1978 JOURNAL OF HERPETOLOGY 12(2):183-196

Status and Nesting Biology of the American Crocodile, *Crocodylus acutus*, (Reptilia, Crocodilidae) in Florida

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ABSTRACT—This project was designed to determine the status of the American Crocodile in Florida and the factors regulating that population. Estimates of the historical and present range show that the nesting range has been considerably reduced during the 20th Century, including continued reduction in Florida Bay since that region became a part of Everglades National Park in 1950.

Crocodiles in Florida Bay and on Key Largo are mound nesters, utilizing well-drained beaches, creek banks and abandoned canal levees as nesting sites. Females usually maintain primary and secondary mounds that are repeatedly used through many years. Average clutch size is 44; about 48% of the eggs hatch in successful nests, while the annual average number of successful nests is 65%. Most nesting failures are due to raccoon predation or failure of eggs to hatch, the latter probably a temperature problem in certain types of nests.

The total number of crocodiles in south Florida early in the 20th Century may have been between 1,000 and 2,000 animals, but that total has steadily declined to the present. Based on an estimated 20 breeding females per year and an average 275 hatchling crocodiles produced annually, the 1970s population is estimated to be between 100 and 400 animals. Factors that regulate the population, including low nesting success, human disturbance, and hurricanes, are discussed.

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INTRODUCTION

The population of American Crocodiles, *Crocodylus acutus,* resident in Florida was placed on the U.S. Fish and Wildlife Services' Endangered Species List on 25 September 1975 (Federal Reg. 40 (187): 44149). An important part of the data used by the Fish and Wildlife Service to support classifying this population as endangered was provided by the study reported here. This study was conducted between 1968 and 1975, primarily in Florida Bay, Monroe County, Florida, and was designed to measure the size and range, general habitat characteristics and factors regulating nesting success of *C. acutus* in Florida. In the following report, information on the total Florida population is given, although emphasis in some sections is on the crocodiles in Florida Bay where most of this study was conducted and where most remaining crocodiles occur. These data are intended to update and supplement those presented by Moore (1953a).

METHODS

An attempt was made to locate all active crocodile nests in Florida Bay and on the upper Florida Keys by slowly scanning the shore along canals, creeks and shorelines from a small boat. Sites located by this technique that appeared to be acceptable crocodile nesting habitat were searched by foot one or more times. All known nesting sites were regularly checked during breeding seasons, March through August, to determine characteristics of sites and success at each. At some nest sites, additional information was collected, such as number of eggs laid, number that hatched and nest temperatures. Infrared, time-sequence 35 mm cameras were

mounted near some nests to record activity patterns of adult crocodiles related to nesting. My visits to each nest were usually brief, and nests were minimally disturbed so as not to attract nest predators. No attempts were made to discourage predators, however, through use of chemical repellents or physical barriers placed on nests, as we wished to measure the true level of nesting success. Post-hatching survival rates were determined for one group of newly hatched crocodiles that were radio-tracked for varying numbers of days during a six week period in 1973. Additional information on the range and numbers of crocodiles was obtained through interviews with several long-time residents, particularly from commercial and sports fishermen of the region.

RANGE

The present range of crocodiles between Florida Bay, Card Sound and the upper Florida Keys is shown in Fig. 1. This range is derived by plotting locations of active nests and sightings of crocodiles away from known nests, for the years 1970-1975. The crocodile sightings are my own, plus those reported by National Park Service employees Randy Cooley, William Hill, Richard W. Klukas, Ralph E. Miele, William B. Robertson, Jr., and Stanley R. Robins; and by Jeffery W. Lang, University of Minnesota; and by local residents Harry Grigsby and Alan Litman. All nest sites shown are on the Florida Bay mainland or on Key Largo, with the exception of one remaining island site on Black Betsy Key. I assume that most sightings of crocodiles away from these known nests represent nonbreeding animals or animals that have wandered from known nests, rather than animals close to unknown nests. The region west of Big Madeira Bay, and the shore lines of Long Sound, Blackwater and Little Blackwater Sounds and Lake Surprise were particularly searched for nests without success. Some crocodiles at non-nesting sites were adult-size animals that were seen regularly during different times of the year, for example at McCormick and Oyster Creeks on the mainland, Lake Surprise on Key Largo, and Venetian Shore on Plantation Key. The presence of these animals where no nests were located indicates that rather long-distance movements by crocodiles may occur. Long-distance movement by adult crocodiles has previously been reported by Graham (1968).

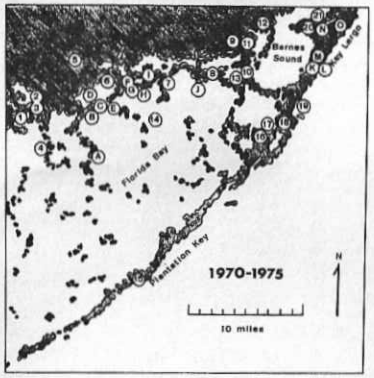

FIGURE 1. Locations of American Crocodile nests (letters) and regular sightings (numbers) in Florida Bay and the upper Florida Keys, 1970-1975. A. Black Betsy Key, B. Madeira Beach, C. Madeira Point, D. Taylor River, E. Fan Palm Hammock, F. Mud Creek, G. Alligator Cove, H. Cocoa Point, I. Davis Creek, J. Snipe Point, K. Central Basin Hills #1, L. Central Basin Hills #2, M. North Basin Hills Canal, N. East of Steamboat Creek, O. Army Radar Station borrow pit (young seen); 1. McCormick Creek, 2. lower Seven Palm Lake, 3. pond east of Terrapin Bay, 4. Samphire Keys, 5. upper Taylor River, 6. East Creek, 7. Trout Cove, 8. Western Long Sound, 9. northeastern Long Sound, 10. Manatee Creek, 11. mainland shore east of Highway One, 12. North Manatee Bay, 13. eastern Little Blackwater Sound, 14. Tern Key, 15. Venetian Shores, Plantation Key, 16. canals east of Dusenbury Creek, Key Largo, 17. Stillwright Point, 18. Sexton Cove, 19. Lake Surprise, 20. Steamboat Creek, 21. Crocodile Lake.

