

ECOLOGY OF THE AMERICAN CROCODILE, *CROCODYLUS ACUTUS*

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SPECIES IDENTIFICATION AND DISTRIBUTION

The American crocodile, *Crocodylus acutus*, is a large, relatively longirostrine crocodile widely distributed in the coastal regions of the northern neotropics. Although individuals have been reported historically to reach lengths of up to 6.25 m (Alvarez del Toro 1974) and 7.0 m (Schmidt 1924, Medem 1981), today *C. acutus* longer than 4 m are rare. The general morphological characteristics of the species have been described elsewhere (Mertens 1943, Brazaitis 1973), yet because of morphological similarities with two other species (*Crocodylus moreletii* and *Crocodylus intermedius*), misidentifications of the species have not been uncommon, even among herpetologists. Frequent past confusion among these and other New World crocodylians has created nightmarish problems for nomenclatural review (Smith and Smith 1977).

Among all living crocodylians, *C. acutus* has the most reduced and irregular arrangement of dorsal osteoderms, usually with no more than 4 scutes in any of the 14-17 continuous precaudal scute rows (Ross and Mayer 1983). The American crocodile is also unique in the degree of development of a median preorbital elevation (MPE) on the snouts of adults and subadults (Brazaitis 1973, Alvarez del Toro 1974, Medem 1981). Although the size and shape of the MPE appears to vary somewhat geographically, and some preliminary evidence suggests that its size may be sexually dimorphic (pers. obs.), the MPE is a consistent and distinctive morphological feature among adults. Other species of crocodiles may have an MPE, but never as pronounced as in *C. acutus*. The combination of these two characteristics, irregular reduced dorsal scutes and the MPE, is sufficient to distinguish *C. acutus* from other crocodiles, with the possible exception of *C. moreletii* which has both characters developed to a slightly lesser degree. Morelet's crocodiles are best distinguished from *C. acutus* on the basis of ventrolateral scute intrusions on the base of the tail (Ross and Ross 1974).

The general distribution of the American crocodile includes both the Atlantic and Pacific coasts of southern Mexico, Central America, and northern South America, as well as the Caribbean islands of Cuba, Jamaica, Hispaniola and the southern tip of Florida, USA. The exact limits of the past and present mainland distribution of the species are somewhat confused due to a lack of systematic survey work, and the past misidentification of species. This is especially true for the Atlantic coast drainage. On the Mexican Gulf coast, *C. acutus* has definitely been recorded as far north as Cozumel Island (Field Museum of Natural History, FMNH 34563), Bahia de la Ascencion and Isla de Mujeres (Quintana Roo), and Laguna de Catemaco (Vera Cruz; Ross and Ross 1974). Literature accounts of *C. acutus* north of Vera Cruz on the Gulf coast appear to be based largely on misidentified *C. moreletii*.

The southernmost limit of *C. acutus* on the Atlantic coast of South America is similarly confused. Specimens of the American crocodile have been reported from the Paria Peninsula in Venezuela and on Trinidad, although the latter records probably represent vagrant animals (Medem 1983). Large crocodylians are known from the Orinoco delta region (F. Pannier, S. Gorzula, pers. comm.), but their specific identity is not known. Apparently, no members of the Crocodylidae are found south of the Orinoco delta.

The limits of the Pacific mainland distribution are better known due to the lack of congeners, and habitat limits to distribution. Crocodiles have been recorded from as far south as the Rio Tumbes and Rio Chira in northern Peru (Hofmann 1970, Medem 1983). In Mexico, the northwestern limit of crocodile distribution historically was the state of Sinaloa (Ross and Ross 1974, King et al. 1982).

The American crocodile reaches the northernmost limit of its range in Florida, USA. Although once found as far north as Lake Worth on the eastern coast of Florida, the current crocodile distribution now centers on Florida Bay. The present and past distribution of crocodiles in Florida are reviewed by Ogden (1978) and Kushlan and Mazzotti (1986).

Outside of its currently recognized range, *C. acutus* was also apparently found on the Bahamas (based on pre-Columbian fossils; King et al. 1982), and on the Cayman Islands, where specimens were collected as recently as 1939 (Grant 1940).

HABITAT RELATIONS

Macrohabitat

The American crocodile is typically found in freshwater or brackish water coastal habitats including, but not restricted to: the estuarine sections of rivers, coastal lagoons, and mangrove swamps (Alvarez del Toro 1974, Medem 1981). Although it is principally a coastal species, *C. acutus* is ecologically adaptable and is known to extend its distribution inland, especially along the courses of larger rivers and their associated wetlands habitat (Medem 1981). Individuals have been reported at altitudes of up to 610 m in Honduras (Schmidt 1924) and 1220 m in Mexico (Rio Tehuantepec: American Museum of Natural History, AMNH 100634). The species also inhabits landlocked lakes of varying salinities: freshwater (Schmidt 1924), brackish (Thorbjarnarson 1984, 1988), and hypersaline (Inchaustegui et al. 1980).

The American crocodile is regularly found on small offshore islands and atolls throughout its range. On many of these islands adult crocodiles can apparently exist without access to freshwater, although the presence of a freshwater source may be critical for the survival of hatchlings (see Temperature and Salinity Relations).

The adaptability of *C. acutus* in terms of habitat requirements extends to the use of disturbed, or man-made habitats. Although crocodiles are known to occupy man-made bodies of water in Venezuela (Embalse de Pueblo Viejo, Embalse de Tacarigua; Seijas 1986b), and Panama (Gatun Lake; Dugan et al. 1981, Rodda 1984), the most extensive use of disturbed habitats is in southern Florida. On Key Largo, crocodiles commonly occupy borrow pits and canals. Indeed, virtually all the nesting on Key Largo (which accounts for some 30% of the total nesting in Florida) is done on peat spoil banks created by dredging canals in mangrove areas (P. Moler, pers. comm.). A small population of crocodiles also inhabits the cooling canal system of the nuclear power plant at Turkey

Point. Nesting has occurred on several occasions in the spoil banks along the cooling canals (Gaby et al. 1985). Crocodiles are also known to occur in the cooling canal system of another power plant in Ft. Lauderdale (P. Moler, pers. comm.).

Microhabitat, Activity and Movements

Within the broad definition of *C. acutus* habitat outlined above, certain microhabitat features strongly influence the distribution of crocodiles in any given area. Crocodiles are principally inhabitants of shoreline habitats, preferring an amalgam of shallow and deep water areas, land for basking or nesting, and aquatic or semiaquatic vegetation for cover or increased habitat productivity. In addition to micro-environmental features, social factors play an important role in determining crocodile distribution. Crocodile size, population density, and population size-class structure all probably interact with environmental factors to define the overall pattern of habitat usage for any given population. Aside from these factors, the presence of humans or pattern of human activity may also modify crocodile habitat use. In most situations crocodiles are retiring and avoid areas frequented by humans. For instance, in Etang Saumatre, Haiti, a temporal habitat segregation was noted with crocodiles nocturnally entering areas used by people during the day (pers. obs.).

Because detailed information on many aspects of habitat selection is lacking, the following discussion centers on some of the more obvious factors that influence crocodile distribution and activity. This information is based primarily on work done on three crocodile populations: southern Florida; Etang Saumatre, Haiti; and Gatun Lake, Panama.

Hatchlings and Juveniles - Among nesting females (see following section) and recently hatched young, terrestrial habitat features are important in defining habitat requirements, as they determine where nesting can occur and the type of habitat into which the young are born. When nests are located adjacent to suitable habitat for hatchlings, the young may remain in the vicinity of the nest for several weeks, months, or even years (Alvarez del Toro 1974; Thorbjarnarson 1984, 1988; Rodda 1984).

In Florida, hatchling crocodiles frequently prefer to remain hidden in vegetation during the day, using such areas as mangrove prop roots, shoreline ledges or beach wrack for cover (Lang 1975b, Mazzotti 1983). In Panama, Rodda (1984) found 10 and 22 month old *C. acutus* along shorelines protected from waves and usually bordered by woody vegetation. In these areas the young crocodiles were frequently seen in floating mats of *Hydrilla*. In Etang Saumatre, Haiti, juvenile and hatchling crocodiles would spend most of the day hidden in root mats of *Conocarpus erectus* that grew in shallow water near the nesting beaches. At dusk, the crocodiles would leave their protected retreat sites and move to more open shoreline habitats or floating algae mats where they would forage (Thorbjarnarson 1984, 1988). Juvenile and hatchling crocodiles in Etang Saumatre were mostly sedentary. Of 10 recaptures, 8 were found at the original point of capture (mean interval 143 days). One juvenile dispersed 1.8 km over 339 days.

When the habitats adjacent to the nest are unsuitable for hatchlings, the neonates may disperse almost immediately. Factors which may cause dispersal are probably diverse, but are known to include wave exposure (Ogden 1978, Mazzotti 1983), and hypersaline aquatic environments (Inchaustegui and Ottenwalder pers. comm., pers. obs.). Mazzotti (1983) found hatchling *C. acutus* would disperse from wave exposed nest sites soon after hatching, moving up to 1.5 km from the nest in the following month. Lang (1975) and Ogden (1978), reported similar results from their studies in south Florida. Movements were either along the shore or inland into

protected, interior, shallow water habitats. In some cases hatchlings were noted to move overland for periods of up to 10 days without access to water (Mazzotti 1983). The general pattern of movements was away from exposed habitats and into sheltered mangrove lined creeks. Hatchlings from nests along creek sites dispersed less and tended to remain in the nest area for at least one year. Virtually all hatchling movements were nocturnal.

