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Mortality of Eggs of the Crocodile *Crocodylus porosus* in Northern Australia*

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ABSTRACT.—Most mortality of eggs of *Crocodylus porosus* in northern Australia is caused by flooding. Floods are of two types, short-term caused by the interaction of rainfall and tidal movements, and long-term caused by heavy rain. The duration of inundation necessary to kill eggs in laboratory experiments is longer than that normally experienced during tidal flooding, but less than that experienced during long-term flooding. Nests beside rivers are more likely to be flooded than those in swamps. Predation by varanids and humans causes fewer losses but this is probably because eggs are killed by floods in most years before predators have a chance to take them. The presence of an adult crocodile at the nest appears to deter varanids. Aboriginal hunters apparently are less efficient at finding nests in swamps than nests along rivers.

No detailed life tables are available for any species of crocodilian. However, they might be expected to follow the pattern typical for other reptiles and for mammals, in which mortality is highest for very young age classes (Caughley, 1977:102). The decline of most crocodilian populations as a result of over hunting has made the study of the earliest and probably most vulnerable, age classes of crocodilians a matter of some urgency to biologists, conservationists, and wildlife managers. Mortality of eggs has been reported for *Crocodylus niloticus* (Attwell, 1970; Blake and Loveridge, 1975; Cott, 1961, 1969; Pooley, 1969), *Alligator mississippiensis* (Goodwin and Marion, 1978; Hines et al., 1968; Joanen, 1969; Kushlan and Kushlan, 1980*a*), *C. intermedius* (Medem, 1958), *C. acutus* (Ogden, 1978; Moore, 1953) and *Caiman crocodilus* (Crawshaw and Schaller, 1980; Staton and Dixon, 1977). Except in the case of *C. acutus* predators caused most losses where humans had not altered the natural flooding regime. Ogden (1978) reported that mortality of eggs of *C. acutus* occurred when the crocodiles used an unsuitable soil type for the nest but this may be a matter of elevation of the egg cavity rather than the soil type used (Kushlan and Mazzotti, pers. comm.). In contrast to the results for other species Webb et al. (1977) found that natural flooding is the major cause of mortality of eggs of *C. porosus* in northern Australia. This initial study prompted the following, more detailed, study of the factors causing mortality of eggs of *C. porosus* in northern Australia which addresses the following questions:

(1) What is the extent of mortality caused by floods?
(2) What is the extent of predation by varanids and humans?
(3) What would be the extent of mortality due to predators in the absence of flooding and how is this affected by the behavior and habitat preferences of the crocodiles?

METHODS

The study was undertaken in the Liverpool and Tomkinson Rivers system, Arnhem Land, northern Australia. The area is subject to distinct wet (October–May) and dry (June–Septem-

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ber) seasons. Most of the annual rainfall (average 1958–1973, 1140 mm) occurs during the wet season. Floods are common in the area during the wet season and result from exceptional rainfall in the catchments of the major rivers or from an interaction between river levels and the amplitude of tides. Floods due to exceptional rainfall may be described as catastrophic, last from 2–14 days, and produce water levels up to 4 m above the bank. Tidal flooding with freshwater lasts less than 6 h (although it may occur twice daily) and water levels are usually less than 2 m above the bank. Tidal flooding is generally restricted to lower sections of rivers; catastrophic flooding affects the whole river.

Maximum daily temperatures vary little throughout the year (averages for 1958–1973, January = 32.7°C, July = 30.0°C). Most nesting by *C. porosus* occurs during the wet season or the early part of the dry season (Webb et al., 1977). The Liverpool/Tomkinson system contains a variety of habitats found throughout the coastal wetlands of northern Australia, including freshwater swamps, turbid meandering tidal rivers, and clear fast-flowing upstream areas. It can be regarded as typifying much of the crocodile nesting habitat of northern Australia (Magnusson et al., 1978*b*, 1980).

An attempt was made to locate all nests in the Liverpool/Tomkinson system by searching from the air, from the ground and from the river (Magnusson, 1980*a*). Each nest was monitored to determine, where possible, the fate of the eggs. The fates of eggs in 38 nests beside rivers and 14 nests in swamps were documented. Nests were visited at weekly intervals. Evidence of the presence of varanids during the previous week (tracks, holes made in the nests, scratch marks on trees) was noted. At three nests that had been opened and eggs removed, between 2 and 4 varanids were shot in the vicinity of the nest and their stomach contents examined. Several varanids remained in the vicinity of these nests and it is unlikely that the number shot had any significant effect on predation on other nests.

