Title

THE EFFECTS OF BODY SIZE ON DEFENSIVE STRIKE PERFORMANCE OF PRAIRIE RATTLESNAKES, CROTALUS VIRIDUS

Author
Ho, Christina M

Publication Date
2023-03-09

THE EFFECTS OF BODY SIZE ON DEFENSIVE STRIKE PERFORMANCE OF PRAIRIE RATTLESNAKES, *CROTALUS VIRIDUS*

By

Christina Mariko Ho

A capstone project submitted for Graduation with University Honors

March 9th, 2023

University Honors

University of California, Riverside

APPROVED

Dr. Timothy Higham

Department of Evolution, Ecology, and Organismal Biology

Dr. Richard Cardullo, Howard H Hayes Jr. Chair

University Honors

TABLE OF CONTENTS

ABSTRACT

Body size is one of the major influences on predator-prey relationships, specifically on its biomechanical performances in terrestrial ambush hunters. Rattlesnakes are ambush hunters that typically specialize on small rodent prey. Although there are previous studies that focus on how fast rattlesnakes can strike, it is not clear how ontogenetic changes in body size might influence strike performance. Past studies in other snakes have found that velocity is constant across a range of body sizes. Whether this is similar in rattlesnakes is not known. Here we investigate the influence of ontogenetic changes in body size on the defensive strike performances in a terrestrial ambush pit viper, *Crotalus viridus*. Using high-speed 3D videography, we examined 9 individuals ranging from 24 to 303 grams. There was a significant positive correlation between body mass and maximum strike velocity, with larger snakes striking at higher velocities than smaller snakes. In contrast to our predictions, acceleration is independent of body mass, and higher maximum acceleration does not lead to higher maximum velocities. Our results, which differ from previous studies of other snakes, highlight the potential for different attack strategies that are likely related to ecology.

ACKNOWLEDGEMENTS

I would like to thank Dr. Timothy Higham for accepting and guiding me as a wonderful faculty mentor throughout this program. His expertise and kindness have allowed me to study an animal I was always interested in, and helped me understand a beautiful perspective into the research field of biology.

I would also like to thank David Ryan for assisting in the data collection and video digitizing. I would also like to thank the graduate students in the Higham Lab for helping take care of the snakes. Finally, I would like to thank Ryan Hanscom for collecting the snakes and allowing UC Riverside to study them.

INTRODUCTION

Predation is fundamental to many intertwining ecosystems. Predators must catch, kill, and eat prey (Hanscom et al., In Press). Predators and their prey can develop adaptations and strategies to survive against one another. For predators, survival depends on the ability to capture and subdue prey efficiently for food, whereas prey must be able to avoid getting consumed or defend themselves. An important factor in these interactions is body size. Body size affects various aspects of an individual's physiology, kinematics/movement, and overall morphology, all necessary to determine the individual's defensive or offensive efforts (Herrel et al., 2011).

In terrestrial animals, body size can influence variables from life history, interactions with both predator and prey, performance, and function. Body size in predators is often related to the group of prey they can capture and consume (Griffiths, 1980; Carbone et al., 1999; Enders, 1975). Despite the extensive diversity among species, many terrestrial carnivores feed on either large vertebrates or invertebrates and small vertebrates. In these mass-related energy requirements, bigger animals require more energy to survive, so they tend to hunt prey large enough to provide those energy needs (Carbone et al., 199). Predators can also utilize their body sizes to assist with their hunting, such as decreasing their search costs (Enders, 1975), or assisting in prey selection and influencing foraging costs in relation to prey size (Griffiths, 1980).

Predators often exhibit a change in prey size selection as their body size increases. Some predators can shift to larger prey as their body size increases, while others continue to consume large and small prey (e.g., Carbone et al., 1999). For example, ontogenetic niche shifts can occur when snakes change their diet or habit due to growth in body size and efficiency for energy feeding, especially away from smaller prey (Hampton, 2018).

Here, we study the snakes, animals that display both predatory and defensive behaviors. Behaviors such as rapid strikes are key to survival for snakes, both in offensive (consuming prey) and defensive (dissuading a predator from attacking) situations (Hanscom et al., In Press). As predators, snakes can be classified as either active or sit-and-wait (ambush) predators, although both share the need to strike at prey (Hanscom et al., In Press). Although few studies have directly quantified whether a certain family of snakes is strictly ambush or active, many studies state that the family Viperidae consists primarily of ambush hunters (Hanscom et al., In Press; Young, 2010).

In most ambush hunting situations, snakes utilize the sit-and-wait method which consists of the initial search for a waiting (ambush) site, waiting in the ambush coil for a period of time, and then striking at an endothermic prey (Hanscom et al., In Press). During defensive behaviors, snakes display warning signs which can include elevating their head between their coiled body, hissing, or producing rattling sounds with their tails (Hanscom et al., In Press; LaDuc, 2002). These signs are then usually followed by a quick strike, which can include delivering venom to the target (LaDuc, 2002).

