

RESEARCH ARTICLE

The effects of temperature on the defensive strikes of rattlesnakes

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ABSTRACT

Movements of ectotherms are constrained by their body temperature owing to the effects of temperature on muscle physiology. As physical performance often affects the outcome of predator–prey interactions, environmental temperature can influence the ability of ectotherms to capture prey and/or defend themselves against predators. However, previous research on the kinematics of ectotherms suggests that some species may use elastic storage mechanisms when attacking or defending, thereby mitigating the effects of sub-optimal temperature. Rattlesnakes (*Crotalus* spp.) are a speciose group of ectothermic viperid snakes that rely on crypsis, rattling and striking to deter predators. We examined the influence of body temperature on the behavior and kinematics of two rattlesnake species (*Crotalus oreganus helleri* and *Crotalus scutulatus*) when defensively striking towards a threatening stimulus. We recorded defensive strikes at body temperatures ranging from 15–35°C. We found that strike speed and speed of mouth gaping during the strike were positively correlated with temperature. We also found a marginal effect of temperature on the probability of striking, latency to strike and strike outcome. Overall, warmer snakes are more likely to strike, strike faster, open their mouth faster and reach maximum gape earlier than colder snakes. However, the effects of temperature were less than would be expected for purely muscle-driven movements. Our results suggest that, although rattlesnakes are at a greater risk of predation at colder body temperatures, their decrease in strike performance may be mitigated to some extent by employing mechanisms in addition to skeletal muscle contraction (e.g. elastic energy storage) to power strikes.

KEY WORDS: Predator–prey, Temperature, Kinematics, Gape, Elastic storage

INTRODUCTION

Most animals must contend with predators, and the risk imposed by predation is a fundamental force shaping morphology and behavior. Encounters with predators can involve vigorous movements where both predator and prey benefit from exerting maximal performance. Although a variety of intrinsic (e.g. muscle size, nutrition, motivation etc.) and extrinsic (e.g. wind speed, light level, substrate etc.) factors affect performance and interaction outcome, some factors are broadly important across many contexts. For ectothermic species, environmental temperature holds substantial

influence over muscle-driven movements (Angilletta et al., 2002; Herrera et al., 2018; Huey and Kingsolver, 1989).

Temperature has large impacts on muscle-driven movements (Bennett, 1985). In general, the contractile rates of skeletal muscle doubles with a 10°C increase in temperature (i.e. a Q_{10} value of ~2), and the effects of temperature on the capacity for many ectothermic species to perform muscle-driven movement has been well documented (Angilletta et al., 2002; Bennett, 1985; Peplowski and Marsh, 1997). This strong correlation between muscle physiology and performance is often deleterious, as it can hinder the ability of ectotherms to capture prey and flee from predators at lower body temperatures (Kruse et al., 2008). As a result, many ectotherms have mechanisms that act to mitigate the deleterious effects of low temperature on performance (Anderson et al., 2014; Deban and Richardson, 2011; Deban and Scales, 2016; Higham and Irschick, 2013; Scales et al., 2016). For example, chameleons project their tongue by using muscles to stretch and store energy in elastic structures which, upon release, rapidly propel the tongue forward (Anderson and Deban, 2010). Temperature has less influence on performance traits that rely on energy stored in elastic structures because the rate of recoil is a product of the material property of the elastic structure (Roberts and Azizi, 2011). Elastic recoil mechanisms similar to the one used by chameleons have been found repeatedly in animals that use ballistic movements to capture prey or flee predators (Burrows, 2009; Deban and Lappin, 2011; Patek et al., 2011, 2004; Van Wassenbergh et al., 2008).

Vipers (family Viperidae) are a near globally distributed family of venomous snakes that can be highly abundant mesopredators in tropical and temperate environments. Relative to many other snake families, vipers tend to be heavy-bodied (Feldman and Meiri, 2013; Pough and Groves, 1983), relying on crypsis and defensive displays to dissuade attacks by predators, rather than rapid flight (Araujo and Martins, 2006; Shine et al., 2002). The defensive displays of vipers are bolstered by their potential to inflict a painful and potentially harmful bite on an attacking predator. As vipers are active across a wide range of temperatures (Ayers and Shine, 1997; Putman and Clark, 2017), a strong positive correlation between defensive strike performance and temperature would indicate that they experience a higher risk of predation when confronted by an endothermic predator at colder temperatures. However, recent studies suggest vipers may have mechanisms to diminish the effects of temperature on strike performance. Young (2010) conducted an electromyographic study of puff adder (*Bitis arietans*) musculature and found that they contracted their dominant epaxial musculature prior to, but not during, defensive strikes. This pattern suggests that the adders may be stretching and storing energy in elastic structures prior to the strike, and then using the stored energy to propel their heads forward rather than relying primarily on temperature-dependent muscle contractions. As the storage and release of energy from elastic structures is controlled by the material properties of the structure and not chemical energy – unlike a muscle contraction – the strike performance of heavy-bodied vipers, such as puff adders and rattlesnakes, may be relatively resistant to change in temperature.

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In North and Central America, rattlesnakes (genus *Crotalus*) are the most abundant and diverse viperid group and, despite their defensive capabilities, are killed and eaten by a variety of mammalian and avian predators (Cartron et al., 2004; Greene, 1992; Hernández et al., 1994; Steenhof and Kochert, 1985). Rattlesnakes are well known for their active defensive rattling displays that often incorporate repeated strikes towards a potential predator (LaDuc, 2002). When defensively striking, rattlesnakes typically raise the anterior portion of their body off the substrate and into a position to propel their head towards the predator by rapidly straightening their body, opening their mouth to ~100 deg, biting and potentially injecting venom upon contact with the predator (Hayes et al., 2002; LaDuc, 2002). Defensive striking may also be performed to reduce the likelihood that a predator or dangerous animal (e.g. large mammal) approaches (Moon et al., 2019). Defensive strikes that do not result in snakes contacting the putative target can function as a warning or bluff, meant to increase the distance between the snake and the perceived threat. Strikes intended to startle, bluff or make contact all involve vigorous movements that are likely to be affected by temperature.