A Minolta 8 mm movie camera with intervalometer (Telonics Ltd.) was used to photograph seven nests and the surrounding areas automatically at 3-min intervals for periods of up to 16 days. On most days lighting limited interpretation of photographs to those taken between 0830 and 1740 h. The nests were between one and two months old during the period of monitoring except for No. 3 which was estimated to be 14 days old and No. 7 which was estimated to be more than 3 months old.

Disturbance by predators of 12 nests on an adjacent river system was also investigated. Although it was not possible to tell whether the eggs were alive when taken from these nests, it was possible to estimate which predator had attacked the nest from the form of disturbance. Lizards tunnel into the nest, pull the eggs out, and strew the shells around. Aboriginal hunters generally remove the eggs and repack the nest, leaving it apparently undisturbed but with a cavity inside that retains the imprints of the eggs.

A water level gauge was erected at each nest located on the Liverpool/Tomkinson system. Rises in water level lifted a float which unrolled sewing thread from a reel. The gauge was reset at intervals of one week. The maximum height of water during the previous week was determined by lifting the float until the thread was taut against the reel. The base line of the gauge was the same height relative to the level of the river at high tide at each location. Apart from those measured during the study there are no records of flood heights for the Liverpool River within the study area. However, the Water Resources Branch of the Department of the Northern Territory recorded discharge rates for the Liverpool River near Cuthbertson Falls from 1965 to 1975. Cuthbertson Falls are below the major catchment area of the Liverpool

River and flooding of the lower reaches is closely related to the rate of discharge at the falls. During the 1974/75 wet season the lower reaches of the Liverpool River suffered catastrophic flooding only on days when the average rate of discharge at Cuthbertson Falls exceeded 80 m^3 per second. It was thus possible to estimate the number of days with catastrophic flooding during each month between 1965 and 1975. It was not possible to determine the frequency of tidal flooding as this is determined only partially by the input from upstream. Nevertheless tidal flooding probably occurs with a similar pattern, but slightly more frequently than catastrophic flooding. Likewise, flooding on the Tomkinson River does not necessarily correspond with flooding on the Liverpool River but they are likely to be highly correlated.

To ascertain the conditions in nests subject to flooding, Po_2 and temperature in two nests—one composed primarily of grass, the other primarily of mud—were measured with an IBC dissolved oxygen meter (limit of reading 1 mm Hg), and a Dobros mercury thermometer (limit of reading 0.5°C) before and during flooding.

To determine the duration of flooding required to kill eggs of different ages, two groups of eggs were inundated under conditions simulating those in flooded nests. Conditions for experimental inundation were set at temperatures of 25–27°C (the smallest range that could be maintained) and 155 mm Hg Po_2. Groups of 5 eggs from each of two nests containing 30-day-old embryos were submerged for 8, 9, 10, 11, 12 and 13 h, the treatments being independent. Sixty-day-old embryos from the same two nests were treated similarly. To allow for delayed mortality after inundation, the eggs were replaced in a natural nest for 24 h. They were then opened to see whether the hearts of the embryos were beating.

To determine the relative efficiencies of aboriginal hunters at finding nests in swamps and nests along rivers two aboriginal hunters were asked to search representative areas intensively. The number of nests found can be measured directly, but the data do not measure predation pressure unless they can be represented as a proportion of nests actually present. The estimate of the total number of nests present in the swamp and the details of the methods used to obtain this have been given by Magnusson et al. (1978*a*). The same techniques were used to estimate the number of nests along the river for comparison.

Results

Mortality Due to Flooding.—Frequency, height and time of flooding vary between years. In general, flooding was more severe in the years of the study at upstream nests than at downstream nests, but there was no consistent pattern. Using flow rates at Cuthbertson Falls as indicators of probable flooding of the nesting areas on the lower reaches of the Liverpool River it is possible to estimate the numbers of days in each month that the Liverpool River flooded between 1965 and 1975 (Table 1). The incubation period of *C. porosus* varies considerably (Magnusson, 1979*b*), probably was a result of factors associated with nest opening by the parent (Magnusson, 1980*b*). However, a reasonable time for incubation would be 90 days. Periods of 90 days or more without heavy flooding during the breeding seasons between 1965 and 1975 are marked on Table 1. Of the ten years, five had such periods commencing in April, three had such periods commencing in March, and one had such a period at the beginning of the wet season (November).

