

The American Crocodile in Florida Bay

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ABSTRACT: The American crocodile was declared endangered in the United States in 1975. At that time 75% of the remaining crocodile nests were in Everglades National Park, in Florida Bay. In 1980, the National Park Service established a crocodile sanctuary in northeastern Florida Bay to protect nesting and nursery habitat. In 1985, a monitoring program, focused on nesting, growth, and survival, was established to evaluate the effects of modified water deliveries on crocodiles in Florida Bay. The number and range of crocodile nests increased between 1970 and 1995, but nesting success decreased slightly. Nests on artificial substrates in the Greater Flamingo-Cape Sable area accounted for most of the increase in nests. Nests on artificial substrates were more prone to predation by raccoons. At least 1.5% of marked hatchlings survived for more than 12 mo, and growth rates were variable. Detailed information on growth and survival of crocodiles is still lacking. It is no longer a question of whether crocodiles will survive in Florida Bay, but how ecosystem restoration and management can be applied to improve conditions for crocodiles.

Introduction

The American crocodile (*Crocodylus acutus*) is primarily a coastal crocodilian that occurs in parts of Mexico, Central and South America, the Caribbean, and, at the northern end of its range, in southern Florida. As with other species of crocodilians, killing (for hides, meat, collections, and out of fear) and habitat loss have made the American crocodile endangered throughout its range. In Florida, habitat loss, due to development required to support a rapidly growing human population along coastal areas of Palm Beach, Broward, Dade, and Monroe counties has been the primary malefactor in endangering the United States crocodile population. This loss of habitat principally affected the nesting range of crocodiles, restricting nesting to a small area of northeastern Florida Bay and northern Key Largo by the early 1970s (Ogden 1978; Kushlan and Mazzotti 1989a). At that time most of the remaining crocodiles (about 75% of known nests) were in Florida Bay in Everglades National Park. Hence, when the American crocodile was declared endangered in 1975 in the United States (Federal Register 40: 44149), crocodiles in Florida Bay assumed a position of importance in conservation efforts for this endangered species. Adequate data were not available for making informed management decisions. Available field and laboratory data suggested that low nest success, combined with high hatchling mortality, provided a dim prognosis for survival

(Dunson 1970; Evans and Ellis 1977; Ogden 1978). Results of an intensive 5-yr study (1977 to 1981) conducted by the National Park Service resulted in a more optimistic outlook for crocodiles in Everglades National Park (Mazzotti 1983). At the conclusion of that study, the National Park Service established a crocodile sanctuary in northeastern Florida Bay in 1980 (Fig. 1; Federal Register 45: 10350-10355). Since then Florida Bay has undergone a number of changes which have caused a great deal of concern for the ecological health of this ecosystem. Efforts have been, and continue to be, made to improve Florida Bay (United States Army Corps of Engineers 1993, 1994). Crocodile monitoring has continued with the dual objectives of assessing the status of the population and evaluating ecosystem restoration efforts.

An endangered species monitoring program in Florida Bay should investigate population parameters that reflect the long-term status of the population and the parameters likely to be affected by alternatives proposed for ecosystem restoration, such as plans for hydrological restoration. Hydrological conditions that will be affected by restoration alternatives include water levels and salinities. For crocodiles, population parameters most representative of changes in population status and in hydrological conditions are distribution, abundance, growth, survival, and nesting effort and success. For economy, monitoring focused on nesting, growth, and survival. This paper reports the results of monitoring conducted between 1985 and 1997 and discusses the relationship between crocodile

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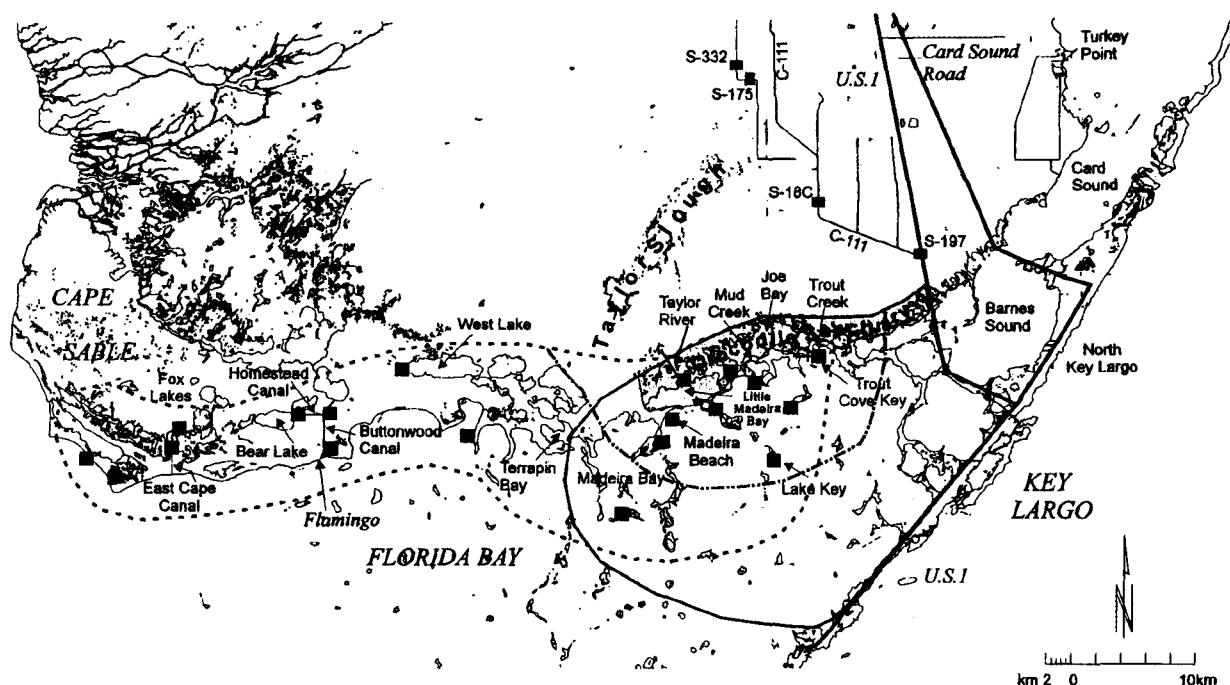


