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Behavior of Nile Crocodiles in a Seasonal River in Zimbabwe

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Nile crocodiles congregated in the Chipinda Pools of the Runde River in the Gonarezhou National Park in Zimbabwe during the dry winter of two drought years, and adults and subadults dispersed upriver when the river flowed during the wet summer. Juvenile crocodiles moved overland through forest during the wet season and inhabited temporary ponds. Crocodiles courted and mated in a shared courtship-mating arena in front of a shared basking ground during winter; after courting and mating, individuals basked and slept. Crocodiles basked most frequently during cold July, first coming onto shore when direct sunlight was on the basking ground, and least during summer. The group of basking crocodiles consisted of reproductive and nonreproductive individuals, adults and subadults of both sexes, including dominant breeding bulls. Aside from exclusion of juveniles, spacing and distribution of basking crocodiles was without regard to sex, dominance, or reproductive status. Basking sites were never defended as exclusive territories. Gaping by basking crocodiles during winter was usually a threat display, used when another animal drew near (e.g., crocodile, hippopotamus, bird, human). Hippopotamuses also basked during winter and often displaced crocodiles from their basking sites. Crocodiles did not congregate at Chipinda Pools during a nondrought year, even for courtship and mating.

NILE crocodiles (*Crocodylus niloticus*) are large and obvious predators, with which humans have been fascinated for centuries (e.g., Pliny, 1601). However, much remains unknown about behavior of Nile crocodiles, and unfortunately their numbers and habitats are now diminished throughout much of the geographic range. Most recently, an overview of crocodilian behavior was presented by Lang (1987), with references to the Nile crocodile.

I studied Nile crocodiles in a seasonally flowing river in Zimbabwe from July 1983 through Oct. 1985. One purpose was to examine their behavior in a highly seasonal environment, with emphasis on movement, basking and gaping, and interaction with hippopotamuses. Reproduction, courtship and mating, nesting ecology, and genetics of the same crocodile population were reported previously (Kofron, 1989a, 1990, 1991; Lawson et al., 1989, respectively).

During the breeding season at Lake Turkana, Kenya, hundreds of Nile crocodiles congregated at Central Island for courtship and mating

(Modha, 1967, 1968b), some having traveled considerable distances (Graham, 1968). Seasonal movement of Nile crocodiles in a river and floodplain in South Africa was noted by Pooley (1969), with individuals > 2.5 m in length moving more than smaller individuals. Hutton (1982) studied movement in relation to age in an impounded river-lake in Zimbabwe and found subadults and young adults moving greater distances than juveniles and older adults.

At Central Island, the crocodiles basked in groups during the breeding season (Modha, 1968a), and at Murchison Falls, Uganda, they also aggregated for group basking during the nonbreeding season (Cott, 1961). The daily basking patterns of Nile crocodiles were documented by Cloudsley-Thompson (1964), Modha (1968a), and Loveridge (1984). However, the sexes and reproductive status of individuals within basking groups have not been determined, nor has basking been considered on a seasonal basis, until now.

The effect of gaping on heat gain by Nile

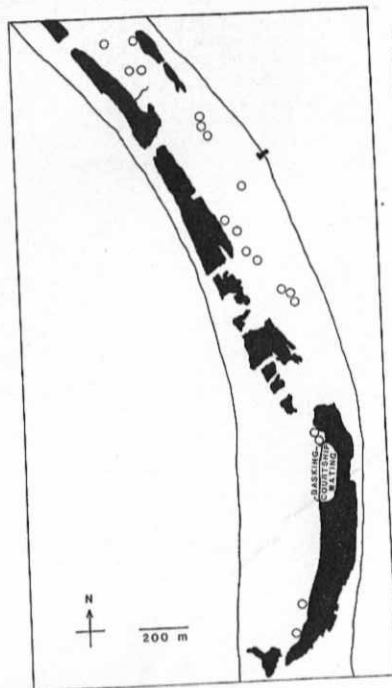


Fig. 1. Map of the Runde River at Chipinda Pools (black; dry season) where most Nile crocodiles were observed and captured. The shared basking ground and shared courtship-mating arena are indicated, and circles represent nesting sites.

crocodiles has received conflicting views, as with American alligators *Alligator mississippiensis* (Spotila et al., 1977; Johnson et al., 1978). Diefenbach (1975) concluded that gaping played no role in cooling for Nile crocodiles; but Cloudsley-Thompson (1969), Cott (1961), and Loveridge (1984) showed that gaping by heated individuals enhanced cooling. However, this does not explain gaping during early morning or night (Cott, 1961; Loveridge, 1984) or by cool individuals during winter.

