PROFILES

Conservation and Management of the American Crocodile

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ABSTRACT / The American crocodile is a rare and endangered species, the range of which has contracted to disjunct locations such as Hispaniola, Jamaica, Cuba, Panama, and southern Florida. In an attempt to determine what factors might be limiting population growth, an extensive collaborative research program was conducted in 1978–82 in southern Florida. Limiting factors explicitly studied included climate, hurricanes, population dispersion, nesting habitat, fertility, predation, nest chamber environment, juvenile survivorship, artificial mortality, disturbance, and environmental contamination. No single natural factor limits the population, although in concert various factors result in low adult recruitment rates. Such natural limitations explain the natural rarity of this tropical species at the temperate limits of its range. Two artificial sources of mortality are death of adults on roads and the flooding of nests by high groundwater tables. These sources of mortality are potentially controllable by the appropriate management agencies. Active management, by such means as protection of individuals, habitat preservation and enhancement, nest site protection, and captive breeding, is also appropriate for assuring the survival of a rare species. The American crocodile has survived in southern Florida in face of extensive human occupancy of parts of its former nesting habitat, demonstrating the resilience of a threatened species. This case history illustrates the efficacy of conducting research aimed at testing specific management hypotheses, the importance of considering biographical constraints limiting population status in peripheral populations, the need for active management of rare species, and the role of multiple reserves in a conservation and management strategy.

The American crocodile (*Crocodylus acutus*) ranges naturally along the tropical coasts of South and Central America and the West Indies (Figure 1). It is presently patchily distributed along the Pacific coast from Peru to Mexico, along the Caribbean Coast from Venezuela to Mexico, and from the Greater Antilles to Florida. Because of hunting and habitat alteration, most American crocodiles are confined to a few disjunct population centers in Hispaniola, Jamaica, Cuba, and Florida, with smaller population segments in Venezuela, Panama, Costa Rica, and Mexico. The northernmost population of this otherwise tropical species occurs on the southeastern tip of the Florida, USA, peninsula in Florida Bay and lower Biscayne Bay (Figure 2) (Kushlan and Mazzotti 1988a).

Because of its restricted distribution, small population sizes, and potential risk from hunting, the American crocodile is listed as endangered by the United States federal government (USFWS 1979) and the International Union for the Conservation of Nature and Natural Resources (Honegger 1968, IUCN 1986). It is further protected in international trade by CITES (Convention on the International Trade in Endangered Species). Owing to its location in the United States, the Florida population may be the one most amenable to management and long-term protection. However, limited data on its biology and potential response to management action has rendered the planning of appropriate management action and conservation policy tenuous at best. Such information is now becoming available from recent studies in various parts of its range, including the Dominican Republic (J. Ottenwalder, personal communication), Haiti (J. Thorbjarnarsen, personal communication), and Florida (Kushlan and Mazzotti 1988a, 1988b, Mazzotti and others 1988, Gaby and others 1985, this article, P. Moler, personal communication).

The risky position of any species that is endangered because of rarity, such as the American crocodile, demands caution in planning and initiating conservation schemes, yet makes the imperative for such schemes all the more compelling. The biological information required for management is twofold: an understanding of the factors that may be limiting the population and an assessment of the efficacy of various management actions. Several possible constraints to population stability have been proposed for the American crocodile in Florida, including nesting failure, human-caused death and disturbance, hurricanes, and water salinity (Moore 1953a, Evans and Ellis 1977, Ogden 1978, Hines and others 1984). In 1978–1982, a program of research was conducted to assess poten-

KEY WORDS: Crocodiles; Conservation; Endangered species; Florida; Florida Bay; Park management; Resources management

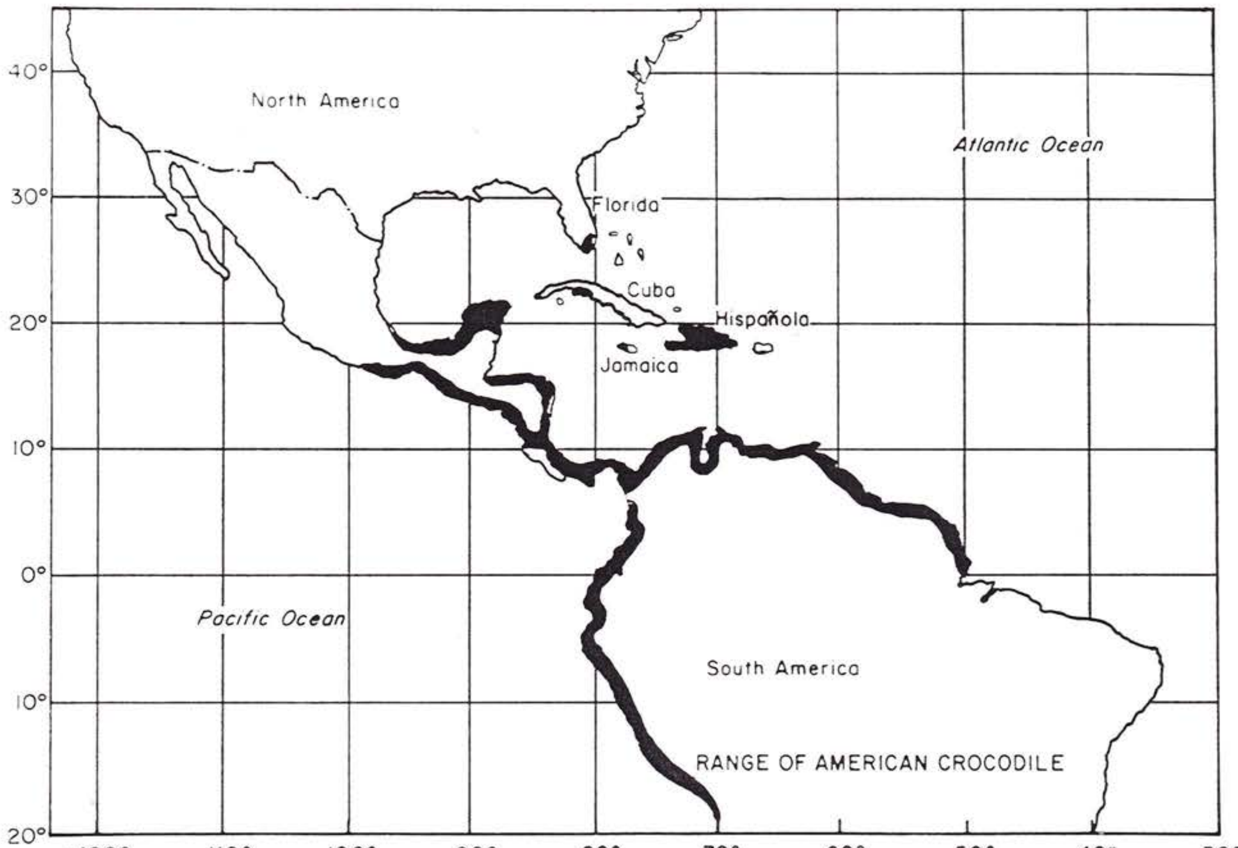

Figure 1. Map of the overall range of the American crocodile in the American tropics.

