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THE STATUS AND ECOLOGY OF THE AMERICAN CROCODILE IN HAITI

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THE STATUS AND ECOLOGY OF THE AMERICAN CROCODILE IN HAITI

John B. Thorbjarnarson*

ABSTRACT

The American crocodile (*Crocodylus acutus*) is the most widely distributed of the New World crocodiles. Due to a combination of hunting for its hide, habitat destruction, and malicious killing, the American crocodile is currently in danger of extinction, with isolated populations existing for the most part only in relatively undisturbed areas. Conservation and management programs are sorely needed to protect this species, but are hampered by a lack of knowledge concerning the current status of many of the extant populations and biological data concerning many aspects of the crocodile's natural history.

In Haiti, crocodiles were once widely distributed throughout coastal and lowland areas where suitable habitat was available. Today, the range of the crocodile in this country has been greatly reduced, and the few extant populations have been severely depleted, remaining only in those areas that have a combination of relatively low human population density and sufficient mangrove habitat.

Presently, no commercial hide hunting is occurring, and the taking of crocodiles for food or the use of their by-products are restricted to two areas bordering the Dominican Republic. Habitat destruction and incidental killings, primarily by fishermen, represent the greatest threat to crocodiles in Haiti today.

The largest remaining population is found in Etang Saumâtre, Haiti's largest lake (113 sq km). Etang Saumâtre is a brackish lake, located in a sparsely inhabited region only 30 km from the capital of Port-au-Prince. The total crocodile population in the lake is estimated at 450. Over a 13-month period, various aspects of the demography, reproductive ecology, diet, and habitat selection of these crocodiles were investigated. The results are discussed in the light of other work which has been done on crocodilians.

The final section outlines several recommendations for the conservation of crocodiles in Haiti.

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RESUMEN

El cocodrilo americano (*Crocodylus acutus*) tiene la distribución más amplia entre las 4 especies de los cocodrilos del Nuevo Mundo. Debido a la caza comercial para su piel, destrucción de su habitat, y a la simple matanza por maldad, el cocodrilo americano está en peligro de extinción, y hoy en día solo quedan poblaciones aislados en zonas remotas. Se necesitan urgentemente programas de conservación y manejo para la protección de esta especie, pero el desarrollo de estos programas es limitado por la falta de conocimiento sobre el estado actual de la mayoría de las poblaciones, y muchos aspectos de su historia natural.

En Haiti, cocodrilos tenían una distribución amplia a lo largo de la costa. Hoy, esta distribución se ha reducido drásticamente, y las pocas poblaciones que quedan son muy pequeñas, ubicadas en zonas despobladas donde hay suficiente habitat con manglares. Hoy en día, no existe una cacería comercial para cocodrilos en Haiti, y la gente los utilizan para comida o remedios solamente en dos zonas al lado de la frontera con la Republica Dominicana. Los dos peligros mayores para la supervivencia de los cocodrilos son la destrucción de habitat, y la muerte por inmersión al enredarse en redes de pescadores.

La mayor población de cocodrilos en Haiti está en Etang Saumatre, el lago mas grande del país (113 km²). Etang Saumatre es de agua salobre, y está ubicado en una zona semi-árida a solamente 30 km de la capital; Puerto Principe. Aproximadamente 450 cocodrilos viven en este lago. Durante un periodo de 13 meses, se estudiaron aspectos de la demografía, reproducción, dieta, y uso de habitat de esta población de cocodrilos. Los resultados estan discutidos en relación con otras investigaciones sobre cocodrilos.

La sección final presenta algunas recomendaciones para la conservación del cocodrilo en Haiti.

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INTRODUCTION

The American crocodile (*Crocodylus acutus*) is the most widely distributed of the four species of New World crocodiles. Although it may be found well inland in freshwater habitats, the American crocodile lives primarily in coastal areas, preferring brackish water habitats associated with mangrove forests, coastal lagoons, and the estuarine sections of rivers. As with most species of crocodilians, unregulated hide-hunting, malicious killing, and habitat destruction have resulted in drastic population declines of the American crocodile throughout its range. Today, these crocodiles exist mostly in disjunct populations where past exploitation and habitat destruction have not been overly severe. Although the general trend of local extirpations and reductions in numbers clearly has been evident for some time (Barbour 1923, Moore 1953, Casas and Guzman 1970, Alvarez del Toro 1974), very little is known about the status of existing populations. A recent review (King et al. 1982) collated reports for *C. acutus* on a country by country basis. Detailed information was available only for a few countries, and the review pointed out the clear need for surveys to determine the present status and distribution of the remaining populations. Data of this sort are needed for the implementation of effective conservation and management schemes designed to insure the continued survival of the species. Primarily a coastal species, the range of the American crocodile includes southernmost Florida, the Atlantic coast of Mexico south through Central America and northern South America (east to the Peninsula de Paria in Venezuela), and the Caribbean islands of Cuba, Jamaica, and Hispaniola. The American crocodile is also found in Pacific Ocean drainages from northern Mexico (Sinaloa) south to the Rio Tumbes in northernmost Peru. The northern distribution of the American crocodile along the Atlantic coast of Mexico remains a question. While crocodiles are known from the states of Tamaulipas and Veracruz, all confirmed specimens from these areas are *C. moreletii*. Nevertheless literature accounts of *C. acutus* exist for the Atlantic coast north of the Yucatan. Further survey work is needed to determine the range of

these two species in Mexico. Very little was known about the status of crocodiles on Hispaniola prior to the mid-1970's. In 1975 scientists from the Museo Nacional de Historia Natural began an ecological study of crocodiles in Lago Enriquillo, the largest lake in the Dominican Republic. This lake was found to contain what may be the largest remaining *C. acutus* population anywhere (Inchaustegui and Ottenwalder pers. comm.; pers. observ.). Coastal populations in the Dominican Republic, however, appear to have been eliminated completely with the exception of the Rio Massacre along the northwestern border with Haiti. Today, both these populations are protected by law (Decreto de Veda 861, June 1979). Prior to the present study, however, the status of crocodiles in Haiti was completely unknown (Powell 1971, King et al. 1983). The objectives of this investigation were twofold: (1) to determine the status and distribution of crocodiles in Haiti; and (2) to record aspects of the ecology of this poorly known species. The findings of the status survey are somewhat unexpected in that Haiti, a country with twice the population density and a much lower standard of living than the neighboring Dominican Republic, has several coastal crocodile populations as well as a substantial population in Etang Saumâtre, Haiti's largest lake. The ecological study was done in Etang Saumâtre, which is, at its closest, only 5 km from Lago Enriquillo in the Dominican Republic. The crocodile population in this lake was somewhat unusual, as it was not found in typical coastal wetland habitat. The crocodiles, however, were relatively easy to locate and capture due to the limited amount of vegetative cover. In addition, the lake represented a closed system, containing an easily defined population. In contrast, coastal populations are often widespread over large areas and are not easily delimited. The inaccessible nature of many of these habitats also precludes any easily accomplished quantitative work on population parameters. Based on the findings of the status survey and the ecological investigation, the last section outlines several recommendations for the conservation of crocodiles in Haiti.

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METHODS

Survey of Status and Distribution

Surveys of coastal areas and inland lakes (other than Etang Saumâtre) were conducted primarily during May-June 1983. Potential crocodile habitats were initially identified on the basis of information provided by reliable informants familiar with wildlife in Haiti. Next, 1:50,000 topographic maps were used to pinpoint areas of possible crocodile habitat prior to visiting those areas. The bulk of the information on the presence or absence of crocodiles was obtained from conversations with knowledgeable local residents (mostly fishermen). Areas were surveyed on foot or by boat during the day to determine the quantity and the quality of the available habitat. Whenever possible, night surveys were also made using a headlamp to spot crocodiles or their reflected eyeshine. However, due to the limited amount of time available to conduct the surveys and the frequent lack of a suitable boat, night surveys were not conducted at all locations. The past distribution of crocodiles in Haiti was reconstructed based on (1) historical accounts of crocodiles in specific locations, (2) place names referring to "caiman," the

local word for crocodiles, and (3) the distribution of suitable crocodile habitat in coastal areas. Regions containing extirpated and extant crocodile populations were then compared on the basis of amount of mangrove habitat (determined from 1:50,000 topographic maps) and human population density based on recent population census (IHSI 1983).

Ecological Study: Etang Saumâtre

Demography

Crocodiles were censused at night from a boat using a Q-Beam spotlight (200,000 candle power) run off a 12-volt marine cell. Two censuses of the entire lakeshore were performed, one requiring three nights (11, 17, 18 August 1983) and the other two nights (7, 8 January 1984). The August survey was not conducted in consecutive nights because of boat trouble. It appears, however, that crocodile movements between survey sections were not sufficiently large to introduce significant error. Surveys were conducted at an average speed of 7 km/hr, approximately 30 m from shore. The light was swept along the shoreline and periodically out into the lake. Crocodiles were spotted by their reflected eyeshine and approached to estimate size (0.3-0.9 m, 0.9-1.8 m, 1.8-2.7 m, > 2.7 m). Because hatchlings did not form pods and were frequently found in dense vegetation along with yearlings, it was unfeasible to separate these two size classes during counts. If the crocodile submerged before an accurate estimate of size could be made, it was placed into one of the following categories: EO > 1.8 m (eyes only, greater than 1.8 m total length), EO < 1.8 m (eyes only, less than 1.8 m), or EO (eyes only). The location of all crocodiles sighted was plotted on a map of the lake as they were spotted. Surveys produced a base estimate of population size and size-class distribution. These data were then corrected for: (1) reduced sightability in areas of dense shoreline vegetation; (2) known animals that were not seen during the survey; and (3) in the January 1984 survey, line transects were conducted in two dense *Conocarpus* swamps to estimate the number of crocodiles that could not be seen from the lake. A full description of the correction procedures is given in Appendix III.

After determining the size-class distribution of the population, the EO, EO < 1.8 m, and EO > 1.8 m sighting classes were divided proportionately between the four known-length size classes. As large animals generally are more wary than small ones, this may have resulted in a slight bias against the larger size classes. Sex ratio and a length-weight relationship were determined from captured individuals. Large crocodiles (> 1.8 m) were caught at night from a boat. Smaller individuals usually were captured when

wading through shallow water habitats. Crocodiles were caught by hand, with pilsstrom tongs, or by using breakaway locking cable snares mounted on the end of a pole (Jones 1965). Crocodiles were weighed on Homs spring scales (100 g, 2 kg, or 10 kg capacity) or Hansen spring scales (136 kg capacity). All captured crocodiles were marked in two ways; by placing self-piercing monel tags in the webbing of the hind foot, and cutting numerical sequence of dorsal caudal scutes. Due to uncertainties in the sexing procedure of juveniles (> 1 m) during 1983, sex data from these animals were not used. Because of the difficulty of sexing small animals based on morphological differences in the penis/clitoris (Joanen and McNease 1979), data on the sex of animals less than 40 cm long were not taken. Growth rates were obtained using successive lengths from recaptured animals. Hatchling growth rate also was estimated by assuming a mean hatching date and length, based on hatchlings found in recently opened nests. In this manner the age and growth of first-year animals could be estimated.

Biomass was determined from the length-weight relationship of captured animals and the size-class distribution of the population. The mass of a crocodile at the midpoint of each size class was used as an estimate of the average mass of a crocodile in that size class. These values then were multiplied by the total number of crocodiles for each class and summed for all four size classes. For the > 2.7 m size class, mean size was assumed to be 2.9 m.

Reproductive Ecology

The location of the crocodile nesting beaches and the number of 1983 nests were determined by extensively searching lakeshore habitats during May 1983. Active nests were identified by the presence of an open hole surrounded by eggshells and egg membrane fragments.

In 1984, nesting beaches were monitored beginning in early January for signs of activity. Nests were located by following the tracks left by females and probing by hand under the substrate in areas where obvious digging had occurred. Once located, nests were carefully excavated to determine clutch size and egg fertility rate (by egg banding, Ferguson and Joanen 1983) and to measure nest hole dimensions. Measurements of egg dimensions and egg mass were made on a sample ($n = 5$) of eggs from each clutch. A 100-200 g soil sample was taken for later analysis of water content (by drying over a butane stove) and soil particle size distribution (by passing through a series of sieves). All weights were measured on a 200 g Pesola spring scale (0.5% accuracy). A variety of other parameters were recorded at each nest site. Height of vegetation was estimated to the nearest 0.5 m, height above the

lake to the nearest 0.3 m. Percent of shrub, grass, and leaf litter cover was estimated to the nearest 10%.

In six nests copper-constantan thermocouples were implanted at the top and the bottom of the clutch. Nest temperatures were recorded over a 30-hour period using an Omega 871 digital thermometer.

To determine the environmental parameters important in the selection of nest sites, 15 null sites were randomly chosen along the major nesting shore. The same environmental parameters measured at the nest sites were recorded at each of the null sites (except distance to lake which was standardized at 25 m) and a stepwise discriminant analysis performed on the data set.

Dietary Analysis

Stomach contents from crocodiles under 1 m total length were obtained using the stomach flushing technique described in Taylor et al. (1978). For crocodiles longer than 1 m a modified scooping technique was used. Crocodiles were strapped to a wood plank with their taped jaws immobilized in an open position around a 7.6 cm diameter section of PVC pipe. Stomach contents were extracted using natural latex (Paramold, Imperial Adhesives and Chemicals, Inc.) scoops moulded from small funnels (opening diameter 6.5 cm, 7.0 cm long). The narrow end of the funnel-shaped scoop was pushed down the esophagus using a 2.5 cm diameter rod until the scoop was felt to reach the end of the stomach. The scoop and rod were generously lubricated with vegetable oil to reduce the chance of trauma to the esophagus during this procedure. Once in the stomach, the rod was extracted and the scoop was slowly pulled out using two strings attached to opposite sides of the funnel rim. The narrow, open end of the scoop was covered with cheesecloth to allow fluids to pass through as it was drawn through the stomach. This procedure was repeated at least three times and was used on animals up to 2.88 m total length. All stomach contents were preserved in alcohol for later identification and analysis. Stomach contents were categorized into three groups: fresh, partly digested, and fragments. Items from the first two groups were individually weighed on an Ainsworth 21N analytical balance to the nearest 0.1 g. The presence of gastroliths, vegetation, and nematodes was noted. For purposes of comparison, invertebrate prey items generally were classified to the ordinal level. Representative invertebrate prey items were identified to family or genus to allow analysis of prey ecology and, by inference, crocodile foraging modes. Vertebrate prey was identified to genus or species in all cases.

Habitat Selection

The various lakeshore habitat types were categorized by physiognomy of the vegetation or shoreline features. The extent of the habitat types was mapped on 1:25,000 topographic maps of the lake during day surveys by boat. The locations of all crocodiles seen during the population surveys were marked on a map of the lake and later assigned to one of the habitat types. Shorelines or the lake-vegetation interface also were assigned an exposure index (protected, moderate, or exposed) based on the amount of wave action they received from the predominant eastern winds.

Spatial distribution of crocodiles around the lake was examined by dividing the lake into eight segments of varying length (4.3-16.0 km long) and comparing the crocodile population in each of these segments.

PRESENT STATUS AND DISTRIBUTION IN HAITI

Introduction

The Republic of Haiti (Fig. 1) occupies 27,700 sq km of the western third of the island of Hispaniola, the second largest of the Greater Antilles (Woodring et al. 1924). A French colony until 1804, Haiti became the world's first black republic following a bloody revolution that lasted nearly 15 years. The name Haiti is derived from an Arawak Indian word meaning "mountainous land" and provides a very apt description of this country, which has peaks up to 2680 m and more than 65% of its surface area sloped greater than 20 degrees (AID 1982).

Within its diverse topography, Haiti supports a wide variety of ecological life zones and associated plant communities ranging from dry thorn scrub to mountain pine forests. In fact, the Holdridge life zone classification system was first developed during work on the mountain vegetation of the La Selle ridge of southeastern Haiti (Holdridge 1947). Today, however, very little of the natural vegetation remains because of extensive deforestation. With an estimated population of more than 5 million, Haiti has one of the world's highest population densities. This, in combination with a paucity of arable land, has resulted in a degree of environmental degradation that is perhaps without equal in the world today. The chief problem is one of rampant erosion, resulting from the nearly complete deforestation of many hillsides

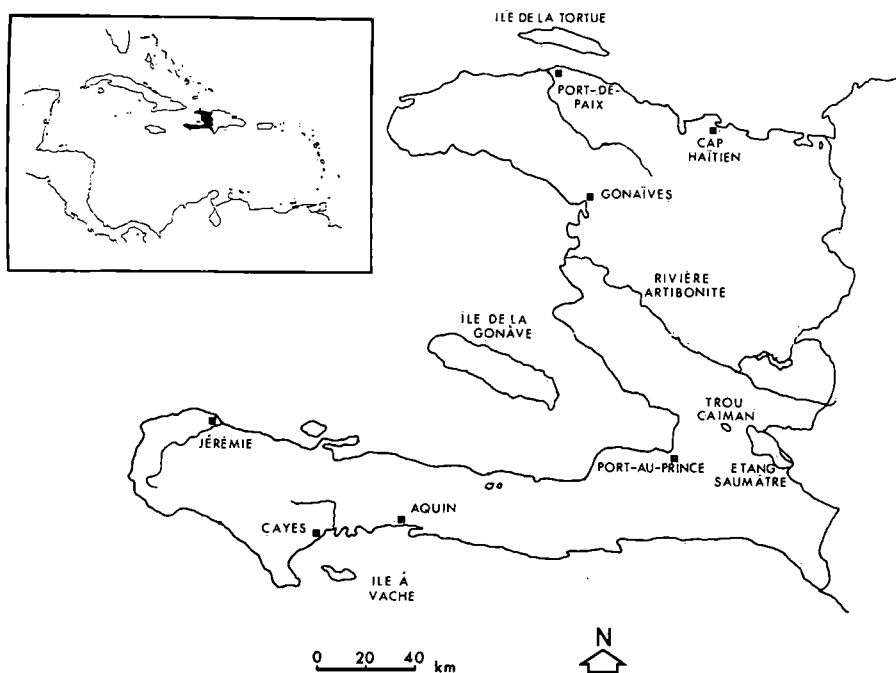


FIGURE 1. Map of Haiti including some major landmarks. Inset is a map of the West Indies with the relative location of Haiti shown as a solid black area.

without the implementation of any soil conservation techniques. Today, the effects of such past practices are being sorely felt by the Haitian people who have the lowest per capita income in the western hemisphere. Recognition of the problem has been slow, but currently the Haitian government, in cooperation with several foreign aid agencies and volunteer organizations, is beginning to implement reforestation projects.

Centuries of human depredation and the virtually complete loss of lowland forested regions have had drastic effects on the local fauna. The hardest hit have been the endemic non-volant mammals, as out of a pre-Colombian total of 25, today only 2 species survive, and both of these are quite rare, persisting in only a few relatively undisturbed areas of suitable habitat (C. Woods pers. comm.). Similarly with reptiles, the giant rock iguanas (*Cyclura cornuta* and *C. ricordi*) have become very rare and today are found only in a few dry, rocky areas inhospitable to man.

The crocodile has managed to survive in Haiti principally because man and American crocodiles are essentially allopatric in their distribution, as man finds the coastal wetlands the crocodiles prefer marginal for agriculture or habitation. In contrast to the near total destruction of the terrestrial forests, the coastal forests, especially mangrove, have fared considerably better. During the period between 1956 and 1977 only 7% of the existing mangrove disappeared. The corresponding figure for loss of pine forest was 40-70% (FAO 1978). While the mangroves are not cleared for agricultural use as are the terrestrial forests, mangrove is used for firewood in bakeries, home cooking, distilleries, and dry cleaners. Mangrove wood also is used as fuel for burning coral rock to produce lime for cement, making charcoal, and for construction purposes. Mangrove has been spared to a large degree in the past, but as the human population continues to grow, more and more pressure will come to bear on these forests. Already the pace of mangrove destruction appears to have been accelerated (pers. observ.).

Although less apparent than the cutting of mangrove, diversion of freshwater for agriculture has probably had more lasting, although as of yet largely undetermined, effects upon some of these ecosystems. This is most notable in the l'Ester region, which contains Haiti's largest mangrove swamp. Mangrove forest still remains in many parts of Haiti, however, and these areas serve as nuclei for the present coastal distribution of crocodiles (see Appendix I).

This section will present the results of a country-wide survey to determine the present status of crocodiles in Haiti. The findings will then be examined in relation to the past distribution of crocodiles, as determined from historical records, to document the retreat of the crocodiles into isolated populations and to provide some useful insights into the ability of crocodiles to survive in man-dominated ecosystems.

Results

Past Distribution of Crocodiles in Haiti

Fourteen historical accounts and eight place names were found that made reference to crocodiles (Fig. 2). These sources, plus information on the distribution of suitable crocodile habitat, were used to reconstruct the probable former distribution of crocodiles in Haiti (Fig. 3).