Nile crocodiles and hippopotamuses inhabit similar aquatic habitats. In Zimbabwe, both are often locally numerous and share the same aquatic ecosystem. A few accounts of crocodile-hippopotamus encounters were reviewed by Cott (1961).

In my study of Nile crocodiles, I addressed the following questions: (1) Do crocodiles move away from their dry season area when the aquatic habitat floods and expands during the wet season? (2) Does frequency of basking change seasonally? (3) What is the social arrangement within a group of basking crocodiles? (4) What is the purpose of gaping by basking crocodiles during winter? and (5) What interactions occur between crocodiles and hippopotamuses when confined to the same pool of water?

STUDY AREA

The study site was the Runde River in Gonarezhou National Park of southeastern Zimbabwe at 350 m elevation. The Runde River is seasonal, flowing only during the wet season. During the dry season, it becomes a series of pools, the source being several smaller seasonal rivers. During this study, the Runde River flowed from Oct. 1983 through April 1984, and Sept. 1984 through July 1985. Most observations were at the Chipinda Pools (Fig. 1), 1–4 km from the park boundary. Here the Runde River is 500 m wide, with four large pools (main pool up to 1000 m long, 100 m wide, 3 m deep) during the dry season. Most of the river bed is coarse sand, but some bedrock is exposed. When the river flows, extensive bedrock below pools forms rapids and a waterfall, and the sand ridges in the middle with reeds (*Phragmites*) and shrubs (*Ficus*) become islands. The river banks are steeply sloping and several meters high. The adjacent land is fine sandy soil with tropical deciduous forest. Tall riverine trees grow next to the river and mopane woodland (*Colophospermum mopane*) away from it.

The years 1982 through 1984 were drought years, with normal rains returning in late 1984. In general, summer months were characterized by rains and winter months by their absence (Fig. 2). Peak rainfall was in Dec. 1983 and Jan. 1985 (191.5 mm and 163.5 mm, respectively). The hottest months were Nov. through Jan. and coldest June and July. Air temperatures ranged from 4–47°C during the study period.

MATERIALS AND METHODS

Three size classes of Nile crocodiles were recognized: adults, subadults and juveniles (up to about 180 cm total length). Adults and subadults were captured by baited mouth snares (Kofron, 1989b), the reproductive states determined, total lengths measured, individually tagged and released. Large plastic tags (8 cm

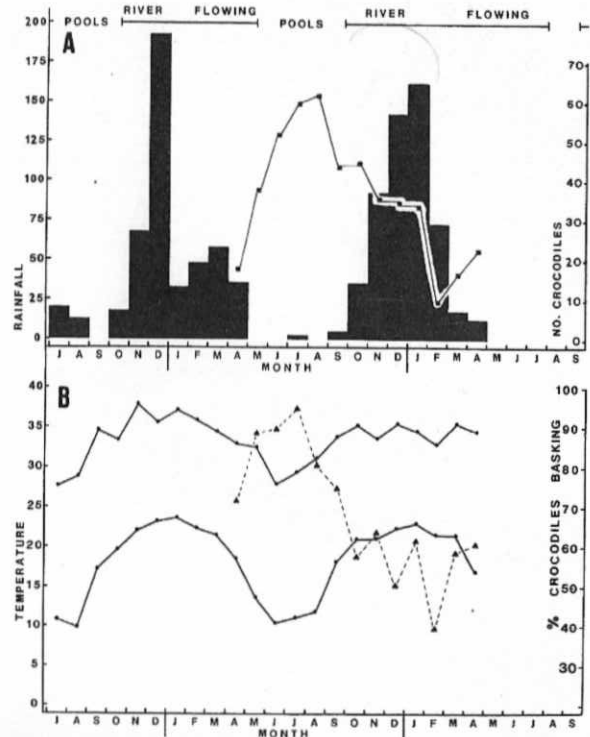


Fig. 2. (A) Rainfall (mm) at Chipinda Pools, Gonarezhou National Park [1983–85 (bar graph)]; and numbers of Nile crocodiles at main pool area (squares and solid line). Crocodiles in water and on shore were counted three times per day (0700, 1200, 1700), three days per week, for 13 months. The highest count of each month is plotted. (B) Minimum and maximum air temperatures (C) at Chipinda Pools (dots and solid lines); and the seasonal incidence of basking by Nile crocodiles (triangles and dashed line indicate the percent of crocodiles at the main pool area that were basking). Climatic data courtesy of G. Sharp, Gonarezhou National Park.

