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### The Strike Behavior of a Congenitally Blind Rattlesnake

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The view that pit vipers denied visual cues depend instead upon thermal cues to launch strikes dates to early experimental work (Noble and Schmidt, 1937; Bullock and Cowles, 1952). What is not known is how specific and accurate this predatory strike might be in the absence of visual information. In rattlesnakes,

the primary sensory organs employed during the strike behavior are the eyes and heat sensitive facial pits (Dullemeijer, 1961; de Cock Buning et al., 1981a, b). Information from the facial pit arrives in the medulla oblongata via the trigeminal nerve and in turn is relayed via the reticularis caloris nucleus to the optic tectum (Schroeder and Loop, 1976; Terashima and Goris, 1977; Gruberg et al., 1979; Newman et al., 1980; Meszler et al., 1981; Schroeder, 1981), which also receives projections from the eye. Bimodal neurons in the tectum thus receive input from the eyes and facial pits, suggesting that visual and thermal sensory information are brought together and processed here in the tectum (Newman and Hartline, 1981). Ascending pathways from the tectum further convey infrared and visual information to the forebrain (Berson and Hartline, 1988). This organization could be functionally important in rattlesnakes that hunt nocturnally and in burrows where visual information is reduced or absent. Here the snake might switch to thermal information; just such conditions are often proposed as those first favoring the evolution of the heat sensitive pits in rodent-eating vipers (e.g., Klauber, 1956).

A growing literature on the general features of rattlesnake predatory behavior (Dullemeijer, 1961; Naulleau, 1965; Kardong, 1975, 1982, 1986b; Estep et al., 1981; Chiszar and Radcliffe, 1976; Chiszar et al., 1982; Duvall et al., 1980; Gillingham and Clark, 1981; Scudder et al., 1983), and an extensive study on the northern Pacific rattlesnake in particular (Kardong, 1986a) provide a baseline ethogram of the strike and the qualitative role played by proximate factors. The laboratory birth of a young rattlesnake with no vestiges of eyes provided the opportunity to examine the role eyes might play in eliciting and controlling the strike behavior. Further, by artificially blocking the facial pits in this same individual so as to deny it the use of this sensory organ as well, we also gained information regarding the contribution the heat-sensitive pit makes to the strike. The purpose of this study was to test the strike behavior of the blind individual and to compare its performance quantitatively with that of normal rattlesnakes.

The mother of this sightless individual, a northern Pacific rattlesnake (*Crotalus viridis oreganus*), was collected in San Luis Obispo County, California. She was maintained in a warm room (24-27 C) with 12:12 L:D cycle; three months later, four young were born, one blind, the subject of this study, and 3 normal. When small, this blind snake was fed hairless live pups ("pink" mice); when larger it was fed 10-20 g mice, about half of which were dead (frozen, thawed), and about half alive (struck and eaten). Feeding was on an irregular basis until the blind snake was about 18 months old at which time it had reached approximately 48 cm snout-vent length (SVL). Formal feeding trials reported here began at this age (size). When hand-held and examined under a dissecting microscope, we could confirm the absence of any vestige of eyes. In their place, the location was instead covered by integument bearing numerous small scales that appeared to be equivalent to scales covering the rest of the head. Other external facial features were normal including presence of paired nostrils and paired facial pits.

The blind snake was housed in a glass terrarium

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TABLE 1. Comparison of predatory performance between normal rattlesnakes and the blind rattlesnake with its facial pits exposed or covered.

	Normal rattlesnakes	Blind rattlesnake	
		Pits exposed	Pits covered
Strike frequency (%) (strikes/trials)	98.7 (150/152)	98.0 (48/49)	26.7 (4/15)
Time-to-death (sec) (N)	288.2 (150) (range 5.0-5700, SD $\pm$ 907.1)	242.6 (40) (range 113.1-4511.1, SD $\pm$ 715)	423.3 (4) (range 44.0-922.0, SD = 366.3)
Released (%) (released/strikes)	88.7% (133/150)	92.5% (37/40)	100% (4/4)
Region struck (%)			
Anterior (N)	79.7 (114)	70.0 (28)	(1)
Mid-section (N)	16.8 (24)	15.0 (6)	(0)
Posterior (N)	3.5 (5)	15.0 (6)	(3)