For a strike to be successful, the snake must be able to cover the strike distance and reach the prey before they react and escape, and the snake must be able to make physical contact with the target (Young, 2010). For capture success, biomechanics and morphology come into play where it is critical to not only strike fast and far (Herrel et al., 2011) but also have the correct aim and timing (Hanscom et al., In Press). In defensive strikes, there can be two reasons to strike. The first is to actively bite and injure the predator, and the second can be a possible tactic to warn predators away (Whitford et al., 2020), potentially missing the target.

So how could snakes miss their targets? There can possibly be a trade-off between strike accuracy and velocity (Higham et al., 2006; Hanscom et al., In Press). Hanscom found that there tend to be higher maximum velocities in defensive strikes, and on the other hand, maximum accelerations were usually higher in predatory strikes. They suggested that this may be due to the importance of accuracy, where defensive strikes might not need to have as much accuracy as predatory strikes. The success of strikes can also be due to body size and body morphology, possibly where bigger snakes can have higher chances of succeeding due to their mass and length. There are many factors that can be the reason for a failed strike, whether it be due to kinematics, miscalculation, or abiotic factors, but in this study, we will only note if the subject misses or not, as we do not have enough information and sample size to deduce a correlation between body size and strike miss rates.

Despite the differences in the purpose of defensive and predatory strikes, defensive strikes should not be overlooked, as they can reach similar levels of performance as predatory strikes (Araujo, 2006; 2007; Kardong and Bels, 1998; LaDuc, 2002). Defensive strikes, accompanied by rattling sounds, usually originate from a series of elevated and vertical S-shaped coil positions or loose positions (LaDuc, 2002; Hanscom et al., In Press; Araujo, 2006) and can change from one position to another. After the initiation of the strike, the behaviors can be categorized into stages (Kardong and Bels, 1998; Hanscom et al., In Press). Kardong and Bels organize these strike stages in order of occurrence: 1) extend stage, 2) contact stage, 3) release stage, and 4) retract stage. In this study, we will be focusing on the extend and contact stages, looking at the comparisons of the initial stages of performance amongst the variety of body masses, from juvenile to adult, before they potentially hit the targets.

There have been many other studies that examined other variables, such as internal temperature effects on the defensive behavior and strikes of snakes (Mori and Burghardt, 2004; Whitford et al., 2020). As snakes are ectotherms, snakes can be moderately influenced by temperature, found in one study by Whitford (2020) where warmer snakes were found to be more open to strike, strike faster, and strike more often. Although we cannot exclude the morphology of the skeletal and muscle mechanisms, a major factor in the performance of strikes, it is important to note that body temperatures can be a possible factor for some correlations.

Past studies (Herrel et al., 2011; Young, 2010) found that strike velocities are relatively similar across a range of body sizes, stating that juvenile, or small animals, will perform equally to adult, larger animals. Herrel et al. (2011), centered their research on the effects of body size on strike performance in an arboreal pit viper, *Trimeresurus (cryptelytrops) albolabris*, another subspecies under the subfamily of Crotalinae. They found that larger snakes tend to have relatively smaller heads compared to their body mass due to the significant negative allometry between head mass/dimensions and body mass. There was also isometry relative to the overall body measurements and mass, such as masses for anterior and middle sections and tails. Despite the smaller body lengths and mass of juveniles, they were able to strike and perform at high speeds and distances similarly to adults. They suggest that speed variables such as velocity are independent of body mass because juveniles experience considerable predation pressure in the wild.

To further understand the relationship between body size and strike performance, we studied defensive strikes of prairie rattlesnakes, *Crotalus viridis*, a venomous terrestrial pit viper species commonly found in many diverse habitats and temperatures (Ashton, 2001; Hanscom et al., In Press). We studied how the differences in body size influenced their defensive performance as terrestrial ambush hunters.

As Herrel (2011) found that body mass did not impact performance in a relatively closely related pit viper, I predicted that strike velocity and strike distance will be independent of body mass, where all snakes will perform similarly to one another despite their body mass for the *Crotalus viridis* species. This study will utilize high-speed videography and digitization software to quantify performance.

METHODS AND APPROACH

Subjects

Twenty-one prairie rattlesnakes (*Crotalus viridus*) were collected from Texas and Nebraska and transported to the University of California, Riverside under Professor Tim Higham's research laboratory. All 21 subjects were kept in a vivarium. The subjects were checked daily in a room with an average temperature of 75.5 degrees Fahrenheit and an average humidity of 55%. Snakes were individually housed in sterile containers lined with newspaper, water, and a plastic cave. Each snake was fed thawed-out dead mice once a month and water was provided ad libitum. These experiments were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of California, Riverside.