Present Distribution of Crocodiles in Haiti

Four regions containing extant coastal crocodile populations were identified: (1) the southern coast of the Tiburon Peninsula from Cote-de-Fer west to the Rivière l'Acul, including Ile-à-Vache, (2) Ile de La Gonâve, (3) the l'Ester-Artibonite mangrove swamp, and (4) the Rivière Massacre-Lagon aux Boeufs region bordering on the Dominican Republic. In addition, the largest remaining crocodile population is found in Etang Saumâtre, an inland lake not far from the capital of Port-au-Prince. The present range of crocodiles in Haiti is summarized in Figure 4. A comparison of the present and past distributions of crocodiles reveals that crocodiles have been

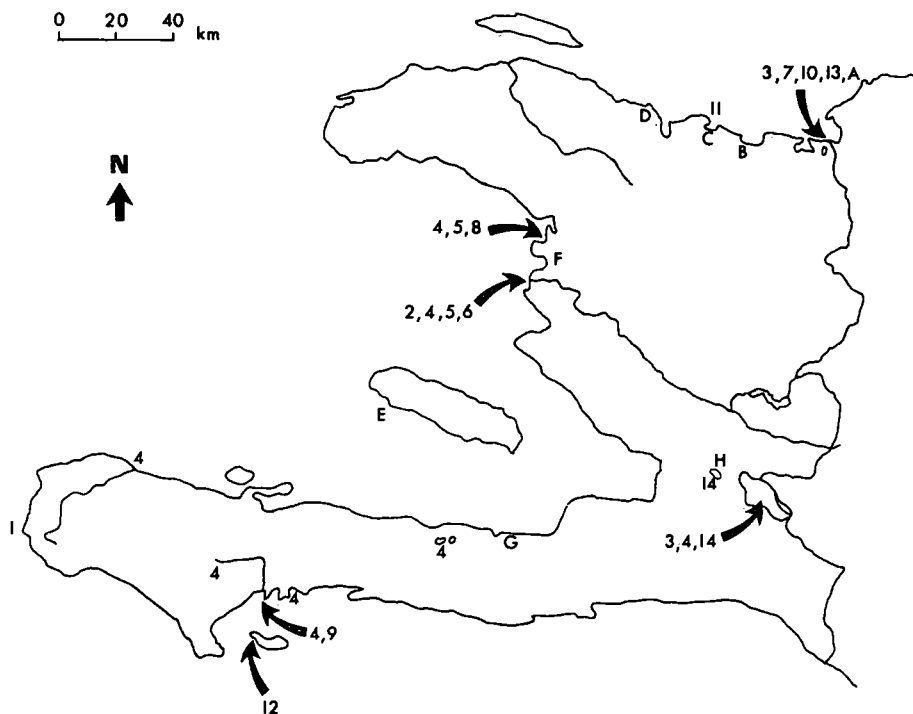


FIGURE 2. Locations of historical records of crocodiles and place names referring to "caïman" in Haiti. (Historical Accounts: 1 - Las Casas 1561, 2 - Lescallier 1764, 3 - Moreau de St. Mery 1796, 4 - Moreau de St. Mery 1797-8, 5 - Descourtilz 1809, 6 - Hearne 1834, 7 - Ritter 1836, 8 - Gosse 1851, 9 - Fortunat 1889, 10 - Hazard 1873, 11 - Rodriguez 1915, 12 - Wetmore Perrygo 1931, 13 - Loederer 1935, 14 - Steedman 1939. Place Names: A - Isleta de los Caimanes, B - Bassin Caïman, C - Caïman, D - Bassin Caïman, E - Caïman, F - Trou Caïman, G - Rivière Caïman, H - Trou Caïman.)

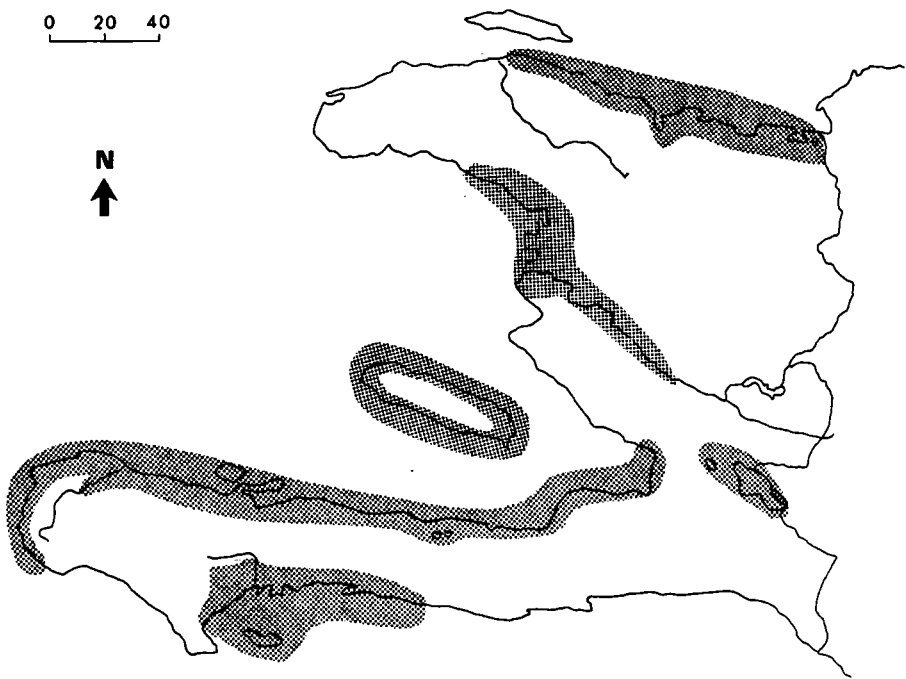


FIGURE 3. Reconstructed historical range of crocodiles in Haiti, based on Figure 2, the present crocodile distribution, and the availability of suitable habitat.

extirpated from approximately 70% of their former coastal range, and two of the three inland lake systems where they were once found (Etang Laborde, Etang Miragoâne).

Southern Coast of the Tiburon Peninsula. A diffuse crocodile population exists in this region from immediately west of Cotes-de-Fer, west to the vicinity of the Rivière l'Acul (Fig. 5). Crocodiles are regularly seen in a number of the more isolated coastal wetlands, specifically: the vicinity of Laborieux-L'Osiendieu, the Aquin-Rivière Capolo region, the Rivière Cavaillon, and the Rivière Bondonne. Crocodiles are sporadically seen in pockets of suitable habitat between these areas, primarily associated with mangrove swamps or the dense vegetative cover at river mouths.

Nesting reportedly occurs in vegetated beach strand habitats along the lower reaches of the Rivières Cavaillon and Bondonne. During surveys, crocodiles were only seen in the Laborieux region (5 subadults seen, 17 April 1983), but according to local residents the largest population remains in a

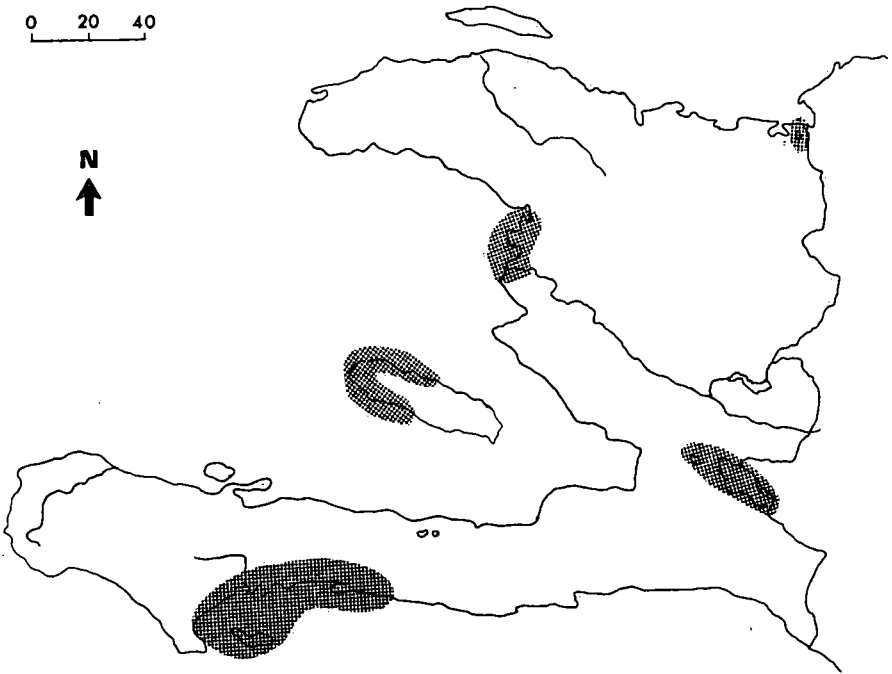


FIGURE 4. Present range of crocodiles in Haiti.

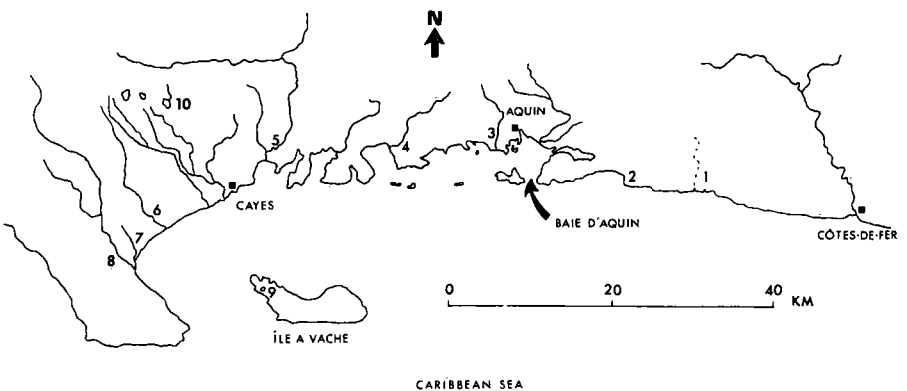


FIGURE 5. South-central Tiburon Peninsula; marked locations indicate the position of extant or former crocodile populations (1 - Laborieux, 2 - Osiendieu, 3 - Rivière Capolo, 4 - Rivière Millionaire, 5 - Rivière Cavaillon, 6 - Rivière Torbeck, 7 - Rivière Bondonne, 8 - Rivière l'Acul, 9 - l'Etang, 10 - Etang Laborde).

mangrove swamp at the mouth of the Rivière Cavaillon. A recently killed specimen (1.2 m total length) was found in the Rivière Capolo (25 June 1983, UF 54208).

Crocodiles were also reported from a small freshwater lake (called L'Etang) on the northwestern end of Ile à Vache, located approximately 10 km off the southern coast of Haiti.

Ile de La Gonâve. La Gonâve is the largest of Hispaniola's satellite islands (658 sq km), or about 2.3% of Haiti's land surface. Much of the coast is protected from wave action by a barrier reef, permitting the growth of a mangrove fringe even though freshwater runoff is almost non-existent. Crocodiles were reported from several of the coastal lagoons on the western end of the island. During a night survey of Lagon Blanch (11-12 June 1983), a shallow water lagoon along the north coast near the town of Richard, a total of five subadult crocodiles (to 1.5 m total length) were observed.

L'Ester-Artibonite. Hispaniola's largest mangrove swamp (8490 ha) is found in the L'Ester region just south of the town of Gonaïves. Immediately to the south of the L'Ester region is the mouth of the Rivière Artibonite, Hispaniola's longest river (240 km). Crocodiles were well documented historically from this area by Descourtilz (1809) in his treatise on the "crocodile du St. Domingue." Today, crocodiles are well known to local fishermen, although they are not seen with any frequency. During a daytime survey by sailboat (4 June 1983) and a night survey of mangroves near Gonaïves (5 June 1983), no crocodiles were seen.

Crocodiles were also sporadically observed by local residents of Grande Saline, at the mouth of the Rivière Artibonite, which lacks any protective mangrove forests.

Rivière Massacre-Lagon aux Boefs. Lagon aux Boefs is a 4-sq-km, mangrove-lined, freshwater lagoon connected at its northern end to the Rivière Massacre, which forms the northeastern boundary between Haiti and the Dominican Republic. The estuarine section of the Rivière Massacre has a mixed riverine-fringe type mangrove swamp (after Lugo and Snedaker 1974) of approximately 1030 ha, most of which is in the neighboring Dominican Republic. Local Haitians were very familiar with crocodiles, which they would catch and eat whenever possible. This is in stark contrast to the rest of Haiti where crocodiles are not eaten. A daytime survey of Lagon aux Boefs (16 June 1983) revealed no crocodiles. During a previous night survey of the lower Rivière Massacre in December 1981 one 3 m crocodile was seen approximately 2 km upstream from the river's mouth.

Etang Saumâtre and Trou Caïman. Haiti's largest remaining crocodile population, approximately 450 individuals of all sizes, is found in Etang Saumâtre, located in the Cul-de-Sac valley 30 km northeast of Port-au-Prince (see *Ecological Study: Etang Saumâtre*). A large lake (113 sq km), Etang Saumâtre is surrounded by a relatively sparsely inhabited region of the

country. The uninhabited eastern lakeshore, bordering the Dominican Republic, contains a significant amount of juvenile crocodile habitat and virtually all the nesting sites.

Trou Caïman is a marshy freshwater lake (6.9 sq km) located 6 km west of Etang Saumâtre. The two are connected by a small canal. The sporadic accounts of crocodiles in this lake suggest that it does not contain a breeding population but probably serves as a dispersal area for crocodiles from Etang Saumâtre.

Extirpated Populations

North Coast West of Ft. Liberté. Crocodiles were known historically as far west as the mouth of the Rivière Limbé (Bassin Cayman). It is not known exactly when the last crocodiles in this region were extirpated, but none has been seen for many years. It is likely that at one time crocodiles ranged as far west as Port-de-Paix, as pockets of suitable habitat exist at regular intervals along the coast. West of Port-de-Paix, a rocky, high-energy coast predominates, providing little in the way of crocodile habitat. Crocodiles also were reported historically in the vicinity of Cap Haïtien (Rodriguez 1915) where a moderate-sized (760 ha) mangrove forest still exists along the lower reaches of the Rivière Haut-du-Cap.

Crocodiles were also found in the Caracol region between Cap Haïtien and Fort Liberté. The only published account is that of Ritter (1836), who mentions seeing crocodiles at Ft. Real, which may have been the old site of Puerto Real, a Spanish colonial settlement in the Caracol region. The presence of a small lagoon (the old river bed of the Grand Rivière du Nord) called Bassin Cayman, and the finding of crocodile mandibles in Indian middens from the area (W. Hodges pers. comm.), however, attest to the fact that crocodiles were indeed in the area at one time.

North and West Coasts of the Tiburon Peninsula. Historically crocodiles were found in the vicinity of Petit Goâve (Rivière Caïman), the Rivière Grande Anse near Jérémie (Moreau de St. Mery 1797), and the Tiburon region at the tip of the peninsula (Las Casas 1552). They also were formerly found in several inland lakes in the area (see following section).

Currently there are no verified populations anywhere in this part of Haiti. Crocodiles may still be found in small numbers in the Baradères region, although this is doubtful. The small individuals reported from Petit Goâve and Jérémie (all in the 1.2-1.5 m range) probably represent vagrant individuals.

Inland Lakes: Etang Laborde. Etang Laborde is the largest of four lakes located on the coastal plain 12 km north of Cayes (1978 size estimate

0.9 sq km). The region is heavily populated and extensive agriculture occurs around the lake. The lake itself is very shallow and reportedly dried up in 1975 after an extended drought. Moreau de St. Mery (1797) stated that crocodiles were found in this lake (then called Etang Vert) but had long since disappeared, making this the earliest known extirpation of crocodiles in Haiti. No crocodiles are currently found in Etang Laborde or any of the other lakes in the region.

Inland Lakes: Etang Miragoâne. Etang Miragoâne presently consists of two lakes (8.3 and 1.3 sq km) near the north coast of the Tiburon peninsula, adjacent to the town of Miragoâne. This region also is densely populated, and there is currently much fishing activity in the lake. The lake is fresh water with extensive grass fringes. Other vegetation includes *Nuphar*, *Nelumbo*, *Typha*, and *Potamogeton*. Moreau de St. Mery (1797) mentioned that the lake had many crocodiles 2.5-3.5 m long which nested in sandy areas surrounding the lake during the summer. Etang Miragoâne has no crocodiles, and no one interviewed could remember there ever being crocodiles in the area.

Discussion

Analysis of the Present Distribution of Crocodiles

Coastal Crocodile Movements. *Crocodylus acutus* is one of two primarily coastal dwelling crocodiles, the other being *C. porosus* from northern Australia, the Indo-Malayan Archipelago, and Southeast Asia. The wide coastal distribution and probable recent evolutionary derivation of both these species (Densmore 1981) suggests that they are adept at moving along coasts and possibly even making transoceanic journeys. This is best documented in the case of *C. porosus* (Bustard and Choudhury 1980) where specimens have been spotted at sea nearly 500 km north of New Zealand (Robb 1980), on Cocos-Keeling Island in the Indian Ocean nearly 1000 km from the closest known population in Indonesia, and on Ponape in the Western Caroline Islands some 1360 km from the nearest population (Allen 1974).

Messel et al. (1982) developed a model of *C. porosus* population dynamics for tidal rivers in northern Australia which proposes that a large fraction of the subadult crocodiles leave the productive nesting rivers when they reach a size (0.9-1.8 m) that brings them into conflict with larger territorial adults. Such individuals, if not killed outright, are forced to leave the river and find other, usually marginal, habitats. Some perhaps move along the coast and manage to find another river where territorial adults are less common (rivers less suitable for nesting) and take up residence there.

The majority, however, probably never survive. As adults it is possible the crocodiles will move back into more suitable rivers for reproduction. The model proposes, then, that movement and mortality are quite high for these intermediate-sized crocodiles.

Logically, a similar pattern may hold for *C. acutus*, which is ecologically similar but poorer known from a biological standpoint. Both Alvarez del Toro (1974) and Medem (1981) reported *C. acutus* moving from river to river using overland routes. Alvarez del Toro (1974) stated that such movements are in response to territorial fighting and the drying up of temporary lagoons. Mazzotti (1983) found *C. acutus* moved considerable distances in the coastal regions of southern Florida. The presence of *C. acutus* on several mid-oceanic islands (Cuba, Jamaica, Hispaniola, and formerly the Cayman Islands) as well as a number of near-shore islands (Isla Margarita, Venezuela; Islas del Rosario, Islas de Sn. Bernardo, Isla Fuerte, Isla Tortuguilla, Colombia; and the Archipelago de los Canarreos, Cuba; as well as Ile á Vache and Ile de La Gonâve off Haiti) strongly suggests the species is adept at moving long distances along the coast or across open water.

Fishermen in Haiti reported that on occasion crocodiles could be seen in the ocean. Crocodile movement along the coast would explain many of the unusual reports of local residents along the southern coast of the Tiburon peninsula. In this region, crocodiles were said to be found in several areas with little or no suitable habitat, and their presence in many of these areas was reported to be of irregular occurrence.

Similarly, reports of crocodiles on the northern coast of the Tiburon peninsula are most likely transient individuals, as are the ones reported from Anse-a-Galets on eastern La Gonâve. A pertinent point concerning these last reports was that all the animals were 1.2-1.5 m individuals, the size class that would be dispersing the most according to the Messel model.

Adult crocodiles will also move along the coast, resulting in large individuals being reported in small coastal wetlands. Most of the areas where crocodiles have been reported along the Tiburon peninsula contain more than 60 ha of habitat. Only a fraction of this area, however, is available to the crocodiles because of extensive fishing, rice cultivation, and other human activities. The habitat at the mouth of the Rivière Capolo is much smaller, however; so small it is impossible to make a size estimate from 1:50,000 topographic maps. A similar situation is found on the southern coast of Jamaica where crocodiles may be found in almost any coastal wetland one hectare or larger in size (Plotkin and Faibairn MS, referenced in Groombridge 1982). This frequent usage of small coastal habitats suggests considerable movement by crocodiles along the coast.

Human-related Mortality. Five direct causes of human-related crocodile mortality can be identified in Haiti (other than habitat destruction): (1) incidental capture in fishing nets or traps, (2) malicious killing, (3)

hunting for sport, (4) hunting for food, and (5) nest raiding. By far the most important of these is being trapped in fishing nets and traps. When caught, crocodiles either drown or are killed by the fishermen when pulled to the surface. In most cases the body is simply discarded in the water. Occasionally crocodiles may be eaten (see below) or the body may be disposed of by burial or by dumping it at sea (see **Folk Beliefs** section below). In Etang Saumâtre, where gill netting is not commonplace, one 1.5 m crocodile was drowned in a net during the 10-month period of time I spent there. As most bodies of shallow water in Haiti are heavily fished, this source of mortality probably is considerable.

Malicious killings often occur in response to crocodiles taking livestock or, in one reported case, killing humans. A large crocodile, approximately 3 m long, was killed at Tete Source in Etang Saumâtre after it had taken livestock on several occasions (goats and sheep). This crocodile was also considered a nuisance because it would take fish from gill nets, leaving gaping holes. The crocodile was caught using a baited hook and then beaten to death with a long stick. Large crocodiles also are killed occasionally when they accidentally wander into populated areas. Likewise, hunting for sport claims adult crocodiles in certain areas, although the incidence of this appears to have declined in the recent past. Throughout Haiti, the people are so poor that the number of firearms is very limited, being restricted in rural areas to certain local leaders and the military. Hunting excursions from Port-au-Prince were popular in the past, especially during the 1917-1934 United States Marine occupation (Steedman 1939, Cave 1952). Crocodile hunting was also a popular pastime of the colonial French prior to the independence of Haiti (Descourtiz 1809).

Use of crocodiles for food is limited to only two areas in Haiti, the Rivière Massacre and, to a much smaller extent, in Etang Saumâtre. Both these regions border on the Dominican Republic, and the usage of crocodiles is undoubtedly due to a Dominican cultural influence (where crocodiles are eaten and their by-products used). Although the better educated people in Haiti will occasionally eat crocodiles, the vast majority of Haitians will not. Active hunting of crocodiles only occurs near the Rivière Massacre, where they are caught with harpoons, set nets, cast nets, and baited hooks. Most of the hunting in this region centers on Lagon aux Boeufs, with a smaller number caught in the river itself. The meat is eaten and the fat is used to render an oil to treat pneumonia and rheumatism.

The only other account of crocodile by-products being used comes from the Cayes region. Although unconfirmed, three separate sources claimed that crocodile teeth are sometimes used for false teeth in people, the work being done in a hospital in Cayes.

Nest robbing probably is not a major source of mortality, although nests may be dug up and the eggs left to die. In most areas, residents reported

nests as being very difficult to find and stated that like crocodile meat, they did not eat the eggs. The only area where eggs were reported eaten (other than the Rivière Massacre region) was Etang Saumâtre. Residents of the town of Fonds Parisien, on the southern shore of the lake, will eat them on occasion (F. Conway pers. comm.). One nest near Tete Source was excavated in 1983 and the eggs sold in the local market of Thomazeau (I. Lange pers. comm.).

There is no present market for crocodile skins in Haiti, and hide hunting is non-existent. Interest was shown by an Italian firm during the 1950's when it approached Mr. E. Lempke of Port-au-Prince about obtaining crocodile hides. Nothing came of this, however, and little interest in commercial hide production has surfaced since. There is a tannery in Port-au-Prince that deals with reptile leathers (mostly lizard and snake skins from South America [J. Wilson pers. comm.]). The skin of the crocodile that was killed for taking livestock in Etang Saumâtre was reportedly taken to this tannery. Until recently there also was a small export trade in live juvenile crocodiles for pets. This apparently has stopped in the last few years.

