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 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 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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Bay. Where appropriate, we compare information from studies conducted simultaneously and cooperatively with our own on other segments of the population (Gaby et al., 1975; P. Moler, pers. comm.). Other aspects of our overall study program are discussed elsewhere (Behler, 1978; Hall et al., 1979; Dunson, 1982; Lutz and Dunbar-Cooper, 1984; Stoneburner and Kushlan, 1984; Kushlan, 1988; Mazzotti et al., 1988; Kushlan and Mazzotti, 1989).

STUDY SITE

The study was conducted in southern Florida in the core range of the North American population (Kushlan and Mazzotti, 1989), primarily in northeastern Florida Bay (Fig. 1). Much of the Florida peninsula is covered by freshwater marshes, including the Everglades, which are confluent along the coast with mangrove swamps dominated by red mangrove (*Rhyzophora mangle*). Within the swamps are relatively deep-water pools, lakes, creeks, and flats that are protected from wind and wave action. Pools and lakes tend to be about 1 m deep, lack emergent vegetation, and are surrounded by mangrove trees. Creeks are short rivers, in places bordered by an elevated bank. Sand beaches are limited to the shores of islands and spits in Florida Bay, which averages 1.25 m deep. The shoreline of Florida Bay is exposed to wind and wave action except in coves.

Rainfall is seasonal; 75 to 80% of the 1150–1400 mm annual precipitation falls during a May to October rainy season. Salinity fluctuates with rainfall, runoff, and evaporation, and is highest in coastal bays and lower in inland mangrove swamps. Lunar tidal fluctuation in the northeastern portion of Florida Bay is minimal because circulation is dampened by islands (called keys) and mud banks. Water levels fluctuate in response to upland water discharge, seasonal changes in sea surface elevation, and wind.

METHODS

The study was conducted from 1977 to 1982. Crocodiles were located on standardized monthly surveys using boat, canoe, fixed-wing airplane, and helicopter (Kushlan and Mazzotti, 1989). For each crocodile seen, we recorded the location, time, size (estimated to the nearest quarter meter), and habitat. An extensive capture/mark/release program was conducted using boats at night. After capturing a crocodile by hand or neck noose, we determined total length (TL), snout–vent length (SVL; to posterior margin of the cloaca), and sex (Chabreck, 1966). Crocodiles were marked by toe web-tags (monel poultry tags), a unique combination of cut scutes, and numbered cattle ear tags at-

tached to tail scutes and to a flexible plastic neck collar. At capture sites, and at observation sites during helicopter and boat surveys, we measured air and water temperatures, salinity, wave action, and water depth. Water level, salinity, and temperature were monitored at several sites.

We captured and tagged 57 adults and subadults and 359 hatchlings from 23 clutches (40% of estimated production); 192 were tagged within 24 hours of hatching. Most captures of non-hatchlings were made away from nests, but in one year 8 females were trapped near, but not on, nest sites. Because of the responses of these animals in abandoning their nests (see below), the exercise was not repeated. It did provide an inadvertent experiment on disturbance effects. Observations of adults and hatchlings in other years were made with considerable care to avoid disturbance.

The wariness and difficulty of capture of American crocodiles and its endangered status made recapture difficult, and thus we could not use mark/recapture methods to calculate population size. We use the method devised by Chabreck (1966): $P = N/AFE$, where N is the number of nests, A is the percentage of adults in the population, F is the percentage of females in the adult population, and E is the percentage of the females nesting. Values are given ± 1 standard error.

Nests were found by searching the shoreline on foot or using helicopters. Each potential nest site was excavated for eggs, which were immediately reburied without turning. Fertility of each egg was determined by its banding (Ferguson, 1982). Sites were monitored through incubation to determine the fate of the eggs. Signs of predation, flooding, adult visitation, and hatching were noted. Temperature, rainfall, and salinity at each site were monitored. In the first year, we excavated and frequently visited only 4 of 11 sites to test whether these activities affected their survival (Dietz and Hines, 1980) or the return of the female at hatching. Because one test site and one control site were predated, and all were opened at hatching, we concluded that our activities had no adverse effect.

We attempted to obtain all available information on nests and nesting in southern Florida. These data came from the literature (Moore, 1953; Ogden, 1978; Gaby et al., 1985), from personal communications with those also studying Florida crocodiles (J. Lang, R. Gaby, and P. Moler), and from the files of Everglades National Park and of Joseph Moore (pers. comm.), who carefully assembled previous information and interviewed long-term residents of Florida Bay in the 1950s.

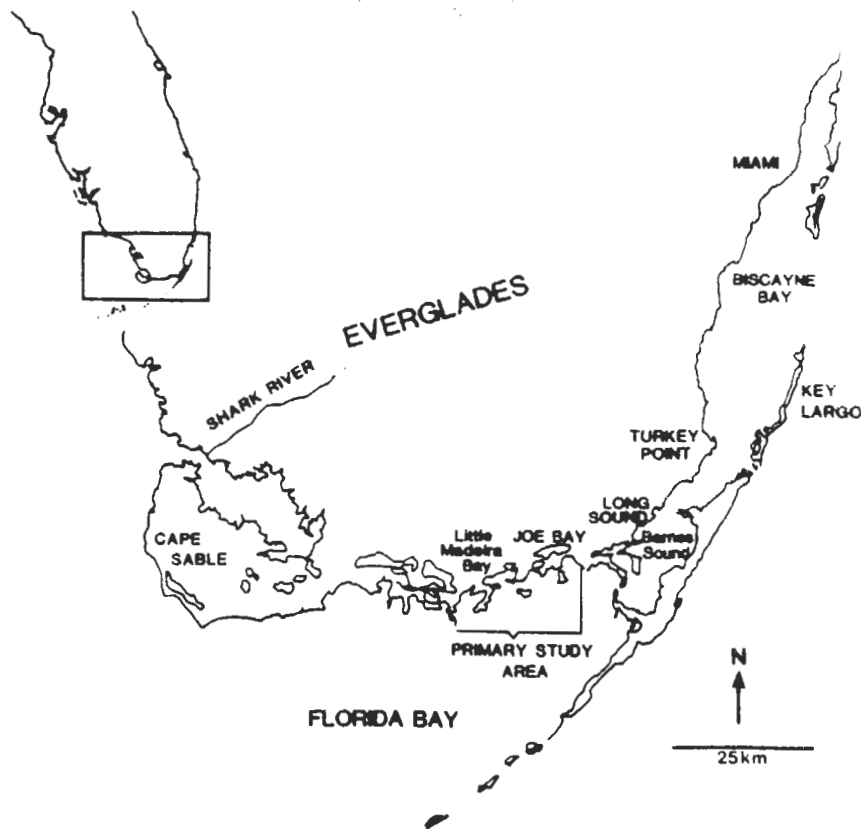Radio transmitters (SB2 for adults and 5 gram

FIG. 1. Map of southern Florida, showing principal localities mentioned in the text.

neapolis, Minnesota) were attached to neck collars (having a 1 yr life) or dacron back harnesses. Telemetered and non-telemetered hatchlings moved together, indicating that telemeters did not restrict movement. Fixes were obtained on weekly fixed-wing aircraft flights. Activity areas were calculated from telemetry fixes using the modified minimum area method (Harvey and Barbour, 1965).