Flooding for 24 h reduced the Po_2 from 155 mm Hg to 135 mm Hg in the mud nest and from 155 mm Hg to 137 mm Hg in the grass nest. The temperature dropped from 28 to 26°C in the mud nest and from 30.5 to 26.0°C in the grass nest.

TABLE 1. Number of days of catastrophic flooding on the Liverpool River in each month between 1965 and 1975. Data based on flow rates at Cuthbertson Falls. Lines indicate continuous periods of more than 90 days when successful nesting could have occurred. *Flooding occurred during the first two days of April 1974 only. For all practical purposes this represents a flood-free month. NR—no flooding recorded for this month but water levels not recorded for some days.

Year	Month							
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.
1974/75	0	2	8	8	13	1	1	0
1973/74	NR	NR	0	14	24	2*	0	0
1972/73	0	0	3	5	0	0	0	0
1971/72	0	1	0	2	10	0	0	0
1970/71	0	1	0	3	7	2	0	0
1969/70	NR	NR	2	1	0	0	0	NR
1968/69	0	0	1	6	7	0	0	0
1967/68	0	0	0	6	2	0	0	0
1966/67	0	0	6	0	15	0	0	0
1965/66	0	3	9	11	0	0	0	0

Flooding killed all embryos in 37 of 38 nests beside rivers. None of the 14 nests in swamps suffered mortality from floods. The timing of flooding seems to be critical. Only one flood during 1976 was high enough to kill embryos on the lower reaches of the Liverpool River, but its effect was catastrophic. All embryos present at the time of the flood were killed. The only eggs beside the river that were not flooded that year were in a nest built after the flood.

Tolerance of Eggs to Inundation.—Eight to 13 h of submersion appears to be lethal for the eggs. Eggs submerged for 8 h survived, but all eggs submerged for 13 h were killed (Table 2). The experiment failed to indicate a significant difference in the tolerance of 30- and 60-day-old embryos to inundation ($F_{5,5} = 0.43, P > 0.5$). However, the trend of the data suggest a slightly longer survival for younger stages and it is possible that an experiment with greater replication would indicate a significant difference.

TABLE 2. Effects of various periods of inundation on crocodile eggs (10 eggs per treatment).

Hours submerged	Number of eggs killed	
	30-day embryos	60-day embryos
8	0	0
9	0	3
10	5	5
11	6	8
12	6	10
13	10	10

Predation by Lizards.—*Varanus indicus* was common along river banks and frequently was seen close to nests. Crocodile eggs were found in the stomachs of 6 of 8 varanids shot in the vicinity of opened nests. All 6 *V. indicus* shot in other areas contained only crabs. Another species of varanid, *V. gouldi*, was seen occasionally near river banks but was not observed feeding on eggs.

Lizards opened and took all eggs from 2 of 14 nests in swamps and from all 38 nests beside rivers. The eggs in 37 of the nests beside rivers had been killed by flooding 2–10 weeks before the nests were raided, but eggs in the two nests in swamps and the remaining nest beside the river had not been flooded and the embryos presumably were still alive. On three occasions when varanids were disturbed while at these nests, live embryos were found in partially eaten eggs. There was no evidence that any of the eggs in these nests was putrid before the lizards opened the nest though this possibility cannot be discounted.

Adult crocodiles in the study area are too wary for direct observation of behavior so almost all behavioral data at nests were obtained by time-lapse photography. Periods that nests were under surveillance and days on which crocodiles and varanids were present at the nest site are diagrammed in Fig. 1. Crocodiles were photographed at 4 of the 7 nests during the surveillance period, indicating that crocodiles were still taking an interest in these nests. Crocodiles may have been present more frequently than indicated because bushes obscured deep water close to these nests and their presence there could have gone unnoticed. The camera recorded a crocodile regularly only at one nest. This nest was 10 m from the river, and the only deep water from which the crocodile could watch the nest was in a wallow less than 1 m from the nest and within view of the camera. Varanids were photographed taking eggs from 3 nests, and crocodiles were not seen at any of these. The 3 nests were situated well away from deep water so it is unlikely that a crocodile was in attendance but not photographed. At nests where a crocodile was not present varanids returned repeatedly until all eggs were eaten. Only once were a varanid and a crocodile recorded together at a nest. On this occasion a varanid appeared in a frame taken at 1500 h. At 1503 h it had dug into the nest and by 1509 h it had made an obvious hole but had not reached the egg cavity. The varanid was not present in the next frame but in its place was a large crocodile. These data suggest that crocodiles, if present, guard their eggs from varanids.

