

## PREY-HANDLING BEHAVIOR IN THE GULF CRAYFISH SNAKE (*LIODYTES RIGIDA*)

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**Abstract.**—Most snakes orient their prey to be consumed head first or have no preference for orientation. However, snakes that commonly consume crayfish must deal with both the defensive power of chelae of a live animal or the difficulty of getting spread chelipeds of dead prey into the mouth if prey orientation is head first. The Gulf Crayfish Snake (*Liodytes rigida*) avoids these difficulties by its prey-handling strategy of attack then coiling to immobilize the chelipeds of the crayfish. We discovered an unreported subsequent handling technique of orienting the abdomen so the upper jaw of the snake can bite the soft tissues of the ventral abdomen, resulting in immobilization or death of the prey, followed by consumption from the caudal end.

**Key Words.**—caudal ingestion; Duvernoy's gland; food; Glossy Swampsnake; prey

### INTRODUCTION

The Gulf Crayfish Snake (*Liodytes rigida*), also known as the Glossy Swampsnake, is a highly aquatic species found in lowlands from eastern Texas and southern Arkansas through southern regions of Alabama, then disjunctly through northern Florida and eastern regions of Atlantic coastal states to Virginia (Powell et al. 2016). The species is brownish to olive greenish above and is most easily identified by two distinct rows of dark dots along the ventral scales. *Liodytes rigida* feeds on crayfishes that can pass through the jaws of its relatively small head. The teeth of *L. rigida* are the least curved and least sharp of the crayfish snakes, and the closely set, stout, chisel-like teeth likely represent a special adaptation to handle crayfish, making them more able to grip the hard exoskeleton of their prey (Nakamura and Smith 1960; Rossman 1963) while the snake coils to secure its catch. However, Dwyer and Kaiser (1997) argued that specialized skull shape probably allowed greater crushing capacity in *Liodytes*. Shapes of skulls and teeth in snakes have become coadapted complexes allowing specialized feeding, and dental attachment is especially important for predators of durophagic prey (Savitzky 1983).

Snakes in the genera *Liodytes* and *Regina* (see McVay and Carstens 2013) specialize on crayfishes as their primary prey (Huheey and Palmer 1962; Godley 1980). Graham's Crayfish Snake (*Regina grahamii*) and the Queen Snake (*R. septemvittata*) hatch with chemosensory prey preferences that reflect their specialized diets (Waters and Burghardt 2005), and chemosensory responses in the Striped Swamp Snake (*R.*

*alleni*) increase with exposure during ontogeny (Waters and Burghardt 2013). *Regina grahamii* specializes on molting crayfish (Mushinsky and Hebrard 1977; Seigel 1992) as does *R. septemvittata*, apparently stimulated by chemical cues of ecdysone, which is released when crayfishes molt (Burghardt 1968; Jackrel and Reinert 2011). In contrast, *L. alleni* and *L. rigida* regularly consume intermolt crayfishes in addition to molting ones (Kofron 1978; Godley 1980).

Based on orientation of prey in the stomach, Godley et al. (1984) found no difference in the probability of frontal versus caudal orientation of crayfish in *R. grahamii* (which feeds only on soft, fresh-molted crayfish), whereas *R. septemvittata* oriented prey only caudally. *Liodytes alleni* consumes crayfish abdomen first (Franz 1977; Godley 1980) but very little has been reported for *L. rigida* (only an unpublished dissertation [Waters 2000] has described prey-handling behavior in *L. rigida*). Although it is well documented that *Liodytes* and *Regina* feed almost exclusively on crayfishes, and most orient their prey for caudal ingestion, few studies have examined the strategy by which any of these snakes capture and handle their prey for caudal-oriented consumption. Our goal was to examine how *L. rigida* can successfully manipulate their difficult prey for easiest consumption while avoiding injury to themselves.

