

Nest opening response of the Nile crocodile *Crocodylus niloticus*

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(With 2 plates in the text)

Observations on captive Nile crocodiles, *Crocodylus niloticus* confirm earlier reports on parental care of nests and of young. Male and female appear to form a pair bond after courtship, the male defending nesting territory with the female rarely leaving the nest until the sounds of the young hatching stimulate her to open the nest to release them. The female transports unhatched eggs and live young in her buccal pouch to water and establishes a nursery where the young are defended for several weeks. Experiments involving playback of distress calls by tape recorder, offering of live young and eggs to the adults, the parent opening an artificial nest and vocalisations and resultant interactions between adults and young are described.

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Introduction

The apocryphal and observational literature on the Nile crocodile has long contained credent reports that this species and some other crocodylians dig up their eggs at the time hatching and carry the young to the water (Bartram, 1792; Goldsmith, 1805; Cott, 1933). In recent summaries of the crocodylians, such reports have generally been ignored or set aside as untrustworthy (Neill, 1971; Guggisberg, 1972).

The present paper reports a series of experiments carried out as part of the Natal Parks Board's crocodile rearing and research programme at Ndumu and St. Lucia Game Reserves in Zululand, Natal, South Africa (see Pooley, 1974 for a popular account with coloured illustrations). It supports other recent reports that some of the original observations were correct and the scepticism of later authors unfounded.

Ndumu Game Reserve

All observations at Ndumu were made in two large crocodile breeding pens, each 32 m and interconnected through a short passageway. The first enclosure contains ponds, each approximately 15 x 7 m and varying in depths from 15 cm to 1 m. The

second pen encloses a pond some 45 m long and 16 m wide with a depth between 15 cm and 1.5 m. These pens are well planted with stands of the grasses *Panicum* spp. and *Sorghum verticilliflorum* along the banks. *Echinochloa pyramidalis* grass, marginal to the water and the aquatic plants *Phragmites* sp., *Nymphaea lotus*, *Pistia stratiotes*, *Trapa natans* and *Typha latifolia* provide cover, and small thickets of *Ficus capreifolia* and *Vernonia colorata* furnish additional shade.

The first experiment involved nine adult crocodiles, five of them females, four of them males. These were captured on the following dates: 24 March 1972; 26 March 1972; 2 November 1972; 18 December 1972; 9 March 1973; 28 April 1973; 23 July 1973; 2 August 1973; and 5 December 1973. The animals were sexed in the manner described by Brazaitis (1969). The largest male measured 4.5 m total length whilst the smallest was 2.59 m. The females were all adults according to criteria derived from the data of Cot (1961) and ranged from 2.69 to 3.50 m in total length.

Courtship behaviour was observed during July and August 1973. A female moved to a nesting site on 23 October 1973 and was observed to have laid eggs on 1 November and thereafter rested on or in the immediate vicinity of the nest. Over the following 117 days she was found absent from guard duties only twice, both times on particularly hot days and soon returned from the pool to the nest after my arrival nearby. The nest site was situated 15 m from the pool and 4 m from the perimeter fence. Random observations at night confirmed that the female continues nest guarding during the hours of darkness. No once during the incubation period was the female seen to feed. Toward the end of the incubation period, it was obvious that this female had lost a considerable amount of weight and it was also noted that she was torpid and sluggish in her movements.

Experiments at Ndumu

In Zululand, the normal crocodile incubation period is from 84 to 96 days (Pooley, 1969). During our initial experiment, after 117 days had passed without signs of hatching, we recognised that the eggs were infertile. Thereupon, it was decided to play pre-recorded sounds of crocodile eggs hatching and various juvenile distress calls to the female, who still remained in the vicinity of the nest.

Tapes of these calls were played on a Stereo Cassette recorder, model Tc-124; the two speakers masked by a reed curtain were placed at the base of the fence. In addition, a box containing unhatched eggs and some live hatchlings was placed nearby, also screened from the crocodile.

On 27 February 1974, during the late afternoon, the first recordings were played. As soon as the sound started, the female emerged from the pool, walked past the nest toward the speakers. With fore-feet she commenced digging at the base of the fence, scraping away earth, grass and small shrubs to a depth of 15 cm in line with the speakers. The experiment then had to be interrupted because of the arrival of, and disturbance from, visitors nearby. The following morning, the same conditions were set up at 0500 hrs. The box of eggs and

PLATE I. (a) The female attempting to pick up the hatchling with her teeth. (b) Delicately grasping the hatchling between sharp conical teeth it is manoeuvred into her jaws. (c) The female demonstrated almost continuous antero-posterior rocking motions of the head once the young were contained within the mouth.