Fig. 1. Crocodile habitat in Florida Bay. Solid line represents the historical nesting area. The dashed and dotted line is the 1970 nesting range retraction into northeastern Florida Bay. Dashed line is the current nesting range. Solid squares are current nest sites.

conservation and ecology and ecosystem restoration and management.

Methods

Crocodile nesting effort (number of nests laid) and success (number of nests that produce at least one hatchling) were determined by searching known and potential nesting habitats in Everglades National Park. Searches were conducted by skiff, foot, canoe, and helicopter during April and May for nesting effort, and during July and August for signs of hatching activity, including tail drags, digging or scraping, or the presence of eggs or hatchlings. When nests were located, vegetation, substrate, distance from shore, and nest dimensions ($l \times w \times h$), and the salinity of adjacent waters were recorded. Shells of hatched eggs or hatchling crocodiles were considered evidence of successful nests. The number of unhatched eggs and causes of egg failure were noted whenever possible.

Growth and survival of crocodiles in northeastern Florida Bay were assessed by capturing and marking hatchlings during nest surveys, followed up with periodic efforts to recapture marked animals. When crocodiles were captured they were checked for marks (if not marked they were then marked); crocodiles were marked by removing tail scutes according to a prescribed sequence. Captured crocodiles were measured for total length

and snout-vent length, weighed, and released. Information for each capture included salinity (by refractometer) and depth of water, type of habitat (pond, creek, cove, canal, or bay), air and water temperature, and location. Unlike evaluating nesting activities, which requires only a few visits during the nesting season, capturing crocodiles requires an intensive, consistent effort. Although crocodiles were captured whenever they were encountered, deliberate efforts to capture crocodiles were restricted to 1987 to 1989 and 1995 to 1997, and were focused in northeastern Florida Bay.

Flow data (cfs) for structures S-18C, S-197, S-175, and S-332 were obtained from the United States Geological Survey and the South Florida Water Management District for the period 1970–1993. Negative flows were recorded as zero. Flow in C-111 Canal was calculated by subtracting the flow in S-197 from that of S-18C. Flow in Taylor Slough was calculated by adding the flow in S-175 and S-332. Months with more than 5 d of missing data were excluded from the analysis.

Rainfall data were obtained for the Royal Palm Ranger Station for 1970 to 1993. Trace amounts of rainfall were recorded as zero. All data were summarized monthly and aggregated by quarter, half-year, and year. The quarters were designated as winter (December to February), courtship and nesting (March to May), incubation and hatching

TABLE 1. Summary of locations and habitats of American crocodile nests in Everglades National Park (Bean 1953; Moore 1953a, b; Ogden 1978; Mazzotti 1989, Present study).

Habitat/Location	Number (%) of Known Clutches							Total
	< 1,930	1,930-1,950	1,950-1,959	1,960-1,969	1,970-1,979	1,980-1,989	1,990-1,995	
Creek	2 (67%)	3 (18%)	1 (8%)	2 (9%)	28 (35%)	12 (13%)	7 (7%)	55 (17%)
Mainland shoreline	1 (33%)	4 (23%)	5 (38%)	16 (69%)	38 (48%)	53 (58%)	55 (54%)	172 (52%)
Island shoreline	0	10 (59%)	7 (54%)	5 (22%)	14 (17%)	17 (19%)	18 (18%)	71 (22%)
Man-made	0	0	0	0	0	9 (10%)	21 (21%)	30 (9%)
Florida Bay	3 (100%)	17 (100%)	13 (100%)	23 (100%)	80 (100%)	82 (90%)	78 (77%)	296 (90%)
Greater Flamingo	0	0	0	0	0	9 (10%)	23 (23%)	32 (10%)
Number of clutches	3	17	13	23	80	91	101	328

area, nests in immediate danger of harm were re-located to artificial sand nests by National Park Service rangers. Nests in the Greater Flamingo area failed to hatch 71% of the time, while 72% of the nests in northeastern Florida Bay were successful. Raccoons (*Procyon lotor*) are the only documented predator of crocodile nests. During the period 1987 to 1993 raccoon depredation was 23% (39 of 166) of nests, occurred only at sand nests, and accounted for 71% of all nest failure.

