Observations on the Behaviour of Nile Crocodiles Crocodylus niloticus, in Captivity

David K. Blake¹ and John P. Loveridge²

WHEN crocodile rearing stations were established in Zimbabwe in the 1960's, most of the emphasis was on raising juvenile Nile crocodiles, Crocodylus niloticus. Some adults were maintained on rearing stations for exhibition purposes, and they occasionally laid eggs, but these were considered something of a positive "spinoff" rather than being the central aim of keeping adults. In 1970, the then Department of Wildlife Conservation set up a holding pen in the Kyle Game Reserve, Zimbabwe, to investigate generally whether or not captive breeding of C. niloticus was possible.

Having adult crocodiles in captivity provided opportunities for observing behaviours that were not easily duplicated in the wild, and it soon became apparent that some behaviours being observed were different from those reported in the wild by Cott (1961), Modha (1967) and Pooley (1969, 1982). For example, nest defence by females against man rarely occurred in the wild, but was common in captivity.

In this chapter, we summarize observations made on captive adult C. niloticus both in Zimbabwe and later at St Lucia, Zululand, over the past ten years. Some of the behaviours remain poorly understood and require further investigation.

OBSERVATIONS

Nest Site Selection

In October 1981, at Spencer's Creek Crocodile Ranch, Victoria Falls, we observed nest sites being selected by female C. niloticus that were eleven years of age. The females were digging "test" holes with their hind feet, and were alternating the use of each foot. When the holes were 10-15 cm deep, the females would turn and insert their snouts into the holes — a behaviour termed "nuzzling" by Hutton (1984). The female would then either continue to dig at the same site or select a new site. In this pen, the ground was flat and the females could not greatly alter their choice of terrain.

At St Lucia, a mature female was observed digging a hole on the evening of 1 December 1984, and she repeatedly backed up (rather than turned) and inserted her snout into it. After some two hours she abandoned the site, but the following evening the same site was selected and the same procedure followed; this time the site was abandoned after three hours. On the evening of 3 December 1984 the same behaviour was repeated at the same site only this time she laid eggs. This particular female was 3 m total length (TL), very fat and had a missing right front leg; her backing up rather than turning (like the females at Victoria Falls) may simply reflect the greater difficult involved in turning her bulk.

Competition for Nest Sites

Where sufficiently large populations exist in the wild, C. niloticus are communal nesters (Cott 1961; Pooley 1982). In captivity, with limited nesting space, the equivalent of communal nesting occurs and can lead to females competing for the same nest site. At Spencer's Creek Crocodile Ranch, Zimbabwe, females sometimes dig up the nests of other females when attempting to lay (R. Gee, unpublished observation).

At the St Lucia holding pens, a 2.5 m female laid eggs on 22 November 1984 and remained at the nest site. On 5 December 1984 a 3 m female attacked her, drove her from the site, and then proceeded to dig and lay eggs at the exact same site. In the process, she dug up and destroyed a number of eggs of the first female.

The one-legged female mentioned under "Nest Site Selection" above, nested within 1 m of where another female had nested earlier. During the processes of both "test" hole digging and the actual digging of the nest, the other female ignored her except for an occasional growl. However, at 0730 hours on the morning after laying, the one-legged female attacked the other one, inflicting bites to her

P.O. Box 127, St Lucia Estuary, Natal 3936, South Africa.

²Department of Biological Sciences, University of Zimbabwe, P.O. Box MP 167, Harare, Zimbabwe

Pages 295-300 in WILDLIFE MANAGEMENT: CROCODILES AND ALLIGATORS ed by Grahame J. W. Webb. S. Charlie Manolis and Peter J. Whitehead. Surrey Beatty and Sons Pty Limited in association with the Conservation Commussion of the Northern Territory

head, forelimbs and the sides of her body. After some 15 minutes of combat they were forcibly separated, after which the first female left the nest site. In her absence, a plank fence was erected between the two nests. The first female began to return to the nest at night, and after some two weeks remained there during both day and night.

