

Observations on Maternal Behavior of the American Alligator, *Alligator mississippiensis*

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ABSTRACT.—Maternal behavior of four female alligators was observed over a six year period at Okefenokee Swamp, Georgia. Nursery areas and dens were noted and described. Mother-offspring interactions involving vocalizations were observed including two instances of mothers vocalizing while moving their pods to new nursery areas. Three of the females attacked without injuring juveniles mixing with pods of younger animals and females guarded nests and young from human intrusion. Vocal interactions between mothers and offspring indicate the possibility of a temporal relationship between maternal vocalizations and/or movements and offspring vocalizations and/or movements but this cannot be confirmed statistically at this time.

Although a minority of alligators actively defend their nests from humans (Joanen, 1969; Kushlan and Kushlan, 1980; Metzner, 1978; Reese, 1915; Watanabe, 1980), most if not all, tend their nests through the incubation period (Garrick, 1975; Joanen, 1971; Joanen and McNease, 1970; Watanabe, 1980; Dietz, 1970). Far from terminating maternal behavior, the post-hatching period seems to initiate a complex relationship between mother and offspring. In 1976, Watanabe (1980) observed and photographed a female scraping her nest open with her forefeet and carrying some of the hatchlings to water in her mouth. Kushlan (1973) reported a mother carrying one of her vocalizing hatchlings from a roadbed where he had taken it. The early researcher, McIlhenny (1935) observed a female alligator grunting to her young, who, in turn vocalized. This paper describes the post-hatching behavior of four female alligators (Table I) uniquely suited for long-term observations because of their habituation to approach by humans.

MATERIALS AND METHODS

Study animals were in two areas of the Okefenokee Swamp: AZP (Atlanta Zoological Park) 10 and 11 were located at Cowhouse Island, Okefenokee

Swamp Park, approximately 10 km SE of Waycross, Georgia; AZP 12 and 13 were in Chesser Prairie, Okefenokee National Wildlife Refuge, approximately 30 km S of Folkston, Georgia (Table 1). The four females had body flaws or other visible abnormalities which provided identification. The collapsed condition of both eyes indicated that AZP 10 was blind. Study animals were observed with binoculars. A blind was not used but observers sat far enough away so as not to disturb the alligators. AZP 13 would tolerate being observed from a distance of 1 m; AZP 11 often could be observed from a minimum distance of 10 m. At Cowhouse Island observations were made from land. AZP 12 was observed from paddle craft, motorized canoe or nearby islands. AZP 13 was viewed from a boardwalk.

This paper reports on studies carried out between 1975 and 1980. Observations were made throughout the year but were more frequent during the periods from June through September. When hatching was imminent or when interactions between adults and young seemed especially interesting 24-hour vigils were maintained.

Study females were not captured but occasionally their young were noosed,

TABLE 1. Okefenokee study alligators.

Females	Total length (m)	Approx. minimum home range (km ²)	Date of hatching	Vocalize to offspring	Aggressive to juveniles
AZP 10 Blind	2.5	4.8	22 Aug. 1975 (12) 2 Sept. 1976 (8)	Yes	Yes
AZP 11 Rt. eye blind	2.75	3.2	1975 (0) 1976 (0) 1977 (0) 31 Aug. 1978 (31)	None heard	Yes
AZP 12 Notched caudal	2.5	6.4	30 Aug. 1976 (30) 31 Aug. 1978 (20)	Yes	Not observed
AZP 13 Scarred earflap	2.25	3.2	1 Sept. 1976 (33)	Yes	Yes

measured and tagged with colored plastic rings (#4, National Band and Tag Co.) or monel fish tags (#1, Style 4-1005, National Band and Tag Co.) inserted through caudal scutes.

The following terms are used for sub-adult alligators: hatchling—total length 23–45 cm; yearling—45–70 cm; juvenile—70–135 cm.

RESULTS

Nurseries.—As used here, nursery refers to an area occupied by a female and her pod and has the following characteristics. Typically, such areas are grassy, open to sunlight and have shallow water except for small ponds or holes excavated by the females. In crawling through the grasses females mash and scrape a network of trails. Small fish, crayfish, frogs and insects funnel into the shallow water trails where the hatchlings wait to prey on them. With broken grass stems blending with their dorsal yellow bars and light colored ventral scales, the camouflaged hatchlings are afforded a degree of protection from aquatic and aerial predators.