In 1988 hatching occurred later than usual. Kushlan and Mazzotti (1989b) determined the mean hatching date for 27 nests was July 29 $\pm$ 6.7 days SD. The six nests that hatched naturally in 1988 were opened between August 2 and August 14. Hatchlings from successful nests had much larger, and less enclosed yolksacs than average. Nest temperatures were spot recorded from the end of July to mid August; temperatures ranged from 30 °C to 32°C. Failed nests opened by crocodiles were examined and revealed that embryonic mortality occurred in lower layers of eggs during the fourth to fifth week of incubation (due to

flooding) and that some embryos in the upper layers were near fullterm but had not absorbed their eggsacs. Some of these embryos were still developing but appeared to be several weeks short of hatching. Since none of these embryos were capable of vocalizing, I presumed the crocodile that opened the nest did so because it was "time to" and not in response to vocalizations. These nests were subsequently depredated by raccoons. Other nests were apparently abandoned; no attempts to open them were visible. Rainfall recorded during the 1988 incubation period was the highest recorded for previous 14 yr.

A weakly significant correlation was found between the flow through C-111 Canal and nesting effort during March to May (courtship and egg laying season) of the same year (Spearman's Rho = 0.48, $p < 0.05$). No other correlations between nesting effort and flow or rainfall were significant.

Groundwater levels were correlated with surface water at Trout Creek (Spearman's Rho = 0.90, $p < 0.05$) and less strongly at Mud Creek (Spearman's Rho = 0.560, $p < 0.05$); it should be noted

TABLE 2. Significant nonparametric correlations (Spearman's Rho) between creek nest site ground water levels, and changes in ground water levels during the 1987 (June 16 to September 1) and 1988 (April 15 to September 1) crocodile nesting seasons and some local and regional hydrological parameters. Flow is estimated C-111 discharge calculated by subtracting flow through S-197 from flow through 18C. Flow + # indicates number of days the flow was lagged.

Year	Location	Rainfall	Flow	Flow + 1	Flow + 2
1987	Trout Creek		0.7090	0.6683	0.5550
	Ground Water		(0.0001)	(0.0001)	(0.0004)
	Trout Creek				-0.3427
	Change in Ground Water				(0.0408)
	Mud Creek		0.4165	0.4012	0.2759
	Ground Water		(0.0003)	(0.0005)	(0.0208)
1988	Mud Creek	0.3918	-0.2411	-0.4050	-0.5283
	Change in Ground Water	(0.0004)	(0.0428)	(0.0005)	(0.00001)
	Trout Creek		0.3841	0.3712	0.2443
	Ground Water		(0.0001)	(0.0002)	(0.0159)
	Trout Creek	0.4238			
	Change in Ground Water	(0.0001)			
	Mud Creek		0.6420	0.6809	0.6399
	Ground Water		(0.0001)	(0.0001)	(0.0010)
	Mud Creek	0.4804	-0.2355	-0.2162	-0.2888
	Change in Ground Water	(0.0001)	(0.0216)	(0.0353)	(0.0043)

TABLE 3. Recapture data for crocodiles. TL = total length; Δ TL = change in total length; Δ Mass = change in mass; nd = not determined.

Clip #/ID #	Date recaptured	Sex	TL (cm)	Days between captures	Δ TL (cm d ⁻¹)	Δ Mass (g d ⁻¹)
114	Feb 7, 1996	F	213	5,303	0.035376	7.908354
140	Feb 22, 1997	F	262	5,684	0.041696	nd
227	Jan 27, 1989	M	120	902	0.103104	6.594235
229	Jan 27, 1989	M	126	902	0.109534	7.424058
272	Jan 29, 1997	nd	98	3,471	0.02083	0.54019
321	Feb 28, 1988	nd	46	207	0.092271	0.47343
309	Feb 8, 1996	F	180	3,110	0.049164	0.6209
460	Feb 7, 1996	F	260	2,574	0.028749	10.87801
509	Feb 7, 1996	F	226	2,377	0.053429	17.54312
580	Dec 27, 1996	nd	194.6	2,340	0.072051	9.804915
643	Feb 6, 1996	M	77	562	0.088968	2.030249
653	Jan 22, 1996	M	76.9	547	0.093053	2.61426
715	Feb 7, 1996	nd	108.5	340	0.33235	0.441176
770	Feb 8, 1996	F	57.5	66	0.03333	0.454545
771	Feb 8, 1996	M	58.3	66	0.013636	-0.45455
775	Jan 29, 1997	F	105.11	358	0.032989	2.960894
C6	Jan 22, 1987	F	199	3,096	0.055943	12.44871

that interference (wasp nest) occurred with the readings from Mud Creek. Groundwater levels were also correlated with flow; this correlation weakened as flow was lagged by day steps (Table 2). Flow in the C-111 Canal was negatively correlated with changes in groundwater levels. Although groundwater levels were high when flow was high, groundwater levels were already receding by the time flow was peaking. Changes in groundwater levels, when extreme, caused nest flooding and were weakly correlated with rainfall (Table 2).

