TINKLE, D. W., H. M. WILBUR, AND S. G. TILLEY. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.
VITT, L. J. 1982. Reproductive tactics of *Ameiva ameiva* (Lacertilia: Teiidae) in a seasonally fluctuating tropical habitat. Can. J. Zool. 60:3113–3120.
———. 1983. Reproduction and sexual dimorphism in the tropical lizard *Cnemidophorus ocellifer*. Copeia 1983:359–366.
———. 1986. Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. Copeia 1986:773–786.
VITT, L. J., AND J. D. CONGDON. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: Resolution of a paradox. Am. Nat. 112:596–608.
VITT, L. J., AND S. R. GOLDBERG. 1983. Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. Copeia 1983:131–141.

Accepted: 27 December 1990
Associate Editor: Robert Kaplan

Herpetologica, 47(4), 1991, 403–406

DOES THE AMERICAN ALLIGATOR DISCRIMINATE BETWEEN VENOMOUS AND NONVENOMOUS SNAKE PREY?

PAUL J. WELDON[1,3] AND LARRY MCNEASE[2]

[1]*Department of Biology, Texas A&M University, College Station, TX 77843, USA*
[2]*Rockefeller Wildlife Refuge, Rt. 1, Box 20B, Grand Chenier, LA 70643, USA*

ABSTRACT: McIlhenny reported that the American alligator (*Alligator mississippiensis*) vigorously shakes venomous (Crotalinae) but not nonvenomous (Colubridae) snakes during predatory attacks. He suggested that these snakes are discriminated by chemical cues. Juvenile and adult alligators in our study ingested whole carcasses or carcass pieces of crotaline and colubrid snakes without shaking them. Moreover, no significant differences were detected in the times spent by juveniles ingesting pieces of the carcasses of these snakes. Snake scent gland secretions, a source of chemicals to which alligators may respond, did not elicit vigorous head-shaking when presented on pieces of chicken; alligators generally disgorged chicken pieces treated with these exudates. Observations of staged encounters between juvenile alligators and live snakes indicated that alligators vigorously shake a variety of snakes, not just crotalines, during predatory attacks.

Key words: *Alligator mississippiensis*; Snakes; Crotalinae; Colubridae

MCILHENNY (1935:44–55) reported that the American alligator (*Alligator mississippiensis*) adopts special methods to dispatch venomous snakes, a claim repeated in popular (Graham and Graham, 1979), semi-popular (Neill, 1971), and scientific (Weldon and Schell, 1984; Wolfe et al., 1987) accounts. He wrote: "When an alligator catches a cotton-mouth moccasin [*Agkistrodon piscivorus*] . . . as soon as the snake is grasped in its mouth it is shaken vigorously until quite dead. This shaking makes it impossible for the snake to bite the alligator, possibly in the eye. . . . When a non-poisonous snake is caught it is not shaken, but killed by being crushed between the jaws." In addition to cottonmouth moccasins, copperheads (*A. contortrix*), and rattlesnakes (*Crotalus* spp.)—all crotalines—were reported to be shaken by alligators (McIlhenny in Klauber, 1972: 1110). McIlhenny suggested that alligators use chemoreception to distinguish between snakes, because he observed an alligator shake the carcass of a canebrake rattlesnake (*C. horridus atricaudatus*) bereft of head and skin.

Two reports of alligators feeding on crotalines have appeared since McIlhenny

[3] PRESENT ADDRESS: Department of Herpetology, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008, USA.

(1935) published his observations of head-shaking attacks on these snakes. Carr (1967) reported that an adult alligator systematically bit along the length of a live diamondback rattlesnake (probably *C. adamanteus*) before swallowing it head-first; head-shaking, however, was not mentioned. In Scott and Weldon's (1989) study, ground meat from the carcasses of western diamondback rattlesnakes (*C. atrox*) was one of several food items contained in paper bags and offered to alligators in a semi-natural enclosure to test their responses to food chemicals. Alligators removed bags containing rattlesnake meat (and other meats) more than controls, but head-shaking was not observed.

We report here attempts to corroborate McIlhenny's claim that alligators shake crotaline, but not colubrid, snakes. Whole carcasses, carcass pieces, or scent gland secretions of snakes were presented to juvenile or adult alligators. Scent glands, paired sacs opening through ducts at the posterolateral margin of the cloaca, release secretions when snakes are disturbed. Scent gland secretions were presented because they are a potential source of chemicals to which alligators respond. In addition, we report observations of staged encounters between alligators and live snakes.

Materials and Methods

Alligators hatched from eggs obtained in Cameron Parish, Louisiana, and they were maintained at the Rockefeller Wildlife Refuge, Grand Chenier, Louisiana. Twenty juvenile alligators ($\bar{x}$ total length = 69 cm), 10–12 mo old, were housed in two 2.1 × 0.9 m concrete enclosures provided with a platform and shelter and filled with water to a depth of approximately 10 cm. They were fed pellets (Burris 45% Alligator Food, Burris Pet Food, Franklinton, Louisiana) ad libidum for 6 mo and were then fed primarily ground nutria (*Myocastor coypus*). Adult alligators ($\bar{x}$ TL = 2.9 m) were housed in three semi-natural enclosures for 17 or 18 yr. Each enclosure was approximately 3.7 ha and contained 13–16 individuals. Adult alligators were offered nutria meat amounting to 6% of their combined mass at regular sites near canals. All tests were conducted outdoors at 26–30 C during August and September, 5–8 days after subjects had been offered their normal ration of food.

