The Feeding Process in *Conus victoriae*

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**Abstract** – The toxoglossan gastropod *Conus victoriae* preys on other prosobranch gastropods, and its mode of prey capture is shown to be behaviorally more complex and time-consuming than in congeners that feed on polychaetes and fishes. The major difference is that while the latter species capture prey by injecting venom with a single radular tooth, *C. victoriae* shot five teeth into a single prey snail, *Cantharus erythrostomus*, at intervals of 5–15 min in the feeding episode observed in an aquarium. The feeding process, over nearly one hour, was videotaped in its entirety from the first evidence of interest in the prey to its final engulfment by the rhynchodaeum. The use of repeated venom injections in capturing a single prey confirms a prediction based on recovery of multiple radular teeth from alimentary tracts and feces of other molluscivorous *Conus* species, and previous briefly reported observations.

**INTRODUCTION**

In the gastropod genus *Conus*, each radular tooth functions independently as a critical component of the delivery system for conotoxins, neurotoxic venoms that are injected into prey organisms and paralyze them prior to feeding. The morphology of *Conus* radular teeth varies among species according to their specialization on a major prey type, primarily polychaete annelids, other gastropods, or fishes (Lim, 1969; Kohn, Nishi & Pernet, 1999). Only a few prior studies describe details of the feeding process, primarily in piscivorous (Kohn, 1956; Johnson & Stablum, 1971) and vermivorous (Kohn & Hunter, 2001) species. Here I describe the behaviorally much more complex feeding process in a molluscivorous species for the first time and confirm earlier briefly published observations (Schoenberg, 1981; Yoshiba, 1983, 1987) that molluscivorous *Conus* inject more than one tooth into a single prey.

**MATERIALS AND METHODS**

*Conus victoriae* Reeve is rather narrowly distributed along west coast of Australia, from North West Cape northward to the western portion of the Northern Territory (Röckel et al., 1995). In that work we considered the southern form “*C. victoriae nodulosus* Sowerby II, 1866” (Shark Bay to Fremantle), to be a subspecies of *C. victoriae*. However, Kohn (1997) determined that it should be accorded species status (see also Nishi & Kohn, 1999).

Specimens of *Conus victoriae* collected in the vicinity of Dampier, Western Australia, were placed in an aquarium containing seawater at ambient temperature (19ºC) on a substrate of marine sand. Various gastropods of species that *C. victoriae* was observed to feed on in nature and that occurred in the same habitat (Kohn, 2003) were introduced, as were other gastropods...
present there. The feeding process was videotaped at night, when most Conus species are known to feed (Kohn, 1959; Leviten and Kohn, 1980), 9–10 August 2000.

RESULTS

Specimens of Trochus histrio Reeve and Cypraea moneta Linnaeus introduced into the aquarium elicited no response from several C. victoriae. These potential prey organisms appeared to sense the presence of the predator, as they crawled rapidly away from it.

The buccinid gastropod Cantharus erythrostomus (Reeve) elicited a feeding response from one specimen of C. victoriae, that measured 53 x 27 mm in shell length and maximum diameter and had been collected at Cleaverville on 5 August 2000. The complete sequence of feeding behavior was observed and videotaped during the night of 9–10 August, and is described below.

After about 1.5 min of active crawling toward the Cantharus, the Conus proboscis became visible as it extended from the rhynchodaeum toward the Cantharus (Figure 1). It made contact and 27 seconds later injected a radular tooth into the Cantharus foot (Figure 2), at 1:52 from the initiation of activity, then contracted and withdrew the proboscis again into the rhynchodaeum, leaving the tooth embedded in the prey. The Cantharus responded by rapidly withdrawing the foot into the shell, which toppled over. However, within 5 seconds the foot extended again, partially righting the shell to the position shown in Figure 3. The foot remained extended, apparently unable to contract and withdraw completely within the shell. At 2:35, the C. victoriae extended its proboscis again, and its siphon moved over the Cantharus shell simultaneously. The proboscis remained extended until 3:50, but did not sting. The proboscis withdrew, then extended again and delivered a radular tooth at 5:41, but this tooth appeared to land harmlessly on the Cantharus shell, missing the body. Again the proboscis withdrew briefly, but extended and injected a second tooth successfully one minute later (Figure 3). After initial withdrawal, the Cantharus recovered somewhat, righting itself and crawling slowly. It extended its siphon and was able to lift the visceral mass and shell above the foot. This activity continued for about 3 min, until 9:25, when the Cantharus fell over, again extending the foot in a vulnerable position.