Folk Beliefs. The fact that crocodile meat generally is considered inedible is undoubtedly one of the major reasons why there are still crocodiles in Haiti today. Such folk beliefs evolved with the culture of the Haitian people and are deeply tied to their religious beliefs. The indigenous Indians ate crocodiles, as is evidenced by the presence of crocodile bones in middens near the Caracol mangrove swamp (W. Hodges pers. comm.). Personal observation, however, has shown that today there is a widespread cultural taboo against eating crocodiles or their eggs. In most areas crocodiles are considered inedible and simply thrown away when killed; however, there is local variation in the method of disposal. In some areas (e.g. Gonaïves), dead crocodiles are buried in a grave, often in coffin-like boxes with a grave marker. Around Etang Saumâtre crocodiles are beheaded, with only the head being buried, usually away from the rest of the body. This represents an attempt to keep the spirit of the dead crocodile (which resides in the head) separate from the body so that it can create no "mischief" after death (pers. obs.). On the island of La Gonâve crocodiles actually are considered poisonous. When crocodiles are killed in this region, they are disposed of by being weighed down with rocks and towed out to sea.

Crocodiles are eaten only in areas where there is cross-cultural exchange with Dominicans. Around the Rivière Massacre crocodiles are accepted as being edible. Near Etang Saumâtre some Haitians also will eat crocodile, but it is considered poor repast, equivalent to the *Cyclura* iguanas in the area. An interesting example of cultural differences occurred at Las Lajas, a border military post in the Dominican Republic. A Dominican guard had shot a 2.7 m crocodile in Etang Saumâtre, dragged it ashore and cut out the tail meat to eat and the penis (which is widely believed to be an aphrodisiac in the

Dominican Republic). Afterward, Haitians chopped off the head and buried it several meters from the carcass to prevent the crocodile's spirit (called its loa) from doing any harm.

Crocodile Distribution in Relation to Habitat. Crocodiles are found only where there is suitable habitat. The habitat provides two important functions: an environment that meets the biological needs of the animal and, if it is to sustain a crocodile population, sufficient cover to protect the crocodiles from man. Because of the extremely dense human population in Haiti, the only significant coastal habitat type that satisfies both these criteria is mangrove swamp. In areas where human densities are considerably less, the second criterion obviously becomes less important. In historical times, crocodiles probably were commonly associated with virtually all coastal wetland habitats. The pattern of disappearance from these habitats is inversely correlated with the degree of human activity in the area. Mangrove swamps provide good habitat because they are relatively impenetrable to humans and offer a wealth of hiding places. Mangroves also are a very common form of tropical coastal wetlands, growing under a variety of physiognomic conditions and, as such, have been well documented as a preferred habitat of the American crocodile throughout its range (Alvarez del Toro 1974; Ogden 1978, Medem 1981).

In Haiti, there is a correlation between the amount of mangrove habitat and crocodile presence in each of the coastal Départements (a political subdivision) and the major satellite islands (Table 1). Coastal regions with crocodiles contain, on average, significantly more mangrove (0.390 sq km/km shoreline, as measured from 1:50,000 topographic maps) than areas without (0.05 sq km/km shoreline) (t -test, $p < 0.05$).

The limited occurrence of crocodiles in coastal non-mangrove habitats emphasizes the need for sufficient cover in which crocodiles can hide. Although much of Haiti's coastal wetlands are dominated by mangroves, there are a number of other small estuarine environments that could support crocodiles. Most of these are on the north coast between Cap Haïtien and Port-de-Paix, or on the southern peninsula (e.g. Cayes Plain rivers, Rivière Grande Anse near Jérémie). Of the non-mangrove habitats, only two still have crocodiles, both of which offer sufficient cover for the crocodiles in them: the Rivière Artibonite (deep, murky water) and the Rivière Bondonne (extensive herbaceous vegetation). Even with cover, however, the presence of crocodiles in these areas probably is related strongly to the nearby occurrence of mangrove habitat.

When considering the suitability of mangrove habitat for crocodiles, however, there are considerations other than total area that need to be addressed. Perhaps the most important are freshwater input and the availability of nesting habitat. As Dunson (1982) demonstrated, hatchling *C. acutus* can osmoregulate properly in water up to approximately 20 parts per

thousand (ppt), but cannot tolerate full strength sea water (35 ppt) for extended periods of time. Periodic access to areas of fresh or brackish water therefore is essential for hatchling recruitment (Mazzotti 1983). The apparent lack of crocodiles in the extensive mangrove swamp at Caracol may, in fact, be due to a lack of freshwater input into the region. One river, the Rivière Trou du Nord, does empty into the mangrove adjacent to the town of Caracol (population 3982). The heavy human use of the area and a possible lack of suitable nesting habitat provide unsuitable conditions for crocodile reproduction and recruitment. The xeric nature of the surrounding area suggests also that periodic access to freshwater lenses formed by rainfall also is unlikely.

In fact, in most of the mangrove areas in Haiti, freshwater influx is very low. The majority of mangrove habitat is located in the subtropical dry forest life zone, areas receiving less than 100 cm of rain annually. The lack of freshwater runoff also is related to the high coastline to total country area ratio. The amount of freshwater runoff is proportional to the amount of land that receives rain, but mangrove habitat is a function of the length of the coastline. Hence, Haiti, with a long irregular coast and a small surface area, provides little freshwater runoff for its coastal mangrove forests. This situation is further aggravated by the fact that much of Haiti is arid, and in several areas (such as the l'Ester region) freshwater runoff is diverted for agriculture.

The fringe forest of the l'Ester historically had a much larger freshwater influx than at present, because of irrigation and channelization, and this region once supported a very large crocodile population (Descourtilz 1809). Diversion of freshwater probably had a significant effect on the habitat which, in combination with intense fishing activity and past crocodile hunting, has resulted in a drastic decline in the crocodile population.

The situation on the island of La Gonâve also is worth mentioning in regard to freshwater availability. No surface streams exist on the island; instead, rainfall percolates down through the limestone bedrock, emerging in springs, some below sea level. In this respect, suitable hatchling habitat may be severely limiting, being restricted to the vicinity of freshwater springs that feed into coastal lagoons. The area visited on the north coast of La Gonâve did, in fact, have at least one small spring adjacent to a mangrove swamp in which juvenile recruitment was occurring.

Crocodile Distribution in Relation to Human Population Density. Most human-related crocodile mortality in Haiti is accidental, therefore it can be assumed to be directly proportional to the frequency of human-crocodile encounters. This, in turn, is related to the prevalence of activities that bring people into crocodile habitat or to accidentally kill crocodiles; these activities include fishing, cutting mangrove, or collecting mangrove oysters. Although it is virtually impossible to quantify such activities, they can be assumed to be

more or less directly proportional to human population density in the area. In Haiti, population densities are, in fact, higher in areas where crocodiles have been extirpated than in those regions which have extant crocodile populations (Tables 2, 3). Because of the large variances involved, the differences are not significant for the coastal areas (Table 2, t -test $p > 0.05$). Inland lakes with crocodiles, however, are in areas of significantly lower human population density (Table 3, t -test $p < 0.05$).

A noteworthy relationship exists between the status of crocodile populations and the ecological life zone in which they are found (Table 4). All historical crocodile populations were located in the two life zones that predominate in the lowland regions: the subtropical moist and the subtropical dry life zones (OAS 1972). The majority of the crocodile populations in the moist zone (100-200 cm rain annually) have been extirpated, only remaining today on the south coast of the Tiburon peninsula and Ile á Vache. On the other hand, only two populations in the dry forest zone have disappeared (Caracol region, L'Etang near Gonaïves). In the latter cases the crocodile populations were probably vulnerable because of a lack of freshwater habitat, and small population size and ephemeral habitat respectively. As adult crocodiles are often found in freshwater and hatchlings require at least some freshwater, this relationship is not due to the availability of freshwater per se. Apparently the presence or absence of crocodiles in these areas is moderated indirectly through human population density, which is higher in the greater rainfall moist zone, leading to the unexpected result of finding crocodiles primarily in areas surrounded by semi-arid habitat.

In the previous discussion, crocodile distribution in Haiti has been examined in relation to habitat availability and human population density. It is reasonable to assume, however, that crocodile distribution is affected simultaneously by both factors. Ranking coastal regions by population density and the amount of mangrove habitat, neither parameter alone is significantly correlated with the presence or absence of crocodiles (Wilcoxon Rank test, $p > 0.05$). A composite rank combining both parameters (Table 5), however, is significant ($p < 0.05$), indicating that the combination of mangrove habitat and population density is a better indicator of an area's suitability for crocodiles than either parameter alone. The extirpation of crocodile populations then appears to be synergistically related to human population density and the amount of suitable habitat. As crocodiles are rather long-lived, prolific, and secretive animals, given sufficient habitat offering retreats (mostly mangrove in Haiti), they can survive even in areas of dense human populations (as along the south coast of the Tiburon peninsula). This is due in no small part to their ability to move along coasts between pockets of suitable habitat. Human-related mortality is, however, quite high and can result in extirpation, especially where crocodiles are not afforded sufficient cover (non-mangrove habitats) or where they are vulnerable (e.g. lack of

freshwater). These generalizations, however, only apply to areas where mortality is mostly incidental, that is where there is no economic motivation for killing crocodiles. Where active hunting occurs for food, or more importantly for hides, crocodilian populations are much more likely to be extirpated.

ECOLOGICAL STUDY: ETANG SAUMATRE

Introduction

General Features of the Region

Etang Saumâtre is Haiti's largest lake (113 sq km) and is located in the Cul-de-Sac Valley approximately 30 km northeast of Port-au-Prince (Fig. 6). The Cul-de-Sac graben, which has been referred to as perhaps the most

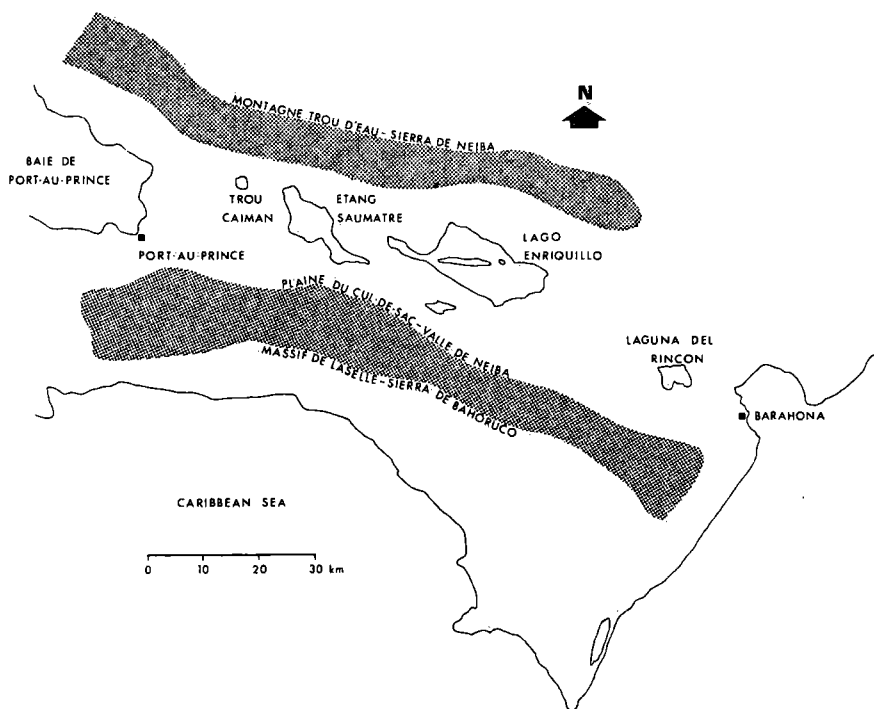


FIGURE 6. Map of the Cul-de-Sac/Valle de Neiba region.

striking surface feature in Haiti (Woodring et al. 1924), is a low-lying valley extending east-southeast from Port-au-Prince Bay completely across the island to the Caribbean coast of the Dominican Republic, where it is referred to as the Valle de Neiba. Mountains border the valley to the north and the south, with Morne La Selle, Haiti's highest point (2680 m) lying directly south of Etang Saumâtre. The abrupt changes in elevation provide a great diversity of ecological life zones within a relatively small area (Holdridge 1947).

The Cul-de-Sac/Valle de Neiba depression contains a series of lakes, from east to west: Laguna del Rincon, Lago Enriquillo, Etang Saumâtre, and Trou Caïman. Lago Enriquillo, in the Dominican Republic, is the largest (180 sq km) and most unusual of the four, as it is one of the lowest lakes in the world (35 m below sea level) and is hypersaline (50 ppt in 1981). Because of hypersaline lake water, the distribution of flora and fauna of the lake are restricted principally to the fringing freshwater habitats.

Etang Saumâtre (elevation 15 m) is located along the Haitian-Dominican Republic border approximately 10 km west of Lago Enriquillo; the two lakes are separated by a ridge of Pleistocene limestone and alluvial

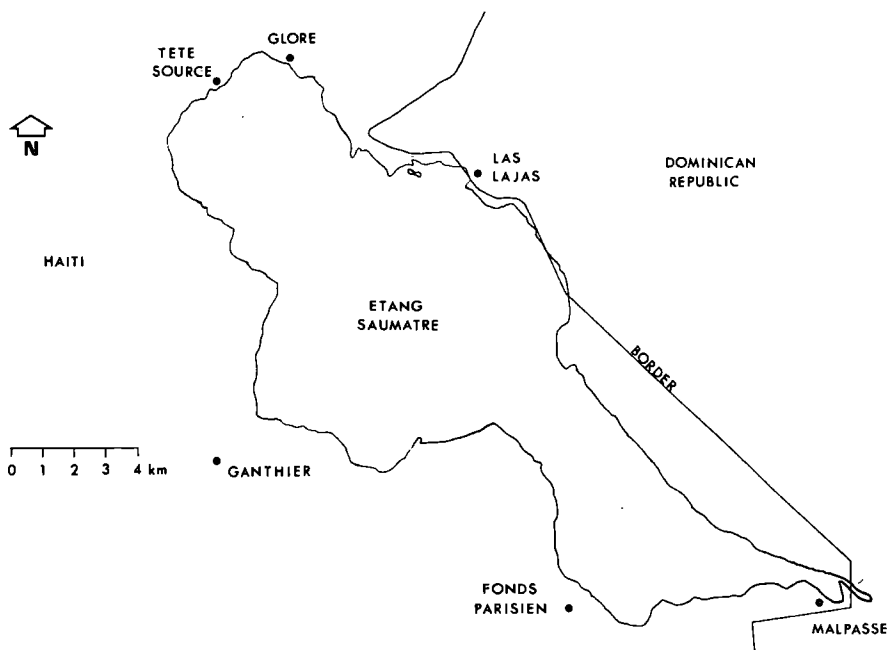


FIGURE 7. Map of Etang Saumâtre.

deposits. Although the vast majority of the lake lies in Haiti, two small sections (at Malpasse and south of Las Lajas) extend into the Dominican Republic (Fig. 7). Like Lago Enriquillo, Etang Saumâtre has no surface outlets, although the possibility of subsurface drainage into Lago Enriquillo cannot be ruled out. Etang Saumâtre is only slightly saline, and because of this its ecology is quite different from that of Lago Enriquillo, in general supporting a much more diverse flora and fauna.

Geology and Shoreline Features

Within the last several million years the Cul-de-Sac valley was a shallow water marine strait that separated the Sierra de Neiba/Montagnes de Trou d'Eau to the north from the Sierra de Bahoruco/Morne La Selle ridge to the south (Woodring et al. 1924). This prior separation of Hispaniola into "north" and "south" islands still is reflected in the biogeographical relations of many taxa, as has been perhaps best documented for reptiles and amphibians (Schwartz 1980).

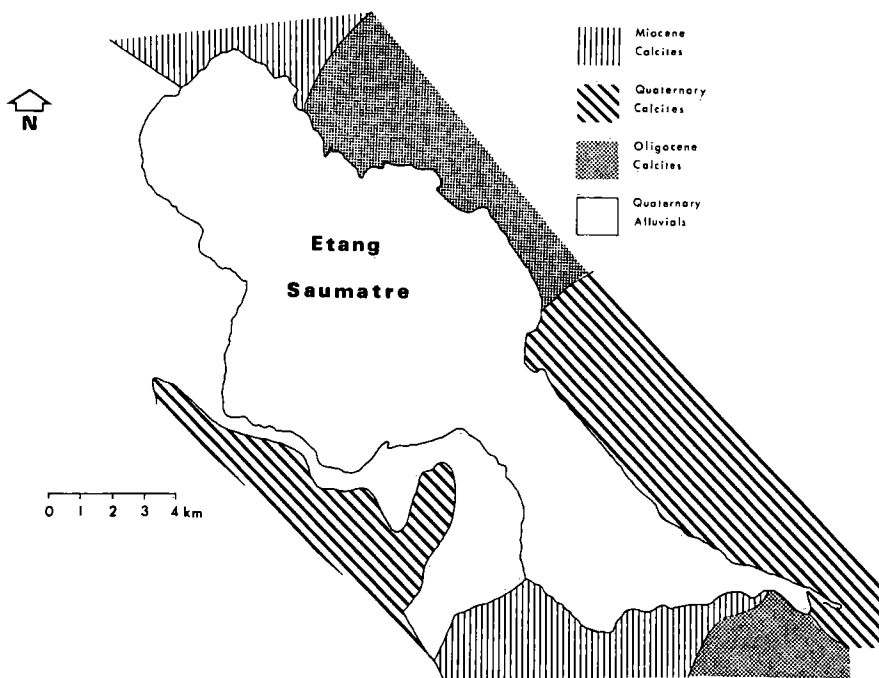


FIGURE 8. Geology of the Etang Saumâtre region.

The abundance of Quaternary limestones composed of extant coral species is evidence of the recent marine inundation of the valley floor (Woodring et al. 1924). In many areas throughout the region coraliferous deposits are still recognizable, and in a few areas, such as Isla Cabritos in Lago Enriquillo, virtually intact exposed coral reefs can be observed.

The placement of the lakes within the valley has been attributed by Woodring et al. (1924) to uneven alluvial deposition from streams draining the mountain watersheds to the north and the south. Areas that did not accumulate sediments are now depressions that have filled with water and remain as a series of lakes. The maximum known depth of the Etang Saumâtre depression is 30 m below the lake's surface, or about 15 m below sea level.

The shoreline features of the lake reflect the geology of the area (Fig. 8). The western lake margin, from Tete Source south to the vicinity of Ganthier, is composed of Quaternary alluvial deposits, creating a shallow lakeshore gradient. Continuing east along the south shore, Quaternary alluvials are mixed with similar-aged limestones creating a mosaic of shallow gradient and rocky, medium gradient shorelines. Just east of Fonds Parisien, older limestones (Miocene and Oligocene) form the northern flanks of the Morne La Selle ridge, and descend abruptly to the lake creating a rocky, steep gradient shoreline. A similar rocky coast is found along the north shore from Gloire east to the vicinity of Las Lajas. However, along the north coast a number of prominent valleys, filled with recent alluvial deposits, extend down to the lake and create shallow gradient, non-rocky shoreline (coves). The eastern shore, northwest of Malpasse, is a medium gradient shoreline dominated by Quaternary limestone, containing several areas of shallow gradient mudflats at the openings of arroyos.

Limnology

Etang Saumâtre is a brackish lake, with a salinity range of 8-10 ppt. In the shallow northwestern lake region where much of the freshwater input occurs, salinity is at the lower end of this range. The lake level fluctuates periodically, apparently as a function of rainfall. During the period 1979-1983, following a series of hurricanes, the lake rose approximately 2 m. At the turn of the century, the lake level apparently was even higher than at present. Tippenhauer (1901) reported its elevation as 20 m above sea level (5 m above present), and Wells (1893) stated that the water was potable, being only slightly brackish. Similar fluctuations in lake level and salinity are known from adjacent Lago Enriquillo (La Fuente 1976).

A number of freshwater springs (conductivity 500-600 mohmos/cm) empty into the lake, primarily in the northwestern section of the lake, the largest being at Tete Source. Several small springs are found in the southeastern section of the lake near Malpasse, located directly along a fault, giving them a high hydrogen sulfide content. Although much of the freshwater input into the lake comes from these solution channel springs, a significant amount of water enters the lake in seepage areas and, to a lesser extent, through freshwater irrigation canals.

Various chemical analyses have been done on Etang Saumâtre lakewater since 1921 (Table 6). The fluctuations in salinity probably reflect changes in lake volume associated with variable rainfall. The high phosphate content of the water indicates the lake is eutrophic (M. Binford and M. Brenner pers. comm.). Bond (1935) termed Etang Saumâtre eutrophic and "thalassohaline," meaning its ion concentrations are in the same relative proportion as seawater. Bond (1935) argued that this was evidence of the lake's marine origin.

Climate

The area surrounding the lake receives an annual average of 70-90 cm of rain. With a mean monthly temperature of 26°C, the region is classified in the subtropical dry zone, as defined by Holdridge (1967). Rainfall follows a predictable annual pattern (Fig. 9), peaking in May and October with a long winter (November-March) and a short summer dry season (June-July). Mean monthly temperature varies from 27.9°C in August to a low of 23.7°C in February.

Winds are predominantly from the east, and steady 18-36 kph winds were not unusual. Under these conditions whitecaps cover the lake, with wave amplitudes in excess of 1 m. The less common westerly winds were usually associated with rainfall.

