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Interactions Between Nesting Crocodiles and Iguanas

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ABSTRACT—Green iguanas *(Iguana iguana)* and American crocodiles *(Crocodylus acutus)* nest in association on Slothia, a small island in Gatun Lake, Panama. In the three nesting seasons that we observed on Slothia a crocodile remained near her nest and frequently charged the nesting iguanas. Observations indicated that the crocodile emerged from the lake significantly more often when iguanas were present in the nest clearing. We observed the crocodile seize an iguana on 12 occasions; five iguanas were eaten, five escaped, and the fate of two was unknown. In addition to the charges and captures, the crocodile's mere presence in the nest clearing interfered with iguana nesting activity. Conversely, the iguanas disturbed the crocodile nest and were observed to dig up crocodile eggs. The crocodile's behavior involved both nest defense and predatory behavior, although the exact motivational sequence is still unclear.

Crocodiles and iguanas share nest sites in several other locations near Slothia. Presumably, similar nest site requirements and common nesting seasons bring the two species together.

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INTRODUCTION

It is well known that where nesting sites are limited, competition within a species can be intense. Less well documented are cases involving direct interspecific competition at nest sites. Usually closely related species are involved and spatial and/or temporal partitioning minimizes overt conflict. Non-predatory agonistic behavior between species is thus either rare or fleeting. Here we detail aspects of the interspecific competition between nesting iguanas *(Iguana iguana)* and American crocodiles *(Crocodylus acutus)* in a type of nest clearing that is seemingly highly favored by both species but may be in short supply in lowland tropical forest habitat.

Slothia is a tiny islet adjacent to Barro Colorado Island (BCI) in Gatun Lake, Panama, where a small (6 × 7 m) clearing has been used as a nesting site by both crocodiles and iguanas during the dry season for at least the past 15 years (Campbell, 1972; Rand, 1968 and unpubl. data). Turtles *(Chrysemys scripta)* and basilisk lizards *(Basiliscus basiliscus)* also use the islet but do not restrict their nesting exclusively to the clearing. The communally nesting iguanas compete with one another for nest burrows (Rand, 1968) and expend considerable energy in nest disputes (Rand and Rand, 1976). Nesting females sometimes open the nests of others and dig out the eggs (Rand, 1968; Sexton, 1975). In addition to these intraspecific interferences between nesting iguanas, observations on Slothia from 1978 to 1980 showed important interactions between the female iguanas and a crocodile which also nested there. In this report we describe the crocodile's predatory and nest-guarding behavior, the reaction of the iguanas to the crocodile, and the disturbance of the crocodile nest by the iguanas. We also present data suggesting that interactions between nesting crocodiles and iguanas are not unique to Slothia.

METHODS

The nest clearing was observed for 66 daylight hours in 1978 (Feb. 14–Mar. 4), 150 daylight hours in 1979 (Feb. 8–Mar. 7), and 210 daylight hours in 1980 (Feb. 7–Mar. 10). Observations were conducted from a small blind on the edge of the clearing (all years), from the BCI laboratory clearing with a telescope (1978), and from a launch anchored in the bay between BCI and Slothia (1979). Only activity on Slothia was visible from the blind; activity both in the water and on land could be seen from the laboratory clearing and from the boat. (See Rand, 1968 for a more complete description of Slothia, the nest clearing and the iguana nesting).

In 1978 and 1979, observers scanned the clearing every 10 min and recorded the crocodile's location, the number of iguanas in the clearing and (1978 only) their activities (i.e. exavating a nest, filling a nest, or resting). We also recorded the crocodile's arrivals at and departures from the nest clearing, and her activities. In 1978 we visited Slothia five times on three different nights between 2100 and 0330 hrs, and we spent one evening on Slothia from 1945 to 2040 hrs in 1979, and one evening from 1800 to 1930 hrs in 1980. In 1979, the clearing was observed from the boat with a night vision scope on an irregular basis. Excavations of the nest clearing confirmed the presence of a crocodile nest in both 1978 and 1979. In addition to observations on Slothia, mainland and island banks north of BCI were examined for signs of crocodile and iguana nesting activity.

