Paper No 18

PARENTAL CARE IN THE CROCODILIA, WITH SPECIAL REFERENCE TO CROCODYLUS NILOTICUS

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Maternal Care during the Incubation Period

Care at the nest

It was well known to writers of the ancient world that the Nile crocodile mounts guard over the nest. Aristotle (trs. Cresswell, 1862) writing in the fourth century B.C., says: "The river crocodile produces as many as 60 eggs, which are white. She sits upon them for 60 days". According to Pliny (trs. Holland, 1601), "The female layeth eggs as big as geese do, and sitteth ever upon them out of the water". Both writers correctly assumed that parental duties devolved upon the mother; and Solinus (trs. Golding, 1587), who writes "In cherishing up their young, the male and female keep their turns", was mistaken in believing that the male of this species takes any share in these duties.

During the whole three-month incubation period, the female remains in attendance, at or near the nest, though her behaviour differs in accordance with the selected site. When the nest is beneath a tree, surrounded by bush or otherwise shaded, the parent generally lies directly on the nest, with the throat or thorax above the egg-chamber. Nests in more open situations are watched from nearby sites affording shade to the guardian crocodile. In Zululand, Pooley (1969a) found nests that were guarded from as many as three additional sites, where shade ranged from light cover to dense tunnels of vegetation from which only the animal's snout protruded. In places where the rookery is fully exposed to insolation, for example on open sand-bars or beaches, brooding females visit the water periodically during the heat of the day, in accordance with requirements of thermal control, discussed elsewhere (Cott, 1961). Such behaviour has been seen at many breeding grounds on the Victoria Nile. On Central Island, Lake Rudolf, Modha (1967) found that even during the hottest hours when other crocodiles were in the water, females were seen on the rookeries: "At intervals they would go down to the water to cool off but were soon out again and lying near the nest".

In some species the female constructs a special shelter from which she can keep watch over the nest. Writing of the Marsh crocodile C. palustris in Ceylon, Waytialingham (1880) states that the females will sometimes go for a quarter to half a mile to find a suitable sandy site for the nest. "They make, first, a large hole for themselves to live in during the day in order to watch their eggs, and then make a small hole near and sometimes at the very mouth of the previous one, and lay eggs in layers ..." He further states that the females will not allow anybody to go near the nests, that they make a fearful roaring and attempt to attack anyone who approaches; and that they keep a strict watch and seldom or never quit the nesting place during the day.

Referring to the Estuarine crocodile C. porosus Loveridge (1946) reports that the mother digs two wallows wider than, but not so long as, her body, close to the nest. These wallows soon fill with water, and in one or the other the crocodile remains during the period of incubation. The female of the American alligator A. mississippiensis similarly constructs a nest-side wallow or den from which the nest can be guarded during the incubation period (Clarke, 1888; Reese, 1907).

Predatory enemies of the eggs

Egg-eating predators take a heavy toll of unguarded clutches, both by day and night. On the Victoria Nile below Murchison Falls important diurnal predators include the Olive baboon Papio anubis, Marabou stork Leptoptilos crumeniferus and Nile monitor Varanus niloticus; with Black kites Milvus migrans and Palmnut vultures Gypohierax angolensis as camp-followers. At night the work is taken over by the Honey badger Mellivora capensis, White-tailed mongoose Ichneumia albicauda and Spotted hyaena Crocuta crocuta; and less commonly by serval Felis serval (Cott, 1969). Mammalian enemies in other parts of Africa include the Egyptian mongoose Herpestes ichneumon in Egypt (Anderson, 1898); and Water mongoose Atilax paludinosus in South Africa (Stevenson-Hamilton, 1954). In Lake Rudolf (Modha, 1967) Grey heron Ardea cinerea, Goliath heron A. goliath and Sacred ibis Threskiornis aethiopicus are known to prey on the eggs.