approximately 50 × 50 × 90 cm and kept in a warm room (22-30 C) maintained at L:D 12:12 year round under standard safety conditions (Gans and Taub, 1964). The feeding trials were also performed while this individual was in this cage and followed methods detailed elsewhere (Kardong, 1986a). Prior (> 1 hr) to presentation of a preweighed "white" mouse (Swiss/Webster strain), the wire cage top was replaced with a sheet of clear plexiglass with two holes (6 cm diam.) cut at opposite ends. Opaque plastic tubes (6 cm diam., 30 cm long) were placed through and suspended from these holes into the cage, but ended about 7 cm above the bottom of the cage. Several sheets of newspaper were taped around the outside of the cage. When introduced, mice were dropped down these tubes at the end of the cage farthest from the snake's head. After introduction of a mouse, the investigator left the room and monitored (and videotaped) the ensuing events via a remote video camera held by a tripod directly above the cage. Such trials were run approximately once per month but no more frequently than every 14 days. In all, 49 feeding trials were performed to determine the strike frequency (number of strikes per presentations). In 40 of these trials additional performance variables of the strike were scored, including the site struck on the mouse, whether the mouse was held or released, and envenomation success as measured by the time-to-death (absolute time from strike to last movement by the prey). Kardong (1986a) presents more detailed discussion of each variable. In fifteen separate feeding trials, a small ball of Styrofoam® was fitted into each facial pit and then additionally covered with thermally opaque tape (standard black electrician's tape) to deny this sightless individual use of the sensory facial pits. The blind and now pit-covered rattlesnake was then tested again in similar feeding trials. Its strike behavior was compared to "normal" (sighted, pits uncovered) rattlesnakes of the same species run in similar feeding trials, 152 trials for strike frequency, and 143 trials while scoring other variables. Thirty-three normal rattlesnakes were used to produce these frequency and variable data; no single individual contributed more than 5% of the trials. These 33 were part of the database in earlier studies and used rattlesnakes of the same size class as the blind rattlesnake (Kardong, 1986a). Tests for statistical significance in these comparisons used analysis of variance (ANOVA), in par-

ticular the general least squares (GLM) algorithm part of the SAS79 package (Helwig and Council, 1979).

As summarized in Table 1, the blind rattlesnake struck live mice frequently but this frequency fell when the facial pit was covered. The blind snake also tended to deliver its strikes to the anterior end of the mouse, producing an average time-to-death following the strike of 242.6 sec. Compared to normal sighted rattlesnakes, there was no significant difference in this time-to-death ( $P > 0.7$ ), nor in the propensity to strike the anterior region of the mouse ( $P > 0.2$ ). As with sighted rattlesnakes, the mice struck by the blind snake were commonly released after the strike (88.5% of the trials). On those few occasions when mice were held, they were generally small (<15 g). However, unlike normal rattlesnakes (Kardong, 1986a), envenomation by the blind individual led to no significant differences ( $P > 0.5$ ) in time-to-death between mice released compared to those held.

Without benefit of visual information, the blind snake was statistically similar to normal rattlesnakes in striking frequency, targeting of the anterior end of the prey, and inclination to release prey following the strike. (Only in time-to-death following strike-and-hold did the blind snake differ from normal snakes, perhaps due to differences in venom composition between California and Washington *Crotalus viridis oregonus*). However, during trials when pits were covered in the sightless individual, strike frequency decreased to almost one-fourth that of normal rattlesnakes.

The fact that this sightless snake struck and usually made contact with the prey is consistent with the view (Dullemeijer, 1961) that senses other than or in addition to vision play a large role in eliciting and directing the strike. When pits were covered, the sightless snake was less able to initiate a strike. This implies that the facial pits which monitor thermal information exclusively (de Cock Buning et al., 1981a, b) are, along with the eyes, primary sensory receptors in the strike. Certainly snakes possess other possible sensory systems, including chemoreceptors such as the vomeronasal organ and nasal passage (Chiszar and Radcliffe, 1976; Graves and Duvall, 1985), mechanoreceptors in the skin (Proske, 1969), and possible accessory thermal organs (Hensel, 1973; Chiszar et al., 1986). However, the inability or disinclination to strike when the eyes and facial pits were covered implies that

these remaining sensory organs are collectively insufficient to compensate equally for the absence of visual and thermal information. Conversely, this implies that the eyes and facial pits, as many have argued (e.g., de Cock Buning, 1983a, b), are the primary sensory systems, at least for the rattlesnake strike. The ability of the sightless snake to produce near-normal strikes based largely upon thermal information gathered via the facial pit supports the idea that the facial pits can allow the snake to strike prey effectively when visual information is unavailable. The extent to which learning during the first 18 months of life contributed to this snake's performance is unknown.

Earlier studies noted that "blind" rattlesnakes could still strike (Dullemeijer, 1961). Our trials show that this sightless individual not only made successful contact with prey but accurately targeted the strikes to the more vulnerable (Kardong, 1986a) anterior region. This ability to aim the strike at specific regions supports the suggestion (Kardong, 1986a) that rattlesnakes use the thermal image presented by the mouse to form a differentiated regional image of the prey. Results of the present study also support the suggestion based upon nervous system circuitry that the infrared system is used not only in orientation but also in discrimination of form (Berson and Hartline, 1988).

