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DESICCATION AND CRYPTIC NEST FLOODING AS PROBABLE CAUSES OF EGG MORTALITY IN THE AMERICAN CROCODILE, *CROCODYLUS ACUTUS*, IN EVERGLADES NATIONAL PARK, FLORIDA[1]

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ABSTRACT: *Flooding and desiccation probably caused mortality of eggs of the American Crocodile* (Crocodylus acutus) *in Everglades National Park. Flooding was subterranean with no sign evident above ground. Apparent desiccation occurred in a year (1981) of abnormally low rainfall. The timing of nesting seems to be rigidly scheduled, with the developmental period bracketed by possibly desiccating and flooding conditions. The success of this strategy is shown by the relatively low rate of embryonic mortality in most years.*

THE status and population dynamics of the American crocodile *(Crocodylus acutus)* have long been a matter of concern and controversy. Ogden (1978) concluded that the number of American crocodiles in the United States was not increasing, and that an important factor regulating their numbers was mediocre nesting success, caused primarily by embryonic mortality.

Most crocodile nesting activity in Everglades National Park occurs near Florida Bay in an area circumscribed around Little Madeira and Joe Bays (Moore, 1953; Ogden, 1978; Mazzotti, 1983; Kushlan and Mazzotti, 1988a). The nesting season occurs in March through August and is divided into nest preparation (beginning of March to mid-May), egg-laying (mid-April to mid-May), development (mid-April to mid-August), hatching (mid-July to mid-August), and post-hatching (mid-July to end-of-August) periods.

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Crocodiles deposit eggs in cavities dug in soil along creek banks or exposed shorelines. The clutch of eggs is subsequently covered for the duration of development. Conditions within the nest cavity may adversely affect the growth and development of crocodile embryos. Ogden (1978) suggested that embryonic mortality was probably caused by low nest temperatures in marl substrate. The environment of nest cavities of crocodiles in Florida Bay has been documented by Lutz and Dunbar-Cooper (1984). The nest temperature regime they found during their study did not kill developing embryos. However, they hypothesized that embryonic death could result from desiccation. As part of their study, gas and temperature probes were placed in three crocodile nests during 1980. While taking a sample of gas, water was withdrawn from the middle of the clutch, providing the first evidence that subterranean flooding was occurring in crocodile nests. The purpose of the present paper is to describe flooding and desiccating events as probable causes of hatching failure in nests of the American crocodile in Florida.

METHODS—Crocodile nests were located by searching shorelines and creek banks carefully by boat, helicopter, and on foot. Nest sites were characterized by morphometry (mound or hole) and by substrate (marl or sand). To provide an objective criterion for morphometry, the elevation of the top of the substrate above the egg cavity was compared to that of the surrounding area. If there was no difference in height, the nest was considered to be a hole nest. The elevation of the bottom of the clutch was measured relative to Florida Bay or creek water levels during 1980.

We defined hatching failure to be the lack of successful emergence from the egg. Hatching failure could be the result of infertility or embryonic mortality. Embryonic mortality may be

Table 1. Nesting of American crocodiles in Florida during 1980 and 1981. Mean clutch size was 39.3 ± 9.1 (SD), n = 8 nests.

Clutch number	Nest morphometry	Nest location	Nest substrate	Elevation of bottom of clutch above sea level (cm)	Number of eggs lost to flooding	Number of eggs presumed lost to desiccation
			1980			
1	Mound	Shore	Sand	72	0	0
2	Mound	Shore	Sand	64	0	0
3	Mound	Shore	Sand	45	0	0
4	Hole	Creek	Marl	−22	40	0
5	Hole	Shore	Sand	6	14	0
6	Mound	Shore	Sand	25	0	0
7	Hole	Creek	Marl	24.5	0	0
8	Hole	Shore	Sand	14	6	0
			1981			
9	Hole	Shore	Sand	–	0	22
10	Mound	Shore	Sand	–	0	0
11	Mound	Shore	Sand	–	0	10
12	Mound	Creek	Marl	–	0	0
13	Hole	Shore	Sand	–	35	0
14	Hole	Shore	Sand	–	0	9
15	Hole	Creek	Marl	–	0	0
16	Mound	Creek	Marl	–	0	0
17	Hole	Shore	Sand	–	0	13

