

# Predatory Strike Behavior of the Rattlesnake, *Crotalus viridis oreganus*

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The purpose of this study was to identify how various proximate factors of the rapid rattlesnake strike affect predatory behavior and thus in turn affect the resulting envenomation and capture of the prey. The results indicate that the larger the snake, the more likely it was to hold, rather than quickly release, prey. Snakes possessed a ready reserve of venom sufficient to envenomate up to four mice in close succession without loss of killing effectiveness. The head/thorax site on mice was the region most frequently struck and also the site of venom injection that led to the fastest prey death. Small mice were more often retained in the jaws rather than released and occasionally evoked no envenomation at all. A retaliatory bite to the head or body of an attacking snake encouraged a quick release of the prey. Retention of mice following the strike enhanced the severity of envenomation. Poor envenomation on the first strike led to a second or even a third follow-up strike. Unlike defensive strikes, offensive (predatory) strikes resulted in no "dry" bites. This suggests that jaw mechanics may be disrupted during defensive strikes or that the snake can actually control its expenditure of venom. Artificial reduction of venom reserves by "milking" the venom glands resulted in poor envenomation but stimulated no change in the basic hold/release behavior.

The predatory strike of the rattlesnake includes a wide repertoire of behavioral options. The rattlesnake may hold or release the prey, strike the prey at different sites along its body, strike the same prey once or several times, and release variable quantities of venom. In turn, these options may be affected by the size of the snake, the reaction of the prey, and the number of prey already struck. Certainly the feeding behavior includes other options (Klauber, 1956) and is subject to modification by other factors (Chiszar, Radcliffe, O'Connell, & Smith, 1981; Chiszar, Radcliffe, & Scudder, 1977; Gillingham & Clark, 1981). However, the results of previous studies (Kardong, 1982; Naulleau, 1965) suggest that these factors are the most likely proximate influences on the predatory strike of the rattlesnake.

Thus, the immediate intent of this study was to experimentally isolate, within reasonable boundaries, several of these likely interacting variables to test their effects on the predatory strike and envenomation success of the Northern Pacific rattlesnake, *Crotalus viridis oreganus*.

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## Method

### General Procedures

All snakes used were Northern Pacific rattlesnakes, *C. v. oreganus* collected from sites in eastern counties (Grant and Whitman) of the state of Washington. All were housed individually in glass terraria approximately 50 × 50 × 90 cm. The room in which snakes were housed and experimental trials were conducted was kept warm year round (22–30 °C) and maintained on a 12:12 hr light/dark cycle. A newly caught snake was considered acclimated when it began striking and swallowing live mice presented. Access to the room was limited to authorized personnel (four persons) familiar with the experiments and safety procedures (Gans & Taub, 1964).

### Statistical Tests

Two tests for statistical significance were used, analysis of variance (ANOVA) and chi-square. All data from feeding bouts were analyzed by ANOVA, in particular the general least squares (GLM) algorithm part of the SAS79 package (Helwig & Council, 1979). This computer package is especially good for its strength in handling unbalanced design. The technique starts by including all variables in the model; then by matrix transformation, the effects of each variable are statistically eliminated in a stepwise fashion. Thus, each variable was separately isolated and tested for its single effects on snake behavior.

Although the same snake was used in several trials, no single snake contributed to more than 10% of the total observations. Most contributed to about 5%. Further, by performing a snake-within-size operation (SAS, PROC GLM), differences between individual strikes were statistically removed. Reported in Tables 1–4, then, are within-snakes analyses based on incomplete, split-block design.

## Experiment 1: Feeding Trials

### Feeding Bouts

Each snake was entered in a set of up to four "feeding trials." Each feeding trial entailed presentation of a Swiss-Webster mouse, observation of the ensuing behavior, timing the envenomation effects, and allowing the snake to swallow the dispatched mouse. The second, third, and fourth feeding trials with the same snake were carried out in the same fashion, and the snake was allowed to swallow each dispatched mouse in succession. Mice used in each set of feeding trials were presented in close succession, usually all in less than 3 hr but never totaling more than four mice on the same day. If during a feeding trial the snake failed to strike the mouse within 10 min, that mouse was removed and no more trials were performed. At least 7 days separated the sets of feeding trials.

The lid of the cage was lifted, and a live preweighed mouse was introduced opposite the snake. The investigator was not hidden at this moment, although care was taken not to move quickly or to alarm the snake. If the snake withdrew from the mouse, began rattling, or drew itself up into coils just before striking, the strike was considered a "defensive strike" (*sensu* Minton, 1969), and the data were not included in this study. Only data from "offensive strikes" were included, namely, strikes preceded by the snake's approaching the mouse, not rattling, and forming its neck into S-shaped curves (*cf.* Kardong, 1975). Five rattlesnakes were filmed before photoflood lights with high-speed camera (after Kardong, 1975). By checking these high-speed films of strikes against direct observation, I confirmed that visual observation was sufficiently accurate to reliably score the snake strike and mouse reaction.

### Variables

Many factors could conceivably contribute to variation in strike behavior and envenomation success. However, in this study, eight variables were examined and scored during each feeding trial. From previous qualitative (Kardong, 1975) and quantitative (Kardong, 1982) observations, the following variables seemed the most promising.

**Snake size.** Initially, three size classes of snakes were designated as measured by snout-to-vent lengths, small (less than 30 cm), medium (30–70 cm), and large (more than 70 cm). In each size class, there were, respectively, 12, 28, and 14 individuals. Unless a snake is born in captivity, age is difficult to determine. However, from records of captive-raised *C. v. oreganus* and from mark-and-recapture records in the field (Kardong, 1974), these three size classes corresponded roughly to first year–18 months, 18 months–3 years, and over 3 years of age.