Each individual was anesthetized and measured, which included both body mass and snout-vent lengths (SVL). Subjects were placed in plastic cylindrical tubes based on their thickness. A cotton ball, soaked in 0.2 mL of isoflurane, was dropped on the opening facing the snake's head, compelling the snake to inhale the anesthesia. The top of the tube was then fastened tight with a plastic bag and rubber band. The anesthesia period varied from 20 to 40 minutes until the subjects gained consciousness. Snout-vent length measures the length (in cm) from the snout to the cloaca, with the body and head held linear, while body mass is measured with a lab-scale (weighted days after feeding). SVL ranged from 34 cm to 86 cm, and body mass ranged from 24 to 303 grams.

Filming Materials and Conditions

Two Phantom Miro M110 high-speed cameras were used to record the strikes. The two cameras were placed at different angles to record the dorsal and lateral views of the snake. The lateral camera had a 50 mm lens and the dorsal camera had a 28 mm lens, creating image sizes of 1280 x 800 pixels. Both cameras were synchronized and simultaneously recorded videos in black/white scale. Additional lighting was provided by four infrared lights placed at each corner of the experiment enclosure. Each trial was captured at 800 frames per second in order to capture the snake strike that occurs in less than a second. Each strike occupies 100-300 frames, or 0.125 to 0.375 seconds for every attempt.

The subjects were transported from their housing containers to the experiment enclosure after body measurements were collected. The enclosure was a see-through acrylic box, where each side of the enclosure, except the front lateral view, was covered with white cardstock to eliminate any outside light and disturbances. The enclosure was around 35x70 cm with an average temperature of 75 degrees Fahrenheit. The snakes were put on either side of the enclosure and were given around 10 minutes to adjust to the new environment before recording.

The threat target, used to initiate a defensive strike, was a filled balloon attached to the end of a rod. The balloons served as an effective threat subject as it was soft, harmless towards snakes, and allowed for easy contact visualization. Each balloon was blown up to around 20 cm and tied to a 1.5-meter rod. This provided a safe distance away from the snakes. This balloon was placed at the opposite end of the filming arena and slowly moved towards the snake until a strike was initiated (Figure 1). Since the snakes might not strike from the balloon's physical appearance, we rubbed the bottom of the enclosure with the balloon and rod to potentially generate vibrations, similar to previous studies (Whitford et al., 2020). Most snakes immediately struck at the prey target, but some needed mild agitation to provoke the defensive behavior, similar to previous studies (Penning et al., 2020). After a couple of test runs to see if the 21 snakes would display defensive behavior, ten individuals displayed the behavior. Due to these previous trials, this experiment focused on the ten individuals who expressed defensive strike behavior. Each subject had at least one recorded trial, with a total of 16 trials in the end. Only the strike trials with the maximum results were analyzed, so we used a total of nine trials for this data set to see the effectiveness of the influence of body size. One individual's trial was deemed as the outlier of the data, and therefore excluded from the data analysis.

VIDEO ANALYSES

I analyzed two variables from each strike trial by digitizing points with Matlab and DLTcal8/DLTdv8 programs. Prior to the analysis, we used Lego pieces and their dimensions to calibrate the XYZ points using the DLTcal8 program. The lego was placed in the enclosure and photographed before every experimental trial. Calibrations were made after every experimental day. Then using these calibrations, I used a program called DLTdv8 to digitize videos and annotate them frame by frame. In each video frame, a digital point was placed the snake's eye closest to the lateral camera in both videos. It can then be translated into a file of XYZ points in the three-dimensional space. Digitized XYZ points were then exported from DLTdv8 into Matlab to calculate measurements of the velocity, acceleration, strike distance, and duration. We used a Butterworth filter with a displacement of 50 Hz similar to other past studies (Penning et al., 2020; Herrel et al., 2011) to filter the data.

Statistics

All data, including body mass and performance variables, were analyzed using a least-squares linear regression to correlate body size to the strike performance variables. The R2 and p-value were determined from these regressions, and $p<0.05$ was considered statistically significant.

RESULTS

Strike Performance

All ten test subjects readily struck at the target. Maximum performance was calculated by selecting the trial with the maximum velocity. Five subjects were only willing to strike once, while the other five subjects striked two or three times in total. None of the subjects striked more than once during a trial, so each trial was considered a single strike. Out of the 16 trials, one trial was a missed defensive strike, where the individual failed to make contact with the target. All strikes started in a coiled position with the rattling warning sign behavior, and then led to a horizontal strike toward the target. Similar to Herrel et al., (2011), after initial contact with the target, all strikes continued forward and were displaced posteriorly.