At 10:40, the Conus proboscis extended again but withdrew without stinging a minute later. During this time the Cantharus siphon remained extended, as did its foot, and the animal appeared to attempt to move, but did not. At 12:06, the Conus proboscis extended again, but withdrew 18 sec. later, when the Cantharus succeeded in turning away. At 12:58, the Conus proboscis extended again briefly, but was now behind the Cantharus. Over the next two minutes, the Cantharus succeeded in lurching away from the Conus in a “drunken” fashion, but
made little progress (Figure 4). At 13:45, the Conus proboscis extended again, and at 14:20, the Conus began to follow the Cantharus. At 14:29, the proboscis withdrew but extended again 8 sec. later, and at this time the siphon also extended toward the Cantharus. The proboscis again withdrew, re-extending only after about 2 min, at 17:00. During this interval the Cantharus had extended its foot and siphon and apparently tried to crawl, but it made little progress and yawed from side to side. It also appeared to try to flip over, but succeeded only in turning on its side with the foot exposed.

At 22:02, the Conus injected a third radular tooth, and the Cantharus remained unmoving with the aperture up thereafter. At 35:42, the Conus proboscis extended intermittently again, and at 37:17 it delivered the fourth sting (Figure 5), following which it contracted its columellar muscle strongly, perhaps to expel fluid from the mantle cavity. After each of the first four stings, a cloud of venom rose in the water following release of the radular tooth from the proboscis. It is visible in the videotape, but not in the figures made from single frames. Because the venom remaining within the proboscis is under positive pressure from the proboscis musculature, it escapes into the water when the proboscis tip separates from the proximal end of the tooth. Some venom settled in the aperture of the Cantharus shell (Figure 5).

At 40:00, the Conus approached the Cantharus, still on its back, and extended the anterior part of its foot toward the victim. Forty seconds later, the Conus extended its rhynchodaeum for the first time, but it did not envelop the prey. The siphon also contacted and probed the foot of the Cantharus. After about 30 sec, it withdrew the rhynchodaeum and pulled the Cantharus toward it by contracting the anterior part of the foot. At 42:12, the proboscis re-extended, and at 43:29 it injected the fifth radular tooth (Figure 6). No venom appeared to rise in the water following this injection, suggesting that the Conus may have exhausted its supply, although some excess venom is visible in the aperture in Figure 6.

At 48:07, the rhynchodaeum extended again, withdrew briefly, and at 49:30 began the definitive enveloping of the Cantharus. Within a half minute, the prey’s head and foot were fully enveloped by the rhynchodaeum, now extended into the aperture (Figure 7). From this point, the rhynchodaeum probably continued to extend into the aperture around the Cantharus body, but this was not possible to observe. Both participants now appeared to remain motionless, and the videotaping was terminated at 52:37, nearly one hour after the initial evidence of interest by the Conus in its potential prey and approximately 12:30 a.m. local time. When examined again 6.5 hr later, the Conus had moved away from the now empty Cantharus shell and had left its operculum lying on the sand (Figure 8). Swallowing of the prey’s body was thus completed sometime during that 6.5-hr period.

The Conus victoriae was fixed two hours later and observed to be a female. It was later dissected to determine the progress of the prey approximately nine hours after the rhynchodaeum had apparently engulfed its body. The lip of the rhynchodaeum was still expanded to a width of about 4.2mm. No tooth was in place within the proboscis. The animal had certainly not used up all of its complete teeth, because the radula caecum or short arm of the radular sheath contained 20 fully formed teeth. The anterior portion of the esophagus was empty but expanded and flaccid, in contrast to the generally contracted and firm state in an animal that has not fed in some time. Dissection revealed that the Cantharus body was intact and occupied the posterior portion of the esophagus and the short stomach at the base of the U-shaped alimentary tract, both of which expanded greatly to accommodate it. The prey presumably remained in the position it was swallowed in, as the posterior part of its now twisted foot was oriented toward the intestine of the Conus and the posterior coil of its visceral mass,
The body of *Cantharus erythrostomus* within and extracted from the esophagus and stomach of *Conus victoriae*. 9. The esophagus and stomach *C. victoriae* dissected from the body. e, edge of the esophagus cut proximally, i.e. toward the pharynx; s, edge of the stomach cut distally, i.e. before it joins the intestine; piece of columella of *C. victoriae* shell. *C. erythrostomus* within the *C. victoriae* stomach: d, partially digested area of foot that had already been affected by digestive gland secretions; df, dorsum of foot; pf, posterior extremity of foot; vm, visceral mass. 10. *C. erythrostomus* body removed from the *C. victoriae* stomach. rt, two *C. victoriae* radular teeth embedded in the *C. erythrostomus* foot. 11. As Figure 10, but rotated to show the left side and additional structures. h, head; m, mantle edge; s, siphon; sf, sole of foot (the foot is twisted both dorso-ventrally and antero-posteriorly); t, tentacles. Other lettering as in Figure 10.
toward the anterior part of the esophagus (Figure 9). The only evidence of digestion was on that part of the dorsum of the foot that extended most posteriad, toward the entrance of the digestive gland ducts at the stomach-intestine junction. Here foot tissue had been dissolved to a depth of 0.8–1.2 mm, with loss of pigmented epithelium and some underlying muscle in the region (Figures 9–11). Removal of the prey body from the Conus digestive tract revealed two teeth remaining embedded in the foot (Figures 10, 11). Presumably the other three had been scraped off during passage of the prey through the tract.