Double Nesting

Double nesting has not been reported in C. niloticus, but may have taken place at St Lucia in 1984. A large female that was recognisable because of a tail disfigurement, laid eggs on 3 November 1984. She aggressively defended her nest site, which was close to the perimeter fence, and during hot periods of the day lay in heavy shade some 10 m from it. Between 11-12 December 1984, she abandoned the nest site and began digging some 5 m away from it. She subsequently became extremely defensive of the new site and completely ignored the old one. On 29 December, 1984, a smaller female started digging at the first site (1145 hours) but ceased after an hour. At 1615 hours the smaller female was observed back at the site and a number of eggs, both broken and whole, had been dug up: during the next hour, she dug up 19 eggs. The mean size of five embryos from these eggs was 148 mm TL, which was consistent with them being from the first female's nest laid on 3 November 1984. After an estimated 120 days on her new nest site, the female was chased away and the area dug up. Seven eggs in an extremely decomposed state were found.

Trance-like State During Laying

Zimbabwe crocodile farmers have observed that once *C. niloticus* start laying eggs they enter a trance-like state; the back leg can be moved and the eggs can be taken from the nest or even as they drop from the cloaca (R. Gee and P. Arnold, unpublished data).

To confirm this observation, one of us (DB) attempted to remove eggs from beneath three females that were laying eggs in November-December 1984. In each case, the females were approached only after they were well into the egglaying process. Initially they were prodded on the hind leg, belly and shoulder of one side, but apart from growling, no other response occurred. A hand was then slipped in front of the hind leg and an egg was removed. The first two crocodiles were approached in darkness and the third in daylight; the third female growled when the hand touched her abdomen.

Fating of Eggs and Hatchlings

At St Lucia, on the night of 22 November 1984, a gravid female started digging a nest hole on a site that had been used for nesting the previous season. During the process, she began excavating whole and

broken eggs from a nest that had been flooded during a cyclone in February 1984. The eggs were dark grey in colour and contained near full-term embryos that were dead and badly decomposed. A larger female, presumably attracted by the smell, came to the nest and proceeded to pick up and eat the eggs. Some were swallowed whole and others were pressed against the roof of the mouth by the tongue, broken, and then swallowed amidst a stream of grey liquid running out of the jaws.

In October 1981, we examined *C. niloticus* nests at Spencer's Creek Crocodile Ranch, Zimbabwe, which had been made by females laying eggs for the first time. The nests were on a steep bank some 3 m above the water, in which the female crocodiles lay watching the proceedings. The nests contained a large number of infertile eggs, one of which was rolled down the bank to observe the reaction; it was promptly seized and swallowed. More eggs were rolled down the bank and all were eaten by a number of different females.

At the Kyle Game Reserve holding pen in Zimbabwe, during January 1973, an overdue nest was excavated (by DB) and the live hatchlings were removed from their eggs and placed at the water's edge. The parent female, which was known to us, immediately became extremely defensive of the hatchlings, with respect to both humans and other crocodiles in the pond. The Senior Game Scout in charge of the pen (C. Basera), subsequently reported that an immature female *C. niloticus*, which had not nested, systematically ate the hatchlings over a number of days, as and when she found them undefended by the parent female.

Nest Defence

Female *C. niloticus* remain in the vicinity of their nest during the incubation period, and it is generally accepted that they are protecting the nest against predators (Cott 1961; Modha 1967; Blake and Loveridge 1975; Pooley 1982; Hutton 1984). However, defence against human intruders by wild nesting females is extremely uncommon. Hutton's (1984) report of humans being threatened refers to females threatening from the water, and Pooley (1982) gives only two instances in which wild females remained at their nest site when it was approached by humans.

Cott (1961) states that "females become torpid and most reluctant to leave the grounds even when approached". This torpid condition in females at nests was also observed by Pitman, Hippel and Savidge (Cott 1961) and occurs when nests are located well away from the water. One of us (DB) observed a torpid, nesting female when collecting eggs with a crocodile rancher (R. van der Rict) at Lake Kariba. Due to a fall in the water level of the lake, the female and her nest were some 400 m from

water. She was lying in the shade of a dense bush some 4 m from her nest, and all attempts to dislodge her by throwing stones or prodding her with a long pole were in vain. Apart from closing her eyes, she took no action and made no noise, even when the eggs were collected.

This reluctance of wild *C. niloticus* females to defend their nests against humans can also be confirmed from the collective experiences of the crocodile ranchers in Zimbabwe. Over the years they have collected eggs from thousands of wild *C. niloticus* nests and have not yet experienced direct aggression from a nesting female. One rancher (K. Yates) reported a collecting party being scattered by a female charging down to the water, but she made no attempt to prevent the eggs from being collected, nor did she engage in any aggressive behaviour.