### MATERIALS AND METHODS

We studied prey handling by five specimens of *L. rigida* (200–305 mm SVL) collected in Clark, Faulkner, and Saline Counties of central Arkansas. We

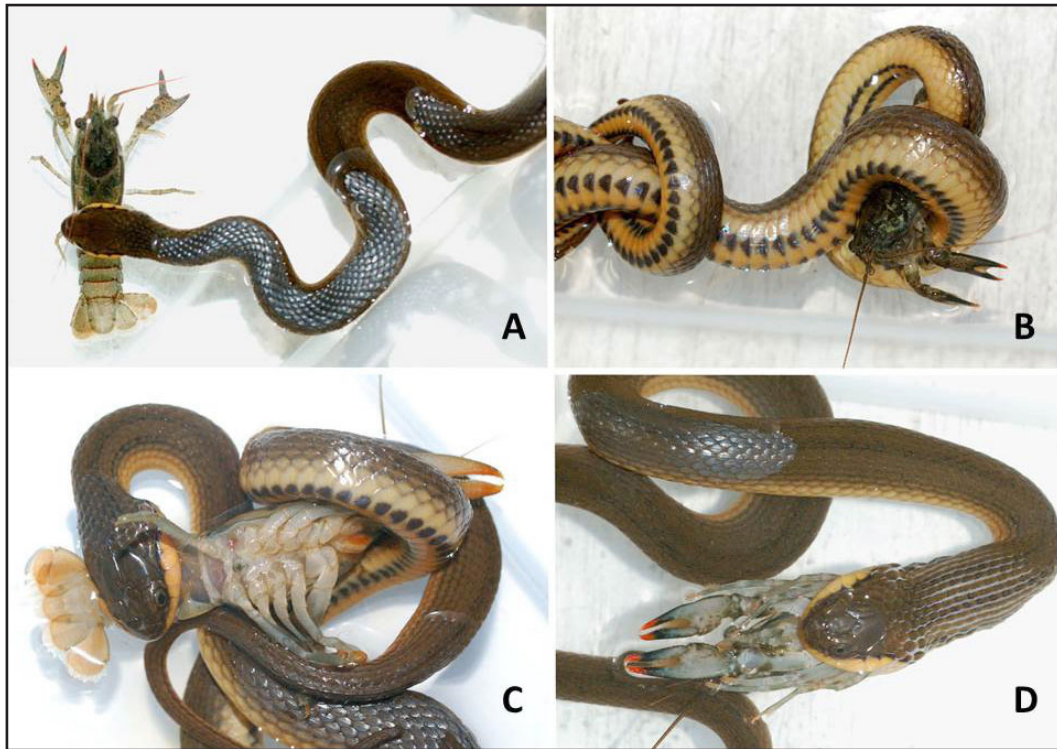


FIGURE 1. Crayfish capture, handling, and consumption behavior by the Gulf Crayfish Snake (*Liodytes rigida*): (A) the snake attacks from the side, (B) rapidly coils to secure the prey and isolate the chelipeds, (C) releases its bite at the point of attack and repositions to chew on the ventral abdomen of the crayfish, then after immobilization has occurred, (D) orients the prey so that the legs will fold forward during ingestion. (Photographed by Renn Tumilson).

fed available small crayfishes (mostly *Procambarus* sp.) 25–50 mm total length to snakes over 17 feeding trials to examine and record prey-handling behaviors. We caught individual snakes initially for use in educational programs and we held them as briefly as possible before we released them at their locations of capture, so opportunities for feeding trials varied per snake, and ranged from 1–4. We used crayfishes whose cephalothorax width was equal to or less than the greatest width of the snake to reduce chances of damage to the GI tract caused by spines (Godley 1980). We placed individual *L. rigida* in an 18 × 30 cm plastic container in about 2.5 cm of water and a crayfish was added. No anchor points were added to which the snake might stabilize its position, as feeding of snakes before the study began fed freely without anchors provided. We recorded behaviors and examined whether these were performed variably or consistently, and the time involved in each observed step of the process.

After each feeding trial, we returned a snake to a container with water and appropriate bedding to reduce any stress to the animal resulting from handling. We released snakes back into their location of origin after feeding trials were conducted. The following description of behavior was consistent among all trials, with any exceptions noted.

