Biomechanics

Debunking the viper’s strike: harmless snakes kill a common assumption

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To survive, organisms must avoid predation and acquire nutrients and energy. Sensory systems must correctly differentiate between potential predators and prey, and elicit behaviours that adjust distances accordingly. For snakes, strikes can serve both purposes. Vipers are thought to have the fastest strikes among snakes. However, strike performance has been measured in very few species, especially non-vipers. We measured defensive strike performance in harmless Texas ratsnakes and two species of vipers, western cottonmouths and western diamond-backed rattlesnakes, using high-speed video recordings. We show that ratsnake strike performance matches or exceeds that of vipers. In contrast with the literature over the past century, vipers do not represent the pinnacle of strike performance in snakes. Both harmless and venomous snakes can strike with very high accelerations that have two key consequences: the accelerations exceed values that can cause loss of consciousness in other animals, such as the accelerations experienced by jet pilots during extreme manoeuvres, and they make the strikes faster than the sensory and motor responses of mammalian prey and predators. Both harmless and venomous snakes can strike faster than the blink of an eye and often reach a target before it can move.

1. Introduction

For many organisms, defence and feeding involve different behaviours or different levels of performance during the same behaviour [1–4]. For many snakes, striking can be used both to catch prey and defend against predators [1,2]. Scientific descriptions of viper strikes date at least as far back as the early nineteenth century [5], and one of the first animal behaviours viewed with high-speed imagery was a rattlesnake strike [6,7]. For much of the twentieth century, the assumption that a viper strike represents ‘the fastest thing in nature’ has dominated our understanding of strike performance in snakes [5–8]. This assumption was tested with high-speed photography in 1954, which showed markedly slower strike velocities in rattlesnakes than generally expected [7]. However, the belief persists that vipers have the fastest strikes among snakes [9,10]. In order for a strike to be successful—regardless of the species involved—a snake must contact prey before it escapes or deter a threat before it causes harm. We used high-speed video recordings to test whether or not harmless ratsnakes can strike as fast as two species of vipers that often feed on similar prey and encounter similar kinds of predators.

We compared defensive strike distances, durations, and peak accelerations and velocities among species using data from 14 Texas ratsnakes (*Pantherophis obsoletus*; mean mass ± s.e. = 348 ± 71 g, snout–vent length = 91 ± 5.6 cm), 6 western cottonmouth vipers (*Agkistrodon piscivorus*; 273 ± 15.8 g, 68 ± 2.4 cm), 12 western diamond-backed rattlesnakes (*Crotalus atrox*; 634 ± 38 g, 95 ± 2.0 cm) and previously published studies [2,4,10,11]. We discuss the accelerations of snake strikes in relation to the known physiological effects...
2. Material and methods

We presented each snake with a target (stuffed glove) and recorded 4–8 defensive strikes per snake. We performed all trials at 27°C. To record strikes, we used a Redlake (San Diego, CA, USA) MotionScope high-speed camera set at 250 Hz and a shutter speed of less than or equal to 0.004 s. Depending on their size, we recorded snakes in an arena measuring 30 × 30 × 60 cm or 65 × 95 × 37 cm with a scale grid visible in the same plane as each snake’s strike.

We analysed only strikes that were perpendicular to the camera. From the high-speed videos, we derived strike distance as the linear distance between the snake’s snout and the target at the onset of the strike, and strike duration as the total time from the initiation of strike movement to first contact with the target. Maximum velocities and accelerations are the highest single (frame-to-frame) values obtained from analyses of filtered coordinates ([2]; 50 Hz cut-off Butterworth filter). We analysed peak values for each variable (often from different strikes [2]) from each snake and obtained by digitizing videos using Tracker 4.87 software (Open Source Physics, http://www.opensourcephysics.org/index.cfm).

We log-transformed the data and treated strike duration (s), distance (m), maximum acceleration (ms⁻²) and maximum velocity (ms⁻¹) as dependent variables. We used an ANCOVA for each dependent variable with species as the independent variable and body mass as the covariate. We also compared maximum accelerations and velocities with more complex models (one for acceleration and one for velocity) incorporating mass, species, strike distance (from the same strike that produced the maximum values) and their interactions, and subsequently excluded non-significant interactions. All model assumptions were tested and met. For maximum strike distance, two outliers were removed (standardized residual > 2) to meet assumptions. We used JMP Pro 11.0.0 and RStudio (0.99.441) for analyses, and determined significance whenever \( p < 0.05 \). We lack sufficient data for analysing muscle cross-sectional areas in these species.