tial limiting factors and to evaluate the effectiveness of possible management action. In this article, I summarize the results of that program and discuss their bearing on management of this species. This case history has general applicability in illustrating the need to understand population limitation in a biogeographic context and the desirability of active management of species that are endangered because of natural rarity. The discussion also addresses a role for multiple nature reserves and captive management in such a conservation strategy.

Study Area

Studies were carried out in the core of the crocodile's Florida range, northeastern Florida Bay (Figure 2). Other concentrations of crocodiles are found on northern Key Largo and at Turkey Point, both in southern Biscayne Bay (Figure 3). The population segments at these sites were being studied by P. Moler and R. Gaby (personal communication) contemporaneously with studies in Florida Bay. All study sites were primarily mangrove swamps and associated creeks, canals, ponds, and the nearby open waters of Florida and Biscayne bays (Figure 4). The Key Largo site features old canals that provided secluded deep water and high ground nesting sites. The Turkey Point site is a series of canals associated with a nuclear power plant (Gaby and others 1985).

Potential Limiting Factors

Factors considered to be potentially limiting to population stability and growth were explicitly examined. These factors included climate, hurricanes, population dispersion, nesting habitat, causes of nesting failure, juvenile survival, salinity, unnatural mortality, disturbance, and environmental contaminants.

Historic Range

All available evidence suggests that the overall range of the American crocodile in Florida has not changed from its historical extent and that the core of the nesting population was always where it is today, in northeastern Florida Bay (Kushlan and Mazzotti 1988a). Thus the species was always restricted in its

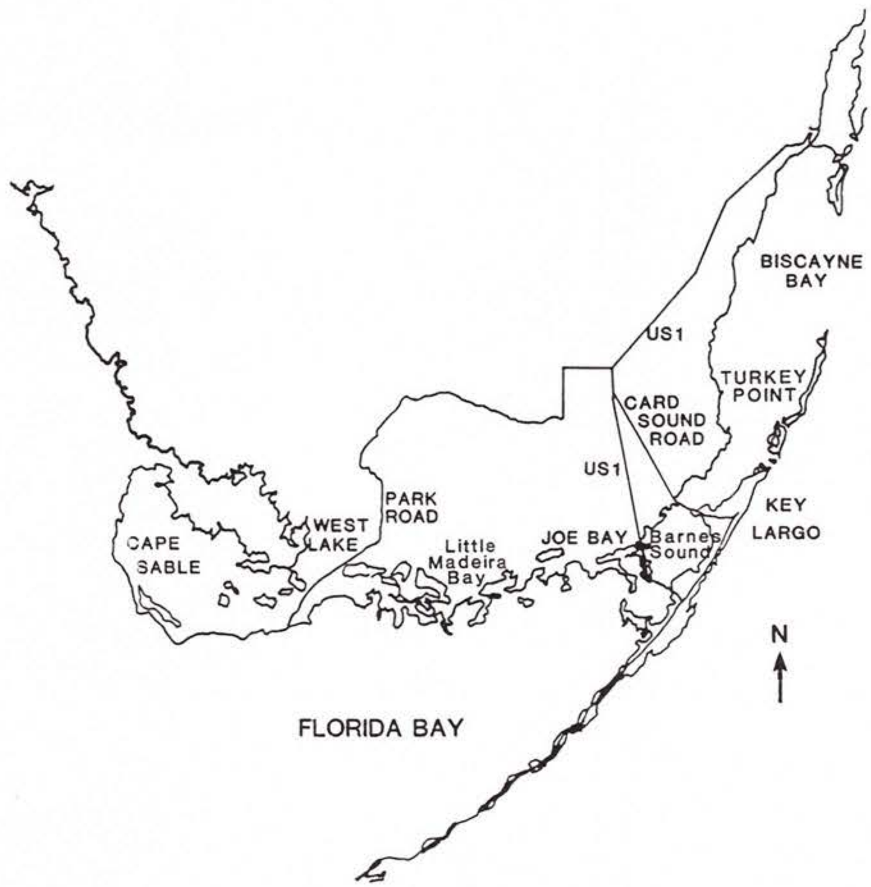

Figure 2. Map of southern Florida showing the primary study area and place names.

distribution at the northern extremity of its range and therefore could have maintained only a small population.

Climate

The range of the American crocodile in Florida coincides closely with that of mangrove swamp (Figure 4), which is restricted by freezing temperature (Chapman 1976, Lugo and Zucca 1977). Scattered evidence suggests that freezing temperatures can kill crocodiles. We found one subadult animal dead the day after air temperatures fell to freezing, as was similarly reported by Barbour (1923). The range in Florida coincides with winter 16° January air isotherms, and the crocodile's breeding range on the southeastern tip of the peninsula is the warmest zone on the Florida mainland (Kushlan and Mazzotti 1988a). Thus it appears that the overall range of the American crocodile in Florida and the restriction of breeding to the extreme southeastern tip of the peninsula appear to be related to seasonally cool temperatures.

Mortality from naturally occurring hot temperatures has not been found. Under experimental conditions hatchlings are stressed by temperatures above 40°C (Mazzotti and others 1988).

Hurricanes

It has been proposed that hurricanes adversely affect the crocodile population through death and displacement (Ogden 1978). To test this we radio-monitored crocodiles after two tropical storms, David in 1979 and Dennis in 1981, both of which were accompanied by high rainfall, winds, waves, and storm surge. Although some telemetered hatchlings were not found after the storm, several hatchlings were relocated near their previous fixes in shallow mangrove flats flooded by the storm. Telemetered hatchlings at Turkey Point also survived the storm (B. Bohnsack, personal communication). We saw no indication of mortality or of unnatural dispersal by telemetered adults as a result of the storms. On the basis of this evidence it seems that tropical storms do not limit the crocodile population.