**Sequence of presentation.** During a set of feeding trials, up to four mice were presented separately. The order presented, first through fourth, was recorded. The mass of the mouse presented in each trial varied and was randomized. Statistical tests confirmed that prey size presented and prey sequence did not covary.

**Site struck.** The length of the mouse was arbitrarily divided into three regions, site 1 (the head and shoulders/thorax), site 2 (middle—region from the posterior edge of the thorax through the pelvic girdles), and site 3 (rump—region behind the pelvic girdle). On each strike, the site penetrated by both fangs was recorded. If fangs fell in different, adjacent sites, the trial was not included in the statistical analysis. Confirmation from the independently filmed high-speed movies (see above) gave me confidence that direct visual scoring during the trials was accurate. These were cross-checked by observing envenomation response of tissue (reddening, fang puncture sites, etc.)

before the struck mouse was swallowed. Only in a few trials was there reasonable doubt about the site struck. These trials were, of course, not included.

**Mouse weight.** Mice used ranged in weight from 4 to 41 g as measured to the nearest 0.1 g. This represents a weight range comparable to mouse sizes likely encountered by rattlesnakes in the wild (Slater, 1941).

Swiss-Webster "white" mice were used as prey in all experiments. This strain of mouse proved to be easily raised to desired sizes. It is a readily available, conventional mouse whose use serves as a way of standardizing results of strike behavior and envenomation dose effects.

**Bite.** Occasionally, a struck mouse turned and with its incisor teeth bit the attacking snake while the snake held the mouse in its jaws. Such successful retaliation by the mouse was also recorded.

**Hold/release behavior.** Usually, a snake immediately (1–2 s) released a struck mouse. However, on occasion a snake would continue to grasp the mouse in its jaws for a longer period of time. This could last several minutes. This aspect of the strike behavior was recorded at each feeding trial to determine whether the snake released (within 1–2 s) or held (longer than 2 s) the struck prey.

**Number of strikes.** In most feeding trials, the snake struck a mouse once and then let the injected venom kill the prey before searching for and swallowing the dispatched mouse. Despite repeated opportunities to strike again as the envenomated mouse dashed about the cage, the snake usually did not do so (Chiszar, 1978, 1981a, 1981b, 1982). In fact, in most trials, the snake did not strike offensively again until it had swallowed the prey, a behavior noted in other rattlesnake species as well (Chiszar & Radcliffe, 1976). However, variation was noted in this single strike behavior, too. During some feeding trials, a rattlesnake struck once and then quickly (within 30 s) struck again at the same mouse. The number of strikes received by a single mouse was recorded.

**Envenomation.** A hand-held stopwatch was used to record the length of time-to-death of the mouse (elapsed time in seconds from strike to last muscular twitch or motion). Others (Minton, 1969) have used "knockdown time" (time until the mouse seemed incapable of further voluntary escape movements) or "death time" (elapsed time to cessation of respiration) to express effects of envenomation. Because the rattlesnake must usually relocate the envenomated mouse to swallow its dispatched meal, "knockdown time" is perhaps the measure of strike effectiveness most meaningful from the standpoint of the snake. However, there is some degree of subjectivity in deciding the point at which a mouse is judged to be incapable of voluntary escape. Thus, in the present study, time-to-death was used, because it could be more objectively scored by the observer. This measure of prey death was not intended to be a venom assay. Rather, it was intended to express the effectiveness of the strike, namely, the chemical effects of the venom plus any mechanical effects of fang puncture. Time-to-death thus expresses the sum of biologically significant factors for the snake that determine the success of the strike in killing the prey.

From the time-to-death, a "death rate" was computed for each envenomated mouse by dividing the total time-to-death by the mass of the mouse. Clinical studies have shown that venom effects are affected, inversely, by a human patient's weight (Reid, 1970). Thus, the calculated death rate (in seconds/gram) seems a reasonable way to make comparisons of envenomation effects from mice of varying masses.

### Technique of Venom Extraction

Rattlesnakes, different from those used in feeding trials, were subjected to extraction of venom. Each snake was removed from its

cage with a long snake hook, placed on a flat counter top, and pinned behind the head with a long aluminum rod. The snake was then grasped behind the head with one hand, and the body was held with the other hand. The jaws of the snake were forced over the edge of a small glass funnel covered with a taut membrane (Parafilm). Usually this prompted the snake to erect its fangs, penetrate the membrane, and release venom. No electrical stimulator or manual squeezing of the venom glands was used to promote ejection of venom. This extracted venom drained to the bottom of the funnel where it was collected in a small test tube. At this point, the yield of liquid venom gathered from each snake was visually estimated, and the health of the snake was evaluated. Thereafter distilled, deionized water was often used to wash venom from the sides of the funnel into the collecting test tube at the bottom. The venom was then immediately frozen, lyophilized, and weighed. The snake was then returned to its cage.

### *Dose Effects of Venom*

Lyophilized rattlesnake venom was reconstituted in 0.9% physiological saline in a total volume of 0.25 ml. By means of a hypodermic syringe, it was then injected into the tail vein of Swiss-Webster mice weighing between 18 and 24 g. The mice were divided into three groups of 24 mice each. Mice in each group received graded doses of pooled venom extracted from snakes belonging to one of the three size classes of rattlesnakes. Thus, for each size class of snake, it was possible to draw a dose-effect curve that expressed the percentage of mortality at various levels of venom administration (Litchfield & Wilcoxon, 1949). These effective dose (ED) levels were based on 24-hr mortality. Experiments on groups of 24 mice were repeated three times for each snake size class, and the results were averaged.