The relative abundance of each habitat type was determined by placing a 0.5 cm acetate grid over a USGS T-map (1:20,000) of the study area. The habitat under each grid intersection was identified and tallied.

RESULTS

Habitat Use.—Crocodiles in southern Florida used mangrove swamps. Their use of habitat was nonrandom for all but one comparison of distribution among habitats (Table 1). Over 50% of our observations were in inland ponds and creeks, and an additional 25% were in protected coves. Only 6% were along exposed shorelines, and a few were on shallow mud flats in the interiors of large islands. The habitats used frequently were characterized by relatively deep water (>1 m) and protection from wind and wave action. Creek banks provided cave and basking sites. Crocodiles tended to remain near shorelines; only two crocodiles were observed in open water.

Crocodiles used habitats characterized by low salinities, averaging 14 ppt ($\bar{x} = 13.8$, SD $= 10.0$, range 0–35 ppt, $N = 111$). Crocodiles were found in higher salinities in spring and summer ($\bar{x} = 17.8$, SD $= 9.5$, range $= 0$–35 ppt, $N = 53$) than

TABLE 1. Habitat use by subadult and adult American crocodiles, given as percent of all habitats. The percent of habitat area available is noted under each habitat. Preference tested using a chi-square test.

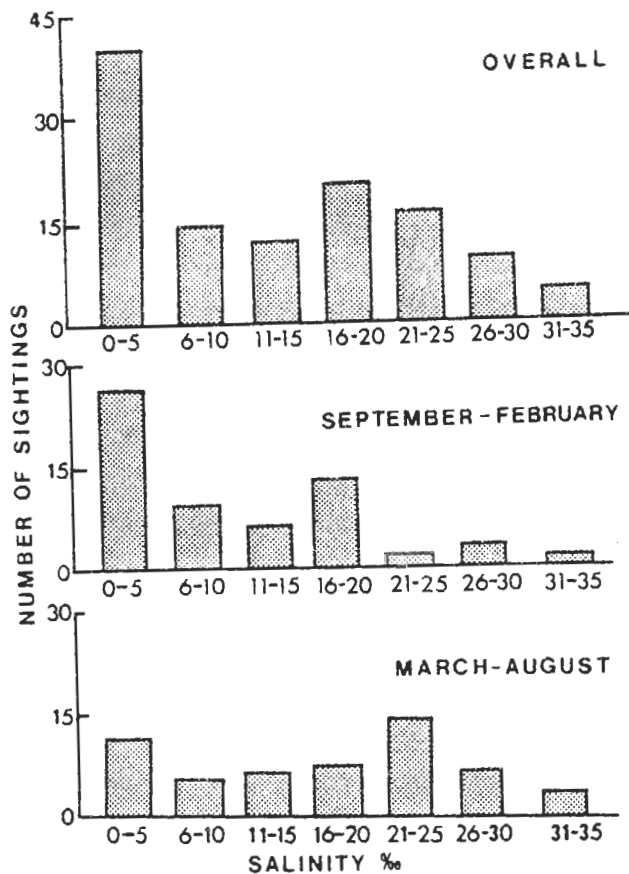|	Number of observations	Ponds (15%)	Creeks (10%)	Coves (43%)	Mangrove flats (8%)	Exposed shoreline (24%)	P
Total	280	29	25	36	8	6	<0.001
Non-breeding	162	25	27	43	4	1	<0.001
Breeding	118	35	24	25	0.4	14	<0.001
Adult	148	38	14	34	3	10	<0.001
Subadult	78	33	10	47	5	4	ns
Males	38	30	29	21	11	0	<0.001
Females	90	31	22	39	6	2	<0.001

FIG. 2. Crocodile sightings in different salinities, overall and for the breeding (Mar.–Aug.) and non-breeding (Sept.–Feb.) seasons.

in winter and fall ($\bar{x}$ = 9.8, SD = 8.8, range = 0–31 ppt, N = 58), when the animals were inland and fresh water discharge was highest (U-test, P < 0.001). In view of the seasonally high salinities present in Florida Bay (often >35 ppt), the relatively low salinities used by crocodiles show a distinct habitat preference for fresh to brackish water. This preferential use is demonstrated by the preponderance of sightings in fresh to brackish water (Fig. 2).

Seasonal differences in crocodile distribution (Fig. 2) are attributable to excursions into Florida Bay for nesting. In fall and winter, crocodiles confine themselves to the inland swamps, bays, and creeks (Fig. 3). In spring and summer, animals also occurred on exposed shorelines and coves of Florida Bay, a shift reflected in differences in habitat use during the breeding vs. non-breeding seasons (Table 1).

Hatchling crocodiles occurred in clumps of mangrove roots, under shoreline ledges, in holes, or under beach wrack by day, and in the water at the shore at night. Use of such areas minimizes exposure to temperature extremes, high salinity, wave action, and perhaps predation. Older juveniles used creeks and ponds, which seemed to constitute the primary nursery habitats in that they were characterized by long-term juvenile occupancy. Swift currents in the

middle of the creek were normally avoided. A combination of shoreline vegetation and ledges at water level provided protection from wave action and current.

Activity Areas and Movements.--Activity areas of 5 animals with >18 fixes averaged 107 ha (SD = 71.3, range 86–262 ha). These activity areas overlapped considerably (Figs. 4, 5). These results were derived from repeated radiotelemetry fixes, over as many as 28 months per individual, on 10 adult and subadult crocodiles (2 males, 8 females, 1.85–2.96 m TL). Telemetered crocodiles were frequently observed near other crocodiles. We located one female with other crocodiles on 6 occasions, 5 times near a telemetered male. Thus the activity areas were geographically and temporally non-exclusive.

Telemetry data demonstrated conclusively that the seasonal use of Florida Bay was related to nesting. Four telemetered females, known to be associated previously with nest sites on islands in Florida Bay, moved into the bay only during the nesting season. Three females left their nest sites immediately after their young hatched and returned to the inland mangrove swamps. One female moved after hatching to a flooded flat within the nesting island where she remained for 5 months prior to returning inland. Neither telemetered male was located in Florida Bay.

Telemetry data also showed that individual females return to the same nesting area in subsequent years. One returned to the same area over three years but alternated her nest site from one side of a creek to the other.

The pattern of area use included substantial movement interspersed with periods of residency (Fig. 5). One female stayed 38 days in a pond. Some animals appeared to have two separated activity areas. Females nesting in Florida Bay showed this pattern. A male using two separated areas had two periods of residency in a pond containing an active wading bird nesting colony. Some recorded excursions include: a female moving 4.2 km in 6 days, a male moving 6 km in 6 days, and another male moving 16.2 km in 22 days. A subadult female, which appeared to move more than the older animals over the 7 months that she was followed, moved an average of 1.4 km between consecutive fixes.

