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Historic and Present Distribution of the American Crocodile in Florida

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ABSTRACT.—The historic and recent distribution of the American crocodile (*Crocodylus acutus*) in Florida is from Vero Beach and Tampa south to the lower Florida Keys. Its nesting distribution is southern Biscayne Bay and northeastern Florida Bay. Both distributions reflect winter temperature. Nesting sites and non-nesting habitat have been lost to development on Miami Beach and the upper Florida Keys, but this loss has been compensated by the creation of artificial nesting sites on spoil banks along southern Biscayne Bay and a westward addition to the nesting range in Florida Bay. Except for the shift in nesting away from developed areas, the general distribution of the American crocodile in Florida is the same as that historically documentable.

Habitat loss and concomitant decreases in distributional range are important factors in the changing status of many crocodylian populations. The American crocodile (*Crocodylus acutus*), although ranging widely in the neotropics, is presently concentrated in a few population centers in Jamaica, Hispaniola, Cuba, and southern Florida. These populations are relatively isolated from each other and have achieved a degree of genetic distinctiveness (Menzies and Kushlan, unpubl. obs.). It has long been thought that the southern Florida population is at risk of extirpation owing to excessive mortality and habitat loss (Barbour, 1923; Ogden, 1978; Hines et al. 1984), but such conclusions have been based on limited information. Here we review the historic distribution of the American crocodile in Florida, present data that document its present distribution, and discuss factors that might account for the observed distributional patterns.

METHODS

Field work was concentrated at the southern tip of Florida, USA. Surveys covered the entire coastal zone, concentrating in Florida Bay from Key Largo to Cape Sable. We observed crocodiles on standardized surveys using power boat, canoe, fixed-wing airplanes, and helicopter between July 1977 and September 1980. Information on the intensity and effectiveness of our methods is provided in Table 1. Efficiency averaged one sighting every 3 hours during 456 survey hours. Night surveys were attempted by helicopter without much success. Standardized

night surveys using power boat and canoe were conducted monthly over accessible habitat adjacent to Florida Bay and along a west coast river system. Sightings from boats were few because of the small area covered, difficulty of access to much of the habitat, and wariness of the animals. We also recorded the locations of all crocodiles sighted or captured by project biologists or by National Park Service field personnel outside the survey. We do not include in this paper multiple locations of hatching, tagged, or radio-telemetered animals.

The most comprehensive and useful information on crocodile distribution comes from daytime helicopter and airplane surveys, which were conducted monthly from July 1977 to July 1978 between Key Largo and Cape Sable. Fixed-wing aircraft were flown at an air speed of 120 km/hr, and helicopters, at 80–100 km/hr, both at altitudes of 50 to 80 m.

Nesting sites were found by observing, from the air or on foot, signs of terrestrial activity, followed by excavating each site for eggs.

Information on the historic occurrence of the crocodile in Florida comes from the published literature and unpublished information in the files of Everglades National Park, and of Joseph Moore (pers. comm.), who interviewed many long-term residents of Florida Bay in the 1950s.

RESULTS

Historic Range.—Rafinesque (1822) suspected that a crocodile occurred in Florida, but a specimen was not collected until 1869, in the Miami River off Biscayne Bay (Wyman, 1870). From that date through the 1960s, many scattered observations and second-hand reports of crocodiles were published (Table 2), which together provide a reasonable estimate of the historic

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TABLE 1. Number of crocodile sightings per survey hour. Number of hours is in parentheses.

Survey	Overall	Breeding season	Non-breeding season
Boat	0.21 (289)	0.13 (132)	0.29 (157)
Helicopter	0.60 (133)	0.57 (81)	0.65 (52)
Fixed-wing	0.63 (34)	0.36 (11)	0.75 (23)
Mean (total)	0.35 (456)	0.30 (224)	0.42 (232)

distribution of the American crocodile in Florida (Fig. 1).