While the thermal ecology of rattlesnakes has been studied from many different perspectives (Dorcas et al., 2004; Martin and Bagby, 1972; Zaidan and Beaupre, 2003), surprisingly few studies have examined how strike performance varies with temperature, and those that have present data that are contradictory and do not account for the effect of strike distance on performance metrics. The distance between the snake and the target at strike initiation is an important factor because it has been shown to have substantial influence on strike performance metrics (Herrel et al., 2011; LaDuc, 2002) and therefore must be taken into account. Rowe and Owings (1990) found that western rattlesnake (*Crotalus oreganus* Holbrook 1840) strike velocity was unaffected by temperatures between 18 and 27°C, but increased at temperatures above 27°C and decreased at temperatures below 18°C. Stepp-Bolling (2012), however, found that strike performance of the same rattlesnake species was unchanged at 26–37°C, but strike velocity and acceleration increased at 16–29°C. As these studies disagree on how temperature influences rattlesnake strike performance across the typical range of active temperatures, between 15 and 35°C (Putman and Clark, 2017; Taylor et al., 2004), the role of temperature remains unclear. Additionally, the data from Rowe and Owings (1990) suggest that temperature effects on strike performance could be relatively low, as the highest back calculated Q_{10} for their data is approximately 1.6 for temperatures of 10–18°C.

Here, we studied rattlesnake defensive strike performance in an experimental laboratory arena in order to quantify the degree to which rattlesnake strike performance changes with temperature. If snakes are striking with maximal effort and their movements do not include the use of elastic recoil, we expect relatively high thermal dependence ($Q_{10} \approx 2$). Alternatively, if snakes do not utilize maximal effort in defensive strikes and/or employ elastic recoil elements, we expect relatively low thermal dependence ($Q_{10} \approx 1$). Using high-speed videography, we recorded defensive strikes from western rattlesnakes (*C. o. helleri* Meek 1905), the same species used in previous studies, and Mohave rattlesnakes [*Crotalus scutulatus* (Kennicott 1861)], a similar-sized crotalid native to desert environment. We addressed the following questions. (1) Are the likelihood, accuracy, and latency of a rattlesnake striking associated with body temperature? (2) Is rattlesnake defensive strike performance (linear velocity and acceleration) robust to changes in temperature? (3) Is the ability of rattlesnakes to inflict a bite (angular velocity and acceleration of jaw) robust to changes in temperature?

(4) Do strike performance and the effects of temperature differ between these two species?

MATERIALS AND METHODS

Animals

Mojave rattlesnakes were collected from Hidalgo County, New Mexico, USA from 2015 to 2018, while western rattlesnakes were collected in San Diego County (USA) from 2015 to 2018. Although the site in New Mexico is hotter and drier, free-ranging snakes at both sites naturally experience the full range of temperatures we tested in our study. All rattlesnakes were housed at San Diego State University as part of a permanent captive collection. They were given *ad libitum* water, fed a lab mouse every other week, and maintained at a room temperature of 28–30°C with a 12 h light:12 h dark cycle. All procedures herein were approved by the San Diego State University Institutional Animal Care and Use Committee (APF 19-08-009C).

Strike recording

To record defensive strikes, snakes were first placed in cloth snake bags and housed overnight in a temperature-controlled room. Snakes were given at least 12 h to acclimate to the test room temperature. Once acclimated, individual snakes were placed in a 50 cm (w)×50 cm (l)×30 cm (h) plywood enclosure with a transparent acrylic front wall and a calibration grid attached to the back wall of the enclosure. The enclosure was also housed in the temperature-controlled room. We recorded during photophase (room lights on) and used supplemental short wavelength infrared lighting (outside the range of long wavelength infrared detectable by pit organs; Goris, 2011) to further illuminate the enclosure (Univivi 8LED IR illuminators). We positioned a single Edgertronic (model SC2) high-speed camera recording at 250 frames s⁻¹ and 1/1000 shutter speed for 10 s to record strikes through the transparent side of the enclosure. To ensure recorded strikes were perpendicular to the back of the enclosure, we mounted a mirror above the enclosure at 45 deg to view the horizontal angle of the strike on the high-speed recordings. An additional camera (Sony Handycam DCR85) recorded continuously throughout each trial to allow us to extract behavioral data (e.g. strike probability, latency and accuracy).

After the snakes were placed in the enclosure, we used a snake hook to corral the snake into the back right corner of the enclosure, then used a balloon attached to another snake hook to elicit a defensive strike perpendicular to the camera view and near the grid background of the enclosure. Strikes that were not perpendicular (more than ~8 deg off parallel) were not analyzed. We used balloons to elicit strikes to reduce the probability that the snakes would damage their fangs while repeatedly striking over the course of the study (Movies 1 and 2). Previous snake strike studies have also used balloons to elicit strikes (Breidenbach, 1990; Safer and Grace, 2004; Stepp-Bolling, 2012; Van Riper, 1955). As many of the snakes would not strike from the presentation of the balloon alone, we attempted to elicit strikes by moving the balloon in an aggressive manner, simulating a predator by repeatedly moving the balloon closer and farther from the snake, touching the snake and then backing away, and rubbing the bottom of the enclosure with the attached snake stick to generate vibrations. We initially tried to elicit strikes from the farthest distance possible, but made closer approaches with the balloon if snakes did not strike. We attempted to record 3 strikes per snake at each temperature, with all strikes at each temperature occurring in the same trial. Each snake was given 10 min to complete 3 strikes, with the time between

strikes equal to the time required to save the video files and attach a new balloon if the original balloon was popped (in total this process took ~1 min). If the snake did not strike in 10 min, it was recorded as no strike. If the snake struck fewer than 3 times, we did not attempt to record additional strikes and included the recorded strikes in our analyses. Following each trial, we recorded the cloacal temperature of the snake using a thermocouple probe (Extech HD500 Type K). Strikes were filmed at 15, 20, 25, 30, 35°C. These temperatures were chosen because they represent nearly the entire range of temperatures utilized by free-ranging rattlesnakes for moving and hunting (Putman and Clark, 2017; Taylor et al., 2004). Trials for each snake at every temperature treatment were recorded within 2 weeks of each other in a randomized order.