### *Artificial Envenomation*

Lyophilized venom reconstituted as above was injected into one of two sites in mice, namely, site 1 or site 3 (see variables above). An attempt was made to insert the needle into each site as deeply as the fang of a rattlesnake might penetrate, although this was, of course, only roughly possible. Similarly, the injection in each site was placed in approximately the same spot within the site each time. Doses of 1.375 mg (about 45 × the iv dose that causes 50% mortality [LD<sub>50</sub>]) per each mouse were injected with a glass tuberculin syringe, 25-ga. needle. Mice, all Swiss-Webster, weighed between 18.7 and 21.2 g. Control injections of 0.25 ml of physiological saline were also given. No mice died from these control injections. The time-to-death for mice artificially envenomated was recorded, along with the site of administration of the injection. Although the length of time varied, all mice so injected with venom eventually died.

### *Experiment 2: Venom-Extracted Snakes*

Some snakes involved in the feeding trials were removed, and their venom was extracted (see Technique of Venom Extraction above). Within 48 hr of this extraction, these snakes were continued in the feeding trials. The same variables and feeding behavior were subsequently recorded. The purpose of these procedures was to determine whether extraction of venom would alter strike behavior or envenomation success.

## Results

### *Experiment 1: Feeding Trials*

Basically, each snake was presented with up to four mice in succession. It was allowed to strike and swallow each mouse before being offered the next. The effects of eight variables were analyzed with the following results.

#### *Snake Size*

Early in the study, I discovered that snakes in the small size class responded differently to mice presented in the feeding trials or at least responded in such a way as to make it difficult to gather results statistically comparable with results for members of the other two size classes. Snakes of the small size class frequently lost interest in additional mice once the first was struck and swallowed. Further, they showed themselves to be easily intimidated by adult mice and quickly assumed a defensive posture. This was especially true of the shortest snakes (newborn) of the small size class. These same shortest snakes often attempted to swallow a dispatched large adult mouse, but none were successful in working their jaws beyond more than the head of the prey. Thus, feeding trials and statistical comparisons are shown for snakes of only the medium and large size classes.

For snakes of any size, the predominant behavior (83% of the time) was for quick release of the prey following the strike. But, on those occasions (17% of the time) when the prey was retained in the jaws, large snakes were more prone to hold the mouse than were medium-sized snakes (27% and 10% of the time, respectively, large and medium; see Table 1).

Medium-sized snakes were more likely to strike site 1 on the mouse than were large snakes. As shown in Table 2, site 1 (head/thorax) is struck 75% of the time by medium snakes but only 67% of the time by large snakes ( $p < .0056$ ). For the remainder of the time, strikes hit site 2 (middle) or site 3 (rump) of the mouse.

Table 3 shows that mice struck by large snakes on average died more quickly ( $M = 219.4$  s) than did mice struck by medium snakes ( $M = 232.2$  s). However, no significant difference in death rate was found between mice struck by large and those struck by medium snakes.

No differences were evident in strike behavior between male and female snakes.

#### *Sequence Presented*

Sequence had no effect on the time-to-death or on death rate of mice (Table 3). Thus, mice presented first in a feeding trial died, on average, just as quickly as mice presented later.

Sequence had no significant effect on the site struck on the mouse. The distribution of strikes to head/thorax (site 1), middle (site 2), and rump (site 3) remained essentially the same for mice struck first in a feeding bout and those struck later.

Table 1  
Strike Behavior Showing Number of Mice Released or Held for Variables of Snake Size, Sequence, and Site Struck

Mouse condition	Snake size				Sequence				Site							
	Large		Medium		1	2	3	4	1		2		3			
	No.	%	No.	%	No.	No.	No.	No.	No.	%	No.	%	No.	%		
Released	248	73	386	90	634	83	358	148	76	52	449		151		34	
Held	92	27	42	10	134	17	32	40	41	21	100		24		10	
Total							390	188	117	73	549	71	175	23	44	6

Dependent variable: Hold/release behavior

Source	df	SS	F	p
Snake size	1	0.7837	8.73	.0003
Sequence of presentation	3	4.5127	16.76	.0001
Site struck	2	0.7174	4.00	.0188
Mouse weight	4	4.5943	12.80	.0001
Bite by mouse	1	0.0792	0.88	.3478

Note. Site 1 = head/thorax; site 2 = middle; site 3 = rump.

There were only three effects of sequence on feeding behavior. First, mice struck first in feeding trials were more likely to be released than mice struck later (Table 1). Second, mice struck later in a feeding trial were more likely to deliver a successful retaliatory bite to the head of the snake than were mice presented earlier in the trial sequence. Third, snakes tended to lose interest progressively in predation on later mice in the sequence, that is, fewer mice later in the sequence were struck than were mice presented earlier (Table 3).

#### Site Struck

Most strikes (71%) hit site 1 (head/thorax; Table 1). Further, mice struck at site 1 died more quickly than mice struck in the middle of the body or on the rump (Table 3). This effect of site struck was true whether time-to-death or death rate was used as a measure of envenomation success.

When mice were struck in site 3 (rump), 18% of the time they successfully delivered a retaliatory bite to the attacking snake. However, when strikes landed on site 1 or site 2, then the mice much less often bit the snake (Table 4).