Crocodiles were credibly reported as far north as Palm Beach on the Florida east coast. Most reports centered on Biscayne Bay, well-visited as the location of Miami, and the less accessible northeastern Florida Bay. Willoughby (1913) mentioned crocodiles on Cape Sable in northwestern Florida Bay, but no details were provided. Crocodiles definitely occurred in the upper Florida Keys as far south as Lower Matecumbe Key (Carr, 1940). Allen and Neill (1949) and Neill (1971) reported that the crocodile's range extended southward to Key West. A published photograph of a crocodile reportedly taken on a beach in Key West in 1935 is the earliest concrete evidence for the American crocodile in the lower Florida Keys. On the west coast of Florida, crocodiles were observed periodically after 1940 at Naples, Sannibel, Osprey, and Pinellas near Tampa. LeBuff (1957b) provided second-hand reports of west coast sightings, including that of an animal killed in Lee County and another captured near Sarasota.

The documentable historic nesting range of the American crocodile in Florida is more restricted than is the dispersion of individuals. Crocodiles nested on islands (called keys) and shores of Biscayne Bay and Florida Bay (Fig. 2). A famous nesting site of long occupancy was on Miami Beach (photo in Barbour, 1944). A number of reports of nesting in Florida Bay are available (National Park Service records; Moore, pers. comm.). Recorded nesting there dates back to at least 1914, in Alligator Bay. Other Florida Bay locations used historically included Samphire, End, and Club keys in 1930-1950, and Cup-of-Whiskey Key in 1951. Black Betsy Key was used for over 30 years. Before 1950, nesting also took place in eastern Florida Bay, near the main line of the upper Florida Keys. The record of nesting on other islands is sporadic, as were efforts by biologists to locate nest sites.

Recent Distribution.—Our surveys demonstrated that crocodiles are well dispersed across the coastal zone of extreme southern Florida from Cape Sable to southern Biscayne Bay, including Key Largo (Fig. 3). We found animals consistently as far north as southern Biscayne Bay, where they inhabit canals including those as-

TABLE 2. Historic published reports of crocodiles in Florida.

Location	References
Florida east coast	Henshall, 1884; Hornaday, 1891; Cope, 1898; Barbour, 1923; Pierce, 1970; Behler, 1978
Biscayne Bay, Miami Beach	Wyman, 1870; Henshall, 1884; Hornaday, 1891; Cory, 1896; Barbour, 1923, 1944; Pierce, 1970; Monroe and Gilpin, 1980
South Biscayne Bay	Cory, 1896; Smith, 1896; Dimock and Dimock, 1908; Willoughby, 1913; Dickinson, 1953
Northeastern Florida Bay	Dimock and Dimock, 1908; Dimock, 1918; Dickinson, 1953; Moore, 1953
Northwestern Florida Bay	Willoughby, 1913
Upper Florida Keys	Carr, 1940
Lower Florida Keys	Carr, 1940; Allen and Neill, 1949; Neill, 1971
Florida west coast, central Florida	Willoughby, 1913; Barbour, 1923 (but see Maynard, 1929); LeBuff, 1957a, b; Behler, 1978

sociated with the Turkey Point nuclear power plant (see also Gaby et al., 1985). The easternmost observations were on northern Key Largo, where crocodiles occur primarily in old canals, coves, and ponds in mangrove swamps (also P. Moler, pers. comm.). Our observations were concentrated in northeastern Florida Bay. Sixty-nine percent of all sightings were in that area during surveys that uniformly covered the entire range of the crocodile in Florida Bay.

Crocodiles are periodically observed and reported in Florida outside of Florida and Biscayne bays (Ogden, 1978; Campbell, 1980; Irvine et al., 1981; Alvarez, 1984; Hines et al., 1984; D. Hubbard, pers. comm.; P. Moler, pers. comm.). During the study period, crocodiles resided in power plant canals in Fort Lauderdale, and one was observed as far north as Vero Beach on the east coast in 1974 (Behler, 1978). Along the west coast, crocodiles were periodically reported from Naples (recent records include 1973, 1975, 1976, 1980, and 1983). More northern observations have been made at Sannibel Island and Tampa.