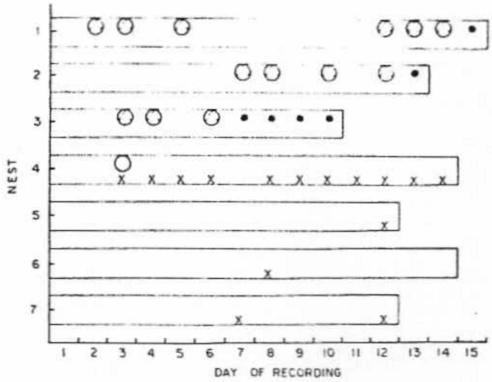

FIG. 1. Days on which varanids and crocodiles were recorded at nests by time lapse photography. O varanid. ⊛ a varanid taking eggs. X crocodile present at nest. * no eggs remaining in nest.

Predation by Humans.—So that other mortality factors could be investigated, aborigines living near the Liverpool/Tomkinson system were asked not to take eggs from nests. They largely complied with this request. Previously, crocodile eggs formed a seasonally important part of their diet. All nests found on the Blyth and Cadell Rivers, near aboriginal settlements, were raided for eggs by aborigines.

The aboriginal hunters found six of the 13 nests estimated to be present in the swamp and all of the seven nests estimated to be present along the section of river bank they surveyed. The method used to estimate the total number present cannot give a standard error if one method of search (in this case aboriginal hunters) finds all of the nests found by the other method. However, the ratios of nests found by aboriginal hunters to the number estimated to be present differ between habitats sufficiently to suggest that aborigines are more efficient at finding nests beside rivers.

Other Causes of Eggs Failing to Hatch.—Other causes of mortality of eggs, such as fungus infections or inappropriate temperature regimes due to poor nest construction, undoubtedly occur. However, the overwhelming influence of flooding and predation prevented an investigation of these during the present study. A few of the eggs examined for embryological studies appeared to be infertile. This is often difficult to determine as the earliest developmental stages are hard to detect. All of the eggs judged to be infertile exhibited aberrant characteristics. The shell lacked the opaque ring around the center typical of eggs of *C. porosus* (Webb et al., 1977) and the yolk was situated in the center of the egg.

Discussion

This study demonstrated that the lizard *Varanus indicus* is a common predator and that it will eat both fresh and dead eggs. Presently varanids do not kill many embryos but this may be because eggs are usually killed by flooding before lizards find the nests. Once a nest is located varanids return to the nest repeatedly until all eggs are taken. Joanen (1969) recorded similar behavior by raccoons raiding alligator nests.

During this study varanids did not successfully attack nests at which adult crocodiles were present. This is in contrast to observations made during preliminary work (Webb et al., 1977) which suggested that crocodiles sometimes tolerate the presence of varanids at nests. The reasons for this difference may be related to the method of collecting data. During the earlier study, observations were made from a motor boat rather than with a time lapse camera. Sound from a motor boat carries for some distance on these rivers and can be heard clearly at the nest for 5–10 min before the boat arrives. If the crocodiles were alarmed by the approaching boat they may not have shown the same responses to the presence of varanids as if undisturbed. Cott (1971) discussed the need for caution when interpreting observations of the behavior of animals that have learned to fear man. One cannot overlook the possibility that nests were attacked by varanids as a result of disturbance by the investigator making them more attractive. Deitz and Hines (1980) found that disturbance by humans doubled the rate of attacks by raccoons on alligator nests. However, as most of the nests in this study were not attacked until 14–30 days after the nest was last disturbed by the investigator this seems unlikely to be a major factor. Because of the high densities of varanids along rivers, it is difficult to imagine any nests in these areas producing young if adult crocodiles did not protect nests.