GROWTH AND SURVIVAL

Four hundred eighty-nine hatchlings were marked from 44 of 103 successful nests between 1986 to 1995. Three hundred twenty-four (66%) were from shoreline nests, 63 (13%) were from relocated nests, 57 (12%) were from island nests, 31 (6%) were from creek nests, and 14 (3%) from nests on artificial substrates. The number of hatchlings marked per year ranged from 3 to 126 and was directly related to effort expended on catching them.

Nonhatchling crocodiles were captured between August 1987 and April 1989, and between February 1995 and February 1997. Twenty-five crocodiles were captured during 1987 to 1989, one in October 1990, and 43 crocodiles during 1995 to 1997. Forty percent were caught in Joe Bay. Recaptures increased from 20% (5 of 25) between 1987 and 1989 to 37% (16 of 43) between 1995 and 1997. Crocodiles ranged in size from 34 cm to 390 cm; 50% were less than 1 m total length. Fifty-four crocodiles were sexed: 28 were female and 26 were male.

Thirteen of the 21 recaptures had been tagged as hatchlings, and had survived for more than 12

mo (range: 18–198 mo). Five were from shoreline nests, three from an island nest, three from canals, and two from creek nests. Two of the canal hatchlings had been released from a relocated nest, and one was originally marked over 25 km distant on North Key Largo. All were recaptured in mangrove-lined ponds, creeks, and coves. This provides a lower limit of 1.5% of hatchlings tagged that survived for more than 1 yr.

Growth data for four crocodiles recaptured in 1988 to 1989 and for 13 crocodiles recaptured during 1994 to 1996 are shown in Table 3. Crocodile growth rates were calculated based on change in mass or total length divided by the number of days between captures. Growth rates varied greatly as did the period between recaptures. Growth (total length) ranged from 4 cm yr⁻¹ to 40 cm yr⁻¹, and change in mass ranged from 8 kg yr⁻¹ to 0.180 kg yr⁻¹ (crocodile lost weight). The crocodiles that grew most rapidly in total length did not necessarily have the greatest rate of gain in mass (Table 3).

MOVEMENTS AND HABITAT RELATIONS

No hatchlings were found at a shoreline nest more than 3 d after hatching. On four occasions, nests were visited the morning after hatching, and, except for a few eggshells, nothing was found. Searches of the shoreline surrounding the nest did not reveal any hatchlings. On six occasions, hatchlings and eggshells were moved, probably by an adult crocodile, 50–200 m away from the nest before being released.

Patterns of habitat use and movements by hatchling crocodiles were similar to that reported by Mazzotti (1983). Island and mainland shoreline hatchlings hid during the day, avoided wave action, and moved rapidly away from nest sites. Creek and

canal hatchlings were active during the day and lingered near the nest site. Hatchling crocodiles from relocated nests were released in East Cape Canal, Homestead Canal, and West Lake.

Non-hatchling crocodiles were captured in coves (51%), ponds (21%), canals (15%), and creeks (13%). Salinities recorded at capture sites were low ($\bar{x} = 6 \pm 3.85$ SD). Some crocodiles moved long distances, usually over long time periods, between captures.

Individual crocodiles moved over the entire study area in northeastern Florida Bay (see Fig. 2 for named locations). In addition to the crocodile that moved from North Key Largo to Mud Bay (25 km), crocodiles moved from Lake Key to Joe Bay (10 km), Joe Bay to Little Madeira Bay (10 km), Trout Cove Key to Taylor River (12 km), and Madeira Beach to Joe Bay (13 km).

Discussion

No one has been able to estimate accurately the numbers of crocodiles in Florida Bay, but we have been able to follow closely the numbers of crocodiles nesting. Although some of the increase in observed numbers of crocodiles nesting is the result of an increase in our ability to find nests, the presence of new adult females nesting in new locations indicates a real increase. This increase in numbers and range of crocodiles nesting in Everglades National Park is encouraging. That crocodiles are now nesting in areas outside of northeastern Florida Bay (in Everglades National Park), and outside of Everglades National Park (at the Florida Power and Light Company Turkey Point Power Plant site and the Crocodile Lakes National Wildlife Refuge on North Key Largo) provides some security against the effects of catastrophic events such as hurricanes. However, most of the increase in nesting is on artificial substrates and nests on artificial substrates are more prone to failure, especially by predation. Why crocodiles started nesting in the Greater Flamingo area is not known. Crocodiles became more noticeable around this area, especially in Buttonwood Canal, after that canal was plugged in the early 1980s to prevent saltwater intrusion into Whitewater Bay and to retain fresh water.

The number of nests per year is variable. There is a weak correlation between the number of nests and spring rainfall, but no obvious reason for this relationship. Depending on the period selected, a 3 or 4 yr study of crocodile nesting in Florida Bay could yield a very different view of the population. For example, looking at nesting from 1989 to 1992 would indicate that crocodiles were declining; shifting the study period 1 yr to 1990 to 1993 would indicate an increasing population. Neither

would provide an accurate assessment of the actual status of the population. In endangered species monitoring programs, only a consistent long-term effort can provide the information needed to separate long-term trends from short-term fluctuations.