Information on the recent status of crocodiles in the lower Florida Keys is scarce. Reports in the 1960s and 1970s, especially by J. Watson (*in* Ogden, 1978), were the last regular sightings of animals there. Jacobsen (1983) accepted only three recent reports as being reliable. Disjunct

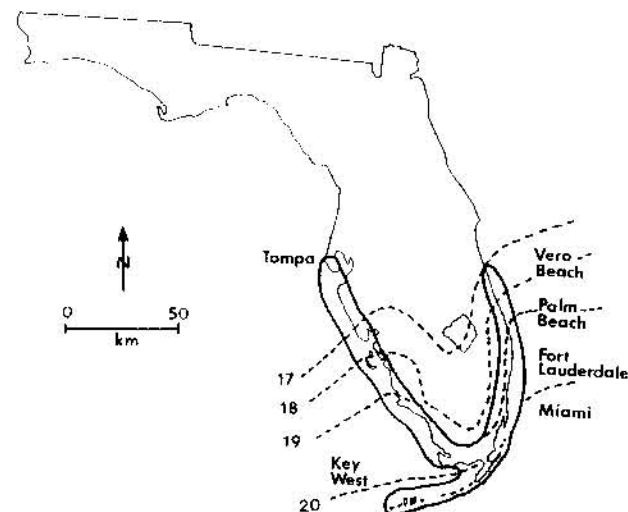


FIG. 1. The overall distribution of the American crocodile in Florida (solid line) and average January air isotherms (C; dashed lines).

sightings of crocodiles near Lake Okeechobee are of animals formerly captive at a tourist attraction (C. Clemmons and J. Lang, pers. comm.).

The present nesting range of the American crocodile is centered in northeastern Florida Bay. Fig. 2 shows the location of nest sites discovered in 1981 and 1982 (our data; Moler, pers. comm.,

for Key Largo; Gaby, pers. comm., for Turkey Point). From 1970 to 1982, 74% of 141 clutches of eggs found in southern Florida were associated with Florida Bay. Most of the remaining nests occurred at Turkey Point and on Key Largo. Single nests have been found near Cape Sable. As a result of these observations, the pres-

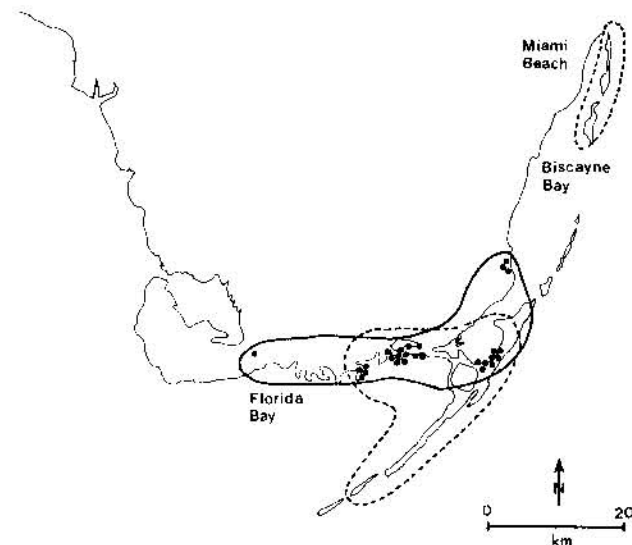


FIG. 2. Historic nesting distribution of the American crocodile in Florida (dashed line) and present nesting distribution (solid line). Each dot represents a nest site used in 1981 and 1982.