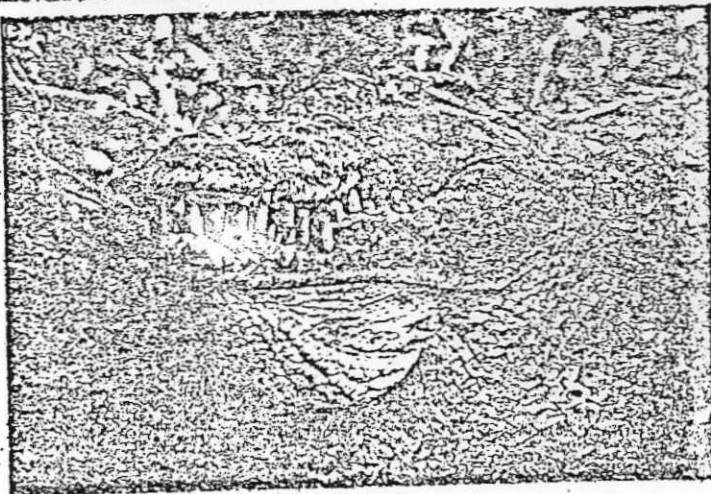
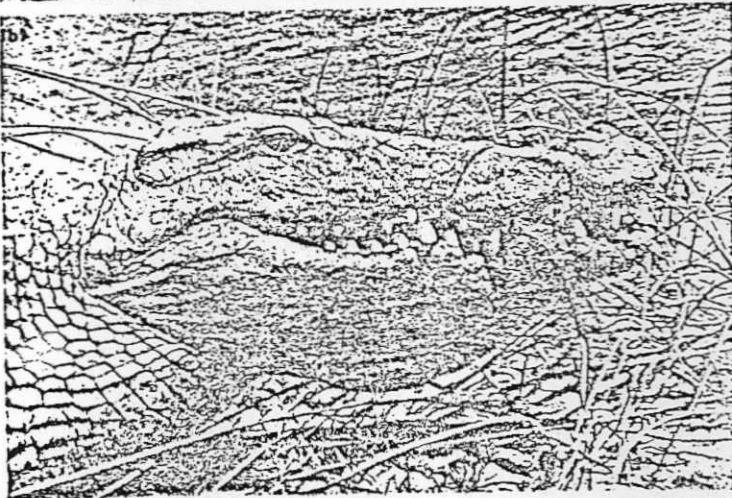
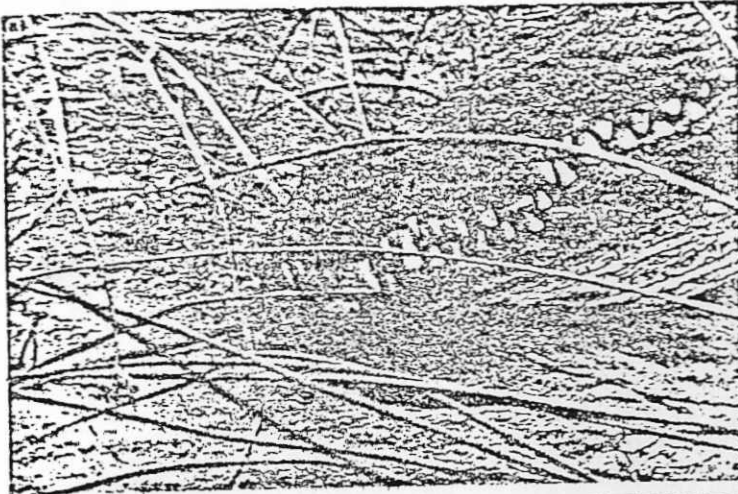


PLATE I

hatchlings was concealed in the same position as before. In response to the tape recording, the female left the nest, which she had been guarding, and approached the fence; however, this time she made no attempt to dig as on the previous occasion, so playback of calls was discontinued.