Juvenile alligators were tested individually in two experiments for responses to pieces of snake carcasses. Each experiment was conducted over one day. Once a week, several weeks before testing began, alligators were fed in a manner similar to that used in experiments with snake tissues: the water in their enclosure was drained, they were placed individually in a 0.9 × 0.9 m area screened off in their home enclosure, and they were offered nutria or pieces of chicken (*Gallus* sp.) on plastic plates (diameter = 16 cm; height = 1.5 cm).

In the first experiment, 10 × 1.5 cm pieces containing both integument and muscle tissue were cut from the dorsolateral aspect of a cottonmouth moccasin and a banded water snake (*Nerodia fasciata*), both freshly sacrificed. A piece from each snake was placed on a plate, and the two plates were placed edge to edge in a corner of the test area; the positions of plates containing pieces of each snake were alternated with each trial. We observed each alligator for 45 min, or until it ingested both snake pieces. The time spent ingesting each piece—beginning with its removal from the plate to swallowing—was recorded. Alligators failing to seize both snake pieces during a trial were not considered in the data pool.

In the second experiment, responses by alligators to pieces cut from the carcasses of a copperhead and a rat snake (*Elaphe obsoleta*) were observed. The same experimental protocol and pool of subjects described for the first experiment were used. This experiment was conducted 2 wk after the first experiment.

Juvenile alligators were tested in two experiments for responses to the scent gland secretions of snakes. The same alligators tested with pieces of snake carcasses served as subjects in these experiments. Each experiment was conducted over one day, and experiments were conducted 1 wk apart.

A total of 4.5 g and 5.4 g of secretions were obtained from 13 live western diamondback rattlesnakes and 12 live bull snakes (*Pituophis melanoleucus*), respectively, by manually pressing the base of the tail and allowing the secretions to flow into glass vials. The secretions were pooled separately for each species. They were stored at −90 C for 2–3 wk and were thawed and reconstituted with 0.5 ml of distilled water several hours before use. Thirty to 40 mg of secretions were applied by brush to individual 7 × 1.5 cm pieces of chicken (*Gallus* sp.); distilled water was applied by brush to control pieces.

Alligators were presented simultaneously with secretion-treated and control pieces of chicken, as described for tests with pieces of snake carcasses. The ingestion or disgorgement of each piece was noted.

Adult alligators were tested in their enclosures for responses to whole carcasses of 12 western diamondback rattlesnakes (TL = 100–146 cm) and 12 bull snakes (TL = 112–202 cm). This experiment was conducted over two days, 1 wk apart. Adult alligators could not be identified individually, so our data may not be independent. Free-living king snakes (*Lampropeltis getulus*), ribbon snakes (*Thamnophis proximus*), and water snakes (*Nerodia* spp.) had been observed in the alligators' enclosures over the years.

Snakes were sacrificed by hypothermia and stored at −90 C for 3 wk and then at −10 C for 5–7 days before testing. The carcasses were thawed for approximately 10 h before being tied with a light string to the end of a 2.3 m pole and were then presented to alligators. Rattlesnake and bull snake carcasses were offered one at a time in alternating order to alligators appearing at their regular feeding sites. Alligators removed carcasses from the string and were observed as they ingested them.

Results

We observed 12 juvenile alligators ingesting pieces of both cottonmouth moccasin and banded water snake, with mean (±SE) ingestion times of 20.0 ± 4.1 s and 32.0 ± 11.5 s, respectively. Eight immature alligators were observed ingesting pieces of both copperhead and rat snake, with mean ingestion times of 13.9 ± 4.5 s and 9.3 ± 1.1 s, respectively. The Wilcoxon matched-pairs test failed to detect significant differences in the times spent by alligators ingesting crotaline versus colubrid snake pieces (t = 22.5 and 12.0, respectively; $P > 0.05$ in both cases). Headshaking was not observed.

We observed 10 juvenile alligators in experiments with the scent gland secretions of bull snakes and rattlesnakes. Alligators disgorged eight pieces of chicken treated with the secretions of bullsnakes—one individual scraped a secretion-treated piece out of its mouth with its hindleg—and disgorged one control piece. Alligators disgorged four pieces of chicken treated with the scent gland secretions of rattlesnakes and ingested all control pieces. The McNemar test indicated that significantly more chicken pieces treated with bull snake secretions were disgorged than were control pieces ($\chi^2 = 6.1, P \leq 0.05$), but it failed to detect a significant difference in the disgorgement of rattlesnake secretion-treated versus control pieces ($\chi^2 = 2.3, 0.20 > P > 0.10$). Alligators opened their mouths and waved their heads during the disgorgement of chicken pieces, but vigorous head-shaking was not observed.