Data analysis

From the recorded trials, we extracted several behavioral variables, including whether a strike occurred (i.e. strike probability), strike latency and strike accuracy. Strike latency was measured as the duration between when the balloon entered the enclosure until the first strike. Strike accuracy was recorded as a 'miss' if the snake did not touch the balloon with its head, or a 'hit' if the snake's head touched the balloon. For the analyses on strike kinematics, we digitized 4 points on each snake using OpenPhysics Tracker (<https://physlets.org/tracker/>): the neck in-line with the posterior edge of the venom glands, tip of the upper jaw, tip of the lower jaw and the corner of the mouth. The calibrated X – Y coordinates for the neck and the angle of the mouth calculated from the remaining 3 points were then extracted and used in the analyses. All point–point displacement values for the X – Y points of the neck and mouth angle data were filtered using a low pass, 50 Hz cut-off Butterworth filter (Herrel et al., 2011; Penning et al., 2016) in Rstudio using the package 'signal' (<http://r-forge.r-project.org/projects/signal/>). Velocity and acceleration, both linear (using the neck point) and angular (mouth opening angle), were calculated from the filtered data. Strike distance was measured as the distance between the tip of the snake's upper jaw and the balloon in the frame in which the snake initiated the strike using OpenPhysics Tracker. We also extracted the time from strike initiation to maximum gape to assess whether temperature influences when snakes attain maximum gape.

Statistical analyses

For all analyses, we used Rstudio 'stats' package for all linear models or the package 'lme4' (<https://cran.r-project.org/web/packages/lme4>) for all mixed models. To determine the variation in kinematic measures attributable to digitizing error, we randomly selected a single strike from our study and digitized it 4 additional times (i.e. 5 times total). We then calculated the coefficient of variation for maximum strike velocity and acceleration, and maximum angular velocity and acceleration of the gape. To assess whether snakes became fatigued after striking multiple times within a treatment, we used a separate mixed model for the two rattlesnake species and for each temperature treatment. We used either maximum strike velocity or maximum acceleration as the dependent variable and included strike number (1, 2 or 3) as a fixed effect and snake ID as a random effect. To test for the effects of temperature and to test for differences between species, we used a 3-step analysis pathway modeled after Deban and Scales (2016) for all performance and behavior variables except for strike probability and strike accuracy, which follow a binomial distribution. Additionally, all dependent variables except for strike probability and strike accuracy were \log_{10} -transformed. To ensure that our models assessed maximum performance capabilities for each individual, we included only the maximum value for each

dependent variable for each snake within each temperature treatment (i.e. only 1 observation per snake per temperature treatment), except for time to maximum gape, where we used the minimum value. As such, for any given snake and treatment, the maximum value for each variable did not necessarily come from the same strike.

Following Deban and Scales (2016), we divided data from the temperature treatments into 4 overlapping treatment pairs (15–25, 15–35, 20–30 and 25–35°C). For each treatment pair, we constructed a generalized linear mixed model for each dependent variable and included cloacal temperature and strike distance as fixed effects and snake ID as a random effect. To increase statistical power, we removed strike distance from models if the P -value was less than 0.15. For each model, we then calculated Q_{10} values by taking the base 10 antilogarithm of the partial regression coefficient for temperature multiplied by 10 (Anderson et al., 2014; Deban and Lappin, 2011); for variables that indicate durations, we used inverse Q_{10} values ($1/Q_{10}$). Second, we tested for interactions between species and temperature within each temperature treatment pair. We used generalized linear mixed models for each dependent variable and included temperature treatment, species, the interaction between temperature treatment and species, and strike distance as fixed effects, and included snake ID as a random effect. Lastly, to test for differences between species within each temperature treatment we used generalized linear models for each dependent variable with species being the sole predictor variable and each model only including data from a single temperature treatment. For all models, we adjusted P -values to account for false discovery rates (Benjamini and Hochberg, 1995). To test for the effects of temperature on strike probability and strike accuracy, we used binomial generalized linear mixed models with either strike occurrence (0 for no or 1 for yes) or strike accuracy (miss=0, hit=1) as the dependent variable. In each model, we included cloacal temperature, an orthogonal quadratic effect of cloacal temperature, species, and the interaction between cloacal temperature and species as fixed effects and snake ID as a random effect. As thermal performance curves are typically best described using a polynomial model (Condon et al., 2010; Huey and Kingsolver, 1989; Klepsatel et al., 2013), for the models assessing strike probability and accuracy we used a likelihood ratio test (LRT) to determine whether the quadratic temperature effect improved the model, and removed the quadratic term if it did not improve the model. On occasion, not all the points on the snake were visible and able to be digitized; thus, the exact sample sizes for each model are not identical.

RESULTS

Summary of strikes

We recorded a total of 179 strikes from 12 western rattlesnakes, and 125 strikes from 12 Mohave rattlesnakes. All snakes used in our study were adults with an average snout–vent length of 79 cm (range 68.5–91.6 cm) and 84 cm (71.5–91.5 cm) and an average mass of 332 g (249–451 g) and 463 g (300–641 g) for Mohave rattlesnakes and western rattlesnakes, respectively. Western rattlesnakes struck in all trials; however, Mohave rattlesnakes did not strike in 33.3% of trials. Both western rattlesnakes and Mohave rattlesnakes contacted the balloon in most strikes, hitting the balloon in 82.6% and 86.4% of all strikes, respectively. Both species tended to strike early in each trial with average strike latencies of 35.3 s for western rattlesnakes and 69.4 s for Mohave rattlesnakes. Similarly, if a snake struck once during a trial, they nearly always performed at least 3 strikes; both species only failed to complete 3 strikes in 2 trials each. Summary statistics are presented in Table 1 (maximum values) and Table S6 (all values). Q_{10} values were relatively low across all measured

Table 1. Summary table of maximum performance values for western rattlesnakes and Mohave rattlesnakes