In the holding pen at Kyle Game Reserve and in various pens on the rearing stations in Zimbabwe that now keep adult C. niloticus, females have rapidly overcome their reluctance to defend nests against human intruders. For example, at the Kyle holding pen in November 1973, we were both chased away from a nest by the 2.8 m parent female, which had been introduced into the pen three years earlier. To collect the eggs in January (1974), a canvas sheet was erected between the nest and the water, where the female was, but after a time she left the water and attacked the canvas, ripping it in several places. It was suggested that this behaviour may have been purely display and that the female would not press home her attack, if given the opportunity. As neither of us was prepared to stand their ground to test this hypothesis, it was decided to experiment using a shop-window manikin - the dummy.

The same crocodile laid eggs in a pile of sand within the pen the following year (14 September 1975). On 18 November, 1975, she was reported (by C. Basera) as spending most of her time lying in shallow water, allowing no one between her and her nest. In addition, she was defending the shallow water adjacent to the nest against another female *C. niloticus* in the pen.

On 19 November, the dummy, dressed in a National Parks uniform complete with stockings and hat, was erected at the nest at 0850 hours. The female immediately left the water and lay down in front of the dummy, snapping her jaws (Fig. 1). After a short period, she attacked the dummy, gripped a leg and tore it off. She showed no further hostility until the dummy was made to move by prodding it with a stick from a concealed position. She attacked it again, this time breaking it into two pieces. In the process, the pole supporting the dummy unearthed eggs from the nest and it was decided to chase off the crocodile and repair both the nest and dummy.

When the dummy was re-erected at 0930 hours, the crocodile again approached it and lay in front of it. After 15 minutes, she suddenly attacked it, first knocking it down and then breaking it into two pieces again. She then took the upper half in her jaws and periodically shook it. After 20 minutes, she carried this top half down to the pond (Fig. 2), swam out and tried to submerge with it. This she was unable to do as the head was made from a large fishing-net float. She then dismembered the upper half into head, arms and torso by shaking it.

At this stage, the 4 m long male in the same pen entered the water and began to investigate the debris. The female moved in stages back to the nest, where she nudged the lower half of the dummy and then bit it. Over the next 20 minutes, she periodically shook or bit this half before finally gripping it and running down to the water where she swam out and abandoned it.

DISCUSSION

Nest Site Selection

"Nuzzling" of test holes by female C. niloticus has also been observed by Modha (1967) and Hutton (1984), and Bustard (1980) reports a similar behaviour with Gavialis gangeticus constructing "test" nests. Hutton (1984) suggested that the females may be sensing soil temperature or marking the nest site with secretions from the two glands in the gular region of the throat (he tended to favour the temperature hypothesis). We cannot throw any additional light on the function of nuzzling, but suggest that substrate water content and/or particle size are two additional factors that could perhaps be assessed during such behaviour. Sense organs potentially capable of one or more of these functions are present in the skin of crocodilians (Reese 1921) and are pronounced along the lower jaw (M. Ferguson, pers. comm.).

Competition for Nest Sites

Communal nesting in wild populations of C. niloticus has been well documented (Cott 1961; Pooley 1982), but it is unclear whether this behaviour represents an adaptation to maximize the effect of nest guarding, or is the result of a shortage of prime nesting sites. That competition for nest sites occurs between females in a pen has obvious implications for managing captive populations of breeding adults. To reduce egg breakages by females excavating the nests of other females, sufficient nesting sites must be provided, or, individual nest bays may be established such as those in the Samutprakan Crocodile Farm in Thailand (Yangprapakorn et al. 1971; Suvanakorn and Youngprapakorn Chapter 33) and those in some South African crocodile farms.



Fig. 1. A 2.8 m captive female Crocodylus niloticus threatening a dummy erected at her nest in a pen at Kyle Game Reserve, Zimbabwe.