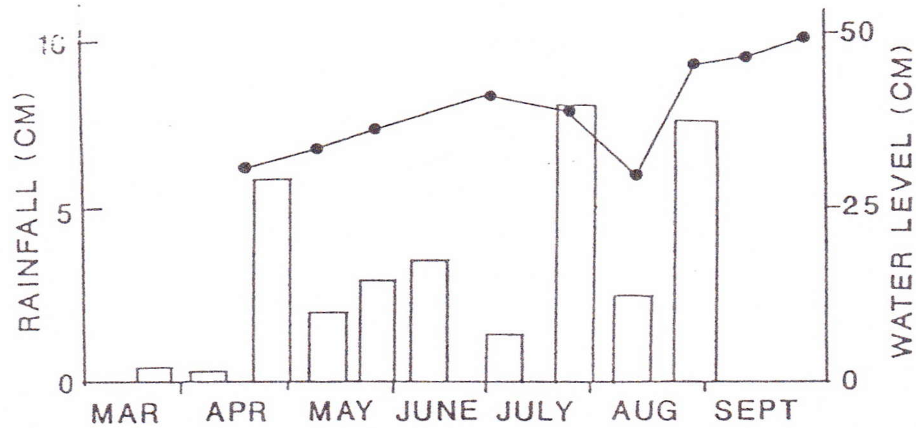

FIG. 1. Rainfall and changes in water levels measured at the Little Madeira Bay environmental station during the 1980 breeding season. Similar trends were found at the other environmental stations.

caused by predation or by environmental factors. Egg fertility was determined by the presence of external banding on the egg shell (Ferguson, 1982). The stage of development of dead embryos was determined by opening and examining eggs that failed to hatch.

After the first clutch was discovered to be flooded in 1980, the water level within the cavity was monitored every two to four days for the duration of flooding, by measuring the elevation of ground water in a small pit dug next to the nest. Water salinity was measured with a temperature-compensated refractometer (American Optical Co.) Water levels and salinity in the creek adjacent to the clutch were also monitored simultaneously. Flooding of three other nests was discovered during 1980 and 1981.

Changes in surface water level were measured bi-weekly at five locations in the nesting area. Rainfall was measured at the same locations by a direct reading rain gauge. Water level fluctuations were measured on a meter stick fixed to the bedrock. The change in water level was plotted relative to the lowest water level recorded during 1979-1980.

Rainfall records (U.S. Department of Commerce) were obtained for two climatological stations near the study area. A 25-year period of record, 1957-81, was used to determine the rainfall for the incubation period.

RESULTS AND DISCUSSION—Twelve clutches were found in 1980 and nine in 1981. Eight of the 1980 clutches were located prior to hatching and are discussed here. Mean clutch size was 39.3 eggs (SD 9.11, n=8). Eighty-nine percent of eggs laid in these eight clutches were fertile. In no clutch were all eggs fertile. Location, morphometry, and substrate of each clutch are described in Table 1.

Rainfall in southern Florida is seasonal, with 60-80% of the annual rainfall occurring from May through October. During the wet season the rainfall is bimodal, with peaks occurring early and late in the wet season (Fig. 1). The onset of the rainy season coincided with egg laying.

Water levels in northeastern Florida Bay fluctuate both seasonally and over shorter time periods. These fluctuations are caused by rainfall, evaporation, and wind. Lunar tides have little effect in this area (Tabb et al., 1962).

Water level changes in the study area, as represented by the Little Madeira Bay station, during the 1980 nesting season are shown in Figure 1. Although short-term fluctuations occur, water levels generally increase during the incubation period (May-July) and peak after hatching (Fig. 1).

Flooding completely destroyed one clutch in 1980 (4), one in 1981 (13), and partially destroyed two clutches in 1980 (5 and 8) (Table 1). Flooding events were closely monitored for clutch 4 during 1980 (Fig. 2). The eggs were flooded twice, yet no above-ground water was observed during either episode. During the first flooding, at least 60 % of the egg cavity was flooding with 36 ppt sea water, and peak water levels may have occurred before moni-