Population Dispersion and Structure

The dispersion of relatively rare and inherently social animals (Garrick and Lang 1977) might be too

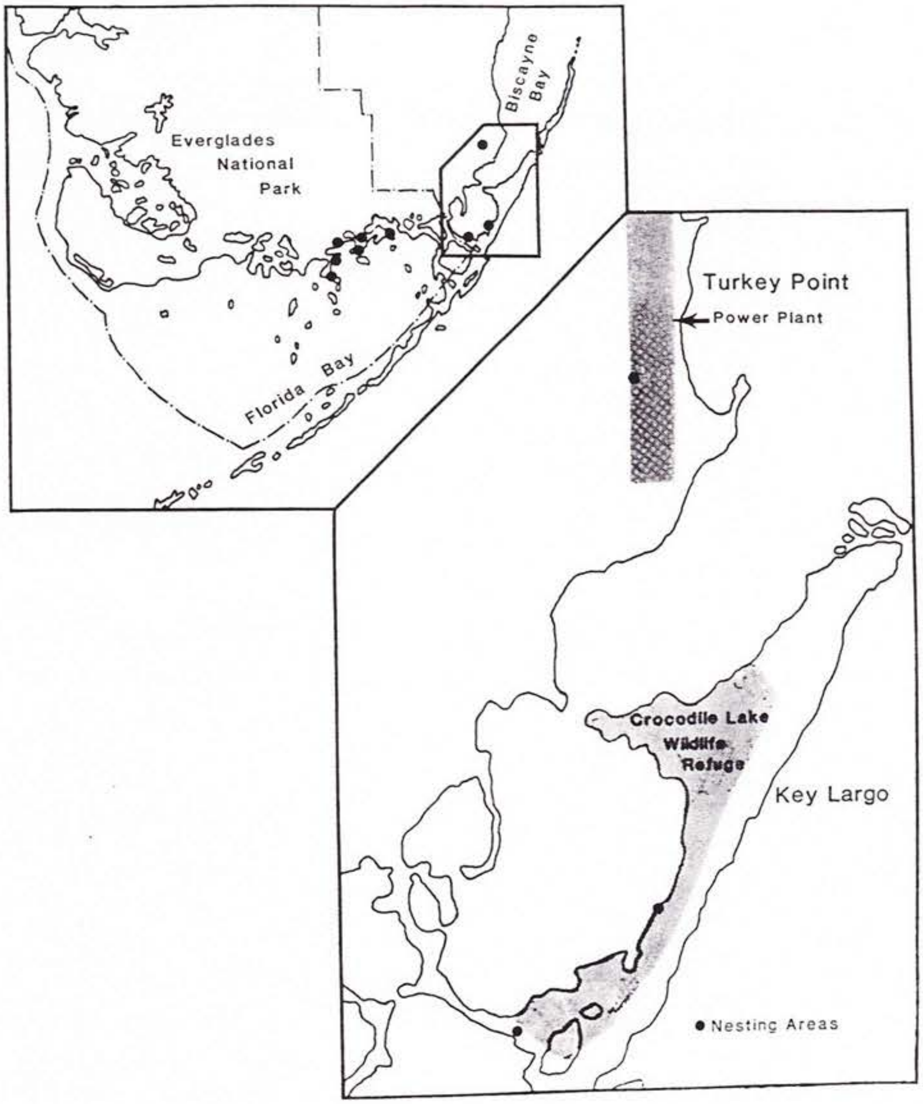

Figure 3. Institutional entities responsible for management of crocodile nesting habitat, showing Everglades National Park (National Park Services), Turkey Point Nuclear Power Plant site (Florida Power and Light Corp.), and the proposed boundaries of the Crocodile Lake Wildlife Refuge (US Fish and Wildlife Service). Dots indicate nesting areas.

great for proper social interactions to occur. But radio telemetry demonstrated that individual crocodiles had overlapping, although large (mean = 107 ha), activity areas (Kushlan and Mazzotti 1988b). We often saw crocodiles together, including telemetered animals of different sexes. We also found that the sex ratio was not significantly different from 50/50, indicating no deficiency of one sex (Kushlan and Mazzotti 1988b). These observations suggest that the small population size and dispersion of individuals does not interfere with social interactions.

Nesting Habitat

Crocodiles lay eggs (clutches) in cavities that they dig in relatively high ground. In Florida Bay, these are marl banks of creeks that run through the mangrove swamp and the sandy beaches fronting the bay (Figure 4). They also nest on artificial substrates, including peat and crushed rock banks of canals outside our primary study area, on Key Largo and Turkey Point. Thus, high ground nesting habitat might be limiting. However, given the many kilometers of beach and creek bank available for nesting, there would seem to be no lack of nest sites.

Territorial behavior might, however, restrict use of available sites. But rather than nesting in territories, the American crocodile can nest communally, individuals placing clutches as near to each other as one meter (Kushlan and Mazzotti 1988b, Ottenwalder personal communication). Thus, there seems to be no behavioral limitation on site use.

Some nesting habitat hsitorically available to crocodiles can no longer be used, including Miami Beach and the upper Florida Keys where human develop-

