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FUNCTION OF NEST ATTENDANCE IN THE AMERICAN ALLIGATOR

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Abstract: Alligators are known to remain in attendance at their nest, but the nature and function of this behavior have not been demonstrated. The response of an attending alligator to an intruder may include an ordered sequence of up to ten progressively more agonistic behaviors which terminate in an attack. The function of these behaviors appears to be to guard the nest against potential predators. Attending alligators respond differently to various potential predators depending in part on the intensity of the threat. Several factors, especially experience, modulate the response and determine the behavior of individual alligators.

Key words: Reptilia; Crocodilia; Alligatoridae; *Alligator*; Agonistic behavior; Nest attendance

Some American alligators (*Alligator mississippiensis*) remain in attendance near their nest during incubation (McIlhenny, 1935; Neill, 1971; Kushlan, 1973). However, the nature and function of nest attendance remain unclear because of the lack of systematic study. Neill (1971) stated that the behavioral components of nest attendance consisted completely of "ritualized bluffs" and did not include actual attacks. Others have suggested that nest attendance behaviors include agonistic components (Kushlan, 1973; Gunter, 1978). Understanding this phenomenon acquires added significance because nest attendance and parental behaviors are rare among reptiles (Burghardt, 1977*a*). We resolved the behavioral components of nest attendance and tested its function experimentally. We present here evidence that nest attendance functions in nest defense against potential egg predators, contains both bluff and attack components, and is modifiable by experience.

Materials and Methods

This study was conducted in the Everglades marsh in Everglades National Park, Florida, during the June through September nesting seasons of 1975–78. Data were collected in 5–10 km² areas of Everglades marsh and adjacent to an 11.3 km road running through Everglades habitat. We visited 132 active nests before they hatched and recorded the behavior of adult alligators present at each nest site. Two visits were made to most nests although the 77 nests in our two major study areas were observed as often as ten times in a season. Several of these nests were selected for experimental work.

Guarding behaviors were elicited in several ways. Initial observations at each nest were made when one or more persons walked or waded to the nest. We also conducted five experiments using alligators that were tenacious in their nest attendance. In experiment 1 we studied the response of an alligator to a natural egg predator by presenting a stuffed racoon (*Procyon lotor*). The racoon was hung from a light-weight line stretched above the nest. Standing 5 m away from and on either side of the nest, we pulled the line and simulated the racoon's approach to and onto the nest. In experiment 2 we tested the response of an alligator near the nest to a human by using a model made of clothing stuffed with rags and attached to a 3 m-long pole. The model was presented gradually to the alligator near the nest. The human model was also used to test the response of an alligator at a nest after hatching (experiment 3) and to a young alligator giving a distress call away

from the nest (experiment 4). In experiment 5, we tested the alligator's reaction to an unnatural intruder using a racoon-sized (20 × 10 × 10 cm) polystyrene block hanging from a 3 m-long pole. Each experiment was conducted once. Experiments 1 and 5 were conducted on different alligators in 1978. Experiments 2–4 were conducted in 1977; it is possible that experiments 2 and 4 involved the same animal two weeks apart. As far as we could tell, during the experiments the alligators responded only to the models and not to the more distant humans presenting them.

Results

Behavioral repertoire.—To understand clearly the experimental results, we first catalogued the behaviors associated with nest attendance. Garrick et al. (1978) have named some of these behaviors although their observations were incomplete and we follow their nomenclature wherever possible. We recognize ten behaviors and postures associated with nest attendance.

Submerged: The alligator lies under water near its nest. This is the usual case. If the area is dry, the alligator lies in shallow water or mud.

Approach (AP): The alligator moves toward the nest generally from its nearby den or pond. It usually swims or uses a low walk but may use a high walk (Garrick et al., 1978).

Head-emergent (HE): The alligator's snout and eyes or entire head are emerged from the water, near and often facing the nest. It may hiss (Hs) with the mouth closed or slightly open.

Head-emergent-tail-arched (HETA): The alligator remains submerged with its head and tail out of the water and may hiss and tail wag.

Nest-posture (NP): The alligator positions itself on or adjacent to the nest. Its head is rested on the nest or is raised slightly. When raised, the head remains horizontal but the neck is arched upward elevating the head well above the ground. The body appears inflated and this posture may be a terrestrial variation of the inflated posture used by alligators in a territorial context (Garrick and Lang, 1977). The posture may be accompanied by a hiss or deep growl.

Open-mouthed-posture (OMP): The alligator holds its mouth open and often hisses or growls. This behavior is part of what Garrick et al. (1978) called hiss posture. This name is inappropriate because hissing is frequently used in other postures and does not always accompany this posture.

Open-mouthed-lunge (OML): The alligator lunges forward about one half its body length usually with a hiss and terminal growl.