Adult alligators readily ingested both rattlesnake and bull snake carcasses; neither species was shaken.

Discussion

Our study failed to corroborate McIlhenny's (1935; cited in Klauber, 1972) claim that alligators shake crotaline, but not colubrid, snakes. Neither juvenile nor adult alligators shook the carcasses or the carcass pieces of any snake. Comparisons of the times spent by juvenile alligators ingesting pieces of snake carcasses also failed to indicate that crotalines and colubrids are treated differently. McIlhenny (1935) wrote primarily about free-living alligators from Avery Island (Iberia Parish), Louisiana. It is possible that the alligators he observed had encountered more snakes than had our subjects, and that the influence of different experiences with snakes account for our discrepant results.

The disgorgement by juvenile alligators of pieces of chicken treated with the scent

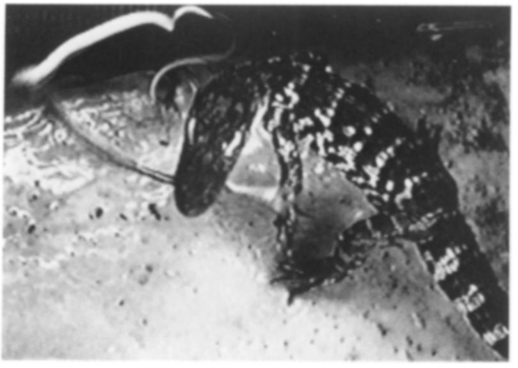

FIG. 1.—A juvenile alligator raises its forefeet off the substrate while shaking a ribbon snake.

gland secretions of bull snakes is consistent with the antipredator function generally attributed to these exudates (see Wright and Weldon, 1990, for recent references). More pieces of chicken treated with the scent gland secretions of rattlesnakes were disgorged than were control pieces, but a significant effect was not detected. A more complex experimental design and greater sample sizes than ours are required to determine the relative palatability of scent gland secretions. Our experiments were designed to test whether these exudates elicit vigorous head-shaking in alligators; we failed to demonstrate that they do.

Our observations of staged encounters between juvenile alligators and various live snakes—copperhead, ribbon snake, water snakes, kingsnake, and mud snake (*Farancia abacura*)—indicate that vigorous head-shaking, during which alligators sometimes raise their forefeet off the substrate, frequently is exhibited during predatory attacks (Fig. 1). Head-shaking usually occurred immediately after alligators had seized snakes, and in some cases after snakes had wrapped around an alligator's head or upper trunk. Additional observations are needed to determine whether alligators shake other live prey.

Acknowledgments.—W. Breaux, T. Joanen, J. Nunez, and G. Perry (Louisiana Department of Wildlife and Fisheries, Rockefeller Wildlife Refuge) made facilities available for this study. M. Banta, C. Chandler, A. Salinas, and E. Santry provided expert field assistance. J. Massey, R. Miller (First Strike, Sinton, TX), G. Wills (Maverick Trading Post, Farmers Branch, TX), and D. Sebolt (Snake-A-Torium, Panama City Beach, FL) provided snakes. G. Shearer (Harrington Media Center, Texas A&M University) provided photographic equipment. D. Pitts (Video Digital Analysis Laboratory, Flight Science Support Office, Lyndon B. Johnson Space Center, NASA, Houston, TX) prepared the figure. H. Drummond, H. Greene, and J. Murphy commented on the manuscript. This study was supported by a grant from the National Geographic Society.

LITERATURE CITED

CARR, A. 1967. Alligators: Dragons in distress. Nat. Geog. Mag. 131:132–148.

GRAHAM, A., AND F. GRAHAM. 1979. Alligators. Delacourte Press, New York.

KLAUBER, L. M. 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind, Vol. 2. University of California Press, Berkeley.

MCILHENNY, E. A. 1935. The Alligator's Life History. Christopher Publishing House, Boston.

NEILL, W. T. 1971. The Last of the Ruling Reptiles: Alligators, Crocodiles and Their Kin. Columbia University Press, New York.

SCOTT, T., AND P. J. WELDON. 1990. Chemoreception in the feeding behaviour of adult American alligators, *Alligator mississippiensis*. Anim. Behav. 39:398–400.

WELDON, P. J., AND F. M. SCHELL. 1984. Responses by king snakes (*Lampropeltis getulus*) to chemicals from colubrid and crotaline snakes. J. Chem. Ecol. 5:141–151.

WOLFE, J. L., D. K. BRADSHAW, AND R. H. CHABRECK. 1987. Alligator feeding habits: New data and a review. Northeast Gulf Sci. 9:1–8.

WRIGHT, J., AND P. J. WELDON. 1990. Responses by domestic cats (*Felis catus*) to snake scent gland secretions. J. Chem. Ecol. 16:2947–2953.

Accepted: 13 December 1990
Associate Editor: Daniel Formanowicz, Jr.