Other crocodilian species have different, though often related, nest enemies. Thus, in Colombia, eggs of the Orinoco crocodile C. intermedius are eaten by the Great tegu Tupinambis teguixin and by the South American Black vulture Coragyps atratus (Medem, 1958b). In North Australia, eggs of C. porosus are rooted out and eaten by Wild pigs (Barrett, 1939), just as those of C. niloticus are destroyed in West Africa by warthog Phacochoerus aethiopicus and Bush-pig Potamochoerus porcus (Lavauden, 1934). Again, in Ceylon, the kaberagoya Varanus salvator fills the niche, occupied by V. niloticus in Africa, as an enemy of C. porosus (Deraniyagala, 1939).

Active defence of the clutch

The need for nest-protection is apparent enough. The question remains: do the attendant crocodiles actively defend the clutches when they are threatened by predators? Here it is necessary to distinguish between the behaviour of the reptiles in a natural undisturbed state, on the one hand and, on the other, in areas where they have been harried and hunted and have in consequence learned to fear man. Observations made under the latter conditions -- of crocodiles readily deserting the rookery and failing to drive away marauders -- may give a false picture of primeval nesting behaviour.

I have on several occasions seen nesting crocodiles make sorties against predators. In 1961, while observing a rookery near the Namsika confluent below Murchison Falls at close range from a grass hide, I witnessed a determined attack: a crocodile that had been lying about 15 yards from, and facing the hide suddenly rose up and ran straight in my direction. When it reached the front of the hide -- and as I was preparing to leave -- there was a rustle of dead leaves and I caught a glimpse of a Nile monitor in rapid retreat. Crocodiles that have been frightened from their nests by launches passing the grounds have on a number of occasions been seen to return to the rookery to chase away a foraging monitor or baboon. The presence of monitors in crocodiles' stomachs, as recorded elsewhere (Cott, 1961), indicates that these egg thieves are sometimes taken unawares.

Opportunities for observing crocodiles in the pristine state are diminishing, and Modha's (1967) prolonged studies at Central Island, Lake Rudolf, on what is one of the largest remaining undisturbed populations of the Nile crocodile, are therefore of special interest. He found that guardian females never tolerated the presence on the rookeries of predatory birds such as Grey and Goliath heron, Little and Great White egret, Sacred ibis and Fan-tailed raven. Crocodiles were seen chasing these birds away from the nests. On the other hand, innocuous species which regularly frequent the grounds, such as Egyptian goose, Spurwing plover and Water dikkop, were ignored.

The literature contains several accounts of attacks upon man by nesting crocodiles -- notably by C. porosus, which is generally believed to be the most dangerous crocodilian. Boake (1870) records that a man who was taking eggs from a nest of this species in Ceylon was repeatedly charged by the guardian crocodile and on being attacked by a second individual at the nest was lucky to escape alive. Shelford (1916) refers to an exciting struggle between a party of hunters and a large female crocodile defending its nest on the Baram River in Borneo. A spirited assault upon himself by C. porosus nesting in a pond near Townsville, Queensland, is described by Robinson (1948): "When I was taking the debris away from the nest she charged at me with open mouth and drove me into the boat. One second later and I would have been in her jaws. She came right out of the water and on to the nest, in clear view of the crowd looking on, and only for my having a long stick to jab

into her mouth I believe she would have come into the boat". From the Llanos Orientales, Colombia, Medem (1958a) reports that a Dwarf caiman Paleosuchus palpebrosus attacked a hunter when he approached the nest containing eggs. Del Toro (1969) gives details of nest defence by both male and female Spectacled caiman Caiman crocodilus breeding in captivity. Both parents remained near the nest, not allowing the keeper or anyone else to approach: and it is interesting to note that in this case it was the male who took the main defensive role.

Comatose state in brooding females

Little is known of the night life of females during the incubation period. The crocodile is nocturnally aquatic: yet females are certainly found occupying the grounds at night. However, no all-night observations on particular individuals have been made, and we do not know to what extend an all-night vigil is maintained. In lake- or river-side rookeries it may happen that brooding females take advantage of the nearby water to feed for short periods. Nevertheless, available evidence suggests that females fast throughout the incubation period. Hippel, a professional hunter who had wide experience 25 years ago in the Lower Semliki and in Lake Kioga, and who made a study of the diet of his victims (1946), told me (pers. comm. 1952) he had never found food in stomachs of females taken at the nest. Pitman's (1930) experience was similar on the islands and shores of northern Lake Victoria. Stomachs of brooding females examined by me were likewise empty.