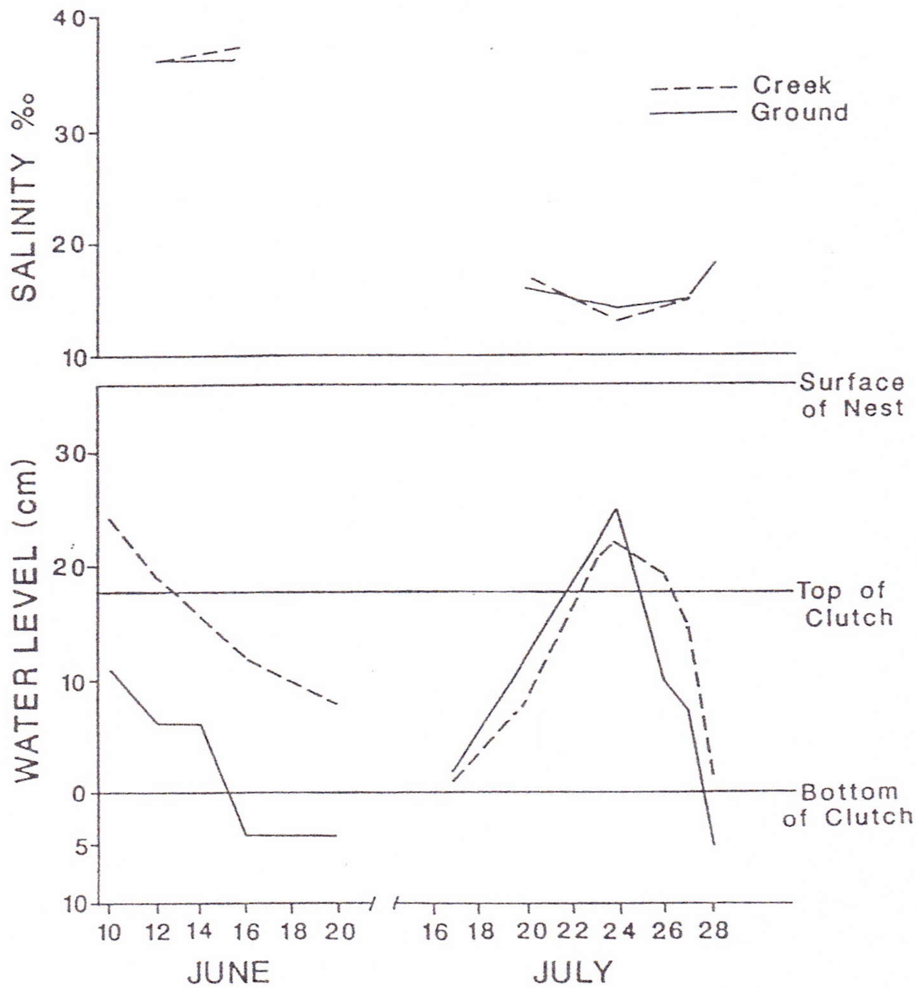

FIG. 2. Water level changes in a crocodile clutch (4, Table 1) during 1980, showing flooding periods.

toring began. Ground water level in clutch 4 during the second flooding episode was 15 cm higher than during the first flooding event. The salinity was lower and the entire clutch was submerged during the second flooding episode (Fig. 2). The rainfall peaks in June and July, 1980 (Fig. 1) occurred close to the flooding episodes.

During the first flooding episode, two other clutches situated at low elevations (5 and 8) were examined. At this time the bottom of clutch 5 was 7 cm above ground water while clutch 8 was 12 cm above ground water. Clutches 5 and 8 were not checked during the second flooding episode. Later examination of eggs that failed to hatch in clutches 5 and 8 indicated that egg mortality probably occurred during the second flooding event.

Timing of flooding and embryonic death could be determined by an examination of the eggs. Little development was observed in clutch 4. Eggs higher in the egg cavity were slightly more developed (larger embryos) than eggs lower in the cavity. This observation suggests that mortality occurred at different times with the lowest eggs dying first. All of the eggs examined from clutches 5 and 8 had embryos in a more advanced developmental stage than eggs from clutch 4. Clutches 5 and 8 also contained eggs at various developmental stages, with the most developed embryos occupying the top of the clutches. This pattern of differential loss of eggs from flooding was also observed by Webb et al. (1977) in Australian *Crocodylus porosus*.

Flooding as a cause of embryonic mortality has been documented for *Alligator mississippiensis* (Joanen, 1969; Metzen, 1977; Goodwin and Marion, 1978; Dietz and Hines, 1980; Kushlan and Kushlan, 1980); for *Crocodylus niloticus* (Pooley, 1969); for *Crocodylus porosus* (Webb et al., 1977; Magnusson, 1982; Webb et al., 1983); for *Crocodylus johnstoni* (Webb et al., 1983); for *Caiman crocodylus* (Staton and Dixon, 1977); and for *Caiman yacare* (Crawshaw and Schaller, 1979). This is the first time nest flooding has been documented for the *Crocodylus acutus*, and the first time that flooding was discovered to be subterranean or cryptic, with no surface water present.

