PREDATION AND DEFENSIVE BEHAVIOR OF THE STRIPED SWAMP SNAKE (*REGINA ALLENI*)

J. STEVE GODLEY

Birds and other predators are known to influence many aspects of the ecology of their prey, such as the prey's distribution, habitat use, behavior, food, and even reproductive output (e.g., Wilbur et al. 1974, Sterns 1976). Reptiles often are common vertebrates in many environments and as such provide an important food resource to many predators, including birds. However for many species of reptiles we lack even anecdotal information about their predators or the effects of predation on reptilian populations (Greene et al. 1978).

In this paper I summarize information on predation, tail loss, and defensive behavior of the striped swamp snake (*Regina alleni* (Garman)). This small (to 530 mm snout-vent length), secretive, highly aquatic snake inhabits many of the marshes, streams, and ponds of Florida where it feeds primarily on crayfish. In some Florida water hyacinth communities this snake may be very abundant, reaching densities of 1287 individuals per hectare (Godley 1980). Previously, the only known predator of striped swamp snakes was the cottonmouth (*Agkistrodon piscivorus*) (Loennberg 1894).

STUDY AREA AND METHODS

Most of my observations of striped swamp snakes and their predators were made from 1974-1978 during a study of the herpetofauna of a 2.71 ha water hyacinth (*Eichhornia crassipes*) community at Rainey Slough, Glades Co., Florida. This site consisted of two hyacinth-choked canals on either side of an elevated road-bed. Each canal was 1.1 km long and adjoined a seasonally flooded (June-September) wet prairie-marsh. The canals were connected under a bridge near the center of Rainey Slough. I (Godley 1980) provided a detailed description of the study area, collection methods, and foraging ecology of striped swamp snakes at this site elsewhere. Additional observations of predation on *R. alleni* were recorded from other localities and in the laboratory. In this paper all snake body sizes are given as snout-vent lengths.

RESULTS AND DISCUSSION

PREDATION

Observations of predation on striped swamp snakes are given in this section.

GREAT BLUE HERON (*Ardea herodias*).—On 12 February 1977 at 1105, F. Ackerman and I observed a Great Blue Heron with an adult (ca. 300 mm) striped swamp snake thrashing in its beak. The heron stood in shallow water repeatedly dropping, pecking, and picking up the snake. After watching the bird through binoculars for about 3 minutes I waded across the canal to attempt to rob it, but the heron flew with the snake in its beak and landed 150 m away. C. E. Winegarner saw a Great Blue Heron catch and swallow a striped swamp snake of unrecorded size on 13 March 1977 at Myakka River State Park, Sarasota Co., Florida. It foraged by walking slowly along the bank, striking in hyacinths that floated near the riverbank.

GREAT EGRET (*Casmerodius albus*).—At 1430 on 24 February 1978, B. Jayne, R. Jennings, M. Martin and I saw a Great Egret fly up from a mixed flock of foraging wading birds in the Rainey Slough marsh with a ca. 300 mm striped swamp snake in its beak. A Great Blue Heron chased the egret for about a minute (ca. 0.7 km) before returning to the flock. The egret flew another 0.5 km before landing out of view in the marsh. C. E. Winegarner (pers. comm.) also observed a Great Egret catch and eat a juvenile (ca. 200 mm) *R. alleni* on 2 February 1978 in a marsh 3.8 km W of Fisheating Creek along SR 70 in Highlands Co., Florida. He noted that the snake twisted and struck weakly at the bird.

RIVER OTTER (*Lutra canadensis*).—At 1342, on 17 December 1974, D. Worley and I observed with binoculars an adult and two 3/4 grown river otters moving eastward across the dry prairie toward the Rainey Slough bridge. The otters entered the west canal and dived beneath a low growth of hyacinths about 40 m from us. Within 10 sec the adult otter surfaced 5 m from shore holding an adult (ca. 400 mm) *R. alleni* mid-body in its jaws. The snake thrashed wildly, with its mouth open and head and neck swaying laterally. The otter bit the snake several times, then turned and swam toward shore. After reaching the bank the otter briefly manipulated the then limp snake with its forepaws and devoured it tail-first within 7 min.

RACCOON (*Procyon lotor*).—Circumstantial evidence suggests that raccoons may be potentially important sources of mortality for striped swamp snakes. Two adult snakes, each probably killed the previous night, were found eviscerated and partially eaten in different marshes (25 August 1977 in Alachua Co., Florida, D. Jackson, pers. comm.; 1 December 1979 in Orange Co., Florida, pers. obs.). Both snakes appeared to have been in good health

before death. No tracks were observed as the substratum was unsuitable in both cases. I suspect that both snakes were killed by raccoons because the sites looked similar to those I had seen previously which did contain numerous raccoon tracks.