Varanids attack a greater proportion of nests along river banks than in swamps. This is probably because *V. indicus* is restricted to mangrove and forest areas bordering rivers (Cogger, 1975; Magnusson, unpubl. data). The two nests in swamps that were attacked were in a small swamp (0.01 km^2) directly adjacent to a mangrove forest along a river bank. The other nests were in much larger swamps (0.2, 1 and 2 km^2), suggesting that apparent protection from predation offered by swamps depends on the area and/or location of the swamp. Joanen (1969) found that *A. mississippiensis* nests in marshes were less likely to be attacked by raccoons than those on levees. A similar situation occurs in Florida, almost all losses due to raccoons occurring along levees (J. Kushlan, pers. comm.). Losses that would be caused by aborigines in the absence of other agents of mortality could not be determined, but the evidence suggests they would be considerable. Because aboriginal hunters found all nests also found from the aircraft, no statistical conclusions could be drawn from the experiment testing the efficiency of aborigines at finding nests on river banks as opposed to in swamps. However, the results are consistent with the claim made by aboriginal hunters that nests are more difficult to find in swamps than along river banks.

Direct predation is not the only way that humans may affect the survival of eggs. This study has shown that the presence of adult crocodiles at the nest may be important in protecting the nest from varanids. Regular disturbance by humans may cause the adult to abandon the nest, or at least to leave the nest for extended periods during the day when varanids are active. This has been reported as a factor in predation on nests of *C. niloticus* in Uganda (Cott, 1969). Kushlan and Kushlan (1980*b*) demonstrated that *A. mississipiensis* actively defends its nest against predators but suggested that the alligators do not defend nests in areas in which they are regularly harassed by humans.

Overall, flooding caused most mortality of eggs. However, its effect was limited to nests along river banks: no swamp nest was flooded. The frequency and magnitude of flooding is unpredictable. Although almost all eggs laid beside rivers were killed by flooding in the three years of this study, in some years riverside nests produce large numbers of hatchlings. Grahame Webb (pers. comm.) found numerous hatchlings from the 1972/73 breeding season in the upper reaches of the Liverpool River. That breeding season was notable for the lack of major flooding from the beginning of March. Flooding occurred on the Liverpool River until the beginning of April in 1974 but some very late nests on the Tomkinson River, which has a slightly different flooding regime, still produced hatchlings (Webb et al., 1977). If this pattern of survival holds it would appear that of the previous ten years three would have had conditions suitable for the production of large numbers of hatchlings and an additional five, conditions suitable for survival of eggs in very late nests, at least on the Tomkinson River. During the 1967/68 breeding season and possibly in 1973/74 there was a suitable interval for incubation of eggs at the beginning of the breeding season but whether this was utilized by the crocodilians is not known. A similar period occurred at the beginning of the 1976/77 season but no crocodilians took advantage of it on the Liverpool/Tomkinson system. It may be that heavy rainfall is the proximal stimulus to breeding. Clarke (1891) has suggested that oviposition by *A. mississippiensis* may be delayed in particularly dry years and that in these years early development of embryos may take place in the oviduct.

It would seem that on the Liverpool/Tomkinson system survival of eggs deposited in nests beside rivers before the end of February is negligible in most years. The question therefore arises as to why early nesting has not been selected against. The only hypothesis that I can suggest is that early nesting is advantageous in swamps in this area. All of the nests in swamps located during this study were constructed early in the wet season. Hatchlings emerging early would be able to take advantage of the higher growth rates possible during the wet season (Magnusson and Taylor, in press) and hence outgrow their predators. Many other species of crocodilians have limited nesting seasons. In any one area, most nests are made within a few weeks (Clarke, 1891; Joanen, 1969; McIlhenny, 1935; Pooley, 1969; Reese, 1907) or at most a few months (Crawshaw and Schaller, 1980; Modha, 1967; Staton and Dixon, 1977). It may be that the protracted nesting season allows *C. porosus* to take advantage of habitats varying spatially, temporally and qualitatively. Such a strategy that would seem appropriate for the species of crocodilian with the widest geographical and, possibly, ecological range. However, this generalised approach may mean that the efficiency of reproductive effort is not maximised for any one habitat.