The active nests are located in the only regions of Florida Bay and the upper Keys that have high, well-drained beaches, creek banks or canal levees suitable for nest sites and also remain largely undisturbed by humans. All Florida Bay sites are within Everglades National Park, while northern Key Largo is the only section of that Key that still has large tracts of undeveloped coastline and woodlands. The north shore of Joe Bay, Long Sound and mainland shores of Card and Barnes Sounds, although generally undeveloped, apparently provide suitable crocodile feeding habitat but lack high-ground nesting sites.

All known nests on northern Key Largo are on abandoned borrow-pit banks or canal levees in mangrove swamps. These sites were originally created during the 1920s (pers. comm., many local residents) during early and unsuccessful attempts to develop north Key Largo during the "boom" years preceding the 1929 depression. Crocodiles may not have nested on northern Key Largo as frequently prior to creation of these unnatural soil banks since the natural coastline there is low and swampy, with few beaches or elevated creek banks. Almost all recent sightings of crocodiles on the Key Largo side of Blackwater Sound and at Venetian Shores have also occurred in canals or old water-filled rock pits. Apparently such sites, when partially or wholly surrounded by mangroves or similar vegetation, provide very acceptable crocodile habitat, a fact that illustrates the apparent preference these animals have for protected, deep-water sites. Crocodiles presumably would nest at more of these unnatural sites were it not for the relatively high levels of human activities at most.

The former nesting range of crocodiles in Florida Bay and upper Keys region is shown in Fig. 2. The records used in this figure represent known nest sites between 1930 and 1969. I purposefully exclude earlier reports because information from prior to 1930 is so scanty as to preclude useful range mapping based on nests. There are, however, old, hard to precisely locate, nesting sites described in Willoughby (1913) and Dimock and Dimock (1908) on the shores of Florida Bay or Card Sound, and nesting on Davis Creek prior to 1910 (Moore, 1953b). The data used in Fig. 2 are from Carr (1940), Dickinson (1953), Moore (1953a, 1953b), field reports of Park Service rangers stationed on Key Largo in the 1950s and from interviews or field notes of former N.P.S. ranger Erwin Winte, National Audubon biologist R. P. Allen, former Key Deer Refuge manager Jack Watson, and long-time local fishermen Hubert Johnson, Buck McGray, Luther Roberts, Lawrence Santini, and Haywood Smith.

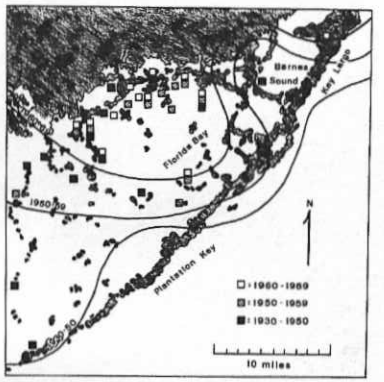

FIGURE 2. Nesting range of the American Crocodile in Florida Bay and the upper Florida Keys, 1930-1969, as indicated by distribution of known nests, showing extent of range reduction.

The major reduction in range shown in Fig. 2 is the gradual disappearance of nesting on islands in Florida Bay, from 7 known sites prior to 1950 to 4 sites in the 1950s, 2 sites in the 1960s, and 1 site in the 1970s, (Fig. 1). This decline has occurred in spite of the fact that Florida Bay became a part of the Everglades National Park in 1950. No such decline is evident on the mainland shore of Florida Bay, where the 11 sites known to be active between 1930 and 1960, or the 9 sites active during the 1960s, are approximately the same as the 9 mainland sites active in the 1970s (Fig. 1). This sort of analysis may underestimate the magnitude of the decline, however, for almost surely there were nesting sites prior to 1960 that were never recorded.

Fig. 2 also shows that crocodile nesting had fairly well disappeared on central Key Largo and adjacent Cross Key to the mainland by 1950. Crocodiles probably nested regularly on northern Key Largo, at least since the 1920s when the borrow pits or canals referred to above made those swamps more suitable for nesting. The scarcity of actual nest observations on northern Key Largo between 1930 and 1970, compared to the number known there in the

1970s, must be because that part of Key Largo has received relatively little attention by people interested in crocodiles.

The east coast of Florida, northward from Biscayne Bay, does not appear to support a viable crocodile population at present. The crocodiles that formerly occurred more commonly in Biscayne Bay were contiguous with crocodiles on northern Key Largo and Card Sound and interchange surely took place. One or more adult sized crocodiles are still seen (1975) on canal banks near Turkey Point on the southwestern mainland shore of Biscayne Bay, but no nesting is known there. A few recent, isolated observations of crocodiles of unknown origin have been reported from further north. A six-foot crocodile was shot by police on Miami Beach in June, 1967, and a large adult was captured at Vero Beach, Indian River County, in January, 1974, and transported to Key Largo.