Rodda (1984) radio-tracked a group of 10 month old ($N = 9$), and 22 month old ($N = 1$) *C. acutus* along a sheltered shoreline in Gatun Lake, Panama. Census work in the area suggested that some of the crocodiles would remain near their nest for at least 22 months after hatching. Over a two-month period the radio-equipped crocodiles were found to remain within relatively restricted home ranges. The 10 month old crocodiles moved within an average of 330 m of shoreline, and spent approximately 80% of their time within a narrower core range of 200 m. The one 22 month old individual moved over 650 m of shoreline.

In the same study, Rodda (1984) examined a series of factors (water temperature, wind speed and direction, sun or moon visibility and altitude, moon phase, cloud cover, and water level) in relation to activity levels. Crocodiles were found to move significantly less during moonlit periods (no clouds, moon more than half full and $> 30^\circ$ from the horizon). A diurnal pattern of movements was found with activity showing a sharp increase just prior to dusk, then increasing steadily until 0300 h. A similar pattern was noted for the mean percentage of animals at the water's surface. Movements during the day (0900- 1700 h) were unusual.

Larger juvenile crocodiles (and subadults) may enter a dispersal phase and move much more than smaller individuals (see following section). Some juvenile crocodiles in southern Florida are known to disperse well away from their nest sites (P. Moler, pers. comm). One individual (84.5 cm TL) moved a minimum distance of 13.1 km over 18 months from its point of origin at the Turkey Point power station (Gaby et al. 1985).

Adults and Subadults - In southern Florida, Mazzotti (1983) reported that adult crocodiles spend most of their time in protected red mangrove (*Rhizophora mangle*) habitats. Over 75% of their observations of adults were in inland or protected coves characterized by deep water, often with undercut banks (see Burrows section) or overhung by mangrove prop roots. Some adults were also found to move to areas of high food availability such as active bird rookeries.

In Etang Saumatre, a brackish water lake in Haiti, adult and subadult crocodiles were found to be significantly more abundant in 5 of the 11 defined lakeshore habitat types (*Conocarpus* fringe, *Conocarpus* flats, *Salicornia* flats, submerged forest, and canal marsh), and were noted to avoid two habitats (rocky shore with medium and steep gradients (Thorbjarnarson 1984, 1988). Three principal environmental factors were considered to be important in determining habitat use: exposure to wave action, food availability and the presence of nesting habitat. The preference of certain habitats over others was attributed in part to the availability of suitable nesting beaches, or to food availability; an active heron rookery in the submerged forest, and the abundance of fish prey species in the *Conocarpus* flats. However, for all habitats the degree of wave exposure was apparently the overriding factor. Classifying lakeshore areas by the degree of wave exposure, crocodiles of all size classes were found in the highest density in protected areas (11.76/km) and in the lowest density in exposed areas (0.83/km) with an intermediate value for moderately exposed areas (7.79/km). A similar avoidance of wave action was noted in adjacent Lago Enriquillo (pers. obs.) and has been reported for *C. acutus* in Florida (P. Moler, pers. comm.), as well as for other crocodylians (Cott 1961, Graham 1968, Woodward and Marion 1978, Messel et al. 1981). Considering that the crocodile's respiratory and visual systems may be severely compromised by waves, avoidance of wave action is a very understandable feature of habitat preference and probably is a general attribute of habitat selection among all crocodylians.

A radio-telemetry study of adult crocodiles in Florida conducted by J. Kushlan and F. Mazzotti (Mazzotti 1983) determined that among 7 adult females (> 2.5 m TL) minimum activity areas averaged 89 ha, and demonstrated seasonal shifts in range associated with the nesting season. Main activity areas were located in protected creeks or ponds, but during the nesting season females would move to the more exposed nest sites in Florida Bay. This study and others have shown that habitat preference in adult females is strongly influenced by the availability of nesting habitat. Females demonstrate an increase in activity and movements during the breeding season (Gaby et al. 1985, Mazzotti 1983) which are often reflected in seasonal differences in habitat selection.

The two radio-equipped male crocodiles (2.3 m, 2.9 m TL) had larger activity areas (98 ha, 216 ha respectively) but did not enter the exposed Florida Bay to any significant degree. One male was noted to have a disjunct activity range occupying a river site, and interior ponds. One stay in the pond region coincided with the active nesting phase of a colony of wood storks (*Mycteria americana*; Mazzotti 1983).

Another type of seasonal activity shift was noted for *C. acutus* by Medem (1981) in freshwater riverine habitats in Colombia. Crocodiles were reported to leave the larger rivers during the wet season to avoid the swift currents and move into lagoons or other inundated areas adjacent to the main river course. Use of the main river channel was restricted primarily to the dry season.

Seasonal activity shifts associated with drought have also been commented on by various authors. Medem (1981) reports that *C. acutus* will bury itself in the mud for periods of up to 2-3 months, or remain in burrows (see below) when its normal habitat dries out. Similar accounts have been given by Varona (1980) for Cuba, Donoso Barros (1966) for Venezuela, and Casas and Guzman (1970) for Mexico.

No quantitative data exist describing daily variation in activity levels in adult or subadult *C. acutus*. Although most data suggest that hatchling and juvenile crocodiles are almost completely nocturnal, possibly to avoid diurnal predators such as raptors and wading birds, adult crocodiles are frequently active during daylight hours. Various behaviors, such as basking (Alvarez del Toro 1974), territorial defense and mating (Alvarez del Toro 1974, Garrick and Lang 1977, Inchaustegui et al. 1980) have been observed during the day. However, for adults as well as juveniles, foraging appears to be mainly a nocturnal activity (Alvarez del Toro 1974, pers. obs.).

Intermediate size-classes of *C. acutus* (large juveniles- subadults, 1.0-2.0 m total length) are frequently found in somewhat marginal habitats. Mazzotti (1983) noted that crocodiles in this size range were often found isolated from the adults and hatchlings and to be located in somewhat inaccessible areas. Gaby et al. (1981, 1985) observed a higher percentage of juveniles and subadult (27% of total) in hypersaline water than adults (5%). In Etang Saumatre subadult crocodiles were more likely to be found along exposed shorelines, and in fact one such marginal habitat (sand-grass-mud) was a statistically "preferred" habitat for subadults (Thorbjarnarson 1984, 1988). In coastal Haiti, juvenile and subadult crocodiles were more frequently reported from small, isolated patches of habitat away from breeding populations.

In the radio-telemetry study in Everglades National Park, Florida (Mazzotti 1983), the one subadult animal followed, a female, was found to move more than adults, and to have a larger minimal activity range (262 ha, 262 fixes), averaging 1.4 km between fixes. In Etang Saumatre, some subadults would also move considerable distances. One subadult male was found to have shifted entirely across the lake, a shoreline distance of 22 km, over a period of 306 days.

The dispersal phase of large juveniles and subadult crocodiles may be an integral part of the population dynamics of *C. acutus* and other crocodylians. The population model proposed by Messel et al (1982) for *C. porosus* may have broad applicability to other species of crocodylians, especially *C. acutus* which is very similar in ecology to *C. porosus*. The data on habitat selection and movement that do exist for *C. acutus* seem to support the presence of dispersal and segregation phases of large juvenile and subadult crocodiles at a time when they may be coming into territorial conflict with adults.

Segregation of Size-Classes - In Florida, the spatial segregation of crocodiles by size-class has been observed in all three sub-populations. As noted above, Mazzotti (1983) reported intermediate-sized crocodiles were not frequently found together with hatchlings or adults. In the cooling canal system at Turkey Point, adult, subadult, and juvenile crocodiles were found in different habitats, with segregation taking place mostly with respect to water salinity (Gaby et al. 1981, 1985). A similar segregation has been noted among the crocodiles on Key Largo (P. Moler, pers. comm.) where physical habitat structure may play an important role. The spatial segregation of crocodiles by size-class may represent a difference in the physical habitat requirements of different sized crocodiles, or it may reflect social factors and agonistic encounters between size-classes as proposed in the Messel et al. (1982) model for *C. porosus*.

However, in other populations of *C. acutus* that have been studied, size-class segregation by habitat type is less clear-cut. In both Etang Saumatre and Lago Enriquillo, hatchling, juvenile, subadult and adult crocodiles were all found together in the same areas (Thorbjarnarson 1984, 1988). In these situations, an important regulatory factor determining the degree (or absence of) size-class segregation, may be population density. It may not be a spurious fact that size-class segregation has been noted in a population inhabiting coastal mangrove habitat in Florida, where population density was lower (see Population Ecology), and the available spectrum of habitats is greater. In the lacustrine crocodile populations on Hispaniola, greater crocodile densities and more limited habitat availability may result in a greater degree of size-class overlap in habitat usage. At the other extreme is the situation reported by Schmidt (1924) in Lago Ticamaya, Honduras, which had an extremely high crocodile density with a total lack of small juveniles. In this case the extremely high density may have triggered density-dependent population control measures which may have lead to the complete exclusion of smaller individuals from the main population body, or mortality via mechanisms such as cannibalism. Schmidt does report finding the remains of a 1.2-1.5 m crocodile in the stomach of a larger specimen, but under circumstances such as these cannibalism is difficult to distinguish from scavenging.

Temperature and Salinity Relations

Studies of the temperature relations of *C. acutus* have primarily involved hatchling (Mazzotti 1983) and juvenile (Lang 1979) crocodiles. Lang (1979) noted that under laboratory conditions the preferred body temperature of fasting *C. acutus* was similar at night (28.0° C) and during the day (27.9° C), but was slightly elevated following feeding (day 29.5° C, night 29.3° C). Testing for the upper limits of thermal tolerance in hatchlings, Mazzotti (1983) found observable signs of heat stress when cloacal temperatures exceeded 38° C.