Nesting.--The principal nesting area of the American crocodile in Florida is northeastern Florida Bay. Eighty-two percent of all nests found in southern Florida from 1970 through 1982 were in this area (Table 2). Maximum numbers of nests found in any year were 13 in Florida Bay, 7 on Key Largo, 2 at Turkey Point, and 1 on Cape Sable, for a southern Florida total of 23. It can be expected that other nesting sites and nesting areas exist.
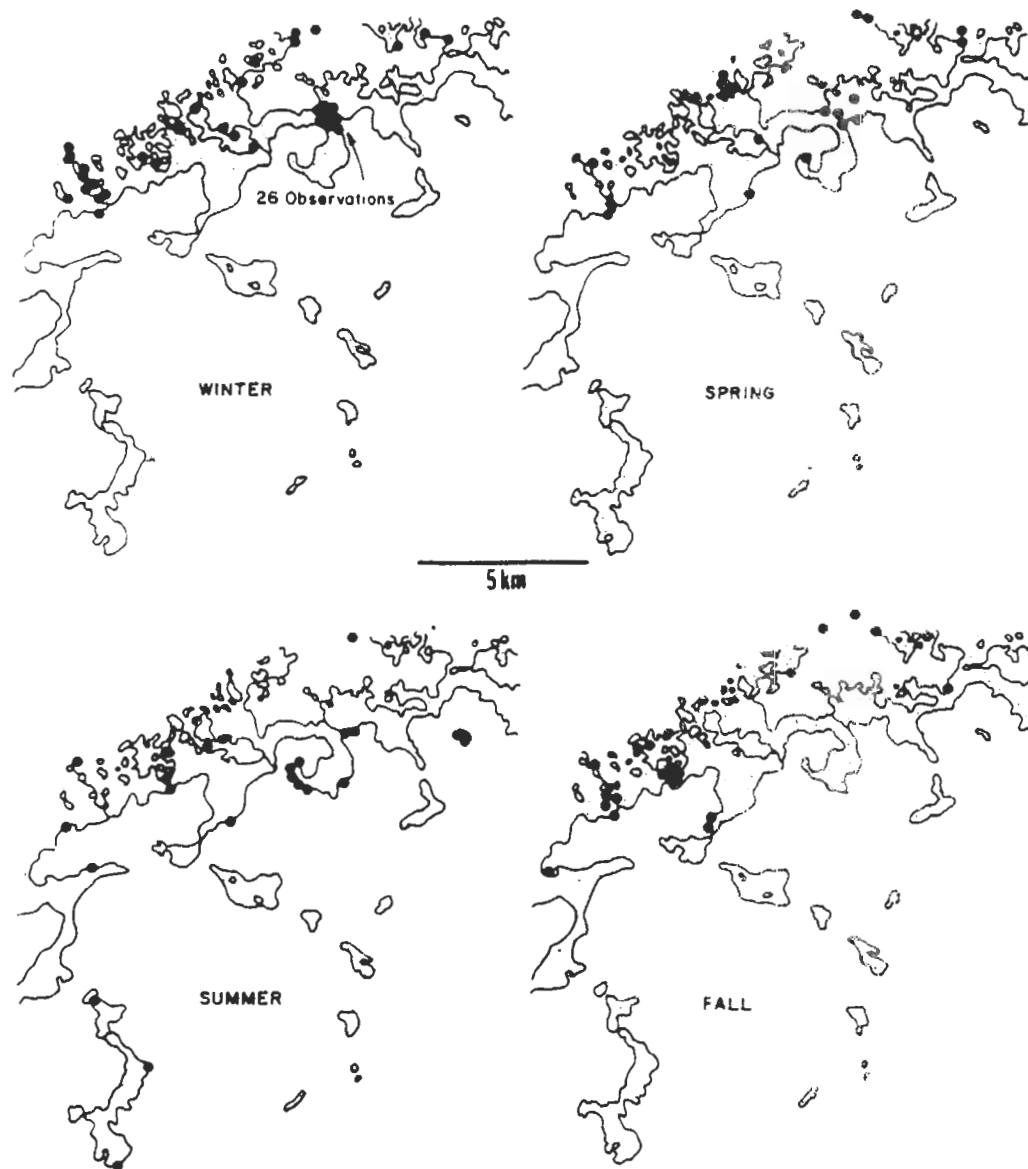
cut scutes and numbered cattle ear tags at

FIG. 3. Seasonal distribution of American crocodiles in northeastern Florida Bay. Land areas are stippled, and dots indicate sightings made during the surveys restricted to the main study area. Winter (non-nesting season, Dec.–Feb.); Spring (early nesting season, Mar.–May); Summer (late nesting season, Jun.–Aug.); Fall (post-nesting season, Sept.–Nov.).

We found documentation for 188 clutches of crocodile eggs in southern Florida since 1930 (Table 3; see Methods for sources). Early data are scattered, but the number of known nests increased substantially from the early to late 1970s. In that the number of clutches found depended on the effort expended in looking for them, the higher numbers are primarily indicative of greater search effort. However, we note that the available data cannot support the proposal that an overall decrease in crocodile nesting has taken place in southern Florida (cf. Ogden, 1978).

Most nests have been found on Key Largo, Alligator Bay, and Madeira Beach (Table 3); these account for over half of the known clutches. Seven of 10 nesting areas were also active historically, in 1930–1950. Reports of nesting near

Alligator Bay go back to 1914, and on Madeira Beach to 1946. Nesting on Cape Sable and at Turkey Point has been known only in the last decade.

American crocodiles nest in spring and summer in Florida. It is likely that courtship occurs in late January and February, as is the case for captive crocodiles in Florida (Moore, 1953; Garrick and Lang, 1977). During this period, crocodiles remained in their typical inland habitat where we saw telemetered animals together, indicating that courtship and mating occur in the mangrove swamps rather than in Florida Bay. Based on the literature (Lang, 1975; Garrick and Lang, 1977), it is likely that males maintain short-term courtship territories within the broadly-overlapping activity areas.