Strike velocity in the snakes tested ranged from 2.22 ms^{-1} to 3.61 ms^{-1} (mean: 2.98±0.52 ms^{-1}). Maximum strike accelerations ranged from 60.2 ms^{-2} to 105.69 ms^{-2} (mean: 78.9±16.65 ms^{-2}). The longest strikes approached 0.23 cm with the longest strike duration of 0.15 ms (mean: 0.12±0.048 cm, 0.09±0.026 ms, respectively).

Maximum velocity occurred either before or at the initial contact with the target for eight of 10 strikes. (Throughout the overall trials, 12 of 15 strikes showed this trend as well, excluding the unsuccessful strike trial). In the eight strikes that reached maximum velocity before making contact with the target, max velocity was reached in less than 0.02 milliseconds prior to contact. Overall, the ten strikes reached a range of 0.0013 to 0.019 milliseconds (1 to 15 frames) before or after the initial contact (mean: 0.0095 ± 0.0054 ms). Maximum acceleration occurred before initial contact with the target for all ten strikes. (Overall, 15 of 15 strikes trials showed this trend). In the ten strikes that reached maximum acceleration before making contact with the target, the max acceleration was reached in less than 0.02 milliseconds in four strikes, between 0.02 and 0.04 milliseconds in four strikes, and over 0.04 milliseconds in two strikes. Overall, the ten strikes had a range of 0.0088 to 0.064 milliseconds (7 to 51 frames) before initial contact with the target (mean: 0.028 ± 0.018 ms).

Out of the ten strikes, one was considered an outlier due to its low values of maximum acceleration and velocity compared to the other nine. Out of the nine strikes, the strike distance had a range from 0.07 to 0.23 meters (mean: 0.12 ± 0.048 m). The strike duration had a range from 0.063 to 0.015 ms (mean: 0.09 ± 0.026 ms).

Scaling

Strike performance, specifically maximum velocity, increased significantly with body size in the nine snakes used for analyses ($R^2 = 0.48$; $P = 0.026$, $DF = 8$) (Figure 2A). However, this increased strike performance was not significantly predicted by strike distance or maximum acceleration (Figure 4). Larger animals did not reach the maximum acceleration, where acceleration is independent to body mass ($R^2 = 0.2$; $P = 0.2$, $DF = 8$) (Figure 2B). Higher maximum velocities were also not a result of high maximum acceleration ($R^2 = 0.03$; $P = 0.58$, $DF = 8$). Snout-vent-length scaled with isometry relative to the overall body mass, indicated that the snakes maintained a similar shape throughout ontogeny (Figure 3).

DISCUSSION

Strike Performance

In our study, velocity from the terrestrial rattlesnake was positively correlated with body mass (Figure 2A). We also found that maximum acceleration was independent of body mass (Figure 2B) through weak correlation. We found opposing results for the correlation of body mass and velocity, acceleration, and strike distance compared to previous studies on pit vipers (Herrel et al., 2011). By taking the maximum values of each subject, we conclude that larger animals have higher velocities, but do not accelerate faster. Having a higher maximum acceleration also does not lead to higher maximum velocities, showing independence from one another. Finally, we found that snakes grow isometrically, maintaining a constant shape.

Scaling to Velocity

Contrary to my predictions, the results showed that larger snakes, those who have higher body mass, reach higher maximum velocities than smaller snakes (Figure 2A). There is a significant correlation between velocity and body mass, unlike previous studies such as Herrel et al., (2011). It is currently not known whether the higher velocity correlation is related to terrestrial behavior and ambush hunting styles, but it is possible that there are key differences in behavior and performance between terrestrial and arboreal pit vipers. Herrel et al., (2011) identified a trend where larger animals are underperforming biomechanically, having lower acceleration and velocities compared to the values of juveniles. The correlation we found where larger animals are maximizing their abilities to perform and strike can be due to terrestrial, ground ambush hunting, which allows for animals to strike at their maximum capabilities, without having to consider outside factors, such as balance and gravity, that arboreal snakes face.

Scaling to Acceleration

We note that larger animals do not show that they significantly accelerate faster than smaller animals (Figure 2b). Although there is a weak correlation, it is not strong enough to state that there is a certain correlation between body mass and acceleration, contradicting the study by Herrel et al., (2011) and our predictions. One of the possible reasons for this is that large animals might achieve higher values of forward momentum since this depends on body mass (Young, 2010). High momentum can be generated with increased muscle force, which can lead to higher strike velocity, and the use of extension (initial stage) is shown to need minimal acceleration (Kardong and Bels, 1998; Young, 2010). Young (2010) studied how the axial muscles and initial position, coiled position, influence the power amplification that enables large animals to exceed minimal forces and acceleration to successfully strike at the target during a defensive strike. Since extension is when the snake straightens from a previous initial coiled position (Young, 2010), it is possible that acceleration was independent of body mass due to the use of the initial extend stage position, where all *C. viridus* subjects were in a coiled position, to fully extend, causing a high velocity but not acceleration. Although this study did not test how the effects of elastic muscular mechanisms influence performance similar to the study from Young (2010), we can note that it is a possibility that vipers are not using as much elastic recoiling as the puff adders (Young, 2010) to achieve such rapid accelerations during the strikes.