diameter; yellow/males, white/females) with bold numerals were sewn onto each side of the tail, enabling identification of sexes and individuals at 100 m. Reproductive states were determined by cloacal palpation, penile mucous smears, surgical examination, measurement of plasma calcium (Kofron and Trembath, 1987; Kofron, 1990); and observations of tagged individuals during courtship, mating, and nest attendance (Kofron, 1989a, 1991). Crocodiles were observed through binoculars from behind bushes at 155–100 m distance. Densities of crocodiles at the main pool were determined by day-

time counts: crocodiles in water and on shore were counted three times per day (0700, 1200, 1700), three days per week for 13 months. Several nighttime counts confirmed the accuracy of the counting method.

RESULTS AND DISCUSSION

Ninety-nine individual crocodiles were captured (35 males, 63 females, 1 unknown) in the Runde River, with 226 recaptures. Males ranged from 155–408 cm total length, and females 144–343 cm. Males attained sexual maturity from

about 270–295 cm, and females 262–287 cm (Kofron, 1990).

Movement.—Nile crocodiles congregated in the Chipinda Pools of Gonarezhou National Park during the dry winters (May through Sept.) of two drought years. The highest density of crocodiles at Chipinda Pools was from June through Aug. 1984 ($n = 52-62$ crocodiles in main pool; Fig. 2), when the river dried to pools. Later, with rains during the summer (Oct. through March), the Runde River flowed, and most adults and subadults moved upriver away from Chipinda Pools (Feb., $n = 10$ in main pool area) and beyond the park boundary. Movement of crocodiles downriver from Chipinda Pools was restricted largely by the rapids and waterfall. Pooley (1969) made similar observations of Nile crocodiles moving into seasonally flooded habitats in South Africa. The greatest known distances that crocodiles moved in the Runde River were 18 km by one individual (unknown size) and 13 km by four subadults (201–266 cm), concurring with the observations of Pooley (1969) and Hutton (1982). Then later as the Runde River was ceasing to flow, crocodiles returned to Chipinda Pools (April, $n = 23$ in main pool). The pools upriver outside the park were heavily used by local people during the dry season (e.g., bathing, washing clothes, drawing water, watering cattle), and very few crocodiles remained there. In general, crocodiles in the Runde River avoided humans, moving away and keeping distance from people on shore.

During Aug. 1984, density of crocodiles decreased at the main pool (Fig. 2), which was the end of dry season and before the river flowed. At this time, some reproductive females moved from the main pool into smaller pools adjacent to nesting sites. For example, three reproductive females were in the main pool on 29 June, 29 June, and 2 Aug.; and then subsequently in smaller pools on 18 Aug., 1 Sept., and 18 Aug., respectively. These three females nested adjacent to the smaller pools. No females nested on the shared basking ground of the main pool but instead moved to higher sites. However, for unknown reasons, movement from the main pool into smaller pools also included some nonreproductive females and adult and immature males. Crocodiles that changed pools ranged from 214–360 cm.

Crocodiles moved on land beyond the steep banks of the river during two situations. Large crocodiles walked up to 20 m beyond the steep banks at night to feed on carcasses of large dead animals (e.g., hippopotamus). When possible, carcasses were dragged back to the river. Also,

during the wet season, juvenile crocodiles (about 75–180 cm) moved overland through forest to inhabit the numerous temporary ponds (pans). In a sample of nine ponds near the river, seven were inhabited by at least one crocodile; and one pond, at 1.5 km distance, had three individuals. Later, as ponds were drying, the juvenile crocodiles disappeared, presumably going back to the river. However, herds of Cape buffalo frequented the ponds for drinking and wallowing, and some crocodiles may have been trampled.

The current of the flooded Runde River was probably too strong for juvenile crocodiles, possibly also inhibiting their capture of food. The temporary ponds offered calm shallow water with insects, important prey for juveniles (Hutton, 1984). Juvenile crocodiles also moved overland through forest and inhabited temporary ponds during the wet season at Lake Kariba, Zimbabwe (J. P. Loveridge, pers. comm.).