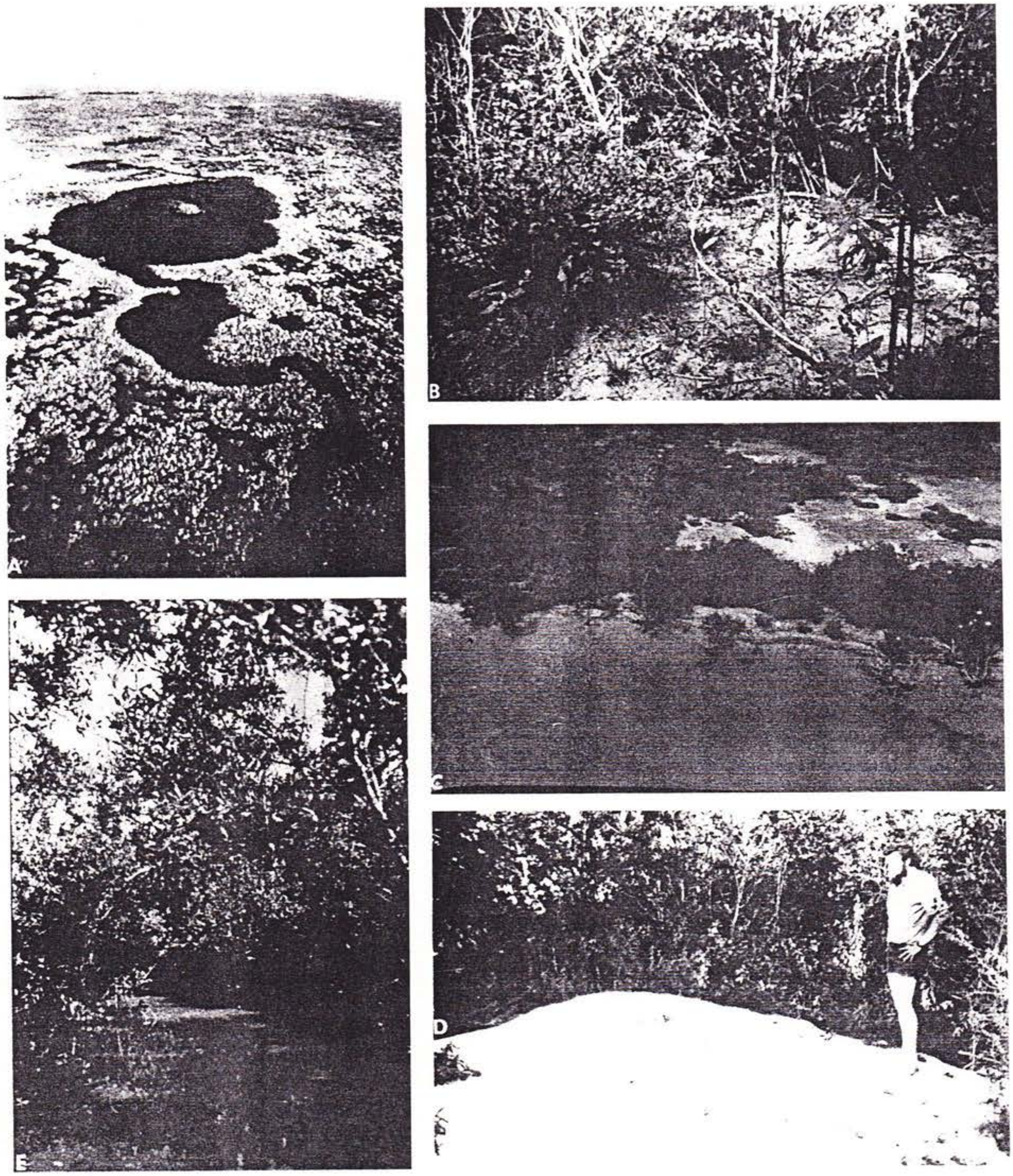

Figure 4. Crocodile habitats in southern Florida. **A.** Mangrove swamp from the air showing creeks and inland ponds. **B.** Nest site along the bank of a creek. **C.** Beach shoreline of an island in Florida Bay. **D.** Crocodile nest mound on a sandy beach. **E.** Mangrove-lined creek off Florida Bay.

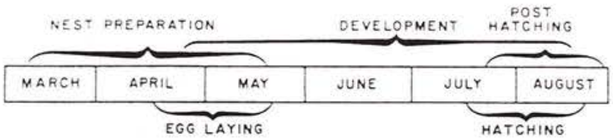

Figure 5. Nesting season of the American crocodile in Florida.

ment has considerably transformed the natural landscape (e.g., Barbour 1923). However these losses have been compensated for by artificial nesting habitat on dredge banks on northern Key Largo and Turkey Point. Crocodiles also have nested in fill on Cape Sable, along the road from the mainland to the Florida Keys, and previously along the railroad embankment that the modern road follows. These areas contained limited suitable nesting habitat prior to deposition of the fill, so their development tends to compensate for habitat losses elsewhere.

Nesting Failure

Crocodiles nest in spring and summer (Figure 5), following the cool temperatures of winter and prior to the height of the rainy season (Kushlan and Mazzotti 1988b). Failure to hatch may be due to any of several causes including infertility, predation, and embryonic mortality.

The fertility rate was 90% ($n = 314$ eggs); all but 1 of 20 clutches had a fertility rate of 84% or higher (Kushlan and Mazzotti 1988b), indicating that infertility is not limiting the population.

Predation, by raccoons (*Procyon lotor*), accounted for the loss of 14 of 99 clutches from 1971 to 1982 (Kushlan and Mazzotti 1988b). The 14% loss is somewhat exaggerated because some clutches would not have been discovered if they had not previously been dug up by raccoons. The inclusion in the calculation of other undiscovered and eaten clutches would have decreased the total proportion of predated nests. No particular nest site, location, or substrate was disproportionately susceptible to predation (Kushlan and Mazzotti 1988b).

Embryonic mortality accounted for 14% loss of clutches ($n = 99$). Death of fertile eggs can be caused by a number of adverse conditions in the nest cavity during the period of development, including temperature, low oxygen levels, high carbon dioxide levels, and low or high moisture levels. These possibilities were tested directly.

Temperatures, monitored in clutches throughout the development period, were the same in marl (31.6°C) and sand nests (30.0°C) (T test, $p > 0.05$). Thus, lower temperatures in marl nests were not responsible for embryonic mortality (contra Ogden 1978). The temperature ranges of continuously monitored nests (28.6°–35.0° in marl nests and 26.0°–33.6° in sand nests, $n = 8$) are those expected for crocodilians (Bustard 1969). The maximum temperature recorded at any nest, 37°C in a marl nest, did not inhibit hatching. Hatchlings from a nest cavity that reached 36.5°C had crooked tails, a sign of heat stress (Bustard 1969). Thus, heat stress occurred rarely (1 nest of 41 examined for signs of hatchling abnormality).

Gas levels in nest cavities varied during the incubation period (Lutz and Dunbar-Cooper 1984). A decrease in oxygen levels and an increase in carbon dioxide levels occurred over the incubation period, but there was no evidence that the normal shift in gas concentration limited survival.