Table 2  
Site on Mouse Struck by Large and Medium Snakes

Site	Snake size			
	Large		Medium	
	No.	%	No.	%
1 (head/thorax)	230	67	319	75
2 (middle)	82	25	93	22
3 (rump)	28	8	16	3

Dependent variable: Site struck

Source	df	SS	F	p
Snake size	1	7.5337	7.72	.0056

Separately from these feeding trials, an attempt was made to determine whether reconstituted lyophilized venom injected by hypodermic syringe into two of these sites would produce relative differences in effects on mice. The results of these "artificial" envenomations show that, in fact, mice injected with venom by hypodermic syringe in site 1 died significantly more quickly than mice injected in site 3 ( $n = 22$ ; paired  $t$  test,  $p < .0001$ ).

#### Mouse Weight

The smallest mice (less than 10 g) were more likely to be held than were larger mice (more than 10 g). Of these small mice, 27% were held following a bite, compared with 13% for mice of larger size.

Mice less than 15 g died more quickly than mice 15 g or larger, at least as measured by time-to-death. However, there was no correlation between mouse size and death rate.

#### Bite

It was unusual for a mouse to successfully deliver a retaliatory bite to the snake (only 6% of the trials). In the few trials in which the mouse did bite the snake, no overall effect could be statistically detected on the subsequent time-to-death or on the death rate of the mouse. However, a limited correlation between mouse bite and time-to-death was discovered; namely, mice that were held and that also delivered a retaliatory bite died more slowly (344.8 s) than mice that were held and that did not bite the attacking snake (116.1 s). No such difference in time-to-death could be found for mice that were released.

No significant correlation emerged between the retaliatory bite of the mouse and the snake's behavior of holding or releasing a mouse following the strike.

Table 3  
Envenomation Success as Measured by Mean Time-To-Death and Mean Death Rate

Variable	Time-to-death (in s)		Death rate (in s/g)		
	No.	%	No.	%	
Large snakes	219.4	340	14.3	340	
Medium snakes	232.2	428	19.0	428	
Site 1 (head/thorax)	199.3	549	14.2	549	
Site 2 (middle)	262.0	175	22.1	175	
Site 3 (rump)	425	44	31.3	44	
Single strike	226.5	768	16.9	768	94
Multiple strike	551.8	48	33.8	48	6
Unextracted snakes	226.5	768	17.4	768	
Extracted snakes	332.1	101	8.9	101	

Source	Dependent variable: Time-to-death				Dependent variable: Death rate			
	df	SS	F	p	df	SS	F	p
Snake size	1	832760.5	5.63	.0179	1	4029.75	4.74	.0298
Sequence of presentation	3	1010920.2	2.28	.0770	3	2779.24	1.09	.3530
Site struck	2	2779539.0	9.40	.0001	2	19391.58	11.41	.0001
Mouse weight	4	2188683.4	3.70	.0054	4	4560.84	1.34	.2529
Bite by mouse	1	280395.9	1.90	.1690	1	861.21	1.01	.3145
Release/hold behavior	1	995968.1	6.73	.0097	1	3795.04	4.47	.0349
Single/multiple strikes	1	3254735.3	11.98	.0006	1	11377.36	8.88	.0030
Extracted snakes	1	962902.4	6.12	.0136	1	1117.59	1.32	.2501

#### Hold/Release Behavior

Most mice (83%) were released immediately following the strike (Table 1).

The hold or release feature of the snake's strike behavior had a profound statistical effect on envenomation success as

Table 4  
Retaliatory Bite By Mouse

Variable	Retaliatory bite			
	No		Yes	
	No.	%	No.	%
Large snakes	309	91	31	9
Medium snakes	418	98	10	2
Sequence 1	382	98	8	2
Sequence 2	175	93	13	7
Sequence 3	103	88	14	12
Sequence 4	67	92	6	8
Release	612	97	22	3
Hold	115	86	19	14
Site 1 (head/thorax)	531	97	18	3
Site 2 (middle)	160	91	15	9
Site 3 (rump)	36	82	8	18

Source	Dependent variable: Bite			
	df	SS	F	p
Snake size	1	0.00241	0.05	.8162
Sequence of presentation	3	0.82283	6.14	.0005
Site struck	2	0.76961	8.61	.0002
Mouse weight	4	0.29464	1.65	.1602
Release/hold behavior	1	0.39432	0.88	.3478

measured either by time-to-death or by death rate (Table 3). A mouse held following the strike died much more quickly ( $M = 148.5$  s) than a mouse released (243.0 s).

#### Number of Strikes

Usually, after striking a mouse, the snake showed no interest in again striking the envenomated prey, even if the struck prey repeatedly came into the vicinity of the snake. Interest in striking returned after the dispatched mouse had been swallowed. However, on a few occasions (6% of the trials), the snake did immediately (within 30 s) strike the same mouse a second and even a third time (Table 3). These mice multiply struck were timed and compared with mice in the more usual trial in which mice were struck but once. The result was that multiply struck mice took more than twice as long to die as did singly struck mice.

No change in hold/release behavior attended multiple strikes relative to single strikes.

#### Envenomation

Results of test for  $ED_{50}$  are shown in Figure 1 for large, medium, and small snakes. Note that venom toxicity drops (curve shifts right) in large compared with medium and small snakes.

Of the 768 mice struck, all showed definite signs of envenomation. There were no "dry" strikes. More than 40% of the mice died within 1.5 min, 95% were dead within 12 min, and the longest time to die was 81 min.

