Use of the vomeronasal system during predatory episodes by bull snakes (*Pituophis melanoleucus*)

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Four bull snakes *(Pituophis melanoleucus)* exhibited a higher rate of tongue flicking after constricting mice than after seeing and/or smelling mice for an equivalent length of time. Accordingly, it was concluded that the act of constriction potentiates chemosensory investigation mediated by the vomeronasal system. A comparably high rate of tongue flicking was also observed after the snakes swallowed a mouse. Since constriction and swallowing both involve grasping prey with the mouth but differ greatly in body postures, it is suggested that oral contact with prey (which stimulates the vomeronasal chemoreceptors) is the causative factor in the activation of chemosensory investigation.

Previous work in this laboratory has shown that rattlesnakes do not exhibit chemosensory interest in odors derived from rodent prey (as measured by rate of tongue flicking) until after they have struck and envenomated a rodent. Accordingly, it appears that striking, which is released by visual and thermal aspects of prey, is itself a necessary event for the activation of chemosensory searching (Chiszar & Radcliffe, 1976; Chiszar, Radcliffe, & Scudder, 1977; Chiszar, Radcliffe, & Smith, 1978). Bull snakes are constrictors that grasp and suffocate rodent prey prior to swallowing them. The purpose of the present study was to examine the extent to which constriction activates chemosensory searching in these snakes. Perhaps constriction plays a role in bull snake predation that is analogous to the role played by striking in rattlesnakes.

METHOD

Subjects and Maintenance Conditions

Four bull snakes *(Pituophis melanoleucus)* captured in Boulder County, Colorado, were subjects. All animals were at least 3 years old and had been in captivity for at least 2 months prior to this experiment. All snakes were kept in individual glass cages (50 x 27.5 x 30 cm) at 26°C-28°C during the dark period. Each animal was fed to satiation (three to four live adult mice) 1 week before the present observations.

Procedure

Just prior to a regularly scheduled feeding session, each snake was observed for 5 min, during which all tongue flicks (TFs) were counted with the aid of a hand-held counter. This was regarded as an undisturbed baseline.

The bull snakes required a mean of 126 sec (SEM = 20) to constrict a mouse. After a snake loosened its coils, the mouse was gently removed, and all TFs during the next 5 min were recorded. However, these TFs cannot be considered to reflect only the effect of constriction; perhaps a snake would emit just as many TFs if it had simply been exposed to a mouse for an equivalent length of time with no opportunity to constrict it. Accordingly, a control condition was also included in the experiment. A clear plastic box (10 x 10 x 10 cm with 10 perforations in each surface) containing a live mouse was placed into each snake's cage for 126 sec and then removed. All TFs emitted during the next 5 min were recorded. Two snakes received the control condition before the constriction condition, and two snakes experienced these conditions in the reverse order.

Finally, all snakes were allowed to swallow their mice after the above observations were made, and all TFs were recorded during the 5 min after the completion of swallowing. This condition was included for two reasons. First, it was necessary to ensure that feeding motivation was not disrupted as a consequence of the disturbances incorporated into the control and constriction conditions. We assume that the occurrence of swallowing is adequate demonstration of the continuity of predatory motivation throughout the experimental session. In fact, all snakes swallowed their mice. Second, it is our hypothesis that constriction will induce a high TF rate partially because the mouse is held in the snake's mouth (and, therefore, stimulates the vomeronasal organs) during this period. Identical stimulation should occur during ingestion and, therefore, an elevation of TF rate above the control level should be seen after the snake swallows a mouse. It should be noted that swallowing was a longer process than constriction (mean time required to swallow = 223 sec, SEM = 49). Hence, a proper control would

Table 1
Mean Number of Tongue Flicks (TFs) Emitted by
Bull Snakes During Four Conditions

		Condition		
TFs	Baseline	Control	After Constric-tion	After Swallow-ing
During 1st min	3	32(44)	69	67
Overall (5 min)	31	124(161)	275	252

Note—Numbers in parentheses are results of a second control, run after the completion of the experiment. In the second control condition, a live mouse was suspended by forceps into the snakes' cages for 3 sec; TFs were recorded for the next 5 min. Data from the two control conditions do not differ significantly, indicating that a 3-sec exposure to a mouse activates as much lingual air sampling as a 126-sec exposure.

involve a longer exposure to the plastic box (containing a mouse) than was used in this study. The authors suspect, however, that increasing the control exposure would not elevate TF rate beyond the level obtained with the present 126-sec condition.

RESULTS

Table 1 presents mean number of TFs seen in each of the four conditions. The first row shows means for the first 1 min of each of the conditions; the second row shows means over all 5 min of each condition. Repeated-measures ANOVAs revealed significant effects of conditions for both rows of Table 1 [$Fs(3,9) = 9.55$ and 5.13, respectively; $ps < .025$]. Multiple comparisons applied to both rows of Table 1 showed that baseline differed from control, that constriction did not differ from swallowing, and that control differed from both constriction and swallowing.

DISCUSSION

When rodent prey were offered to our bull snakes, attack occurred immediately and very few TFs were seen. Accordingly, we conclude that well-acclimated captive bull snakes under 1 week of food deprivation do not rely upon their vomeronasal chemoreceptors during initial phases of predatory episodes. Attack appears to be released by visual cues arising from live mice. Yet, if attack was prevented, as in the control condition, then an elevation of TF rate occurred as the snakes investigated the plastic box. Hence, visual and/or airborne chemical cues can activate the vomeronasal system. Perhaps this represents the initiation of chemosensory foraging.

After constriction and after swallowing, large elevation in TF rate were observed. Since the mean numbers of TFs under these conditions were higher than those seen in the control condition, it is here suggested that contact between prey and the vomero-nasal receptors (which occurs during both constriction and swallowing) caused these differences (see below).

Since the dead rodent ordinarily remains in the snake's coils, no searching or trailing behavior is required for the snake to locate its prey after constriction. However, it may be that chemical cues are required for initiation of swallowing (Duvall, Chiszar, Trupiano, & Radcliffe, 1978; Duvall, Scudder, & Chiszar, in press). For this reason it may be adaptive for bull snakes to exhibit heightened interest in chemical cues after constricting a rodent, even though trailing behavior is not necessary.

The elevation in TF rate after swallowing may represent an adaptation that ensures that the snake will take advantage of additional prey remaining in the vicinity. It has often been observed that a constricting snake may be induced to swallow several dead prey after it has constricted and swallowed one that was alive at the start of the feeding episode. Heightened interest in chemical cues consequent to constricting and swallowing may be the basis for this phenomenon.

It appears that constriction may function in bull snake predation much like striking functions in rattlesnake predation. In both cases, the animal's special prey-subduing response releases a high level of chemosensory investigation mediated by the vomeronasal system. Yet, it must be recognized that constriction is a complex action involving oral stimulation as well as proprioception arising from the body musculature (Greene, 1977; Greene & Burghardt, 1978). It will be interesting to determine the contribution of these respective components to the activation of lingual air sampling. Because swallowing and constriction generate equally high TF rates while differing greatly in muscular involvement (and, presumably, in proprio-ceptive consequences), we hypothesize that oral stimulation (common to the two behaviors) is the major determinant of the increase in TF rate.

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