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The Hold-Release Mechanism in the Family Crotalidae

Ronald K. Easter
Eastern Illinois University

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THE HOLD-RELEASE MECHANISM

IN THE FAMILY CROTALIDAE

BY

RONALD K. EASTER

B.S., Eastern Illinois University, 1977

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

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CHARLESTON, ILLINOIS

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I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING THIS PART OF THE GRADUATE DEGREE CITED ABOVE

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THE HOLD-RELEASE MECHANISM
IN THE FAMILY CROTALIDAE

BY

RONALD K. EASTER
B. S. in Zoology, Eastern Illinois University, 1977

ABSTRACT OF A THESIS

Submitted in partial fulfillment of the requirements for the degree of Master of Science in Zoology at the Graduate School of Eastern Illinois University.

Charleston, Illinois
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ABSTRACT

Strike/release vs. strike/hold feeding behavior was observed for 5 Crotalus atrox and 5 Agkistrodon piscivorus. Two sizes of warm-blooded prey were offered to the rattlesnakes on alternate weeks. Cottonmouths were offered, alternately, fish or mice of equal size. Although data varied among individual subjects, cottonmouths offered fish demonstrated the strike/hold behavior significantly more often than the strike/release behavior; cottonmouths offered mice struck and released significantly more often than they struck and held. It is concluded that the strike/hold strategy in response to fish is advantageous because the danger of holding such prey is minimal and the release of such prey in an aquatic environment often results in escape. Strike/release strategy in response to mice is advantageous because of the potential danger to the predator from incisors and claws. Rattlesnakes gave the strike/release response significantly more often toward large warm-blooded prey than the strike/hold response; small warm-blooded prey were struck and held significantly more often than larger prey. It is concluded that this is due to the greater potential danger from larger prey.
ACKNOWLEDGEMENTS

I wish to thank Drs. Richard Andrews, Patrick Docter, and Richard Funk for serving on my committee and offering valuable editorial comments on this manuscript. I wish to give a special thanks to Dr. Michael A. Goodrich, chairman of my graduate committee, for all his sincere support and hours of meticulous editing. Working with all of these gentlemen, in and out of the classroom, has been an honor for me.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>i</td>
</tr>
<tr>
<td>TABLE OF CONTENTS</td>
<td>ii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>iv</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>4</td>
</tr>
<tr>
<td>RESULTS</td>
<td>7</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>10</td>
</tr>
<tr>
<td>CONCLUSIONS</td>
<td>14</td>
</tr>
<tr>
<td>REFERENCES CITED</td>
<td>21</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Comparison of prey struck/held vs. number of prey struck/released by each of the 5 <em>Agkistrodon piscivorus</em>, when offered mice and fish</td>
<td>15</td>
</tr>
<tr>
<td>2. Comparison of prey struck/held vs. number of prey struck/released by each of the 5 <em>Crotalus atrox</em>, when offered small prey and large prey</td>
<td>16</td>
</tr>
</tbody>
</table>
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Dimensions and arrangement of housing and water bowl for experimental <em>Crotalus atrox</em> and <em>Agkistrodon piscivorous</em></td>
</tr>
<tr>
<td>2.</td>
<td>Number of prey struck and released vs. number of prey struck and held by each of the 5 <em>Agkistrodon piscivorous</em> according to prey type</td>
</tr>
<tr>
<td>3.</td>
<td>Number of prey struck and released vs. number of prey struck and held by each of the 5 <em>Crotalus atrox</em> according to prey size</td>
</tr>
<tr>
<td>4.</td>
<td>Comparison of the shortest to longest latency periods from strike and release to initiation of swallowing between each group of subjects and their corresponding prey</td>
</tr>
</tbody>
</table>
INTRODUCTION

Rattlesnake and cottonmouth feeding and defense behaviors have been the subject of wonder and study ever since pioneers first began crossing the North American continent. Many myths and legends (along with a few facts) have flourished as to the length of striking distance, the fang penetration and the swallowing capacity of these pit vipers. Until recently, however, few of these descriptions were backed with accurate scientific evidence.

Walker Van Riper (1953), set out to answer the question: does a rattlesnake stab you with its fangs or close its jaws in a true bite? Most experts agree that harmless snakes bite by closing their jaws. There was much debate as to whether rattlesnakes demonstrated similar tendencies. High speed photography was used to study the sequence of movements just at the point of contact. Even though preliminary observations showed the "stab" to be the method of envenomation, Van Riper's herpetological friends assured him that they had witnessed rattlers grabbing and holding prey animals, especially small prey. With a modification of his procedures (offering varying sizes of targets), Van Riper found that half of his subjects bit the targets while the other half consistently "stabbed" it. The conclusion reached by such results, according to Van Riper, seemed to demonstrate the validity of the "Harvard Law of Animal Behavior": "Under carefully controlled conditions, animals
behave as they damn well please."