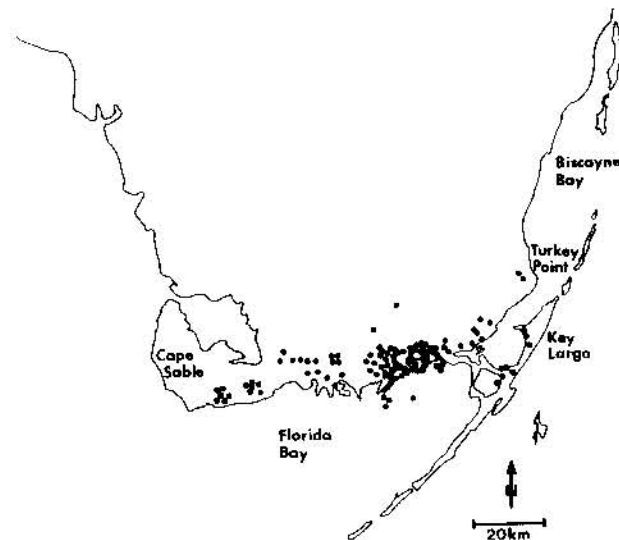


FIG. 3. Locations of crocodiles observed in southern Florida in 1977 to 1980. Each dot represents a sighting.

ent nesting range of the American crocodile can be delineated as southern Biscayne Bay, including Turkey Point and Key Largo, and northern Florida Bay to Cape Sable (Fig. 2).

Factors Affecting Distribution.—The American crocodile is a tropical species, and it is likely that climate limits the northern extent of its range in Florida. Its overall range reflects winter air isotherms (Fig. 1), corresponding generally to the 17°C January isotherm. This similarity suggests that winter temperatures may ultimately be limiting the distribution of the American crocodile in Florida. The only permanent population north of extreme southern Florida is in the warm cooling canals of a Fort Lauderdale power plant.

The nesting range coincides with the warmest winter location on the Florida mainland (Figs. 1, 2). The American crocodile appears to prefer relatively deep estuarine habitats that are protected from wind and wave action (Kushlan and Mazzotti, 1989), and these preferences appear to account for the details of distribution within the overall breeding range.

DISCUSSION

Historic Range.—The historic range of the American crocodile has been a matter of some disagreement (Moore, 1953; LeBuff, 1957b; Ogden, 1978) and requires re-evaluation. The historical presence of the American crocodile in south Florida is well documented (Table 2). Available reports make it clear that northeastern Florida Bay, at the extreme tip of the Florida

peninsula, was the center of the crocodile's historic distribution. Dimock (1918, p. 452) provided a precise description at the turn of the century. He said crocodiles were "definitely limited to the region at the extreme southern end of the peninsula of Florida, a strip ten miles long by three wide."

Individual crocodiles were reported sporadically outside these limits. LeBuff (1957a) concluded that crocodiles historically occurred sparsely on the Florida west coast, a view disputed by Moore (1953), who concluded that there is no evidence that the American crocodile occurred there naturally. Ogden (1978) stated that such records were of escaped, released, or storm-displaced animals. Certainly any of these factors might contribute to displacement of a crocodile, and it is likely that some of these sightings were of previously captive animals. Nevertheless, the record of observations is so long and persistent as to suggest that the west coast of Florida has been part of the overall range since at least the 1940s. However, there is no evidence that crocodiles lived there continuously during that period, and it is likely that sightings were of transient individuals. A similar explanation accounts for sightings in the lower Florida Keys. Jacobsen (1983) concluded that there is no evidence to suggest that crocodiles ever occurred in substantial numbers or permanently in the lower Florida Keys.

Reports from inland central Florida are especially tenuous. Barbour (1923) reported that C. J. Maynard claimed to have killed a large

crocodile near Lake Harney in Volusia County, central Florida, but Maynard (1929) later retracted this record, admitting that he had misidentified an alligator. Interestingly, Maynard based his retraction on a comparison made with a crocodile that reportedly had been killed near Lake Okeechobee by F. A. Ober. Willoughby (1913) also reported a crocodile having been killed near Lake Okeechobee, perhaps the same one. Because of this report, we cannot rule out the possibility that crocodiles have occurred in the lake, although there is no evidence that they lived there regularly.