When struck, a mouse showed onset of various signs typical to the envenomation by this species. Initially, the mouse began to walk along the side of the cage. Vocalizations were some-

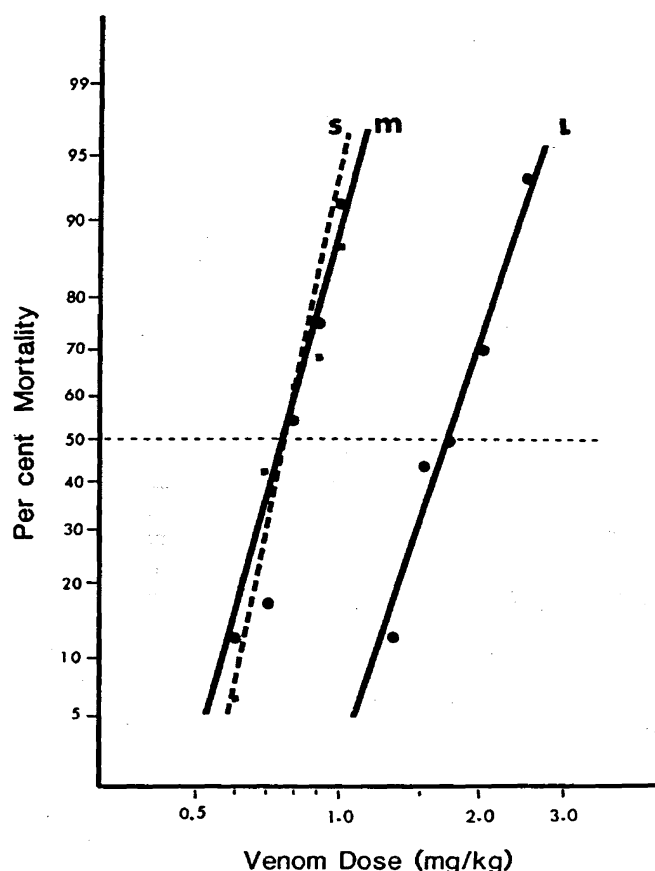


Figure 1. Mortality of venom doses. (The percentage of mortality for graded doses of venom taken from small [S], medium [M], and large [L] snakes. The plot for venom from small [dashed] and medium [solid] snakes closely coincide. To their right, the plot for large snakes [solid] indicates a drop in venom toxicity. Graded doses were continued beyond the high and low points indicated on each curve, but because these extreme doses gave complete or no mortality, respectively, they are not included in the plots. Multiple-range test:  $S = M \neq L$ .)

times emitted as well. Shortly, signs of locomotor disruption in the limbs appeared, and the path of the mouse became erratic. Next, hindlimbs became functionless and were dragged behind the body, and the mouse continued to move only under the power of its forelimbs. Soon the forelimbs also became functionless, and the mouse now either stopped forward motion or fell to its side. Convulsive, running motions of the limbs ensued, but these were ineffective and produced no forward progression for the toppled mouse. These running motions gradually decreased as the mouse next showed the onset of a deep but reduced respiratory rate. Final movements were usually sporadic abdominal spasms which gradually decreased in intensity. Just before or immediately after the last of these spasms, a drop of urine occasionally was released.

#### Experiment 2: Venom-Extracted Snakes

There proved to be a significant difference ( $p < .0136$ , PROC GLM) between mice struck by extracted snakes and

those struck by unextracted snakes (Table 3). Mice struck by extracted snakes took longer to die ( $M = 332.1$  s compared with 226.6 s). However, extracted snakes showed no change in hold/release behavior or in any other aspect of the strike that was recorded.

## Discussion

### Experiment 1: Feeding Trials

#### Snake Size

Small snakes often struck the first mouse presented but seldom struck any additional mice. Small snakes were easily intimidated by adult mice and were quick to switch from an offensive to a defensive posture. The loss of interest in additional mice could simply reflect satiation after the first mouse was struck and consumed. The easy intimidation by adult mice is likely more complex. On the one hand, small snakes are capable of killing adult mice. When small rattlesnakes did strike large mice, the mice showed rapid onset of envenomation effects, and all died soon thereafter. On the other hand, even though newborn rattlesnakes could kill adult mice, these small snakes were physically unable to swallow these dispatched adult mice. Not until these newborn snakes grew to near the 30-cm upper break-off point of their size class were they able to swallow adult mice. All newborn snakes that tried failed. This might explain the preference for small prey by young rattlesnakes studied in the wild (Fitch, 1949). As the snakes grew larger, larger prey could be swallowed, and prey size preference expanded. This, too, has been observed in natural populations (Fitch, 1949).

This ontogenetic shift, small prey preference changing to include larger prey as snakes grow, is apparently reflected in the basic character of the strike behavior and perhaps accounts for the reluctance of small snakes to stalk large mice.

Finally, rattlesnake size was also correlated with hold or release behavior. Following the strike, large snakes more often retained hold of the prey than did medium-sized snakes. Because muscular strength is roughly proportional to size, large snakes are likely stronger than medium snakes and so better able to control struggling mice. This better physical control over mice may account for the more frequent tendency of large snakes to hold prey.

#### Sequence

There was no loss of killing effectiveness throughout a single set of up to four feeding trials in those snakes that responded on all four trials. Mice struck last died as quickly as mice struck first in the sequence. This retention of killing effectiveness is not likely based on a quick synthesis of new venom. Typically, viperid snakes do not empty their glands in a single bite, and the venom spent is resynthesized slowly (Kochva, 1960, 1978a). Estimates vary from 15 days (Schaeffer, Bernick, Rosenquist, & Russell, 1972) to 54 days (Klauber, 1956) for replenishment of rattlesnake venom. It is unlikely that synthesis of new venom during only the hour or two of trials

would be sufficient to account for the sustained effectiveness of strikes to quickly kill the first through the fourth mouse struck. Thus, there must then be present sufficient stores of ready venom at the beginning of a feeding series.