Where cover is dense on a crocodile's breeding ground, and especially where the site is at a distance from the water, the reptiles are very loath to move from their nests. In such places, as incubation proceeds, females are frequently found in a comatose state, unwilling to shift even under the greatest provocation. Pitman (1941) reported from Lake Victoria that shots have been fired close to such crocodiles without evoking the slightest response. In 1957, I examined a rookery in a sand-river below Murchison Falls where some nests were nearly a quarter of a mile from the water. Females in their trance-like state lay motionless, like felled logs: one refused to move even when large stones were thrown on her back; others hissed their remonstrance and shifted a few feet into thicker cover. Similar behaviour has been witnessed by Pooley (1969a) in Zululand. He writes: "One female at St Lucia withstood a barrage of sticks thrown at her, adopting an attitude of defiance during the attempt to chase her off the nest. She lay with head held almost vertical, jaws slightly agape, uttering a deep throaty growl each time a missile landed nearby or actually hit her. Our attempts to dislodge her failed".

It seems almost certain that such crocodiles remain on the rookery until hatching time, without once visiting the water. The physiological condition

f these animals, especially in regard to dehydration, is doubtless comparble to that of torpid crocodiles which, under different circumstances, are nown to survive long periods of drought, aestivating in caves and holes dug n dry pans or river-beds. Many observers have recorded such behaviour, is, for example, from Lake Rukwa (Swynnerton and Nicholson, in Cott, 1961); Abyssinia (Emin Pasha, 1890); Somaliland (Eliot, 1905); West Nile Province of Uganda (Kittenberger, 1929); and Mali (Lhote, 1948): the atter states that crocodiles inhabiting a temporary lake near Ménaka spend it least six months of the year aestivating in the mud after the lake has dried up.

Parental Care at Hatching Time

Calling of the young

When ready to hatch the young respond to airborne sounds and to terrestrial vibration by calling. Under artificial conditions -- if, for instance, eggs are stored in boxes indoors – the human voice, a tape recording of a hatchling's grunt, the slamming of a door, or the shaking of an egg in the hand, will elicit the vocal response; and when one hatchling calls others may join in the chorus. In the field, a pat of the palm above the nest will stimulate calling, and this reaction provides a ready means of ascertaining the time when hatching is due. Under natural conditions the step of the mother or the sweep of her tail near the nest will doubtless have a similar effect. Hunt (1969) reports a like response in hatchlings of the Spectacled caiman: when he lightly brushed the roof of the nest so as to simulate a mother crawling on the ground, croaking was heard.

Maternal reaction to vocalization

The sounds uttered by the unhatched young stimulate the guardian parent to visit the nest and open it, thus enabling the hatchlings to escape from the shells. Experiments to test the female's response to a tape recording of the cries of unhatched crocodiles were carried out on different rookeries below Murchison Falls in 1968 and 1969. At one site the recorder was concealed in an observation hide. The female that had been floating off shore when the recorded was switched on, soon submerged and promptly surfaced at the bank and climbed up towards the hide without hesitation. On another occasion when the recorder was hidden in grass on a sand-bar close to several nests, three crocodiles swam towards the sound. One of them hauled out and came to rest just short of the playing recorder. Modha (1967) had previously

obtained generally similar results on Lake Rudolf. There is, then, no doubt that the croaking of the unhatched brood does alert, and attract, the nesting mother to her brood.

Exhumation of the eggs

It is well known that the female unearths the eggs at hatching time, but details of the process have rarely been observed. Examination of nests that have been opened by the parent shows that alternative methods may be used, according to the situation of the nest. Normally, and where the brood-chamber is covered with hard, firm earth, the crocodile lies with her snout near the nest, and digs down to the eggs with the fore-limbs. At such nest sites one can often clearly see a platform, wedge-shaped in front where the throat had rested, with a trench on each side made by the fore-limbs, with two heaps of excavated spoil that had been thrown back beside the body, and claw-marks left in the wall of the egg-chamber.