It is also possible that rattlesnakes reach these high velocities and not high accelerations due to the distance they cover (LaDuc, 2002). Although our results do not show a strong correlation of strike distance to both higher velocities or acceleration patterns (Figure 4) due to $p>0.05$, this can be due to the limited sample size of strikes. This can also be a reason why having a higher acceleration did not lead to having a higher velocity in this study, as they are independent variables from one another.

Scaling in Relation to Ecology and Mechanics

The values of maximum velocity in defensive strikes were reached prior to initial target contact in the majority of the strikes, (8 of 10), similar to results found by defensive strikes in *C. atrox* by LaDuc (2002) and predatory strikes in Kardong and Bels (1998). The values of maximum acceleration were reached prior to initial contact with the target in all ten strike trials, similar to findings from Kardong and Bels (1998) where they also found that strikes showed deceleration of the head before the target contact. There can be several possible reasons why these maximum values are achieved before target contact. Kardong and Bels (1998) found that many strikes show this performance as a safety mechanism to prevent the jaw from experiencing too much force that can cause damage and harm. Another possibility can be that the strike was intended as a warning sign, rather than a more successful strike (Whitford et al., 2020). They can be underperforming or striking with higher velocity and acceleration a bit before contact to simply reduce their encounter with the predator and to avoid fighting (Whitford et al., 2020). Although rattlesnakes have their rattling sounds as the initial warning sign, striking faster and potentially unsuccessfully can be their backup defense mechanism.

There are also adaptations, such as camouflage and crypsis (Whitford, 2020) that can cause underperformance of strikes. Snakes with patterns on their back allow them to hide and remain unspotted from predators, where they will only defend themselves if they feel threatened or get injured. As our subjects were housed in the lab for several months, they may have a reduced level of motivation defensively striking to the maximum of their abilities, which can lead to variance in our data. However, this is unlikely given comparable results from lab and field studies of rattlesnakes.

Although the body temperatures of this study's subjects were not taken, there is a possibility that larger animals have a higher body temperature, allowing them to strike successfully and perform at better speeds. This can be studied as a further investigation to see the correlation between body temperature, body mass, and kinematics. Our snakes likely all had the same temperature (room temperature of around 70 degrees Fahrenheit), but an additional follow-up study is to examine the effects of temperature on the relationship between body mass, maximum velocity, and acceleration. This is especially important given that prairie rattlesnakes live over a very wide range of temperatures from southern Canada to northern Mexico.

CONCLUSION

Prairie rattlesnakes, ambush terrestrial snakes, are well known for their distinct behaviors as a predator against prey, or defensively when threatened or injured. These predators are important to study as they are a prime example of displaying both characteristics, widening our understanding of predator-prey interactions in the study of animal biomechanics and behavior in snakes.

Although we found that large terrestrial snakes perform with higher velocities and constant acceleration, this is only one species. Given the discrepancies between our study and the previous work by Herrel et al. (2011), the correlations between body size and performance should be examined in many other ambush-hunting species of snake. We predict that our scaling relationship will hold for other terrestrial snakes, but might differ among ecologically-distinct species.

For further studies, there should be more consideration about various factors that can contribute to the performance of strikes, internal factors such as individual stress levels, feeding, and acclimation periods, and external factors such as feeding period relative to the experiment day. Both external and internal factors can have a huge influence on behavior, along with phenotypic differences.

Ongoing studies of the muscular system of *C. viridis* can possibly explain more about the performance of the defensive strikes, by directly looking at the muscle activity during both strikes. These studies can investigate the relationship between muscle morphology, and possible elastic storage mechanisms in vipers, with kinematics to further understand the relationship between body mass with performance. It can also find more data on kinematically active regions, where it is said that defensive strikes use more than half of its body to strike (Kardong and Bels, 1998), and see if that influences their strike performance. There have been previous studies that investigate this such as Whitford et al. (2020), but more species would be needed to make any general conclusions about snake strike kinematics. Further studies can also compare the predatory and defensive strikes in this species to be able to analyze any comparisons. For any future studies including the *C. viridis*, it will also be useful to use a bigger sample size with multiple trials per subject to possibly see a stronger correlation.