Under field conditions, Mazzotti (1983) noted that hatchling *C. acutus* selected the coolest available microhabitats during the day, becoming active when surrounding temperatures dropped to within 1° C of the microhabitat temperature. The resulting pattern of activity indicates that hatchlings seek out the lowest available temperatures in order to avoid heat stress (Mazzotti 1983).

These data for hatchling *C. acutus* agree with the hypothesis of Lang (1975c) of *Crocodylus* as thermoconformers whose basic thermoregulatory strategy is to avoid rapid heating during the day.

No specific studies have examined the thermal relations of adult *C. acutus* but, in contrast to hatchlings, adults are well known to bask, especially during the morning or late afternoon hours. Basking is usually accomplished by hauling out on land, but in areas where suitable terrestrial habitat is not available, or a disturbing human presence is found, crocodiles will bask in a high emergent floating posture in the water (Alvarez del Toro 1974, Medem 1981, pers. obs.). Conversely, during the heat of the day adults are known to remain hidden in deep water (Alvarez del Toro 1974), or in cool, shaded aquatic situations (pers. obs.).

At times crocodiles will remain on land at night, and this behavior results in lowered body temperatures (Cott 1961, Graham 1968, Lang 1975c). In Lago Enriquillo and Etang Saumatre, this behavior was frequently noted in response to intense wave action (pers. obs.), but it may also occur in calm water areas. Crocodiles on land have also been observed gaping both during the day and at night, an action considered by various authors to be thermoregulatory in nature (Alvarez del Toro 1974, Loveridge 1984). Besides a temperature regulation function, gaping may also be used to dry out the mouth lining to control the growth of algae or fungi, or to desiccate aquatic ectoparasites (pers. obs.).

The salinity relations of *C. acutus* are of obvious importance as the species is frequently found in saline environments. A relatively large literature exists on the osmoregulation of *C. acutus* and other crocodylians.

Mazzotti (1983) found crocodiles in Everglades National Park occupied a wide range of salinities (0-35 parts per thousand (ppt)), with mean salinity values varying somewhat between size classes (adults 12.1 ppt, subadults 12.6 ppt, juveniles 20.1 ppt) and time of year (winter 12.4 ppt, spring 19.6 ppt, summer 17.3 ppt, and fall 15.1 ppt). The seasonal shift in mean salinity was associated with a population move towards the Florida Bay during the spring and the greater use of inland areas during the fall when freshwater discharge was at its highest. Average salinity for females (17.3 ppt) was higher than for males (10.8 ppt) and reflected to some degree the use of nesting sites in the higher salinity Florida Bay region.

Also in south Florida, Gaby et al (1985) reported finding crocodiles in salinities ranging from 0 to 40 ppt, and Dunson (1982) observed hatchlings in water up to 43 ppt. Gaby et al. (1985) also noted a size-class segregation by water salinity with adults more frequently observed in freshwater areas (38% of observations), as opposed to only 13% for juveniles and subadults. These two smaller size-classes had a greater tendency to be found in brackish (53%) or hypersaline water (27%). The mean water salinity for captured juveniles was 25.2 ppt.

In terms of osmoregulation, body size plays an extremely important role. Individuals larger than 200 g can fast in seawater for long periods without developing severe salt balance problems (Ellis 1981, Mazzotti 1983). Adult crocodiles, with a relatively small surface area to volume ratio, can presumably remain in saline water for extended periods. In Lago Enriquillo, crocodiles lived in water of up to 70-80 ppt for many years prior to the hurricanes of 1979 and 1980. However, in the same lake hatchling crocodiles would perish as a consequence of the hypersaline water unless they happened to disperse into one of the freshwater marsh areas that fringe the lake (Inchaustegui and Ottenwalder, pers. comm.).

The most crucial period for *C. acutus* in terms of osmoregulation is the first year or two of life. At small body sizes, a large surface area to volume ratio results in an increased capacity for water flux in relation to body mass. Hatchling crocodiles under laboratory conditions do not

maintain mass in full strength sea water (35 ppt), even when fed fish *ad lib* (Dunson 1970, Evans and Ellis 1977, Ellis 1981). However, field observations indicate that hatchlings not only tolerate salinities of up to 43 ppt, but under some circumstances grow extremely rapidly in hypersaline environments (Carney 1971, Gaby et al. 1981). An extra-renal salt excreting gland has been found in the tongue of *C. acutus* and all *Crocodylus* examined to date (Taplin and Grigg 1981). But under natural conditions of blood plasma salt levels, this extra renal excretory pathway apparently plays little or no osmoregulatory role in *C. acutus* (Dunson 1982). In the absence of major physiological adaptations for life in saline water, Mazzotti (1983) suggested that osmoregulation is accomplished primarily by behavioral means. The principal behavioral mechanism for maintaining water balance is probably drinking brackish water made available ephemerally by rains (Mazzotti 1983). Under laboratory conditions it was found that small *C. acutus* maintained in saline water will drink brackish water. Over a 10 day period, hatchlings were found to maintain mass in seawater (35 ppt) if provided with fish to eat, and placed in brackish water (4 ppt) for one day per week (Mazzotti 1983).

Burrows

The construction and use of burrows or dens by *C. acutus* has been widely observed and commented upon throughout the species range: Florida (Hornaday 1904, Dimock and Dimock 1908, Ogden 1979), Mexico (Casas and Guzman 1970, Alvarez del Toro 1974), Honduras (Schmidt 1924), Nicaragua (Camacho 1983), Colombia (Medem 1981), Venezuela (Donoso Barros 1966), Jamaica (L. Garrick, pers. comm.), Haiti and the Dominican Republic (pers. obs.). Burrows are used principally by adult crocodiles living in riverine habitats, although Medem (1981) also reports dens from lakes and mangrove swamps in Colombia. Other accounts of *C. acutus* from lacustrine habitats indicate that crocodiles do not dig burrows in these areas, perhaps because of a lack of suitable shorebank conditions or less seasonal variability in water levels (Etang Saumatre, Lago Enriquillo, pers. obs.; Lago Ticamaya, Schmidt 1924).

According to Medem (1981), burrow construction differs in relation to habitat type. Along rivers or in lakes, burrows are excavated in elevated banks and have from one to three entrances. In mangrove swamps they are usually found in the most elevated areas under the roots of mangroves or dead trees, or even in mounds of decomposing leaf litter. Varona (1980) reports that in Cuba, *C. acutus* burrows have an oval entrance, exposed at low tide, widening inwards. The burrow ascends and the roof of the terminal chamber is above the water level, sometimes even with "ventilation" holes to the surface. Crocodiles are reported to enter and leave the burrow head first so the terminal chamber needs to be large enough to allow the crocodile to turn around.

Burrows can be quite large. One burrow measured by Medem (1981) along the Rio Palenque in Colombia had two entrance tunnels (2.75 m, 5.80 m in length), one above the water, the other submerged, with a very large terminal chamber (8.5 m x 7.2 m). Ogden (1979) reported that in Florida crocodile burrows were often maintained near creek bank nest sites and were 3-9 m in length with entrances at or below the water line.

Burrows are probably used under various circumstances, as a refuge for resting and thermoregulation, an aestivation site for prolonged drought, or for protection from natural predators or man.

Habitat Relations with Other Crocodilians

Over its extensive range in the northern Neotropics, *C. acutus* overlaps, partially or entirely, the range of four (and possibly five) crocodilians: *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus rhombifer*, *C. moreletii* and possibly *C. intermedius*. The range of distribution overlap is: *Alligator*, southern Florida; *Caiman*, Caribbean drainage Honduras-Venezuela, Pacific drainage Oaxaca, Mexico-southern Ecuador; *C. rhombifer*, Cuba and the Isle of Pines; *C. moreletii*, Atlantic drainage southern Mexico-Guatemala; and *C. intermedius* possibly in the vicinity of the Orinoco delta. Indeed, on a macroscopic scale, the only parts of the range of *C. acutus* where it is not sympatric with another crocodilian are on the islands of Jamaica and Hispaniola, and in northwestern Mexico (Sinaloa-Guerrero).

Reports of ecological relations between *C. acutus* and other crocodilians are restricted primarily to habitat partitioning, and in some areas even this situation is confused. Where *C. acutus* is sympatric with another large, primarily freshwater species, it is generally restricted to brackish water habitats, and does not penetrate far into interior, freshwater areas (*Alligator* (Kushlan and Mazzotti 1986), *C. rhombifer* (Gundlach 1880; Barbour and Ramsden 1919; Varona 1966)), although the situation with *Alligator* is somewhat complicated by potential temperature limitations (Kushlan 1982). In Cuba, *C. rhombifer* is reportedly behaviorally dominant over even larger *C. acutus* in captivity (Varona 1966) and may actively exclude *C. acutus* from freshwater habitats. Although *C. acutus* ranges far up into freshwater rivers along the northern coasts of Colombia and Venezuela, it apparently never has been found far up into the Orinoco river, habitat of the large, freshwater *C. intermedius* (Medem 1981).