Nest success remains high compared to other populations of crocodilians (Mazzotti 1989). Egg mortality due to hydrological extremes is low. Fewer nests are flooding because fewer nests are being laid at creek sites. Predation has increased and is associated with the increase in nests on artificial substrates. Nests on artificial substrates may be more vulnerable to predation because there may be more raccoons near these sites; increased densities of raccoons near human activities are not unusual in South Florida.

Although mortality due to flooding is decreasing, nesting at creek sites is also decreasing. Are fewer nests being laid at creek sites because crocodiles have abandoned these sites due to regular failure or because of better success at other sites? The cause is unknown; however, the decline in creek nests has been of concern because failure of these nests has been related to groundwater levels (Mazzotti et al. 1988), which may be affected by water management decisions. In Everglades National Park, upstream water releases, made by deliberate management decision, regularly flood alligator nests (Mazzotti and Brandt 1994). Could decisions to increase flow from C-111 Canal jeopardize crocodile nests?

Groundwater levels at creek sites were correlated with flow, but negatively correlated with changes in groundwater level (Table 2). Hence, the highest water levels occur as the groundwater levels are receding. Changes in groundwater levels were weakly correlated to rainfall. Based on these observations, the most likely scenario for a nest-flooding event can be described as rainfall sufficient to cause a rapid increase in groundwater, resulting in flooding of the nest cavity. Groundwater levels peak at the end of rainfall or shortly thereafter. Groundwater levels fall slowly, inhibited by the relatively impermeable marl soil. As groundwater ebbs, flow from C-111 Canal increases. Egg mortality is associated with rainfall rather than flow, although flow-induced groundwater levels could increase the frequency of rainfall-driven flooding events. In any case, the loss of creek nests due to high water could be more than compensated for if an associated drop in salinity increased survival of hatchlings from successful nests. However, this would not be the case if sea-level rise is causing an increase in the frequency of nest flooding; an increase in water levels would be accompanied by an increase in salinities (Wanless et al. 1994). At least

one long-time observer of the natural history of South Florida has noticed a decline in creek crocodile nests related to sea-level rise (Simmons and Ogden 1998).

Excessive rain can have effects other than flooding nests. Abundant rain can lower sand temperatures and delay incubation, as it has for sea turtles (Kraemer and Bell 1980). Spot nest temperatures recorded in a high rainfall year (1988) were 4–8°C less than those measured in other years (Mazzotti 1989). Lower nest temperatures lengthened incubation in other crocodilians (Webb et al. 1983; Jonen et al. 1987; Webb et al. 1987). A longer than normal incubation period resulted in failure of some nests due to abandonment, and due to depredation following a premature excavation. Apparently not all crocodiles require vocalizations to initiate nest opening.

American crocodiles readily take advantage of artificial nest sites. In 1986 a crocodile nested in new bags of concrete used to plug East Cape Canal. The crocodile nested between the time the last bag was left at 1630 h and maintenance workers returned at 0900 h the next morning. This suggests that, at least in some areas, nest sites are limited. Kushlan and Mazzotti (1989a) pointed out that the creation of nest sites where none were previously available has to some extent compensated for the loss of nest sites elsewhere in South Florida. Creation or enhancement of nest sites where lack of natural nest sites are limited can be an effective management tool for recovery of endangered crocodile populations.

Most hatchlings marked (78% of hatchlings marked between 1986 and 1995, and 89% of hatchlings marked between 1978 and 1981) come from nests on shorelines of the mainland or keys in Florida Bay. Most of the successful nests are located here, and hatchlings are easiest to capture at these locations. Hatchlings disperse most rapidly from these sites. Marking shoreline hatchlings depends on being at the nest the morning after hatching, when the hatchlings are still concentrated in one or two groups. In most cases, these pods are gone after 1 d, and all of the hatchlings are gone by the third day. In some cases, being at the nest the morning after hatching is not soon enough.

The fate of hatchlings and eggs from these nests remains a mystery. On one occasion a nest was visited at 2030 h in the evening, then at 0900 h the following morning. The nest had hatched, the egg cavity was empty, and two ("hatched") shells were found nearby. Nothing else was found in an exhaustive and immediate search of the shoreline (hundreds of meters) around the nest and a thorough search of the shoreline (kilometers) at night using lights from a boat. We have found hatchlings

and eggs carried by adults en masse for a distance of several hundred meters along a shoreline before release, and can only speculate that adults are capable of doing the same thing for greater distances. The closer the hatchlings are moved to a nursery habitat before release, the less they have to disperse, and presumably more survive. Circumstantial evidence for long distance (8–10 km) dispersal aided by an adult occurred on North Key Largo (Moler 1991).

Thirty-one nonhatchling crocodiles were captured between 1978 and 1981, 25 between 1987 and 1989, and 43 between 1995 and 1997. In explaining this increase in numbers of crocodiles captured we can not separate an increase in abundance of crocodiles from an increase in our ability to capture them. From 1977 to 1981 capture surveys were done monthly in all accessible bodies of water from Little Madeira Bay east through the creeks and ponds north of Long Sound. During 1987 to 1989 and 1995 to 1997, we focused capture efforts on prime locations for crocodiles during January and February. We also sent out several capture crews at once to provide a thorough sweep of selected areas. The efficiency of this method is demonstrated by the increase in numbers of crocodiles captured, and by the increase in proportion of recaptures.