At 0730 hrs, after the temperature had risen by about 4°C, vocal activity was heard from the box. The calls caused the female to move closer to the fence, where she pressed and prodded with her snout against the wire mesh to reach the box. At this point, a live hatchling was introduced into the pen (through a slit in the fence); the female lunged forward with head angled sideways and attempted to pick up the hatchling with her teeth (Plate I(a)). The hatchling yelped several times and tried to climb back through the fence. Delicately grasping it round mid-body, the female pulled it back. With a quick gulping motion, she manoeuvred it into her jaws (Plate I(b)), and with a rocking motion of the head, into the buccal pouch.

Over the next two hours, 18 more hatchlings were introduced into the pen, and each was captured and taken into the buccal pouch. The female demonstrated almost continuous antero-posterior rocking motions of the head once the young were contained within the mouth (Plate I(c)), presumably to prevent the young from climbing out of her jaws. The following points are of particular interest: (a) The female accepted the foster brood; after some hesitation, she even accepted some of the hatchlings from my hand. (b) When a group was introduced, those young that did disperse into long grass were located by sound and not by sight or scent. The parent followed them into the long grass, waited motionless with head held just above the position from which the last call had emanated and then captured the hatchling when it commenced yelping again. (c) Some hatchlings walked straight towards the jaws of the female, and climbed inside of their own accord, after she lowered her partly opened jaws towards the ground. (d) Other hatchlings became excited at the close approach of the adult, yelped almost continuously and flicked their tails from side to side, which made them more noticeable. (e) As both the number and weight of live young contained in the buccal pouch increased, the pouch was seen to become more distended and to hang heavily below her jaws (Plate I(c)). Furthermore, when all of the 19 young offered were contained in the pouch, one could see, through her partly opened jaws, that there appeared to be space available for at least that many again. (f) Once inside her jaws, and although the jaws were often half open, not one hatchling attempted to escape. In fact, when observed closely, several appeared to be sleeping. It was also noted that the female continued rocking motions of the head once young were in the pouch, and this seemed to discourage attempts to climb out of the pouch. (g) Vocal communication among hatchlings may be important, as the arrival inside the pouch of each newly caught young stimulated those within to yelp; in turn, any left on the ground answered. (h) Once the full complement of available young had been captured and, having observed that no more were forthcoming, the female became aggressive towards me, exhaling and growling loudly, making mock thrusts against the fence at any movement made by me. (i) After an interval of five minutes or so, the female then turned around and lumbered off down to the pool, entered the water and disappeared behind thick aquatic vegetation. Almost immediately a chorus of young could be heard uttering chirruping yelps presumably as they entered the water. These yelps were different in tone from the vocalizations previously heard. The adults, in turn, responded by emitting long, drawn out roars from various parts of the enclosure but did not approach the area where the young were released. (j) The

female never returned to her nest; when it was opened, the eggs were found to be infertile.

Over the following weeks, the female could be seen in one corner of the pool with the young in immediate proximity, either basking on a mudbank or on floating vegetation. Spot samples at all times of the day and night showed that the young remained adjacent to the foster parent. In a series of tests carried out at weekly intervals over the next two months the female responded by coming to collect live young offered to her. It was significant that she would only respond if the young uttered distress cries when dangled through the fence, or if tape recordings of these sounds were played.

On the 53rd day, 20 April, the female accepted the last of the live young; these were 37.5 cm in length. It was obvious from the slow approach to the fence, the reluctant manner in which the young were accepted, and the fact that they were allowed to climb out of her jaws before getting to the water's edge, that maternal interest was waning.

A dispersal of young away from the nursery area started about 14 April, and all had dispersed by 2 May. The female then commenced feeding. The establishment of a nursery area by females has already been described by Cott (1971).

St. Lucia Game Reserve

A new experimental breeding enclosure was established at St. Lucia during June 1974. This measured approximately 180 x 150 m and contains two ponds, one of about 15 x 10 m averaging 15 cm in depth, the other 120 x 10 m varying in depth from 15 cm to 1.5 m. The smaller pond is well planted with stands of *Phragmites* sp. and *Typha latifolia*. The larger pond contains scattered small thickets of the sedge *Scirpus littoralis*. Within the enclosure, there are areas of well grassed banks, sandbanks, and shade in the form of large *Syzygium cordatum* trees and thickets of the same species.

St. Lucia experiments

Two adult males, an adult female, and six sub-adults (three males and three females) in the 1.5 to 2 m size group were transferred to this enclosure.