In regions where *C. acutus* is sympatric with a smaller crocodilian, habitat use normally includes a greater variety of freshwater environments. In Mexico, *C. acutus* ranges well upstream in many of the larger rivers, and also was frequently found in lakes (Alvarez del Toro 1974). In the same areas, the smaller species of crocodilians are found principally in small streams, or swampy, slow moving sections of rivers (*Caiman crocodilus*), or in small, turbid streams, swamps or swampy lakes (*C. moreletii*; Alvarez del Toro 1974). Similarly, in the Rio Atrato in Colombia, Medem (1981) noted a definite habitat segregation existed with *C. acutus* in the river and major tributaries, and *Caiman* confined to the surrounding swamps and smaller tributaries. A similar situation is presently found in eastern Honduras (pers. obs). In northern Venezuelan rivers, Seijas (1986b) found a broad overlap in the habitat usage between *C. acutus* and *Caiman crocodilus*. It was noted, however, that in areas where the two species were found together, the population levels of *Caiman* were considerably reduced. Other studies have also found that in the recent absence of *C. acutus*, other crocodilians have expanded into typical *C. acutus* coastal habitat: *C. moreletii* (Belize; Quintana Roo, Mexico; C. Abercrombie and M. Lazcano-Barrero, pers. comm.), *C. crocodilus* (Colombia, Medem 1981; Venezuela, Seijas 1986a). Medem (1981) and Seijas (1986a) have pointed out that in many instances, the ecological niche expansion of *Caiman* may be a direct result of the over-exploitation of the more commercially valuable *C. acutus* populations.

REPRODUCTIVE ECOLOGY

Territoriality, Courtship and Mating

Based on studies of captive crocodiles in Florida (Lang 1975a, Garrick and Lang 1977), and observations made on wild crocodiles in Mexico (Alvarez del Toro 1974) and the Dominican Republic (Inchaustegui, Ottenwalder, Robinson, pers. comm.) the breeding system of *C. acutus* is

polygynous. Adult males defend territories during the breeding season, excluding other males but permitting females to enter for courtship. Males are reported to interrupt the courtship activities of smaller neighboring males (S.Inchaustegui, J.A.Ottenwalder, D.Robinson, pers. comm.). Male territorial defense is composed of a series of stereotyped postures, frequently followed by actual or mock fighting. Territorial intruders are often approached in a head-emergent, tail-arched posture prior to fighting. Combat frequently includes lunges and chases. Following an aggressive encounter, dominant males commonly assume a raised "inflated posture" (Garrick and Lang 1977). Alvarez del Toro (1974) reported that, when encountering one another, territorial males would lift their snouts out of the water, snort loudly, and spurt water through their nostrils ("narial geysering" of Garrick and Lang 1977).

Indirect evidence of a polygynous mating system was also found in Etang Saumatre, Haiti (Thorbjarnarson 1984, 1988). Twenty-seven adult crocodiles were located in four distinct groups adjacent to the major nesting beaches one month prior to the peak oviposition period. The groups were well defined during the day, with a mean intergroup distance of 4.7 km, but at night would break up as individuals dispersed along the shoreline. These groups were inferred to be courtship assemblages, and contained one large male, and several smaller adults (presumably females but possibly including subdominant males). The male:female sex ratio of adult crocodiles captured in the same area shortly following the oviposition period was 1:3. At the same time, the corresponding sex ratio for another section of the lake, removed from the nesting beaches, was highly male biased (5 males:0 females) and indicated that a certain fraction of the adult male population may have been excluded from breeding.

Courtship and mating are exclusively aquatic activities. The main advertisement display of male *C. acutus* is a series of one to three headslaps (Garrick and Lang 1977). Courtship is usually initiated by the female, and typically consists of a somewhat stereotyped sequence of behaviors with females snout-lifting, swimming in slow circles around the male, or placing her head on the snout or back of the male. Males frequently respond to this activity by emitting a very low frequency sound, termed a sub-audible vibration (SAV) by Garrick and Lang (1977). The SAV is given from a typical "head-emergent tail-arched" posture, and causes the water on the males back to agitate upwards in what has been termed a "water dance" in alligators (Vliet 1987). Following the SAV are a further series of behaviors that include snout lifting and rubbing, bubbling, and temporary submergences. Copulation is done in shallow water and usually lasts several minutes (Lang 1975a, Garrick and Lang 1977).

The role of vocal signals in the establishment of territories, and courtship in *C. acutus* is not well understood. Garrick and Lang (1977) reported no bellowing in their study of captive individuals, but Herzog (1974) noted one instance of a captive *C. acutus* bellowing on land. Alvarez del Toro (1974) described bellowing in *C. acutus* in Mexico, noting that bellows are primarily heard during the early nighttime or morning hours, and were more frequent during the courtship season. The bellows are said to be answered by other males in the vicinity. A similar account is given by Medem (1981) for *C. acutus*, who also states that bellows can sometimes be heard in the afternoon, and are audible from afar.

Alvarez del Toro (1974) reported that females are territorial towards one another, but upon the approach of an adult male would snout lift and roar in an unusual fashion. Varona (1980) also indicated that in Cuba nesting females are territorial, and up to 5-6 may compete for one nest site. In other parts of its range, however, female *C. acutus* are apparently less territorial around the nest site and may nest colonially or in small groups: Florida (Kushlan 1982), Haiti (Thorbjarnarson 1984, 1988), Dominican Republic (pers. obs.).

Minimum Reproductive Size and Breeding Effort

The minimum reproductive size of male *C. acutus* is somewhat problematical as estimates must be based on size estimates of animals copulating (and producing fertile clutches), or anatomical examination. A further complication is that individuals may be physiologically mature, but excluded from breeding due to social factors.

Medem (1981) reported a captive 2.19 m total length (TL) male that mated with a 2.36 m TL female in Colombia. The resulting clutch, however, was infertile and suggests that the male was not yet sexually mature. The smallest reported lengths of mature males come from Etang Saumatre, Haiti, where two males captured adjacent to the nesting beaches during the breeding season, and assumed to be mature, were 2.82 m and 2.88 m TL (Thorbjarnarson 1984, 1988).

More data exist on the size of sexually mature females based on nesting individuals. Nevertheless, estimates vary considerably throughout the range of the species, suggesting that minimal size for reproduction needs to be treated as a population parameter, perhaps reflecting environmental or genetic differences in growth rates, and/or age at sexual maturity.

Alvarez del Toro (1974) reported never finding a reproductive female less than 2.8 m TL. Similarly, in Cuba, the reported minimum reproductive size of females is 2.7-3.0 m TL (Varona 1980). However, in other areas females are known to nest at much smaller sizes. Klein (1977) suggested 2.4 m TL as a minimum reproductive size for female *C. acutus* in eastern Honduras. In Etang Saumatre, females begin nesting at around 2.2-2.3 m TL, and never attain lengths over 2.5 m TL (Thorbjarnarson 1984, 1988). Based on the growth rates from recaptured individuals, the minimum reproductive age of females in Etang Saumatre is approximately 10 years. A similar minimum reproductive size in females was noted for nearby Lago Enriquillo (pers. obs.) as well as in Jamaica (L. Garrick, pers. comm.).

In Florida, Ogden (1978) estimated the total lengths of 8 *C. acutus* seen at nesting beaches was 3.9 m, 3.5 m, 3.1 m, 2.8 m (two nests), and 2.5 m (three nests; mean = 2.95 m). Also in Florida, Mazzotti (1983) estimated minimum nesting size to be 2.25 m TL, and captured 6 females at nests with total lengths of: 2.28 m, 2.47 m, 2.57 m, 2.59 m, 2.96 m, 3.08 m (mean = 2.66 m).

Estimates of breeding effort (the annual percentage of adult females that nest) have been made for two crocodile populations, Everglades National Park (Mazzotti 1983), and Etang Saumatre (Thorbjarnarson 1984, 1988). Both values were derived indirectly from estimates of the total adult female population size, and the known number of nests. The two populations had similar values: Florida 72%; Haiti 63.8%, and are comparable to published values for other populations: *A. mississippiensis*, 68.1% (although see Wilkinson (1984) for a much lower value); *C. niloticus*, 80% (Cott 1961); 67% (Blomberg et al. 1982); 87.6% (Graham 1968); 63% (Hutton 1984); and *C. johnsoni*, 90% (Webb et al. 1983).

Nest Site Selection

The American crocodile typically lays its eggs in a hole nest excavated into sand or soil near the waters edge. However, *C. acutus* appears to be one of the most adaptable of crocodilians in terms of nesting requirements and has been known to nest in a variety of situations. The use of soil or mangrove peat "mound" nests have been well documented in Florida (Campbell 1972,

Ogden 1978, Mazzotti 1983). Even more noteworthy are accounts that *C. acutus* will make small mound nests of scraped up vegetative litter. Under these circumstances the females are reported to dig a shallow hole into which the eggs are laid, then covered with leaf litter, grass or dead branches, forming a definite mound (although smaller in size than the nest mounds made by the sympatric *C. moreletii* and *Caiman crocodilus* (Alvarez del Toro 1974, Medem 1981). However, this behavior has not been well documented in the wild and probably plays an insignificant role in overall nesting ecology.

The ecological significance of hole versus mound nesting was discussed by Campbell (1972), who refuted the phylogenetic importance attributed to nesting mode described by Greer (1970, 1971). Campbell noted that mound nests are found most frequently in species that inhabit low-lying areas, swamps and marshes. He went on to speculate that individual differences in nest morphometry within a population may reflect the past nesting experience of specific females.

Perhaps of even greater importance in defining nesting mode is the timing of nesting in relation to rainfall or water level variation. True mound nesters (e.g. the Alligatoridae) typically nest in the rainy season, frequently during peak water levels. Hole nesting crocodiles normally nest during periods of falling water levels (i.e. the dry season), with hatching taking place towards the beginning of the rainy season (see Timing of Nesting). However, with a hole nesting species such as *C. acutus*, the tendency to "mound" nests may be an adaptive response to nesting in low-lying areas where the probability of nest flooding is high (see Clutch Size, Fertility and Egg Mortality).