Hopefully, further investigation can identify general defensive strike patterns for terrestrial snakes that ambush prey. By understanding the relationship between body mass, velocity, and acceleration, we can further enhance our understanding of how biomechanics can influence the biology of snakes. Similarly, combining ecological and biomechanical studies will uncover potential ecological drivers of different attack strategies and performance.

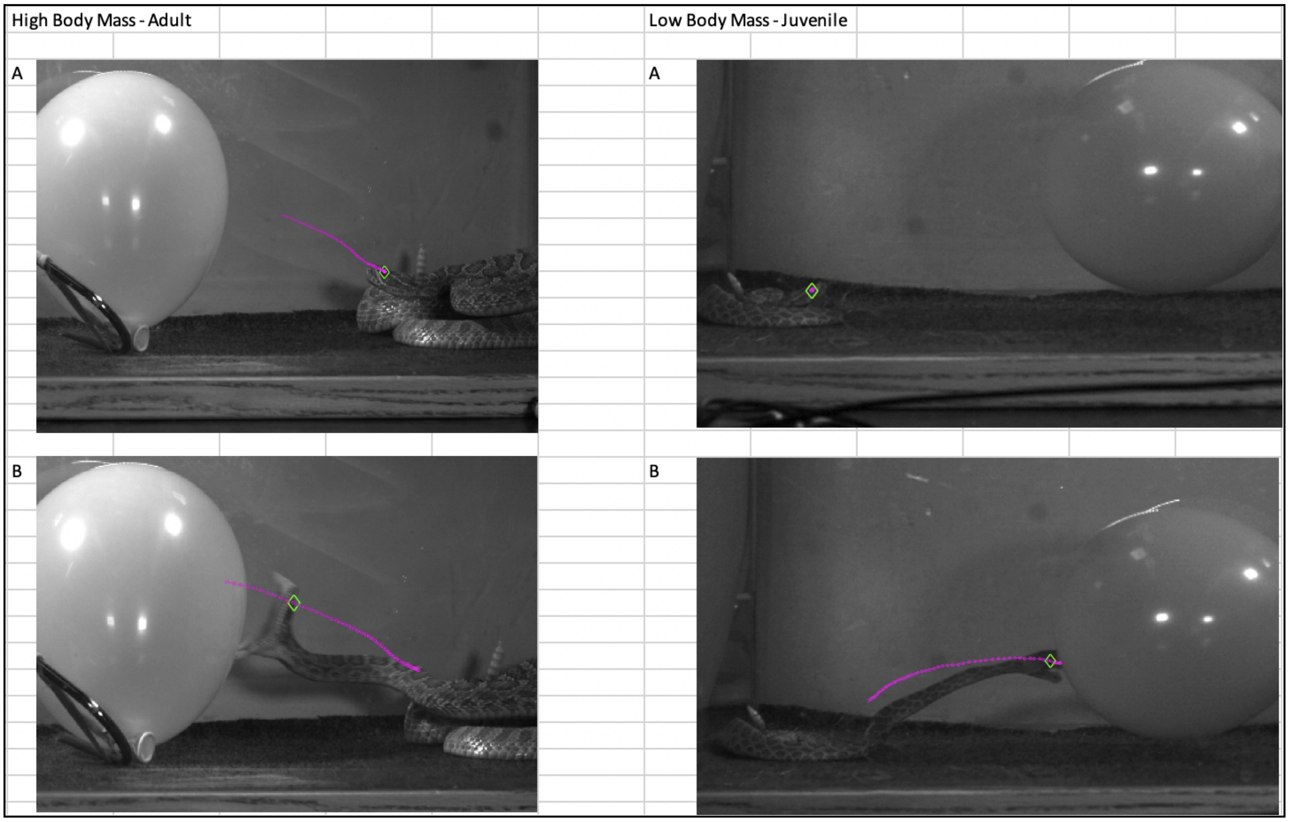

Figure 1: Defensive strikes of Crotalus viridus for high body mass (left) and low body mass (right) either (A) stationary or (B) striking at the target and making contact. The points are placed on the eye for digitizing purposes.