Double Nesting

The laying of two separate clutches by a single female C. niloticus in one breeding season has not previously been recorded. None of Cott's (1961) data imply double nesting and Turner (1977) states that it does not occur in wild C. niloticus or Alligator mississippiensis. However, regular double nesting has been recorded for Crocodylus palustris at the Madras Crocodile Bank in India (Whitaker and Whitaker 1984), with about 40 days between the two layings. There were 38-40 days between the construction of the two C. niloticus nests we observed. However, although the female's defensive behaviour is consistent with two nest holes being made and two periods of egg-laving, our observations may be indicative of "staged" nesting. Staged nesting, where all eggs in a clutch are not laid at the same time, may account for very small clutches of eggs found in the wild for other crocodilians (Webb, pers. comm.), and may be mistaken to indicate dual nesting (two separate clutches of eggs). It is of interest that the female's guarding of the first nest ceased when the second nest was made.

Trance-like State during Laying

Cott (1961) reported the trance-like state of female *C. niloticus* guarding nests, but made no mention of a similar behaviour during egg-laying. The phenomenon does not seem to have been

reported in crocodilians, although it has long been known to occur in turtles (McAllister et al. 1965). The trance-like state and the opportunity for close approach to the nest hole and eggs during egg-laying may be useful for crocodile farmers and researchers. It should be possible to remove eggs as they are laid for artificial incubation or to insert nest environment sensors in among the eggs at the time of laying, rather than having to disturb the nest later. A temporary barrier at right angles to the female in the vicinity of her foreleg, would give handlers a little added protection.

Eating of Eggs and Hatchlings

Pooley and Gans (1976) and Pooley (1982) report that when both a female and a male *C. niloticus* were offered fully developed eggs from a hatchery, they gently rolled them in their mouths, between the tongue and palate, and released the hatchlings. The shell was then swallowed. On being offered a rotten egg, the male swallowed it whole (Pooley 1982). The present observations add the following: a female spontaneously eating rotten eggs excavated from an old nest; the eating of eggs (infertile) when they were presented to females during the nesting season; and, the predation on hatchlings by an immature female sharing a pen with the parental female.

Hadley (1969), Cott (1971), Lang (1980) and Kushlan (1973) all describe the defence of hatchling



Fig. 2. The female Grocodylus niloticus in Figure 1 attacked the dummy and carried the top half down to the water.

crocodilians against conspecifics, although this is not always successful, as reported here. From a management point of view, allowing nests to hatch in pens can be expected to result in high hatchling mortality or, at best, the nuisance of having to catch hatchlings from a pen. As artificial incubation of crocodilian eggs is likely to proceed better if eggs are collected at the time of laying (Ferguson 1985), there would simply seem to be little utility in leaving eggs laid in captivity in the nests.

The eating of eggs by crocodiles in the wild may occur if a female excavates an old nest, but is probably largely restricted to when nests are hatching. The various circumstances of egg-eating described by Pooley (1977) may explain the discovery of eggs in the stomach contents of *C. niloticus* in East Africa (Welman and Worthington 1943).

Nest Defence

The females of nearly all species of crocodilians appear to defend nest sites against at least some potential predators (Cott 1961; Pooley 1969; Kushlan and Kushlan 1980; Bustard and Singh 1981). Cott (1971) reviews the literature on this behaviour and also discusses the torpid state sometimes observed in *C. niloticus* females at nests. We have rarely

encountered that state, and then only when females and their nests are a long way from water.

Attacks on man by female crocodilians at their nests are equally uncommon, and in our experience, have only occurred when captive females have become accustomed to the presence of man. Cott (1971) does not record any such attacks for C. niloticus, but does discuss three attacks by nesting Crocodylus porosus. Bustard and Singh (1981) describe a warning "nip" inflicted on a man by a nesting Gavialis gangeticus, and Bustard and Kar (1981) describe how egg-collectors had to remain in a tree for 30 minutes because of a protective female C. porosus. Kushlan (1973) describes nest protective behaviour in wild Alligator mississippiensis, and later (Kushlan and Kushlan 1980) the results of presenting wild nesting females with stuffed racoons and a human model. The human model was attacked as we report here for C. niloticus, but after ripping the model's clothing, the alligator withdrew, Each aggressive act was preceded by a threat (e.g. jaw snapping before biting) as reported here.

CONCLUSIONS

Observations of the behaviour of captive crocodilians are relatively easily made once animals have settled in their pens. If interpreted in the light of field experience, matters such as nest site selection, competition for nest sites and nest defence could have conservation implications, whilst all the matters discussed have potential importance to farmers managing captive populations of adult crocodilians.

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