Historically, crocodiles were known to have nested on the east coast at two locations, Biscayne Bay and vicinity near Miami in Dade and adjacent Broward Counties, and Lake Worth in Palm Beach County. Crocodiles apparently occurred in most creeks and rivers flowing from the mainland into Biscayne Bay, in creeks and swamps north to Hallendale, and on Virginia Key, and were known to nest at "Crocodile hole" near Indian Creek on the Dade County mainland (Smith, 1896:177; Barbour, 1923). Crocodiles were also well known on Lake Worth (C. W. Pierce ms., fide G. L. Voss). Pierce reported that crocodiles were regular on parts of Lake Worth in the 1870s and 1880s, especially in the southern end in the vicinity of Spanish Creek. Young crocodiles were sometimes numerous at Spanish Creek, fairly good evidence that they were produced locally. The last crocodiles in Lake Worth remembered by Voss was one adult killed in the early 1940s near Lantana.

The sometimes cited report of the northernmost crocodile in Florida, an animal killed by Maynard near Lake Harney, Volusia County (in Barbour, 1923), was later withdrawn by Maynard (1929); the animal was actually an alligator. Reports of one or more crocodiles killed near Lake Okeechobee (in Willoughby, 1913, and Maynard, 1929) are too brief to be evaluated.

The status of crocodiles on Florida's west coast is vague at best. Crocodiles, including adults, have been occasionally seen along the southwest coast, from Cape Sable north to Sarasota County (observation files, Everglades National Park; LeBuff, 1957). No crocodile nest has been found on the west coast, however, and only once, to my knowledge, have crocodiles been seen repeatedly at one site. One or more adult-sized crocodiles were seen by several observers during 1973 through 1975 in a backwater region of Rookery Bay, Collier County (J. Allen, pers. comm.). The likely explanation for west coast crocodiles is that they escaped, were released or were storm-displaced animals that may survive long periods in the wild, but that no wild, reproducing population has ever existed.

The role that large hurricanes may have in displacing crocodiles has not been previously considered. Several crocodiles that were killed south of Everglades City, Collier County, late in 1960 by illegal alligator hunters were reportedly the only crocodiles these men had ever seen on the west coast (F. Dayhoff, pers. comm.). During the same fall, several crocodiles, both living and dead, were located in the lower Florida Keys at sites where crocodiles did not normally occur (J. Watson, pers. comm.). These sets of observations happened immediately following the passage of a major hurricane ("Donna") through the crocodile range in Florida Bay in early September, 1960. No other explanation for the appearance of these displaced crocodiles seems reasonable, except that these animals were either moved by the storm or moved because of it.

The occurrence of crocodiles in the lower Florida Keys (below Marathon and the Seven-Mile Bridge) is almost unrecorded historically, although apparently they have long been there. The only historical evidence known to me of crocodiles in the lower Keys is a photograph in Neill (1971:332) showing a crocodile on a beach, reportedly taken at Key West in 1935.

During the late 1960s and 1970s small numbers of crocodiles were regularly reported in the lower Keys in the vicinity of the Key Deer and Great White Heron National Wildlife Refuges. Sightings came primarily from Big Pine, Little Pine, Howe, Johnson and upper Sugarloaf Keys, with one or more crocodile nests found on Little Pine in 1971 (J. Watson, pers. comm.). This population of crocodiles apparently is disjunct by about 50 miles from the nearest Florida Bay-upper Keys crocodiles, although the two populations were once closer (Fig. 2), and may have had regular interchange of animals at one time.

NESTING BIOLOGY AND PRODUCTIVITY

Crocodile nesting sites (N = 19; including some now abandoned) that I examined were located in a variety of substrates and vegetation, and differed widely in their conspicuousness as viewed from the water. There was uniformity, however, in that each was in relatively well-drained soil and was adjacent to water deep enough for an adult crocodile to approach by a water route. Nests in Florida Bay were located (1) in open thickets of hardwood trees along the edges of 4 to 8 m wide, deep-water creeks with vertical, .5 to 1.0 m marl or muck banks, (b) surrounded by varying amounts of hardwood shrubs and trees at the heads of narrow, shell-sand beaches, or (c) in thickets of shrubby Black Mangroves (*Avicennia nitida*) behind marl banks rising 15 to 30 cm above water. These nests were constructed of the local soils and/or sands, usually mangrove or hardwood peats, marl and/or sand. Several nests on northern Key Largo were located on levees of abandoned canals or excavation pits in Red Mangrove (*Rhizophora mangle*)-Black Mangrove swamps, and these nests were composed of mangrove peat and/or marl soils. Nests on some canal levees and beaches were conspicuously open to view, while some nests in hardwood thickets at the heads of beaches or in mangroves were well hidden at distances as close as 4 m.

Crocodiles were seen at certain nest sites on the keys and on exposed points of land or beaches on the mainland of Florida Bay only when these nests contained eggs. As a generalization it appears that these sites were only seasonally favorable to crocodiles because they provided high ground for nests but lacked shelter and protection from rough water and perhaps were less favorable feeding sites than other regions of the Bay. Following hatching the adults and hatchlings disappeared within 3-7 days from these sites and presumably moved to more protected waters in creeks or ponds on the mainland or the interior of larger keys. Cott (1961:218) and Graham (1968:25) reported a similar avoidance of unprotected, rough water by *C. niloticus*. At more protected Florida Bay nesting sites, for example, along narrow creeks on the mainland, signs indicated that crocodiles occurred throughout each year.

Greer (1970, 1971) and Campbell (1972) discussed possible correlations between nest types (hole nests vs. mound nests) with either crocodilian phylogony or location of nests. In the latter case, it was suggested that mound nests are characteristic of species or populations that nest in marshy sites, while hole nests occur where a species nests on banks or beaches. Crocodiles in southern Florida construct both types of nests, without correlation between nest

TABLE 1. Sizes[1] of *Crocodylus acutus* primary nests in Florida.