3. Results and discussion

All snakes struck with very high accelerations (range = 98–279 ms⁻²) and velocities (2.10–3.53 ms⁻¹), over short distances (8.6–27.0 cm), and with short durations (48–84 ms). Strike performance was not significantly different among species for three of the four variables (figure 1; table 1). Snakes displayed similar strike accelerations (\( F_{2,28} = 1.5, p > 0.23 \)), velocities (\( F_{2,28} = 1.8, p > 0.17 \)) and durations (\( F_{2,28} = 2.6, p > 0.09 \)). However, peak strike distance differed significantly (\( F_{2,26} = 7.2, p < 0.01 \)), with rattlesnakes striking shorter distances than ratsnakes. The lack of corresponding differences in duration or velocity was owing to peak values coming from different and variable strikes. There was no difference among species in maximum accelerations (\( F_{2,27} = 0.91, p > 0.38 \)) or velocities (\( F_{2,27} = 1.9, p > 0.16 \)) in models where both mass and strike distance were included as covariates. Rattlesnake strikes matched or exceeded the performance of viper strikes in other studies (table 1).

Strike accelerations were similar and impressively high in all three species that we studied (table 1) and are similar to those of feeding strikes [1]. Strike accelerations are probably more important than the peak velocities [2] because strikes do not involve a chase. These accelerations have two sets of important consequences. First, the high accelerations keep the strike durations shorter than the response times of mammalian predators and prey. Mammalian startle responses can activate muscles in 14–151 ms, and produce observable movement in as little as 60–395 ms [12,13]; non-mammalian response times are not well known. Our results demonstrate that both harmless and venomous snake strikes can reach their targets in \( ca 50–90 \) ms, which is often faster than mammals can respond. These strikes are literally faster than the blink of an eye, which takes 202 ms in humans [14]. However, strike performance and prey capture in nature may not always be this high [15]. If strike durations are longer than the response times of the targets, then strike accelerations and reaches must be high enough to overcome the predator or prey once it has initiated a response. Our two highest strike accelerations (274 ms⁻² from a ratsnake and 279 ms⁻² from a rattlesnake) were approximately an order of magnitude greater than the jumping accelerations of black-tailed jackrabbits [16], and 30% faster than those of kangaroo rats [17,18], whose escape behaviour may have evolved in response to snake predators [18]. The impressive strike performance across species indicates that selection for rapid strike performance acts on many snakes. Snakes that defend against similar kinds of predators or feed on similar kinds of prey, such as small mammals, probably all need to have comparably high accelerations and short strike durations.

A second important consequence of strike performance involves physiological tolerances to high accelerations. Blood flow to the brain may be reduced during rapid head-first accelerations [19], such as those in snake strikes. Humans rarely experience accelerations as high as those of snake strikes. Fighter-jet pilots launching from an aircraft carrier experience take-off accelerations of only 27–49 ms⁻² [20]. Without the aid of anti-gravity suits, pilots can lose consciousness at accelerations that are 21–23% of the values achieved by our snakes [19]. Even with anti-G suits, pilots lose the ability to stand up from sitting at accelerations of \( ca 30 \) ms⁻² and lose the ability to move their limbs when...
accelerations reach 78 ms\(^{-2}\) [19]. Acceleration duration and heart-to-head distance are important in physiological responses to acceleration [19], as is size [21], which complicates our ability to understand how acceleration affects other animals. The long distances between the heart and head in many snakes could make them susceptible to impaired cranial blood flow during strikes, similar to the impairment that can occur during climbing [22], but the very short strike durations may preclude such physiological disruptions. The events at the end of a strike may have additional effects [19], but the effects of rapid deceleration and impact on a soft-bodied target are well tolerated by snakes.

Despite statements in the literature [9,10], vipers do not strike faster than all other snakes. Ratsnakes and vipers alike have similarly impressive strikes. Such high accelerations disrupt the physiology of other animals, but are well tolerated by the snakes and allow them to make contact before their targets can respond. Selection for high strike performance may be heavily influenced by the target’s sensory and motor response capacities, which are an understudied aspect of predator–prey interactions. With so few snakes having been studied thus far, it seems likely that future research will reveal a greater range of performance in these diverse and successful predators.

**Ethics.** This work was approved by the University of Louisiana at Lafayette’s Institutional Animal Care and Use Committee.

**Data accessibility.** Complete dataset (https://figshare.com/s/156f2bf10d5767051cc9).

**Authors’ contributions.** D.A.P. conceptualized the project, collected data and drafted the manuscript. B.R.M. helped with data collection and writing. B.R.M. helped with project design, data collection and writing. All authors agree to be held accountable for the content herein and gave approval for publication.

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### References


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**Table 1.** Defensive strike performance by *Pantherophis obsoletus* and several vipers. Our data (top three) are means ± s.e.m. (covariate-adjusted mean in parentheses). Other data are means except for medians of best-performance values from five *Bothrops* species [11]; emdashes indicate no data. *Trimeresurus albolabris* values are composite means from male and female means [2].