The observed loss of interest in predation on later mice in the sequence likely reflects the progressive loss of appetite as each previous mouse is struck and swallowed.

### Site Struck

A strike to the rump of a mouse increases the chance that a snake will receive a retaliatory bite. However, this higher incidence of retaliatory bites by the mice to snakes striking site 3 (rump) probably reflects only the relative ease of turning on a snake holding the back end of the mouse. Strikes to the head or shoulders place the head of the mouse, and hence its teeth, under the control of the snake's jaws and thus prevent the mouse from turning on the snake.

The part of the mouse most often struck was the head/thorax (site 1). Both natural strikes and artificial envenomations with syringe injections of venom proved most effective in quickly killing the prey when delivered to site 1. The heavily vascularized lungs lie within this region. Perhaps venom is quickly absorbed by the pulmonary capillary beds and spread to bring about the characteristic rapid interruption of locomotion. Venom injected elsewhere along the body has no such comparable capillary system, so that onset of envenomation effects takes longer.

Whatever the anatomical/physiological basis, site 1 is the route bringing quickest effects of venom injection. The high rate of strikes to this site (71%) suggests that rattlesnake strike behavior is targeted to this, the most vulnerable site on the mouse.

In crotaline snakes, vision and thermoreception are the most important senses affecting orientation to prey and the strike (de Cock Buning, 1983a). Chemoreception (smell), via the vomernasal organ, becomes more important after the strike when the snake searches to recover the dispatched victim (Chiszar, 1983; Chiszar, Duvall, Scudder, & Radcliffe, 1980; Cowles & Phelan, 1958; Dullemeijer, 1961; Duvall,

Scudder, & Chiszar, 1980; Gillingham & Baker, 1981; O'Connell, Chiszar, & Smith, 1981). But, for the strike itself, visual and thermal information predominate. Thus, the accuracy discovered in the present study wherein site 1 (head/thorax) receives most of the strikes might be dependent upon the visual or thermal image a mouse presents. For the strike to be accurately placed, the mouse must be differentiated, and the critical target must be consistently recognizable.

A possible visual image is shown in Figure 2A. The head and body are roughly oval shapes but of unequal size. Because the visual image thus presents a differentiated shape, the target site could be distinguished. If the mouse should move, its direction of travel could give a polarity to the mouse, head to posterior. This could conceivably provide additional sensory information to help differentiate the most vulnerable region of the mouse (head/thorax).

A thermal image is shown in Figure 2B (after Bosch, 1983). The concentric lines define different temperature regions. As the figure indicates, the live mouse is not uniformly warm, but it has regions of significantly different temperatures. Note especially the set of concentric isotherms centered around the eye. To a crotaline snake with a heat sensory pit (de Cock Buning, 1983b), these temperature isotherms could form targets detectable by the facial pit and help the snake aim its strike.

The exact role played by vision and thermoreception in directing the strike is not known. Sometimes awkward, blindfolded crotaline snakes will strike at live mice (de Cock Buning, Goris & Terashima, 1981). If the facial pit is plugged, some crotalines will (de Cock Buning et al., 1981) and others will not (Dullemeijer, 1961) strike at mice. The roles are complicated, perhaps interrelated, but vision and thermoreception seem to be important factors in the strike. They are thus likely the senses most important in forming the prey into a differentiated image within the central nervous system.

### Mouse Weight

Twice as many small mice (less than 10 g) were held as were larger mice. In fact, these small mice were often not

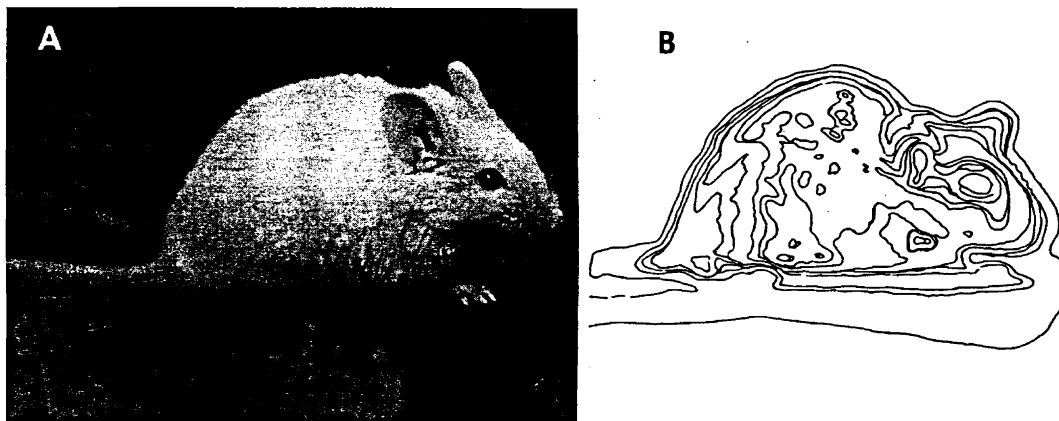


Figure 2. Visual (A) and thermal (B) images of a mouse. (The concentric lines for the thermal image define isotherms [from Bosch, 1983]. Note that the eye forms the center of such isotherms of the head.)

envenomated at all. The snake frequently did not even erect its fangs but just began to swallow the tiny mouse. A similar tendency to hold small but release large prey has been reported in other viperids (Allon & Kochva, 1974; Kardong, 1982; Kochva, 1978a). Small mice possess no or only poorly developed incisor teeth. They could thus deliver no troublesome retaliatory bite to the snake. This general retention of small and release of large mice might be taken as evidence that the bite of a mouse can be severe enough to affect the strike behavior (Radcliffe, Chiszar, & O'Connell, 1980).