Location	Substrate	1970	1971	1972	1973
Davis Creek	soil			1.0 m X 15 cm	1.2 m X 25 cm
Mud Creek	soil			3.0 m X 32 cm	
Cocoa Point	sand	1.0 m X 0 cm			
Alligator Cove	sand			3.7 m X 55 cm	
Taylor River	soil			1.2 m X 20 cm	
Madeira Point	sand			4.6 m X 65 cm	
Madeira Beach	sand		2.4 m X 9 cm		3.6 m X 47 cm
Black Betsy South	sand			1.9 m X 25 cm	
Black Betsy North	sand				2.2 m X 20 cm
North Basin Hills	soil			3.0 m X 45 cm	
Central Basin Hills #1	soil			4.2 m X 30 cm	
Central Basin Hills # 2	soil				1.2 m X 20 cm

[1]Measurements are longest diameter and height at center, expressed in meters and centimeter respectively.

type and location or soil type (Table 1). Some females deposit eggs in holes that subsequently are covered over level with the surrounding substrate, but most lay in varying sizes of mounds.

Although there are exceptions for every statement made about crocodile nests in Florida, my impression is that new nests are usually hole or small mound nests, and that these nests develop mounds of increasing size with consecutive years of use. Exceptions to this general statement include a crocodile on Madeira Beach that constructed a typical hole nest for two consecutive years, then abruptly (same female?) constructed a mound 3.6 m in diameter and 55 cm high on the same spot the third year. A new nest on western Madeira Beach in 1974 was a moderate sized mound 2.1 m by 30 cm in its first year. There probably is no correlation between size of a female and size of a nest mound, except where a female used the same mound for many years and both increase in size through the years. A large, 3.5 m female at Cocoa Point laid 52 eggs in a hole nest in 1970 at a spot where there had been no nest in previous years.

I assumed that adult crocodiles that made repeated visits to active nests were breeding females and was able to estimate the length of eight that were well seen. These eight were estimated at 3.9 m (Madeira Pt.), 3.5 m (Cocoa Pt.), 3.1 m (Black Betsy), 2.8 m (2 sites: Alligator Cove and Mud Creek), and 2.5 m (3 sites: Madeira Beach, Taylor River and Davis Creek).

Individual female crocodiles apparently return for several consecutive years, and perhaps many years to nest at a site. During the years 1970-1974, 7 out of 10 nest sites in Florida Bay were used each year (Table 2). The nest at Taylor Slough was first active in 1972, apparently the work of a young female that was a new breeder that year. The remaining two sites (Fan Palm Hammock and Cocoa Point) were abandoned during the study for unknown reasons. A crocodile continued to return each spring and do some digging or scraping on the Cocoa Point nests but laid no eggs. This particular female was one of the larger I saw, and it seems possible that she had become senescent. Graham (1968:59) showed that senescence probably does occur in older females of *C. niloticus,* in his study at Lake Rudolf.

Each nest site contains one primary nest that receives eggs for several consecutive years and one or more secondary nests that may occasionally receive eggs. The secondary nests are scattered within 35 m of the primary nests, but on Black Betsy Key one secondary nest was 500 m from the primary nest. Primary and secondary nests are often interconnected by trails. The maximum number of secondary nests at a site was five at Cocoa Point. At some sites the primary nest is a mound, reflecting its repeated use, and secondary nests resemble hole nests. New secondary nests are occasionally created during the spring digging period and once dug may or may not receive eggs that first year. After a period of years a female may shift primary nests by making one of the secondary nests into the new primary nest.

Nest sites are generally not visited by crocodiles during fall and winter months. An adult (presumably female) may make occasional, nocturnal visits to each site beginning in March and usually does some shallow digging or scratching on one or more nests. The frequency of nest visits increases through April with increased digging at primary nests and occasional digging at some or all secondary nests. During these weeks each nightly visit tends to be brief, less than one hour, and digging is primarily on the nest surface or only a few inches deep. This prolonged period of digging and re-digging serves to gradually convert nests that hardened through the winter into mounds of loose, porous soil. Egg laying is preceded by several nights of greatly increased digging at primary mounds and prolonged visitation to nesting sites. During this peak in activity, some females come ashore several times each night at different spots within 100 m of the nest and wander parallel to the water's edge.

Most nests receive eggs between 25 April and 5 May, while most eggs hatch between 25 July and 10 August. The earliest and latest hatching dates were 19 July 1970 at Madeira Point and 15 August 1974 at Taylor River. Eggs were all laid in a single nest at each site, except 1971 at Alligator Cove and 1975 at Taylor River where clutches were split between primary and secondary nests that were 8 and 4 m apart, respectively. Each clutch of eggs was apparently laid on a single night at most sites, but three nests contained two groups of eggs separated by

TABLE 2. History of Florida Bay (1-10) and Key Largo (11-14) crocodile nests, 1970-1974.