Kenneth Kardong (1975) presented evidence, via frame by frame analysis of high speed motion pictures, of prey capture in the cottonmouth. He divided this process into six observable phases (Approach, Glide, Bite, Release and Post-release) with a seventh assumed phase of "Search" in which the snake would move through its environment in such a fashion as to increase the likelihood of locating prey. The "Search" phase, therefore, would precede all other phases in sequence. Kardong mentions that on occasion the rapid and immediate release of prey subjects did not occur.

Based on these published studies and on long-term observations of the feeding behavior of captured pit vipers at Eastern Illinois University (Goodrich, pers. comm.) developed the following hypotheses: cottonmouths strike/release warm blooded prey more often than strike/hold; cottonmouths strike/hold cold blooded prey more often than strike/release; rattlesnakes strike/release larger warm blooded prey more often than smaller warm blooded prey.

Cottonmouths feed on a wide range of cold blooded as well as warm blooded prey (Kofron, 1978). Bothner (1974) made some interesting observations on three subjects regarding how they located, captured and swallowed fish on a July day in 1972. A small pool (7m long x 2m wide x 15-20cm deep), left isolated by falling stream levels and containing many fishes, was the "hunting ground". Bothner recorded each snake's feeding behavior and success rate for 85 minutes.
Snake B was the most active and the most successful. Much of its exploring was done with its head under water, moving from right to left as it glided through the pool. Upon finding a fish, it would immediately seize and carry its prey well onto the bank. Only then was it manipulated in the jaws and swallowed. If the prey slipped, as it did on three occasions, it did not escape. Snakes A and C, which "hunted" only with their heads above the water surface, seemed to have more difficulty in locating and capturing prey. Snake C caught only one fish and took it to the bank to swallow it. Although snake A caught five fish, it never went to the bank before trying to manipulate and swallow its prey. Consequently, two of the five captures resulted in escapes by fish which flopped loose and swam away. These observations will later be compared with the author's laboratory results.
MATERIALS AND METHODS

Ten adult North American pit vipers, 5 western diamondback rattlesnakes (*Crotalus atrox*) and 5 cottonmouths (*Agkistrodon piscivorous*), were used in the experiment. All were housed in the Eastern Illinois University Vivarium in wooden cages with sliding glass fronts containing water bowls and paper flooring (Fig. 1). Four rattlesnake and four cottonmouth cages were 46cm wide x 34cm high x 31cm deep while one rattlesnake and one cottonmouth were housed in cages 95cm wide x 30cm high x 60cm deep. The difference in cage sizes was relative to the difference in snake sizes, larger individuals requiring larger quarters.

Room temperature was maintained between 25-30° C. All subjects had been maintained in a similar environment in the Vivarium for a minimum of two years. Depending upon the size of the snake, each had been offered one mouse or rat each week since housed in captivity. Fresh water was available at all times. Cages were cleaned as needed.

All snakes remained in their own cages throughout the experimental procedure. Care for the subjects remained the same as before except that no cage cleaning or water bowl changing activities were conducted prior to experimental observations for that day.

The five *Agkistrodon piscivorous* were offered a mouse (25-30g) or comparable size green sunfish on alternate weeks. This was done to compare feeding behavior on cold blooded
prey and warm blooded prey.

Four adult *Crotalus atrox* (size range 100-140cm) were offered an adult mouse (25-30g) or a young mouse approximately 1/2 the size (12-15g) on alternate weeks. The largest *C. atrox* (approx. 190cm) was offered alternately a small rat (60-70g) or an adult mouse (25-30g) approximately 1/2 the size of the rat. This was done to observe differences between feeding behavior on large and small prey of similar type.

Each experimental feeding was conducted in the evening between 2100 and 2300 hours. The room lights were turned off and the cage being observed was illuminated by three 60 watt lights placed six feet in front of the cages. This had the effect of concealing the observer from the snakes, while at the same time illuminating the cages and making accurate observations possible.

To begin a trial, the glass front of the cage was slid open only far enough to quickly introduce the prey and then rapidly closed. Timing with a hand held stopwatch began immediately upon the placement of the prey into the cage. The observer would then step behind the lights so not to distract the subjects. Data collected for each test were: date; prey type and size; whether first contact was a strike/release or a strike/hold (3 seconds or longer); if released, latency until second contact; and whether prey was swallowed head first or tail first and whether swallowed alive or dead. The behavior of each subject was recorded for
a maximum of 15 minutes for each trial, starting from the introduction of the prey, and ending with either a completed swallow or 15 minutes, whichever came first.
RESULTS

Ten snakes (5 rattlesnakes and 5 cottonmouths) were offered a total of 200 prey subjects, 20 each. Feeding response (strike/release or strike/hold) occurred in 173 of the 200 trials (99 of 100 trials with Crotalus atrox and 74 of 100 trials with Agkistrodon piscivorous).