The documentable historic nesting range includes northeastern Florida Bay and Biscayne Bay as far north as Miami Beach. Evidence for long-term nesting elsewhere in Florida seems unconvincing at present. Pierce reported nesting at Fort Worth (C. Voss in Ogden, 1978), but supporting evidence is lacking.

Present Distribution.—Our systematic surveys provided the first comprehensive data on the distribution of this species in southern Florida. Based on these data and other observations, the present distribution over the core of its range is well delineated (Figs. 2, 3).

Reports of crocodiles outside the breeding range occur fairly regularly. As noted above, this may be a natural result of the ability of individual crocodiles to move long distances, and/or the occurrence of previously captive animals. In that records of introduced animals are indistinguishable from those of native animals and the presence of any crocodile indicates conditions are appropriate for survival, distribution is appropriately evaluated using all recorded observations.

The ability of crocodiles to move long distances was well demonstrated in 1978 when a crocodile made several long-distance movements after being transported by wildlife officers. This animal, captured in Fort Lauderdale (Grimm and Bubman, 1978) and transported to Key Largo (T. Regan, pers. comm.), moved 100 km south before being recaptured on Big Pine Key (W. Dunson, pers. comm.). Re-released on Key Largo (J. Simon, pers. comm.), it was recaptured 20 km south (P. Patty, pers. comm.), and was released at the Fort Lauderdale power plant (P. Rose and R. Wilcox, pers. comm.). Later that year, after moving 10 km inland via canals, it was recaptured and released near Naples on the west coast (P. Moler, pers. comm.). It then moved to Cape Sable, 150 km south (pers. obs.). This individual undertook a succession of long-distance movements and, with help from government agents, covered most of the known range of the crocodile in Florida. Thus it is clearly possible for crocodiles to periodically occur well outside the nesting range.

Recent vs. Historic Distribution.—We find no change in the overall distribution of the American crocodile in Florida. The Florida population is, and apparently always was, restricted to the southern part of the Florida peninsula, along both coasts from Tampa and Vero Beach–Palm Beach to the lower Florida Keys. Similarly, the American crocodile is, and apparently always was, most commonly reported from southern Biscayne Bay to northeast Florida Bay, its present breeding range. The concurrence of this distribution with winter temperatures suggests that climate is the primary factor affecting crocodile distribution in southern Florida.

However, the nesting distribution of the American crocodile has changed. Crocodiles no longer nest on Miami Beach or frequent northern Biscayne Bay. It is not known how important Miami Beach was as a nesting habitat, but it is likely suitable nest sites were limited along the mangrove swamp-lined bay shore. Nesting still occurs on both sides of Barnes and Card sounds, the southern extensions of Biscayne Bay. Nests there, at Turkey Point, and on Key Largo, are on the spoil banks of canals dug through mangrove swamps. It is probable that few suitable nest sites occurred naturally in these areas. The current nesting activity in southern Biscayne Bay in part compensates for the loss of nesting habitat in northern Biscayne Bay and Miami Beach.

Crocodiles also no longer nest on the Florida Keys or on islands in nearby eastern Florida Bay. We agree with Ogden (1978) that such a loss must have been caused by the reduction in suitable non-nesting habitat on the main line of the Florida Keys. Our information from surveys and telemetry conclusively shows that crocodiles seldom occur in Florida Bay itself, except for nesting, at the conclusion of which they return to protected habitat (Kushlan and Mazzotti, 1989). The off-season habitat for crocodiles nesting on islands in eastern Florida Bay would have been the upper Florida Keys. Much of the land area of the main line keys has been developed, and conflicts between human residents and crocodiles, fatal to the crocodile, have occurred in this area for over 40 years (R. P. Allen, in litt.). The loss of habitat on the main line of the Florida Keys, occupied for most of the year, rather than conditions on or around the Florida Bay nesting islands, undoubtedly led to the decrease in the nesting range of crocodiles in eastern Florida Bay and the Florida Keys.