Site	Nest Composition	1970	1971	1972	1973	1974
1. Snipe Point	sand	Active not checked	Unsuccessful raccoons	Successful	Unsuccessful raccoons	Worked, no eggs
2. Davis Creek	soil	Successful	Unsuccessful embry. mort.	Unsuccessful embry. mort.	Successful	Successful
3. Cocoa Point	sand	Successful	Worked, no eggs	Worked, no eggs	Worked, no eggs	Inactive
4. Alligator Cove	sand	Successful	Unsuccessful raccoons	Successful	Successful	Unsuccessful raccoons
5. Mud Creek	soil	Successful	Unsuccessful human dist.	Unsuccessful embry. mort.	Successful	Worked, no eggs
6. Fan Palm Hammock	sand	Inactive	Successful	Worked no eggs	Inactive	Inactive
7. Taylor River	soil	No nest	No nest	Successful	Worked, no eggs	Successful
8. Madeira Point	sand	Successful	Unsuccessful raccoons	Successful	Successful	Successful
9. Madeira Beach	sand	Active not checked	Unsuccessful raccoons	Successful	Unsuccessful human dist.	Successful
10. Black Betsy Key	sand	Active not checked	Successful	Successful	Successful	Unsuccessful embry. Mort.
11. E. of Steamboat Creek	soil	Successful	Successful	Inactive human dist.	Inactive	Inactive
12. North Basin Hills Canal	soil	Not checked	Not checked	Successful	Destroyed, land develop.	Inactive
13. Central Basin Hills #1	soil	Not checked	Not checked	Unsuccessful embry, mort.	Successful	Not checked
14. Central Basin Hills #2	soil	Not checked	Not checked	Not checked	Unsuccessful embry. mort.	Not checked
Totals		6 successful 0 unsuccessful	3 successful 6 unsuccessful	7 successful 3 unsuccessful	6 successful 3 unsuccessful	4 successful 2 unsuccessful

TABLE 3. Clutch size, and number of eggs that hatched at some sites.

Location	Clutch size (number hatched)				
	1970	1971	1972	1973	1974
Davis Creek	44	41	29		
Mud Creek		41	81	55 (7)	
Cocoa Point	52				
Alligator Cove	28 (11)	56	73		
Taylor River			25 (7)		
Madeira Point	40 (25)		78 (40+)	45	
Madeira Beach					
Black Betsy			44 (35)	44 (20)	46
E. of Steamboat	19 (16)				
Central Basin Hills #1			41		
North Basin Hills			22		

several inches of soil. These nests, plus the above mentioned Alligator Cove and Taylor River nestings, may indicate eggs laid on more than a single night or by more than one female. Clutches ranged between 19 and 81 eggs, based on examination of 20 nests, with a mean clutch of 44 (Table 3). It is logical to suspect that the three large clutches were each produced by more than one female. The 78 eggs at Madeira Point in 1972 were separated into two groups in the nest, as if two females were involved, but the large clutches at Mud Creek and Alligator Cove were both contained within single cavities in these two nests. It is also interesting that all three large clutches occurred during the same year, 1972.

Forty nesting attempts resulted in 26 successful and 14 unsuccessful nests (Table 2). A nest was considered successful if signs at the site indicated that one or more young hatched from the nest, while unsuccessful nests were those that received eggs and produced no young. Regularly used sites that did not receive eggs some years (example: Mud Creek and Snipe Point in 1974) were not considered unsuccessful those years. Chabreck (1966) has shown that mature female American Alligators do not necessarily lay every year and presumably this could be true of crocodiles as well.

It was not possible to examine a hatched nest and determine the number of young produced since counts of egg shells and unhatched eggs remaining in a nest rarely equaled the number of eggs known to originally have been in the same nest. Presumably the activities of the females carrying eggs from the nests account for some of the missing eggs or shells (Ogden and Singletary, 1973). We did determine the approximate number of eggs that hatched in eight successful nests, however, by repeatedly examining the eggs in each nest during a 7 to 10 day period immediately prior to the hatch. We assumed eggs were viable and likely to hatch if they were swollen and showed numerous horizontal cracks in the brittle, outer shell, and/or showed some movement, or sound could be detected inside the egg. An egg was considered "bad" if the egg was obviously rotten, seemed to contain only liquid (sloshed), and/or was not swollen or laterally cracked. Our criteria for assigning eggs into viable or "bad" categories were determined by opening a limited number of eggs, and through frequent examination of eggs during the hatching period. Table 3 shows that in these eight nests, approximately 48 percent of the eggs hatched (161 of 333). The three of these nests constructed of soil produced 30 young from 99 eggs (30 percent), while 131 of 234 eggs hatched in five sand nests (56 percent).

Seventeen soil nests produced 11 successful hatches (64 percent) while 23 sand nests produced 15 successful hatches (65 percent). Failure in the two groups, however, occurred for different reasons. Five of six unsuccessful soil nests experienced embryonic mortality in all eggs. Six of eight unsuccessful sand nests (all in Florida Bay) failed due to raccoon predation. No dirt nest suffered predation and only one sand nest failed due to total embryonic mortality. Total embryonic mortality in a Florida Bay crocodile nest was previously reported by Moore (1953a).

A possible explanation for why total embryonic mortality is more frequent in soil nests may be temperature differences between soil and sand nests. In 1973, sand nests averaged slightly warmer than soil nests, as recorded by a telemeter probe at about 25 cm depth in five sand and four soil nests. Average early May temperatures in soil nests was 27.5°C (range 26.5 to 29.5), and in sand nests 27.8°C (27.0 to 29.0). Average late July temperature in soil nests was 29.7° (29.0 to 30.4) and in sand nests 31.4° (30.0 to 33.0). Little is known of temperature requirements for successful incubation in crocodilians, although Bustard (1971) found that eggs of *C. novaeguinae* did not hatch at 26°C and did hatch well at 32°C. Somewhere between these two measurements there must be a threshold for success, which could be close to temperatures recorded in south Florida nests. Soil nests are cooler than sand nests possibly because as a group soil nests are more shaded. Although I did not quantify shade differences at nests, soil sites generally supported larger and more lush vegetation than did sand sites. I detected no other difference between soil and sand nests that might explain the different embryonic mortality rates. Eggs in both types of nests were laid at similar depths, and were similarly located in cavities in the tests with air spaces between eggs. I took no measure of moisture in nests.