Vegetation

Terrestrial Vegetation. The riparian vegetation is a virtual monoculture of buttonwood mangrove (*Conocarpus erectus*) growing in fringe 5-20 m wide around the lake where there is sufficient soil. Because of the recent rise in lake level, the *Conocarpus* frequently extended out into shallow water to a depth of approximately 1 m. The most prolific *Conocarpus* stands are found along the shallow gradient alluvial shorelines on the western shore between

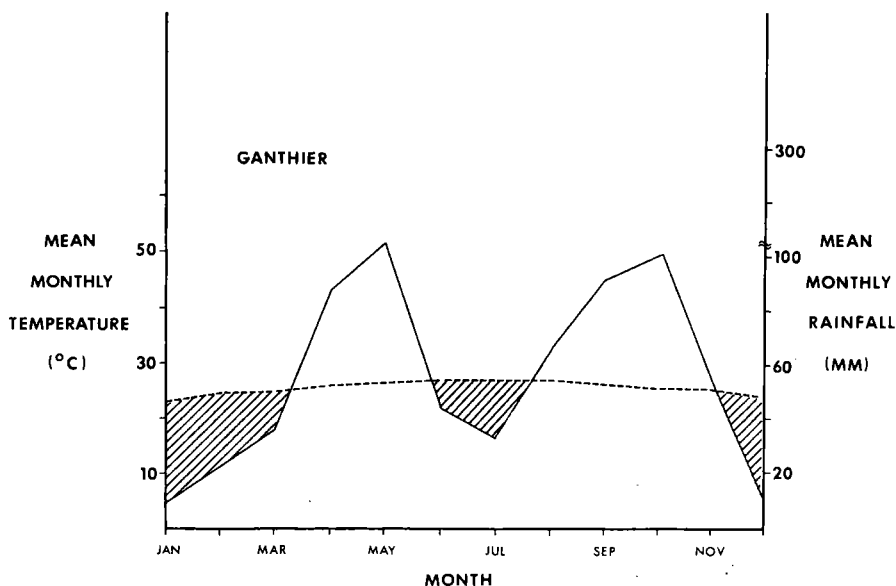


FIGURE 9. Walter diagram of rainfall and temperature variation in Thomazeau, adjacent Etang Saumâtre. Shaded areas represent the dry season (after Walter 1973).

Tete Source and Ganthier, and on the western shore between Las Lajas and Malpasse. Most of the *Conocarpus* is of low stature, rarely exceeding 4 m in height. The upland areas immediately surrounding the lake are vegetated with a xeric *Acacia*, *Prosopis*, and cactus association (Appendix II).

Aquatic Vegetation. The freshwater flora is restricted to a few springs, canals, and freshwater seeps around the lake. In these areas the dominant vegetation consisted of grasses (*Echinochloa crusgalli*, *Paspalidium geminatum*), sedges (*Eleocharis cellulosa*, *Scirpus pungens*), floating vines (*Ludwigia leptocarpa*, *L. repens*, *Enhydra sessilis*, *Commelina geniculata*), submerged plants (*Najas marina*, *Nitella* sp., *Sagittaria* sp.), and cattails (*Typha domingensis*).

The flora of the lake itself is rather limited, being restricted to several halophytic algae and a few vascular plants. Shallow water sublittoral areas usually supported dense bottom mats of algae (*Chara hornemannii* and *Batophora oerstedii*). These were the most productive areas of the lake and supported large numbers of fish (mostly *Tilapia*). Another alga (*Cladophora*

sp.) frequently was found growing attached to *Conocarpus* roots. *Ruppia maritima* forms dense mats in shallow water in several parts of the lake, usually adjacent to freshwater seeps. The grass *Halodule beaudettei* was often encountered along shores or in shallow water areas on mud or marl, usually under *Conocarpus*. In the southeastern section of the lake near Malpasse, *Salicornia perennis* grows along the lakeshore and out into shallow water.

Vertebrate Fauna

Fish. West Indian freshwater fish communities generally are lacking in diversity (Myers 1937). Etang Saumâtre only supports eight native species (Appendix II), three of which (*Strongylura notata*, *Gobionellus* sp., and *Dormitator maculatus*) typically are marine-coastal dwellers, reflecting the marine origin of the lake. In terms of biomass the dominant native species are *Cichlasoma hartiensis* (in the lake and springs) and *Cyprinodon bondi* (lake only). The other native fishes all are poeciliids, the two genera (*Limia* and *Gambusia*) being characteristic members of Hispaniolan freshwater fish communities.

Two species of introduced fish also are found in Etang Saumâtre: *Tilapia mossambica* and carp (*Cyprinus carpio*). Both were first introduced into the lake during the early 1950s as part of an FAO fisheries project. The *Tilapia* have become quite abundant and probably are the dominant fish overall in the lake in terms of biomass. The carp, on the other hand, are rarely seen and almost never caught by fishermen. As carp are long-lived fish and generally require cool water conditions for spawning, it is possible that no reproduction has occurred in the lake, and the few seen are remnants of the introduced stock.

Reptiles and Amphibians. Aside from crocodiles, the only aquatic reptile found in Etang Saumâtre is *Trachemys decorata*, a little-known freshwater turtle restricted to the Cul-de-Sac/Valle de Neiba region. Very secretive in their habits, the turtles were rarely seen, with most observations being restricted to shallow water areas in or around *Conocarpus*. No amphibians were found in the lake itself although several anurans (*Bufo guntheri*, *B. marinus*, and *Osteopilus dominicensis*) bred in freshwater areas adjacent to the lake.

Avifauna. Aquatic and semi-aquatic birds are quite common in the lake, especially during the winter when there is an influx of migrants from North America. The aquatic and semi-aquatic avifauna of the lake is listed in Appendix II.

Mammals. No native mammals are found in the Etang Saumâtre area. The only local mammals (besides domestic stock) were rats (*Rattus rattus*, *R.*

norvegicus), mice (*Mus musculus*), feral cats (*Felis domesticus*), and mongoose (*Herpestes auropunctatus*).

Demography

Population Size, Sex Ratio, and Size-class Distribution

Based on the corrected survey data the total population size in Etang Saumâtre was estimated to be approximately 450, including crocodiles of all size classes (Fig. 10).

Because sexing juvenile crocodiles is difficult, much of the juvenile sex data was not used, so sample sizes are small (Table 7). The predominance of males in the two smaller size classes is noticeable; however, it is not significantly different from 50% (chi square, $0.25 < p < 0.10$). All captured crocodiles over 2.4 m were males; the largest female caught was 2.39 m long. In the 1.8-2.7 m size-class the sex ratio of captured crocodiles probably was biased in favor of males. This occurred because most adults were captured in January on shallow-water feeding grounds at a time when many of the females were near the nesting beaches. Nevertheless, the sex ratio of the captured animals in this size-class was predominantly female (58.3%).

The size-class distribution was heavily skewed to the smallest class (0.3-0.9 m), two-thirds of which were concentrated along 16 km of the uninhabited eastern lakeshore (22.5% of the lake perimeter) adjacent to the nesting beaches (see **Habitat Selection**). Breeding-sized animals composed approximately 15.7% of the total population (1.8-2.7 m, > 2.7 m). This may be a slight overestimate as sexual maturity is not attained until 2.2-2.3 m total length (see **Reproductive Ecology**). Nevertheless, the great majority of the animals seen in the 1.8-2.7 m size-class were 2.3-2.5 m long, and the overestimate of reproductive animals is probably quite small. Only 10% of the population was in the subadult (0.9-1.8 m) size-class.

The small number of subadult crocodiles appears to be a general characteristic of most crocodilian populations. Cott (1961) commented on this mysterious "disappearance" of small- and intermediate-sized crocodiles in Africa, quoting Pitman as it being "a conspicuous feature of African inland waters." Messel et al. (1981) noted a similar lack of subadult *C. porosus* in northern Australia, as did Mazzotti (1983) for *C. acutus* in Everglades National Park. This apparent lack of subadults may be a result of: (1) rapid growth of young crocodiles, (2) extremely secretive behavior or occupancy of marginal habitats, or (3) high juvenile mortality. In most populations these factors are not mutually exclusive and may all play a role. Indeed, the last two

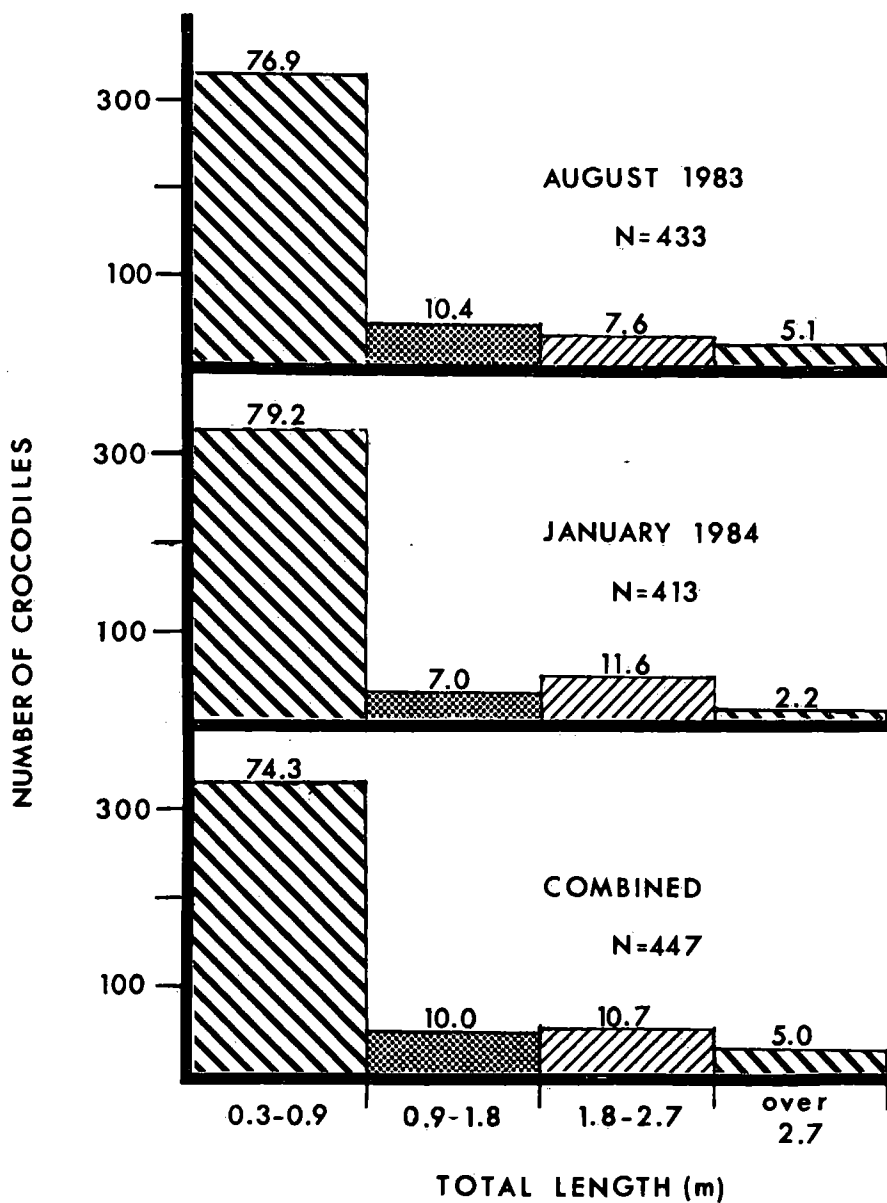


FIGURE 10. Size-class distribution and the total population size estimated from the August 1983, January 1984, and combined survey data.

are major components of the population dynamics model proposed by Messel et al. (1981) for *C. porosus*.

In Etang Saumâtre, rapid growth does not appear to be a factor (see following section). Subadults, however, do have a tendency to be found in more "marginal" habitats (see **Habitat Selection**), and this may have resulted in a slight underrepresentation of these crocodiles in the population surveys. The possibility of movement of subadults out of Etang Saumâtre also cannot be ruled out. Local residents have reported crocodiles moving between Trou Caïman and Etang Saumâtre, especially during periods of heavy rain. Crocodiles also have been reported crossing the arid strip between Lago Enriquillo and Etang Saumâtre (J. Ottenwalder pers. comm.). In both cases, however, the animals seen were most often adults; the incidence of migration of subadults remains unknown.

If we assume that the population in Etang Saumâtre has a stable age distribution, we then would be left with high juvenile mortality as the only explanation for the small number of subadults. While this mortality probably plays an important role, recent past events in the lake also must be considered.

Prior to 1979 the lake was approximately 2 m below its present level. In many areas one can still see *Conocarpus* snags standing in water of this depth. Subsequently, three hurricanes hit Haiti in 1979 and 1980, causing the lake to rise to its present level and flood out into *Conocarpus* habitat over 41% of the lakeshore (*Conocarpus* fringe and *Conocarpus* flats habitats; see **Habitat Selection**). Unless exposed to considerable wave action, these areas were ideal habitat for young crocodiles, hiding by day in the *Conocarpus* root mats and emerging at night to feed on the abundant fiddler crabs and other invertebrates (see **Diet**). Although the amount of suitable juvenile habitat before the hurricanes is unknown, it almost certainly was considerably less than it is today. Aerial photographs of the lake when it was at a similarly low level (Bond 1935) show considerable stretches of barren shoreline.

Furthermore, prior to 5-6 years ago, the major nesting areas on the eastern shore were the sites of temporary human settlements. People lived on the eastern lakeshore, cutting *Conocarpus*, making charcoal, and fishing, bringing freshwater across the lake from Fonds Parisien by boat. Remains of old thatch "ajoupas" were found in the middle of several of the nesting beaches. Nests were robbed and the eggs eaten (F. Conway pers. comm.) by residents of Fond Parisien. Undoubtedly, juvenile crocodiles also were killed. Since that time movement across the lake by boat has been outlawed by the Haitian government because of smuggling across the Dominican border, so no one lives near the nesting beaches.

Consequently, because of reduced habitat availability and increased human disturbance for a period of time prior to 1977-1980, hatchling production and survivorship of juvenile crocodiles may have been

considerably lower than today. Based on growth rates of recaptured crocodiles (see **Growth Rates**), the ones in the 0.9-1.8 m size class would have been born during the period 1977-1980, and recruitment into this size-class would undoubtedly have been adversely affected by these factors. Thus it seems that both natural mortality and past changes in the level of human-related mortality and juvenile habitat availability may be factors contributing to the low observed proportion of subadults.

Density and biomass

Few data exist on any aspect of crocodilian population dynamics. This is especially true for *C. acutus* where the lack of previous studies is due, at least in part, to the difficulty of accurately censusing these animals in their typical habitat (i.e. coastal wetlands). For comparative purposes, however, some information is available for several other crocodilians species, most notably *Crocodylus niloticus*, *C. porosus*, and *Alligator mississippiensis*. Density of crocodiles in Etang Saumâtre was calculated on a linear basis (per km shoreline), as crocodiles are primarily littoral animals and generally do not move far from shore. Therefore, in lacustrine or riverine habitats, density is best described in this fashion. Based on the corrected survey data, the mean density of crocodiles in Etang Saumâtre was 6.3/km (crude density, 71.2 km shore). Eliminating habitats unsuitable for crocodiles (rocky or high wave energy shores), the ecological density was 9.6/km (46.7 km shore).

Density estimates for various crocodilians are presented in Table 8. The high degree of variability among these values undoubtedly results from a variety of factors such as: physical habitat structure, vegetation, water depth, degree of wave exposure, aquatic productivity and the availability of food, population structure, and even terrestrial habitat (inasmuch as it determines the suitability of the area for nesting). Little is known quantitatively about the roles these various factors play in determining population density. Crocodile density in Etang Saumâtre is variable depending on habitat type and the degree of exposure to wave action (see **Habitat Selection**). Wood and Humphrey (1983) found that density in *Alligator mississippiensis* was correlated to lake productivity (nitrogen concentration). Anecdotal accounts relate food availability to crocodile density (Montague 1983, Watson et al. 1971) or vice versa (Cott 1961, Fittkau 1970, 1975, Whitaker 1978, Glastra 1983), suggesting that in some instances crocodilians play a beneficial role in maintaining healthy fish populations.

Although the factors mentioned above determine the attainable density, or carrying capacity of a particular habitat, in reality actual densities are usually held well below this value by human predation. Several hunted and

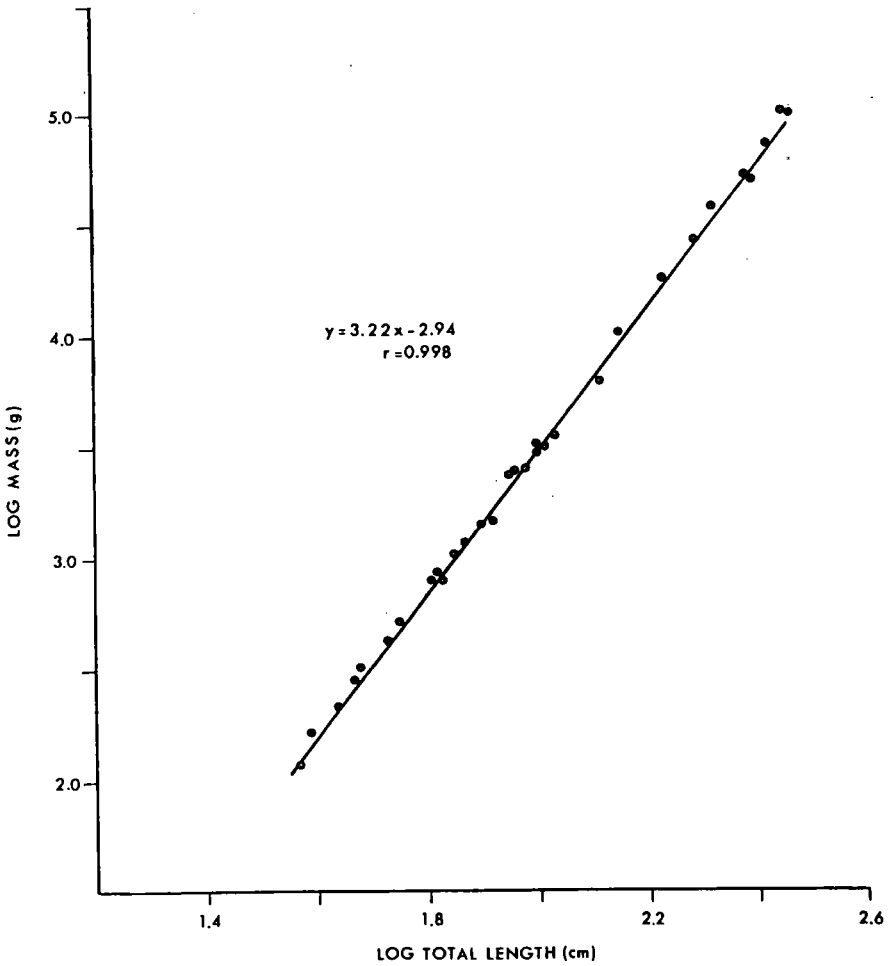


FIGURE 11. Log-log plot of the length-mass relationship of crocodiles captured in Etang Saumâtre. A maximum of 5 randomly chosen values are plotted for each 20 cm size class interval.

non-hunted populations are included in Table 8. At the time of censusing, the non-hunted *Crocodylus niloticus* populations probably existed in a more or less undisturbed state, and densities in these areas are quite high (13.1-21/km). Furthermore, within each of these areas densities were considerably higher in favorable habitats. In parts of Lake Turkana, for example, densities reached 55.8/km (Graham 1968). The highest reported value for *A. mississippiensis* from 40 lakes in Florida was 29.06/km (Wood and Humphrey 1983). The corresponding figure reported for *C. porosus* in the tidal waterways of northern Australia (excluding hatchling crocodiles) was 8.75-10.1/km (95% confidence intervals, Messel et al. 1982). In Etang Saumâtre, the highest density for any section of shoreline was 16.05/km (Habitat Selection, Table 23).

The length-weight relationship of 119 captured crocodiles (0.35-2.88 m total length) is given in Figure 11. Five randomly chosen values are plotted for each 20 cm size class (for size classes with more than 5 data points). From the length-mass relationship ($y=3.220x-2.994$, where $y=\log \text{ mass [g]}$ and $x=\log \text{ total length [cm]}$), and the corrected survey data, the total biomass of crocodiles in Etang Saumâtre is estimated as 4741.8 kg. This represents a crude density biomass of 66.6 kg/km shore, or 101.7 kg/km ecological density (excluding rocky and high wave energy shores that crocodiles avoid). The specific breakdown of biomass by size class is shown in Table 9.

Reported biomass figures of *C. niloticus* populations (Lake Turkana, 350 kg/km; Victoria Nile, 397.5 kg/km; Graham 1968; Parker and Watson 1970) are considerably higher than those found for *C. acutus* in Etang Saumâtre. The greater difference in the biomass values between Etang Saumâtre (corrected census data) and Lake Turkana (66.6 vs 350 kg/km) as compared to the density figures (6.3 vs 13.4 crocodiles/km) reflects differences in the population's size-class distributions and the fact that crocodiles reach larger sizes in Lake Turkana (to 4.7 m), and that the majority of the population biomass is concentrated in the larger size classes (Table 9).

Whether or not the crocodile population in Etang Saumâtre is near an undisturbed state can best be addressed by a comparison with adjacent Lago Enriquillo. A rough estimate of population size in Lago Enriquillo can be made based on the number of nests in that lake and the demographic data gathered in Etang Saumâtre. A maximum of approximately 150 nests has been found in Lago Enriquillo (J. Ottenwalder pers. comm.). Taking a high and low range of 150 and 100 nests and assuming the same population structure in both lakes, the most conservative estimate of adult population in Lago Enriquillo is 336-504. Considering only adult crocodiles, the crude population density in Lago Enriquillo (130 km shoreline) is 2.58-3.88 adults/km. The corresponding value for Etang Saumâtre is 0.98, or 3.2 times lower than in Lago Enriquillo. These data suggest that the crocodiles in Lago Enriquillo may be in a nearly undisturbed state, and indicate that past

hunting and human disturbance has had a significant effect in reducing the crocodile population in Etang Saumâtre.

Mortality

Mortality of young crocodiles always has been assumed to be quite high. Owing to the difficulties of obtaining such data, however, few quantitative estimates of juvenile crocodile mortality are available. What little information is available does, however, indicate that mortality over the first two years is substantial.

Although no quantitative estimates are available for Etang Saumâtre, an approximation of mortality can be obtained based on some of the data from this study. Production of hatchling crocodiles in 1983 can be estimated from nesting data. Twenty nests were located with a mean clutch size of 22.5 (SD=2.7) and a fertility rate of 90.1% (SD=10.5). This resulted in the total 1983 production of approximately 405 viable eggs. To estimate the number of hatchlings egg mortality must be known. Egg mortality results from three primary factors: predation, nest flooding, and egg dessication (Mazzotti 1983). No nest predation was observed in 1983, but one nest (5.8%) was lost to flooding from heavy rainfall. In Florida Bay, egg loss from dessication accounted for 0% and 15% egg mortality during a normal rainfall and very dry year respectively (Mazzotti 1983). Using these as high and low estimates for Etang Saumâtre, we obtain a range of 5.8-20.8% egg loss due to embryonic mortality. This results in an estimated production of 321-381 hatchlings in 1983.