RESULTS AND DISCUSSION

During February and early March 1978, 1979 and 1980 several dozen female iguanas visited the clearing and many nested there. The crocodile was observed in the clearing in all three years. She was approximately 3 m in total length, and recognizable as the same individual by a distinctive pattern of worn tail scutes.

When the crocodile moved from the water onto land, she climbed a slide until her head was just over the edge of the bank. In 39 of 75 arrivals observed in 1978 (the only year in which details of the crocodile's behavior were systematically recorded) she then entered the clearing slowly and rested at its edge. In 36 of the 75 arrivals, she looked quickly around the clearing, then charged with mouth slightly open towards iguanas in the clearing. Thirty of the 36 initial charges were followed by a series of charges directed towards iguanas at the edge of the clearing. The crocodile's behavior upon entering the clearing seemed to follow the same general pattern in 1979 and 1980. If the crocodile stayed on land more than about 20 min the iguanas usually moved from the bushes to the clearing edge. The crocodile on occasion rushed towards these iguanas and at other times she ignored them.

When the crocodile first appeared over the bank, all iguanas in the clearing fled at least to the clearing edge, except those in the process of egg laying. Some females lay their eggs with head and shoulders exposed. These egg-laying iguanas did not flee until the crocodile had charged to within about 1 m, even though they could see the crocodile in the clearing. Digging and laying iguanas and iguanas emerging from under ground near the crocodile were the only ones we saw captured. Typically, the crocodile slowly moved to within 2 m of an occupied nest hole, then rushed towards the iguana with mouth open. If the charged iguana fled safely, the crocodile either continued the pursuit or stopped with her head over the nest hole. Jaw-snapping often occurred when the crocodile lunged forward and attempted to grab the fleeing iguana. Unsuccessful charges sometimes ended with the crocodile emitting a low growl through open jaws. On several occasions after a near capture, the crocodile placed her snout into the iguana's nest burrow and rotated her head.

Predatory Behavior.—We saw the crocodile seize 12 iguanas—six in 1978, one in 1979, and five in 1980. Of the 12, five were eaten, five escaped, and the fate of two was unknown. In most cases, the crocodile seized the iguana by the hind quarters so that it was crosswide to her snout.

The iguana usually extended her dewlap, thrashed the forepart of her body back and forth, and lashed her tail across the crocodile's head. After a brief (10 s to 2 min) pause during which the iguana might be bitten several times, the crocodile carried the iguana into the water.

Two of the five iguanas known to have escaped were observed with the crocodile in the water. One of these iguanas was held under water for several minutes, then was mouthed at the surface. The crocodile apparently did not apply pressure to the iguana for she was able to swim away. It was not clear whether the iguana was released or escaped. The second iguana swam away after the crocodile, holding her by the tail, pulled her under the water several times.

Iguanas eaten were alternately submerged and held above the surface. The crocodile chewed the iguana and shifted its position, using inertial feeding movements (Gans, 1961) before swallowing it head first. On one occasion the crocodile lifted the struggling iguana from the water and slapped it against the water (and possibly against the bank) by lifting her head vertically, rotating it to one side, then bringing it down quickly. After the third strike, the iguana's tail broke at the base; the iguana flew from the crocodile's mouth and hung limply in a bush overhanging the bank. The crocodile swallowed the tail, then grabbed the iguana by the hindquarters as she fell from the bush, positioned and swallowed it.

Two iguanas were found dead one afternoon in the water at the base of the crocodile's slide. One was bloated and missing a lower jaw; the other, on the bottom, had puncture wounds in the head as if bitten by a crocodile. We suspect that the crocodile killed both of these, but if she ate them she did not do so immediately.

Nest Attendance.—Beyond the dramatic charges and captures, the crocodile's mere presence on Slothia had a significant effect on the iguanas' behavior. Iguanas were observed in the clearing less often when the crocodile was present than when she was absent ($X^2 = 54.2$, df = 1, $P < .001$) and fewer iguanas worked in the crocodile's presence ($X^2 = 60.3$, df = 1, $P < .001$). At least one iguana was sighted in the clearing in 75.7% (165/218) of intervals when the crocodile was absent, but in only 38% (61/160) when she was present. When iguanas were in the clearing, at least one was observed to be working in 58.2% (96/165) of intervals when the crocodile was absent, but in only 6.6% (4/61) of intervals when the crocodile was present (Table 1). When iguanas crossed the clearing in the crocodile's presence, they traveled as far from her as possible and moved nervously in an alert posture. They appeared very much aware of the crocodile even after she had lain motionless for some minutes.