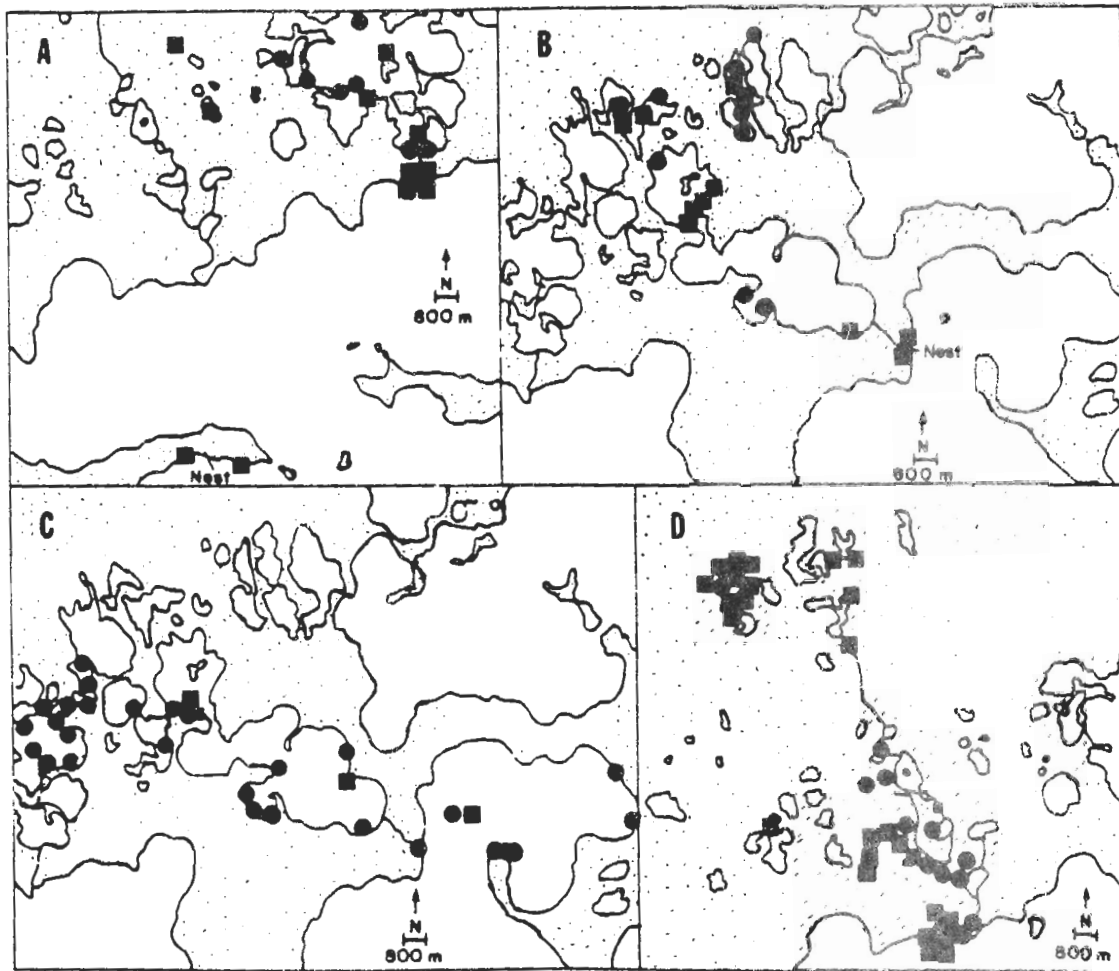Crocodiles first visit potential nesting sites in

FIG. 4.   Locations of four adult crocodiles along the northern shore of Florida Bay as determined by radio telemetry. Dots represent fixes in the non-breeding season; squares represent fixes in the breeding season.

mid March, continuing for over a month. We observed fewer animals, less frequent nest visitation, and delays in initiating nesting during periods of storms or high winds. Physical evidence suggested that March–April is a period of nest-site selection. At a site, crocodiles typically visited, crawled over, and dug at numerous places. Substantial digging began in mid April, with eggs being laid in late April to May. Based on clutches for which we had good information, we estimate that the average laying date was 5 May (SD = 12.1 days, $N = 12$). The average incubation period was 85 days. The average hatching date was 29 July (SD = 6.7 days, $N = 27$ clutches).

A nesting crocodile deposits its eggs in a cavity dug in soil, which is then covered. Nest site dimensions ranged from a hole 1×1 m to a mound $7 \times 5 \times 1$ m tall. In general, nests were dug on high ground, in an open area cleared of vegetation. Open areas ranged from 2×3 m to 10×15 m. The nest was placed an average of 5 m from the water's edge ($\bar{x} = 5.3$ m, SD = 4.26 m, $N = 20$ clutches) but also as far as 17 m from shore.

Egg deposition sites may be divided into creek nests and shore nests. The former are on the raised banks of relatively deep creeks; the latter are on the beach shores of Florida Bay. Nests on canal banks at Turkey Point and Key Largo are analogous to creek nests in natural habitats. Creek nests appeared to be in more suitable nesting habitat than did shore nests because they were located on high, well-drained soil adjacent to deep (>1 m) water protected from the effects of wind and wave action, and within the habitat used by crocodiles throughout the year. Nests on beaches fronted shallow water exposed to wind and wave action. As noted above, such sites were abandoned by adult crocodiles soon after their eggs hatched.

The amount of soil mounding at nest sites was variable. Although American crocodile nests have been divided into "hole nests" and "mound nests" (Campbell, 1972; Ogden, 1978), our data indicate that there exists a continuum between the two. The average height of nests measured was 0.39 m (SD = 0.331, $N = 20$) We defined a mound nest as one in which the elevation of the top of the soil material above the cavity was higher than the surrounding ground level. By this criterion we found that 40% ($N = 20$) of the
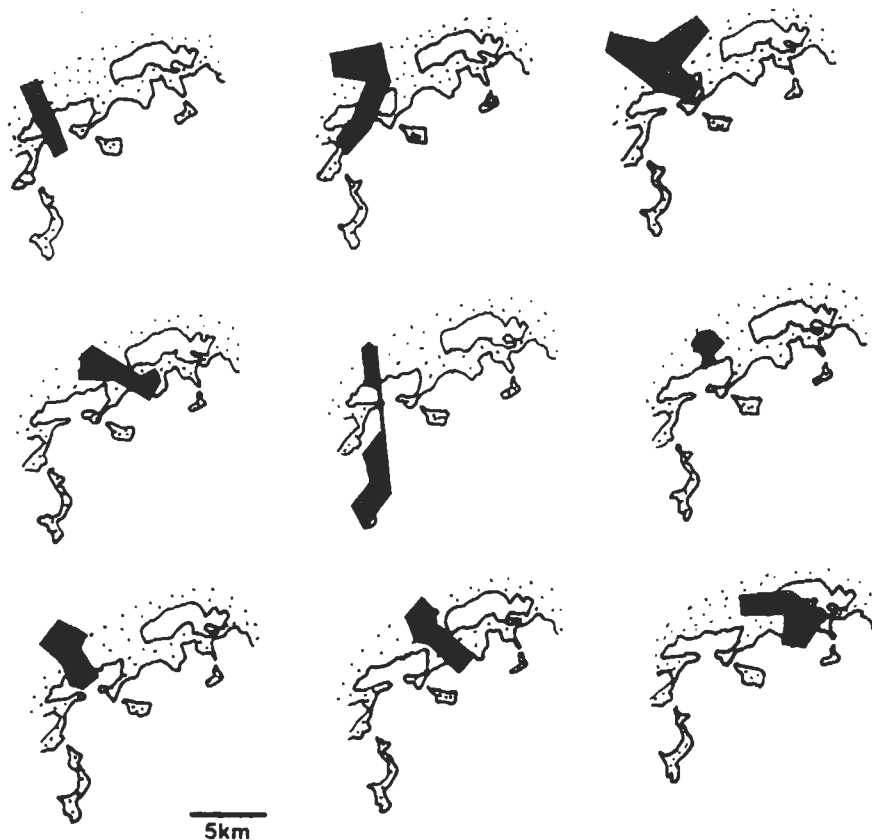
FIG. 5. Activity areas of nine adult and subadult American crocodiles in Florida Bay. Polygons enclose the activity areas of individual crocodiles as determined by radiotelemetry.

nest sites could be classified as mounds. Some mounds were relatively permanent and received clutches in most years. One well-known location, called Madeira Mound, may have been in use since the 1940s and certainly since the 1950s (Campbell, 1972). Variability in nest morphology appears to occur at individual nest sites, and therefore perhaps among nesting events of a single individual. At some traditional sites such as Mud Creek, the clutch was placed in a hole one year and a mound the next. Not all mounds constructed in a year received eggs. At one site with a reworked mound, the clutch of eggs was laid in a hole in the trail leading to the nest. It is likely that egg laying takes place when appropriate substrate conditions are encountered irrespective of whether a mound had developed from the scraping and other exploratory activity.