Variable	15°C			20°C			25°C			30°C			35°C		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Western rattlesnakes															
Max. strike velocity (m s^{-1})	3.23	2.54	3.73	3.57	2.61	4.41	4.01	3.02	5.17	4.10	2.92	5.09	4.06	3.22	5.15
Max. strike acceleration (m s^{-2})	87.99	61.23	112.83	106.21	80.94	134.96	133.53	74.85	319.88	117.44	98.48	146.43	119.26	74.81	160.31
Max. gape angular velocity (rad s^{-1})	57.28	45.62	86.14	66.18	49.35	83.48	77.75	56.38	92.21	90.85	79.19	116.31	94.12	60.05	136.86
Max. gape angular acceleration (rad s^{-2})	6477.09	3165.57	18,397.41	6591.44	2612.31	11,419.93	6966.68	3717.24	11,482.01	11,272.41	5753.32	20,899.15	9866.95	3563.83	18,514.58
Min. time to max gape (ms)	86.33	72.00	104.00	76.67	64.00	88.00	75.67	48.00	88.00	67.00	40.00	100.00	69.67	44.00	96.00
Strike distance (cm)	16.27	7.70	27.60	20.04	12.40	34.10	20.42	6.60	31.30	20.72	9.90	30.40	23.97	10.70	35.50
Strike latency (s)	28.73	4.00	79.00	23.86	1.00	86.00	18.27	3.00	102.00	41.67	1.00	312.00	41.75	3.00	258.00
Mohave rattlesnakes															
Max. strike velocity (m s^{-1})	2.80	2.24	3.18	3.42	2.42	4.20	3.67	3.04	4.81	4.05	3.32	5.32	3.78	1.79	5.26
Max. strike acceleration (m s^{-2})	69.41	50.62	81.51	82.04	46.94	112.13	103.81	78.83	145.33	128.58	108.43	147.13	119.14	71.04	182.20
Max. gape angular velocity (rad s^{-1})	57.91	47.51	73.44	70.87	45.24	85.01	78.36	69.69	94.79	82.85	64.93	107.89	90.40	76.98	108.48
Max. gape angular acceleration (rad s^{-2})	5652.88	3460.96	11,424.00	6902.55	5469.47	8610.11	6541.78	5350.05	9148.76	6450.35	4014.53	10,964.47	8754.76	6099.83	14,397.84
Min. time to max gape (ms)	69.00	60.00	84.00	64.67	56.00	84.00	63.33	56.00	80.00	58.50	40.00	84.00	50.18	32.00	72.00
Strike distance (cm)	14.24	7.30	25.30	16.57	11.70	23.00	17.79	7.50	25.40	20.85	9.10	33.80	17.15	4.50	34.50
Strike latency (s)	112.25	14.00	280.00	18.75	4.00	27.00	75.80	1.00	283.00	57.75	1.00	233.00	83.27	1.00	260.00

variables. The highest Q_{10} for a variable that was significantly influenced by temperature was 1.6 for the maximum gape acceleration of western rattlesnakes in the 20–30°C comparison. Similarly, the average of all Q_{10} values for variables that were found to significantly vary with temperature was 1.29 and 1.31 for Mohave rattlesnakes and western rattlesnakes, respectively (Tables S2 and S3). We found no evidence of fatigue for either species or any temperature treatment ($P>0.05$ for all models; Table S1). We also found that the coefficient of variation in kinematic measures attributable to digitizing error was always less than 10% (1.4–9.7%), and lower for measures of velocity than for measures of acceleration, as would be expected from a first order versus second order derivative.

Strike probability, latency and outcome

We found that the behaviors of both species were moderately influenced by temperature. As western rattlesnakes struck in all trials, our analysis of strike probability was only performed on Mohave rattlesnakes. We found that cloacal temperature had a weak effect on the probability of Mohave rattlesnakes striking, with the estimated probability of a strike occurring increasing from ~75% at the coldest temperature to 100% at the highest (Fig. 1A; Est=0.24, s.e.=0.11, $P=0.036$). Cloacal temperature accounted for ~11% of the variation in strike probability (marginal $R^2=0.11$), while the combination of cloacal temperature and snake ID explained ~86% of the variation (conditional $R^2=0.86$). Thus, a substantial proportion of variation in whether snakes struck is related to inter-individual variation in snake behavior.

For the model assessing the effects of temperature on strike accuracy, we found that both the linear effects of temperature (Est.=−11.57, s.e.=3.67, $P=0.001$) and the interaction between the linear temperature effect and species (Est.=16.06, s.e.=5.79, $P=0.004$) influenced strike accuracy, while the quadratic effect and species were not significant ($P>0.05$) (Fig. 1B). At higher temperatures, both species were more likely to miss; however, the percentage of strikes that missed also decreased at the coldest temperatures for Mohave rattlesnakes (i.e. the percentage of strikes that hit was highest at midrange temperatures for Mohave rattlesnakes). The increase in the percentage of missed strikes at the highest temperatures appears to be driven by strikes that did not reach the balloon, rather than strikes that mistargeted the balloon. For the 30°C and 35°C treatments, ~71% (western rattlesnakes) and ~88% (Mohave rattlesnakes) of strikes missed the balloon because the strikes were too short. Missed strikes at the colder temperatures, however, were predominately inaccurate targeting for both species.

Strike latency did not vary substantially with temperature or between species. The only significant effect of temperature on strike latency was between species within the 15°C treatment, where Mohave rattlesnakes took on average 83.5 s longer to strike than Western rattlesnakes (Fig. 1C).

Strike performance: linear and angular kinematics

The strike performance of both species was substantially influenced by temperature (Fig. 2) as Q_{10} values for most kinematic traits exceeded one, even though the magnitude of the temperature effect was not as large as expected for a primarily muscle-driven movement. In the 15–25°C and 15–35°C comparisons, we found a positive effect of temperature on maximum strike velocity and acceleration for both species (Tables S2 and S3). For Mohave rattlesnakes, we also found a significant effect of temperature on maximum strike acceleration in the 20–30°C and 25–35°C comparisons (Fig. 2B). Mean strike