TABLE 1. Ten minute scan samples classified according to whether or not iguanas were present and/or working, and whether or not the crocodile was present (1978 only).

	Iguanas Present	No Iguanas Present	Iguanas Working	No Iguanas Working
Crocodile Present	61	99	4	156
Crocodile Not Present	165	53	96	122

For the crocodile, an effective nest-guarding strategy would seem to entail remaining in the vicinity of the nest and visible to the iguanas throughout the nesting season. The average percent of daylight observation hours that the crocodile was seen on Slothia ranged from 20 to 40 in the three years. Visit duration ranged from less than a minute to almost three hours, with the mode being 10–15 min. On each visit to Slothia at night we found a large crocodile in the water within 10 m of the clearing. We suspect that this was the same crocodile seen during the day. If so, then during all three iguana nesting seasons the crocodile spent most of her time, both day and night, in the clearing or in the water nearby.

The crocodile's activities did not prevent the iguanas from disturbing her nest, however. The iguanas returned to the clearing and resumed digging soon after the crocodile returned to the water. They dug up three crocodile eggs in 1978, and three or four in 1979, but none in 1980. These eggs were usually pushed about the clearing or into the water by iguanas or vultures *(Coragyps atratus)*. On at least one occasion, the crocodile reburied eggs shortly after dusk.

Although the crocodile did not maintain a constant vigil at the nest-site, her movements onto land were related to the nesting activity of the iguanas. Weak but significant correlations were found between the maximum number of iguanas seen in the clearing daily and 1) the number of crocodile visits per observation hr ($r = .43$, $df = 52$, $P < .01$) and 2) the percent of daily observation hrs the crocodile remained in the clearing ($r = .49$, $df = 52$, $P < .01$). The numbers of iguanas in the clearing prior to each crocodile visit were available for 1978 and 1979, and thus it was possible to look at differences in the crocodile's behavior as a function of the number of iguanas present. The frequency of crocodile visits varied with the number of iguanas in the clearing ($X^2 = 66.32$, $df = 4$, $P < .001$). The crocodile rarely entered the clearing when it was empty, but she often ventured onto land when four or more iguanas were present (Table 2).

TABLE 2. Ten minute observation intervals classified according to the number of iguanas in the clearing and crocodile movements onto land.[1]

	Number of Iguanas in Clearing				
Crocodile	0	1	2	3	4
Enters clearing	12	20	23	27	86
Does not enter clearing	220	87	54	74	120
No. visits/interval	.05	.19	.30	.27	.72

The question arises as to whether the crocodile was monitoring the activity of iguanas in the clearing and timing her movements onto land to coincide with iguana nesting. One problem is that it was impossible to tell how the crocodile could visually assess the presence of iguanas in the clearing from her usual position in the water off Slothia. She was observed to swim several meters out from Slothia's bank and back again, but her view of the clearing from this position is not known. She could be sensitive to sounds made by working iguanas, or to vibrations conveyed via the substrate (the crocodile was probably in contact with the substrate while in the shallow water at the base of Slotha's bank). It is also possible that some other factor(s) influenced the behavior of both the crocodile and the iguanas. For example, both species were at times reacting to disturbance caused by observers in the blind.

The crocodile's activities seem to be only loosely related to iguana nesting activity when the entire nesting period is considered. Systematic observations began earlier and finished later in 1980 than in earlier years, and the seasonal shift in the crocodile's behavior apparent in earlier years was recorded. She made 128 of 132 visits to the clearing between 16 February and 5 March. The average maximum number of iguanas recorded daily during this period was 10.5 (sd = 3.6). During the previous week, 8–15 February, the crocodile remained in the water next to the clearing, even though the iguanas had already begun to nest ($\bar{X}$ maximum number of iguanas recorded daily = 2.9, sd = 1.3, range = 1–5). Between 6 and 10 March, the average maximum number of iguanas recorded was 4 (sd = 2.6, range = 1–7), but the crocodile was seen in the clearing on only one day (4 visits). Though some iguana nesting continued after 10 March, the crocodile was not seen in the clearing at all.