On the other hand, where nests are in loose dry sand, liable to cave-in during excavation, the female scoops out a hollow from above the eggs with her body. Mr L.J. Sim, a crocodile hunter in Tanzania, informed me (pers. comm., 13 March 1958) that just before sunset on 30 January 1956, he saw a crocodile wriggling and squirming on a bare patch of river-bank. On reaching the spot he heard the young croaking from beneath the shallow rimmed crater thus formed. An African assistant told Sim that he had witnessed the same method of liberation, and he was most insistent that the crocodile's feet were not used. This method is certainly consistent with the appearance of shallow basin-like excavations -- some over four yards (3.70 m) in diameter -- such as I found in 1952, in two colonial rookeries at the south end of Lake Albert (Cott, 1961). Loveridge (1953) saw similar crater-like excavations on dune-sand near Mtimbaka, Nyasaland; and a photograph by Adamson (1955) illustrates a rookery of nest-craters on Lake Rudolf sands.

At hatching time the young are absolutely dependent upon maternal assistance. The eggs are covered by many inches of earth: in some soils, such as loamy clay which packs hard, a man would have to use a panga (machete) to chip the covering away and there is no question of the hatchlings escaping unaided. Unless the parent is at hand to expose the eggs, the young perish in the shell. In the course of surveys carried out below Murchison Falls in 1968 and 1969, when some 350 nests were under observation, I have no record of hatching except from nests that had first been excavated. Modha (1967) made similar observations on Lake Rudolf: he reports that from not one of 150 nests had any hatchlings managed to escape without maternal help. In cases where the female fails to revisit her croaking young, the subterranean chorus may continue for four or five days. When the release is overdue, the surviving hatchlings burst the shell and emerge almost

explosively immediately the eggs are unearthed, though a moment before the shells were not even chipped.

Release of the hatchlings

The remarkable determination of the female to reach and liberate her young has been observed on a number of occasions. This was first demonstrated experimentally by Voeltzkow (in Gadow, 1901), who had a nest surrounded with a fence. When the mother had returned several times and partly destroyed the fence, this was replaced by a stronger one. The mother then dug a deep ditch beneath the fence in her efforts to reach the nest. In Zululand, Pooley (1969a) isolated a nest with a structure of stout poles 15 cm in diameter, supporting an 8-gauge wire fence, the latter firmly bound with sacking, and the nest roofed over with the same material. At hatching time the parent was found to have smashed her way through the barrier and to have opened the nest. Pooley (1969b) also reports that screens of heavy wire mesh, laid over nests to protect clutches from predators, were easily displaced by the parent at hatching time, some of the screens being found 3 m from the nest in a twisted heap of wire and pegs. Jones (in Cansdale, 1955) records that in the Bonthe District of Sierra Leone a nest was first discovered in a rest house only when the adult came one night to dig it out.

Whether, in the field, the female assists her offspring in the actual hatching process is not known. But recent observations on crocodilians in captivity suggest that it may be so. Hadley (1969) has described hatchings witnessed by him in Livingstone Game Park in 1966. Having dug her eggs from the ground, the mother C. niloticus "carried three or four of them at a time to the water. They were held very lightly in her mouth and she moved her head from side to side slowly in the water as though washing the eggs. She then applied pressure to the eggs and cracked them. One young crocodile emerged from the egg and swam out of her mouth, and a second dropped to the bottom of the pool and shortly afterwards the young crocodile surfaced. This I witnessed twice".

Even more surprising is the parental care of the Spectacled caiman, witnessed at Tuxtla Gutierrez Zoo and described by del Toro (1969). "After 70 days of incubation ... the male started to break the nest, scratching at it with his hind legs and tossing mouthfuls aside ... Now something very unexpected happened: the male rolled over several of the eggs, crushing them with his hind legs and tail until the young were free. He also took hold of several eggs with his teeth, one at a time, and crushed the shell carefully till the young could escape". The female stayed in the water while this was happening, called to the young, and took them around the pool "just as a hen takes her chicks around the yard".

In the light of these observations, the comment by Vansleb, who wrote of the Nile crocodile in 1678, is of interest. He states that at hatching time the female "then goes and opens the hole and breaks the shell with its Musle for the young to creep out".