In addition to islands, crocodiles nested historically on the natural berm of coastal rivers off Florida Bay. The same locations were used by settlers and farmers as recently as the 1950s. In that river nest sites are in the year-round

habitat of both adult and hatchling crocodiles (Kushlan and Mazzotti, 1989), these seem to be the most advantageous nest sites. In contrast, nesting on offshore island beaches places hatchlings in some jeopardy. It is possible that use of bay islands may have been the result of past disturbance to the theoretically more suitable nesting sites along coastal rivers. Nesting persists on northeastern Florida Bay islands, and there is no evidence that the number of these sites has decreased. Actually documented use of this area has increased in recent years, coincident with an increase in efforts to find nests, and undiscovered nesting sites undoubtedly exist westward in the bay and in the Cape Sable area.

Thus the overall distribution of the American crocodile in Florida remains generally undiminished from its historic extent, although the nesting distribution has shifted away from developed areas. The provision of canal banks in southern Biscayne Bay may have mitigated for some of the loss of nesting habitat. The northernmost population of the American crocodile still occurs within its traditional range, limited, it seems, principally by winter temperatures.

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Population Biology of the American Crocodile

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ABSTRACT.—The population biology of the American crocodile (*Crocodylus acutus*) was studied in southern Florida during 1977-1982. Crocodiles occur primarily in inland mangrove swamps protected from wave action. Females use the open waters of Florida Bay only for access to nesting sites. Individuals have large (86-262 ha), overlapping activity areas. Nesting occurs in spring and summer, avoiding the cold and the wet seasons, either of which can affect incubation. Clutches averaging 38 eggs were laid both in mounds and in holes in the ground, either singly or communally. Available data cannot support the view that the number of nests has decreased in recent years. Hatching failure occurred as a result of infertility, predation, and embryonic mortality from desiccation and flooding. Hole and creek nests were most susceptible to embryonic mortality. Seventy-eight percent of nests hatched some young. We found no evidence of adults defending nests or young, but nest opening by adults was essential for hatching. Disturbance at nest sites caused females to abandon the site. All expected age classes occurred in the population. Size at maturity was 2.25 m TL for females. Documented mortality of adults and subadults of approximately 2 crocodiles per year was predominantly human-caused. At least 45 crocodiles have been released into southern Florida in 17 years. We estimate the southern Florida population to be about 220 ± 78 adults and subadults.

The northernmost population of the American crocodile (*Crocodylus acutus*) occurs on the extreme southern tip of the Florida peninsula, USA. The range of this tropical species has always been limited, probably by temperature constraints (Kushlan and Mazzotti, 1989). Early reports of crocodiles in Florida are notices and discussions of its occurrence (Wyman, 1870; Hornaday, 1891; Smith, 1896; Barbour, 1923); Moore (1953) provided the first detailed account of its status. Ogden (1978) documented aspects of its nesting biology. More recently, Gaby et al. (1985) reported on the population biology of a small number of crocodiles living in a power plant cooling system.

Many crocodilian populations are endangered because their effective population sizes have been reduced by human-related factors such as hunting and habitat loss. Small populations, particularly when isolated, risk extirpation because of the action of natural or artificial forces that erode their numbers. The Florida population of the American crocodile is thought to be of limited size (Ogden, 1978), and therefore susceptible to chance and human interference. As a result it has long been considered to be endangered (Barbour, 1923; Hines et al., 1984). Unfortunately, limited information has inhibited understanding of its population biology, and therefore of its true status or appropriate conservation needs.

In this paper we discuss the population biology of the American crocodile based on a five-year study of the population in the core of its northernmost range, northeastern Florida

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