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### Phalangeal Formulae in the Turtle Genera *Chrysemys*, *Pseudemys*, and *Trachemys* (Testudines: Emydidae)

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The number of phalanges in the fifth toe of the hind foot has been repeatedly mentioned in the literature as a character that can be used to distinguish species groups of emydine turtles. Several authors have used this character to define genera, subgenera, or species in the *Chrysemys-Pseudemys-Trachemys* lineage. McDowell (1964) cited the presence of three phalanges in the fifth toe as diagnostic for *Trachemys*, and four for *Pseudemys*. Weaver and Rose (1967) gave fifth toe phalangeal counts for five species of *Chrysemys* (sensu lato). They reported that *C. concinna* has three; *C. floridana* two; *C. scripta* two or three; *C. picta* two; and *C. terrapin* (= *C. decussata*, sensu Seidel, 1988) two. On the basis of their phalangeal counts they refuted McDowell's observations of three and four fifth-toe phalanges in *Trachemys* and *Pseudemys*, respectively. Fahy (1980) used fifth-toe phalangeal counts to distinguish *Pseudemys concinna* (3 phalanges) from *P. floridana* (with 2). Seidel and Smith (1986) used the character "never more than three phalanges on fifth toe" to distinguish *Trachemys* and *Chrysemys* from *Pseudemys*. McDowell (1964), and Seidel and Smith (1986) included all elongate toe bones in their counts. Weaver and Rose (1967) and Fahy (1980) did not include the proximal bone in each toe (metatarsals), hence the consistent discrepancy in counts. We used the latter method in making the phalangeal counts reported here (see Fahy, 1980, Fig. 7).

Most published phalangeal counts are based on relatively small series of skeletal specimens. There has been no assessment of ontogenetic, individual, or geographic variation of phalangeal numbers based on

large numbers of specimens. We examined a total of 316 specimens of five species, representing *Trachemys*, *Chrysemys*, and both subgenera (*Pseudemys* and *Ptychemys*) of *Pseudemys*. Most of the specimens were X-rayed, and phalangeal counts made directly from the radiographic negatives. In a series of adult *T. scripta* from Perry County, Alabama, phalangeal counts were made by dissection as the specimens were being skeletonized. The phalangeal counts are expressed as a formula giving the number of phalanges in each toe, counted from the first toe to the fifth. Counts were made on both hind feet, resulting in a total of 519 observations. Bilaterally asymmetrical phalangeal numbers were observed in 9 individuals (2.8%). Variation in fifth toe phalangeal number occurs only in the hind foot. The front foot phalangeal formulae of all specimens examined was 2-3-3-3-2 (502 observations). Results are presented in Table 1.

To assess ontogenetic variation a sample of 209 hatchling *T. scripta* from Perry County, Alabama, was compared with 29 adult females from the same population. The adult phalangeal formula was invariably 2-3-3-3-2 (N = 58). The 2-3-3-3-2 formula was found in 91% of the hatchlings (N = 285), and 2-3-3-3-1 in 9% (N = 28). Weaver and Rose (1967) suggested that delayed ossification of the terminal phalanx in some individuals could account for this variation. We cleared and stained one hind foot from each of four hatchlings with the 2-3-3-3-1 phalangeal formula. In two specimens (CM 81398, CM 81472) the terminal phalanx was visible but tiny and poorly ossified. In two others (CM 81381, CM 81468) the terminal phalanx was fused with the penultimate phalanx, giving the appearance in the X-ray radiographs of a single bone. A small sample of adult *T. scripta* from Oklahoma was examined to detect possible geographic variation in the species, and was found to have 100% 2-3-3-3-2 formulae (N = 9). Our results indicate the only ontogenetic component of variation in phalangeal formula, at least in *Trachemys scripta*, results from delayed ossification of the terminal phalanx. Otherwise the 2-3-3-3-2 formula is invariant in *T. scripta*. As 2-3-3-3-3 is the primitive phalangeal formula in emydine turtles (Zug, 1971), occurrence of the derived 2-3-3-3-2 formula in *Trachemys* is consistent with the phylogeny for *Trachemys* and related genera proposed by Seidel and Jackson (1990).

To assess geographic variation we examined 46 adult specimens of *Chrysemys picta* from Maryland, Tennessee, Minnesota, and Colorado (Table 1). These populations represent three of the four recognized subspecies of *C. picta*. The phalangeal formula in this species is highly variable, both within and between populations. The 2-3-3-3-2 formula was found in 52%-83% of individuals in the four populations, and the 2-3-3-3-3 formula in 17%-48% (total N = 88). Thus, the statement of Weaver and Rose (1967) that *Chrysemys* always has two fifth-toe phalanges is incorrect, as is McDowell's (1964) implication (followed by Seidel and Smith, 1986) that *Chrysemys* and *Trachemys* have the same phalangeal formula.

We examined small samples of three species in the genus *Pseudemys*: *P. (Pseudemys) concinna*, *P. (Ptychemys) alabamensis*, and *P. (Ptychemys) rubriventris*. The *P. alabamensis* (N = 8) and *P. rubriventris* (N = 11) all had formulae of 2-3-3-3-2. This observation contra-