No difference was found in the duration of inundation required to kill 30-day-old eggs and 60-day-old eggs in the laboratory experiment (8–13 h). This is greater than that to which eggs would be exposed during the tidal floodings (less than 6 h) but less than that usually experienced during catastrophic floods (more than 24 h). If O_2 is a limiting factor in the survival of eggs when inundated the use of 155 mm Hg pO_2 might have biased the results towards higher survival. However, Kutchai and Stean (1971) have shown that it is the diffusion barrier set up by stagnant water in the pores of the egg shell that kills chicken embryos. If this is true also for crocodiles it may be that, within limits, the PO_2 of the water in which the eggs are immersed has little effect on the time of survival. Also, it should not be overlooked that factors other than anoxia, such as the low osmotic pressure of the water, could be responsible for the deaths of the embryos. While it is never possible to be certain that a laboratory experiment correctly duplicated field conditions, field data support the conclusions. Eggs taken from two nests that had been flooded for 6–8 h were successfully incubated in artificial nests through to hatching. Eggs taken from six nests flooded for 24 h or more were dead. Joanen et al. (1977) found that a similar period of inundation (6 to 12 h) was required to kill eggs of *A. mississippiensis* at the same stage of development but reported that very early stages survived for longer.

Crocodiles appear to nest in suitable habitats in proportion to availability (Magnusson, 1980*a*). For this reason nests in swamps make up only a small proportion of the total. However, as these nests are subject to less predation by varanids and humans and none of them are flooded, they can be expected to contribute hatchlings to the population every year. In areas beside rivers mortality of eggs is extremely high due to flooding. In the absence of flooding, predation by humans (which are not deterred by the presence of a crocodile) and by varanids (which probably are deterred by an attendant adult) could be expected to be significant. In the absence of detailed information on survival of crocodiles post-hatching it is difficult to come to firm conclusions as to the significance of the differential mortality to the population as a whole. On the Liverpool/Tomkinson system most swamps are on the lower reaches. Hatchlings entering these areas from swamp nests disperse upstream away from the nest sites, but hatchlings entering the river further up remain near the nest site (Magnusson, 1979*a*). Perhaps the lower reaches are unfavorable to hatchlings. Whatever the importance of nests in swamps during normal years, it is likely that they are important to overhunted populations which may lack sufficient numbers to buffer them against many consecutive years of unsuccessful nesting.

While the present paper has fairly clearly defined the sources of mortality of eggs of *C. porosus* the implications for management of the species are not as clear cut. The general result, that there is less mortality of eggs in swamps, has already been used as a criterion for the suitability of habitat for nesting by crocodiles in northern Australia (Magnusson, 1980; Magnusson et al., 1978*b*, 1980). However, not all swamps may be equally free from flooding (Grahame Webb, pers. comm.). The dynamics of populations subject to severe temporal and geographical fluctuations in age specific mortality are poorly understood. Any attempt to manipulate the population by such measures as collecting and artificially incubating eggs from areas subject to flooding will require careful monitoring. The presence of investigators in the area could shift the emphasis from mortality due to flooding to mortality due to varanids simply by scaring the attendant crocodiles from the nests. In areas with similar flooding regimes to the Liverpool/Tomkinson system it may be well to limit collecting of eggs to before March in all years. The creation of large reserves with limited human access would seem to be a sensible strategy to maintain the populations while other methods are being tested.

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LITERATURE CITED

ATTWELL, R. I. G. 1970. Some effects of Lake Kariba on the ecology of a floodplain of the mid-Zambezi Valley of Rhodesia. Biol. Conserv. 2:189–196.

BLAKE, D. K., AND J. P. LOVERIDGE. 1975. The role of rearing crocodiles for commercial and conservation purposes in Rhodesia. Rhod. Sci. News 8:315–324.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, London. 234 pp.

CLARKE, S. F. 1891. The habits and embryology of the American Alligator. J. Morphol. 5:181–206.

COGGER, H. G. 1975. Reptiles and amphibians of Australia. Reed, Sydney. 584 pp.

COTT, A. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and northern Rhodesia. Trans. Zool. Lond. 29:211–356.

———. 1969. Tourists and crocodiles in Uganda. Oryx 10:153–160.

———. 1971. Parental care in the Crocodilia with special reference to *Crocodylus niloticus*. I.U.C.N. Public. New Ser. Suppl. Pap. 32:162–180.

CRAWSHAW, P. G., AND G. B. SCHALLER. 1980. Nesting of the Paraguayan Caiman (*Caiman yacare*) in Brasil. Papéis Avulsos Zool., São Paulo 33:283–292.