The following sections will provide accounts of nesting mode in two crocodile populations in very different habitats: the coastal lowlands of southern Florida, and the inland lakes of Hispaniola. The descriptions serve to highlight some of the variability in nest site selection.

South Florida - The principal nesting areas of *C. acutus* in southern Florida are found along creek banks, in exposed sandy beaches in Florida Bay, in man-made canal berms along the mangrove-lined bay side of Key Largo, and in the cooling canal system of the Turkey Point power plant (Ogden 1978, Mazzotti 1983, Gaby et al. 1985). Ogden (1978) noted a diversity of nesting sites in Florida Bay, but that all nests were located in well drained soil and had a deep water approach. Ogden classified nest sites into three major types which are, verbatim:

1. Open thickets of hardwood trees along the edges of 4 to 8 meter wide, deep water creeks with vertical, 0.5 to 1.0 m marl or muck banks.
2. Surrounded by varying amounts of hardwood shrubs and trees at the heads of narrow, shell-sand beaches.
3. In thickets of shrubby black mangrove (*Avicennia nitida*) behind marl banks rising 15 to 30 cm above water.

In Florida Bay two basic nest soil substrates are found: porous sand-shell soil, and marl; the latter having a very fine particle size and a high percentage of organic matter. The soil water content and resultant oxygen diffusion differ widely between the two soil types and play a significant role in determining egg physiology (Lutz and Dunbar-Cooper 1984; see Incubation and Nest Environment).

Ogden (1978) reported that 13 of 14 primary nest sites investigated had significant elevations (mounds) above the surrounding terrain. The elevations ranged from 9 to 65 cm (mean = 31 cm) and were apparently not correlated with location or soil type. Maximum diameters of nest mounds ranged from 1.0 m to 4.6 m (mean = 2.4 m, N = 14).

< 0.01). Percent shrub coverage was significantly higher at null sites ($p < 0.05$), but was correlated with soil moisture.

Nests in Etang Saumatre are hole-type nests with no mounding notable. The nest excavation is angled diagonally back into the soil. Mean perpendicular depth to eggs was: clutch top 24.1 cm (SD 4.7 cm, $N = 13$), and clutch bottom 37.9 cm (SD 4.3 cm, $N = 12$). Mean horizontal width of the egg chamber is 32.4 cm (SD 4.3 cm, $N = 12$). Because of a lower density of nesting females colonial nesting was not evident as it is in nearby Lago Enriquillo. The greatest number of nests found on any one beach was three.

Other Areas - Aspects of the nesting biology have also been noted in Jamaica (L. Garrick, pers. comm.), Cuba (Varona 1980), Mexico (Casas and Guzman 1970, Alvarez del Toro 1974), Panama (Breder 1946, Dugan et al. 1981), Honduras (Schmidt 1924, Klein 1977), Colombia, Venezuela and Ecuador (Medem 1981, 1983). These accounts support the generalization that *C. acutus* prefers to nest in sandy beaches, but is very adaptable and will nest in marginal areas such as gravel (Schmidt 1924, Alvarez del Toro 1974), wet, mucky soils (Varona 1980), wood chips (L. Garrick, pers. comm), or even make small, mound-type nests from vegetative matter (Alvarez del Toro 1974, Medem 1981, 1983).

Alvarez del Toro (1974) described a typical *C. acutus* nest in Chiapas, Mexico as being located in a sandy beach, beyond the bare sand fringe and usually near a shrub thicket. In Jamaica, Garrick (pers. comm.) noted that *C. acutus* nests were mounded, and found in sandy beaches located adjacent to mangrove swamps that provide habitat for the female. Along rivers, nests are positioned high up on banks in areas cleared by the female.

In Honduras, Schmidt (1924) found a crocodile nest in a gravel beach on an island in Lago Ticamaya, and Klein (1977) mentioned nests being located in sandy river bars. In Panama, *C. acutus* nests have been found in a clearing on a small forested island adjacent to Barro Colorado Island (Dugan et al. 1981), in a small lighthouse clearing in a forested mainland peninsula also near BCI (Rodda 1984), and in open, sandy river bars in the Rio Chucunague drainage (Breder 1946).

Table 1: Mean values of nine parameters for *C. acutus* nests in Etang Saumatre, Haiti. From Thorbjarnarson 1988.

Nest Parameter	Mean (SD)	Range	N
Distance to Lake (m)	27.5 (11.8)	7-47	31
Height above Lake (m)	1.2 (0.5)	0.6-2.1	31
Soil pH	6.2 (1.6)	5.2-7.1	15
Soil Moisture (% water)	6.6 (3.1)	3.4-14.3	12
Shrub/Tree Coverage (%)	30.1 (14.5)	10-60	29
Grass Coverage (%)	5.9 (5.8)	0-20	29
Leaf Litter Coverage (%)	18.4 (8.6)	10-30	29
Height of Vegetation (m)	3.4 (0.6)	2.0-4.5	27
Distance to Nearest Tree (m)	2.1 (1.1)	0.5-5.0	27

Nesting Behavior and Parental Care

Although Duval (1977) reports an interval of 84-107 days between observed copulation attempts and nesting in a captive situation, most reports from other captive and wild populations indicate that oviposition follows courtship activity by 1-2 months (Alvarez del Toro 1974, Garrick and Lang 1977, Varona 1980, Inchaustegui et al. 1980). Gravid females will begin visiting potential nest sites up to 4-6 weeks prior to laying (Ogden 1978, Thorbjarnarson 1984, 1988). These early visits are usually brief (less than one hour) and of irregular occurrence and provide the females with the opportunity to make shallow exploratory excavations. The nocturnal visits increase with frequency as the time for oviposition approaches, and egg laying usually follows several nights of more lengthy visits and increased digging activity (Ogden 1978). In Florida, digging is restricted to primary or secondary nest sites, usually found within 35 m of one another (Ogden 1978), but in Etang Saumatre, where more potential nest sites are available, excavations are frequently scattered among several sites (Thorbjarnarson 1984, 1988). Gravid females in both Lago Enriqueillo and Etang Saumatre were noted to infrequently drop their eggs prematurely while walking along the beach searching for nest sites (both lakes), or even in the water (Lago Enriqueillo). The etiology of this premature oviposition is unclear.

Nesting sites in Etang Saumatre are reused regularly. Forty-six percent of the nests located in 1984 were used the previous year, 15 % were used previous to 1983, and 39% were located in apparently new sites (Thorbjarnarson 1984, 1988). Similar to the situation in adjacent Lago Enriqueillo, a rising lake level since 1980 has forced some crocodiles to seek new nesting sites.

Female *C. acutus* in Lago Enriqueillo emerge from the water to nest shortly after dark (pers. obs.). One female was discovered in the final stages of egg laying at 2315h on 12 February 1982. Detailed behavioral observations of oviposition by a captive female were made in Isla Salamanca National Park, Colombia by Pachon, Ramirez and Moreno (cited in Medem 1981). Using her hind legs the female dug a nest cavity on 15 March, and the following night began excavating another hole from 0015h to 0400h. Once the digging was completed, the female remained motionless atop the nest until egg laying began at 0525h. Oviposition was accomplished with the female positioned with her hind legs over the edge of the hole, head slightly elevated, pectoral region pressed against the ground, and abdomen arched upwards. The first abdominal contractions lasted 5 minutes. During the next 21 minutes, 15 eggs were laid, the time interval between eggs diminishing from 5 min. 20 sec., to 5 seconds. Eighteen minutes after the last egg was deposited, the female began covering the eggs with soil and leaf litter, gradually shaping a mound 80 cm in diameter, and 10 cm high. This was apparently the females' (2.36 m TL) first nesting attempt and this may partially account for the small clutch size (Medem 1981).

Female *C. acutus* will remain in the vicinity of the nest during incubation (Alvarez del Toro 1974, Ogden 1978, Thorbjarnarson 1984, 1988). In some areas females are reported to actively protect nests, excluding other crocodiles or potential nest predators from the nest locale: Mexico (Alvarez del Toro 1974), Cuba (Varona 1980), Panama (Dugan et al. 1981); although this behavior is individually variable. In other areas females provide little or no nest protection: Florida (Ogden 1978) and Haiti (pers. obs.). There is no evidence that males play any role in nest defense in the wild.

Dugan et al. (1981) observed an adult female *C. acutus* protecting her nest by chasing away ovipositing iguanas. Iguanas would dig up crocodile eggs during the construction of nest burrows, and on 12 occasions the crocodile seized iguanas near her nest. The authors concluded that this behavior was a mixture of nest defense and predation.

Towards the end of the incubation period, female crocodiles will begin to make nocturnal visits to their nests, laying their heads atop the nest to listen for the release calls of the hatchlings (Ogden and Singletary 1973). Triggered by the grunts of the young, the female opens the nest using her front feet. Photographs of a wild crocodile opening a nest in Florida suggest that the female will help the hatchlings emerge from their eggs by gently squeezing the eggs between the tongue and palate (Ogden and Singletary 1973). Following hatching, the young are gathered in small groups into the female's mouth, where they are carried in the depressed gular pouch, and ferried to the water's edge. The female photographed in Florida (using an automatic device) carried a total of 34 hatchlings in 12 trips between the nest and the water (Ogden and Singletary 1973). Similar nest opening behavior has been observed or inferred for *C. acutus* throughout the species range (Alvarez del Toro 1974, Inchaustegui et al. 1980, Medem 1981, Thorbjarnarson 1984, 1988).