Mock-bite (MB): The alligator bites down lightly and then releases without holding. This behavior appears similar to the biting used by crocodilians in dominance interactions (Garrick and Lang, 1977).

Hard-bite (HB): The alligator bites down and may shake its head sideways while applying pressure.

Withdrawal (W): The alligator withdraws from the confrontation at any stage in the sequence usually with much noise and splashing (WS).

Descriptive results.—Alligators in attendance at their nest used one or more of the ten behaviors. If more than one behavior was employed, it was generally used in succession as part of the sequence shown in Fig. 1. The figure and descriptive results are based on our observations of alligator responses to human intruders and our models. When an intruder arrives at a nest, the alligator remains submerged, moves away, submerges, or approaches the nest usually from its nearby pond or den. If away from the nest, it generally approaches underwater and assumes a head-emergent posture when near the nest. Head-emergent posture seems to be primarily an attentive behavior during which the alligator locates the intruder. In deep water the head-emergent-tail-arched posture may be used at this time.

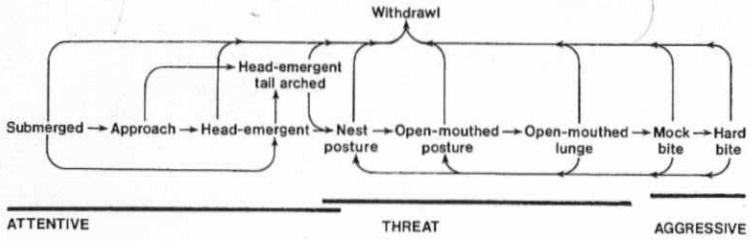

Fig. 1.—Sequence of behaviors used by nest attending alligators in response to intruders. See text for description of behaviors.

The next reaction of an alligator is to come out of water usually using a high walk. It approaches the nest or interposes itself between the nest and intruder. This response seems to be directed initially toward the nest site rather than toward the intruder. Most commonly, the alligator walks over the edge of the nest or on the top of the nest and remains there assuming a nest-posture.

As the encounter continues, the alligator may assume an open-mouthed posture followed by an open-mouthed hiss. If the intruder comes closer to the nest or turns around to retreat, the alligator may make on open-mouthed-lunge. After the lunge, the alligator generally stops and resumes a nest-posture. The sequence of nest-posture, open-mouthed posture, open-mouthed-lunge, nest-posture may be repeated several times with each lunge bringing the alligator further from the nest toward the intruder. The alligator sometimes may high walk a short distance at various times. Although we know of one instance of an alligator that had been continually exposed to people chasing an intruder many meters (Kushlan, 1973), this was highly atypical. Alligators usually confine their display to the nest area and seldom pursue an intruder long distances.

If the intruder neither withdraws nor shows aggression, the open-mouthed-lunges and intervening high walks bring the alligator in striking range and a mock-bite is delivered after a lunge. This involves the alligator biting down and maintaining slight tension before releasing its hold. In contrast, during a hard-bite the force is greater and sometimes the animal shakes its head from side to side.

Experimental results.—In the first experiment we tested the response of an attending alligator to a natural nest robber, the racoon, which may destroy a sizeable proportion of alligator nests in some areas (Joanan, 1970; Goodwin and Marion, 1978). The alligator initially responded to the model with open-mouthed posture and hissing (Fig. 2). After these responses the alligator gave two hard bites, the second of which tore the racoon model from its control line. The alligator then ate the model. This suggests that nest attendance may be effective in guarding against the alligator's most important contemporary nest predator.

In experiment 2 we tested the response of an alligator to a model of a human intruder, a nest predator potentially dangerous to the guardian. The alligator responded to the human model in the same manner as to the racoon but exhibited a more elaborate behavioral sequence (Fig. 2). Upon initial contact with the model it gave a mock-bite and released quickly. Only after this was ineffective did the alligator give a hard-bite that ripped the model's clothing. After this bite the alligator withdrew. As in experiment 1, threat displays preceded aggressive behaviors. In response to the human model,

Experiment

1. Ap → HE → NP → OMP, Hs → OML → OMP, Hs → OMP → NP → OMP, Hs → OML → HB → OMP → OML → HB
2. Ap → NP → OMP, Hs → OML → OMP, Hs → OML → OMP, Hs → OML → MB → OMP → OML → HB → WS
3. Ap → HE → W
4. Ap → HE → OMP → OML → OMP, Hs → OML → W → HE
5. Ap → HE → NP → OMP → OML → OMP, Hs → OML → HB → OMP → OML → HB

FIG. 2.—Results of experiments eliciting nest guarding behavior using models. Abbreviations for behaviors are given in the text. Experiment 1, natural nest predator (stuffed racoon). Experiment 2, human model intruder at nest. Experiment 3, human model intruder at nest after hatching. Experiment 4, human model intruder near young giving distress calls away from nest. Experiment 5, unnatural intruder (plastic block) at nest.

the alligator resorted to a hard-bite only after the model did not retreat (most uncharacteristic of a human). These responses would certainly have been effective in deterring a nonagressive human intruder.