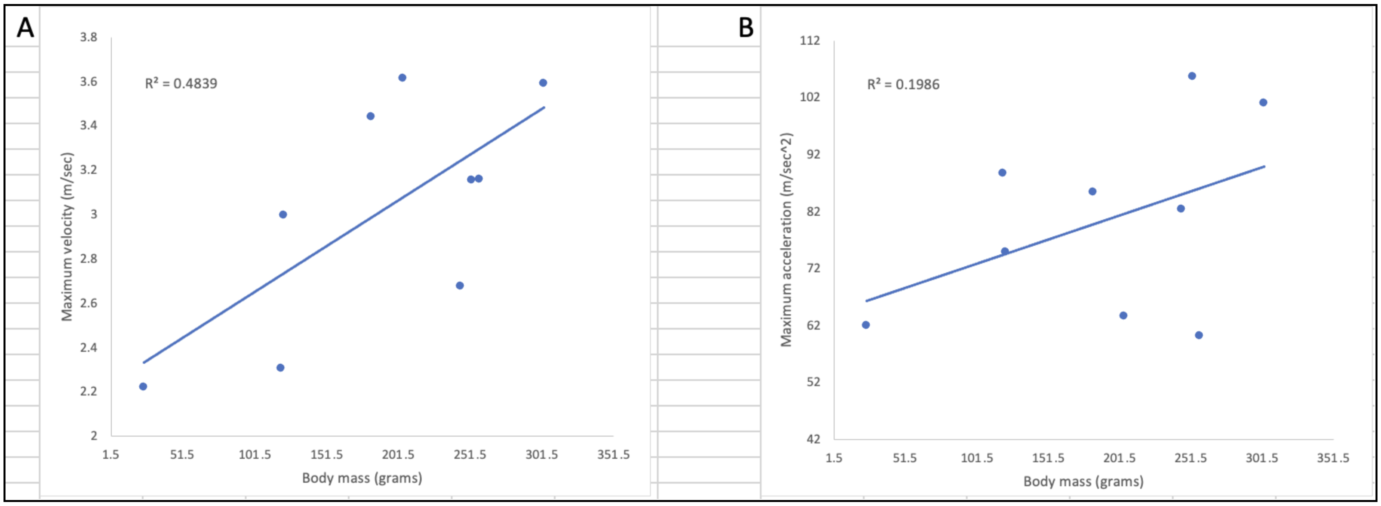

Figure 2: Scatterplots illustrating the scaling of (A) maximum strike velocity and (B) maximum acceleration relative to body mass. Strike velocity increases with body size, whereas strike acceleration is independent of body size.

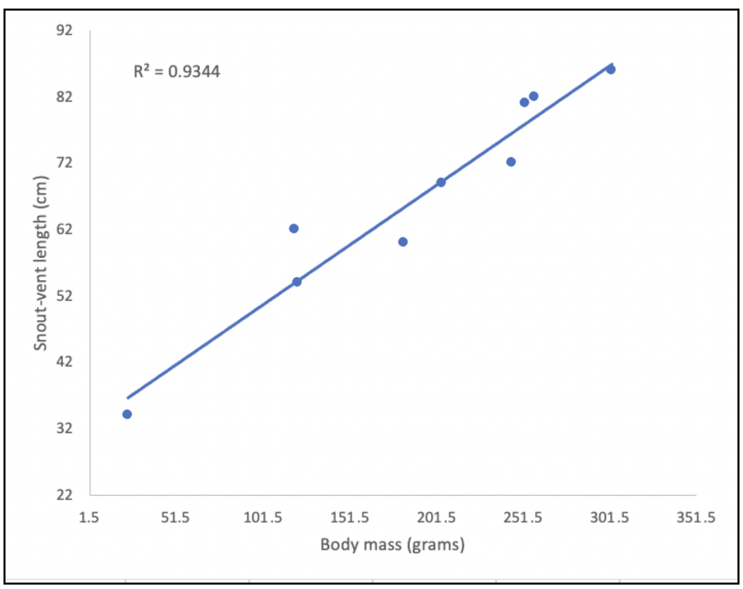

Figure 3: Scatterplot illustrating the scaling of snout-vent-length relative to body mass.