Crocodiles nested in four soil types: sand, marl, peat, and rocky spoil. The latter two substrates were artificially available on Key Largo and Turkey Point, respectively. Marl consisted of very fine soil particles, whereas sand consisted mostly of shell particles (Lutz and Dunbar-Cooper, 1984). Marl nests are on natural creek banks, whereas all sand nests are on beach ridges along the shore of Florida Bay. In 1980–1981, we found 14 clutches (64%) in sand and 6 in marl. Sand nests tend to be mounds and

marl nests, holes, but not always. Sand nests included 10 mounds and 4 hole nests; marl nests included 2 mounds and 4 holes. Mounds in sand tended to be larger ($\bar{x} = 0.61$ m) than those in marl substrate ($\bar{x} = 0.45$ m), but the difference is not significant with the available sample size ($t = 1.49$, $P > 0.05$, $N = 10,2$).

Communal nesting occurred in Florida Bay. This conclusion is based on the evidence that some clutches were laid very close to each other,

TABLE 2. Numbers of clutches of crocodiles located in southern Florida (dashes indicate no data available).

Year	Florida Bay	Cape Sable	Key Largo	Turkey Point	Total
1970	5	—	1	—	6
1971	10	—	1	—	11
1972	10	—	2	—	12
1973	10	—	3	—	13
1974	7	—	—	—	7
1975	—	1	—	—	1
1977	11	—	—	—	11
1978	12	—	7	2	21
1979	13	1	5	1	20
1980	12	1	—	—	13
1981	9	—	4	2	15
1982	5	1	4	1	11
Maximum	13	1	7	2	23

TABLE 3. Temporal and geographic distribution of known crocodile nests in southern Florida.

Area	<1930	1930–1949	1950–1959	1960–1969	1970–1975	1977–1982
Biscayne Bay						
Key Largo		3	0	2	7	20
Miami Beach	1					
Turkey Point		0	0	0	0	6
Florida Bay						
Alligator Bay	1	0	2	5	14	19
Black Betsy		4	1	1	5	7
Davis Cove		1	1	3	5	8
East Florida Bay		3	2	1	0	0
Little Madeira Bay		2	0	1	4	6
Madeira Beach		2	2	5	10	13
Trout Cove		1	4	2	4	9
Western Lakes		0	0	0	3	3

as close as 1 m apart in the same mound, and that in each case the clutches contained eggs of different sizes. (Egg sizes differ among individual alligators [Ferguson, 1982].) It also seems highly unlikely that a single crocodile would be able to produce two complete clutches within the limited egg-laying period. Thus we believe that double clutches were from different females. We found four paired clutches at three sites in three years. Five large clutches reported by Ogden (1978) also consisted of two egg clusters each (Lang, pers. comm.). The inference that Florida Bay crocodiles may nest communally is also supported by the courtship and egg deposition patterns of animals in captivity (Garrick and Lang, 1977), and observations in other locations such as Jamaica and Hispaniola (J. Ottenwalder, pers. comm.).

The average clutch size of crocodiles in southern Florida was 38.0 eggs (SD = 9.45 eggs, N = 46). The smallest clutch we found was 15, the largest 56. The average clutch size calculated by Ogden (1978; 44, range = 19–81, N = 20) is inflated because of the inclusion of five multiple clutches, including nests of 56 eggs in 1971, of 81, 73, and 78 in 1972 (Ogden, 1978), and of 55 in 1973 (Lang, pers. comm.). We now have counts of 46 single clutches, including clutches from 1951, 1967, and 15 from Ogden (1978), providing an acceptable estimate of clutch size in southern Florida.

American crocodiles in Florida Bay did not defend their nest sites against humans. Only twice did we encounter animals at nest sites, although physical evidence suggested frequent visitation by crocodiles through most of the nesting season. One crocodile encountered at a nest site did not respond to our presence; another at a site that did not receive eggs gave a throaty growl and oriented toward the intruder but neither approached nor retreated.

Excessive disturbance of the female at the nest site caused abandonment of the clutch that year and changes of site in subsequent years. Only one of 6 females we captured near but not at nest sites returned to open her nest that year. In all cases nest sites near capture locations were not used the following year. The female photographed opening her nest by Ogden and Singletary (1973) and later captured, moved her nest site the following year (Lang, pers. comm.). Another female captured at a nest site on one key was seen at a freshly-mounded site on another key the next year, although no eggs were laid where she was found.

The failure of crocodile eggs to hatch was due to infertility, predation, and embryonic mortality (Table 4). The fertility rate was 90% (281 of 314 eggs were banded). All clutches examined had fertilities between 84 and 100%, except for one of 46%. From 1971 to 1982, 14% (14 to 99) of known clutches were depredated by raccoons (Procyon lotor). Because predation can call attention to otherwise overlooked nest sites, the percentage loss is an overestimate. We found no predictable pattern of loss among sites, between shore and creek nests, between mound and hole nests, or between nests visited by humans and those not. We believe that the low density of crocodile nesting inhibited the development of nest robbing specialists among local raccoons, and that nest robbing is a chance event.

Embryonic mortality, which affected 14% of all clutches, was caused by either desiccation or flooding. In the relatively dry summer of 1981, 54 embryos from four cavities failed to hatch. Each showed signs of excessive water loss, either the presence of air cavities or incomplete absorption of yolk sacs (Ferguson, pers. comm.; Tracy, pers. comm.). Flooding occurred when ground water entered the egg cavity (Mazzotti

et al., 1988). We found, by monitoring ground water level in cavities, that flooding killed one clutch each in 1980 and 1981 and partially killed two clutches in 1980. Mortality was nonrandom between sand and marl nests ($\chi^2 = 740$, df = 1, $P < 0.01$) and between mound and hole nests ($\chi^2 = 8.51$, df = 1, $P < 0.01$), suggesting that marl and hole nests were more susceptible to embryonic mortality. All flooding occurred in hole nests on creek banks.

During 1977–1980, 46 clutches (78.3%) and an average of 9.4 nests per year hatched some animals. Based on mean clutch size, an average of 357.2 eggs was produced annually. We estimated egg hatching success in 1980 by counting empty egg shells (an underestimate of hatching) and subtracting the number of unhatched eggs from the initial clutch size (an overestimate). Our estimate lies between 42.5% and 72.6% hatching success. Using the midpoint of the range, 57.5%, we calculate that about 200 (205) eggs hatched per year in northeastern Florida Bay. This would be an underestimate to the extent that other nests were undiscovered.

Hatching for the entire population extends over a period of about one month. In 1980, for example, hatching dates of nests ranged from July 23 to August 19 with a mean of August 4 ($N = 9$ clutches). The earliest hatching dates known in southern Florida were July 5 and 7, at Turkey Point (R. Gaby, pers. comm.).