The ratio of 28 females to 26 males captured is consistent with the 1:1 sex ratio found in other studies (Kushlan and Mazzotti 1989b; Moler 1991; Brandt et al. 1995). However, in all of these samples subadults predominate, and these sex ratios may not be representative of the adult population.

Since we can not distinguish between death and dispersal, we can not estimate survival. We can measure minimum survival based on capture of known individuals. This is a minimum estimate of survival in that it still does not distinguish between death and dispersal. The 1.5% estimated here is less than that reported for North Key Largo (Moler 1991) and Turkey Point (Brandt et al. 1995). At both North Key Largo and Turkey Point, nest sites are closer to nursery habitat, and, thus, dispersal distances are less for hatchling crocodiles. At both Key Largo and Turkey Point sites, low survival was associated with high salinity or low rainfall.

Although mortality of hatchling crocodiles can reach 99%, the population can still be stable because of the large clutch size, and long period of reproductive activity (Graham 1968). At a minimum, the subpopulation of American crocodiles in Florida Bay is stable and probably is increasing. In a stable population of crocodiles with good nest success and adequate hatchling survival, mortality of older juveniles and subadults becomes the most likely factor to limit population numbers (Magnus-

son 1986; Abercrombie 1989). The question is no longer will crocodiles survive, but how can we further improve habitat conditions for this endangered species.

Few recaptures and variable growth rates make comparing Florida Bay crocodiles with other groups difficult. Understanding the causes of variability of growth rates will be important. Food obviously plays a role. Mazzotti and Dunson (1984) conducted a series of laboratory experiments and found that even with a constant food supply, changing salinities caused different growth rates, and that hatchling crocodiles could grow quite well in high-salinity water with only periodic access to low-salinity water. They found that when hatchlings reached a size of 200 g, they were more tolerant of immersion in seawater. They further hypothesized that rapid growth to this size before the onset of colder temperatures and higher salinities of the dry season in December would be a major adaptation for survival in saline water. In support of this Moler (1991) reported that in the years when crocodiles attained 200 g by December, first-year survival averaged almost 30%, and only 10% when mass did not. Further, Moler suggested that rainfall and associated lower salinities could influence growth rates and survival. He found low rainfall associated with the years that hatchlings failed to reach 200 g by winter.

The above discussion suggests the number of nests is useful as an indicator of long-term population trends, but less useful as a measure of short-term responses to ecosystem restoration. For example, failure of nests due to flooding by rainfall could be more than compensated for by increased growth rates and survival of hatchlings from successful nests. Because of more direct linkages with rainfall and salinity, growth and survival are better indicators of the success of ecosystem restoration alternatives. More information is needed on patterns of growth and survival of Florida Bay hatchlings.

American crocodiles in Florida continued to show their predilection for low-salinity habitats that are protected from the effects of wind and wave action (Ogden 1978; Kushlan and Mazzotti 1989b). Since our objectives were growth and survival and not relative distribution and abundance, we looked for crocodiles in places where we expected to find them, and did not distribute our capture efforts randomly or systematically. Although able to withstand long immersion in salt water when adequate food is present, American crocodiles clearly prefer fresh and brackish water whenever a gradient occurs (Dunson and Mazzotti 1989; Kushlan and Mazzotti 1989b; Brandt et al. 1995). Surveys to examine the relationship of the relative distribution

and abundance of crocodiles to salinities should be conducted, and the results evaluated for their application for setting restoration success criteria.

SYNTHESIS AND HYPOTHESES

Increasing numbers and range of nests, good nesting success, high fertility of eggs (Mazzotti 1989), adequate growth and survival of hatchlings, and recruitment into the breeding population all indicate crocodiles are doing fairly well in Florida Bay—certainly better than alligators in nearby freshwater marshes (Mazzotti and Brandt 1994). However, Florida Bay crocodiles have lower growth and survival rates than crocodiles on North Key Largo or at Turkey Point. Crocodiles may be secure in Everglades National Park, but there is still opportunity for enhancement of the Florida Bay ecosystem for the benefit of this endangered species.

Do historic and current patterns of nesting, growth, and survival of crocodiles provide any clues for restoration of Florida Bay? The previously unexplained loss of nests sites in central Florida Bay, and the dependence of hatchling crocodiles on local salinities for growth and survival, may provide clues. Crocodiles formerly nested on a line of keys from the mouth of Terrapin Bay to Whipray Basin (10 km south-southwest) (Moore 1953a, b). These central bay key nests and island nests in eastern Florida Bay had disappeared by 1970 (Ogden 1978). Ogden (1978) and Kushlan and Mazzotti (1989a) attributed the loss of eastern bay nests to the loss of year round habitat on Key Largo. In the central bay area, year-round crocodile habitat is still intact and would include the back-country north of Terrapin Bay, including McCormick Creek, west to West Lake. Crocodiles have regularly occurred in these areas and continue to occur there today. If it was not loss of year round habitat, perhaps some combination of a loss of attractiveness of key nest sites and the increased opportunity of nesting on artificial substrates lured crocodiles away from this traditional nesting area.