Courtship was observed during early August 1974 and initially involved a series of subadult males and the adult female. After two weeks, the fully adult males also started to participate. The larger of the adult males started chasing the smaller males, biting them and inflicting minor wounds on tails and hindlimbs. This behaviour continued for three weeks and, over the last few days, fights became serious, resulting in the death of one of the smaller adult males. All sub-dominant males retreated to the small pond in the enclosure and thereafter remained in that area. During the fights, the dominant male of 3.69 m lost most of its teeth. The base of the fourth tooth on the lower jaw was abscessed on either side. For the following six weeks this male did not feed at all, but lay in the shade of a tree.

What appeared to be a successful mating between this male and the female was only observed once, and that on 5 September, the day after serious fighting started. On the morning of 3 November 1974, the female was discovered lying over a nest. During the following 93 days she was found absent from the nest only on two occasions. On the morning of 3 February 1975, the female was found in the water immediately adjacent to 25 young that were floating in the pool close to one another. A deformed dead juvenile was lying on the bank below the nest. Upon noticing observers, the female reared out of the

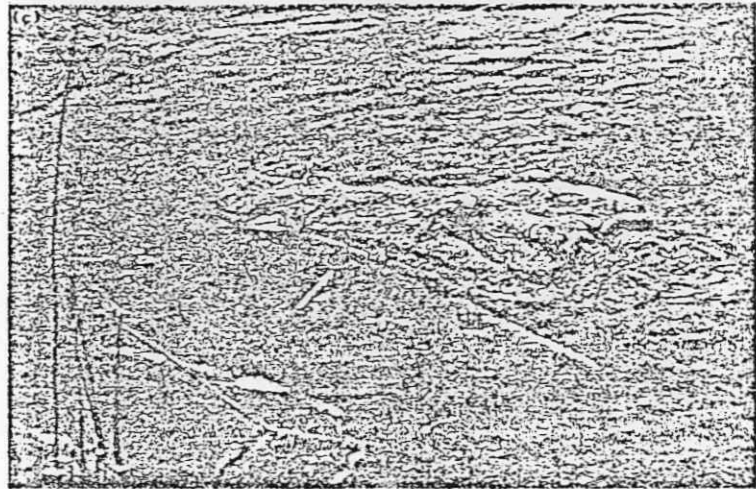
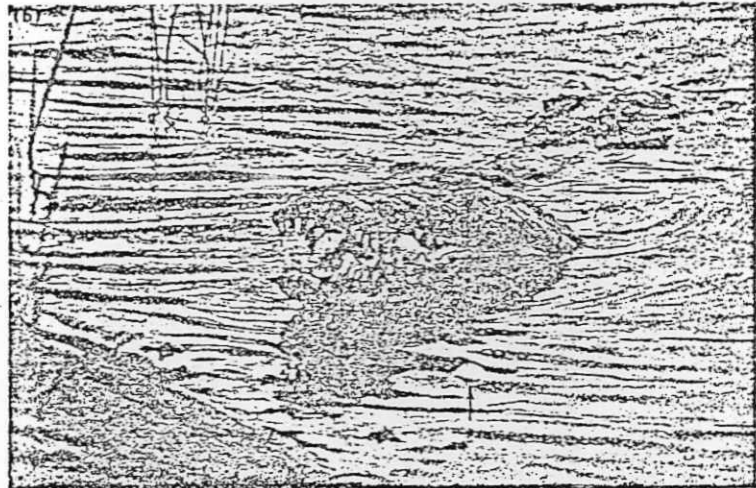
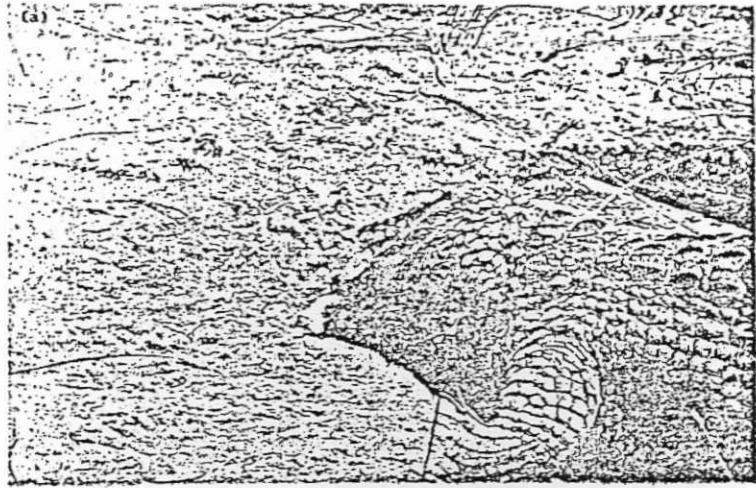