In some instances hatching is not simultaneous for all eggs and females may leave underdeveloped eggs buried in the nest, returning at a later date to open them (Ottenwalder, pers. comm.; pers. obs.). Mazzotti (1983) also noted that in Florida females may leave fully developed, vocalizing eggs in the nest. In one case a female hatched a nest during three visits over a four day period. In Lago Enriquillo, female crocodiles may remain on land in shaded areas with their hatchlings, or leave them under vegetation during the day (Inchaustegui et al. 1980). This behavior may have been related to the hypersaline lake water and resultant osmotic problems for hatchlings (pers. obs.; see Temperature and Salinity Relations).

The degree of maternal care for recently hatched *C. acutus* appears to vary considerably throughout the species range. The results of most studies suggest that the formation of distinct pods of young and maternal care of neonates is minimal in this species (Mazzotti 1983, Thorbjarnarson 1984, 1988; Rodda 1984). However, under certain conditions the formation of pods may be influenced by the habitat into which the young are born. In areas exposed to wave action or in hypersaline water the dispersal of hatchlings is almost immediate (see Habitat Selection, Activity and Movements) and there is virtually no group cohesion among the hatchlings. Nevertheless, in some areas adult crocodiles have been seen in the vicinity of loosely grouped hatchling assemblages (Mazzotti 1983, Thorbjarnarson 1984). Alvarez del Toro (1974) reported that in Mexico, hatchlings would remain grouped together near the female for several weeks following hatching. However, even in suitable juvenile habitats in south Florida and Haiti, pod formation is also ephemeral (Gaby et al. 1985, Thorbjarnarson 1984, 1988; P. Moler, pers. comm.). Campbell (1973) noted that young *C. acutus* are relatively non-vocal, and this observation has been supported in the wild by observations made by Mazzotti (1983). In as much as hatchling vocalizations serve to maintain group integrity, and/or communication with an adult, the non-vocal nature of hatchling *C. acutus* is another indication of lack of social cohesion in the young.

The seemingly unremarkable amount of maternal protection for hatchlings *C. acutus* may be a consistent character of the species, or it may reflect a recent change in behavior associated with human-related disturbance. Rand and Troyer (1980) have suggested that in Gatun Lake, Panama, past hunting has selectively eliminated adults that protected their young. Furthermore, as crocodilians are long lived animals with recognized learning ability (Bustard 1968, Webb and Messel 1979), a diminution in parental care may also be a learned response based on past experience with humans. Indeed, some historical accounts suggest that a higher degree of parental care may have existed in the past (e.g. Esquemeling 1678).

South of Colombia rainfall patterns change drastically, becoming much dryer with a rainy season extending from January to April. The crocodiles in this region adapt accordingly and oviposit from October to December, suggesting that the eggs would hatch during the first half of the wet season (Medem 1981, Fiallos et al. ms).

Data are scanty for crocodile nesting along the Caribbean coast of Colombia and Venezuela, which has a typical Caribbean weather pattern (rains May-Oct/Nov). In Colombia, Medem (1981) reports that *C. acutus* nests hatch in April-May, but it is not clear to which part of the country he is referring. The only site specific datum is from Isla Salamanca where a captive female laid on 16 March (Medem 1981). Information from Venezuela suggests that in most coastal areas *C. acutus* hatch in April (Rio Yaracuy) or May (Lago Maracaibo region) (A.E. Seijas, pers. comm.), but in the arid region of Falcon state, the nests of one crocodile population near Chichiriviche are known to hatch in late August or early September. One nest at the Jatira Reservoir was found in the process of hatching on 28 August 1987 (A.E. Seijas, pers. comm.). However, in this arid region the peak rainfall is in November-December. These data would suggest that nesting in Venezuela follows the general Caribbean pattern, with the exception of the Falcon region where nesting is delayed, perhaps due to arid conditions and a delayed peak in rainfall.

The islands of Cuba, Jamaica, and Hispaniola share the typical Caribbean climatic pattern, and here *C. acutus* have a nesting schedule comparable to other Caribbean areas. Oviposition takes place primarily during March and April, and nests hatch during June-July (Inchaustegui et al. 1980, Varona 1980, L. Garrick, pers. comm.), i.e. during the first half of the rainy season. The notable exception to this is in Etang Saumatre, Haiti, where nests are constructed in late January and early February, and hatch late April-early May at the very beginning of the rainy season (Thorbjarnarson 1984, 1988).

In southern Florida, a similar seasonal rainfall pattern exists, but crocodiles are delayed by low winter and spring temperatures and do not nest until April-May, with the young hatching July-August (Ogden 1978, Kushlan and Mazzotti 1986). Captive crocodiles in southern Florida that originated from Jamaica follow the typical Florida nesting schedule (ovipositing April-May; Garrick and Lang 1977), indicating that at least with respect to temperature limitations timing of nesting is environmentally malleable.

Incubation and Nest Environment

Reported incubation periods for *C. acutus* nests range from 80 to 90 days (Table 3), although in one artificially incubated nest it was 107 days (Duval 1977). The length of incubation is temperature dependent, but under natural conditions nest temperatures appear not to fluctuate greatly. Over a 24 day period, Lutz and Dunbar-Cooper (1984) found a mean daily temperature variation of 1.4° C in a nest in southern Florida. During a 30 hour interval, the maximum temperature fluctuation among 6 nests in Haiti was 0.9° C (top of egg clutch), and 0.6° C (bottom; Thorbjarnarson 1984, 1988). Due to the thermal buffering effects of the soil, in both studies maximum nest temperatures were reached at night.

Among seven nests in Florida, Lutz and Dunbar-Cooper (1984) noted a trend of increasing nest temperature with time. Mean nest temperature increased from 30.9° C in late May-early June, to 34.3° C in early August. The rise in mean nest temperature was correlated with an increasing trend in mean air temperature.

The study of Lutz and Dunbar-Cooper (1984) also examined gas exchange in *C. acutus* nests. In southern Florida crocodiles nest in two distinct soil types, and the physical properties of the soil play an important role in determining gas exchange characteristics of the nest. Marl nests have a much finer soil particle size (primarily less than 246 microns), a higher mean water content (29.2% by weight), and a lower oxygen diffusion (1.96×10^{-4} cm/sec at 15% water content). Sand/shell nests have a larger particle size (0.5-3.3 mm), a lower mean water content (10.3%), and a higher oxygen diffusion (1.51×10^{-4} cm/sec at 16% water). Although the results were more clear-cut in the sand/shell soil, nests in both soil types demonstrated an increase in PCO_2 , and a decrease in PO_2 during incubation. The lower potential for gas diffusion resulted in lower PO_2 and higher PCO_2 levels in the marl nests.

Lutz and Dunbar-Cooper (1984) also noted a 15% decrease in egg mass (water loss) during incubation. Somewhat similar results were reported by Moore (1953) who suggested that under normal conditions a clutch of crocodile eggs loses 8.6% of its mass by day 70 of incubation.

Table 3. Reported egg incubation periods in *C. acutus*. Data from Alvarez del Toro (1974); Varona (1980); Ioc and Kushlan and Mazzotti (1986).

Location	Incubation Period (days)
Cuba	80-90
Florida	85
Mexico	80
Dominican Republic	84

Table 4: Reported values of clutch size for *C. acutus* N is the number of nests examined. Data from Kushlan and (1986); Lutz and Dunbar-Cooper (1984); Ogden (1978); Medem (1981); Breder (1946); Schmidt (1924); Inchausteg (1980); Thorbjarnarson (1988); and Alvarez del Toro (1971).

Location	Clutch Size	N
Florida	38.0	46
	39.1	8
	44	20
Colombia	40-60	-
Panama	46	1
Honduras	22	1
Dominican Republic	23.8	80
Haiti	22.5	14
Mexico	30-60	-

Clutch Size, Fertility and Egg Mortality

Reported values for clutch size in *C. acutus* (Table 4) range from lows of 22 (Schmidt 1924) and 22.5 (Thorbjarnarson 1984, 1988), to high figures of 81 (Ogden 1978) and 105 (Medem 1981). Extremely large clutches of eggs may be the result of more than one female ovipositing at the same nest site (Kushlan and Mazzotti 1986). This interpretation is supported by evidence from Florida and Haiti where two clutches known to have been laid by different females were laid in the same nest hole (Kushlan and Mazzotti 1986, Thorbjarnarson 1984, 1988).

Clutch mass from one nest in Florida was 5.2 kg (Lutz and Dunbar-Cooper 1984). Mean clutch mass from 14 nests in Haiti was 2.18 kg, and averaged 4.4% of adult female body mass (Thorbjarnarson 1984, 1988). Reported values of individual egg masses (early in incubation) are 91.3 g (Lutz and Dunbar-Cooper 1984), 97.0 g (Thorbjarnarson 1984, 1988) and 103.4 g (Duval 1977).

Mean egg dimensions are more often reported in the literature than egg mass and can be used to better show the variation in egg size. However, there is not enough evidence to determine if egg size varies with female size, or between populations. The largest reported mean egg dimensions are from Panama (52.0 x 79.0 mm, N = 46; Breder 1946), and Chiapas, Mexico (54 x 80 mm; Alvarez del Toro 1974). Smaller eggs have been reported from Haiti: 45.4 x 76.5 mm (Thorbjarnarson 1984, 1988), Cuba: 42-47 x 73-81 mm (Barbour and Ramsden 1919), and Honduras: 42-42.5 x 70-76 mm (Schmidt 1924), 46.6 x 75.4 mm (Thorbjarnarson and Vliet, unpubl. data). Large eggs containing two embryos have been reported from Cuba (Barbour and Ramsden 1919), where one nest contained two twin eggs (100 x 50 mm). The embryos were apparently well formed and healthy. A similar twin egg has been reported by Blohm (1948) for *C. intermedius* in Venezuela.