DEITZ, D. C., AND T. C. HINES. 1980. Alligators nesting in north-central Florida. Copeia 1980:249–258.

GOODWIN, T. M., AND W. R. MARION. 1978. Aspects of the nesting ecology of American Alligators (*Alligator mississippiensis*) in north central Florida. J. Herpetol. 34:43–47.

HINES, T. C., M. J. FOGARTY, AND L. C. CHAPPEL. 1968. Alligator research in Florida: a progress report. Proc. S.E. Assoc. Game Fish Comm. 22:166–180.

JOANEN, T. 1969. Nesting ecology of alligators in Louisiana. Proc. S.E. Assoc. Fish Game Comm. 23:141–151.

———, T., L. M. MCNEASE, AND G. PERRY. 1977. Effects of simulated flooding on alligator eggs. Proc. S.E. Assoc. Fish and Game Comm. 31:33–55.

KUSHLAN, JAMES A., AND M. S. KUSHLAN. 1980*a*. Water levels and alligator nesting in the Everglades. Second Conference on Scientific Research in National Parks. San Francisco, California, November 1979.

———, AND ———. 1980*b*. Function of nest attendance in the American alligator (Reptilia: Crocodilia: Crocodilidae). Herpetologica 36:27–32.

KUTCHAI, H., AND J. B. STEAN. 1971. Permeability of the shell and shell membranes of hen's eggs during development. Respir. Physiol. 11:265–278.

MCILHENNY, E. A. 1935. The alligator's life history. Christopher Publishing House, Boston. 177 pp.

MAGNUSSON, W. E. 1979*a*. Dispersal of hatchling crocodiles (*Crocodylus porosus*) (Reptilia, Crocodilidae). J. Herpetol. 13:227–231.

———. 1979*b*. Incubation period of *Crocodylus porosus*. J. Herpetol. 13:362–363.

———. 1980*a*. Habitat required for nesting by *Crocodylus porosus* in northern Australia. Aust. Wildl. Res. 7:149–156.

———. 1980*b*. Hatching and creche formation by *Crocodylus porosus*. Copeia 1980:359–362.

———, G. J. CAUGHLEY, AND G. C. GRIGG. 1978*a*. A double survey estimate of population size from incomplete counts. J. Wildl. Mgmt. 42:174–176.

———, G. C. GRIGG, AND J. A. TAYLOR. 1978*b*. Aerial survey of potential nesting areas of the saltwater crocodile (*Crocodylus porosus* Schneider) on the north coast of Arhem Land, northern Australia. Aust. Wildl. Res. 5:401–415.

———, ———, AND ———. 1980. An aerial survey of potential nesting areas of *Crocodylus porosus* on the west coast of Cape York Peninsula. Aust. Wildl. Res. 7:465–478.

———, AND J. A. TAYLOR. 1981. Growth of juvenile *Crocodylus porosus* as affected by season of hatching. J. Herpetol. 15:242–245.

MEDEM, F. 1958. Informe sobre reptiles Colombianos. III. Investigaciones sobre la anatomía craneal, distribuición geográfica y ecología de *Crocodylus intermedius* (Graves) en Colombia. Caldasia 8:157–215.

MODHA, M. L. 1967. The ecology of the Nile Crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. E. Afr. Wildl. J. 5:74–95.

MOORE, J. C. 1953. The crocodile in the Everglades National Park. Copeia 1953:54–59.

OGDEN, J. C. 1978. Status and nesting biology of the American Crocodile, *Crocodylus acutus* (Reptilia, Crocodilidae), in Florida. J. Herpetol. 12:183–196.

POOLEY, A. C. 1969. Preliminary studies on the breeding of the Nile Crocodile, *Crocodylus niloticus*, in Zululand. The Lammergeyer 3:22–44.

REESE, A. M. 1907. The breeding habitats of the Florida alligator. Smithson. Misc. Collect. 3:381–387.

STATON, M. A., AND J. R. DIXON. 1977. Breeding biology of the spectacled caiman, *Caiman crocodilus*, in the Venezuelan Llanos. U.S. Fish and Wildlife Service Wildlife Report 5. 21 pp.

WEBB, G. J. W., H. MESSEL, AND W. E. MAGNUSSON. 1977. The nesting of *Crocodylus porosus* in Arhem Land, Northern Australia. Copeia 1977:238–249.

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