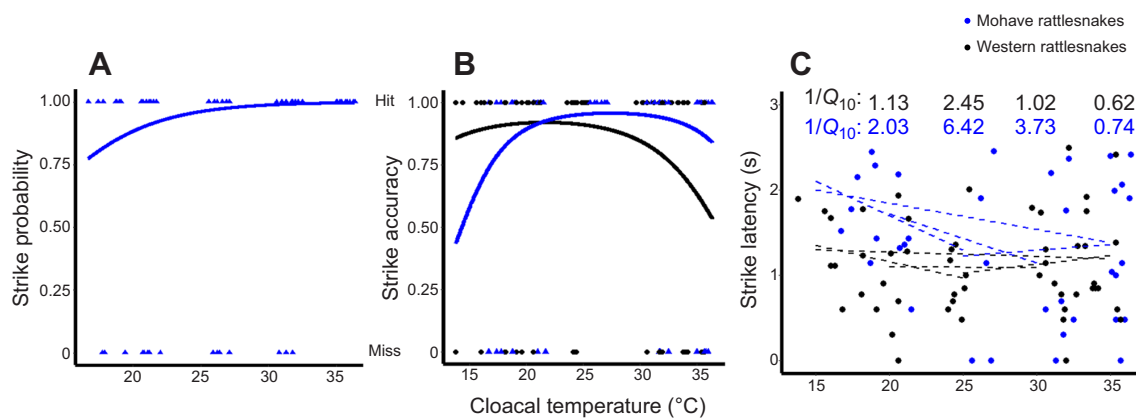


Fig. 1. Strike kinematics for Mohave rattlesnakes and western rattlesnakes. (A) Strike probability, (B) strike accuracy and (C) strike latency with Q_{10} (and $1/Q_{10}$) values ordered according to treatment comparisons at 15–35°C, 15–25°C, 20–30°C and 25–35°C. Dashed lines indicate a nonsignificant effect of temperature for a given treatment comparison, solid lines indicate a significant temperature effect. Values for strike latency are \log_{10} -transformed.

velocity was not affected by temperature in the 25–35°C comparison for either species but did increase with temperature in the 15–25°C and 15–35°C comparisons for both species; the mean strike velocity of Mohave rattlesnakes also increased in the 20–30°C comparison (Fig. 2D). Western rattlesnakes did attain a higher maximum velocity

in the 15°C treatment and higher accelerations in the 15°C and 20°C treatments (Fig. 2A). While we did find several statistically significant interactions (Table S4), the interactions do not appear to be biologically significant, as the overall differences between species was small (Table S5).

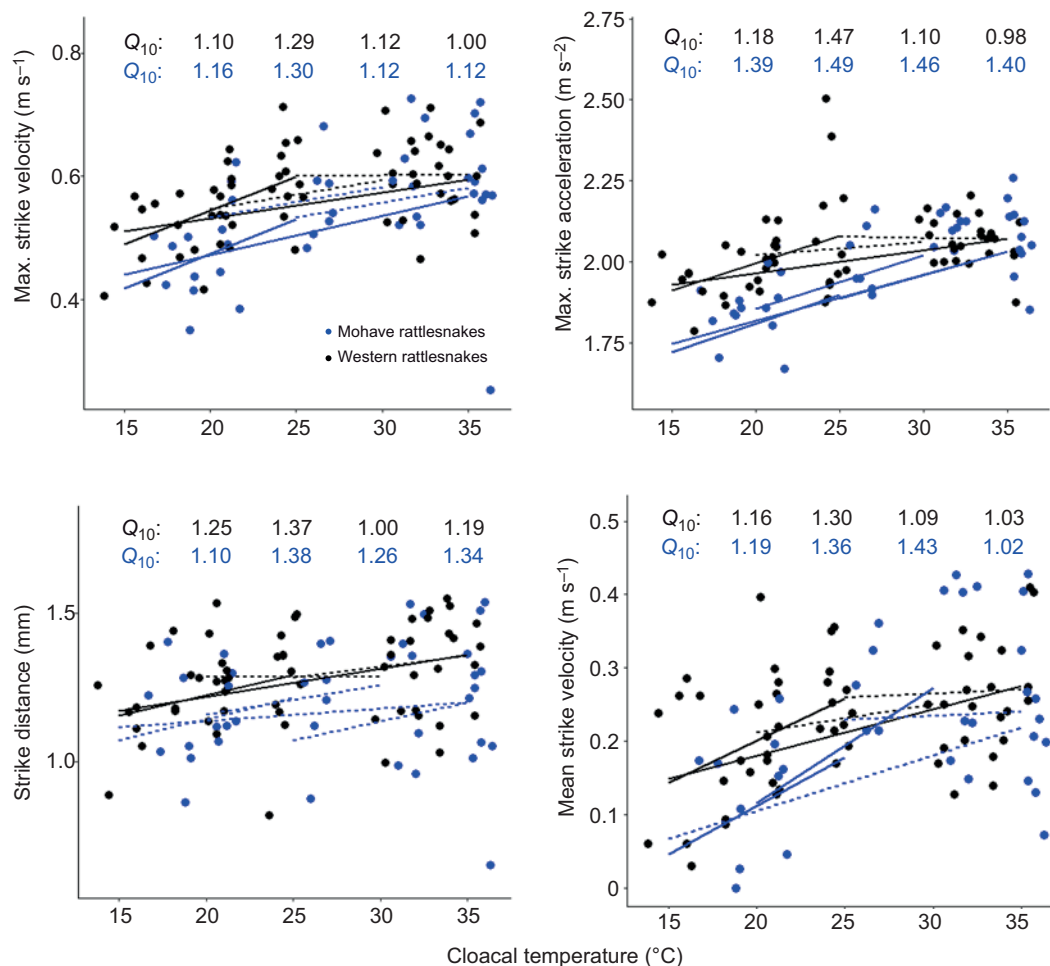


Fig. 2. Scatterplots for linear kinematic variables and strike distance in Mohave rattlesnakes and western rattlesnakes. (A) Maximum strike velocity, (B) maximum strike acceleration, (C) strike distance and (D) mean strike velocity with Q_{10} (and $1/Q_{10}$) values ordered according to treatment comparisons at 15–35°C, 15–25°C, 20–30°C and 25–35°C. Dashed lines indicate a nonsignificant effect of temperature for a given treatment comparison, solid lines indicate a significant temperature effect. All values on the y-axes are \log_{10} -transformed.