Den.—During several dry days in April 1976 the exposed winter den of AZP 11 was examined. Located 10 m from her nesting site, the 80 × 30 cm high entrance hole extended 3 m horizontally and terminated in a chamber

1.5 m in diameter by 1.5 m high. Probing the submerged den entrance in February 1979 revealed a large alligator assumed to be AZP 11. When she terminated hibernation in March her two remaining hatchlings were with her.

Vocalizations.—Hatchlings, yearlings and juveniles vocalized loudly during threats by larger animals including humans. These vocalizations provoked an immediate response from the female who then swam rapidly toward her distressed offspring. On two occasions AZP 10 successfully drove away great blue herons approaching her vocalizing hatchlings. Hatchlings and yearlings vocalized softly when swimming away from the pod. Then the females' only response was to blow bubbles, grunt or burp-trill (Watanabe, 1980) (Fig. 1).

On 18 May 1976, AZP 13 was observed vocalizing and moving her remaining 12 hatchlings from their nursery (and hatching site) to a new area. At 0715, following a chorus of bellowing from distant alligators she bellowed several times. One hatchling grunted. At 0900 and 0945 she grunted softly several times in succession and the hatchlings responded immediately with non-distress grunts. AZP 13 grunted again at 1300 and then crawled from

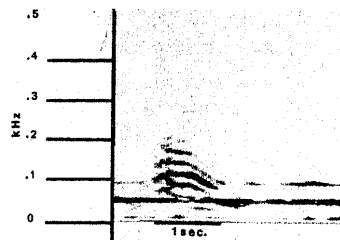


FIG. 1. *A. mississippiensis* adult female vocalization (burp-trill).

the pond followed by three of her still grunting offspring. After an advance of several meters, she hesitated and grunted again and was answered by most of her hatchlings. This procedure was repeated until 1337 when she and her entire pod had advanced 75 m beyond her pond and into an alligator trail where the hatchlings had never before been observed. In following months, AZP 13 inhabited another pond connecting with the alligator trail and 200 m from the previously inhabited nursery.

AZP 13 burp-trilled when leaving the pond on forays into Chesser Prairie. These vocalizations were accompanied by grunts from the hatchlings. At two years of age, one of her offspring burp-trilled when leaving the pond and a sibling responded with grunts.

In the presence of the female, non-distress grunting of hatchlings occurred in continuous and apparently random fashion. The pattern of grunting was the same as shown by unhatched young in the nest. A *t*-test suggested no difference in the average number of grunts per minute between unhatched in piped eggs and fresh hatchlings ($P < 0.05$). A *t*-test also affirmed no differences in the above statistic when yearlings were compared with both hatchlings and young in unhatched eggs (Table 2).

On 13 December 1977 vocalizations

TABLE 2. Comparison of mean numbers of grunts/minute in 30 minute observation periods.

	Mean number grunts/min	Number of observations
Unhatched	.73 ± .67	3
Hatchlings	1.33 ± 1.16	4
Yearlings	1.17 ± 1.30	9

were recorded from AZP 13 and her four yearlings at sequential 10 minute intervals. Their movement coincided with four vocalizations of adult and 15 vocalizations of yearlings at intervals 7, 8 and 9. Over the total 160 minutes, yearlings vocalized 116 times, AZP 13 vocalized five times. Although gross inspection of protocols suggested a temporal relationship between vocalizations and/or movements of the female and vocalizations and/or movements of her young, Kendall's Tau-test did not confirm this ($P < 0.05$).

Hatchlings and yearlings grunted frequently when searching for food or exploring their environment. Such vocalizations occurred more commonly in the presence of the female and this agrees with the findings of Deitz (1979).

Dispersal of Offspring.—Study females rarely wandered from their nursery and hatchlings. It was assumed that juveniles would eat smaller younger individuals and that therefore, they would not be tolerated by nesting, brooding females. AZP 12, however, permitted a juvenile to remain within 5 m of her 1978 nest. This lone juvenile remained near the periphery of her nursery but did not join the hatchlings. It was subsequently noosed for an examination which revealed a deformed tail. During capture, the juvenile vocalized and AZP 12 hissed and made a single 3 m lunge with open mouth at the captor.