Hatchlings.—American crocodiles open their nests and assist eggs in hatching (Ogden and Singletary, 1973), and in Florida Bay the presence of an adult animal was essential for hatching. Some eggs were hatched by the adult at the nest cavity, while others were carried to the water's edge where hatching took place and the shells were discarded. Based on the behavior of other species and our observation that undeveloped eggs and dead clutches were not excavated, we believe that vocalizations initiate release from the nest cavity. The release of young by adults is essential to survival because hatchlings did not escape from a nest cavity by themselves. We found that young partially emerged from their shell, half unburied, and exposed to 38°C temperatures did not complete hatching on their own and died. In some nests, hatching was completed on a single night whereas others were released over several nights.

We have no evidence of parental care by adult crocodiles after hatching. Despite our hundreds of person-days of observation, adult crocodiles were observed near hatchlings only five times. Three were during daylight, and in each instance the adult crocodile left the area when discovered. The rapid movement of a telemetered adult female away from her presumed hatchlings within two days after hatching further suggests a lack of parental care.

TABLE 4. Causes of hatching failure in American crocodile clutches (data from 1971–1974 from Ogden, 1978, with double clutches separated into their components).

Year	Predation		Embryonic mortality	
	Number of clutches	%	Number of clutches	%
1971	5	50	1	10
1972	0	0	3	30
1973	1	10	0	0
1974	1	14	1	14
1977	1	9	2	18
1978	1	8	1	8
1979	3	23	1	8
1980	0	0	1	8
1981	1	11	2	22
1982	1	20	2	40
Total clutches or mean %	14	14.5	14	24.6

Hatchlings were active at night and inactive by day. They initially remained together in the water or on land near their nest site. Microhabitats chosen by hatchlings were those having the lowest temperatures available (χ^2, $P < 0.05$, $N = 42$). They emerged one-half hour before sunset, initially remaining near their groups. Immediately following sunset, we observed them swimming individually between red mangrove clumps, moving both directions along the shore and thereby dispersing the group. We followed one hatchling swimming vigorously at 10 m/min for approximately 125 m from the nest. By daybreak they returned to shore.

By following tagged and telemetered hatchlings we found that animals from shore nests dispersed rapidly. At shore nests, hatchlings became displaced during their nocturnal swimming activity, usually in the direction of longshore currents. Movements of hatchlings up to 300 m per day were observed. By two weeks, some hatchlings from shore nests had moved inland, eventually entering protected interior ponds or flooded flats. We found one hatchling 1.6 km from a shore nest 7 weeks after hatching. By 7 months, hatchlings had disappeared from all shore areas.

Hatchlings remained at creek nests for a number of months. We documented that telemetered hatchlings remained adjacent to their nest site for up to three weeks, until the transmitters failed. Tagged hatchlings remained at a creek nest site 7 months after hatching. We several times observed hatchlings in a creek, displaced more than 50 m downstream by the current during our capture attempts, swim back to their

previous sites immediately. These observations support the contention that creeks are the preferred habitat for young crocodiles, which we believe to be because they offer substantial cover and protection from wind and wave action.

To test directly the hypothesis that wave action determined hatchling habitat use, we observed choice of land or water by 69 hatchlings 1-43 days old in areas having differing wave action (<5 cm and >5 cm wave height), but having similar salinity and temperature. We found that occupancy of land and water habitats was not independent of wave action ($\chi^2 = 38.4$, df = 1, $P < 0.05$). Hatchlings moved onto land when wave action was present but remained in the water when wave action was absent.

Hatchlings remained sedentary, once appropriate habitat was found, through the following spring or longer. We found one 17 month old crocodile from a shore nest in a creek near another nest site. Crocodiles on northern Key Largo have a similar residency period in the protected habitat there (P. Moler, pers. comm.).

Juveniles disperse from such "nursery" areas after their first year. One observation may exemplify the typical situation. A crocodile we tagged at a creek nest on 30 July 1978 was recaptured 36 months later 13 km away (P. Moler, pers. comm.). It had entered an area also occupied by juveniles dispersing from Key Largo, which had covered similar distances. Interchange of young crocodiles also occurred between Turkey Point and Key Largo (Gaby et al., 1985). These findings show that juvenile movement is an important mechanism of dispersal and interchange among nesting areas. Our animal was found because it happened to be in an accessible location near a major highway, whereas most dispersing juveniles would not be seen.

Mortality.—The mortality of juvenile crocodiles in Florida Bay appears to be relatively high. However, the causes of mortality remain elusive, as it is difficult to know whether failure to find hatchlings is due to their death or dispersal. It is notoriously difficult to observe juvenile crocodilians, especially in such inaccessible habitat as mangrove swamp. Nonetheless we have documented survival of tagged hatchlings for 5 months (3 animals), 7 months (1 animal), 17 months (1 animal), and 36 months (1 animal). Documented hatchling survival is very high on Key Largo, where the nursery sites are accessible (P. Moler, pers. comm.).

We eventually lost track of all radiotelemetered hatchlings, but this did not necessarily indicate mortality, as the life span of the transmitters was about two weeks. Four transmitters were recovered without crocodiles. Two were found intact, knots tied, with no evidence as to

the fate of the hatchling. We suspect that one of the remaining hatchlings was eaten because we found holes, probably tooth punctures, in its transmitter casing. The second transmitter was found next to the hatchling's skull. A similar case of possible predation was observed during 1980 when a hatchling was tracked to a land crab (*Cardisoma guanhumi*) burrow (J. Lang, pers. comm.). On four occasions we saw blue crabs (*Callinectes sapidis*) eating living or dead hatchling crocodiles. Although a number of potential predators have the ability and probably the opportunity to eat young crocodiles, the extent of predation remains undetermined. Southern Florida crocodiles grow rapidly (our data suggest a growth rate of 41 cm/yr or 68 cm TL at 1 yr), which would decrease their susceptibility to predation.

With respect to juvenile and adult crocodiles, documented mortality is primarily human-caused. Of 26 documented deaths in 1971–1983, all but 6 were related to human activities; 17 deaths were the result of shooting or being hit by cars (Kushlan, 1988). Of the possible natural deaths, there was reasonable though circumstantial evidence of the death of one subadult from cold and of another during drought. These mortality data are biased because unnatural mortalities were far more likely to be reported than those from natural causes occurring in inaccessible locations. Nonetheless, 10 adult animals were known to have died in 12 years, providing a minimum death rate of 0.8 adults/yr.

Population Structure.—The proportion of females in the southern Florida crocodile population is 0.67 ± 0.10. This value is not different from the expected 1:1 ratio (*t*-test, $P > 0.05$, two-tailed). The proportion in Florida Bay was 0.70 females, based on 12 females and 5 males caught in our indiscriminant capture program. Crocodiles captured at Turkey Point included 2 subadult males, 1 adult male, 1 subadult female, and 3 adult females (R. Gaby, pers. comm.). Adding these captures to those from Florida Bay brings the total to sixteen females to eight males captured in southern Florida. The small sample size and possible bias in capturing males reinforce the conservative position that the sex ratio is not different from 1:1.