We spot-checked Slothia after the iguanas completed their nesting. The crocodile was never sighted in the clearing. In 1978 and 1980 she was seen in the water nearby and returned to the clearing to open the nest in May (1978) and late April (1980). The crocodile did not return to the clearing in 1979. We excavated the nest at the end of May, and 36 unhatched eggs were found, 30 of them fully developed.

Other Nesting Associations.—Though first studied in 1978, interactions between crocodiles and iguanas were observed prior to this time. In 1965 and 1966 iguanas dug up crocodile eggs on Slothia (Rand, unpubl. data). A crocodile was seen eating an iguana in the water in 1973 and capturing one in the clearing on Slothia in 1977.

Crocodiles and iguanas share nest sites in locations other than Slothia. Five of six iguana nest sites examined in Gatun Lake in 1978 had evidence of crocodile nesting activities. All four crocodile nests located in Gatun Lake in 1979 had iguanas nesting near them.

Conclusions.—The disadvantages of nesting together are obvious for both crocodiles and iguanas. The crocodile risks having her eggs disturbed; the iguana risks being caught and perhaps

killed, certainly being disturbed while nesting. The advantages seem less compelling. The crocodile gets an occasional meal of iguana; the iguana who successfully nests near a crocodile nest may have it guarded for her by the crocodile. Though perhaps important, these advantages are probably secondary in explaining why crocodiles and iguanas nest in association. The similarity of nesting requirements of both crocodiles and iguanas and the relative scarcity of nest sites with these requirements, at least on the margins of Gatun Lake, may be the major factor underlying the assocation. Both species select open areas with sun reaching the ground, with soil suitable for digging, and with isolation from nest predators (at least for iguanas, see Rand and Robinson, 1969). Both species nest in early dry season. Thus, similarity of nesting requirements in both time and space brings the crocodiles and iguanas together.

Shared distributions and common nesting requirements have produced a similar conflict between nesting alligators and turtles in Florida (Deitz and Jackson, 1979). Nesting turtles *(Chrysemys nelsoni)* may deposit their eggs in nest mounds constructed by the American alligator *(Alligator mississippiensis),* sometimes breaking alligator eggs in the process. Female alligators were observed to drive *C. nelsoni* away from nests, and dead adult females turtles were found near alligator nests.

The crocodile's activities contain elements of both nest defense and predation; neither the predatory attempts nor the interference with iguana nesting were entirely effective. It is curious that the crocodile did not eat all of the iguanas she caught. Three at least escaped alive; two more were killed but not eaten, at least not immediately. The crocodile's predatory behavior may have been in some way inhibited. Reduced feeding during certain phases of reproduction is known in both birds and mammals (Mrosovsky and Sherry, 1980); *Crocodylus niloticus* females do not eat during the nest-guarding phase (Cott, 1961).

Although we have observed only one crocodile in one location, the ambiguous nature of this crocodile's behavior suggests a potential motivational conflict. Possibly parental behavior is incompatible with normal prey-handling behavior while she is guarding her nest, and her treatment of the iguanas is a mixture of prey-handling and hatchling-transport behavior. Many crocodilians open their nests and carry their young in their mouth to the water (Herzog, 1975; Joanen, 1970; Modha, 1967; Ogden and Singletary, 1973; Pooley, 1969; Pooley and Gans, 1976). We know that this female opened her nest, and it is likely that she also carried her young to the water. Movies of a female *Crocodylus moreletti* (Hunt, 1978) releasing her young were strongly reminiscent of the movements we saw our crocodile making while mouthing an iguana she subsequently released. To the extent that aspects of the hatchling transport situation are roughly approximated or entirely lacking in the situation on Slothia (notably vocalizations of hatchling crocodiles, size of object in mouth, and perhaps the timing of events with respect to the incubation of crocodile eggs) predatory behavior may be only partially inhibited. This hypothesis is consistent with ethological studies of conflict and behavioral inhibition (see Hinde, 1970). A detailed analysis of the motivational conflicts involved would be most illuminating, but is not very easily carried out with such animals in the field or the laboratory. Only observations elsewhere will show how typical are our observation on Slothia.

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