Basking and gaping.—From May through early Aug. 1983 and 1984, adult and subadult crocodiles (180–360 cm, males and females) congregated in the main pool. The highest density of crocodiles in the main pool was during July and the first half of Aug., the time of courtship and mating. Courtship and mating occurred in water (late June through mid-Aug.) usually in front of the basking ground in a shared courtship-mating arena. Crocodiles dispersed from the basking ground by sunset, although some frequently remained on shore into night. Most courtship and mating occurred in the morning shortly after the crocodiles returned in front of the basking ground (0630–0830). After courtship and mating, the individuals basked and slept.

During June and July 1985 after the drought, the river remained flowing, and crocodiles dispersed widely. There was no large aggregation of crocodiles at Chipinda Pools during this non-drought year, even for courtship and mating. Only one small group of nine individuals was observed in a smaller pool, with courtship and mating and group basking.

In general, smaller juvenile crocodiles did not aggregate with adults and subadults, either in water or on the basking ground. However, on one occasion, a juvenile (1 m) was amid a group of larger crocodiles investigating a food item. When the juvenile moved first to take the food, the largest crocodile (3.6 m) grabbed the juvenile in its jaws and flung it several meters through the air.

Crocodiles basked most frequently on cold winter mornings of May, June, and July (80–95% of crocodiles basking; Fig. 2), coming out

of water shortly after sunrise to warm in the sun when early morning air temperatures were 10–13°C. Direct sunlight on the basking ground was the cue for crocodiles to first come onto shore, even though air temperature may have been less than water temperature. A similar observation was noted by Loveridge (1984), although Smith (1979) remarked that, in general, crocodilians bask when air temperature exceeds water temperature.

In winter, the crocodiles basked and slept on shore during much of day and hunted and fed at night. Basking peaked in cold July, and during one observation, 57 of 60 crocodiles in the main pool were basking. Crocodiles basked least during the hot summer months of Oct. through March (40–64% of crocodiles basking), when daily air temperatures ranged from 20–35°C. Similarly in Texas, American alligators basked during spring and fall but rarely during summer (Smith, 1979).

When basking, adult and subadult crocodiles usually positioned themselves parallel to or facing the water (eastward), instead of facing inland, and within one body length of water. For example, during one observation of 25 basking crocodiles, 17 were parallel to water and eight facing it; and all were within one body length of water.

During the winter dry season of two drought years, many larger crocodiles (up to 25 individuals) in the main pool shared a basking ground of 100 m length of sandy shore, although additional sandy shore was available. The daily aggregation of basking crocodiles consisted of reproductive and nonreproductive individuals, adults and subadults of both sexes, including large breeding bulls. The distribution and spacing of crocodiles on the shared basking ground apparently was not influenced by sex, dominance, or reproductive status. Basking crocodiles were frequently near other crocodiles, often touching (even resting the head upon another). The basking aggregation included male/male, male/female, and female/female associations. The following are several examples: large bull (317 cm, producing sperm) basking 1 m from another large bull (322 cm, producing sperm); young adult male (279 cm, producing sperm) basking 2 m from large bull (322 cm, producing sperm); subadult male (277 cm) basking 1 m from dominant bull (360 cm, producing sperm); reproductive female (284 cm) basking 1 m from dominant bull (360 cm, producing sperm); large bull (341 cm) mates and then basks 1 m from subadult female (255 cm); reproductive female (284 cm) basking with chin on head of subadult female (263 cm); and sub-

adult female (286 cm) basking 1 m from another subadult female (263 cm).

Some individual crocodiles used favored basking sites day after day, but the sites were never defended as exclusive territories, even by large breeding bulls. Although courtship, mating, fighting, and submissive behavior occurred in water in front of the basking ground, these activities never occurred on shore. Fights between bulls in water were usually avoided by temporal partitioning of the shared courtship-mating arena. Reproductive females moved away from the shared basking ground to higher sites for nesting after the period of courtship and mating, as at Lake Turkana, Kenya (Modha, 1967).

In Lake Turkana, hundreds of Nile crocodiles congregated at Central Island during the breeding seasons of three consecutive years (Modha, 1967, 1968a, 1968b). Some crocodiles shared basking grounds (Modha, 1968a), but dominant breeding bulls guarded territories and basked separately (Modha, 1967). Cott (1961) documented with photographs large Nile crocodiles aggregating and sharing a basking ground at Murchison Falls, Uganda, outside the breeding season. Other crocodilians in areas of periodic drought may aggregate for basking with suspension of territoriality and dominance (Lang, 1987).