In experiment 3 we tested the hypothesis that nest attendance behavior changes after hatching. In response to a human model approaching the nest on the day after hatching, the previously aggressive nest guardian exhibited only an attentive response (Fig. 2). Thus, nest guarding typically occurs only as long as the eggs remain in the nest.

In experiment 4 we attempted to determine how nest attendance behavior differed from behavior used in guarding hachlings. Alligators and other crocodilians have been shown to respond to young in distress by picking them up in their mouths and carrying them away from danger (Kushlan, 1973; Herzog, 1975; Hunt, 1975; Pooley and Gans, 1976). In response to a human model near a restrained juvenile, the adult used the same behaviors as in nest attendance (Fig. 2). However, no mock-bites or hard-bites were directed toward the model. Interspersed in the response sequence the alligator attempted to pick up the restrained juvenile with its mouth. Failing, it withdrew and maintained an attentive posture nearby.

In experiment 5 we tested whether alligators only guarded against natural predators. For this we used a racoon-sized polystyrene block. The alligator responded to this highly unnatural intruder in the same manner as to the racoon except that it released the block after a hard-bite rather than consuming it (Fig. 2). Thus, the alligator defended against an unusual intruder but recognized it as not being edible.

Frequency of response.—We saw alligators at 57 of 132 or 43% of the nests. This is a minimal estimate as additional animals no doubt remained hidden near their nests and were not seen by us. Overall, 18 nests (14% of all nests or 32% of the visibly attended nests) were actively defended against humans (i.e., attending animal showed at least threat behavior). Differences in response of individual animals were particularly apparent when detailed observations were made at 71 nests in 1978. That year 49% of the nests were known to be attended. Seven (10%) of the animals left at our approach, 8 (11%) remained submerged at the nest, 11 (15%) exhibited head-emergent behavior only, and 9 (13%) defended. Alligators we saw at individual nests were consistent in their response. For example, at one nest an animal was seen four times and defended each time. An animal at another nest was seen three times and exhibited head-emergent behavior each time. In no case did behavior change when an animal was seen more than once at a nest site during the incubation period.

DISCUSSION

Response sequence.—The behaviors discussed from head-emergent through hard-bite appear to include attentive, threat, and aggressive motivations (Fig. 1). Head-emergent is an attentive posture. Head-emergent-tail-arched and nest-posture appear to have both attentive and threat motivational components. Open-mouthed posture, and open-mouthed-lunge appear primarily to be threats. The mock-bite may result in bodily harm. The hard-bite is certainly an aggressive attack behavior. The threat and aggressive behaviors are generally interrupted by episodes of attentive behavior. After giving a mock-bite an alligator may return to an open-mouthed posture or nest-posture (Fig. 1). After several sequences the intervening open-mouthed posture may be eliminated in favor of repetition of more aggressive behaviors.

Such a series of progressively intensive behaviors may allow the alligator to decrease risk and energy cost by using the minimal effective response appropriate to a given situation and to evaluate risks it faces with further agonistic behavior. If the intruder responds aggressively or inappropriately the alligator can withdraw thereby terminating the encounter.

Individual animals differed in extent of guarding. For example, some alligators retreated after head-emergent behavior whereas an experimental animal remained until the intruder model (inappropriately) did not retreat after a hard-bite. Differences in the aggressiveness of individual alligators may be indicated by the stage at which each terminates the guarding sequence. Withdrawal appears to be part of the repertoire in that it seems to involve more noise and splashing than would seem to be required for mere retreat. This movement may serve to distract an intruder.

Nature of nest guarding.—Brattstrom (1974) suggested that nest attendance is best considered territorial behavior rather than parental behavior. However, use of the same behaviors in defense of the nest and young away from the nest suggests a close motivational and functional relationship. Most behaviors used in nest defense differ from those used in territorial defense (Garrick et al., 1978) even though land areas are defended in both cases. Thus, nest defense appears to be considered best as an example of parental behavior.

Our observations indicate that the behavior of nest attending alligators is more complex than previously described by Neill (1971), Garrick et al. (1978), and others. Alligators used a graded series of ten displays some of which are also used in other contexts (Garrick and Lange, 1977). Much of the guarding repertoire appears to function as a threat of attack. For humans and possibly for other large animals such as bears the threat is probably rather effective. Contrary to Neill's (1971) opinion, however, there are aggressive components to nest guarding.