Soil moisture depends on rainfall and the height of the subterranean water tables. Moisture content, which varied from 4.9% to 36.1%, in turn affected soil oxygen and carbon dioxide levels (Lutz and Dunbar-Cooper 1984). Under usual conditions soil moisture remains appropriate for development throughout the nesting period. However, two conditions can adversely affect development: droughts and floods (Mazzotti and others 1988). Drought effects were relatively rare. In the dry summer of 1981, 54 embryos from four nests failed to hatch and showed signs of excessive water loss (Mazzotti and others 1988). This desiccation was in sand mounds and did not affect the entire clutch of any nest. Flooding by a rise in the groundwater table, which may not be visible aboveground, saturates the soil, reduces oxygen levels, and suffocates the embryos. Cryptic flooding killed one clutch in 1980 and 1981 and partially killed two clutches in 1980. Flooding took place only in marl nests soil on creek banks (Kushlan and Mazzotti 1988b, Mazzotti and others 1988) and may account for the embryonic mortality previously attributed to low temperatures (Ogden 1978).

The groundwater table in the mangrove swamps frequented by crocodiles depends on water levels in the creeks, which in turn depend on sea surface elevation, wind tide, and especially the amount of freshwater entering the swamps from upstream. Freshwater movement into the crocodile nesting area in Florida Bay is under the control and responsibility of local water management authorities and Everglades National Park. High spring and summer discharges into the coastal mangrove swamps can result in the unnatural mortality of crocodile eggs.

Juvenile Survivorship

The age structure of the population, determined by extensive boat and aircraft surveys, indicates that hatchlings, subadults, and adults all occur in the population (Figure 4) (Kushlan and Mazzotti 1988b). On Key Largo, hatchling survival is about 40% over the course of the first year (P. Moler, personal communication). Tagging studies demonstrated the survival of hatchlings for 36 months, and we have evidence of recruitment of young females into the breeding population (Kushlan and Mazzotti 1988b). These findings indicate that juvenile crocodiles survive in our study population.

The documented age distribution (Figure 6) lacks the proportion of juveniles one might expect in a stable or growing population. However, this deficiency is probably the result of the difficulty of encountering subadults, a problem characteristic of crocodile studies (T. Joanen and H. Messel, personal communication).

Salinity

Previous studies (Dunson 1970, Evans and Ellis 1977) had indicated that hatchling crocodiles in the laboratory could not maintain body mass in high salinities. Extending this study to the natural habitat, Dunson and Mazzotti found that hatchling crocodiles possess a number of behavioral adaptations for survival in hypertonic conditions (Dunson 1982, Dunson and Mazzotti, in preparation). These include consuming water-laden prey items, drinking freshwater from pools and lenses riding on top of saltwater, and avoidance of salt intake. American crocodiles also possess a salt gland (Taplin and others 1982), although the extent of its functioning is not fully understood (G. Grigg and W. Dunson, personal communication).

In fact, crocodile hatchlings can gain mass even in water as hypersaline as 44 ppt (Mazzotti, personal communication) and the growth rate of Florida crocodiles in their first year (=41 cm/y total length) is among the fastest reported for crocodilians (Cott 1961, Murphy 1976, Grigg and others 1980). Dunson (1970) found that the growth rates of the American crocodile are fastest in brackish water. The appropriate brackish water salinity regime presently occurs through most of the year in the mangrove habitat selected by crocodiles. The average salinity at places where crocodiles were seen was 13.8 ppt (sd = 10.00, n = 111, min = 0.0, max = 35.0 ppt). The average salinity at nest sites at hatching was 24.2 ppt (Figure 7) (sd = 5.14, n = 82, min = 7, max = 29).

Artificial Adult Mortality

To examine the effects of unnatural mortality, we documented the mortality of 27 subadult and adult crocodiles over a 15-yr period (Table 1). Of these, 18 are known to have been caused by humans. The most common cause of death was being struck by automobiles, especially along Highway 1 leading from the mainland to Key Largo. Killing by gunshot is the next most common artificial mortality documented. Deaths of subadult and adult crocodiles to artificial causes have averaged 1.2/yr, which underestimates actual artificial mortality.

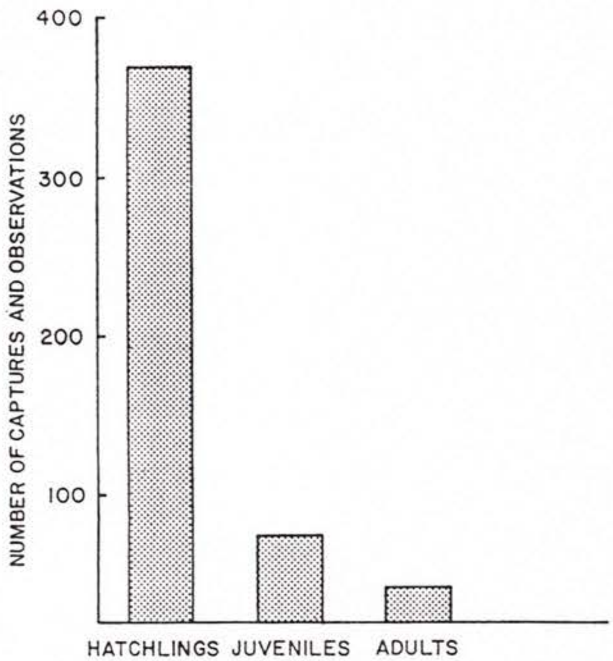

Figure 6. Age category distribution of American crocodiles observed and captured in southern Florida.

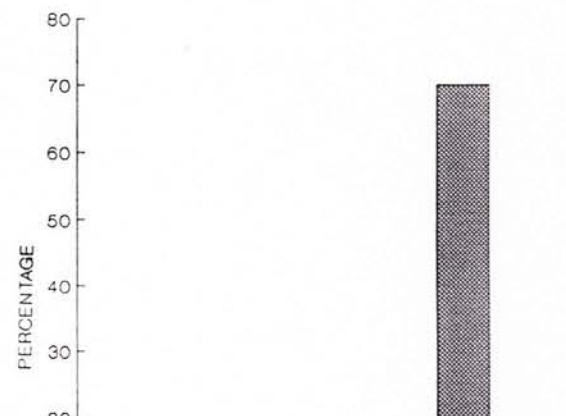

Figure 7. Distribution of hatchling crocodiles according to water salinity. Full seawater is 35 ppt.

Table 1. Documented mortality of crocodiles in southern Florida.