PLATE II

water, lifted her fore-limbs, gaped widely, then dropped the mouth until her lower jaw was below the water level. She then closed the upper jaw on the lower with a resounding crash. For the next five weeks the female gave this response whenever the pen was approached, first swimming, on the surface or underwater, to the side of the pond closest to the observer. During these encounters the male was lying on the bank but did not respond to the disturbance. However, if one of the sub-adults ventured to enter the area, the male gave chase with an impressive turn of speed, pursuing the intruder across the pool, over the bank and into the adjacent pool. The subadults generally took cover in the dense thickets and once out of sight would generally be left in peace.

On occasion, at the approach of visitors to the far end of the semi-circular pool, the male would move to that end to inspect them. He occasionally put on a display by blowing streams of bubbles from between partly opened jaws, or by partly submerging his head and ejecting a spray from the nostrils.

Various experiments were carried out in repetition of the Ndumu ones. Tape recordings of distress calls were repeatedly played at different points of the perimeter. The female always responded immediately, turning to the sound, swimming across the pool and approaching the fence to the site where the speaker was concealed. Her young tended to follow their mother to the edge of the pool and would remain there, obviously listening to the recordings, craning their necks and responding by a chorus of vocalizations.

The experiment was repeated three times at weekly intervals and the results were the same each time; the female was lured to three different spots away from her original nest site and the nursery area of the pool.

The first playing of calls, 10 February, was followed by an offer of two young, previously hatched from eggs collected in the wild. In each case, she accepted the young through the fence, and they thereafter behaved as did her hatchlings.

The following experiment was carried out on 25 February. Near the perimeter fence, across the pool from her nest site, a hole was dug and into it were placed seven eggs from my hatchery which were on the point of hatching. This artificial nest was then covered with a 5 cm layer of sand. The female was called to the site by tape recordings of distress calls. The recorder was switched off as soon as the female reached the position of the nest, and she then sank down in a resting position. At this point the young in the eggs beneath her commenced vocalising. The female backed up until her snout was above the nest and pushed the snout slightly into the depression. She then started to scrape away the sand with her snout and, after some minutes, followed this by alternate movements of the forelegs.

One of the young had partially emerged from the egg by this time and it and its attached membranes were picked up by a sideways movement of the female's head (Plate II(a)) and propelled into the back of the significantly depressed buccal pouch by an inertial flick. An unhatched egg was picked up in the same manner and both were carried down to

PLATE II. (a) The female picking up a hatchling from the artificial nest which she has uncovered. (b) The female shifting eggs between palate and tongue. The male has discarded the egg shell (arrowed) in the foreground and is moving in to the shore to release the hatchling. (c) The male releasing a hatchling (arrowed) after rolling the egg for fourteen and a half minutes between its jaws.

water. The first young snapped its umbilical cord rapidly and was seen to climb over the female's tooth row into the water. The female followed it right into the shallows and then remained motionless for some minutes. The young could then be heard calling within the egg. Thereupon she raised her head, opened her jaws slightly and started to shift the egg from the back of her buccal cavity towards the tip of her jaws, rubbing it against the palate by movements of the tongue. One could see the shell more cracked each time the egg was visible and the snout of the hatchling was then seen to emerge. The young struggled for some minutes until it was completely out of the shell and had left the shelter of the partly opened jaws. Still attached to the eggshell by the yolk stalk which lay between the female teeth, it braced its hind feet against the female's jaw until the cord snapped, and the hatchling shot out into the water. After about five minutes the female raised her head to some 60° and could be seen to swallow the empty eggshell.

Twenty-five minutes after the first interaction, the female returned to the nest when the young remaining in the nest started calling. She immediately dropped her snout into the depression and picked up one egg, took it to water and again manipulated it between her jaws until the young was free. The empty shell was then swallowed. Whilst she was occupied with three of the remaining eggs, exposed to the hot sun, hatched on their own. The young climbed out of the nest depression and started crawling toward the water, one of them dragging the empty shell behind. All three called intermittently and elicited a similar response from all the other young in the pool. The female climbed from the water toward them, made attempts to pick up one of them and then abandoned it. All three young continued to water of their own accord. One egg remained in the nest but was ignored by the female; I later removed it and found it to be infertile.