Strike distance did not change with temperature in any treatment comparison for Mohave rattlesnakes, but did increase in the 15–25°C and 15–35°C comparisons for western rattlesnakes (Fig. 2C). We also found no differences in strike distance between species. However, strike distance was an important covariate in Mohave rattlesnake models assessing maximum strike velocity (all treatment comparisons), average strike velocity (15–25°C and 20–30°C), and maximum gape acceleration (15–35°C and 25–35°C). For western rattlesnakes, strike distance was less important as it was a significant covariate in only the models assessing time to maximum gape (15–35°C) and maximum strike acceleration (25–35°C). In all instances where strike distance was an important covariate, it was positively correlated with the dependent variable.

There were no detectable differences between species in maximum gape velocity. However, in all but the 20–30°C comparison for Mohave rattlesnakes, temperature was positively correlated with maximum gape velocity (Fig. 3A). Similarly, maximum gape acceleration was similar for both species in all but the 30°C treatment and the interaction between species and temperature in the 20–30°C comparison (Fig. 3B). Those species differences were due to western rattlesnakes attaining substantially greater angular accelerations in the 30°C treatment. Maximum gape acceleration was found to positively correlate with temperature in the 15–35°C and 25–35°C comparisons for Mohave rattlesnakes and in all but the 25–35°C comparison for western rattlesnakes. Also, western rattlesnakes were found to take longer than Mohave rattlesnakes to reach maximum gape in the 15°C, 20°C and 35°C treatments. The effects of temperature on time to maximum gape were limited (Fig. 3C). For western rattlesnakes, there was significant negative correlation between temperature and time to maximum gape in the 15–25°C and 15–35°C comparisons and the 15–35°C and 25–35°C comparisons for Mohave rattlesnakes.

DISCUSSION

In our study, the kinematics of defensive strikes from both western rattlesnakes and Mohave rattlesnakes were positively correlated with temperature. Linear strike velocity and acceleration, as well as angular velocity and acceleration of mouth opening, were positively correlated with body temperature over most of the temperature range we tested, whereas time until maximum gape was negatively correlated with body temperature to a minor degree. Behavioral

variables were also moderately influenced by body temperature, with colder Mohave rattlesnakes being less likely to strike, taking longer to strike, and striking less accurately. Both species were less likely to contact the balloon in the 35°C treatment. It is clear from our results that warmer rattlesnakes strike more rapidly, which implies that colder snakes cannot defend themselves from predators as effectively. However, despite numerous performance variables being influenced by temperature, the magnitude of the temperature effect was relatively low ($Q_{10} < 1.6$ for nearly all variables) compared with most muscle-driven movements (Anderson and Deban, 2010; Deban and Scales, 2016), indicating that snake strikes are either partially powered by elements that are not as dependent on temperature as skeletal muscle contraction (such as tendon elasticity), or that the motivation to perform maximally changes with temperature.

Behavioral traits

Our results illustrate that Mohave rattlesnakes were less likely to strike, waited longer prior to striking, and were less accurate at colder temperatures. Both species, however, were less likely to contact their target at higher temperatures. While it is unclear why strike probability and latency to strike in Mohave rattlesnakes was more affected by temperature than western rattlesnakes, the general pattern may stem from the trade-off between vulnerability and defensive striking.

Rattlesnakes strike by rapidly straightening their body, and snakes that have struck are in an elongated position that is vulnerable to counterattack until they can recoil. Some individuals may be less willing to break crypsis and strike at cooler temperatures because they recognize that their strike would put them in a more vulnerable position at those temperatures. In general, animals that rely on crypsis for avoiding predation must decide when the risk of attack or probability of detection by a nearby predator is high enough to abandon crypsis, and either flee or engage in active defense (Cooper and Sherbrooke, 2010). Animals with defenses that can cause substantial physical injury are more likely to exhibit defensive displays and stand their ground against the predator, whereas those that lack defensive capability or are compromised in some way are more likely to flee or continue to maintain crypsis (Cooper and Frederick, 2010, 2007; Stankowich and Blumstein, 2005). Rattlesnakes frequently employ an additional defensive

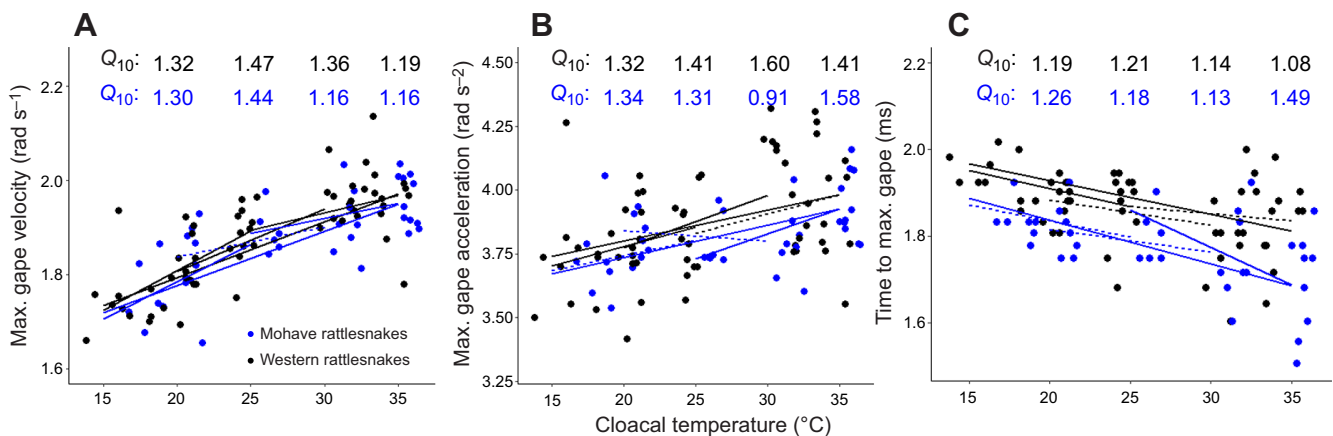


Fig. 3. Scatterplots for mouth gape variables in Mohave rattlesnakes and western rattlesnakes. (A) Maximum gape velocity, (B) maximum gape acceleration and (C) time to maximum gape with Q_{10} (and $1/Q_{10}$) values ordered according to treatment comparisons at 15–35°C, 15–25°C, 20–30°C and 25–35°C. Dashed lines indicate a nonsignificant effect of temperature for a given treatment comparison, solid lines indicate a significant temperature effect. All values on the y-axes are log₁₀-transformed.

display – rattling – that also breaks crypsis, but does so to warn the potential predator of the impending defensive strike. However, the speed with which rattlesnakes can rattle is itself positively correlated with body temperature (Martin and Bagby, 1972). It has even been demonstrated that California ground squirrels can use the sound of the rattle to determine the level of danger posed by the rattlesnakes, with animals being more willing to interact with a cold, more slowly rattling snake (Swaigood et al., 1999). These factors show that suboptimal temperature can deleteriously affect other aspects of rattlesnake antipredator behavior, beyond strike performance.