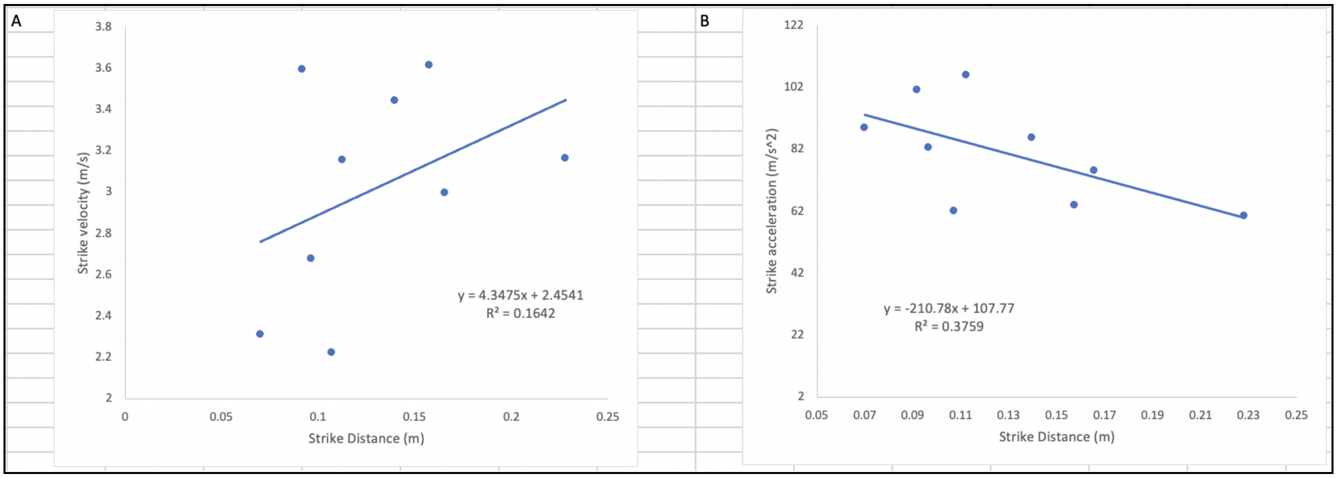

Figure 4: Scatterplots illustrating the scaling of (A) maximum strike velocity and (B) maximum acceleration relative to strike distance. Strike distance is shown to be independent relative to maximum velocity and acceleration due to an insignificant correlation.

REFERENCES

Araujo, Marcio. S. and Martins, Marcio. “Defensive behaviour in pit vipers of the genus Bothrops (Serpentes, Viperidae).” Herpetol. J. 16. 2006. pp. 297-303.

Araújo, M. S., & Martins, M. “The defensive strikes of five species of lanceheads of the genus Bothrops (Viperidae).” Brazilian Journal of Biology, 67. 2007. pp. 327–332. https://doi.org/10.1590/S1519-69842007000200019

Carbone, C., et al. “Energetic constraints on the diet of terrestrial carnivores.” Nature 402, 286–288. 1999. https://doi.org/10.1038/46266

Enders, Frank. “The Influence of Hunting Manner on Prey Size, Particularly in Spiders with Long Attack Distances (Araneidae, Linyphiidae, and Salticidae).” The American Naturalist, vol. 109, no. 970. 1975. pp. 737–63. JSTOR, http://www.jstor.org/stable/2459867

Griffiths, David. “Foraging Costs and Relative Prey Size.” The American Naturalist, vol. 116, no. 5, 1980, pp. 743–52. JSTOR, http://www.jstor.org/stable/2460632

Hampton, Paul M. “Ontogenetic Prey Size Selection in Snakes: Predator Size and Functional Limitations to Handling Minimum Prey Sizes.” Zoology (Jena), vol. 126. 2018. pp. 103–09, https://doi.org/10.1016/j.zool.2017.11.006.

Hanscom, R.J., et al. “Ambush Hunting in Snakes: Behavior, Function, and Diversity.” 2023. In Press.

Herrel, Anthony, et al. “Fast and furious: effects of body size on strike performance in an arboreal viper Trimeresurus (Cryptelytrops) albolabris.” Journal of experimental zoology.

Part A, Ecological genetics and physiology vol. 315, 1. 2011. pp 22-29. http://doi.org/10.1002/jez.645

Kardong, Kenneth V., and Vincent L. Bels. "Rattlesnake Strike Behavior: Kinematics." Journal of Experimental Biology, vol. 201, no. 6. 1998. pp. 837–50, https://doi.org/10.1242/jeb.201.6.837.

Kyle G. Ashton. "Body Size Variation Among Mainland Populations of the Western Rattlesnake (Crotalus Viridis)." Evolution, Volume 55, Issue 12, 1. 2001. pp. 2523–2533, https://doi.org/10.1111/j.0014-3820.2001.tb00766.x

LaDuc, Travid J. "Does a quick offense equal a quick defense? Kinematic comparisons of predatory and defensive strikes in the western diamond-backed rattlesnake (Crotalus atrox)." Biology of the Vipers 2002:267e278. 2002.

Mori, Akira, and Gordon M. Burghardt. "Thermal Effects on the Antipredator Behavior of Snakes: A Review and Proposed Terminology." Herpetology Journal, vol. 14, 2004. Pp. 79-87, http://bhs.org/moriandburghardt

Penning, David A, et al. "The scaling of terrestrial striking performance in western ratsnakes (Pantherophis obsoletus)." J. Exp. Zool. 2020. 333:96–103. https://doi.org/10.1002/jez.2328

Whitford, Malachi D., et al. "The Effects of Temperature on the Defensive Strikes of Rattlesnakes." Journal of Experimental Biology, vol. 223, no. Pt 14. 2020. https://doi.org/10.1242/jeb.223859.

Young, Bruce A. "How a heavy-bodied snake strikes quickly: high-power axial musculature in the puff adder (Bitis arietans)." Journal of Experimental Zoology. Part A, Ecological genetics and physiology vol. 313,2. 2010. pp. 114-121. http://doi.org/10.1002/jez.579