Egg fertility levels (determined by egg banding) have been reported from nests in south Florida and Haiti. Unbanded eggs could be the result of infertility, or early embryonic failure. In Florida, Kushlan and Mazzotti (1986) reported 90% of 314 eggs examined were banded. The range of values for individual nests was 46-100%, with only one nest having fewer than 84% banded eggs. In Haiti a similar value of 9.9% unbanded eggs was determined from seven clutches (range 70.6-100% banded) (Thorbjarnarson 1984, 1988).

Other than egg fertility rates, nest hatching success is influenced by three environmental factors: flooding, desiccation, and predation. An increase in soil moisture reduces soil oxygen diffusion capacity (Lutz and Dunbar-Cooper 1984), as well as that of the eggshell (Ferguson 1985). Although *C. acutus* nests during the dry season, in areas where nests are located in low-lying areas, flooding may be an important factor in egg mortality. In the Florida Bay region, flooding drowned two of 17 (11.8%) of the nests studied by Kushlan and Mazzotti (1986), and partially destroyed two other nests. Flooding was subterranean and hence was not recognizable unless the nests were excavated. It is perhaps significant that four of nine "hole" nests experienced flooding mortality, whereas none of the eight "mound" nests flooded.

In areas where female *C. acutus* have access to higher, well drained nesting sites, flooding mortality is usually minimal. On Key Largo and at Turkey Point in Florida, females nest in raised spoil banks and the nests experience little or no flooding mortality (P. Moler, pers. comm.). In Etang Saumatre, Haiti, only one of 15 (16.7%) nests examined was lost to flooding and this was due to excessive surface runoff from a nearby arroyo.

Egg desiccation has been reported to cause egg mortality in Florida. Mazzotti (1983), found 27 eggs from four different nests to have air sacs, which according to Ferguson and Joanen (1983) are indicative of excessive egg water loss.

Although predation is usually considered to be the most important factor governing nest success in *C. acutus*, few quantitative estimates of predation rates are available. Kushlan and Mazzotti (1986) reported that during 1971-1982, 14% of 99 clutches in Florida were predated. Raccoons (*Procyon lotor*) were the only nest predators observed. Although Dugan et. al. (1981) reported that nesting iguanas would dig up crocodile eggs, all other reported nest predators are mammals: *Procyon lotor*, *P. cancrivora*, *Nasua narica*, *Dusicyon thous*, *Conepatus* sp., *Canis latrans*, *Mephitis macroura*, and *Spilogale augustifrons* (Alvarez del Toro 1974, Medem 1981, Camacho 1983, Kushlan and Mazzotti 1986). On Hispaniola, an island with a depauperate mammalian fauna (both natural and man induced), few natural nest predators are found and nests are rarely depredated other than by man. A 0% natural predation rate was found among nests in Etang Saumatre (Thorbjarnarson 1984, 1988).

DIET

The diet of *C. acutus* follows the typical ontogenetic shift described for other species of crocodylians (Cott 1961, Chabreck 1971, Taylor 1979, Webb et al. 1982). Hatchlings and juvenile crocodiles feed primarily on aquatic and terrestrial invertebrates (Alvarez del Toro 1974, Medem 1981, Thorbjarnarson 1984, 1988) or small fish (Schmidt 1924, Alvarez del Toro 1974). With increasing size, crocodiles feed increasingly on larger vertebrate prey with fish being the dominant food item (Alvarez del Toro 1974, Medem 1981, Thorbjarnarson 1984, 1988).

Among hatchling and juvenile *C. acutus* the most commonly reported prey are aquatic insects (Dyctisidae, Hydrophilidae, Belastomatidae) and their larvae (Libellulidae), and snails (Alvarez del Toro 1974, Medem 1981). In Etang Saumatre, Haiti (Thorbjarnarson 1984, 1988), the dominant prey items flushed from the stomachs of hatchling crocodiles (less than 0.5 m TL; N = 8) in terms of biomass were fiddler crabs (*Uca bergersii*, 33.5% of prey mass), Hymenoptera (25.0%), and amphipods (25.0%). Among juveniles (0.5-0.9 m TL; N = 28), the principal prey were *Uca* (62.3% by mass), odonate larvae (10.3%), and Coleoptera (8.9%). Other frequently encountered prey were: Arachnida, Lepidoptera, Scolopendera, Hymenoptera, and Gerridae. Only 9.3% of the crocodiles under 0.9 m TL contained fish (N = 64), principally small poeciliids (*Limia* sp., *Gambusia hispaniole*). Other than fish the only vertebrate remains found in juveniles' stomachs were one turtle (*Pseudemys decorata*), and unidentified bird remains.

Alvarez del Toro (1974) reported that in Mexico, subadult crocodiles feed on insects (*Belastoma*, *Disticus*, *Hydrophilus*), fish, frogs, small turtles, birds, and small mammals. Two specific crocodiles mentioned (1.1 m, 1.2 m TL) had catfish (*Mollinesia*), a dove (*Zenaidura macroura*) and a marsupial (*Philander laniger*) in their stomachs. Subadult crocodiles in Etang Saumatre (0.9-1.8 m TL; N = 5) fed principally on aquatic invertebrates including odonate larvae (35.3% by mass), *Uca* (32.6%), and spiders (14.5%), but also took an increasing number of birds (17.7%; Thorbjarnarson 1984, 1988).

Adult crocodiles, while primarily piscivorous, feed on a variety of prey. Schmidt (1924) reported that one 3 m crocodile in Honduras contained a turtle shell, remains of a 1.2- 1.5 m crocodile, and peccary hoofs. Besides two marine catfish, Medem (1981) found fragments of *Pomacea* snails in the stomach of a 3.17 m crocodile in Colombia. Medem (1981) also mentions observing a crocodile eat a turtle (*Podocnemis lewyani*). Alvarez del Toro (1974) comments on the

formerly widespread problem of crocodiles eating domestic livestock in Mexico. Based on a small sample of crocodiles in Etang Saumatre, fish (primarily Cichlidae) and birds were the most common prey items. Adults were also seen to eat turtles and domestic animals (dogs, goats; Thorbjarnarson 1984, 1988).

Observations on feeding behavior in Etang Saumatre indicate that crocodiles use both active and passive modes of foraging. Juvenile crocodiles were frequently seen at night along shallow water shorelines making rapid sideswipes at surface disturbances. This method of foraging probably accounted for the high percentage of non-aquatic invertebrates in their diet. The presence of odonate larvae in crocodile stomachs suggests young crocodiles may also actively forage amongst submerged vegetation and/or bottom sediments (Thorbjarnarson 1984, 1988).

Adult crocodiles in Etang Saumatre were also frequently observed in shallow water areas where concentrations of cichlids (*Cichlasoma hatiensis*, *Tilapia mossambica*) were found. Crocodiles were observed to remain stationary on the bottom, occasionally making sideswipes at passing fish. Crocodiles also concentrated under a heron rookery during the birds nesting period, ostensibly to catch young that fall out of the nest (Thorbjarnarson 1984, 1988). Medem (1981) mentions an unconfirmed fishing technique used by crocodiles in Colombia. Floating at the surface with the mouth partially open, the crocodile regurgitates small quantities of partially digested food. The food attracts fish to the vicinity of the crocodile's mouth where they are caught using rapid sideswipes.

POPULATION ECOLOGY

Population Density, Biomass, and Size-Class Structure - Published values for crocodilian population density rarely reflect true steady-state population levels, but tend rather to indicate the intensity of past or present human exploitation of crocodiles. Furthermore, differences in census methodology, and habitat type frequently make interpopulation comparisons difficult. Nevertheless, density values can be informative, and published figures are tabulated for crocodile populations in southern Florida, Honduras, Venezuela, and Haiti (Table 5).

Density values from Florida are expressed in units of time and so are not directly comparable to the other figures which are calculated on the basis of crocodiles per kilometer of shoreline. Nevertheless, the data for Florida indicate a very low density crocodile population.

The density values for Honduras (0.51/km) and Venezuela (1.57/km) are principally from coastal lagoons and mixed coastal habitats respectively, and represent populations severely depleted by hunting.

The highest reported densities of *C. acutus* come from lacustrine habitats. Schmidt (1924) reported an extremely high crocodile density in Lago Ticamaya, Honduras. Etang Saumatre, in Haiti, had an overall crocodile density of 6.3/km (including all crocodile size-classes), even though the population has been somewhat depleted by hunting and other human-related mortality. Excluding the exposed, rocky shorelines avoided by crocodiles, the ecological density in Etang Saumatre was 9.6/km. The crude and ecological densities for crocodiles over 1.8 m total length were 1.0/km and 1.5/km respectively. Within the lake crocodile density varied between habitats. Among the major habitat subdivisions (with more than 1 km shoreline) mean densities ranged from a high of 14.5/km (*Conocarpus* fringe) to 0.2/km for the rocky, steep shore gradient areas (Thorbjarnarson 1984, 1988).

kg/km. Based on the above mentioned population estimate for Lago Enriquillo, Dominican Republic, crude biomass in this lake was calculated to be 188.4-256.1 kg/km.