Post Natal Maternal Care

Early reactions of hatchlings

Observations on clutches of eggs excavated at hatching time show that, as soon as they have broken out of the shell, hatchlings tend to make for a nearby object affording shade and shelter. For example, when in 1968 at Murchison Falls I placed a crude dummy of a crocodile a few yards from eggs that were about to hatch, most of the young, on emergence, made their way to the dummy, some immediately, eagerly and at a run, dragging the umbilical cord and still-attached shell behind them, and took cover beneath the lower jaw and along the flanks of their 'mother'. When in 1969 my African assistant lay down motionless close to an excavated clutch, he likewise became a centre of attraction, and soon had many baby crocodiles sheltering under his chin, arms and sides.

Transit from nest to nursery

This behaviour raises the questions: how do the emergent young react to the presence of the female in a wild state; and what part does the female play at this phase of the breeding cycle? Transit from nest to nursery has never been witnessed. Whether the young are conducted, or carried from the one to the other, is not yet certainly known.

Factors favourable for the nursery site are shallow, confined or still water, with for cover plentiful marginal or floating vegetation such as Pistia stratioides, Cyperus articulatus or Leersia hexandra. The site may be in the lee of a fallen tree, in a creek leading from the main body of water, or inland in a shallow mere. Such nurseries can often only be reached by travel of several hundred yards across country, and in a direction away from the waterside rookery.

As to how the journey is accomplished, accounts vary. An early observation is given by Goldsmith (1805) who states that on being set free the brood "quickly avail themselves of their liberty; a part run unguided to the water; another part ascend the back of the female, and are carried thither

in greater safety". Young have been seen on a number of occasions following the parent. Thus, in Madagascar, Voeltzkov (1899) was reliably informed by his taxidermist that he had seen a large crocodile with a tribe of about twenty young ones travelling over a stretch of sand to the water: the parent was in an excited state -- "Das alte Tier sei auffällig wild gewesen". In Basotseland, Livingstone (1865) was told by his companions that the female leads her brood to the water. Mr F. Wilson (pers. comm., 1952) once saw a crocodile with a brood of newly-hatched young sunning on a bank in Lake Victoria: on being disturbed the parent went into the water, followed by her hatchlings.

With other species, the parent-offspring relationship appears to be similar. In his account of a primeval nesting ground of A. mississippiensis on St John River in northern Florida, Bartram (1792) frequently saw the female "leading about the shore her train of young ones". One alligator which passed close to the side of his boat had young following after her: "they kept close together in a column, without straggling off to the one side or the other". Mitchell (in Kellog, 1929) states that the mother on watch calls the hatchlings to her den, which then becomes their home.

There are other records which suggest that the female may sometimes carry her brood to their new quarters. Chadwick (1931), who witnessed a hatching, states that as each young one crawled from the shell "it swarmed upon the mother and clung to her". In Nigeria, Lamborn (1913) was informed by natives that the young crocodiles, immediately after hatching, attach themselves to the dorsal fringe of the tail of the mother and are thus conveyed by her to the water. Mr J.L. Sim (pers. comm., 13 March 1958) was given similar information in Tanzania: "when the young emerge, they mount the back of the mother, and as soon as it is dark, she transports them through shallow water to a patch of reeds". In Lake Rudolf, Modha (1967) was told by natives that the young are carried to the water on the snout, neck and back of the female. A launch coxwain with long experience of the Victoria Nile at Paraa assured me that in 1967, he personally saw a crocodile on land transporting hatchlings on its back. Similar behaviour has been recorded of the American crocodile C. acutus (Ulloa, in Brehm, 1885). Once established in the nursery site, the young -- over a period of several weeks -- constantly clamber on to their parent's head and back as she lies half-submerged: this I have witnessed and photographed at close range on many occasions in Uganda.