The higher predation rate on sand nests than on soil nests may be due to differences in compactness of nests. Soil nests become much harder and more compact than sand nests after female crocodile complete nest digging. By mid-summer, soil nests are "brick-hard" while sand nests remain porous. Raccoons dug or scraped the surface of nearly all nests, but only penetrated the eight to ten inches to eggs in some sand nests.

Mortality among juvenile crocodiles during the first weeks following hatching may be quite high. Seventeen juvenile crocodiles were radio-tracked for up to six weeks following hatching by Jeffery W. Lang and me in 1973. Of that total, three were eaten by raccoons, one died in a crab hole, five transmitters were recovered minus the crocodiles, and eight disappeared (predation, left study area, or transmitter failure). Transmitters were recovered from three juveniles that were certainly eaten by raccoons, indicating that raccoons were capable of removing them. The other five recovered transmitters likely also resulted from raccoon predation. The transmitters were attached with elastic harnesses and could not have easily pulled off or been removed by any other potential predator in the region. Similar sized captive crocodiles with transmitters appeared to function without stress and operated without losing their equipment. It seems, therefore, safe to assume that one-half or more of these transmittered animals died or were killed during the six week tracking period.

PRESENT AND HISTORIC NUMBERS

Two approaches are used to estimate the present numbers of crocodiles in the Florida Bay-upper Keys region. One technique is based on the number of breeding females in this region. We located 14 nesting sites in Florida Bay and on the upper Keys that were used at least once between 1970 and 1974 (Fig. 1). Although some nesting sites surely were overlooked, our searches were intensive enough so that I doubt that there are over 20 breeding females in this region. Chabreck's (1966) study of the American Alligator in coastal Louisiana, and my calculations from Graham's (1968:117) hypothetical life table for adult female *Crocodylus niloticus,* reveals that adult females of these species made up approximately 4 to 5 percent of the total animals in these two studied populations. If the same is true for crocodiles in Florida, then there are between 280 and 350 in the Florida Bay-upper Keys region. If we assume 20 breeding females, then the total becomes 400 to 500 crocodiles.

The present number of crocodiles may also be estimated from annual production and mortality rates, again assuming 20 females. The problem here is that while some calculations on production can be made, almost nothing is known of mortality rates. Using the figures for nesting and hatching rates presented earlier in this paper, annual production is calculated as follows. Assuming 65 percent of a total 20 nests are successful (13 of 20), and each successful nest hatches 48 percent of an average 44 egg clutch (.48 X 572), then 275 young are hatched each year. Natural juvenile mortality of 50 percent during the first few weeks following hatching, as was suggested by the radio-tracking of juveniles reported above, leaves about 137 alive by mid-September. Although mortality rates surely decline as a successively higher percentage of survivors include the most vigorous animals, the number of juveniles alive by the

following summer (age 1) reasonably might be in the range of 10 to 25 percent of the hatch. I'll also assume relatively low annual mortality rates for subadult crocodiles after the first year (20 to 40 percent), that local crocodiles reach maturity at about 13 years (reported for captive *C. acutus,* LeBuff, 1957; also reasonably consistent with *C. niloticus, C. siamensis* and *C. porosus,* Graham, 1968; Yangprapakorn, et al., 1971), and that there are equal numbers of adult males and females (true for *C. niloticus,* Graham, 1968). Admittedly, calculations derived from manipulations of these figures are rough, but if anywhere near accurate, they suggest the Florida Bay-upper Keys crocodile population, excluding newly hatched juveniles, numbers between 100 and 400.

The only other extant population of crocodiles in Florida (presumably viable) is in the lower Florida Keys. This region has not been systematically searched for crocodiles, although Jack Watson, long familiar with the region, reported nesting at perhaps two sites on Little Pine Key (pers. comm., 1973). The present crocodile population in the Lower Keys, therefore, may be 50 or fewer animals.

There are no estimates of the size of the southern Florida crocodile population prior to extensive human settlement of the region. Some early naturalists and biologists, however, did write enough about their crocodile observations to provide an impression of the numbers of crocodiles between Florida Bay and Biscayne Bay in the years 1889 to 1906 (Dimock, 1918; Dimock and Dimock, 1908; Hornaday, 1904; Smith, 1896; Willoughby, 1913). These authors indicated that crocodiles occurred regularly in small numbers along the mainland coast between central Florida Bay and northern Biscayne Bay. Dimock (1918) thought crocodiles were most common in a region along the coast 10 miles long and 3 miles wide lying west from Card Sound. Although these early observers found crocodiles more easily than is now possible, the impression I get from their accounts is that they saw only a few crocs per day (< 10) while exploring prime habitats.

Much less is known of the historical numbers of crocodiles north of Biscayne Bay to Lake Worth, or south of Florida Bay to Key West. I infer from this scarcity of crocodile reports from these two regions that they were much fewer in numbers and/or much more local in distribution. The present very low numbers of crocodiles in protected areas of the Key Deer National Wildlife Refuge compared to the higher numbers in Florida Bay might be used as circumstantial evidence that crocs have always been relatively scarce in the lower Keys. The only east coast site north of Biscayne Bay with a fairly well documented crocodile history is Lake Worth, where, as mentioned in the previous section, several animals were captured (Neill, 1971) and nesting was reported (Voss, per. comm.).