Year	#/year	Size (m,TL)	Location	Probable cause of death	Reference[a]
1971		ca .3	Key Largo	Shot	1
1971		ca 2.7	Key Largo	Shot	1
1971	3	2.5	Key Largo	Automobile	1
1972	1	ca 2.1	Key Largo	Unknown	1
1974		ca .5	Key Largo	Automobile	1
1974		ca 2.5	Key Largo	Unknown	1
1974	3	ca .3	Key Largo	Shot	1
1975		ca 3.7	Key Largo	Shot	1
1975		1.2	Key Largo	Automobile	1
1975	3	1.0	Card Sound Road	Automobile	1
1976	1	1.0	Key Largo	Shot	1
1977	1	0.5	Card Sound Road	Automobile	
1977	2	ca 3	Mrazek Pond	Unknown, during dry season	
1978		ca 2.5	Fort Lauderdale	Shot	2
1978	2	2–2.25	Intercoastal waterway, Florida Bay	Possibly hit by boat	
1979		3.0	Florida Bay	Unknown, previously captured	
1979	2?	2.37	Turkey Point	Unknown, previously captured	
1980	1	1–1.25	US1, Key Largo	Automobile	2
1981		0.87	Davis Creek, Florida Bay	After a period of low temperature	
1981	2	1.25	US 1, Key Largo	Automobile	2
1982		1.0	US 1, mainland	Automobile	2
1982	2	3.0	US 1, mainland	Automobile	2
1983		3.0	Park road, Everglades National Park	Automobile	
1983		3.0	Cross Key	Automobile	
1983	3	3.9	Turkey Point	Unknown	3
1984	1	2.0	Trout Cove	Unknown	

[a] References:
1. Ogden (1978).
2. P. Moler, personal communication.
3. R. Gaby, personal communication.

The effect of fishing on American crocodiles is unknown, although the adverse effects of fishing nets on the estuarine crocodile (*Crocodylus porosus*) in Australia has been well documented (Jenkins 1980, Messel and others 1981). Crocodiles have been caught in fishing nets in Florida Bay (R. P. Allen, unpublished), and several fishermen have commented that they have "thinned" crocodiles from fishing locations in the past (R. Klukas, personal communication). In February 1976, a crocodile was caught in a shrimp net near Key Largo.

Disturbance

Crocodiles in Florida occur primarily in relatively inaccessible mangrove swamps. However, each year crocodiles are reported from developed areas, especially coastal canals. Such appearances suggest that human presence per se does not inhibit crocodiles. However, our observations indicate that human disturbance can be detrimental at a nest site.

Adult crocodilians typically assist their eggs in hatching (Cott 1961, Pooley 1969, Ogden and Singletary 1973, Kushlan and Simon 1982). Hatchling crocodiles are unable to hatch from their egg on their own (Kushlan and Mazzotti 1988b). During various studies in Florida Bay, females were disturbed and captured near, but not on, their nest sites (Ogden and Singletary 1973, Kushlan and Mazzotti 1988b). In all but one case, the female failed to return later that season to open her nest, and all layed their clutch elsewhere the following year. Thus, drastic disturbance at a nest site causes nest site desertion.

Environmental Contaminants

Organochlorine and heavy metal levels were measured in eggs (Hall and others 1979. Stoneburner and

Kushlan 1984), but in no case were levels sufficient, based on available information, to adversely affect reproductive performance or survival. No change in pesticide contamination was found between 1972 and 1978 except that PCB, mercury, and lead levels increased.

Conclusions

In summary, the various findings provide no evidence to suggest that the overall distribution of the American crocodile has contracted in Florida in recent years, not has its range expanded. The nesting range has decreased due to development, but habitat losses have been compensated for by creation of artificial nesting sites elsewhere. The best indication of population size is the number of nesting females, and the number of known nests has increased in recent years (owing primarily to increased search effort). As a result, available data do not indicate that the population has decreased in recent years.

The American crocodile population in southern Florida faces substantial natural limitations, particularly from a combination of climatic factors, including winter temperatures, flooding, and droughts. On the other hand, it is able to accommodate to such potentially limiting factors as high salinity, inhospitable nest environment, and limited nesting habitat. It does so by such characteristics as a long lifespan, rapid early growth, behavioral osmoregulation, sociality, and habitat choice.

Findings regarding salinity constraints and nesting mortality are most notable. All evidence suggests that high salinity does not limit survival in the wild, and it also supports Dunson's (1970) suggestion that the habitat preference of American crocodiles is for brackish estuarine conditions. With respect to mortality, the loss of entire clutches to predation and hatching failure together is about 28%. Marl creek nests are susceptible to flooding during periods of high water discharge, and sandy shore nests are susceptible to desiccation during drought. Flooding of nest cavities by groundwater rises owing to controlled water discharge poses an artificial threat to low-lying nests along creek banks. Thus the primary artificial constraint on hatching success is subterranian flooding by groundwater. High water levels are known to reduce nesting success for other crocodilian species (Joanen and others 1977, Magnusson 1982, Jacobsen and Kushlan 1986a).

Hatching success is relatively high for crocodilians, in that 78.3% of the nests (n = 46 clutches) hatched some young and that an estimated average of 205 eggs hatch annually in Florida Bay. The relatively low predation rate is unexpected for two reasons. First, we found that the American crocodile leaves its nest site undefended in Florida Bay, which is not the case in most crocodilians (see Kushlan and Kushlan 1979). Second, predation losses in other crocodile populations are higher than those we found. Staton and Dixon (1977) reported losses of 84% of the eggs of the spectacled caiman (*Caiman crocodilus*). Raccoon predation on the nests of alligators (*Alligator mississippiensis*) was reported to be 31% in north Florida and 17% in Louisiana (Goodwin and Marion 1978, Joanen 1969), and most reports of predation losses in the Nile crocodile (*Crocodylus niloticus*) range above 30% (Pooley 1973, Cott 1961). The limited predation rate in Florida Bay crocodiles may be attributable to the small population size and high dispersion of clutches that do not serve to reinforce robbing behavior among local raccoons (see Hopkins and others 1979). Thus, predation appears to be an infrequent and unpredictable event among crocodile nests in Florida Bay.

These natural limitations, although not high in themselves, would tend to place a definite cap on population growth, which is reflected in the naturally restricted range in southern Florida and the rarity of crocodiles within that range. Any artificial inhibitions to population growth are superimposed on these naturally occurring limitations. Thus the question of management concern becomes one of the identifying artificial sources of mortality that can be controlled. These include highway-related deaths and flooding of nests by managed water discharge. The existing balance between recruitment and artificial constraints remains unclear, but any additive artificial limits cannot help that balance.