Predatory enemies of the young

Unguarded hatchlings, like the eggs, are very vulnerable and are preyed upon by many enemies. In the Victoria Nile these are known to include Nile monitor, Great White egret Casmerodius albus, marabou, Saddle-bill stork

Ephippiorhynchus senegalensis, Fish eagle Cuncuma vocifer, Black kite, Ground hornbill Bucorvus leadbeateri and African civet Viverra civetta (Cott, 1968). Records of other species that prey upon hatchlings are: in Egypt (formerly) Egyptian mongoose Herpestes ichneumon and Soft-shelled turtle Trionyx triunguis (Anderson, 1898); on Lake Rudolf, pelican, Sacred ibis, Pied crow Corvus albus and the catfish Clarias lazera (Modha, 1967 and pers. comm.); and in Zululand, Goliath and Grey heron, Little egret Egretta garzetta, Spotted eagle owl Bubo africanus and Rusty-spotted genet Genetta tigrina (Pooley, 1969a).

The situation is closely similar for hatchlings of other crocodilian species. For example, of the American alligator Le Buff (1957) records otters, skunks, raccoons, large wading birds, turtles, snakes and other alligators as enemies. Audubon (1827) referred to White ibis Guara alba (= Eudocimus albus) and Sand-hill crane Grus canadensis as eaters of the young. The American bullfrog Rana catesbiana has the same habit (Wettstein, 1954).

Maternal defence of the young

The female in charge of her brood becomes an aggressive and dangerous animal -- alert and ready to attack any adversary, both by day and night. During two seasons' work on the Victoria Nile I witnessed defensive behaviour on many occasions. The female at one nursery was seen to make a tremendous leap out of the water and over a fallen tree trunk, to drive away a Vervet monkey that had come down to drink. When we approached another nursery that was sited in a creek forty yards (37 m) from the river, the female on more than one occasion came directly for the boat, porpoising and threshing the water with its tail. At a riverside nursery the female unobtrusively submerged, coming up beneath the patrol-launch and striking it a tremendous blow with its head. A fourth female guarding her brood in a ditch was unusually bold: during days of observation this animal made repeated attacks whenever I approached her closely -- hissing, growling, and making lunges, jaws agape, with incredible agility. Seen at point-blank range, such demonstrations are most impressive.

Descourtilz (1809) has an account of C. acutus making a determined attack on two men when surprised at her nest. Dharmakumarsinji (1947) who watched a female Marsh crocodile for a whole day "maintaining a scrupulous guard" over her newly-hatched young, writes: "I saw this crocodile rush out of the water, at least a dozen times, to drive away Black-necked storks Xenorhynchus, herons Ardea and large white egrets Egretta when they ventured to alight near the young which were lying helpless at the water's edge". The crocodile was afterwards shot and confirmed to be a female. Neill (1946) relates that the calling of a juvenile C. novae-guineae that had

been caught by hand at night, provoked the adult into charging savagely in the direction of the sound. Hartwig (1873) described an attack made under somewhat similar circumstances upon Richard Schomburgk by Melanosuchus niger on the Essequibo: "The mother, a creature of prodigeous size, suddenly emerged with an appalling roar, making desperate efforts to reach her wriggling and screeching offspring ... Having been wounded with an arrow, she retired for a few moments, and then again returned with redoubled fury, lashing the waters into foam by the repeated strokes of her tail". McIlhenny (1934) relates how a female American alligator had to be restrained from attacking him when he was handling her young at a nest on Avery Island, Louisiana.

Recent observations have shown that the young remain gregariously with the mother for several weeks, learning to feed and fend for themselves while under close maternal supervision. Thus, on 8 April 1969, a female with her brood was found occupying a waterhole in a narrow ditch opposite Paraa. The hatching date of the clutch was not known. Subsequently this nursery was under observation, at first daily, and later at intervals of a few days. The mother crocodile continued to guard her hatchlings until 28 June -- the last date she was seen in the nursery. Her duties had extended over at least 81 days -- a period about equal to the incubation period. In other words, it appears that for about six months in the year the breeding female is continuously engaged in pre-natal and post-natal care.

Knowledge of the vital part which parental care plays in the successful rearing of offspring has important implications in the field of management and conservation. Disturbance of females on the nesting grounds causes high mortality both through hatching failure and predation. Protection from interference during the successive phases of the reproductive cycle is therefore essential for recruitment and long-term survival of the population (Cott, 1968, 1969).

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