KINGSNAKE (*Lampropeltis getulus*).—I studied kingsnakes at Rainey Slough from November 1975 through August 1978 (J. Godley unpub.). Four of 58 captured individuals contained prey, all of which were snakes. One adult kingsnake (960 mm) found crawling along a canal bank at 1230 hr on 16 November 1975, regurgitated two partially digested striped swamp snakes. I judged that both prey were captured in the water, (water hyacinth rootlets regurgitated with prey), were eaten in rapid succession (similar stages of digestion), and were swallowed head-first (only tail portions undigested). Tail lengths and sexes of the two *R. alleni* were 134 mm (male) and 123 mm (female). Based on regression analyses of this population of *R. alleni* (Godley 1980 and unpub.), the male was 422 mm and the female was 468 mm. These two snakes represented meals of about 14.0% and 19.4% respectively of the kingsnake's body mass. A second adult kingsnake collected 11 March 1977 defecated the remains of 1 adult *R. alleni*, a juvenile *Thamnophis* sp. or *Nerodia* sp., and hyacinth rootlets.

GREATER SIREN (*Siren lacertina*).—Following a night of funnel trapping in a marsh at Lake Conway, Orange Co., Florida, D. Gross and D. Sutphen (pers. comm.) found on 20 December 1979, an adult *Siren lacertina* (435 mm) in a trap with a dead male striped swamp snake. Only the rear portion of the snake's body remained, the rest apparently eaten by the greater siren. The tail of the snake was 105 mm, indicating a body length of about 334 mm.

CRAYFISH (*Procambarus* spp.).—A gravid striped swamp snake and a gravid black swamp snake (*Seminatrix pygaea*), both captured in July 1976 in Fisheating Creek, Highlands Co., Florida, were placed in an aquarium (52 X 26 X 30 cm) stocked with 10 liters of water, water hyacinths, and a dry hide box for cover. One or two crayfish were provided weekly as food for the *R. alleni*. During the night of 4 August the *S. pygaea* gave birth to six young. One newborn apparently was killed and the posterior half of its body eaten by the only crayfish in the tank (an adult male *Procambarus alleni*, carapace length 31 mm), three were alive but had freshly bobbed tails, and two were alive with no obvious injuries. Both adult snakes were uninjured. On 6 August 1979 a 325 mm female striped swamp snake from Orange Co., Florida, gave birth to seven young in the same tank under similar circumstances except that

three adult crayfish (*Procambarus fallax*) were present. The following morning five of the young were found dead: three of these still had portions of their yolk sac attached, and all five showed signs of crayfish predation (i.e. bobbed tails, chaelae scars on body, parts of tail and head eaten). Branson and Baker (1974) noted that adult crayfish. probably *Orconectes juvenalis*, killed and ate juvenile queen snakes (*Regina septemvittata*) in the laboratory.

These laboratory observations suggest that crayfish may be important predators of juvenile aquatic snakes, especially in the snake's first few hours of life. In the laboratory four different female *R. alleni* gave birth in the water, even though terrestrial hide boxes were available and extensively used before and after parturition, suggesting that in the wild *R. alleni* (and *S. pygaea*) probably give birth in the water. During the reproductive season of striped swamp snakes (July-September), the density of two species of crayfish (*Procambarus alleni* and *P. fallax*) in hyacinths averaged $10/m^2$ (Godley 1980). Adults of these crayfish species attain a mass of > 15 g and thus weigh six times as much as the newborn snakes. At such high densities encounters between young snakes and large crayfish should be common, and newborn snakes with yolk sacs still attached may be especially vulnerable to attack. Laboratory observations suggest that crayfish may be responsible for many of the bobbed tails reported in aquatic snakes.

Tail Loss

The loss of portions of the tail has been used as an index of the intensity, or efficiency, of predation on a number of species of snakes (e.g. Greene 1973). In 88 striped swamp snakes from Rainey Slough, 10.2% had lost part of their tail (12.0% of 50 males, 7.9% of 38 females). Combining my data with the 141 specimens in the Florida State Museum analyzed by Spears (1977) and 149 collected by R. Franz (pers. comm.) at Payne's Prairie, Alachua Co., Florida, the mean frequency of abbreviated tails is 12.17%. This value is lower than that reported for 3 of 4 other aquatic snake species from Florida (Spears 1977). Within the sample of *R. alleni*, no significant differences were detected among the 3 sampling "locations" (χ^2 tests, $P>.05$), suggesting that predation intensities, or predatory efficiencies, were similar, or possibly that any real between-site variation was masked by unknown differences in survivorship (cf. Schoener 1979). No significant sexual differences in tail abbreviations were detected (either within or between samples).