Although lower temperatures could also inhibit sensory systems and information processing, these factors are likely not as relevant given the timescale of the behaviors. Even at the warmer temperatures, strike latency was ~20–30 s, indicating that the choice was driven by behavioral decisions rather than physiological constraints. However, the decrease in strike accuracy at the coldest temperature may result from the effect of temperature on coordination and/or the ability of the snakes to perceive their target effectively. Both species were more likely to miss the balloon at higher temperatures, which was largely because warmer snakes often struck short of the target rather than inaccurate aim. Because warmer snakes were more likely to strike and could strike (and presumably recoil) faster, they may have been using strikes to keep the putative predator from approaching rather than trying to actually bite and/or envenomate their target. Thus, striking early in the direction of an approaching threat may decrease the probability of a predator approaching and attacking. Although we were unable to quantify the retraction and recoiling of snakes following strikes, qualitatively, it was apparent that warmer snakes could rapidly recoil into a defensive position. Warmer snakes, particularly those in the 35°C treatment, were also much more difficult to corral, handle and process during the experiment. In the 35°C treatment, snakes moved faster, struck toward the observer and snake handling implements more often, and would frequently attempt to escape the enclosure. In conjunction with the results of our study, this indicates that warmer snakes are much more dangerous to a putative predator.

Kinematic traits

Despite some inconsistencies in previous studies as to how temperature influences rattlesnake strike performance (Rowe and Owings, 1990; Stepp-Bolling, 2012), our study illustrates that the kinematics of rattlesnake defensive strikes are indeed influenced by temperature, but to a lesser degree than would be expected based on muscle physiology alone. In our study, the highest Q_{10} for all measured kinematic and behavioral variables was 1.6, with an average Q_{10} of 1.3 for both species. Our calculated temperature coefficients fall below the range of Q_{10} values (1.6–3.0) typically reported for primarily muscle-driven locomotory movements (Deban and Scales, 2016; Dewar and Graham, 1994; Lailvaux and Irschick, 2007), but it remains unclear whether the low temperature coefficients are due to elastic recoil mechanisms (Anderson and Deban, 2010; Deban and Scales, 2016) or the motivation of the snakes to strike maximally (Astley et al., 2013). While the results of Young (2010) suggest the possibility that strikes from heavy-bodied vipers are ballistic in nature and powered by muscle contraction and subsequent elastic recoil, more research on the muscles and tendons of vipers is needed. Alternatively, the apparent robustness of strike performance to temperature could also result from the motivational state of the snakes. Previous research has illustrated that measures of

maximum performance can be underestimated simply because animals rarely perform maximally (Astley et al., 2013). If the snakes in our study were striking with submaximal performance at warmer temperatures, our Q_{10} calculations could be underestimates. However, our performance values are similar to previous strike studies (LaDuc, 2002; Penning et al., 2016; Young et al., 2001), which could be indirect evidence that they are representative of maximal performance, assuming that differences in subject motivation would lead to substantial variation in performance metrics across independent studies.

Despite relatively low Q_{10} values, most measured kinematic traits for both western rattlesnakes and Mohave rattlesnakes were influenced by temperature, with temperature being positively correlated with performance (except for time until maximum gape). From 15°C to 30°C, Mohave rattlesnakes experienced an average increase in velocity of 1.24 m s^{-1} and 59.17 m s^{-2} in acceleration. Western rattlesnakes experienced an increase in velocity of 0.83 m s^{-1} at 15–35°C and an increase of 45.54 m s^{-2} in acceleration at 15–25°C. This change in performance with temperature is substantial from an ecological perspective, as the reaction times of birds and mammals, taxa that include numerous rattlesnake predators, typically exceed 75 ms (Ghez and Vicario, 1978; Pomeroy and Heppner, 1977), whereas accurate strikes in our study frequently reached the balloon in under 100 ms. In other words, a typical rattlesnake predator would have a very short window of time in which to successfully dodge a fast strike. Over such a short a time period, even small changes in strike performance can be influential in determining whether rattlesnakes successfully defend themselves and/or catch prey, particularly when interacting with endothermic species that would be less impacted by low temperature. To more conclusively determine if these changes in performance are ecologically relevant when interacting with other ectothermic species, it would be necessary to compare the effect of temperature on rattlesnake strike performance with that of the movements of their endothermic predators and prey.

Gape kinematics were also correlated with temperature, which may be attributed to the effects of temperature on muscle performance, the extensibility of tissues, and/or an unknown elastic mechanism that is powering mouth opening. As tissue extensibility correlates with temperature, snakes may reach maximum gape sooner even when applying the same muscle force due to changes in the mechanical properties of the tissues responsible for mouth opening. However, it remains unclear why the Q_{10} values for mouth gapes kinematics is relatively low ($Q_{10} < 1.6$). Low Q_{10} values may be the result of a trade-off between defense and sensory capabilities. Reaching maximum gape earlier may be advantageous for snakes when defensively striking, as gaping early could increase their apparent size (heads are substantially larger when at maximum gape) and ensure that their fangs are pointed toward the threat as soon as possible. In support of this notion, rattlesnake defensive strikes involve higher maximum gapes than predatory strikes, and reach maximum gape earlier in the strike sequence (LaDuc, 2002). Additionally, if a predator manages to get close, being able to reach maximum gape rapidly may allow vipers to still inflict a venomous bite despite being potentially limited in distance and/or time. However, when rattlesnakes open their mouth fully, their ability to see their target with their eyes or infrared pits is likely to be diminished as these senses are occluded by the gaping mouth. Thus, snakes may open their mouth fast enough and early enough to be well defended but may not be attempting to maximize their rate of mouth opening.