The size-class distribution of three *C. acutus* populations have been reported: Florida (Gaby et al. 1985, Mazzotti 1983), eastern Honduras (Klein 1977), and Etang Saumatre, Haiti (Thorbjarnarson 1984, 1988; Table 6). Whereas the values for Florida and Haiti represent data obtained during nocturnal boat surveys, the Honduras figures are from commercially harvested animals and hence may be somewhat biased towards larger individuals, and do not include crocodiles less than one meter total length.

A large percentage of the crocodiles sighted in Everglades National Park (46.9%) were subadults (1.5-2.0 m TL).

Although the size-class limits vary somewhat, a smaller percentage of the population at Turkey Point, Florida (18.7%, 1.21-1.83 m TL, Gaby et al. 1981) and Etang Saumatre (10.7%, 0.9-1.8 m TL, Thorbjarnarson 1984, 1988) were in the subadult size range. In both these two populations, a larger percentage of small crocodiles was found: 56.3% Turkey Point, 74.3% Etang Saumatre (less than 1.21 m and 0.9 m TL respectively).

Among these three crocodile populations the percent composition of adults was similar: Everglades 24.5%, Turkey Point 25.0%, Etang Saumatre 15.7%. As the Etang Saumatre figures include hatchling crocodiles, a comparable figure to the Florida values for percentage of adults would be somewhat higher. Seijas (1986b) estimated that only 35 of 293 (11.9%) of the crocodiles (including hatchlings) seen in Venezuela were adults. An even smaller percentage of adults (3.7%) was noted by Garrick (pers. comm.) from a sample of 268 crocodiles captured in Jamaica.

Sex Ratio - Figures for *C. acutus* population sex ratios are available for Florida, Etang Saumatre, Haiti, and eastern Honduras. Among adult and subadult crocodiles captured in the Everglades National Park, Mazzotti (1983) found a female biased sex ratio of 2.4:1 (N = 17). At the nearby Turkey Point site, a slightly male biased ratio (0.75:1, N = 7) was noted (Gaby et al. 1985). Together these data suggest an overall 2:1 female biased sex ratio (Kushlan and Mazzotti 1986).

In Etang Saumatre, the sex ratio of 28 adult and subadult crocodiles captured was 0.75:1. Including juveniles, the overall sex ratio was still male biased 0.69:1 (N = 54; Thorbjarnarson 1984, 1988) although the difference was not found to be significant (binomial test $Z = 1.22$).

Based on a sample of 32 *C. acutus* commercially harvested in Honduras, Klein (1977) reported 14 females and 18 males (0.78:1). A larger sample of 92 wild captured crocodiles over 1.83 m TL was sexed at the Hacienda El Tumbador crocodile farm in Honduras (King, Thorbjarnarson and Vliet, unpubl. data). The majority of crocodiles in this sample came from the Rio Aguan and were composed of 40.2% males, 59.7% females. Although strongly female biased, this difference was not significantly different.

Growth Rates - Published values of growth rates in *C. acutus* are mostly from the first year or two of life (Table 7) and indicate that during this period animals can grow extremely rapidly. Over the first several months following hatching, growth rates are very high, and in some instances (e.g. Florida) may exceed 0.3 cm TL/day, although the more normal value for this time are in the 0.1-0.2 cm TL/day range (P. Moler, pers. comm.).

In most populations the initial rapid burst of growth slows considerably in older hatchlings and juveniles (Haiti and Panama 0.05-0.10 cm TL/day), but in Florida crocodiles up to 621 days old have been reported with mean growth rates of up to 0.134 cm TL/day (Gaby et al. 1981).

Table 6: Size-class distributions of four *C. acutus* populations. SC=Size class, PP=Percent of population. References in text.

LOCATION							
Florida				Honduras		Haiti	
Everglades NP		Turkey Pt					
SC	PP	SC	PP	SC	PP	SC	PP
						0.3- 0.9	74.3
0.50	6.1						
0.75	12.2	0.60-					
1.00	8.2	1.20	56.3	1.0-			
1.25	2.0			1.5	20.3	0.9-	
1.50	20.4	1.21-				1.8	10.0
1.75	14.3	1.83	18.7	1.5-			
2.00	12.2			2.0	31.3		
2.25	18.4					1.8-	
2.50	2.0	>1.83	25.0	2.0-		2.7	10.7
2.75	4.1			2.5-	26.6		
				2.5-		>2.7	5.0
				3.0	14.1		
				3.0-			
				3.5	6.2		
				>3.5	1.6		
Sample size	49		16		64		447

Table 7: Reported growth rates of free-living juvenile *C. acutus*. Sources: Thorbjarnarson (1988); P. Moler (pers. comm.); Gaby et al. (1981), Mazzotti (1983), Rodda (1984).

Location	Size or Age Class	Mean Growth Rate (cm TL/day)	N
Haiti	0-3 months	0.111-0.135	13
	0.3-0.9 m	0.058	10
	0.9-1.8 m	0.090	2
Florida	0-81 days	0.117-0.214	85
	0-124 days	0.158	9
	0-621 days	0.134	5
	0-17 months	0.112	-
Panama	0-10 months	0.088-0.105	-
	0-22 months	0.052-0.070	-

These latter data, from Turkey Point, may be considered somewhat anomalous in that the crocodiles are inhabiting cooling canals with elevated temperatures. However, comparable growth rates in *C. acutus* have been noted in other parts of Florida (Lang 1975b, P. Moler, pers. comm.). The rapid growth of Florida crocodiles is all the more remarkable as due to low winter temperatures, crocodiles do not grow during 4 months of the year (December-March, P. Moler, pers. comm.).

Growth data from crocodiles more than two years old are scanty. Two crocodiles in the 0.9-1.8 m size class in Etang Saumatre grew at an average rate of 0.09 cm TL/day (Thorbjarnarson 1984, 1988). Garrick (pers. comm.) recaptured a 6 year old crocodile (tagged when 58.7 cm long) that grew at an average rate of 0.05 cm TL/day over the interval. A six year 11 month old crocodile from Key Largo was 2.03 m TL (P. Moler, pers. comm.). This indicates an average growth rate of approximately 0.08 cm TL/day.

Mortality - Mortality in post-hatching *C. acutus* is highest during the first few years of life when the crocodiles are small and vulnerable to a host of predators, or environmental problems (e.g salt balance, low temperature). Quantitative estimates of survivorship of hatchling crocodiles in southern Florida indicate that mortality rates vary considerably from place to place. Gaby et al (1985) noted that at Turkey Point, approximately 11% of captured hatchlings survived at least one year. Ogden (1978) and Lang (1975b) radio tracked a group of 17 hatchlings for periods of up to 6 weeks. Ogden (1978) reported that at least one half of this sample died during the course of the study. On Key Largo, based on recaptures and resightings of marked individuals, hatchling survivorship can be much higher and in some years > 50% of the hatchlings may survive their first year (P. Moler, pers. comm.). Based on recaptures from one cohort, an estimate of minimal survivorship to 4 years is 25%. However, hatchling and juvenile mortality vary considerably from year to year, and these values may represent near maximum survivorship values (P. Moler, pers. comm.).

Potential predators of young crocodiles are numerous and include large wading birds (*Ardea herodias*, *Nycticorax nycticorax*, *Casmerodius albus*), raptors (*Buteo magnirostris*, *Herpetotheres cachinnans*, *Heterocnus mexicanus*) and mammals (*Procyon lotor*, *Felis pardalis*, *F. weidii*, *F. jagourandi*, *Canis latrans*; Alvarez del Toro 1974, Inchaustegui et al. 1980, Medem 1981, Camacho 1983, Thorbjarnarson 1984, 1988). Crabs (*Callinectes* sp., *Cardisoma guanhumi*) have also been observed depredating, or implicated in predation on hatchling crocodiles in Florida (Lang 1975b, Ogden 1978). Several species of predatory fishes have been reported to eat small crocodiles (*Pseudoplatystoma fasciatus* (Medem 1981), *Lepisosteus tropicus* (Camacho 1983)). Mazzotti (1983) mentions lemon sharks (*Negaprion brevirostris*), snook (*Centropomis undecimalis*) and tarpon (*Megalops atlantica*) as potential natural predators of *C. acutus* in Florida coastal waters.

With increasing crocodile size the predators of *C. acutus* diminish rapidly in number. Other than man, large crocodiles have few potential predators. Alvarez del Toro (1974) reports that jaguar (*Panthera onca*) will kill subadult crocodiles and mentions one instance of an adult jaguar killing a 2.5 m *C. acutus*. Medem (1981) states that near Isla Fuerte, Colombia, fatal attacks by white sharks (*Carcharodon carcharias*) on adult crocodiles were not uncommon in the past.

Mortality due to cannibalism in *C. acutus* is not well understood, but apparently occurs under certain circumstances, particularly in high density situations. In the formerly dense *C. acutus* population in Lago Ticamaya, Schmidt (1924) reported finding the remains of a 1.2-1.5 m crocodile in the stomach of a 3 m individual. He also reports a colleague seeing a large crocodile eating a smaller one. Varona (1980) cites Gundlach reporting that large *C. acutus* will eat small ones.

Under certain circumstances mortality of hatchling or small juvenile crocodiles may be directly related to environmental factors. The cool winters in Florida are known to limit growth in small crocodiles, and it is possible that short-term cold spells could cause mortality. Osmoregulatory failure is also important in some areas. In at least one population, Lago Enriqueillo, it is the primary source of hatchling mortality (Inchaustegui et al. 1980, pers. obs.). Ogden (1978) and Mazzotti (1983) also mention hurricanes as potential factors in crocodile mortality in southern Florida.

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