Crocodiles frequently gaped while basking. Loveridge (1984) demonstrated that gaping by heated Nile crocodiles permitted evaporative cooling through exposed oral mucosa; however, he could not explain gaping at night or by cool individuals. Having also observed gaping crocodiles on crowded sandbanks, Loveridge (1984) suggested interpretation in a social context. At Chipinda Pools, gaping by basking crocodiles during winter was usually a threat display, used when another animal drew near (e.g., crocodile, hippo, bird, human).

In a sample of 54 observations of gaping by basking crocodiles during winter, 45 were threat displays: 19 crocodiles gaped when another crocodile drew near; seven when I approached; six when hippopotamuses drew near; six when splashing occurred; five when touched by another crocodile; one when touched by a hippopotamus; and one when birds drew near. On seven occasions, crocodiles gaped immediately after emerging to bask and twice with no apparent reason. Also, on two other occasions, basking, sleeping crocodiles were alerted and gaped; and several even returned to water, in response to alarm calls of disturbed Egyptian Geese and White-crowned Plovers. In addition, during capture (Kofron, 1989b), many croco-

diles gaped when pulled to face humans, which also was a threat display, previously noted by Hutton (1982). During gaping, the rear of the oral cavity was sealed by the gular folds, flaps of tissue at the posteriors of the soft palate and tongue (Pooley and Gans, 1976).

Sometimes the first crocodile coming out to bask on a cold winter morning gaped immediately without apparent reason. Possibly it was a threat display elicited by daily habit on a shared basking ground; or exposing of oral mucosa may have enhanced the sensitivity of senses to smell or airborne taste; or possibly air temperature was assessed through exposed oral mucosa; or perhaps, when facing the sun, there was warming of blood routed to the exposed oral mucosa.

On numerous occasions, subadult and young adult crocodiles of both sexes bellowed during capture, which were probably distress calls. Normally the sound was emitted by gaping individuals with open mouth, but a muffled version was produced when jaws were held closed with cable and tape. Two tones were effected by vibrating the gular folds in moving air, one at inhalation, followed immediately by the louder at exhalation. Pooley (1982) elaborated on vocalizations of Nile crocodiles and reported that wounded individuals bellowed, but molested adults remained silent.

Crocodiles used a high walk (Cott, 1961) when coming onto shore, moving about the basking ground, and returning to water (unless startled, which resulted in quicker movements and a belly run (Cott, 1961)). A high walk was used also when moving long distances over land (e.g., when changing pools or enroute to nests). Some individuals walked more than 100 m before resting on the venter.

Interaction with hippopotamuses.—Two types of interaction occurred between crocodiles and hippopotamuses, one in water and one on the basking ground. Most interactions occurred during the dry season when the two large species shared the same pools. Hippopotamuses in water did not tolerate crocodiles within 2 m of themselves. Crocodiles usually avoided hippopotamuses in water and, when near, submerged to swim past them underwater. Hippopotamuses snorted at, charged, and shoved crocodiles that were too close.

Hippopotamuses also basked and slept in the sun during the cold month of July, when crocodiles basked most frequently, and there was apparent competition for basking sites. The crocodiles basked as a group, usually on the same reach of shore daily. On at least eight occasions, the hippopotamuses came onto the

basking ground and displaced the crocodiles. Each hippopotamus placed its nose to the ground 1–2 m from the posterior half of a crocodile and, gradually moved closer until touching. Crocodiles responded by lifting their heads to alert positions (Cott, 1961), gaping, or moving their tails away. Next the hippopotamuses pushed the crocodiles, and the latter moved to new sites or returned to water, with the hippopotamuses settling into their spaces.

A hippopotamus sometimes expended more than 1 h displacing a crocodile. Other basking crocodiles also moved after being disturbed by hippopotamuses moving nearby. In this manner, most crocodiles of a basking group were displaced, except the largest (greater than 350 cm) which hippopotamuses avoided. However, later, the largest crocodiles also relinquished their sites and moved to stay with the basking group. Several days later, the hippopotamuses usually again displaced the crocodiles from their new basking sites. This interaction on the basking ground occurred during drought and non-drought years. Hippopotamuses exercising dominance on a crocodile basking ground were observed also by Cott (1961) and Modha (1968a).

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