The population censuses in both August 1983 and January 1984 show that there are only approximately 320-340 crocodiles in the smallest size class (0.3-0.9 m) which, based on the known rate of growth (see **Growth Rate**), includes 3-year cohorts. If the 1981 and 1982 production of hatchlings was comparable to the estimate for 1983, then clearly a significant fraction of each year class has disappeared. As it is very unlikely these small crocodiles dispersed from the lake, this loss must be assumed to be mortality.

Two population surveys revealed nearly identical estimates of 0.3-0.9 m crocodiles over a 6-month interval (August-January). The first survey was done 3-4 months after the 1983 hatch. If indeed there was little mortality in this size class during the interval between surveys, it suggests that much of the mortality takes place in the first 3-4 months after hatching. This hypothesis is consistent with the predation that is presumed to account for a large part of this mortality (i.e. from wading birds). Observation in Lago Enriquillo suggests that yellow-crowned night herons (*Nyctanassa violacea*) take a large number of freshly emerged hatchlings (J. Ottenwalder pers. comm.).

Undoubtedly, other wading birds such as great blue herons (*Ardea herodias*) or great egrets (*Casmerodius albus*) also take hatchlings. After growing to 40-50 cm, crocodiles are probably immune to this predation, with the exception of the great blue heron (however, Gorzula [1978] reported that a white-necked heron, *Ardea cocoi*, took an 80 cm long *Caiman crocodilus*).

Messel et al. (1982) suggested that mortality of 0.9-1.8 m crocodiles associated with intraspecific aggression may be quite high. They found that up to 80% of the crocodiles in this size class may be excluded from river systems, presumably by adult aggression. The juveniles and subadults either are lost through direct mortality or by being forced to move into marginal habitats where many may perish. This hypothesis is supported by independent observations of crocodilian behavior. Agonistic interactions between adult and subadult crocodiles have been noted in captivity with *Crocodylus moreletii* (Hunt 1977) and *Alligator mississippiensis* (Hunt and Watanabe 1982). Juvenile *C. porosus* apparently first begin demonstrating territorial and aggressive behavior in the 0.9-1.8 m size range (Bustard and Kar 1980). Negative interactions between adult and subadult *C. acutus* also have been inferred from data on size-class specific habitat selection in Florida (Gaby et al. 1981).

Cannibalism has been implicated in a number of crocodilians, and in most cases adults are eating subadults (as opposed to juveniles) (*Caiman crocodilus*, Staton and Dixon 1975; *Alligator mississippiensis*, C. Abercrombie and A. Woodward pers. comm.; *Crocodylus niloticus*, Cott 1961; and *C. acutus*, Schmidt 1924).

Adult crocodile mortality is primarily human-related. During the 14-month interval of this study at least three adults and one subadult were killed. Fishermen occasionally will try to kill juveniles and subadults they encounter. This was evidenced by a machete wound found on a 90-cm crocodile in an area frequented by fishermen.

The frequency of injury of crocodiles in Etang Saumâtre is quite low (2.6% of the captured crocodiles had injuries). The lowest reported frequency of injury among four populations reviewed in Webb and Manolis (1983) was 6.5% for *C. porosus* in Australia (from Webb and Messel 1977). A Jamaican population of *C. acutus* had an injury frequency of 14.1% (from Garrick unpubl.). In the past, frequency of injury sometimes was assumed to reflect predation pressure (Webb and Messel 1977, Dietz 1979). Most evidence, however, indicates that while predation may lead to some injuries, the majority are sustained during intraspecific social encounters (Cott 1961, Staton and Dixon 1975, Gorzula 1978, Webb and Manolis 1983).

Growth Rate

The growth rates of crocodiles to 1.6 m total length were estimated from the recapture of 12 individuals, one of which was recaptured three times. Mean growth rate of the 0.3-0.9 m crocodiles was 0.058 cm/day (10 recaptures; SD=0.043). Due to the small sample size, no statistical analyses could be done to test the effects of season, habitat type, or sex on the rate of growth.

With a mean hatching date of 1 May, and a mean hatchling length of 24.4 cm (from six hatchlings found in a nest just prior to emerging), the average hatchling growth rate over the first 65-86 days of life was 0.135 cm/day (SD=0.043, n=13), with a low estimate of 0.111 cm/day (mean hatching date 15 April, SD=0.035, n=13). Both these values are substantially higher than the growth rates of the recaptured 0.3-0.9 m crocodiles, all of whom were at least 9 months old.

Based on the two 0.9-1.8 m crocodiles recaptured, there does not appear to be any slowing of growth in males of this size class (mean growth rate 0.090 cm/day). As no females in this size class were recaptured, no data exist for 0.9-1.8 m females. Females do not grow as large as the males; consequently, it is apparent that female growth slows sooner than that of the males. Messel and Vorlicek (in press) have noted consistent differences in male and female growth in *C. porosus* less than 1 m total length; however, these differences were not significant. In animals over 1 m total length, sexual differences in growth rates have been found to be significant (Webb et al. 1978, Chabreck and Joanen 1979, Webb et al. 1983).

Although the sample size is small, several conclusions can be drawn concerning the growth rates of crocodiles in Etang Saumâtre. Hatchlings appear to grow rapidly (0.111-0.135 cm/day) over at least the first three months of life, thereafter slowing to 0.05-0.06 cm/day in the 1-2 year age classes. Although growth among hatchlings was consistently high (range 0.059-0.204 cm/day), growth in larger animals was more unpredictable. Two 1-2 year old animals exhibited almost no growth (0.000 and 0.008 cm/day) over a period of 168 days.

Seasonal differences in growth rate have been noted in a number of crocodilians: *Alligator mississippiensis* (Chabreck and Joanen 1979), *Crocodylus porosus* (Webb et al. 1978, Magnusson 1981, Messel and Vorlicek in press), *C. acutus* (P. Moler pers. comm.), *C. johnsoni* (Webb et al. 1983), *C. niloticus* (Pooley 1962), and *Caiman crocodilus* (Gorzula 1978). These seasonal changes have been variously attributed to temperature and/or food availability. Little information exists concerning seasonal differences in growth rates in Etang Saumâtre as the great majority of the recaptures (10 of

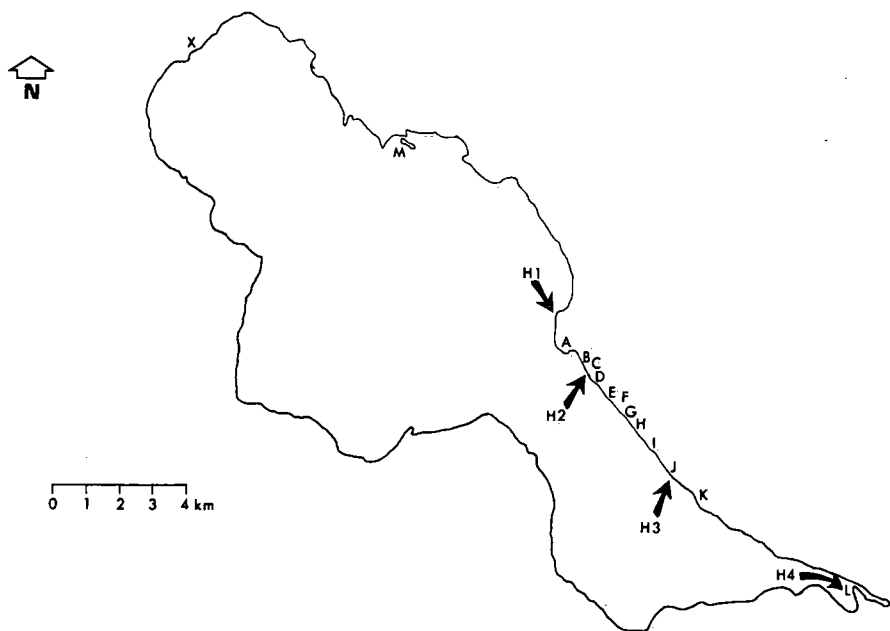


FIGURE 12. Location of nesting areas and "harem" groups in Etang Saumâtre. (A-M are nesting beaches. X marks the location of a human-predated nest in 1983. Harem locations are marked h.)

12) included both wet and dry season growth periods. One animal recaptured 3 times did grow at a slower rate over the winter dry season (0.088 cm/day, interval 118 days) than during the summer wet season (0.155 cm/day, interval 58 days). Seasonal variation in growth rate, if it does occur, would most likely be related to temperature. Mean monthly air temperature varies 4.1°C annually, and reptiles, being ectotherms, are sensitive to changes in temperature because metabolic rate is temperature dependent. Although rainfall does increase in the wet season, it has little effect on lake level or food abundance (the primary food item of juveniles, *Uca*, being abundant at all times of the year).

A comparison of the growth rates of *C. acutus* from Etang Saumâtre with rates reported from other *C. acutus* populations and those reported from *C. porosus* (Table 10) indicates the Haitian crocodiles are growing at a slow rate. This occurs despite the fact that in the other populations the crocodiles are not growing during significant portions of the year because of low temperatures (Florida, P. Moler pers. comm.) or possibly food availability

(Australia, Webb et al. 1978). The Etang Saumâtre crocodiles apparently are growing throughout the year but at reduced rates.

The slow growth of the Etang Saumâtre crocodiles is manifested in the small size of adults. Males and females only reach lengths of 3.5 m and 2.4 m respectively, whereas in other parts of its range *C. acutus* is reported to grow considerably larger (Alvarez del Toro 1974, Ogden 1978, Medem 1980, Mazzotti 1983). The maximum reported size of *C. acutus* is 6.25 m (Alvarez del Toro 1974). A similar situation appears to hold in the large Lago Enriquillo population, where crocodiles may grow slightly larger (males 4.0 m, females 2.6-2.7 m). Jamaican crocodiles are also reported to reach similar lengths (Garrick in litt.), so relatively small size may be characteristic of the *C. acutus* in these Greater Antillean islands. The reasons for the slow growth in Etang Saumâtre, whether environmental or genetic, are unknown.

Reproductive Ecology

Courtship and Mating

Courtship and mating activity was not observed in Etang Saumâtre, but based on the timing in relation to nesting (Garrick and Lang 1977) was assumed to take place during late December and early January. The courtship of crocodiles in Lago Enriquillo was observed in 1979 by S. Inchaustegui, J. A. Ottenwalder, and D. Robinson (pers. comm.). Three males were observed to establish adjacent territories. The largest male was dominant, excluding the other males from his territory. Females would move freely through the territories of the males. One copulation was observed by the dominant male (0900 h, 27 January 1979) during 15.5 hr of observation. During this period the same male was observed courting several females and interrupting the courtship of a neighboring male. The pattern and behavioral inventory of courtship and mating was similar to that described in Garrick and Lang (1977), with the exception of the "sub-audible vibration" which never was observed at Lago Enriquillo.

In Etang Saumâtre during early January 1984, 27 adult crocodiles were observed in four distinct groups (mean intergroup distance 4.7 km, SD=2.9) along the eastern lakeshore adjacent to the nesting beaches (Fig. 12). These groups were quite distinct during the day, but at night the adults would disperse along the lakeshore. These aggregations were inferred to be courtship groups or "harems," as they contained one large male and several smaller adults (presumably females, although possibly smaller males). The sex ratio of males to females captured near the nesting beaches shortly after the nesting period was 1:3. During roughly the same period of time, five

adults were captured in the northwestern section of the lake, away from any known nesting areas, and these all proved to be males. This suggests that a certain fraction of the adult males were excluded from breeding, a hypothesis consistent with a polygynous mating system. This argument is strengthened further by the fact that the "excluded" males were smaller (mean length=2.63 m, SD=0.16 m, n=5) than the males caught adjacent to the nesting areas (mean=2.86 m, SD=0.04 m, n=2).

Minimum Size for Reproduction and Percentage of Population Breeding

The smallest female captured near the nesting beaches, and presumed reproductively active, was 2.30 m, the largest was 2.39 m. The minimum size for reproduction in either sex of *C. acutus* is not well known, but the length at sexual maturity undoubtedly varies between populations. Alvarez del Toro (1974), for instance, never found a reproductive female less than 2.8 m, in Chiapas, Mexico, which is longer than the longest female in Etang Saumâtre. In Florida, Ogden (1978) estimated the sizes of nesting females to range from 2.5 m to 3.9 m. Also in Florida, Mazzotti (1983) estimated minimum female breeding size at 2.25 m and found six females at nests ranging from 2.28 m to 3.08 m. Similar variation in the minimum breeding size of females has been noted in *Crocodylus niloticus* (Cott 1961, Graham 1968). Assuming a minimum breeding size of 2.25 m, age at sexual maturity is probably at least 8 years for females in Etang Saumâtre (assuming no slowing of growth with age up to 2.25 m).

The minimum breeding size of males is even more difficult to ascertain, as the reproductive state of a male can be determined only by killing the animal. Evidence from Lake Turkana indicates that male *C. niloticus* may be sexually mature at lengths of 2.12 m (Graham 1968), although in other parts of Africa 2.30 m may be the minimum (Cott 1961). Medem (1981) reported that a 2.19 m captive *C. acutus* mated with a 2.36 m female, but produced an infertile clutch. In all probability, however, males in the wild may be sexually mature, but excluded from breeding by larger males, so minimum size at reproduction needs to be considered from a behavioral, as well as a physiological standpoint.

The percentage of adult females breeding in 1983 was estimated based on demographic and nesting data, using the formula of Chabreck (1966): $E = N / (P * A * F)$; where E = percent of adult females nesting, N = total number of nests, P = total population size, A = percent of population sexually mature, and F = percent of females among mature crocodiles. In 1983, 20 nests were located and another was reported, but not seen, making a total of 21 nests. Based on the data in the preceding section, P=450, A=15.7%, and F=46.6%,

suggesting that 63.8% of the mature females nested that year. This figure is comparable with values reported for other crocodilian populations (Table 11). Reasons why an individual female may not breed in any particular year are not well understood, but probably are related to energetic constraints or reproductive senescence (Graham 1968).

Timing of Nesting

In 1984, all 13 known nesting attempts occurred between 22 January and 12 February. Hatching takes place in late April and early May after an incubation period of approximately 90 days. This timing is similar to that found in other soil-hole nesting crocodiles in that egg laying takes place during the dry season and eggs hatch at the beginning of the rainy season (Fig. 13). Oviposition during the dry season means incubation will take place when water levels are dropping, thereby reducing the chance that the nests

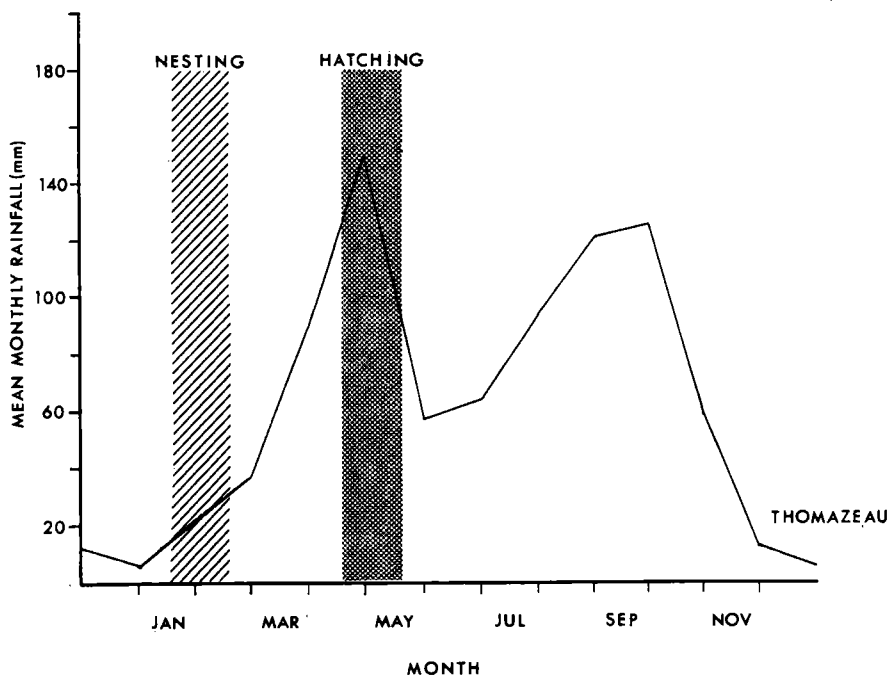


FIGURE 13. Timing of nesting and hatching in relation to rainfall (Thomazeau rainfall data).

will be flooded. It also allows the newly emerged hatchlings to take advantage of the increased invertebrate food and habitat availability associated with the rainy season (Cott 1961). Similar timing of nesting in *C. acutus* has been noted in Mexico (Alvarez del Toro 1974).

Although this pattern of reproduction is fairly typical of soil-hole nesting crocodiles (as opposed to crocodiles that build vegetation mound nests), a degree of asynchrony in breeding has been noted in some populations of *Crocodylus niloticus* in Lake Turkana (Graham 1968) and Lakes Victoria and Kioga (Cott 1961). Graham (1968) found evidence of reproductive activity at all times of the year, although a definite peak occurred during the dry season (late fall-early winter) when Modha (1967) noted courtship and mating. Cott (1961) reported two nesting seasons in Lakes Victoria and Kioga, each associated with one of the two annual rainy seasons. Interestingly, 15.1% of the females examined by Graham (1968) that were ovulating or had just ovulated contained another clutch of developing eggs, suggesting that females may produce more than one clutch of eggs a year. Double clutching has been noted in *Crocodylus palustris* in India (R. Whitaker pers. comm.), although all evidence indicates that *C. acutus* nests only once a year.

A comparison of the timing of nesting with adjacent Lago Enriquillo produces some unexpected results. Both lakes experience the same temperature and rainfall regimes, and being located only 5-10 km apart, the annual photoperiod is identical. Yet, crocodile courtship/mating and nesting in Etang Saumâtre appears to be 2 weeks to one month ahead of Lago Enriquillo. The reasons for this asynchrony are unclear. The role of environmental cues in determining the onset of reproduction has yet to be examined in crocodilians and would merit future investigation.

Nest Site Characteristics

Physical Characteristics. Crocodile nests can be divided into two basic types, eggs being deposited either in holes dug into the substrate or in vegetation or soil mounds built up above the level of the surrounding terrain. Under natural conditions, this dichotomy usually is consistent within species; however, *C. acutus* will use hole nests or mounds constructed from soil (Campbell 1972, Ogden 1978) or, rarely, from vegetation (Alvarez del Toro 1974, Medem 1981). All nests at Etang Saumâtre were hole nests (Table 12).

The purpose of constructing mound nests presumably is to raise the elevation of the egg clutch, thereby minimizing the possibility of nest flooding (Mazzotti 1983). Some mound nests on Key Largo, Florida, however, are constructed on spoil banks where the possibility of flooding is minimal (P. Moler pers. comm.).

The mean height of nests in Etang Saumâtre was 1.2 m (SD=0.5 m, n=25) above lake level (Table 13) at the beginning of the incubation period. The bottom of the average clutch is approximately 80 cm above lake level, as the mean hole depth is 37.9 cm (Table 12). Because the lake only fluctuates 0.3-0.4 m annually (excluding years with hurricanes), egg mortality from rising lake water would be minimal. The only flooding found to occur was associated with surface inundation from heavy rainfall (one nest, 1983).

Along the eastern lakeshore, nests were located on coralliferous limestone outcrops that extend down to the lakeshore. These outcrops often were separated from one another by low-lying salt pans that supported little vegetation other than frequently dense *Conocarpus* stands along the lakeshore. Old beaches, formed when the lake level was higher, frequently would create deep sand areas on these outcroppings, providing suitable nesting habitat. Besides furnishing sand beaches close to the lakeshore, these outcroppings provided deep-water approaches to the nesting area. Although apparently suitable nesting areas were located behind the salt pans, these were farther away from the lake (usually more than 50 m), and water approaches were frequently through shallow water or over mudflats. These two parameters, well-drained soil and deep water approaches, also were noted by Ogden (1978) as being important in determining the suitability of habitats for *C. acutus* nesting in Florida.

Besides using the deep sand of old beaches, crocodiles frequently would nest in old charcoal mounds, usually located on the same raised, well-drained banks where sand nests were found. The term "mound" refers only to the fact that when the charcoal is being made, the slowly burning wood is covered with a layer of soil, creating a mound. Upon finishing, the charcoal makers scatter the remains of the mound more or less evenly with the surrounding terrain. Out of 26 nest sites active in 1983 and 1984, 15 (57.7%) were either in or adjacent to these old charcoal mounds.

To more closely examine the factors that are important in determining nest site selection, a stepwise discriminant analysis (Barr et al. 1976) was performed comparing the 1984 nest sites with 15 null sites randomly selected within the range of the nesting beaches along the eastern lakeshore. Of the eight nest parameters examined (Table 13), distance to lake was not used, as this was standardized at 25 m for all null sites. The discriminant analysis revealed only soil moisture content to be important in separating nest sites (drier) from null sites (wetter) ($p < 0.01$). Percent shrub coverage was significantly higher at null sites ($p < 0.05$) but was correlated with soil moisture content so did not account for much of the difference between nests and null sites once the variation due to soil moisture was removed ($p > 0.38$).

The importance of soil moisture content in selecting nesting areas is obvious as eggs depend on oxygen diffusion for respiration (Ackerman 1980), and gas diffusion rates are negatively correlated with the amount of water in

the soil. The mean water content of the nest soil (6.62%, SD=3.13, n=12) was significantly lower than for null sites (20.33%, SD=5.01, n=15) and reflected the fact that the areas selected for nesting were the well-drained old beach or charcoal mound sites. The mean water content for three sand nests measured in Florida was 10.3% (calculated from Lutz and Dunbar-Cooper 1982) and ranged from 4.89% to 19.25%, these extremes being recorded from a single nest over the period of incubation.