The duration of submergence was not determined precisely in this study, but twelve hours of submergence in fresh water is the critical tolerance limit for the eggs of *Alligator mississippiensis* (Joanen et al., 1977) and *Crocodylus porosus* (Magnusson, 1982). Given such a short critical submergence time, and, because of the absence of standing water, it is obvious that flood-induced embryonic mortality can occur in American crocodile nests yet not be documented by observers monitoring the fate of the eggs.

Lutz and Dunbar-Cooper (1984) concluded that with the exception of flooding events, nest moisture depended upon rainfall. Rainfall during the 1981 incubation period was the lowest amount of rainfall for the 25-year period of record at both the Royal Palm (Everglades National Park) and Tavernier, Florida stations.

Packard and co-workers (1982) stated that although rigid-shelled eggs of reptiles are usually insensitive to the hydric environment, there may be some sensitivity if the nest is very dry. Ferguson (1982) has found that the presence of air chambers in alligator eggs is caused by excessive water loss. Tracy (1981, pers. comm.) has found, also in alligators, that incomplete yolk metabolism is caused by excessive water loss from eggs due to dry nest substrate. If we assume that these relationships are also true for the American crocodile, 54 eggs from four nests failed to hatch in 1981 apparently due to desiccation (Table 1). After a nest was abandoned by the adult crocodile, the unhatched eggs were opened and examined. Twenty-seven of these eggs had air sacs and lacked developed embryos. The other 27 had full-term embryos with incompletely absorbed yolk sacs. There was no evidence of embryos in eggs with air sacs. Thus it appears that low rainfall during 1981 apparently caused desiccating nest conditions, resulting in egg mortality.

Modha (1967, for *Crocodylus niloticus*) and Staton and Dixon (1977, for *Caiman crocodilus*) found that eggs in nests in desiccating substrates had low hatching success. In addition to loss of eggs, newly hatched crocodiles in 1981 looked different than in previous years. They had swollen abdomens and umbilical scars that had barely closed enough to encompass the remaining yolk. Also, as predicted by Packard et al. (1982), the apparently desiccation-stressed hatchlings measured in 1981 were smaller in mass and snout-vent length (Kruskal-Wallis test, $p < 0.001$) than similarly measured hatchlings in 1978-1980 (Mazzotti and Kushlan, unpub. obs.). An alternate explanation is that egg mortality was not caused by desiccation per se but rather by elevated temperatures in dry nests. However, abnormalities of embryos and hatchlings caused by high temperatures, such as kinked tails (Bustard, 1971; Webb et al, 1983) were not observed, further supporting the interpretation that desiccation, and not high temperatures, killed the developing embryos.

In Florida, *Crocodylus acutus* nest in the spring, avoiding the low temperatures of winter and high temperatures of late summer. This timing also avoids the dry season, when desiccation is a threat, and peak water levels, when flooding is likely. On this schedule only extremely wet or dry years cause the level of embryonic mortality described here. In a more unpredictable environment in northern Australia, Magnusson (1978) suggested that the prolonged breeding season of *Crocodylus porosus* was the result of the unpredictable timing of floods. In Florida a more predictable seasonal cycle of rainfall at the northern limits of the range of the American crocodile provides selection pressure for marked seasonality in nesting.

Distribution of embryonic mortality (Table 2) was non-random between sand and marl (X^2 test, $p < 0.01$, $n = 17$) and mound and hole nests (X^2 test, $p < 0.05$, $n = 17$). Flooding of hole nests was the most frequent cause of egg mortality. The discovery of cryptic nest flooding was the most significant finding of this study. Currently this level of embryonic mortality is low in most years (Mazzotti, unpub. obs.), however, an important implication of cryptic nest flooding is that low elevation hole nests, like those along creek banks, may be subject to increasing failure due to flooding, caused by high fresh water discharges into the northeastern Florida Bay mangrove zone. Fresh water discharge can be caused by local rainfall or water releases resulting from upstream water management practices. Increased loss of creek nests would be detrimental to the population of American crocodiles in Everglades National Park, since most of the surviving hatchling crocodiles come from creek nests (Ogden, 1978; Kushlan and Mazzotti, 1988b).

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