Radular teeth removed from the radula caecum were 4.68 mm long, or 9% as long as the shell, and conformed with a prior morphometric analysis of C. victoriae teeth (Nishi and Kohn, 1999: Table 1, Fig. 2).

**DISCUSSION**

Prior observations of more than one of the predator’s own radular teeth in the intestine or feces of several molluscivorous species of Conus (Kohn, unpublished data), including two individuals of C. victoriae that each defecated three teeth (Kohn, 2003), suggested the hypothesis that in nature these species may inject more than one tubular, hypodermic tooth into the victim in each predation episode. Schoenberg (1981) appears to have been the first to observe multiple envenomation by a molluscivorous Conus in an aquarium. She reported that a C. textile injected 17 radular teeth into a Harpa amouretta in a single feeding episode, after the latter had autotomized the posterior portion of its foot. Yoshiha (1983) reported that both C. textile and C. bandanus injected several radular teeth into prey gastropods. Yoshiha (1987) kept a single C. textile, 72mm in shell length, in an aquarium for five years, during which it fed 190 times and injected an average of 3 teeth per episode.

In the videotaped observation of Conus victoriae preying on the buccinid gastropod Cantharus erythrostomus reported here, the feeding process required nearly an hour from the first evidence of interest by the predator to its extending the expanded rhynchodaeum into the prey’s shell to engulf its body. During this period, the C. victoriae attempted to inject six radular teeth into the prey, at intervals of 5–15 min. Five of these successfully impaled the prey’s foot, injected venom, and were the released from the C. victoriae proboscis tip. One tooth hit the shell harmlessly, was immediately released, and the Conus was able to move another tooth into position and inject it just one minute later. Following release of the first four successfully injected teeth from the proboscis, a cloud of venom escaped from the proboscis mouth due to the positive pressure exerted on its lumen by the circular and longitudinal muscles (Greene and Kohn, 1989). No excess venom was seen after the last tooth was injected, suggesting that all available venom may have been used. It is unlikely that all available radular teeth were used, because later dissection revealed that after six were used, 20 fully formed teeth remained in the radula caecum.

Although continuous observation ceased after the rhynchodaeum was inserted well into the aperture of the Cantharus shell, by 6.5 hr later, the C. victoriae had completed feeding and moved away from the prey’s empty shell. Because the ambient sea temperature was 18–19ºC during these observations in the austral winter, the feeding process of C. victoriae may not require as much time during warmer seasons, and may be slower than that of molluscivorous Conus species that occur in lower latitudes.

In vermivorous and piscivorous Conus species, a single radular tooth typically functions both as a hypodermic needle and harpoon, and after its injection the proboscis shortens to pull the
impaled and paralyzed prey into the rhynchodaeum (Kohn, 1998). One known case of feeding by a vernivore, C. imperialis preying on the amphinomid polychaete Eurythoe complanata, partially resembles that of C. victoriae in that the single injected tooth is released by the proboscis prior to engulfment (Kohn and Hunter, 2001).

ACKNOWLEDGEMENTS

I thank David Armstrong for providing research facilities at the School of Aquatic and Fisheries Sciences, University of Washington. I thank David Hurley for preparing the single video frames, Ritsuko Kurima for translating the abstracts by Yoshiba (1983, 1987), and an anonymous reviewer for calling attention to the note by Schoenberg (1981). I thank David Armstrong for providing research facilities at the School of Aquatic and Fisheries Sciences, University of Washington.

LITERATURE CITED