For crocodiles nesting on islands there is a trade-off between the high success of beach sites with the long distance dispersal and associated high mortality of hatchlings. Hatchlings not only have to disperse to suitable nursery habitat during the 3–4 mo posthatching period, but they must grow to a mass of 200 g to have a good chance of surviving the winter dry season. Growth and survival of hatchlings have been linked to the availability of fresh water, including rainfall, and surface waters. I hypothesize that past patterns of water delivery to the central bay were more conducive to the survival of hatchlings from island nests. Crocodile nests that fail to produce surviving hatchlings

eventually are abandoned. What happened to Florida Bay in the period leading up to the early 1950s when these nest sites were deserted, or, perhaps more importantly, how did Florida Bay function for crocodiles before disturbance?

Recognizable since the early 1930s, water management practices have changed the natural patterns of freshwater inflow to Florida Bay (Smith et al. 1989; McIvor et al. 1994). Taylor Slough was a major source of fresh water for north-central Florida Bay. During the wet season, fresh water would pool behind a series of marl and sand berms along the north shore of the bay. Restricted by berms, fresh water would flow into the central bay primarily through McCormick Creek. Potentially large amounts of water would continue to flow into the bay during the dry season. This historical, early dry season flow from Taylor Slough coupled with rainfall could have provided saline conditions suitable for hatchling growth. Historical flow patterns probably also pushed isohalines farther out into the bay, reducing the distance hatchlings would have to disperse to find suitable nursery habitat. Less fresh water in the central bay means that crocodiles would not only grow slower but have to disperse farther. Both factors negatively impact survival and the suitability of island nest sites. The hypothesis is that in northeastern Florida Bay, the combination of saline water and long distance dispersal limits hatchling survival. In the central Bay, the lack of flow and increased salinities have eliminated survival of hatchlings from island nests.

An ecosystem restoration goal for crocodiles in Florida Bay would be to restore Taylor Slough as a main source of fresh water for the eastern and central bay areas and, specifically, to restore the early dry season flow (October to December) from Taylor Slough to Florida Bay. Measurable objectives of success would be

1. A fluctuating mangrove backcountry salinity that rarely exceeded 20‰;
2. Increased growth and survival of hatchling crocodiles; and
3. Reestablishment of crocodile nesting on keys in the central bay.

In Florida Bay we have the unique opportunity to integrate habitat enhancement for an endangered species with ecosystem restoration and management.

The effects of sea-level rise on crocodiles in Florida Bay have not been evaluated, but should give reason for concern. Nest sites are obviously limiting in some locations. Currently, the only natural nest sites left in Florida are in Florida Bay. These nests, on exposed shorelines and creek banks, could become limiting or even disappear depend-

ing upon conditions of sea-level rise. All potential crocodile nesting habitat should be identified and mapped. A forecasting model should be developed to evaluate the rate of loss of nesting habitat compared to the rate of sea-level rise. That crocodiles readily use artificial substrates for nests provides a management option to compensate for negative impacts to existing nesting areas.

This study underscores the importance of a long-term, consistent research and monitoring program for the endangered American crocodile. When we apply a consistent monitoring effort, we get proportional results. The biggest gaps in our current knowledge of crocodiles are information on growth and survival of all size classes, especially subadults, and the relationship of relative distribution and abundance of crocodiles to salinities. This information could contribute to evaluating restoration alternatives and establishing success criteria for ecosystem restoration.

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LITERATURE CITED

- ABERCROMBIE, C. L. 1989. Population dynamics of the American alligator. Crocodiles their ecology, management and conservation. Crocodile Specialist Group Special Publication. Gland, Switzerland.
- BEAN, N. M. 1953. Crocodile nest at Trout Creek. *Everglades Natural History* 1:100-102.
- BOX, G. E. P. AND G. M. JENKINS. 1976. Time Series Analysis Forecasting and Control. Holden-Day, Inc., San Francisco, California.
- BRANDT, L. A., F. J. MAZZOTTI, J. R. WILCOX, P. D. BARKER, JR., G. F. HASTY, JR., AND J. WASILEWSKI. 1995. Status of the American crocodile (*Crocodylus acutus*) at a power plant site in Florida, USA. *Herpetological Natural History* 8:29-36.
- DUNSON, W. A. 1970. Some aspects of electrolyte and water balance in three estuarine reptiles, the diamondback terrapin, American and "salt water" crocodiles. *Comparative Biochemistry and Physiology* 32:161-174.
- DUNSON, W. A. AND F. J. MAZZOTTI. 1989. Salinity as a limiting factor in the distribution of reptiles in Florida Bay: A theory for the estuarine origin of marine snakes and turtles. *Bulletin of Marine Science* 44:229-244.
- EVANS, D. H. AND T. M. ELLIS. 1977. Sodium balance in the hatchling American crocodile *Crocodylus acutus*. *Comparative Biochemistry and Physiology* 58:159-162.
- GRAHAM, A. 1968. The Lake Rudolph crocodile (*Crocodylus niloticus* Laurenti) population. Report to the Kenya Game Commission, Kenya Game Department, Kenya.
- JOANEN, T., L. MCNEASE, AND M. W. J. FERGUSON. 1987. The