Each subject was given a two letter and one number code for the purpose of identification. The letters came from the scientific names, Agkistrodon piscivorus = AP, Crotalus atrox = CA. Subjects were numbered 1, 2, 3, 4 or 5.

All subjects completed a feeding response in at least 40% of the trials (AP-5) and some (CA-1, CA-2, CA-3, CA-5) responded 100% of the time.

Table 1 shows the responses of each individual cottonmouth and the summation of the responses to a particular prey species. It can be seen that mice accepted were struck and released significantly more often than struck and held. Conversely, sunfish accepted were significantly more often struck and held than struck and released. The results are illustrated in figure 2.

Cottonmouths offered mice showed a latency from strike/release to initiation of swallowing of 66 to 833 seconds with a mean of 321 seconds (Fig. 4). When offered fish, the time elapsed from strike/release to initiation of swallowing was 225 to 900 seconds, with a mean of 625 seconds. However, the sample size for this response was only 7.
Table 2 shows the responses of each individual rattlesnake and the summation of these responses to large versus small prey. Collectively, it is seen that small prey were struck and held significantly more often than struck and released, and larger prey were struck and released significantly more often than struck and held. Results for individual subjects varied considerably, however, in every case the strike/release behavior occurred more frequently in response to larger prey. These results are illustrated in figure 3.

Rattlesnakes, striking and releasing small prey, later recovered the prey and began the swallowing process within a range of 114 seconds to 693 seconds with a mean of 286 seconds (Fig. 4). Rattlesnakes, striking and releasing larger prey, showed a latency to recovery of 96 seconds to 900 seconds, with a mean of 356 seconds.

Of the 50 small prey offered to the rattlesnakes, 31 were swallowed head first, 15 were swallowed tail first and 4 were swallowed sideways. Of larger prey, 43 were swallowed head first versus only 5 tail first and none swallowed sideways. Larger prey were swallowed head first significantly more frequently than small prey; the differences significant at P<0.05 (X^2 cal.= 5.65).

The cottonmouths swallowed 29 mice head first, 2 tail first and none sideways. When offered fish, 35 prey were swallowed head first, only 1 tail first and none sideways. The overall lower number of swallowings by the cottonmouths
is a reflection of the lowered acceptance of prey by this species.

Determining whether a prey subject is alive or dead upon the initiation of swallowing by its predator is often subjective. The following data reflecting the number of times that prey were still alive during the swallowing behavior were arrived at by observing visible, active movement by the prey during this process. If the prey remained limp and motionless, it was classified as "apparently dead" when swallowed. Six of 35 (17.1%) mice were noticeably alive while being swallowed by cottonmouths, compared to 10 of 39 (25.6%) fish. For rattlesnakes, 11 of 50 (22%) small prey were noticeably alive while being swallowed compared to 1 of 49 (2%) of larger prey.
DISCUSSION

Table 1 shows that 30 out of the 35 (86%) mice accepted by the cottonmouth were struck and released, whereas, the strike/release behavior was demonstrated in only 5 out of the 39 (13%) trials in which fish were accepted. The strike/hold behavior, conversely, was found to be 14% for mice compared to 87% for fish. As observed by Bothner (1974), grabbing and holding cold blooded prey (fish) until reaching a site where escape is less likely can prove very beneficial in improving the success rate of swallowing prey that have been captured.

The striking and releasing of warm blooded prey (in this case mice) may also be of value to pit vipers. According to Kardong (1982), claws and incisors (neither of which are possessed by fish) can prove to be formidable weapons against an attacking snake. On the relatively few occasions throughout the course of these experiments that cottonmouths and rattlesnakes attempted to swallow living rodents, they were occasionally bitten badly enough to elicit a release and momentary retreat from their prey. Live fish being swallowed were never observed to cause any kind of harm to the cottonmouths.

Table 2 shows that for *Crotalus atrox* only 14 out of 50 (28%) small rodents accepted were struck and released, whereas the strike and release pattern occurred in 34 out of 49 (69%) acceptances of larger rodents. The strike/hold behavior appeared 72% of the time when small rodents were offered compared to only 31% of the time when larger rodents
were utilized.

If claws and incisors of moderate size rodents could prove dangerous to a snake as suggested by Kardong (1982), then the avoidance of claws and incisors of larger prey would be even more important. The advantage for snakes being able to envenomate their prey and then remain a safe distance away until death or paralysis rendered such prey harmless can easily be imagined. It would appear that snakes follow specific innate behaviors for survival purposes instead of just "behavior as they damn well please" as stated by Van Riper (1953).