One of the stimuli for dispersal of young alligators from nurseries is presumed to be the increasing aggression of the mother toward growing offspring. On several occasions, AZP 10, 11 and 13 attacked without injuring ju-

veniles of unknown origin when they mixed with hatchlings.

Although unable to judge length of offspring by sight, the blind female AZP 10 could possibly judge length by sound for as her offspring grew larger, their vocalizations grew lower in frequency. On 5 October 1975 two stunted alligators (two years of age, total length 35 cm) escaped from an exhibit at the Okefenokee Swamp Park and she immediately accepted them into her pod. On 24 March 1976 she seized a vocalizing juvenile (estimated total length 1 m) then released it after five minutes of shifting it about in her mouth. The juvenile quickly swam from her nursery.

On 21 March 1977, AZP 13 seized and held a juvenile (total length 72 cm) when it attempted to pass through her hatchlings who then called in distress. After four minutes, she released it. Examination of the juvenile revealed no apparent injury except for a slight tooth impression on the mandible. Several weeks later under similar circumstances, AZP 13 did not attack a yearling (total estimated length 40 cm).

AZP 11 stalked and finally lunged at a juvenile (estimated total length 1 m) who swam near her two eight month old offspring. But by August the two had become wary of their mother and quickly vocalized and fled when she approached. This behavior pattern continued into September after AZP 11 excavated her nest mound.

Aggression Toward Humans.—At any time of the year when alligators were active, humans capturing hatchlings, yearlings or juveniles risked attack but the study alligators were most aggressive during nesting. In the prairie study area, other alligators tending but not defending their nests from humans lost eggs to predators. Day or night the study alligators were consistently visible near their nests and hissed with open mouth when approached by humans. Typically this display continued with the guarding female at times partially covering the nest with her body

or making short lunges at the intruder. In one case AZP 13 jumped at the chest of a researcher who walked by her nest. Under these circumstances touching nests was impossible. Presumably egg consuming predators are similarly thwarted. Metzén (1978) noted the black bear as primary predator of alligator eggs in the Okefenokee Swamp and perhaps alligators see humans as facsimiles of bears as suggested by Deitz and Hines (1980).

DISCUSSION

McNease and Joanen (1974) reported a 12 to 600 ha dispersal of subadult alligators (total length 1-1.5 m). Although Neill (1971) claimed that hatchlings dispersed immediately after emerging from the egg, it now seems certain that some offspring remain close to their mother for the first year and sometimes into the second or even third year (Fogarty, 1974; Garrick and Lang, 1977). However, mixing and the resulting competition between hatchlings and juveniles for food and maternal care would adversely affect survival of hatchlings. Even cannibalism might result. Juveniles sometimes linger at the periphery of nurseries but AZP 10, 12 and 13 acted aggressively toward juveniles mixing with hatchlings. Similar behavior in captive Morelet's crocodiles, *Crocodylus moreletii*, made juveniles wary of their mother and inhibited their feeding or moving near hatchlings (Hunt, 1977). With juveniles dispersed, the study alligators could perhaps direct their vigilance more advantageously to younger more vulnerable offspring. This is the type of parent-offspring conflict situation envisioned by Trivers (1974) in which older offspring are rejected by the parent in favor of younger offspring.

Vocalizations are an important aspect of alligator social behavior from hatching to adult (Campbell, 1973; Garrick, Lang and Herzog, 1978; Herzog and Burghardt, 1977; Watanabe, 1980) and the survival of young alligators de-

pends on their ability to stay together in suitable habitat with their protecting mother. When the blind female, AZP 10, successfully protected her young, she demonstrated the importance of vocalizations in maternal behavior (Hunt, 1978).

Herzog and Burghardt (1977) suggested and Watanabe (1980) has recently elaborated on the theory that the vocalization system of *A. mississippiensis* is comparable to that of avians and mammals as described by Morton (1977), in that the frequency and sonographic shape of the call determines its social definition. Thus high-pitched chevron-shaped cells, such as distress grunts, indicate distress and/or appeasement. The adults respond protectively to this call. Harsh, low frequency calls, such as a hiss are threats. Other vocalizations of intermediate frequency range, such as non-distress grunts may aid in determining individual identity and maintaining group (pod) cohesion.

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