We found all expected size classes in the southern Florida crocodile population during surveys and capture programs (Fig. 6). Lacking information on growth rates for all but hatchlings, it is not possible to construct a detailed age-class distribution for southern Florida crocodiles. However, we can define three age groups (hatchling, juvenile, adult) by size; the Florida Bay population is distributed across all three age categories (77% hatchling, 16% juveniles, 6%

adults). The size structure of the breeding females appears well distributed, with a 1:3:1 ratio among crocodiles in the 2.25–2.5, >2.5 < 3.0, and >3.0 m TL size classes.

The age categories were determined as follows: (1) crocodiles less than 0.5 m total length are in their first 6 months of life and are considered hatchlings; (2) juveniles were from 0.5 m to the size at first breeding, 2.25 m; (3) adults were larger than the size at first breeding, which was determined through several lines of evidence. Female crocodiles associated with specific nest sites during the nesting season were 2.28, 2.47, 2.57, 2.59, 2.96, and 3.08 m TL. All but one, captured in early April, had distended cloacae when captured, indicating breeding (Webb, pers. comm.). In 1981, a small female, 2.28 m TL, was captured at a nest site that had not been used previously, suggesting that it may have been her first breeding attempt. LeBuff (1957) reported nesting in captivity by crocodiles 7–9 ft TL (2.1–2.7 m, but probably measured only to the nearest 1 foot). We assume males are capable of mating at the same size as females.

The largest crocodiles captured in Florida Bay were around 3 m TL. The largest female captured was 308.0 cm TL (166.5 cm SV); the largest male was 289.3 cm TL (147.5 cm SV). On surveys we made 10 sightings of animals we placed in the 3 m class (class center, 25 cm intervals), and one in the 3.5 m class. Males grow larger. We handled a male at Turkey Point that was 3.75 m TL and a captive male originally from Jamaica that was 3.95 m TL. Our 3 m long female may have been postreproductive when she died of undetermined causes in 1979 in that the eggs laid at the site which she frequented failed to develop in 1977 and 1979 (they were eaten by raccoons in 1978).

Population Size.—Using Chabreck's model, we calculate that 90 ± 32 adult and juvenile crocodiles occurred in our study area and 130 ± 46 in Florida Bay. Adding the number of hatchlings we calculated previously, we estimate a maximum population after hatching of 330 crocodiles in Florida Bay.

To calculate the variables in Chabreck's formula we used survey, capture, and nesting data from our study area in northeastern Florida Bay. The maximum nesting effort (N) was 13 nests in the study area in 1979. The sex ratio (F) was 0.67 ± 0.10. The percentage of females nesting (E) was 0.72 ± 0.09 (the maximum number of nests, 13, divided by our minimum estimate of the adult female population, 18, which included the 13 females we captured plus the 5 nest sites at which we did not capture a female). The proportion of adults (A) was 0.30 ± 0.06 (the number of adults captured, divided by the total
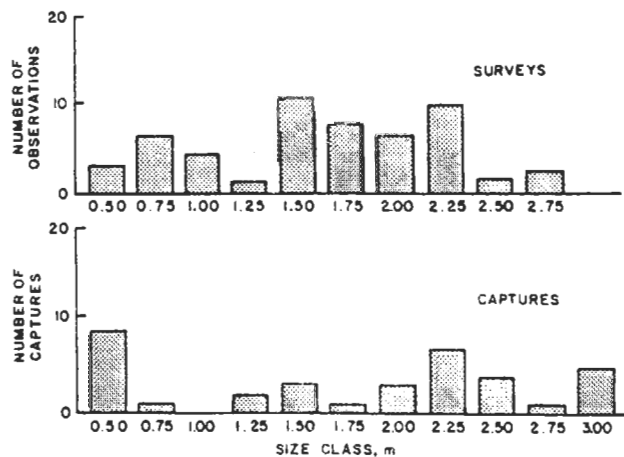

FIG. 6. Size distribution of American crocodiles in southern Florida. To avoid bias these data do not include 369 animals <0.5 m TL captured in concentrated efforts at nests. There was no difference in the size frequency distributions of crocodiles observed on surveys or captured (U-test, P > 0.05).

number of non-hatchling crocodiles captured). Because 69% of all animals tallied on standard surveys were observed in our study area we were able to extrapolate the number in our study area to all of Florida Bay by multiplying by 1.45.

We estimate that the total population of adult and juvenile crocodiles in southern Florida is 220 ± 78 (or between about 150 and 300) animals. After hatching, the total population would on average be over 500 animals. To estimate the total southern Florida population, we assumed that parameters we calculated for Florida Bay hold elsewhere and that the number of animals in Florida Bay is proportional to the percentage of nests there (24/13 = 1.69). Thus to extrapolate, we multiplied our Florida Bay population estimate by 1.69.

The approximately 220 adult and juvenile crocodiles are distributed as follows: 130 near Florida Bay, 70 on northern Key Largo, and 20 at Turkey Point. The latter estimate compares well with the 19 estimated by Gaby et al. (1985). A few additional animals may be expected periodically elsewhere in the overall Florida range (Kushlan and Mazzotti, 1989).

Introductions.—We have found 15 instances of American crocodiles being released in southern Florida, involving about 45 animals over 17 years (see also Behler, 1978). Seven of these releases involve animals known or suspected to be foreign to the resident Florida population. Only 4 of these animals were released in northeastern Florida Bay, the rest having been released near Cape Sable. Most releases were by Federal or state officials in cooperation with zoos or animal attractions seeking to dispose of specimens. Six animals were adults when released; 20 were hatchlings from Panama. Because none was permanently and distinctively marked, there is no

way of knowing whether these animals survived.

DISCUSSION

Habitat.—On the basis of the results of this study, we can now summarize the habitat preference of the American crocodile in Florida. Its overall distribution and probably its nesting range appear to be determined by the distribution of relatively warm winter temperatures (Kushlan and Mazzotti, 1989). Within this range, crocodiles appear to frequent protected coastal areas, particularly mangrove-lined coastal creeks and ponds off Florida Bay and similar artificial habitat on northern Key Largo and at Turkey Point. Crocodiles use the open water of Florida Bay only in transit to nest sites.

These results indicate that the American crocodile is an estuarine species, not a marine one (cf. Barbour, 1923; Moore, 1953; Ogden, 1978), a view supported by Dunson's (1982) demonstration that hatchlings grow faster in brackish water than in either fresh or saline water. We suggest that an important aspect of their occupancy of mangrove swamps is the avoidance of wind and wave action, as has also been reported for other crocodilians (Graham, 1968).

It appears that the salinity of water in Florida Bay does not adversely affect crocodiles, because both adults and hatchlings are able to compensate for high salinity, physiologically and behaviorally, and especially because they do not live in saline water permanently. Although early laboratory studies (Dunson, 1970; Evans and Ellis, 1977) demonstrated that hatchling crocodiles should not be able to survive in the salinity of water found near nest sites, subsequent studies conducted in collaboration with our own revealed behavioral adaptations to high salinity that include eating hydrated prey, drinking fresh water, avoiding salt intake even in relatively high salinity, and a body mass effect (Dunson, 1982). American crocodiles also possess salt glands (Taplin et al., 1982), although their function remains in dispute (G. Grigg and W. Dunson, pers. comm.).

A second aspect of habitat choice is the use of sites for nesting. High-ground marl banks and sand beaches occur in limited numbers, but their overall extent and the ability of crocodiles to nest communally indicate that nesting habitat is not limited in Florida Bay.