## RESULTS

Soon after we added a crayfish to the container, a qualitatively observed increase in the rate of tongue flicks indicated to us predatory interest. Crayfish were approached either from the side or from behind, but the snake always quickly moved to a position perpendicular to the crayfish, paused, then struck from the side. The point of attack was usually the anterior of the abdomen but sometimes the first bite was at the back of the cephalothorax. Once the prey was grabbed, the snake quickly threw coils around the body of the crayfish to restrict its movements (Fig. 1). Coils always isolated the chelipeds, disabling use of the chelae to counterattack the head of the snake, although crayfish did sometimes pinch the body of the snake.

When the body of the crayfish was secured and the chelae isolated, the snake remained coiled but released its bite and moved its head down the abdomen of the crayfish, then turned its prey so the soft muscular ventral side of the crayfish was accessible to the upper jaw (Fig. 1). This was accomplished by the snake moving its head to bite in that position. The bite was held between 45–225 s (mean =  $93.2 \pm [SE] 11.0$  s) while the snake made 6–22 (mean =  $9.9 \pm 1.0$ ) in-place chewing motions on the abdomen of the crayfish until it became limp. The

snake held its bite until swimmerets and legs of the crayfish had ceased to move, leading to variation in the length of time the snake held its prey in this manner.

After the crayfish had succumbed, the snake released its bite and began to move down the tail until it could begin consumption from the caudal end of the prey. At this point, the coils around the crayfish were relaxed. The lateral approach by the mouth of the snake caused the nearest uropod to fold toward the telson, then the first side-to-side consumptive motions folded the opposite uropod. Prey was consumed with the ventral side up in all but one case, in which the ventrally dispatched crayfish became dorsally oriented during consumption. Time from horizontal orientation of the crayfish with the telson of the crayfish in its mouth, to disappearance of the chelae during ingestion of the crayfish, ranged from 15–146 s (mean =  $73.1 \pm 9.4$  s).

On two occasions, crayfish immobilized or killed by *L. rigida* were momentarily rejected. The abdomen of one crayfish was fully inside the mouth of the snake before being expelled, but the snake returned to its prey within a couple of minutes and repeated the strike-coil behavior, then quickly moved to the telson and completed consumption. The second observation involved release after the snake had completed behaviors to the point of orientation to the telson. We believed our flash photography startled the snake and caused the release. However, after 7.5 min the snake returned to the crayfish, struck, coiled, manipulated the crayfish ventrally, and consumed it.

### DISCUSSION

Compared to related snakes of the genera *Liodytes* and *Regina*, the prey-handling behavior of *L. rigida* we describe is unique in a number of aspects, most notably the nature of immobilization of crayfish by chewing prior to ingestion, and consistent ventral orientation for consumption. Crayfishes became limp after the chewing motions on the soft tissues of the ventral abdomen. Total lack of responsiveness of the unrestricted crayfish in the two trials in which crayfish were completely released (then later consumed) verified that the crayfishes were either dead or completely immobilized after the chewing behaviors.

Immobilized crayfishes not only ceased flicking movements of the tail, but the swimmerets and legs also relaxed and remained limp. The steps of predatory behavior were always performed in the same sequence, and in the same manner though with variable lengths of time required to complete each step. Waters (2000) observed similar variation in aspects of prey-handling by *L. rigida*, recording the number of immobilizing bites to average 9.6 (range, 3–21) and the time the crayfish was held before initiating consumption averaging 68.8 s

(range, 8–247 s). Number of bites is correlated with the size of the prey (Waters 2000).

Pooling the observations of our study and those of Waters (2000), prey-handling behaviors arguably are innate fixed-action patterns, given that they occurred consistently with each attempt at predation (including re-strikes of prey that had been attacked and immobilized previously). All steps were performed with each successful strike (although snakes proceeded more quickly to the consumptive phase on the two prey that were previously immobilized and released). Such behavior was not reported in its congener *L. alleni* (Franz 1977).