Based on the evidence cited above, I suspect the number of crocodiles in south Florida at the end of the 19th Century was not more than five times the present population, probably between, 1,000 and 2,000 animals. Some settlement of Biscayne Bay had occurred by the 1870s (Pierce, 1970) and along northeastern Florida Bay by the 1890s (Tebeau, 1963), thus the above estimate probably represents a population already depressed by shooting and habitat loss. Smith (1896) mentioned rather extensive alligator hunting by Seminole Indians on the mainland behind Biscayne Bay; presumably the Indians did not spare crocodiles. Dimock and Dimock (1908:298) reported that all crocodile "caves" they examined showed signs of earlier attempts to capture occupants, a fact verified by Hornaday's (1904) description of crocodile capture techniques.

RECENT HUMAN-RELATED MORTALITY

Any evaluation of the dynamics of the present crocodile population must include consideration of human-related mortality. Crocodiles that have been killed by humans in the Florida Bay-upper Keys region since our study began in 1970 are listed in Table 4. This list reports only those animals killed that I learned about through regular communication with local residents and National Park Service rangers and is not the result of any systematic survey of crocodile mortality on my part. The list, therefore, almost surely is incomplete. Included in the

TABLE 4. Human-related crocodile mortality in south Florida, 1971-1976.

Date	Size	Location	Probable cause of death
Summer 1971	about 3 m	Northern Key Largo	Shot
September 1971	about 2.7 m	Sexton Cove, Key Largo	Shot
September 1971	2.5 m	Lake Surprise, Key Largo	Hit by car on road
July 1972	about 2.1 m	Lake Surprise, Key Largo	Floating dead, next to highway
April 1974	45 cm	Northern Key Largo	Hit by car on road
June 1974	about 2.5 m	Blackwater Sound, Key Largo	Floating dead in canal
Summer 1974	about 3 m	Basin Hills	Shot as trophy
February 1975	about 3.7 m	Northern Key Largo	Shot
March 1975	1.2 m	Northern Key Largo	Hit by car on road
July 1975	1.0 m	Card Sound mainland	Hit by car on road
Spring 1976	1.0 m	Northern Key Largo	Shot and head removed

list are six from northern Key Largo-Basin Hills where crocodile nesting is known, and four from the Lake Suprise-Blackwater Sound region of Key Largo where no recent nesting is known. If some crocodiles wander great distances, then some of those killed in the latter region may have come from the northern Florida Bay nesting sites.

The level of human-related mortality to adult crocodiles conceivably could approximate or exceed recruitment of adults into the breeding segment of this population. I suggest that this may be true, considering the small size of this population, its modiocre reproductive success, the probable high mortality rate of juveniles, and the fact that I saw little evidence that new adults are regularly entering the breeding pool in Florida Bay. This is speculation on my part, however, as real data on rate of adult recruitment versus adult mortality, including human-related mortality, in this species are unavailable.

DISCUSSION

Graham (1968:117) speculates that density-dependent factors may regulate population dynamics in *C. niloticus* on Lake Rudolf, specifically the survival rates of juveniles. No such density-dependent factors are likely to be operating on *acutus* in south Florida, where the population is well below early historical numbers and is showing no sign of recovering where protected. I suspect that three density-independent factors are actually at work regulating *acutus* in Florida, direct and indirect human disturbance, relative poor nesting success, and the occasional severe effects of tropical storms.

The activities of people must be the most important regulating factor. The disappearance of crocodiles on the southeastern Florida coast, and the loss of nesting on Cross Key and most of the upper Florida Keys has been directly due to shooting, frequent disturbance to animals, and habitat loss. Shooting and disturbance to animals have overall been most important in reducing the population and driving animals from nesting sites, as a fair amount of apparently suitable habitat remains on the upper Florida Keys that is now unoccupied by crocodiles. Habitat loss has been widespread on the east coast, however, and is occurring steadily on the Florida Keys. An active nest site on north Key Largo in 1972 was covered over by a newly constructed road by 1973.

Less certain, but probably the most logical explanation, the loss of crocodile nesting in southern and central Florida Bay, within Everglades National Park, is also due to human activities on the adjacent upper Florida Keys. For this to be true, I assume that most nesting sites in the Bay are not close to habitats suitable for year-round use by groups of different age-class crocodiles. Nesting sites on Bay keys generally lack quiet, deep water pools, and perhaps are less favorable feeding grounds. Crocodiles apparently moved after nesting from these unprotected nesting sites to larger keys where habitats were more favorable. Many of these animals that once nested in the central and southeastern Bay probably moved seasonally to Key Largo and Plantation Key where they were susceptible to shooting and where habitat

they required has been destroyed. Thus this segment of the population may have been lost due to what happened away from their nesting grounds. The crocodiles that nest on the north shore of Florida Bay appear to be in more favorable habitat, and if these animals wander I suspect it's not because they are forced to do so because of habitat limitations.

Florida Bay may also be less suitable for year-round activity by crocodiles because of salinity changes. T. W. Schmidt (pers. comm.), biologist at Everglades National Park, recently reported a general increase in average maximum salinities in the eastern and central Bay during recent decades. This rise in salinity has presumably been due to reduced flow of freshwater into the Bay because of drainage and channelization of surface water flow on the mainland. Schmidt's studies revealed maximum prolonged salinities of between 50 and 55 parts per thousand occurred in central and southeastern Florida Bay during winter and spring dry seasons between 1973 and 1976. Dunson (1970) reported that small crocodiles can tolerate "short periods" of exposure to seawater (35 ppt), but implied that they do not do well in seawater during long periods. Large crocodiles maintain "viability" for longer periods in seawater presumably because their large size minimizes surface area relative to volume of the animals. It is possible, therefore, that the disappearance of crocodiles in much of Florida Bay came about at least in part because of increased mortality rates among salt-stressed juveniles.