- effects of egg incubation temperature on post-hatchling growth of American alligators, p. 533-536. In G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.), *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty and Sons Pty Ltd., Chipping Norton, Australia.
- KRAEMER, J. E. AND R. BELL. 1980. Rain induced mortality of eggs and hatchlings of Loggerhead sea turtles (*Caretta caretta*) on the Georgia Coast. *Herpetologica* 36:72-77.
- KUSHLAN, J. A. AND F. J. MAZZOTTI. 1989a. Historic and present distribution of the American crocodile in Florida. *Journal of Herpetology* 23:1-7.
- KUSHLAN, J. A. AND F. J. MAZZOTTI. 1989b. Population biology of the American crocodile. *Journal of Herpetology* 23:7-21.
- MAGNUSSON, W. E. 1986. The peculiarities of crocodilian population dynamics and their possible importance for management strategies. Proceedings of the 7th Working Meeting of the International Union for the Conservation of Nature and Natural Resources, Crocodile Specialists Group. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.
- MAZZOTTI, F. J. 1983. Ecology of *Crocodylus acutus* in Florida. Ph.D. Thesis in Ecology, Pennsylvania State University, University Park, Pennsylvania.
- MAZZOTTI, F. J. 1989. Factors affecting the nesting success of the American crocodile, *Crocodylus acutus*, in Florida Bay. *Bulletin of Marine Science* 44(1):220-228.
- MAZZOTTI, F. J. AND L. A. BRANDT. 1994. Ecology of the American alligator in a seasonally fluctuating environment, p. 485-505. In S. Davis and J. Ogden (eds.), *Everglades: The Ecosystem and Its Restoration*. St Lucie Press, Delray Beach, Florida.
- MAZZOTTI, F. J. AND W. A. DUNSON. 1984. Adaptations of *Crocodylus acutus* and alligator for life in saline water. *Comparative Biochemistry and Physiology* 79A(4):641-646.
- MAZZOTTI, F. J., J. A. KUSHLAN, AND A. DUNBAR-COOPER. 1988. Desiccation and cryptic nest flooding as probable causes of egg mortality in the American crocodile, *Crocodylus acutus*, in Everglades National Park, Florida. *Florida Scientist* 51:65-72.
- MCIVOR, C. C., J. A. LEY, AND R. B. BJORK. 1994. Changes in freshwater inflow from the Everglades to Florida Bay including effects on biota and biotic processes: A review, p. 117-146. In S. M. Davis and J. C. Ogden (eds.), *Everglades: The Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, Florida.
- MOLER, P. E. 1991. American crocodile population dynamics, Final Report, Study Number: 7532. Bureau of Wildlife Research, Florida Game and Fresh Water Fish Commission, Tallahassee, Florida.
- MOORE, J. C. 1953a. The crocodile in Everglades National Park. *Copeia* 1953:54-59.
- MOORE, J. C. 1953b. A mound on a key in Florida Bay. *Everglades Natural History* 1:66-75.
- OGDEN, J. 1978. Status and nesting biology of American crocodile, *Crocodylus acutus* (Reptilia: Crocodylidae) in Florida. *Journal of Herpetology* 12:183-196.
- SIMMONS, G. AND L. OGDEN. 1998. *Gladesmen*. University Press of Florida, Gainesville, Florida.
- SMITH, T. J., J. H. HUDSON, M. B. ROBLEE, G. V. N. POWELL, AND P. J. ISDALE. 1989. Freshwater flow from the Everglades to Florida Bay, A historical reconstruction based on fluorescent banding in the coral *Solenastrea bournoni*. *Bulletin of Marine Science* 44:274-282.
- TANUR, J. M., F. MOSTELLER, W. H. KRUSKAL, R. F. LINK, R. S. PIETERS, AND G. R. RISING. 1972. *Statistics: A Guide to the Unknown*. Holden-Day, Inc., San Francisco, California.
- UNITED STATES ARMY CORPS OF ENGINEERS. 1993. Experimental program of water deliveries to Everglades National Park, Taylor Slough iteration. United States Army Corps of Engineers, Jacksonville, Florida.
- UNITED STATES ARMY CORPS OF ENGINEERS. 1994. Comprehensive review study reconnaissance report. United States Army Corps of Engineers, Jacksonville, Florida.
- WANLESS, H. R. 1994. Sea level control on stability of Everglades wetlands, p. 199-223. In S. M. Davis and J. C. Ogden (eds.), *Everglades: The Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, Florida.
- WEBB, G. J., A. M. BEAL, S. C. MANOLIS, AND K. E. DEMPSEY. 1987. The effects of incubation temperature on sex determination and embryonic development rate in *Crocodylus johnstoni* and *C. porosus*, p. 507-531. In G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.), *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty and Sons Pty Ltd., Chipping Norton, Australia.
- WEBB, G. J., R. BUCKWORTH, AND S. C. MANOLIS. 1983. *Crocodylus johnstoni* in the McKinlay river, NT. VI. Nesting Biology. *Australian Wildlife Resources* 10:607-637.

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