Head-first ingestion by piscivorous snakes allows spiny fins of prey fishes to fold down, reducing chances of injury to the snake during consumption, and is aided by long sharp teeth (Savitzky 1983). In contrast, caudal ingestion was argued to be advantageous for *L. alleni* as a predator of crayfish (Franz 1977; Godley 1980) because: (1) spines of the cephalothorax project forward, which could make ingestion difficult if they were oriented facing the snake; (2) appendages fold forward during consumption, allowing the smoothest possible process; and (3) chelae are rendered useless as a defense. These same advantages apply to the process of consumption by *L. rigida*.

Side attack and immobilization of the chelipeds is important to the predation process for both *L. alleni* and *L. rigida* because it avoids facial contact of the snake with the chelae of the crayfish, which could have been used against the predator in either frontal or caudal attack. *Liodytes alleni*, the closest relative of *L. rigida*, also uses coiling to restrain prey, but then consumes the prey without killing it (Franz 1977). Because chewing of the abdomen physiologically immobilized or killed a crayfish restrained by coils of *L. rigida*, which were then relaxed prior to consumption, we argue that only the first two reasons of Franz (1977) and Godley (1980) are important to *L. rigida* at the point of consumption. The chelae were of no use for prey defense after immobilization by chewing in *L. rigida*, and the snake relaxed its coils, so we believe caudal orientation became important mostly because the appendages folded forward and maximized ease of consumption. Ventral orientation of the crayfish against the upper jaw of the snake probably is most important for allowing the biting behaviors, but it also allows the snake to initiate ingestion by gripping the softest available tissues of the crayfish first. Once the prey is half ingested, the teeth of the snake encounter legs angling forward and outward, again allowing traction for the teeth of the snake and creating the most efficient process for consumption.

Regional variation may occur in prey-handling behavior of this snake. Consistent with our findings, Franz (1976, location unknown) and Myer (1987, in

southern Louisiana) also mentioned coiling and caudal ingestion by *L. rigida*, but not abdominal biting and ventral-up orientation of the prey prior to ingestion. Myer (1987) believed immobilization was achieved by constriction on the cephalothorax, which he observed to cause visceral fluids to exude from the crayfish in 85% of the feeding trials. We witnessed coiling, but not constriction and this effect. Our observations support coiling only as a prey containment behavior because no squeezing, consistent with constrictive killing, appeared to take place. Crayfish shells showed no signs of being crushed or misshapen and there was no evidence of internal fluids being extruded. This is consistent with findings by Waters (2000) for *L. rigida* from Florida and Louisiana. Coiling to immobilize crayfish prey, but without biting, also is exhibited by *L. alleni* (Franz 1977).

As we did not witness crushing during the biting process, we agree that the skulls and specialized teeth may provide greater ability to hold the hardened exoskeletons of intermolt crayfish (see Nakamura and Smith 1960; Rossman 1963). Further, these adaptations might be used during the chewing of the ventral abdomen, where pressure against the ventral nerve cord of the crayfish may hinder its ability to flick the tail and render it immobile. Escape and tail-flip responses, as well as the righting reflex, are inhibited by transection of the nerve at the level of the III-IV abdominal segment (González del Pliego et al. 1998).

The abdominal biting process deserves further study. During the process of biting, we observed cessation of the tail-flip escape response common to crayfishes, as well as loss of movement in swimmerets and legs. It is possible that orientation and biting affects the ventral nerve cord of the crayfish. We believe it is more likely, however, that the bite of the snake may deliver an unknown chemical that immobilizes its prey systemically (Rodríguez-Robles 1994; see also Waters 2000), which would explain the observation that the legs and swimmerets also became limp during the handling process. It is estimated that half of the numerous species of colubrid snakes may have some form of venom produced by Duvernoy's gland, but there are few studies of these glands and their potential venoms (Taub 1967, Hill and MacKessy 2000). Known studies were summarized by Junqueira-de-Azevedo et al. (2016).

Waters (2000) noted *L. rigida* to possess enlarged, ungrooved, posterior maxillary teeth. Duvernoy's gland, associated with these teeth in other snakes, secretes toxins that may affect only specific prey. *Liodytes rigida* is a good candidate for future study of specialized toxins.

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