A final experiment was intended to test whether egg recognition depended upon nest condition and whether the behaviour was exclusively female. Both male and female were called to the fence with the whistle ordinarily employed during feeding sequences. Rather than offering fish, three eggs from my hatchery, about ready to hatch, were individually rolled down the slope, alternately toward male and female. Both male and female caught the rolling eggs between their teeth but did not crush them as they would have pieces of fish. Instead, both adults went through the egg-rolling sequence, moving the egg between tongue and palate until it hatched and the young was released (Plate II(b)).

In the case of one egg, the male rolled the egg fourteen and a half minutes until the young emerged from between the jaws (Plate II(c)). In each case the eggshells and membranes were swallowed. Three eggs were used, two for the male, one for the female. To test discrimination, a rotten egg was next rolled to the male who caught it as before, moved it to the back of the buccal cavity, waited for about one minute, then swallowed it.

Toward the end of the third month, the young could be seen to disperse, moving away from the parents individually or in small groups. Most of these were picked up in the early mornings in small unfenced neighbouring ponds and from which they were moved to rearing ponds. A few times such wandering young were seen to reach the vicinity of a sub-adult crocodile; when they noticed the large animal they immediately turned and retraced their path.

After dispersal of all the young, the sub-adults from the adjacent pool began returning without eliciting apparent animosity from the large adults. In fact it became usual to see five or six animals comprising adults and sub-adults of both sexes basking next to one another on the same bank.

Conclusions

The observations and experiments, while still fragmentary, do permit a series of interesting tentative conclusions.

The dominant male remains associated with the female throughout the post-copulatory period. This confirms the comments of Modha (1967) who noticed such males cruising off the breeding beaches. The females have been recorded returning to the same breeding sites each year; however, they may establish new ones. These observations also confirm the earlier reports that the female remains on guard for the duration of the incubation period and that nest guarding continues during the hours of darkness. It also shows that the female does not feed whilst nest guarding. The female clearly responds to the calls of the hatching young. In the wild, transport to water has never been witnessed but sometime during the night or early morning she presumably digs open the nest and transports them in this manner. Although she is capable of manipulating eggs in order to assist hatching, repeated trips with only a few at a time in her mouth would expose both the open nest and the already hatched young to predation whilst the parent was transporting young between the two points. The rocking movements apparently serve to keep the young in the pouch and the lower level chirping of the trapped youngsters suggests that they may relax once the pouch has been entered. Clearly the young participate in the mouth transport process. On emerging from the nest they yelp continuously, flick tails in such a way as to draw attention to their positions, and have been seen to climb into the mother's jaws. Perhaps they are attracted by the chirping sounds that may be radiated by the distended pouch. If transport occurs during hours of darkness the chirping sounds of the first animals to enter the pouch would aid location of the parent's mouth. Both male and female show spectacular motor control in shifting their large, heavy skulls in order to pick up 100 g hatchlings without injuring them. They can also roll the egg in the mouth to hatch it. Probably the observations represent exceptional circumstances, as manipulation may be difficult once the floor of the mouth has been depressed and multiple young are in the buccal cavity; this is one of the several aspects needing further study. The eggshells and membranes are eaten by the adults, which accounts for the absence of significant amounts of shell remnants in the vicinity of the nests. This may have the advantage of avoiding attracting predators to the young. The nest sites are used every year; however, the willingness of females to establish new sites in semi-natural enclosures suggests that the animals can adjust to the destruction of old nest sites which might occur by flooding or movement of other animals. This has important implications for conservation and management programmes. The juveniles remain together for several weeks after hatching and during this time are defended by the female. This is a critical period during which yolk is resorbed and locomotor and feeding efficiency and escape patterns developed. These observations confirm and enlarge on others made by Hadley (1969) and H. Mendelsohn (pers. comm., February 1975) who observed the mouth transport activities of *C. niloticus* in a Tel-Aviv zoo. D. K. Blake and J. P. Loveridge in a paper entitled "Behavioural observations on the Nile Crocodile during the Breeding Season" at a symposium of the Zoological Society of Southern Africa, September 1975 reported on nest guarding, excavation of the nest, transport of young and parental care.

Mouth transport of the young, as reported by Ogden & Singletary (1973); Hunt (1974); Hadley (1969); Kushlan (1973) and Herzog (1975) working on other species, suggest that this method of transfer from nest to water, is practised by all crocodylians.

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