Random and catastrophic events such as freezes or disease can affect any rare population, particularly one at the edge of its range. These events, which may only set back a robust population, can send a small population reeling toward extinction (Leigh 1981, Strebel 1985). Through management action it is possible to alleviate unnatural threats and provision the population for unmanageable catastrophes, thereby increasing the chance of its survival.

Potential Management Approaches

Individual Protection

For any rare species, protection of individuals, particularly breeding adults, is an important aspect of a conservation strategy. As a federally listed endangered species, the American crocodile in Florida is afforded complete protection from taking, including killing, capture, injury, or harassment. However, as the incidents of shooting deaths reveal, coexistence of large predators with humans is not easy, in that threats to human life will continue to exist (Hines and Keenlyne 1977, Hines and Schaffer 1978). The American crocodile in Florida is further compromised by the perception that the threat posed by the American alligator has increased and its level of protection should be reduced. Continuing communication is required between officials and the public on the status, distinctiveness, degree of threat, and rarity of the American crocodile in Florida. Similarly a mechanism for removing and relocating offending crocodiles from developed areas is required to assure continued protection of individuals. For an endangered species threatened by its rarity, and the similarity of its appearance to harvested species, nonconsumptive management is the only appropriate approach (Jacobsen and Kushlan 1986b).

A specific need for individual protection is to reduce or eliminate roadside mortality. Although expensive, complete protection is possible through structural changes including elevating the roadbed on trestles, constructing large closely spaced culverts elsewhere, fencing, and reducing car speed.

Habitat Protection

Outside nesting areas, protective programs are sufficient to assure the species' continued presence. However, in the nesting range, additional habitat management is appropriate at the several nesting sites, all of which are under institutional protection: Florida Bay population, in Everglades National Park; the Turkey Point population, on a power plant site; and the Key Largo population, on land being purchased by the federal government for the Crocodile Lake Wildlife Refuge. How these areas will be managed depends on the differing objectives of the organizations involved.

On the power company site, the primary land use is for a nuclear power plant, and its radiator network of cooling canals, which are frequented by crocodiles (Gaby and others 1985). Investigations indicate that crocodiles can choose appropriate temperatures within the canal system (Mazzotti and others, in preparation). Therefore no specific manipulations are required in this artificial habitat.

On northern Key Largo, crocodiles occur in both artificial and natural habitats. Nesting sites are the peat banks of old canals. Various habitat improvements such as construction and maintenance of elevated banks and canals, and digging isolated deep-water sites are possible. Such intensive management can enhance the habitat for crocodiles in the wildlife refuges that have been dedicated to their survival.

In Everglades National Park, crocodiles inhabit the natural mangrove swamp. The goal of a national park in the United States is to preserve natural environments; in Everglades National Park this by law explicitly includes preservation of the distinctive tropical plants and animals found there. To accomplish this end, active management is called for, including the curtailing of any current actions that adversely affect crocodiles. As on Key Largo, nesting habitat can be enhanced by supplying additional elevated sites on creek banks, although it does not appear that nest site availability is limiting. Artificial mortality under management control can be eliminated by devising management plans for water control that would avoid subterranian flooding of crocodile nest sites on the creeks of Florida Bay during April through August. Furthermore, at other times of the year, it is necessary not to produce floods of freshwater that replace the preferred natural estuarine conditions.

Disturbance is also a factor that can be controlled. There is demand for human access to the crocodile habitat in Everglades National Park. In 1978 the National Park Service created a crocodile sanctuary encompassing the core habitat and prohibited entry by park visitors throughout the year. Observations on the effects of disturbance reported in this article show the need for protection during the nesting season. Conversely, there has been no demonstration of the need for isolating crocodiles from nonagressive people in the nonbreeding season. Thus the sanctuary could be seasonal.

Predator Control

The raccoon is the primary modern predator of crocodile nests, although beats (*Ursus americanus*) also dug up crocodile nests historically (Moore 1953b). In that no nest site, location, or situation was disproportionately susceptible to predation, it is not feasible to single out risky sites for protection. However, by monitoring sites, the appearance of a raccoon in the area can be determined. Tests in such a situation found that raccoons can be live-trapped near a nest site, thereby providing protection from predation. Such a program of monitoring and selective trapping can be used to reduce predation in all nesting areas.

Introductions

A potentially useful method of managing an endangered species is through population augmentation, a strategy that can take three forms: introduction of foreign animals, captive rearing, and captive breeding.

Unthoughtful introductions of animals into natural populations can have a number of adverse effects

(Kushlan 1980). One of these is the introduction of genes foreign to the specific population. This would be the case with respect to the Florida population of the American crocodile, for Menzies and Kushlan (in preparation) show that the various populations are genetically distinguishable. Furthermore they suggest that these population segments have been isolated for thousands of years. At least 45 crocodiles have been released in southern Florida in 17 yr, and some were definitely from foreign populations. Future introductions would need to be managed with concern for genetic implications. Since we lack a valid management goal of increasing genetic diversity, introductions of animals of unknown origin would be inappropriate. Furthermore, these results imply that the various populations of crocodiles should be managed as separate genetic entities, including the one in Southern Florida.

Captive Rearing

Collecting and incubating eggs and head-starting hatchlings can short-circuit the mortality associated with these life stages, and there is no reason why captive animals should not survive upon release. Such an approach can enhance recruitment into a rare population. Artificial incubation would have to be undertaken only after additional study because it appears that incubation temperature determines the sex of developing crocodilians (Ferguson and Joanen 1983). Thus incubation under artificial conditions can distort sex ratios (Morreale and others 1982).

Captive Breeding

The maintenance of a self-contained captive population can serve two functions. It can provide animals for restocking, especially should catastrophe occur in the natural population, and it can supply animals for research and education purposes. Thus the establishment of a self-sustaining captive population of Florida crocodiles can aid the conservation effort. Behler (1978) demonstrated that maintenance of a captive population of the American crocodile is feasible.

Conclusions

Management of the American crocodile requires protection of individual animals throughout the range as well as management and enhancement of habitat. The latter requires appropriate water management to avoid unnatural nest flooding. Control of predators and augmentation of the population are also potential management activities. Each of these must be carried out in the three management areas, which are under the control of three organizations having differing priorities and philosophies.