It is interesting to note the total number and type of prey being swallowed while still alive versus those being swallowed only after becoming motionless (apparent death). Differences between the percentages of mice swallowed alive versus fish swallowed alive by cottonmouths were negligible. Rattlesnakes, on the other hand, swallowed 11 small prey alive compared to only one large. This reinforces the assumption that detachment from larger, more dangerous prey by pit vipers until the venom can take effect is beneficial for survival.

Variations in prey animals (large vs. small as well as fish and mice) were arbitrarily chosen by the experimenter. Had both the fish and mice, which were offered to the cottonmouths, been considerably larger, but still within the swallowing capabilities of pit vipers as described by Pough and Groves (1983), perhaps the strike/hold behavior and the
percentage of prey swallowed alive would have decreased significantly for mice. These hypotheses based on the behavior of rattlesnakes toward larger rodents, would in effect produce an even greater difference in the feeding behavior of cottonmouths toward cold blooded and warm blooded prey. Likewise, if a larger gap existed between the two sizes of rodents offered to the rattlesnakes, the degree of difference in the strike/release versus strike/hold behavior as well as the swallowing of live prey versus dead might be even more distinct. Even though neither of these hypotheses were tested in this experiment, the data that were obtained support them.

The entire mechanism of envenomating and then releasing prey by pit vipers can only be an effective feeding behavior if there is an efficient way to recovering such prey afterwards. Noble and Schmidt (1937) showed that the facial pits of these snakes are radiant energy receptors. The Jacobson organs, facilitated by tongue flicks, are chemoreceptors. It is thought that both of these work together in locating prey after envenomation. Goodrich and Miller (1984) have demonstrated the potential importance of the pit organs for this function.

Certainly, the release and subsequent recovery of cold blooded prey might not prove effective since venom works more slowly on cold blooded animals than warm. Though figure 4 shows the latency of strike/release to swallowing of fish to be considerably longer than warm blooded prey tested, there
seemed to be a similar correlation of strike/release to death. This would allow the prey to move perhaps some great distance away from its predator before succumbing to the venom, making recovery almost impossible. Heat sensing pits would be less effective in distinguishing a cold blooded prey from its environment.

Table 3 shows that the vast majority of prey are swallowed head first. Tail first swallowing occurred frequently only in the smallest prey. This would be expected when considering the basic mechanics of the swallowing process and the body form of the prey. According to Pough (1983), pit vipers in general can swallow considerably larger prey in relationship to their body size than those offered during this experiment. Had the experimenter utilized larger prey, we might have seen the percentage of posterior and sideways swallowing diminish.
CONCLUSIONS

The data collected from this experiment show that cottonmouths offered fish demonstrate the strike/hold behavior significantly more often than the strike/release behavior. Cottonmouths being offered mice will strike/release significantly more often than strike/hold. The strategy of strike/hold toward fish is advantageous because the danger of holding such prey is minimal and the release of such prey in an aquatic environment often results in escape. The strike/release strategy toward mice is advantageous because of the potential danger to the predator from incisors and claws. The recovery success rate of warm blooded prey released is greatly increased due to the pit organs. Rattlesnakes show a greater strike/release of large prey than they do of smaller prey. This tendancy is undoubtedly related to the greater potential danger from larger prey.
Table 1. Comparison of prey struck/hold vs. number prey struck/release by each of the 5 *Agkistrodon piscivorous*, when offered mice and fish.

* Differences significant at p<0.001 (X² cal.= 40.03)
Table 2. Comparison of prey struck/held vs. number of prey struck/released by each of the 5 Crotalus atrox, when offered small prey and large prey.

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<tr>
<th></th>
<th>CA-1</th>
<th>CA-2</th>
<th>CA-3</th>
<th>CA-4</th>
<th>CA-5</th>
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<tr>
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<tr>
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<td>7</td>
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<td>36</td>
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<td>STRIKE/RELEASE</td>
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<tr>
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<td>3</td>
<td>1</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>STRIKE/RELEASE</td>
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<td>3</td>
<td>7</td>
<td>8</td>
<td>6</td>
<td>34</td>
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</tbody>
</table>

* Differences significant at p<0.001 (X^2 cal. = 15.35)
Figure 1. Dimensions and arrangement of housing and water bowl for experimental Crotalus atrox and Agkistrodon piscivorus.
Figure 2. Number of prey struck and released vs. number of prey struck and held.

- Mouse
- Fish

AP-1 AP-2 AP-3 AP-4 AP-5

Number of prey accepted according to prey type.

STRIKE/HOLD

STRIKE/RELEASE

0 1 2 3 4 5 6 7 8 9 10
Figure 3. Number of prey struck and released vs. number of prey struck and held by each of the 5 *Crotalus atrox* according to prey size.
Figure 4. Comparison of the shortest to longest latency periods from strike and release to initiation of swallowing between each group of subjects and their corresponding prey.
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Pough, F. H. and J. D. Groves. 1983. Specialization of the