As the soil parameter data were taken shortly after oviposition, the moisture values reflect what the females were encountering as they excavated the nests. On examining the nests, however, it was noted that the soil matrix near the eggs appeared to be more moist than the surrounding soil. This was tested by excavating holes of equal depth adjacent to four nests and measuring soil water content. The nest soil was found to be significantly wetter (Table 14, paired *t*-test, $p < 0.05$). The source of this moisture could be from cloacal fluids released by the female during oviposition and/or the mucous covering of the eggs. As during periods of low rainfall dessication can cause egg mortality in *C. acutus* eggs (Mazzotti 1983), this extra moisture may be important in preventing dessication mortality. Bustard (1971), however, found that *Crocodylus novaeguineae* eggs hatched normally in soil with only 2% water content.

Vegetation. Nests generally were located near the ecotone between the *Conocarpus*-dominated riparian strip and the xeric upland flora, the species assemblage being a mixture of both communities (Table 15). The percent of shrub coverage at the nest sites (30.1%) was significantly lower than the null sites (40.6%) (Table 13). The canopy of these trees and shrubs was quite sparse and only provided partial shading. Nests were usually located near to, but not directly under, trees or shrubs. The mean distance from nests to the nearest tree/shrub over 1 m high was 2.1 m (SD=1.05 m). This, however, was not significantly different from the null sites (2.7 m, SD=2.7 m). Herbaceous cover was also sparse on the nesting beaches. The dominant grass, *Uniola virgata*, usually was not found growing on the sand beaches or charcoal mounds used for nesting.

Location of Nesting Beaches

The majority of the nesting occurred over 6.6 km of shoreline on the eastern lakeshore (Fig. 12, containing 18 of the 21 nests in 1983 [2.7 nests/km shore]). At least 13 nests occurred over the same area in 1984. Because of the difficulty of locating nests before hatching, this 1984 figure represents a minimum number and is probably an underestimate.

Colonial nesting in the sense of Cott (1961), or in Lago Enriquillo where one may find 20-30 nests on a single nesting beach, was not in evidence. Nevertheless, several nesting beaches had more than one nest (Table 16).

Single nests also were located on a small island near Malpasse (nesting beach L), and on Osprey Island along the north shore 2 km west of Las Lajas (nesting beach M, Fig. 12).

Location of nesting beaches on the lake was primarily determined by three factors: (1) suitability of the terrestrial habitat for nesting (as discussed above), (2) human population density, and (3) the presence of nearby aquatic habitats protected from wave action.

The effects of human population density can be seen in the case of a 1983 nest reported from the northwestern section of the lake near Tete Source (I. Lange pers. comm.). The nest was discovered by local residents, excavated, and the eggs were brought to a local market for sale. The area where the nest was located provides suitable nesting habitat and in the past may have been an important nesting site. High population density and heavy grazing/browsing by domestic stock today make this area marginal for nesting. Extensive searching failed to reveal any sign of nesting in 1984. All other known nesting areas are located away from areas of high human activity. The two island nest sites are relatively isolated with only occasional use by fishermen or charcoal makers. The nesting beaches along the eastern lakeshore are likewise removed from any significant human activity.

Although the characteristics of the terrestrial environment are important for choosing nesting areas in that they are selected to minimize egg viability, the nature of the adjacent aquatic environment also is important. As mentioned above, deep water approaches are favored as they allow the crocodile easier access to the nest site. Nesting beaches also were located adjacent to areas protected from wave action. With the predominant winds from the east, the eastern lakeshore provides many such areas. In several locations along the western lakeshore suitable terrestrial environments exist for nesting, but these areas invariably are exposed to a high degree of wave action (the nesting area near Tete Source mentioned above is located adjacent to a protected water area).

The relationship between calm water habitat and nesting is closely tied to the habitat preference of adult crocodiles, which tend to avoid areas with any wave action and concentrate in calm water habitats (see *Habitat Selection*). Calm water may be especially important for courtship and mating, as many of the associated behaviors are visually oriented and take place when the animals are floating at the surface of the water, thus requiring low wave amplitude. Once courtship and mating are finished, the females may select the closest available nesting area. I observed a similar pattern of nesting beaches located adjacent to calm water habitat in Lago Enriquillo.

At the opposite extreme is the situation in Florida Bay, where crocodiles spend most of the year in protected mangrove habitat but the females venture out into the more exposed regions of Florida Bay to nest (Ogden 1978; Mazzotti 1983). Reasons for this behavior are not well understood but may be related to a lack of suitable nesting habitat in the protected regions of the bay.

Clutch Size and Fertility

The average clutch size at Etang Saumâtre was 22.5 (SD=2.7) (Table 17), which is at the lower end of reported values for *C. acutus* (Table 18). Overall egg fertility was 90.1% and ranged from 70.6 to 100% within clutches. Mean clutch mass was 2.18 kg, or approximately 4.4% of female body mass (mean female mass=49.7 kg, based on an average length of 236 cm). Clutch size has been demonstrated to be positively correlated with female size in *C. niloticus* (Cott 1961, Graham 1968), and it is reasonable to assume that the same holds true for other crocodiles. Because the crocodiles in Etang Saumâtre and Lago Enriquillo do not reach large sizes, this could explain the small clutch sizes in these lakes. Using data from Graham (1968) relating female length to clutch size ($y=0.2909x-43.34$, $r=0.86$, $n=10$; where y =clutch size and x =total female length in cm), the predicted clutch size for the average length female in Etang Saumâtre (236 cm) is 25.3, which is in good agreement with the observed mean clutch size (22.5).

Using this same relationship together with the mean egg mass (97 g) data and the length-weight relationship from this study, the predicted clutch size and mass can be calculated for females of different lengths. These relationships predict that clutch size remains a fairly constant 3-5% of body mass over a wide range of female lengths, but trending slightly downward with increasing female size (assuming that egg mass is independent of female size). Ferguson and Joanen (1983), however, found that larger female alligators laid larger eggs than smaller females. If this is true for crocodiles, clutch mass as a percentage of body mass may remain remarkably constant throughout life. Webb (1983) also found that clutch mass was approximately 5% of body mass in *Crocodylus johnsoni*.

It should be noted that this relationship is for the average clutch size, and actual clutch size may vary considerably from year to year. Yadav (1979) reported nesting data from a captive pair of *Crocodylus palustris* where the female (2.80 m total length) oviposited annually for 15 consecutive years. Data for 12 years demonstrated that clutch size varied from 22 to 41 (mean=31.2, SD=5.2) with the high and low values being laid in consecutive years.

Nest Temperature

Temperature of incubation determines the sex of *Alligator mississippiensis* (Ferguson and Joanen 1982, 1983), *Crocodylus niloticus* (Hutton 1984), *C. porosus*, *C. johnsoni* (Webb and Smith 1984), and a number of turtles (review in Bull 1980). As all crocodilians lack heteromorphic sex chromosomes (Cohen and Gans 1970), it is reasonable to assume that temperature dependent sex determination is a common feature shared by all crocodilians. As such, information on the temperature regimes of nests is an important aspect of nesting ecology.

Thirteen temperature recordings were made for the top and the bottom of six egg clutches over a 30-hour period on 13-14 February 1984 (Table 19). Overall mean temperature for the egg clutches was 29.3°C (SD=0.41). Temperature at the top of the clutch varied slightly more (mean temperature amplitude=0.9°C) than the bottom (0.6°C). Nevertheless, on average, temperature remained remarkably constant, the largest temperature variation in any one nest being 1.8°C (nest 84-4, top) while air temperature over this period varied 8.9°C. This is even less variation than found by Lutz and Dunbar-Cooper (1982, 1984) for *C. acutus* nests in Florida Bay (mean diel variation=1.4°C), and also less than values reported for vegetation mound nesting species (Chabreck 1973, Webb et al. 1977, Goodwin and Marion 1978). The diel temperature variation for a typical nest (84-8) is shown in Figure 14. The high thermal inertia of the soil results in the nest reaching its highest temperature during the night.

Little can be said about the differences in temperature regimes between sand and charcoal nests. Of the six nests monitored, two were in charcoal mounds (84-2 and 84-8); these nests were the hottest and coolest nests measured, respectively.

Nesting Behavior

Crocodiles began visiting potential nest sites up to 28 days prior to nesting. Similar early visits were noted in *C. acutus* in Florida (Ogden 1978, Mazzotti 1983; P. Moler pers. comm.). During these early visits, females walk along the nesting beach and make periodic shallow digs in the substrate. As the time for nesting approached, deeper test holes were dug, often several in a very small area, or scattered around the nesting beach. These test holes either were left open or were filled in by the female before departing. Nest digging or egg laying were never observed in Etang Saumâtre; however, observations in nearby Lago Enriquillo indicated that females begin nesting

soon after dark. One female was discovered in the final stages of egg laying at 2315 h on 12 February 1982. After oviposition the female, using her tail and body, smoothed out the area surrounding the nest, making it difficult to find the exact location of the hole.

During the incubation period females will remain in the vicinity of the nesting beaches, although they never were observed on land near the nest as has been reported for *C. niloticus* (Cott 1961, Modha 1967). No nest predation was observed in Etang Saumâtre during 1983 or 1984. In Lago Enriquillo dogs, and possibly mongoose (*Herpestes auropunctatus*), were reported to rob crocodile nests (J. Ottenwalder pers. comm.). The incidence of nest predation in Etang Saumâtre, however, is very low.

Crocodiles were not observed to be territorial around nest sites as has been reported for *C. acutus* in Mexico (Alvarez del Toro 1974). In fact, several nests were found within a few meters of one another, and two nests in 1984 (84-8 and 84-12) were laid (approximately 2 weeks apart) with their clutches almost contiguous.

Crocodiles appear to nest on the same beaches year after year. The actual reuse of 1983 nest sites in 1984, however, was only 46%. This figure is similar to the values obtained for *C. niloticus* in the Okavango delta (44.3%, Graham et al. 1976; 44.1%, Blomberg in Graham et al. 1976). Of the 1984 nests, 15% were in areas used as nests prior to 1983 (based on egg shell fragments), and 31% were apparently in new sites.

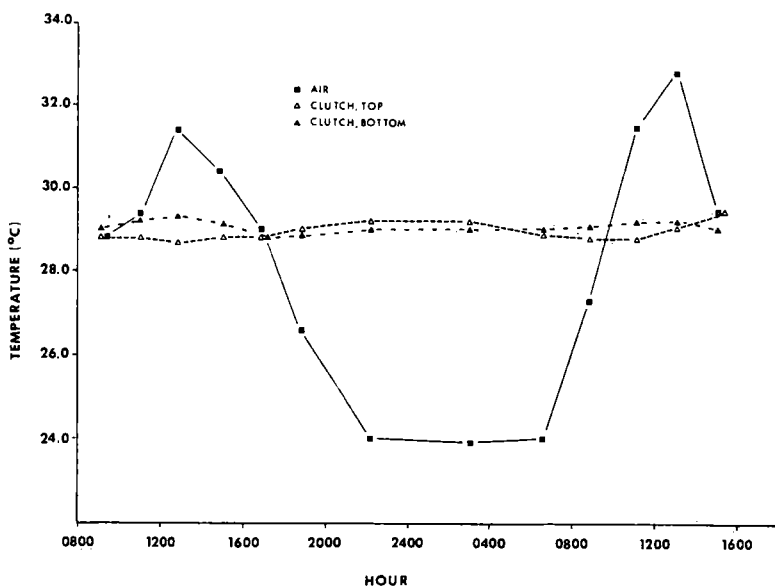


FIGURE 14. Diel nest temperature variation (nest 84-8) over a 30-hour period, 13-14 February 1984.

Tracks of female on nesting beaches in Etang Saumâtre revealed an apparent random search component. Females could locate old nest sites without difficulty, but often would wander considerably during their nocturnal visits, or even come ashore in areas where no suitable nesting habitat occurred. This type of searching behavior may be important because of changes in the characteristics of the previously used nesting sites. In Etang Saumâtre (and in Lago Enriquillo) many old nest sites have been inundated by the rising lake waters since the hurricanes of 1979 and 1980; others are unsuitable because the egg cavities would now be below the water table. This has required females to select entirely new nest sites in the last 5-6 years. This random searching by the female no doubt familiarizes her with potential nest sites in the area and facilitates switching to new nesting areas.

The reuse of nest sites by individual females has been speculated on (Alvarez del Toro 1974, Ogden 1978) but is difficult to document. The only data concerning individual nest reuse for hole nesting crocodiles concerns *C. niloticus* in Botswana (Graham et al. 1976), where aerial photographs of females on nests reveals that in two instances different females were photographed at the same nest site in consecutive years. Obviously, different females may use the same nest site in different years, and annual use of nest sites should not be construed as the work of one female unless other supporting data exists.

Based on tracks, females returned to open the nest at the end of incubation. Some females were visiting the nest sites 2 weeks prior to hatching and probably visited the nest frequently before it finally opened. In several instances, eggshell membranes were found along the shoreline, indicating that females carry their young to the lake, picking up egg fragments in the process. In two of the 1983 nests, females left eggs covered in the nest after opening it. In both nests, two eggs contained pipped young, and the third egg held a dead embryo. Asynchrony in hatching also has been noted in *C. acutus* in Lago Enriquillo (J. Ottenwalder pers. comm.) and Florida (Mazzotti 1983).

Diet

Juvenile Crocodiles

For the purposes of analyzing the differences in diet among crocodiles of varying lengths, four size-classes were defined (Table 20). The largest sample was obtained for juvenile crocodiles (the smallest two size-classes), and for these animals invertebrates composed the vast majority of prey items. No vertebrate remains were found in any crocodile of the smallest size class (< 0.5

m). In the 0.5-0.9 m class, the occurrence of vertebrates increased dramatically. Many of these, however, were samples with a few scattered mammal hairs (*Mus* or *Rattus*) or bird feathers. Prey mass represents a more unbiased estimate of diet because it considers only recently ingested food items (fresh and partly digested categories) so there is less potential for bias due to differential digestibility of prey (Jackson et al. 1974, Garnett 1985). Based on prey biomass (Table 21), invertebrates comprised the great majority (87.2%) of the food for 0.5-0.9 m crocodiles.

The dominant prey item in terms of frequency of occurrence and mass was the fiddler crab, *Uca bergersii*. These crabs were very abundant (23.1-121.8/m²) in all the protected shallow water habitats which juvenile crocodiles preferred. Juvenile crocodiles also ate considerable numbers of beetles (Coleoptera) and odonate larvae (Tables 20, 21). The occurrence of these prey items indicates two separate foraging strategies. The majority of beetles found in crocodile stomachs was of terrestrial origin (Table 22). Crocodiles never were seen foraging on land, but frequently were observed sitting in shallow water making sideswipes at surface disturbances. This method of prey capture probably results in the ingestion of terrestrial insects (Coleoptera, Lepidoptera, and Hymenoptera) that accidentally fall into the water.

The high occurrence of odonate larvae in the diet of these crocodiles suggests that they also actively forage underwater amongst the submerged vegetation and/or bottom sediments. In this manner crocodiles also may acquire gastroliths and accidentally ingest aquatic vegetation (Table 20).

Very few juveniles were found with fish in their stomachs. Of the three juveniles (9.3%) that had recently eaten fish, two were captured in shallow water muddy lagoons where catching fish was perhaps more easily accomplished. All the fish eaten were small poeciliids (*Limia* sp. and *Gambusia hispaniolae*). Predation on mammals by juveniles was restricted to *Conocarpus* swamps or in the thick marshy vegetation surrounding canal mouths.

Subadult and Adult Crocodiles

Only a limited sample (n=9) of stomach contents from crocodiles over 0.9 m total length was obtained (Table 20). Of these, four were over 1.1 m total length (1.20 m, 1.38 m, 1.95 m, and 2.43 m). Scooping was attempted on seven other crocodiles over 2.0 m total length, but extracted no stomach contents. Although this may indicate a high incidence of empty stomachs (Graham 1968), it is equally likely that the scoop simply failed to bring up large food particles.

As has been pointed out by other authors (see Cott 1961) there is a dietary shift with age in crocodilians, from the predominantly invertebrate food of juveniles, to primarily vertebrate prey for adults. The incidence of both birds and fishes increased in the subadult and adult crocodiles in Etang Saumâtre (Table 20). Large crocodiles also were known to take domestic stock (goats or sheep) and sometimes dogs. During January-February 1984, at least three goats were known to be killed and eaten by crocodiles along the nesting beaches on the eastern lakeshore (pers. obs.). One adult (2.82 m male), when captured, had the remains of a goat in his mouth. At least two dogs were killed by a large male (3.5 m) in the spring at Tete Source over a 14-month period.

Nevertheless, the primary food item of adults appears to be fish. Adult crocodiles frequently were seen in water 1-2 m deep where large fish (*Tilapia* and *Cichlasoma*) were abundant. In these areas crocodiles were observed sitting on the bottom making rapid sideways sweeps of the jaws to catch fish. Crocodiles also would take fish trapped in gill nets set by fishermen near Tete Source, and were not infrequently seen at night sitting on the bottom next to these nets.

Habitat Selection

Spatial Crocodile Distribution

The distribution of crocodiles by lakeshore segment and size-class is summarized in Figures 15 (August 1983) and 16 (January 1984). These data are corrected for differences in the lengths of shoreline segments and expressed as density per km shore in Table 23. The highest concentration of hatchling and juvenile crocodiles (0.3-0.9 m) were found in section H, which contains the majority of the nesting beaches. Mazzotti (1983) found that hatchling *C. acutus* would disperse rapidly from nest sites in areas exposed to wave action, moving to more protected waters. Hatchlings from the more protected creek nesting sites were less likely to move and generally remained in the vicinity of the nest. Rodda (1984) noted a high degree of philopatry among 10 first year *C. acutus* in Panama. These animals had average home range sizes of 330 m of shoreline and spent 80% of their time in core areas of only 200 m.

In Etang Saumâtre, of the 10 crocodiles (0.3-0.9 m) that were recaptured, eight were found in the same location where they were originally caught (mean recapture interval 143 days). Of the two that moved, one apparently did so in response to the rising lake waters that exposed a previously protected lagoon to considerable wave action. This juvenile moved

1 km into a temporarily flooded *Conocarpus* zone. The other juvenile moved 1.8 km along the eastern lakeshore over a period of 339 days.

Subadults (0.9-1.8 m) also were found frequently in section H; they were also concentrated in the northwestern region of the lake (section E). The concentration of subadults in this area is interesting, as it also contained several apparently non-breeding males during the 1984 nesting season.

Subadults had a greater tendency to move than did juveniles. Of the two subadults that were recaptured, one had moved (over 306 days) entirely across the lake, a straight-line distance of 10 km. As this individual probably moved along the shore, the actual distance travelled is closer to 22 km. The other subadult moved 0.3-0.4 km over a period of 84 days.

The 1.8-2.7 m crocodiles, composed primarily of adult females, had a high density during the August survey in section G. During January the

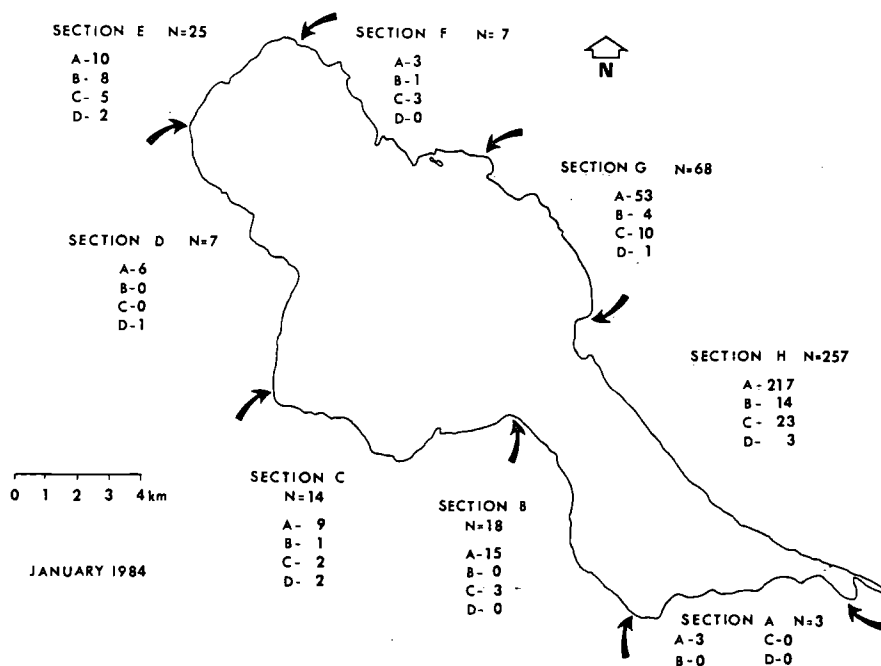


FIGURE 15. Crocodile distribution by size class and lakeshore segments, August 1983. (Crocodile size classes (in m) are: A = 0.3-0.9, B = 0.9-1.8, C = 1.8-2.7, D = > 2.7; all values given represent total length.)

majority of these animals was found in section H. In August, the 1.8-2.7 m crocodiles in section G were concentrated in 2 areas: (1) in shallow water "feeding grounds" that contained abundant *Tilapia*, and (2) under an active heronry. Crocodilians have been reported to congregate under bird or bat colonies (Hopkins 1968, Guggisberg 1972, Messel et al. 1981), presumably to eat young or adults that fall into the water. January marks the beginning of the nesting season and therefore the concentration of 1.8-2.7 m crocodiles in section H (adjacent the nest sites) is not unexpected. Furthermore, the heronry in section G is not active during this time of year. The shift in the maximal abundance of these animals then appears to reflect the concentration of crocodiles in productive feeding grounds during the non-breeding season, and movement to the vicinity of nesting beaches sometime prior to January.