The north Florida Bay crocodiles are fairly secure on their nesting grounds, having been protected since 1950 by the National Park Service. Why the number of crocodiles there has not increased, however, is a puzzle. Most other large vertebrates in the Bay have increased in numbers since this region received protection, including Great White Herons, *Ardea herodias occidentalis,* Roseate Spoonbills, *Ajaia ajaja,* Bald Eagles, *Haliaeetus leucocephalus,* and Ospreys, *Pandion halieatus* (Ogden, pers. obs.; W. B. Robertson, pers. comm.). The low reproductive rate of crocodiles means that any recovery will be slow, but the fact that no recovery is evident after 25 years must indicate that some unnatural limiting factor is at work. Rising salinities in the Bay, if that is part of the problem, may be having an adverse effect here also, although the northern Bay is closer to the source of freshwater flow off the mainland and maintains lower average salinities than to the south. The only other suggestion I can make is that crocodiles being killed on and adjacent to Key Largo include animals that wander from the north shore, and that enough of these are killed to balance recruitment of young adults into the population. The nearest and furthest distances from north Florida Bay to central Key Largo are 9 and 14 miles respectively. Evidence does exist to show that some species of crocodilians do wander that far, and that such wandering is intrinsic to at least some age-classes. Graham (1969:28) reported that *C. niloticus* probably routinely moved up to 9 miles on Lake Rudolf, while Joanen and McNeese (1972) recorded the longest movement by a radio-tracked male alligator as 33 miles from the initial capture site. Chabreck (1965) found that subadult alligators 3 to 5 years old were the age-classes most likely to wander, with individuals moving from three-fourths of a mile to 10 miles during a period of 3 to 4 years after initial capture. These data, along with our observations of crocodiles at sites on the Florida Keys where no nesting is known, suggest strongly that *acutus* does wander, and that crocodiles killed on the upper Keys could include animals from the north shore of Florida Bay.

A second regulating factor for *C. acutus* in Florida appears to be their mediocre nesting success, primarily due to failure of eggs to hatch rather than excessive predation. With 65 percent of nests producing a hatch, and a 48 percent hatching rate by eggs in successful nests, Florida crocodiles have poorer productivity than in other species that have been similarly measured. Joanen (1969) found that 75.6 percent (combining his successful and partially infertile cagegories) of American Alligator nests in coastal Louisiana produced some young and that 58.2 percent of the eggs in successful nests hatched. I examined alligator nests in the everglades region of Everglades National Park in 1971 and 1972 and found that 73 percent (19 of 26) produced a hatch, and that 60.1 percent of the eggs in 9 of the successful nests (175 out of 291) hatched. Graham (1968) used data produced by Modha (1967a) for *C. niloticus* at Central Island, Lake Rudolf (no mammalian predators) to show a hatch by 82.9 percent of the nests and 82.8 percent of eggs in successful nests.

I have suggested that relatively low nest temperatures may be part of the reason why so few eggs hatch in Florida, especially in shaded, soil nests. Bustard (1971) has already been cited for his study showing ideal hatching by *C. novaeglinaea* eggs at 32°C. Successful artificial incubation for crocodile eggs has also been reported by Pooley (1971) at between 28°C and 34°C, by Honegger (1971) at 29° to 31°C, and by Yangprapakorn, et al. (1971) at approximately 35° to 36°C. Modha (1967b) found temperatures at 25-30 cm depths in 26 natural nests of *C. niloticus* to average 32.5°C, and range between 28° and 34.5°C. These various temperature measurements overlap those recorded in Florida, but generally average higher.

Nest predation seems to be less important as a factor regulating Florida *acutus,* at least the 17 percent (6 of 34) rate of predation in Florida Bay (Table 2) is no greater than reported elsewhere. Joanen (1969) reported 44 of 266 (16.5 percent) alligator nests destroyed by predators in Louisiana. Among sparsely dispersed nests of *C. niloticus* predation seldom exceeded 20 percent, but was at least 34 percent at one site where nests were more numerous (Pooley, 1969).

The adverse effects that severe tropical storms have on Florida crocodiles have not been measured, but reports of displaced crocodiles after a 1960 hurricane, described above, suggest that an occasional major storm may significantly reduce total numbers. Considering the slow potential recovery rate of crocodiles, the occurrence of major hurricanes in the Florida Keys at regular intervals may be a factor that serves to hold the local crocodile population at some depressed level. There have been 10 major hurricanes that crossed the Florida Keys or Florida Bay in the 20th Century, in October, 1906; October, 1909; September, 1929; September, 1935; September, 1945; September, 1948; October, 1948. September, 1960; September, 1965; and October, 1966. A major storm is defined as one with 125 mph winds over an area with 100 miles diameter and tides of nine feet or higher (Anon., 1974). These storms, coming as they do shortly after the hatching period for young crocodiles, and sometimes with two or more storms at close intervals such as in the 1940s and 1960s, must adversely affect the local crocodile population.

ACKNOWLEDGMENTS

This study was supported by the U.S. National Park Service and the National Audubon Society. I was assisted in the field by Stanley R. Robins, Randy Cooley and Fred Dayhoff of the National Park Service, and by Caulion Singletary of Homestead, Florida. I especially benefited from discussion or time in the field with Richard W. Klukas, who helped organize the project; Jeffery W. Lang, who radio-tracked crocodiles in Florida Bay in 1973; and Alan L. Litman, who maintains close watch on crocodiles on northern Key Largo. Lynda Gibson and Lorraine Dilling of National Audubon assisted in the preparation of the manuscript.

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Accepted 16 Mar. 1977