### *Bite*

The mice were seldom successful in delivering a retaliatory bite to the striking snake. In only 6% of the trials did mice bite the snake. In these cases when the mouse did succeed, the effect of this retaliatory bite on the snake proved to be subtle. Only in trials in which the mouse was held and retaliated with a bite of its own was there a statistical effect on time-to-death, namely, such a mouse (held and a bite) took longer to die than a corresponding mouse (held and no bite). If the mouse was released following the strike, as was the usual case, then a retaliatory bite by the mouse did not correlate with a change in time-to-death.

On occasion, a rattlesnake reacted vigorously, even violently, to the retaliatory bite of a held mouse. This reaction ranged from a quick flick of its head to a lurch of its entire body, but it always succeeded in dislodging the biting mouse. This, taken with the influence of mouse weight discussed above, suggests that the mouse counterattack can affect the strike behavior, unfavorably from the snake's standpoint. This argues that holding on to a mouse does, in fact, expose the snake to a higher risk of retaliation than if the mouse were quickly released. There is thus some support here for the often stated view that quick release of a mouse following the strike reduces risks to the snake (e.g., Radcliffe et al., 1980). The frequent (here 83%) release of the prey may thus be interpreted as a feeding adaptation that reduces danger to the snake when striking mice with a significant ability to retaliate.

### *Hold and Release*

Risk of injury from the prey may account for the frequent (83%) release of mice following the strike. The snake is actually in contact with the mouse for less than 0.3 s. At least for 12 filmed strikes, contact averaged less than 0.3 s (range, 0.09–0.5 s). Thus, the complete venom dose must be injected during this short period of contact. However, many (17%) mice were also held in the jaws of the snake following the strike. Much of this percentage figure for held mice includes trials with small mice that could not retaliate and were more frequently held anyway. But, even allowing for the effects of small prey size, still 13% of the larger (more than 10 g) mice were held as well. The trade-offs between deployment of these two behaviors, hold or release of prey, suggest an uneven (83%/17%) compromise between conflicting predatory risks for the snake. The chance of injury favors release; the chance of losing released prey favors hold behavior.

Hold behavior could represent a response to poor fang placement. If fang penetration were shallow or poorly positioned and if the snake detected such mistakes, then perhaps holding prey following the strike allows time for delivery of additional venom and compensation for an initially faulty strike. However, a study of observable strike mistakes by *C. v. oregonus* found no ability of snakes to inject extra venom to compensate for mistakes of the strike (Kardong, in press). The present study does not settle, then, whether hold behavior relates more to recovery of prey than to their envenomation.

Nevertheless, the strike is not a simple reflex but, instead, is open to modification. It is modified by prey size, but certainly by other factors as well. Perhaps levels of venom in the gland, struggle by the prey, or success in fang placement affects the inclination to hold prey. Whatever the stimulus, it is clear that the basic hold or release feature of the strike is not a fixed behavior. It can be modified.

### *Strikes*

The usual feeding behavior observed was for a snake to strike the mouse, quickly release, locate, and then swallow the dispatched rodent before striking again. In fact, swallowing must usually occur before the snake will show an interest in striking again (Chiszar et al. 1982). However, in a small percentage of the trials (6%), the snake quickly struck again following the first bite, usually within 30 s. In such cases, the mice, despite sustaining two and sometimes three strikes in quick succession, took longer to die than mice struck only once.

Because such rattlesnakes depart from the usual single-strike pattern and because multiply struck mice take longer to die, this may suggest that a second or a third strike is an adjustment to a poor first-strike envenomation. This implies that the first strike resulted in insufficient venom delivery. At present, it is not possible to correlate such multiple strikes with biomechanical factors of jaw kinesis, with failure of venom secretion, or with poorly placed fangs at the time of contact with the mouse. However, what may be implied is that rattlesnakes are sensitive to success of envenomations. Failure may then lead to modification of the basic strike behavior, namely, more strikes at the same mouse.

These results are consistent, at least in part, with studies on prairie rattlesnakes (O'Connell, Poole, Nelson, Smith, & Chiszar, 1982) in which second, but not first, mice presented tended to receive multiple predatory strikes. However, with Northern Pacific rattlesnakes, the incidence of multiple strikes in third and fourth mice returns to the level of that in first mice struck. If one recalls that decline in appetite results in fewer attempted strikes throughout a series, this seemingly complex pattern of multiple strikes can be deciphered. Essentially, the predatory behavior of Northern Pacific rattlesnakes changes in two ways during a feeding sequence. First, appetite and second envenomation efficiency both decline. The decline in envenomation efficiency is reflected in the higher incidence of multiple strikes to second mice in the sequence. By the third and fourth mouse in the feeding sequence, attempted predatory strikes have declined further, apparently by now eliminating potentially inefficient strikes. This is reflected



statistically in the drop of multiple strikes of third and fourth mice in the sequence.