Sociality.—Based on the use of large, overlapping activity areas, our frequent observation of animals together, and evidence for communal nesting, we suggest that the American crocodile is a social species. This conclusion is supported by studies of captive animals, whose behavior included a substantial social component (Garrick and Lang, 1977). They concluded that the American crocodile was more social than the American alligator (*Alligator mississippiensis*).

Nesting.—Nesting phenology of the American crocodile in southern Florida is in concert with local hydrologic and temperature cycles. Nesting begins after the cold weather of winter, near the end of the dry season, and ends prior to the highest water levels of the wet season. Highest rainfall and lowest salinities of the year occur in the post-hatching period. Thus the incubation period avoids both the low temperature of winter and high temperatures of late summer. This timing tempers the effects of the twin perils to incubating eggs, desiccation and flooding (Lutz and Dunbar-Cooper, 1984; Mazzotti et al., 1988).

The timing of nesting in the American crocodile differs in various parts of its range. Crocodiles nest at the same time in Florida as in Venezuela, Mexico, and Honduras, but they nest in December–February in Ecuador and Panama (Schmidt, 1924; Rand, 1968; Medem, 1973; Alvarez del Toro, 1974). American crocodiles from Jamaica maintained near Lake Okeechobee, Florida, nested several weeks before Florida Bay animals (J. Lang, pers. comm.); and captive Florida crocodiles at Bonita Springs laid eggs from mid March to mid May (Moore, 1953). It is likely that initiation of the nesting season is in part temperature-related, gametogenesis undoubtedly being inhibited in cold temperature.

The variation found in the nest sites of the American crocodile in Florida Bay supports none of the theories proposed to account for crocodilian nest structure. It has been postulated that nest structure has a phylogenetic basis in which hole nesting is a primitive characteristic (Greer, 1970). However, the American crocodile has been described both as a hole-nester and as a mound-nester (Schmidt, 1924; Greer, 1970; Neill, 1971; Campbell, 1972; Ogden, 1978). Our measurements confirm these observations. Webb et al. (1983) suggested that mounds occur in species that nest during wet seasons or in marshes. Neill (1971) suggested that the compactness of the substrate determined whether a nest was a hole or a mound. Our observations suggest that whether a clutch is placed in a mound depends on the individual animal and on its finding an appropriate substrate for the clutch. The existence of a mound is not related to substrate. Moreover, we found no statistical difference in the mean size of mounds in marl and sand. Nonetheless, the largest mounds were made of sand. It seems likely that the mound nests of the American crocodile are not homologous to those of other mound building crocodiles who invariably construct mounds of vegetation.

Hatchlings.—Most crocodilians defend their nest and hatchlings (Cott, 1971; Kushlan, 1973; Alvarez del Toro, 1974; Hunt, 1975; Kushlan and Kushlan, 1979). Our failure to observe nest defense, pod formation, or hatchling defense is atypical, even for American crocodiles in captivity and in other locations (Alvarez del Toro, 1974; Dugan et al., 1981). Ogden and Singletary (1973) documented nest opening, egg opening, and transport of young in the mouth by adult American crocodiles in Florida Bay, and we found that such parental assistance in hatching nests is essential to hatchling survival. The reason for lack of parental behavior after hatching is unclear. It is possible that a past history of human disturbance has eliminated guarding behavior from the local population. Alligators guard nests primarily in areas free from harassment (Kushlan and Kushlan, 1979). Alternatively, limited parental care may be a long-standing, intrinsic characteristic of crocodiles in Florida.

Juvenile crocodiles may remain at suitable "nursery" sites for a year or more, but all evidence suggests that dispersal occurs in the second year. Such dispersal is characteristic of many crocodilians (Webb and Messel, 1978; Messel et al., 1980). However, in Panama Rhodda (1984) found American crocodiles 10 and 22 months old occupying small activity areas near their nest site. Thus the amount and extent of dispersal may differ among populations.

The age distribution of Florida Bay crocodiles demonstrates that long-term recruitment is occurring. That the proportion of juveniles found was somewhat smaller than might be expected in a stable population could reflect either high hatchling mortality or the underrepresentation of subadults in capture and survey data. The latter is probably the case in that such under-representation is found in most crocodilian studies (T. Joanen and H. Messel, pers. comm.). Rapid growth rates also provide a quick passage through the smaller size classes. Furthermore, concurrent studies in southern Florida have demonstrated that hatchling survival is relatively high. Moler (pers. comm.) reported survivorship of 50% of tagged hatchlings in 1 yr in the protected habitats of northern Key Largo, and Bohnsack (pers. comm.) reported survivorship at Turkey Point for 7 years of 5% of hatchlings tagged in 1978 and 15% of hatchlings tagged in 1979 (see also Gaby et al., 1985). Graham (1968) stated that theoretically a crocodile population could remain stable despite a hatchling mortality of 99%.

Population Size.—Our estimate of about 220 animals represents a small but potentially viable population. We were able to calculate this estimate from population parameters of the study population. Previous estimates have been based on data from other species or on assumptions unsecured by data. Ogden (1978) estimated the population to be 400–500 animals based on alligator and Nile crocodile data parameters and assumptions as to female proportions and number of nest sites (Chabreck, 1966; Cott, 1971). Ogden (1978) also applied estimates of mortality and age at maturity to predict a population of 100–400 crocodiles, excluding hatchlings.

We do not believe that there is sufficient information on which to base any estimate of population size prior to human settlement of southern Florida. Ogden (1978) interpreted the writings of explorers and crocodile hunters to indicate that they were able to see "a few crocs per day (< 10)." Contrasting that with his more recent experience, he guessed that "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" (Ogden, 1978, p. 192). Even today, however, one can expect to see at least a few crocodiles per night in areas where they occur, a situation not very different from that reported historically.

By the 1940s it was thought that the number of crocodiles in southern Florida had been greatly reduced from historic numbers (Beard, 1938; Carr, 1940; Allen and Neill, 1949; Dickinson, 1953). However, again, little actual information exists from the 1940s on which to base such an impression. Crocodiles, like other wildlife, certainly were hunted by early settlers and probably before that by Indians (Smith, 1896). Settlement of Biscayne Bay began by the 1870s, so that even before 1900 crocodiles were probably killed there. Documentable hunting was usually for museum or zoo specimens. A decrease in crocodiles may have been initiated by hunting, but habitat loss to development of Miami Beach, Miami, and the Florida Keys was the ultimate cause of changes in the nesting distribution (Kushlan and Mazzotti, 1989). Despite any early reductions, we can conclude crocodiles were not uncommon in northeast Florida Bay and south Biscayne Bay through the early 1950s, but we can have no idea in what numbers they occurred.

The Florida population of the American crocodile clearly is small, restricted to the barely tropical tip of the Florida peninsula, and isolated from other such populations. What seems remarkable to us is not so much the small size of the population but its demonstrated ability to persist in the face of the intensive human occupancy of southern Florida. Its population characteristics fail to suggest any inherent in-

stability (Kushlan, 1988). However, such a small and restricted population is potentially at risk to the vagaries of random processes and catastrophic events, a situation not atypical of any rare species on the periphery of its range.

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