Defensive Behavior

During my studies of *R. alleni* I collected about 120 specimens and maintained and observed a number of these in the laboratory, but I have never been bitten by one. However, eight individuals displayed an unusual "gape and sway" behavior when handled. When grasped firmly near mid-body, these individuals rigidly arched their back, open their mouth nearly 180 degrees exposing the white interior, and swayed their heads and necks laterally. Usually the mouth was closed after 1 to 3 lateral oscillations of the head. One adult striped swamp snake maintained in the laboratory repeatedly displayed this behavior and on several occasions made contact with my hand but never chewed or drew blood. A similar behavior apparently occurred during two predatory encounters in the field. Wright and Wright (1957:422) probably referred to this same response by a freshly captured *R. alleni* from Okefenokee Swamp when they wrote, "In the boat it opened its mouth, and we thought it was about to bite. We noticed the same tendency when we handled it or photoed it."

Other species of *Regina* are noted for their mild temperament (Wood 1949, Nakamura and Smith 1960, Smith and Huheey 1960, Hall 1969, Barbour 1971, Martof et al. 1980). The teeth of *R. alleni* have rounded, chisel-like tips (Rossman, 1963), which penetrate neither the hard exoskeletons of their odonate and crayfish prey (Godley 1980 and pers. obs.) nor the skin of a human finger. Presumably biting would not deter the attacks of most predators. The gape and sway behavior described above may be a "flash display" used to startle predators or mimic more noxious (e.g., water snakes, *Nerodia* spp.), or venomous (e.g., cottonmouth) sympatric snakes that do bite. A defensive and protective function of this behavior is suggested because it apparently is elicited only by a sudden tactile stimulus by a potential predator.

Other presumed defensive behaviors occasionally used by striped swamp snakes include coiling the body into a ball, concealing the head beneath a coil, and laterally flattening the body. Like most natricines, *R. alleni* typically discharges its cloacal contents or anal gland secretions upon capture.

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LITERATURE CITED

BARBOUR, R. W. 1971. The amphibians and reptiles of Kentucky. Univ. Press of Kentucky, Lexington.

BRANSON, B. A., AND E. C. BAKER. 1974. An ecological study of the queen snake *Regina septemvittata* (Say) in Kentucky. Tulane Studies Zool. Bot. 18: 153-171.

GODLEY, J. S. 1980. Foraging ecology of the striped swamp snake, *Regina alleni*, in southern Florida. Ecol. Monogr. 50: 411-436.

GREENE, H. W. 1973. Defensive tail display by snakes and amphisbaenians. J. Herp. 7: 143-161.

GREENE, H. W., G. M. BURGARDT, B. A. DUGAN, AND A. S. RAND. Predation and defensive behavior of green iguanas (Reptilia, Lacertilia, Iguanidae). J. Herp. 12: 169-176.

HALL, R. J. 1969. Ecological observations on Graham's water snake, *Regina grahami* (Baird and Girard). Amer. Midl. Natur. 18: 156-163.

LOENNBERG, E. 1894. Notes on reptiles and batrachians collected in Florida in 1892 and 1893. Proc. U.S. Nat. Mus. 17: 317-339.

MARTOF, B. S., W. M. PALMER, J. R. BAILEY, AND J. R. HARRISON III. 1980. Amphibians and reptiles of the Carolinas and Virginia. Univ. North Carolina Press, Chapel Hill.

NAKAMURA, E. L., AND H. SMITH. 1960. A comparative study of selected characters in certain American species of water snakes. Trans. Kansas Acad. Sci. 63: 102-113.

ROSSMAN, D. A. 1963. Relationships and taxonomic status of the North American natricine snake genera *Liodytes, Regina,* and *Clonophis.* Occ. Pap. Mus. Zool., Louisiana State Univ. 29: 1-29.

SCHOENER, T. W. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. Ecology 60: 1110-1115.

SMITH, H. M., AND J. E. HUHEEY. 1960. The watersnake genus *Regina.* Trans. Kansas Acad. Sci. 63: 156-164.

SPEARS, G. 1977. Predation on colubrid snakes. Masters Thesis. Univ. Florida, Gainesville.

STEARNS, S. C. 1976. Life-history tactics: A review of the ideas. Quart. Rev. Biol. 51: 3-47.

WILBUR, H. M., D. W. TINKLE, AND J. P. COLLINS. 1974. Environmental certainty, trophic level and resource availability in life history evolution. Amer. Natur. 108: 805-817.

WOOD, J. T. 1949. Observations on *Natrix septemvittata* (Say) in southwestern Ohio. Amer. Midl. Natur. 42: 744-750.

WRIGHT, A. H., AND A. A. WRIGHT. 1957. Handbook of snakes of the United States and Canada. Vol. I. Comstock Publ. Assoc., Ithaca, New York.

Department of Biology, University of South Florida, Tampa, Florida 33620 and National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. 20560.