Adult males (> 2.7 m) were distributed throughout the lake (excepting section A), but were found in the highest densities in section E during both the August and the January surveys. Section E contains a productive,

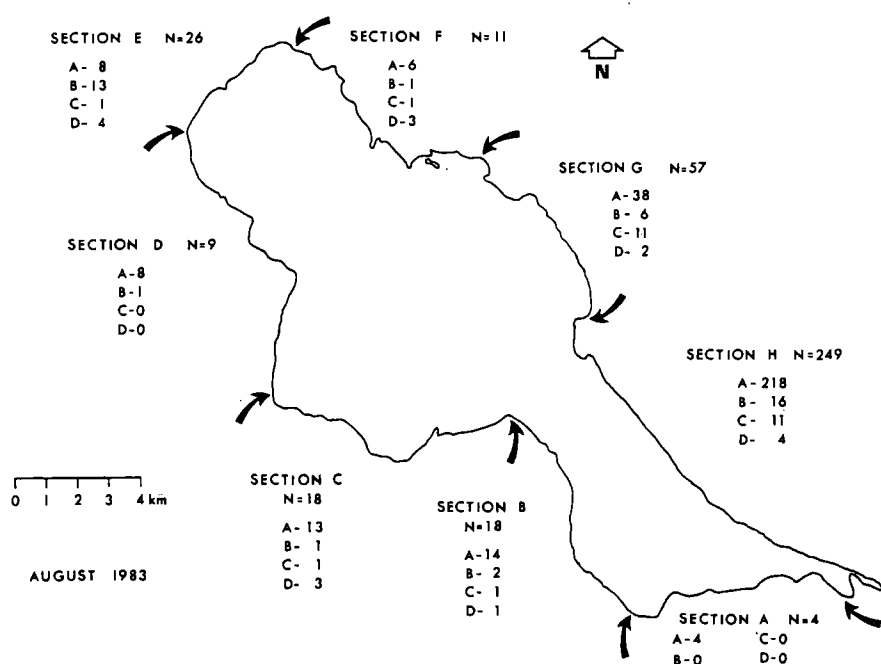


FIGURE 16. Crocodile distribution by size class and lakeshore segments, January 1984. (Size classes as in Fig. 15).

shallow-water (1-2 m) "feeding ground" and an abundance of *Conocarpus* for hiding in during the day, or during periods of rough weather. This area appears to be where the majority of crocodiles on the western lakeshore congregate.

Distribution By Habitat Type

The lakeshore was divided into 11 habitat types, which are listed along with their relative abundance in Table 24. Following is a brief description of each:

Sand-grass-mud. Shallow gradient dropoff, sandy beaches, often ephemeral or constantly changing in conformation, or mudflats. Usually exposed to wave action, often accumulating *Batophora* wrack.

Salicornia flats. Restricted to the extreme southeastern end of the lake. Shallow gradient mud shores covered with *Salicornia perennis*.

Conocarpus flats. Shallow water areas supporting dense or sparse growths of low stature *Conocarpus erectus*.

Seepage marsh. Shoreline marsh areas, identified by the presence of freshwater vegetation, in areas where underground seepage of freshwater occurs.

Canal marsh. Freshwater marsh around the mouth of irrigation runoff canals feeding into the lake.

Conocarpus fringe. Moderate gradient shoreline fringed with *Conocarpus* that may grow out into shallow water, often on partially submerged sandbars, creating small protected lagoons.

Acacia scrub. Moderate gradient sandy or somewhat rocky shores where the xeric upland floral association extends down to the lakeshore.

Rocky shore, medium gradient. Medium dropoff rocky shores usually backed by xeric vegetation.

Submerged forest. Found only on the eastern shore south of Las Lajas. High stature (to 10 m) *Conocarpus* forest extending 20-50 m into the lake.

Cove. Moderate gradient dropoff, gravel beaches located between rocky promontories along the north coast.

Rocky shore, steep gradient. Steep gradient dropoff rocky shores, usually little or no vegetation, usually a high degree of wave exposure.

The density of crocodiles varied greatly in the different habitat types (Table 25). A chi-square goodness of fit test indicated the crocodiles were not randomly distributed throughout the various habitat types. Using a Z test of the form:

$$s = \frac{o(i) - e(i)}{\sqrt{(e(i))(1 - e(i))/n}}$$

(where s = test statistic, $o(i)$ = observed proportion of crocodiles in habitat $i = o_i$, $e(i)$ = proportion of the total lake shoreline in habitat $i = e_i$, n = number of crocodiles observed), the distribution of all crocodiles > 0.9 m was tested on a habitat by habitat basis against the null hypothesis of random distribution around the lake. Crocodiles < 0.9 m were not included in this analysis because they tended to remain in the vicinity of the nesting beaches and would bias the results towards the *Conocarpus* fringe habitat that contained the great majority of the nests. The results of this 2-tailed test show the habitats where the crocodiles are significantly more abundant than would be expected according to the null hypothesis (preferred habitats), and the habitats where they are significantly less abundant (avoided habitats) (Table 26). Preferred habitats included *Conocarpus* fringe, *Conocarpus* flats, *Salicornia* flats, submerged forest, and canal marsh. Both the medium and steep gradient rocky shores were avoided.

Three factors determine why crocodiles are more abundant in the preferred habitats: (1) protection from wave action, (2) food availability, and (3) nesting habitat. Of these, the single most important factor was the degree of wave action. Crocodile density in exposed habitats (0.73/km) was much lower than along moderate exposure shorelines (8.55/km), which in turn had fewer crocodiles than protected habitats (10.93/km). A similar avoidance of wave action has been noted for *C. acutus* (Ogden 1978, Mazzotti 1983) and other crocodilians (Cott 1961, Graham 1968, Woodward and Marion 1978, Messel et al. 1981). Because of the proximity of the eyes and nostrils to the surface of the water in a floating crocodile, any appreciable wave amplitude would interfere significantly with respiration and visibility. Wave action also makes movement more difficult and probably interferes significantly with feeding activity.

The preference for *Salicornia* flats (100% protected) and *Conocarpus* flats (83% moderate exposure, 17% protected) to some degree reflects this avoidance of wave action. However, these areas also were adjacent to productive shallow water areas that appeared to be favored feeding grounds for adults.

The submerged forest habitat was considered to be 100% moderately exposed to wave action, although areas well protected from wave action were located back within the vegetation. The major attraction of this habitat was, however, the presence of the active rookery with an estimated 300-400 pairs of egrets, herons, and ibises. Throughout the 3.2 km of this habitat type, crocodiles were seen only under or adjacent to the rookery. The rookery was not active during the January survey, consequently the submerged forest was not a preferred habitat during this time.

In January, the preferred habitats switched to canal marsh and *Conocarpus* fringe. Crocodiles apparently were attracted by the cover offered by the freshwater vegetation around the canals and always were found in high densities in or around these marshes. One of the two areas of canal marsh habitat type provided the only suitable crocodile habitat over 5 km of shoreline near Fonds Parisien, and so tended to concentrate crocodiles. Although crocodiles were found in high densities in these areas, the small amount of canal marsh did not make this an important habitat for the crocodiles.

The preference for *Conocarpus* fringe in January reflects the congregation of adult crocodiles around the nesting beaches during this time of year. The majority of the crocodiles seen in this habitat during January were 1.8-2.7 m individuals, composed primarily of adult females. Of these, 85% were seen adjacent to nesting beaches.

Habitats avoided by the crocodiles typically were those exposed to wave action and offering no suitable cover. Crocodiles were rarely seen along steep or medium gradient rocky shores. Crocodiles also typically shunned the exposed sand-grass-mud habitats, although this did not show up as significant because of the tendency of some crocodiles, especially subadults (0.9-1.8 m) to use isolated patches along these shorelines (spring mouths and *Conocarpus* clumps). In fact, using the combined August and January surveys, the sand-grass-mud habitat is actually one of the "preferred" subadult habitats (Table 27). The relatively large number of 0.9-1.8 m crocodiles in this marginal habitat supports the suggestion of possible exclusion of some of the subadult population from more favored habitats.

CONSERVATION

Discussion

Currently, there are few laws pertaining to wildlife in Haiti, and none concerning crocodiles. Although laws should be enacted affording protection to species currently endangered with extinction, the mere presence of laws

protecting wildlife would have little effect (besides symbolic) as the arm of the government that deals with wildlife (Bureau des Ressources Forestieres et de la Production de la Faune, Département de L'Agriculture des Ressources Naturelles et de Développement Rural) currently is so understaffed that effective protection could not be achieved. Furthermore, the nature of most of the human-related crocodile mortality (accidental drownings in nets or fish traps) is such that little can be done without making unrealistic attempts to change fishing techniques and/or fishermen's attitudes towards crocodiles.

Even more troublesome for the crocodiles is the present rate of habitat destruction. Loss of coastal wetlands and high human population densities around those that remain have resulted in a sizeable reduction of the range of the crocodile in Haiti. The continued survival of those few, small crocodile populations that do remain, as well as that of other coastal wildlife species will depend on how these wetlands fare in the future. In this respect, perhaps the most positive step that can be taken would be to initiate a plan for the management of coastal resources. Because a significant proportion of the commercially utilized marine species of fish and invertebrates depend, at one point or another during their lifecycle, on mangrove ecosystems, the plan should, at the very least, include fisheries and mangrove harvest. The primary objectives of such a plan would be to insure the viability of these valuable coastal ecosystems which provide a livelihood and food for a significant portion of the Haitian human population. Within the framework of such a program could be included plans to protect wildlife and some of the critical habitat on which they depend. The most important region from this standpoint is the l'Ester area, containing Hispaniola's largest mangrove swamp. The l'Ester and its environs are the site of considerable fishing activity and unmanaged mangrove harvest. This area also contains a significant amount of wildlife including crocodiles, sea turtles, manatees, flamingos, and wading birds. A trial program of coastal resource management in the l'Ester region, if successful, could be expanded to include other coastal areas. Effective protection of the wildlife in coastal Haiti will depend on obtaining detailed information concerning critical habitats. With respect to crocodiles, this especially includes nesting beaches and nursery habitat for the hatchlings. Currently there has been interest shown by two international development organizations (U.S. Agency for International Development and the World Bank) in helping to develop programs fostering coastal resource management in Haiti. It is hoped that if such programs are developed in Haiti, plans will be made to include a wildlife component.

The creation of wildlife preserves also could be done in conjunction with the newly established national parks program, currently being coordinated by the Institute National Haitien de la Culture et des Arts and the Département de L'Agriculture, des Ressources Naturelles et du Développement Rural. Two areas which should be considered for protection in this regard are the

eastern shore of Etang Saumâtre and the Rivière Massacre-Lagon aux Boeufs estuary.

The eastern shore of Etang Saumâtre is uninhabited, and contains virtually all of the lake's crocodile nesting areas. Additionally, this region supports a diversity of other wildlife including wading birds, ospreys, and a significant number of migratory waterfowl and shorebirds. Protection of this area easily could be accomplished as the vast majority of the land is owned by the Haitian government. Because this land parcel borders on the Dominican Republic, a degree of international cooperation will be necessary if this plan is to prove effective. As the land is isolated from the rest of Haiti by water, and boats are prohibited from the lake (because of past smuggling), the area is inaccessible to Haitians. Aside from this, the lack of freshwater prevents any extensive human settlement. Currently, the only use of this land is by Dominican ranchers who graze their cattle and goats seasonally along the lakeshore.

Another, more insidious, problem in Etang Saumâtre is the shooting of adult crocodiles by Dominican (and Haitian) border guards. As both the border stations are adjacent to calm water areas regularly used by crocodiles, the shooting has been a steady drain on the crocodile population. During a 10-month period, at least 2 adult male crocodiles were shot by Dominican guards (the males are preferentially taken because the penis is used as an aphrodisiac). Based on a high and low estimate of 2-4 crocodiles taken in this manner every year, this represents a loss of 10-20% of the adult male population each year. This action is clearly illegal as the government of the Dominican Republic has officially declared the crocodile to be fully protected. Efforts should be made to put a stop to this unnecessary killing by bringing it to the attention of the superiors of the army personnel involved.

The Rivière Massacre, along the northeastern border with the Dominican Republic, contains Haiti's only riverine mangrove ecosystem. Crocodiles are found both in the river and in adjacent Lagon aux Boeufs. The region surrounding these habitats is sparsely inhabited, and recently the Dominican Republic has declared the eastern bank of the river to be a national park. A joint Haitian-Dominican Republic project would be most effective in affording protection to the crocodile.

Recommendations

1. Enact legislation protecting the crocodile.

2. Establish a resource management area in the l'Ester region. Combine managed harvest of mangrove with protection of the region's wildlife, including crocodiles, sea turtles, manatees, flamingos, and wading birds.
3. Establish wildlife reserves on the eastern shore of Etang Saumâtre and in the Rivière Massacre/Lagon aux Boeufs rea.
4. Stop the illegal shooting of crocodiles in Etang Saumâtre by guards at Dominican Republic border stations.

SUMMARY

Prior to its colonization by Western man, probably all low elevation wetland habitats of any size in Haiti were inhabited by crocodiles. Today, the range of crocodiles in Haiti has been greatly reduced, with small populations remaining only in relatively isolated areas, usually associated with mangrove swamps. The largest remaining population (450 crocodiles of all sizes), however, is in Etang Saumâtre, a landlocked lake in a semi-arid region only 30 km from the capital.

The disappearance of crocodiles from their historical range has followed a consistent pattern relative to human population density and the amount of available mangrove habitat. Today, the few remaining populations are found in areas of low human population density that contain sufficient amounts of mangrove habitat for cover. An important modifying factor is the availability of freshwater, which is needed by hatchling crocodiles to maintain an adequate ion balance. Crocodiles are missing from Haiti's second largest mangrove area (Caracol Bay) apparently due to a lack of fresh or brackish water. Because of the tendency of crocodiles, especially subadults (0.9-1.8 m), to move long distances along the coast, in some areas (such as the southern coast of the Tiburon Peninsula and Ile de La Gonâve) crocodiles are not infrequently seen over a wide distribution. In these regions crocodiles are often reported from areas not capable of supporting viable populations, but appear to be transient individuals. Habitat destruction and incidental killing, usually in fishermen's nets, represent the greatest threat to crocodiles in Haiti today. Use of crocodiles for food or their by-products is limited to areas bordering on the Dominican Republic.

The crude density of crocodiles in Etang Saumâtre (6.3/km shoreline) is relatively high compared to most other published values, although well below the values estimated for nearby Lago Enriquillo and several other nearly pristine African populations. This indicates that the population in Etang Saumâtre is below its carrying capacity. In terms of biomass, the mean for the

entire lake is 60.6 kg/km shore, or 92.3 kg/km shore when only considering areas of suitable habitat (ecological biomass). The sex ratio of animals below 1.8 m total length appears to be skewed towards males, over 1.8 m TL it is 1:1. Young crocodiles (> 0.9 m TL) grow at an average rate of 0.058 cm/day (21.2 cm/yr), considerably slower than reported values for *C. acutus* in Florida. The reason for this slow growth rate is unknown. Compared to mainland populations, adults do not appear to grow as large in Etang Saumâtre. The largest males seen were approximately 3.5 m TL, females 2.4 m TL.

Nesting in Etang Saumâtre is almost entirely restricted to the uninhabited eastern lakeshore. Nests are exclusively of the hole type, generally dug in old beaches associated with moderate gradient shoreline promontories. Soil moisture appears to be the most important factor determining selection of nest sites. Egg-laying commences in late January, at the height of the dry season, and lasts approximately three weeks. Hatching begins in late April, coinciding with the start of the rainy season. Mean clutch size is low for this species (mean=22.5) and appears to be related primarily to the small size of the females. During 1983, 21 nests were located, suggesting that only 63.8% of the adult females nested that year. Egg fertility rate was 90.1%, and natural nest predation was almost non-existent.

Crocodiles were found to be opportunistic feeders. The young subsisted primarily on the abundant fiddler crabs (*Uca bergersii*), but also ate a significant number of beetles and odonate larvae. Larger crocodiles consume an increasing proportion of vertebrate prey, the adults feeding primarily on fish.

The most important factor determining the distribution of crocodiles in the lake was the degree of wave exposure. Crocodiles sought out areas that were well protected from the often intense wave action associated with the predominant easterly winds. Secondary factors important for adults were the presence of shallow water feeding areas (both sexes) and the availability of nesting areas (females during the breeding season).

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Table 1. Mangrove area and crocodile distribution in coastal departments (major islands considered separately).

Department	Mangrove area (sq km)	Shoreline (km)	Sq km mangrove per km shore
I. Crocodiles present			
Nord Est	44.6	60	0.74
Artibonite	93.3	140	0.66
Sud	16.9	230	0.07
La Gonâve	11.5	140	0.08
Ile à Vache	16.1	40	0.40
Mean			0.39
II. Crocodiles absent			
Nord	13.4	85	0.16
Nord Ouest	0.7	180	0.00
Ouest	7.5	155	0.05
Grande Anse	18.0	235	0.08
Sud-Est	0.0	145	0.00
Ile Tortue	1.1	85	0.01
Mean			0.05

Table 2. Human population density and crocodile distribution in coastal communes and major islands which historically contained crocodiles.

Crocodiles present		Crocodiles extirpated	
Commune	Population density (per sq km)	Commune	Population density (per sq km)
Ferrier	6	Caracol	10
Terrier Rouge	25	Terre Neuve	51
La Gonâve	72	Baradères	90
Aquin	116	Dame Marie	114
Gonaïves	129	Bas Limbé	154
Ile à Vache	158	Petit Goâve	229
Grande Saline	171	Limonade	235
Cavaillon	237	Jérémie	269
Torbeck	297	Cap Haïtien	1079
Mean density =	134.6	Mean density =	247.9

Table 3. Human population density and crocodile distribution for inland communes which historically contained crocodiles.

Crocodiles present		Crocodiles extirpated	
Commune	Population density (per sq km)	Commune	Population density (per sq km)
Ganthier	72	Miragoâne	234
Thomazeau	112	Cayes	251
Mean density =	92	Mean density =	243

Table 4. Crocodile population status and ecological life zone.

Crocodiles present		Crocodiles extirpated	
Location	Life Zone	Location	Life Zone
Tiburon Peninsula, Laboreaux to Capolo	dry	Caracol	moist
Tiburon Peninsula, St. Louis du Sud- l'Acul	moist	Tiburon Peninsula, north and west coasts	moist
Ile à Vache	moist	La Gonâve (eastern)	moist
La Gonâve (western)	dry	Caracol	dry
Artibonite	dry	Etang Laborde	moist
l'Ester	dry	Etang Miragoâne	moist
Rivière Massacre- Lagon aux Boefs	dry		
Etang Saumâtre- Trou Caïman	dry		

Table 5. Wilcoxon-rank analysis of coastal crocodile distribution in relation to human population density and amount of mangrove habitat. Arrondissements and major islands which historically contained crocodiles.

Arrondissement or island	Population rank	Mangrove rank	Combined rank	Crocodiles present
Gonaïves	4	3	1	yes
La Gonâve	3	8	2.5	yes
Trou-du-Nord	9	2	2.5	no
Ft. Liberté	1	12	4	yes
Nippes	7	6	5	no
Dessalines	13	1	6	yes
St. Marc	5	11	7	yes
Aquin	10	7	8.5	yes
Ile à Vache	12	5	8.5	yes
Tiburon	2	16.5	10	no
Grande Anse	6	13	11	no
Limbé	11	10	12.5	no
Cap Haïtien	17	4	12.5	no
Port-au-Prince	14	9	14.5	no
Port-de-Paix	8	15	14.5	no
Léogâne	15	14	16	no
Borgne	16	16.5	17	no

Note: Arrondissements (the next largest political subdivision above Communes) were used in this analysis as habitat area data were not available for Communes.

Table 6. Chemical analyses of lake water: Etang Saumatre.

	Sources*			
	A	B	C	D
1. Total dissolved Solids (ppm)	7432	10296	12700	11606
2. Conductivity (mohm/cm)	-----	-----	20000	18500
3. Dissolved oxygen	-----	-----	6.2	8.1-8.6
4. total phosphate	-----	-----	0.028	0.35
5. Nitrate	trace	-----	-----	3.9
6. Ca	94	127	-----	118.8
7. Mg	279	393	-----	498.9
8. Na	2159	-----	-----	3180.0
9. K	-----	3040	-----	86.0
10. Cl	3660	5154	-----	6098.0
11. SO ₄	711	1001	-----	500.0
12. CO ₃	46	24	-----	0.0
13. HCO ₃	161	223	-----	348.7
14. Fe	0.48	trace	-----	-----
15. PH	-----	8.5	7.6	8.1
16. Transparency (m)	-----	3.25	2.0-3.6	-----

* Sources:

A = Woodring et al. 1921

B = Bond 1935

C = DARNDR 1979

D = K. Lekkerkerker pers. comm.

Note: In 1921 and 1933 values for Na and K were combined

Table 7. Sex ratio by size class: Etang Saumâtre.

Size class (m)	Males	Females	Males/Females
0.3-0.9	16	10	1.60
0.9-1.8	8	5	1.60
1.8-2.7	5	7	0.71
>2.7	3	0	----

Table 8. Crocodilian density estimates.

Species	Location		Density (per km)	Source
<i>Crocodylus niloticus</i>				
Ethiopia:	Awash River	upper	7	a
		middle	3-20	a
		lower	2	a
	Lake Margherita		1.25	a
		Blue Nile	2-4	a
	Omo River	hunted	7.5	a
		unhunted	21	a
Uganda:	Lower Semiliki River		0.81	b
	Lake Albert		0.06	b
	Albert Nile		0.39	b
	Victoria Nile		13.1	c
Kenya:	Lake Turkana		13.4	d
	Upper Lorian Swamp		8.5	c
Tanzania:	Grumeti River		2.2	c
<i>Crocodylus porosus</i>				
Australia:	Northern Territory	mean	1.61-1.67	e
		highest	8.75-10.1	e
	Western Australia Queensland	Kimberly System	2.02-2.23	e
		Cape York		
		Peninsula	1.47-1.62	e
<i>Crocodylus porosus-novaguineae</i>				
Papua New Guinea:		hunted	0.8	f
		unhunted	1.6	f
<i>Crocodylus acutus</i>				
Haiti:	Etang Saumâtre	crude density	6.3	g
		ecological density	9.6	g
<i>Alligator mississippiensis</i>				
USA:	Florida	lakes	7.8	h
		rivers	2.5	h
		canals	2.5	h

Sources: a = Cott and Pooley 1971 e = Messel et al. 1982a
 b = Parker and Watson 1970 f = Montague 1983
 c = Watson et al. 1971 g = This study
 d = Graham 1968 h = Wood and Humphrey 1983

Note: Figures for Messel et al. 1982 are 95% confidence intervals for non-hatchling crocodiles.

Table 9. Size class contribution to total population biomass: Etang Saumâtre.

Size class (m)	Biomass (kg)	Percent of total biomass
0.3-0.9	201.1	4.2
0.9-1.8	370.4	7.8
1.8-2.7	2,046.6	43.2
> 2.7	2,123.7	44.8
Total	4,741.8	100.0

Table 10. Summary of reported wild crocodile growth rates (cm/day).