Discussion

The management of endangered species is a difficult task, requiring not only biological information but also political support and an agreed-upon philosophical context. If political and fiscal support are not available, of course, nothing can be accomplished. In the case of crocodilians, appropriate management actions are identifiable but philosophical positions are especially strong, ranging from one favoring complete protection to one of using crocodilians as a harvestable resource (Hines and Percival 1986, Jacobsen and Kushlan 1986b). However, the rarity of the American crocodile in Florida has compelled general agreement on the need for management as a completely protected species.

An appropriate goal for management of an endangered species would be to maintain a viable population in the wild. Although viability is necessarily an imprecise goal, it can be met by a population having a relatively low probability of extinction and existing at or above the natural carrying capacity of an ecosystem having no critical unnatural limiting factors. Such a goal would be achieved with respect to the American crocodile if the population were not decreasing and if it were not being limited by unnatural factors amenable to management. On the basis of the findings of the research program discussed above, the American crocodile population in Florida meets the population risk criterion. It is likely, however, that traffic mortality and nest flooding are imposing an artificial limit on population growth. Additional management action is necessary to eliminate nest flooding and human killing. Coupled with the establishment of a self-sustained captive population, these activities can fully meet such a management goal.

Several lessons regarding the management and conservation of endangered species can be drawn from the case of the American crocodile in Florida. The first relates to its status. The species is rare in Florida, and has always been rare for natural biogeographic reasons. Similarly, it is restricted in distribution, but its overall distribution is similar to historic times and the core of its nesting distribution is where it always has been. Thus, the rarity and restricted distribution of this species is a natural condition. In planning for the conservation of endangered species, one tends to presume that endangerment is human-caused. In this case, the crocodile would be rare and, for that reason, endangered in Florida, if the peninsula had never been settled by humans. And under the best of management, it will remain rare and restricted.

The human settlement of southern Florida has been extensive, yet the crocodile has survived and maintained itself in face of the massive human occupancy and development. In retrospect, its well-being was positively influenced by the inadvertent creation of artificial nesting sites. The provisioning of nesting habitat may not only have compensated for habitat lost to development but actually added to the total amount of nesting habitat. This is an example of massive mitigation, which shows the way for future manipulations for habitat enhancement.

Second, the lack of any dominating natural limiting factor suggests that the population is limited by the combined action of a number of mortality factors, each having a small effect. Such a situation is what would be expected to have operated naturally. From a conservation view, the impact of most of these could be reduced in severity by management, and such efforts would enhance the population. Yet is is worthwhile to question the need for artificial enhancement given the overall healthy status of the population.

Third, the need to protect individuals is essential to any management strategy for an inherently rare species. For the American crocodile, human-caused deaths seem still to be a primary problem, and one which may be eroding what recruitment is occurring. In this case, it is not so much legislation or enforcement that is lacking as a clear understanding on the part of citizens and of responsible government agencies (such as those responsible for highway modifications or water management) as to how their actions may be adversely impacting a rare species.

Fourth, protecting habitat is clearly needed for management of a naturally restricted species. However, purchase of the land and establishing appropriate reserves is only the first step. Management of crocodile nest sites is divided among a private organization operating under the multiple permitting authority of federal and state agencies, the US Fish and Wildlife Service in a species-specific wildlife refuge, and the National Park Service in a national park. Each of these entities has its own perception of its mission and appropriate management procedures. The power company attempts to prevent adverse impact of its operations. The federal wildlife agency, responsible for the protection of endangered species and their habitat, should be philosophically prepared to undertake enhancement on its reserve. The park service attempts to mix broad habitat preservation and human use and has a philosophical difficulty undertaking single-species management (Kushlan 1983). Nonetheless, the conservation of endangered species as well as ecosystems often depend on active management of species (Kushlan 1986).

In the present case, the combined effect of three reserves and three management objectives provides a more robust conservation strategy than a single management goal undertaken from a single philosophical position by one of the institutions. Thus, impact avoidance can take place on Turkey Point, enhancement in the wildlife refuge, and natural habitat preservation in the national park. Of the three, the latter strategy is the most risky because the protection of a natural ecosystem does not in itself secure the survival of an endangered species dependent on it (Kushlan 1979, 1983). Such a situation makes even more critical the existence of backup strategies in a nearby refuge dedicated to the endangered species.

Similarly, a self-sustaining captive population provides a backup to all three reserves. The role of self-sustaining captive populations is a matter of some concern in that they are expensive and require a commitment of time and facilities over a long term. Nonetheless, the establishment and maintenance of a captive population is the final leg of an ideal conservation strategy along with enhancement in a wildlife refuge and protection in a natural area reserve.

Thus, the case of the American crocodile in Florida demonstrates the usefulness of multiple management strategies in both the wild and in captivity to maintain a rare species. It further suggests that rarity itself can be both a natural situation and a dominating conservation problem to be managed. What is essential in the management and conservation of a rare species is to avoid the additional impact of unnatural intrusions into survival and recruitment. With this species it is also necessary to gain the philosophical agreement among the citizen groups and government agencies that have to live with crocodiles in their backyards.

Acknowledgments

I thank colleagues and students who have participated in the study of the American crocodile in south Florida, especially John Behler, Ann Dunbar-Cooper, William Dunson, Ronald Gaby, Jeffrey Lang, Peter Lutz, Frank Mazzotti, Robert Menzies, Paul Moler, Jose Ottenwalder, Daniel Stoneburner, and John Thorbjarnarson, and also my field assistants, Robert Austin, Joanna Booser, Linda Campbell, Carol Hewes, Terri Jacobsen, Deborah Jenson, Lori Lagna, Amanda Muller, Paige Patty, Mark Salzburg, and Ronald Wideman. I especially appreciate the criticism and suggestions of William Dunson, Les Garrick, Jeffrey Lang, Earl W. Lathrop, Ted Joanen, William Magnusson, D. B. Means, Harry Messel, and Grahame Webb. This study was funded by the National Park Service in cooperation with the US Fish and Wildlife Service, Florida Game and Fresh Water Fish Commission, Florida Power and Light Company, Conell Asso-

ciates, and by contracts between the National Park Service and Pennsylvania State University (Dunson), University of Georgia Institute of Ecology (Stoneburner), the University of Miami (Lutz and Dunbar-Cooper), and Nova University (Menzies).

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