Comparisons with other studies

Rattlesnake defensive strike kinematics have been the subject of study since the 1950s (Van Riper, 1955). As the majority of previous studies on rattlesnake strike performance have typically recorded strikes at temperatures around 26–27°C, the most salient comparison is with our 25°C treatment. Indeed, our kinematic values from the 30°C and 35°C treatment generally exceed those reported in previous studies. For maximum strike velocity, Van Riper (1954) reported 2.67 m s⁻¹ for a prairie rattlesnake (*Crotalus viridis*) at an unknown temperature. LaDuc (2002), Young et al. (2001), and Penning et al. (2016) reported values for western diamond-back rattlesnakes (*Crotalus atrox*) of 3.71 m s⁻¹, 2.25 m s⁻¹ and 2.95 m s⁻¹, at temperatures of 27, 26 and 27°C, respectively. Penning et al. (2016) also reported a mean maximum acceleration for western diamond-back rattlesnakes of 169 m s⁻². For the western rattlesnake, Rowe and Owings (1990) report a maximum strike velocity of ~1.75 m s⁻¹. Our mean maximum strike velocities of 3.39 m s⁻¹ and 3.73 m s⁻¹ for Mohave rattlesnakes and western rattlesnakes at 25°C, respectively, place our values within 1–2 standard deviations of other studies and each other. While there may be some differences in maximum strike velocity and acceleration between Mohave rattlesnakes, western rattlesnakes (*C. o. helleri* and *C. o. oreganus*), western diamond-back rattlesnakes and prairie rattlesnakes, the differences are relatively minor and may result more from methodological differences (points digitized and data smoothing/splining) between studies and differences between individuals within species rather than biological differences between species. Indeed, in our study, we generally found much more variability between individuals within species than between species themselves, indicating that inter-individual variation in temperament and motivation may heavily influence conclusions made at the level of species or populations. On average, snakes in our study also initiated strikes from farther distances than snakes in other studies, which also contributes to snakes in our study achieving greater maximum strike velocities. In our study, western rattlesnakes and Mohave rattlesnakes initiated strikes from an average of 18.3 and 14.4 cm away from the balloon, respectively, while the average distance at strike initiation from previous studies ranges from 9.43 to 12.7 cm.

When comparing the Q_{10} values we report ($1 < Q_{10} < 1.6$) for rattlesnake defensive strike kinematics, it is noteworthy that they are similar to ectotherm movements that are well known to utilize elastic storage mechanisms. For example, the Q_{10} values for chameleon tongue projection, which incorporates elastic recoil, range from 1.1 to 1.3 (Anderson and Deban, 2010). Similarly, Deban and Scales (2016) calculated Q_{10} for ballistic tongue projection in salamanders that utilize elastic recoil and in those that do not (i.e. those that use muscle contraction only). Again, our values are highly similar to the values reported for salamanders that use elastic recoil and are lower than nearly all values reported for salamanders that do not utilize elastic recoil. While the Q_{10} values of our study do not directly indicate the presence of an elastic recoil mechanism in snake strikes, they do indicate that it is a possibility which warrants further investigation. Given that we do not know exactly which muscles (or amount of muscle) are involved in a rattlesnake strike, it is not possible to determine whether the power output of a strike exceeds what is possible from muscle alone. This is necessary for identifying an elastic mechanism and should be explored in the future.

Although there is a substantial literature on snake strike kinematics and performance (Herrel et al., 2011; Kardong, 1992, 1975, 1986a,b; Kardong and Bels, 1998; LaDuc, 2002; Young et al., 2001), very

limited work has been done on the role of body temperature, and the studies that do exist are somewhat contradictory. Greenwald (1974) found that the velocity of gopher snake (*Pituophis catenifer*, Colubridae) strikes increased with temperature up to 27°C, and then declined. Whitaker et al. (2000) did not find a strong relationship between strike speed and temperature for eastern brown snakes (*Pseudonaja textilis*, Elapidae). Rowe and Owings (1990) found that rattlesnake strike velocity did not change over the majority of active body temperatures (18–27°C) reported for rattlesnakes in the field, whereas Stepp-Bolling (2012) found that rattlesnake strike velocity increased from 16–29°C but did not change at temperatures exceeding 29°C. Although much more work needs to be done to make informative comparisons, differences in the influence of temperature on strike performance between vipers and other snake families is likely attributable to the very divergent foraging behaviors and morphologies between these groups. The relatively sessile behaviors and stout bodies of vipers contrast starkly with those of highly active colubrid and elapid snakes. For vipers, our results illustrate that rattlesnake defensive strike performance does increase with temperature, but less than expected based on muscle physiology, and so may be more robust to temperature variation than many other ectotherm movements.

Our study illustrates that rattlesnakes at colder temperatures are likely to be at greater risk of predation, as they would likely not be as effective at defending themselves if attacked. Whether rattlesnakes also use the elastic energy mechanisms proposed for puff adders (Young, 2010) is unknown. Although our study illustrates that rattlesnake defensive strike performance is relatively robust to temperature changes ($1 < Q_{10} < 1.6$), *in vivo* muscle recordings and comparative myological studies on the trunk musculature, particularly the epaxial muscles that power strikes, are needed to conclusively identify the potential role of an elastic storage mechanism in snake strike mechanics.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.W., G.F., T.H., R.W.C.; Methodology: M.W., G.F., T.H., R.W.C.; Software: M.W.; Formal analysis: M.W.; Investigation: M.W.; Resources: M.W., G.F., T.H., R.W.C.; Writing - original draft: M.W.; Writing - review & editing: M.W., G.F., T.H., R.W.C.; Visualization: M.W.; Supervision: M.W., T.H., R.W.C.; Project administration: M.W., T.H., R.W.C.; Funding acquisition: M.W., G.F., T.H., R.W.C.

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Data availability

Data have been deposited in the Dryad Digital Repository (Whitford et al., 2020): B8903D.

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.223859.supplemental>

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