Age class Species	Location	Growth rate	Source
Hatchlings			
<i>Crocodylus acutus</i>	Florida	0.158	a
		0.112	b
		0.118	c
<i>Crocodylus porosus</i>	Australia	0.188	d
		0.100-0.120	e
1-2 Years			
<i>Crocodylus acutus</i>	Florida	0.107	a
<i>Crocodylus porosus</i>	Australia	0.076	e
3-4 years			
<i>Crocodylus porosus</i>	Australia	0.063	e

Sources: a = Gaby et al. 1981
b = Mazzotti 1983
c = Moler pers. comm.

d = Magnusson 1978
e = Messel and Vorlicek in press

Table 11. Reported values of annual breeding effort for adult female crocodilians.

Species	Location	% breeding	Source
<i>Alligator mississippiensis</i>	Louisiana	68.1	Chabreck 1966
<i>Crocodylus niloticus</i>	Zambia	80.0	Cott 1961
	Botswana	67.0	Blomberg 1982
	Kenya	87.6	Graham 1968
<i>Crocodylus acutus</i>	Florida	72.0	Mazzotti 1983
	Haiti	63.8	This study
<i>Crocodylus johnsoni</i>	Australia	90.0	Webb et al. 1983

Table 12. Nest hole dimensions (cm): Etang Saumâtre.

Dimension	Mean	Standard deviation	Range	N
Depth to top of clutch	24.1	4.7	16-33	13
Depth to bottom of clutch	37.9	4.3	30-45	13
Egg chamber width	32.4	4.3	28-42	12

Table 13. Summary of nest site and null site parameters for Etang Saumâtre.

Parameter	Standard Nest/Null	Mean	deviation	Range	N
Distance from lake (m)	nest null	27.5 -----	11.8 -----	7-47 -----	31 --
Height above lake (m)	nest null	1.2 0.6	0.5 0.4	0.6-2.1 0.3-1.5	31 15
Soil pH	nest null	6.2 ---	1.6 ---	5.2-7.1 -----	15 --
Soil moisture (% water)	nest null	6.62 20.33	3.13 5.01	3.4-14.3 6.25-28.57	12 15
Percent shrub/tree coverage	nest null	30.1 40.6	14.5 34.3	10-60 0-90	29 15
Percent grass cover	nest null	5.9 40.0	5.8 35.1	0-20 0-100	29 15
Percent leaf litter cover	nest null	18.4 8.0	8.6 9.4	10-30 0-30	29 15
Height of vegetation (m)	nest null	3.4 3.0	0.6 1.1	2.0-4.5 0.0-4.5	27 15
Distance to nearest tree	nest null	2.1 2.7	1.1 2.7	0.5-5.0 1.0-8.0	27 15

Table 14. Soil water content: nests vs adjacent holes.

Soil moisture (percent water)			
Nest	Nest	Adjacent hole	Difference
84-1	9.67	3.92	-5.75
84-2	4.55	3.50	-1.05
84-8	6.32	3.17	-3.15
84-11	4.29	1.45	-2.84

Table 15. Incidence of vegetation over 1 m tall within a 5 m radius of 25 nest sites.

Species	%	Species	%
<i>Acacia farnesiana</i>	88	<i>Prosopis juliflora</i>	28
<i>Conocarpus erectus</i>	72	<i>Lemaireocereus hystrix</i>	8
<i>Pithecellobium circinale</i>	32	<i>Consolea moniliformis</i>	4
<i>Guaicum officinale</i>	28	<i>Neoabbottia paniculata</i>	4

Table 16. Number of nests at nesting beaches Etang Saumâtre 1983-1984.

Nesting Beach	1983 Nests	1984 Nests	Nesting Beach	1983 Nests	1984 Nests
A	3	2	H	1	0
B	2	3	I	1	0
C	2	2	J	1	0
D	3	2	K	0	1
E	2	1	L	1	0
F	1	1	M	1	0
G	2	0			

Table 17. Egg clutch data: Etang Saumâtre.

Parameter	Mean	Standard deviation	Range	N
Clutch size	22.5	2.7	17-28	14
Egg mass (g)	97.0	8.1	80-116	68
Egg dimensions (mm)				
width	45.4	1.00	42.4-48.8	83
length	76.5	3.28	70.7-82.4	83
Clutch fertility (%)	90.1	10.5	70.6-100.0	7

Table 18. Reported clutch sizes for *Crocodylus acutus*.

Location	Clutch size	N	Source
Florida	39.3	8	Mazzotti 1983
	39.1	8	Lutz and Dunbar-Cooper 1982
	44	20	Ogden 1978
Colombia	40-60	--	Medem 1981
Panama	46	1	Breder 1946
Honduras	22	1	Schmidt 1924
Dominican Republic	23.8	80	Inchaustegui et al. 1980
Haiti	22.5	14	This study
Mexico	30-60	--	Alvarez del Toro 1974

Table 19. Nest temperature data from six nests at Etang Saumâtre.

Nest	Average clutch temperature			Temperature range	
	Top	Bottom	Mean	Top	Bottom
84-1	29.1	29.3	29.2	28.8-29.4	29.1-30.1
84-2	30.1	30.2	30.1	29.9-30.5	30.0-30.5
84-4	29.5	29.2	29.3	28.8-30.6	29.0-29.6
84-7	28.9	29.2	29.0	28.5-29.4	29.0-29.5
84-8	28.9	29.1	29.0	28.7-29.5	28.9-29.3
84-11	29.1	29.3	29.2	28.8-29.5	29.1-29.6

Table 20. Crocodile diet by frequency in stomach samples.

Prey item	Crocodile size class			
	<0.5 m (N=14)	0.5-0.9 m (N=43)	0.9-1.8 m (N=7)	>1.8 m (N=2)
Crustacea	85.7	90.7	71.4	0.0
Coleoptera	78.6	72.1	14.3	0.0
Odonata	64.3	46.5	42.9	0.0
Arachnida	28.6	30.2	42.9	0.0
Scolopendra	21.4	2.3	0.0	0.0
Hymenoptera	14.3	4.6	0.0	0.0
Lepidoptera	21.4	0.0	0.0	0.0
Amphipoda	14.3	0.0	0.0	0.0
Gerridae	7.1	0.0	0.0	0.0
Mantidae	0.0	2.3	0.0	0.0
Osteichthyes	0.0	11.6	0.0	100.0
Reptilia	0.0	2.3	0.0	0.0
Aves	0.0	2.3	28.6	50.0
Mammalia	0.0	11.6	14.3	0.0
Nematodes	35.7	39.5	57.1	50.0
Gastroliths	0.0	13.9	28.6	50.0
Vegetation	87.5	67.4	57.1	50.0

Table 21. Diet based on percent of mass of fresh and partly digested food items.

Food item	Crocodile size class		
	< 0.5 m (N=8)	0.5-0.9 m (N=28)	0.9-1.8 m (N=5)
Crustacea	33.5	62.3	32.6
Odonata	0.0	10.3	35.3
Coleoptera	0.0	8.9	0.0
Arachnida	4.0	4.9	14.5
Hymenoptera	25.0	0.5	0.0
Gerridae	12.5	0.0	0.0
Amphipoda	25.0	0.0	0.0
Osteichthyes	0.0	9.3	0.0
Aves	0.0	0.0	17.7
Reptilia	0.0	3.5	0.0

Table 22. Prey items identified from the stomach contents or observed ingestion by crocodiles from Etang Saumâtre

Terrestrial prey	IIX. Class-Mammalia
I. Class Insecta	<i>Mus musculus</i> (Muridae)
Coleoptera	<i>Rattus</i> sp. (Muridae)
<i>Bothynus</i> sp. (Scarabeidae)	<i>Capra hircus</i> (Capridae)
<i>Cyclocephala</i> sp. (Scarabeidae)	<i>Canis familiaris</i> (Canidae)
<i>Phyllophaga</i> sp. (Scarabeidae)	
<i>Coneris</i> sp. (Elateridae)	Aquatic prey
<i>Pyrophorus</i> sp. (Elateridae)	I. Class Insecta
<i>Lagocheirus</i> sp. (Cerambycidae)	Coleoptera
<i>Chrysobothris</i> sp. (Buprestidae)	<i>Tropisternus</i> sp. (Hydrophilidae)
<i>Selenophorus</i> sp. (Carabidae)	Hemiptera
<i>Calosoma</i> sp. (Carabidae)	(Belostomatidae)
<i>Cicindela</i> sp. (Cicindelidae)	Odonata
<i>Acalles</i> sp. (Curculionidae)	<i>Macrodiplax</i> sp. (Libellulidae)
<i>Artipus</i> sp. (Tenebrionidae)	<i>Brachymesia</i> sp. (Libellulidae)
Orthoptera	
(Blattidae)	II. Class Crustacea
(Mantidae)	Decapoda
II. Class Crustacea	<i>Uca bergersii</i> (Ocypodidae)
Amphipoda	III. Class Arachnida
<i>Tethorchestia</i> sp. (Talitroidae)	(Pisauridae)
III. Class Chilopoda	IV. Class Osteichthyes
<i>Scolopenera alternans</i>	<i>Limia</i> sp. (Poeciliidae)
(Scolopendridae)	<i>Gambusia hispaniole</i> (Poeciliidae)
IV. Class Arachnida	V. Class Reptilia
<i>Tetragnatha</i> sp. (Araneidae)	<i>Trachemys decorata</i>
VII. Class Aves	(Emydidae)
<i>Dulus dominicus</i> (Dulidae)	
<i>Gallus gallus</i> (Gallidae)	

Table 23. Crocodile density (per km) in Etang Saumâtre by shoreline section and size class.

Shore section	Size class (m)				Total
	0.3-0.9	0.9-1.8	1.8-2.7	>2.7	
August survey					
A	0.49	0.00	0.00	0.00	0.49
B	2.00	0.29	0.14	0.14	2.57
C	1.26	0.10	0.10	0.29	1.75
D	1.07	0.13	0.00	0.00	1.20
E	1.86	3.02*	0.23	0.93*	6.04
F	0.56	0.09	0.09	0.28	1.02
G	5.28	0.83	1.53*	0.28	7.92
H	13.36*	1.00	0.69	0.25	15.24
Total	25.88	5.46	2.78	2.17	
January survey					
A	0.37	0.00	0.00	0.00	0.37
B	2.14	0.00	0.43	0.00	2.57
C	0.87	0.10	0.19	0.19	1.35
D	0.80	0.00	0.00	0.13	0.93
E	2.33	1.86*	1.16	0.46*	5.81
F	0.28	0.09	0.28	0.00	0.65
G	7.36	0.56	1.39	0.14	3.10
H	13.56*	0.87	1.43*	0.19	16.05
Total	27.71	3.38	4.88	1.11	

* denotes highest density for that size class

Table 24. Shoreline habitat categories and amount of each habitat type.

Habitat type	Shoreline occupied (km)	Percent lake shoreline
Sand-grass-mud	3.5	4.92
<i>Salicornia</i> flats	2.9	4.07
<i>Conocarpus</i> flats	8.9	11.94
Seepage marsh	3.6	5.10
Canal marsh	0.4	0.56
<i>Conocarpus</i> fringe	17.2	24.72
<i>Acacia</i> scrub	9.5	13.34
Rocky shore, medium gradient	5.6	7.87
Submerged forest	3.2	4.49
Cove	0.6	0.84
Rocky shore, steep gradient	15.8	22.19
Total	71.2	100.00

Table 25. Crocodile density by habitat type.

Habitat	Survey date	Density (per km)	Mean density (per km)
Sand-grass-mud	August	3.14	
	January	1.14	2.14
<i>Salicornia</i> flats	August	6.21	
	January	9.65	7.93
<i>Conocarpus</i> flats	August	8.54	
	January	8.54	8.54
Seepage Marsh	August	4.44	
	January	3.61	4.03
Canal marsh	August	17.50	
	January	25.00	21.25
<i>Conocarpus</i> fringe	August	14.77	
	January	14.24	14.51
<i>Acacia</i> scrub	August	2.63	
	January	1.89	2.26
Rocky shore medium gradient	August	0.36	
	January	1.07	0.72
Submerged forest	August	3.44	
	January	2.19	2.82
Cove	August	8.33	
	January	0.00	4.17
Rocky shore steep gradient	August	0.13	
	January	0.19	0.16

Table 26. Preferred and avoided habitat types, subadult and adult crocodiles (> 0.9 meters).

	Preferred habitats	Avoided habitats
August	<i>Salicornia</i> flats <i>Conocarpus</i> flats Submerged forest	Rocky shore, medium gradient Rocky shore, steep gradient
January	Canal marsh <i>Conocarpus</i> fringe	Rocky shore, steep gradient

Table 27. Preferred and avoided habitats of subadult crocodiles (0.9-1.8 m): combined survey data.

Preferred habitats	Avoided habitats
Sand-grass-mud <i>Salicornia</i> flats <i>Conocarpus</i> flats	Rocky shore, steep gradient

APPENDIX I

Distribution of Mangrove in Haiti

Haiti, with a shoreline of 1525 km, has approximately 22,300 ha of mangrove forest. While composing only 0.8% of the country's area, mangroves constitute what is probably the least disturbed natural forested ecosystem type in Haiti today. Although mangroves are scattered around the coast in association with sheltered bays, estuaries, and coastal lagoons, approximately 40% (9000 ha) of the mangrove habitat is concentrated in the l'Ester-Artibonite region. Taken together, the four largest mangrove forests contain 70.6% of the mangrove habitat (see below).

Lugo and Snedaker (1974) have developed a classification of mangrove forest types based on physiognomic characteristics. Using this system, the majority of the mangroves in Haiti fall into the fringe mangrove category, growing in relatively protected areas and receiving little freshwater influx. A similar situation has been described by Lugo and Cintron (1975) in Puerto Rico, where fringe mangroves dominate in protected areas that are located in the subtropical dry forest life zone. Lugo and Cintron (1975) noted that in areas with greater rainfall and wave exposure basin and riverine mangroves tended to dominate.

Similarly, in Haiti, the four largest fringe forests (l'Ester, Baie de Caracol, Port-au-Prince, and Aquin) are located in relatively low wave-energy areas which receive less than 100 cm of rain annually (subtropical) dry life zone of the Holdridge system). Basin forests are typically located in the subtropical moist zone (100-200 cm rain annually) and generally along high energy shorelines.

Appendix I continued. List of major mangrove swamps in Haiti.

Location		Area (ha)	Percent of Country total	Forest type
I.	North coast			
A.	Ft. Liberté area			
	1. Rivière Massacre	60	0.27	R,B
	2. Coastal	70	0.31	B,F
	2. Baie de Ft. Liberté	340	1.52	F,B
B.	Baie de Caracol	3,990	17.84	F
C.	Cap Haïtien	760	3.40	B,F
D.	Limbé			
	1. Baie de l'Acul	480	2.15	F,B
	2. Rivière Limbé	100	0.45	B
E.	Port-de-Paix	70	0.31	B
II.	West Coast			
A.	Anse Rouge	350	1.57	F
B.	l'Ester	8,490	37.97	F
C.	Artibonite	490	2.19	F,B
D.	Port-au-Prince	670	3.00	F
III.	Tiburon Peninsula			
A.	Petit Goâve	50	0.22	F
B.	Trouin	70	0.31	B
C.	Miragoâne	350	1.57	F
D.	Baradères	1,200	5.37	F,B
E.	St. Jean du Sud	180	0.81	F
F.	Cayes area			
	1. Marsay	140	0.63	F,B
	2. Cavaillon	350	1.57	B
	3. Mombin	60	0.27	B
	4. Rivière Millionaire	80	0.36	B
	5. Scattered coastal	400	1.79	F,B
G.	Aquin	490	2.19	F
IV.	Satellite islands			
A.	Ile Tortue	110	0.49	F
B.	Ile la Gonâve	1,150	5.14	F
C.	Grand Caymite	250	1.12	F
D.	Ile à Vache	1,610	7.20	B
Total area		22,360		

* Mangrove forest types: F = fringe; B = basin; R = riverine.

APPENDIX II

Aquatic and Semiaquatic Avifauna, Native Fish Fauna, and the Dry Forest Vegetative Association of Etang Saumatre

Common name	Scientific name	Family
AVIFAUNA		
Pied-billed grebe	<i>Podilymbus podiceps</i>	Podicipedidae
Great blue heron	<i>Ardea herodias</i>	Ardeidae
Green heron	<i>Butorides viridescens</i>	Ardeidae
Little blue heron	<i>Florida caerulea</i>	Ardeidae
Great egret	<i>Casmerodius albus</i>	Ardeidae
Snowy egret	<i>Egretta thula</i>	Ardeidae
Tricolored heron	<i>Hydranassa tricolor</i>	Ardeidae
Yellow-crowned night heron	<i>Nyctanassa violacea</i>	Ardeidae
Black-crowned night heron	<i>Nycticorax nycticorax</i>	Ardeidae
Least bittern	<i>Ixobrychus exilis</i>	Ardeidae
Glossy ibis	<i>Plegadis falcinellus</i>	Threskiornithidae
Flamingo	<i>Phoenicopterus ruber</i>	Phoenicopteridae
West Indian tree duck	<i>Dendrocygna arborea</i>	Anatidae
Northern pintail	<i>Anas acta</i>	Anatidae
Bahama pintail	<i>Anas bahamensis</i>	Anatidae
Blue winged teal	<i>Anas discors</i>	Anatidae
American widgeon	<i>Anas americana</i>	Anatidae
Lesser scaup	<i>Aythya affinis</i>	Anatidae
Ruddy duck	<i>Oxyura jamaicensis</i>	Anatidae
Masked duck	<i>Oxyura dominica</i>	Anatidae
Osprey	<i>Pandion haliaetus</i>	Pandionidae
Purple gallinule	<i>Porphyrio martinica</i>	Rallidae
Common gallinule	<i>Gallinula chloropus</i>	Rallidae
Caribbean coot	<i>Fulica caribaea</i>	Rallidae
Northern jacana	<i>Jacana spinosa</i>	Jacanidae
Semipalmated plover	<i>Charadrius semipalmatus</i>	Charadriidae
Thick-billed plover	<i>Charadrius wilsonia</i>	Charadriidae
Killdeer	<i>Charadrius vociferous</i>	Charadriidae
Black-bellied plover	<i>Pluvialis squatarola</i>	Charadriidae
Ruddy turnstone	<i>Arenaria interpres</i>	Charadriidae
Black-necked stilt	<i>Himantopus mexicanus</i>	Recurvirostridae
Spotted sandpiper	<i>Actitis macularia</i>	Scolopacidae
Greater yellowlegs	<i>Tringa melanoleuca</i>	Scolopacidae
Lesser yellowlegs	<i>Tringa flavipes</i>	Scolopacidae
Least sandpiper	<i>Calidris minutilla</i>	Scolopacidae
Western sandpiper	<i>Calidris mauri</i>	Scolopacidae
Laughing gull	<i>Larus atricilla</i>	Laridae
Least tern	<i>Sterna albifrons</i>	Laridae
Royal tern	<i>Thalasseus maximus</i>	Laridae
Caspian tern	<i>Hydroprogne caspia</i>	Laridae
Belted kingfisher	<i>Ceryle alcyon</i>	Alcedinidae

APPENDIX II Continued

Scientific name	Family
ICHTHYOFAUNA	
<i>Cichlasoma haitiensis</i>	Cichlidae
<i>Cyprinodon bondi</i>	Cyprinodontidae
<i>Gobionellus</i> sp.	Gobiidae
<i>Dormitator maculatus</i>	Eleotridae
<i>Strongylura notata</i>	Belontiidae
<i>Limia tridens</i>	Poeciliidae
<i>Limia melanonotata</i>	Poeciliidae
<i>Gambusia hispaniolae</i>	Poeciliidae
DRY FOREST VEGETATIVE ASSOCIATION	
<i>Prosopis juliflora</i>	Leguminosae
<i>Acacia farnesiana</i>	Leguminosae
<i>Bursera simaruba</i>	Burseraceae
<i>Guaicum officinale</i>	Zygophyllaceae
<i>Phyllostylon brasiliensis</i>	Ulmaceae
<i>Zizyphus rignoni</i>	Rhamnaceae
<i>Pithecellobium circinale</i>	Leguminosae
<i>Haematoxylum campechianum</i>	Leguminosae
<i>Calotropis procera</i>	Asclepiadaceae
<i>Comocladia dodonaea</i>	Anacardiaceae
<i>Consolea moniliformis</i>	Cactaceae
<i>Neobabbotia paniculata</i>	Cactaceae
<i>Lemaireocereus hystrix</i>	Cactaceae
<i>Harrisia divaricata</i>	Cactaceae

APPENDIX III

Survey Correction Procedure

1. Base estimate produced from the number of crocodiles observed during night-time boat surveys.
2. Known animals (0.3-0.9 m, 0.9-1.8 m) not seen during the surveys were added.
3. Correction for reduced sightability:
 - A. Mean of three test boat surveys along densely vegetated shore, where the actual number of crocodiles was determined by surveying the area on foot with a spotlight, revealed that only 50% of the 0.3-0.9 m and 0.9-1.8 m crocodiles in these areas were observed from the boat at night. As larger crocodiles tended to avoid these densely vegetated, shallow water areas, it was assumed that reduced sightability from dense vegetation had no effect on the sightability of crocodiles over 1.8 m.
 - B. The amount of densely vegetated shoreline was estimated from aerial photographs of the lake.
 - C. Counts of 0.3-0.9 m and 0.9-1.8 m crocodiles were increased 50%, proportionately between the two size classes, along all densely vegetated shorelines.
4. Line transects were conducted through two especially dense habitats during January 1984 (Trou Caïman Canal swamp, East Bay Swamp). These data were used, rather than reduced sightability estimates, to determine the number of 0.3-0.9 m and 0.9-1.8 m crocodiles in these habitats.
 - A. Line transects were conducted by walking slowly through the area at night, following a single compass direction as closely as possible. Crocodiles were spotted using a headlamp (4v, Mine spot) and their perpendicular distance to the transect line was estimated. In this manner the transect width was estimated to be 50 m.
 - B. Calculation of total transect area was done by multiplying transect width (50 m) by the length (number of strides x 0.6 m). Transect width, divided by the total area being surveyed (determined from 1:25,000 topographic maps) provided an estimate of the fraction of the total area that was surveyed.

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