Perhaps snakes with declining motivation pass up the chance to strike the third and fourth mouse and leave these mice to the snakes with a continuing high motivation. Poorly motivated snakes drop out, highly motivated snakes continue, and envenomation efficiency returns. If this interpretation is substantially correct, it argues that motivation itself is a factor that can affect envenomation success.

### *Envenomation*

Toxicity of venom dropped in large snakes. This decline in toxicity reflects an ontogenetic shift also reported for other species (Bonilla, Faith, & Minton, 1973; Mackessy, 1985). However, despite a drop in toxicity, no change occurred in the mean length of time for struck mice to die. Even though venom toxicity per milligram is lower, mice struck by large snakes died as quickly or more quickly than mice struck by medium or small rattlesnakes. It is conceivable that large snakes could compensate for lower venom toxicity by injection of larger quantities. In fact, larger cobras (Kochva, Tonsing, Louw, Liebenberg, & Viser, 1982) and vipers (Kochva, personal communication, 1985) can store more venom and probably inject more venom than smaller individuals. A direct measure of the quantity of venom delivered during the rattlesnake strike was not attempted in the present study. However, of the variables measured in this study none changed ontogenetically in such a way as to account for the equal, in fact improved, envenomation success of large snakes. It seems most likely, then, that decline in venom toxicity in large snakes is offset by delivery of larger quantities of venom.

The venom of rattlesnakes serves two major biological roles during feeding (Russell, 1980). First, it rapidly immobilizes the prey, and, second, it begins the process of digestion from within (Jansen, 1983; Thomas & Pough, 1979). This drop in venom toxicity with age may reflect a solution to an ecological dilemma created by the dual role of venom. On the one hand, larger snakes can swallow larger prey. But large prey are bulky and, as a consequence, have an unfavorable surface/volume ratio that slows the action of digestive enzymes released by the walls of the gut (Pough & Groves, 1983). To compensate, more venom is injected into the mouse, thus increasing the total quantity of accompanying digestive enzymes available to supplement gut enzymes. On the other hand, more venom creates a problem. The increased volume of venom means a more rapid prey death, perhaps killing too quickly to allow for adequate spread of digestive enzymes. It is conceivable that the drop in venom toxicity with age represents a way out of this dilemma. A drop in toxicity allows an increase in the volume of venom injected without an overall change in speed of prey death. Yet, because more venom is injected, more proteolytic components are carried in to enhance digestion of a large, bulky prey. The ontogenetic drop in venom toxicity may be the compromise required to solve this dilemma between speed of killing and time for spread of the digestive enzymes.

No "dry" strikes occurred during feeding trials of more than 768 mice. This is a marked contrast with clinical cases in-

volving humans. In humans, perhaps as few as 10% or as many as 73% of snakebites result in no envenomation (Parrish, 1959; Reid, 1970; Russell, 1980). This supports the view that rattlesnakes employ two different strikes, an offensive strike used when feeding and a defensive strike used when threatened (Chiszar et al., 1981; Gove, 1979; Klauber, 1956; Minton, 1969). The advantage of consistent delivery of venom during offensive strikes seems straightforward, namely, to reliably obtain prey. Venom helps to immobilize the prey and perhaps to begin the process of digestion. Why venom occasionally is not delivered during a defensive strike proves more complicated to interpret. Perhaps striking a large surface, such as an arm or a leg of a human, requires considerable realignment of the jaws or at least more so than is true for relatively smaller objects such as mice. Striking a large surface could change the geometry of the kinematic jaw linkages, interfere with jaw mechanics, prevent successful engagement of the fangs, and so finally disrupt the venom delivery system. Or perhaps one should look at defensive strikes another way.

Defensive strikes serve a biological role not in food getting but in discouraging predators on snakes or in discouraging large animals, such as ungulates, from inadvertently tromping on a snake and causing injury (Klauber, 1956). The defensive strike itself may function to startle a predator or an inattentive ungulate. Consistent delivery of venom with each defensive bite may be more than is required to earn avoidance by predator or ungulate.

If the explanation for occasionally "dry" defensive strikes lies with a disruption of jaw mechanics, then this would be an insight into the limits of jaw design. If withholding of venom is the explanation, then this would imply some control by the snake over its expenditure of venom supplies. Whatever the explanation, a difference does exist between the types of strike behavior, offensive and defensive.

Although more than half of the mice were dead within 1.5 min, the actual time to immobilize the victim was much less. Usually within 10 to 15 s, the locomotor system was severely disrupted, and the mouse was in a state of distensive paralysis. How this is brought about so quickly is not known. Perhaps components of the venom act on the nervous system directly or act to create hypotensive crisis (shock) which precipitates quick disruption of locomotion. Whatever the physiological basis, disruption of locomotor ability appears quickly, stops much displacement of the mouse from the vicinity of the snake, and thus shortens the recovery distance for the snake.

### *Experiment 2: Extracted Snakes*

When snakes were "milked" of some of their venom, the mice they struck took longer to die. One might conclude that successful envenomation requires ready stores of venom. On the other hand, milking of venom did not result in a change in the hold/release behavior or in the strike behavior generally.

For the time being, however, these results must be carefully qualified. First, by the extraction procedure followed, not all the available venom could be emptied from the gland. Without actual electrical stimulation or mechanical massage of the gland, some reserve of venom remained. If the gland had been depleted of all its venom, changes in the strike behavior might

have surfaced. Second, extraction of venom required handling of the snake. The handling trauma itself could have left the snake disturbed enough to alter its efficiency of envenomation.

Thus, although this set of experiments is in keeping with the view that venom stores are not quickly (within 48 hr) replenished, other explanations for the time being must be entertained as well.

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