The 14% defended nests we found in the Everglades was about the same as that (9.2%) found by Joanan (1970) in Louisiana. In areas of the Everglades outside the park where human harassment is frequent, alligators seldom guard their nests (Schortemeyer, pers. comm.). For example, whereas 43% of the nests in our study were attended, only 15% were attended in north-central Florida (Deitz and Hines, in press). Thus, alligators harassed by humans learn not to guard whereas alligators that do not often encounter humans or are habituated to inoffensive humans guard more often.

Adaptive significance.—The results of experiment 1 suggest that the adaptive significance of nest attendance behavior is the defense of the nest against potential predators. Joanan (1970) found that 16.5% of the nests in his Louisiana study were destroyed by racoons. Goodwin and Marion (1978) found that 31% of a small sample of 13 nests was destroyed by predators (probably ra-

coons). Deitz and Hines (in press) working in the same area, showed that nest opening by humans increased nest predation by racoons. Thus far in our studies few undisturbed nests in the Everglades have suffered predation loss. Our experiment suggested that nest attendance can be an effective defense against racoons and thus increases reproductive success. Presumably nest guarding has been effective against similar predators in the alligator's evolutionary history.

The response to a racoon initially consisted of defensive displays followed by predation whereas the response to humans included more elaborate behaviors with final attacks being initiated only after the model did not retreat. Thus, alligators distinguish between types of potential predators and have the ability to alter their guarding behaviors under various circumstances. They appear to be able to evaluate the intruder's action during each stage of an encounter and from this experience gauge subsequent responses as well as future responses to similar intruders. Such behavioral plasticity and attendant ability to learn quickly from experience is obviously highly adaptive. These results provide a field context for the success obtained in laboratory studies of learning in crocodilians (Burghardt, 1977*b*). Nest attendance behaviors shown by alligators in nature appear to balance benefits in increased reproductive output with potential costs of adult injury to achieve appropriate responses to potential predators.

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SEXUAL DIFFERENTIATION IN HATCHLING LOGGERHEADS (*CARETTA CARETTA*) INCUBATED AT DIFFERENT CONTROLLED TEMPERATURES

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Abstract: A clutch of *Caretta caretta* eggs was divided into subgroups and incubated at constant temperatures ranging from 22°–36°C in 2° steps. Hatching occurred at 26°–34°C. At 30°C both males and females developed. Above 30°C only females resulted; below 30°C only males resulted. At hatching the gonads were differentiated as ovaries with a conspicuous germinal epithelium, or as testes with well developed primary sex cords. The oviducts in males were not resorbed at hatching.

Key words: Reptilia; Testudines; Cheloniidae; *Caretta*; Development; Eggs; Temperature; Sex

Gonads of the turtles *Sternotherus odoratus*, *Emys orbicularis*, and *Testudo graeca* have been shown to be histologically differentiated into testes and ovaries by the time of hatching (Risley, 1933; Pieau, 1971). In some formes (e.g., *Sternotherus odoratus*, *Chelydra serpentina*), the oviduct in the male has regressed sufficiently to permit determination of sex by dissection (Risley, 1933; Yntema, 1976). The purposes of this report are to describe sexual characteristics of the gonads and oviducts in hatchling loggerheads (*Caretta caretta*), and to provide histological information needed to determine their sex. In addition, we investigated the effect of incubation temperature on incidence of sex.

Materials and Methods

This report is based on 30 animals preserved within a day after hatching and 11 animals reared for 1–7 weeks. The animals were hatched from a clutch of eggs that was collected on Little Cumberland Island, Georgia on 23 July 1978 and promptly shipped to Syracuse, New York. Upon arrival, the vitalline membrane had not as yet adhered to the inner shell membrane. Cohesion of these membranes in *Chelydra* eggs occurs 1–2 days after removal from the oviduct. The eggs were incubated at temperatures ranging from 22°–36°C.

The hatchlings were killed and fixed in Bouin's solution after the body cavity was opened. The gonad and oviduct were removed along with the adjacent kidney. In addition, the oviduct anterior to the gonad was removed along with the adjacent body wall. These parts were sectioned at 12 micra and stained with hematoxylin and triosin or with hematoxylin and the periodic acid-Schiff reaction (PAS); the latter gave better results.

Results

Female.—At low magnification (Fig. 1A) the gonad of the female hatchling is seen as an elongated structure extending from anterior to postero-medial on the ventral surface of the kidney. The lateral border is serrated. The ventral surface is marked off in irregular areas by shallow grooves; these are detectable in photographs with adequate lighting. The oviduct runs lateral to the ovary; the diameter of the former approximates 0.05 mm and is uniform (Figs. 1A, 2C).

In histological sections (Fig. 2A) the germinal epithelium is seen to form the outer surface of the ovary except in the region of the mesovarium which extends from the ovary to the kidney. This covering is relatively thick on the ventral surface. The epi-