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Is There Always a Need for Speed? Testing for Differences in the Striking Behavior of Western Ratsnakes (*Pantherophis obsoletus*) When Encountering Predators and Prey

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ABSTRACT.—**Prior to both offensive and defensive striking, snakes can display notable differences in prestrike behaviors between offensive and defensive contexts. However, few studies have investigated strike movements during the different scenarios with which snakes are faced. To better understand how snakes strike, we measured the strikes of Western Ratsnakes (*Pantherophis obsoletus*; $N = 11$) presented with two different targets: one simulated predator (a gloved human hand) and one prey (pre-killed mice). For each strike, we recorded strike distance, duration, velocity (average and peak), acceleration (average and peak), and time to start mouth gape. In both encounters, ratsnakes displayed similar time to the initiation of a mouth gape while all peak performances were significantly different between strike types with performances being higher in defensive strikes. Defensive strikes took longer (mean = 122 ± 13 ms), reached greater distances (mean = 15.1 ± 1.7 cm), had higher maximum velocities (mean = 1.80 ± 0.11 ms^{-1}), and maximum accelerations (mean = 101.4 ± 15.2 ms^{-2}). Offensive strikes had much shorter durations (mean = 49 ± 5 ms), distances (mean = 4.3 ± 0.6 cm), maximum velocities (mean = 1.06 ± 0.10 ms^{-1}), and maximum accelerations (mean = 81.4 ± 18.9 ms^{-2}). The results for average performance measurements are similar to those for the maximum performance comparisons. Our results show that snakes can recognize and differentiate prey from threats and respond differently in each situation. Our results also show that predatory and defensive strikes are quantitatively and situationally distinct, should be treated as separate behaviors, and therefore should be evaluated and analyzed separately from one another.**

For all animals, survival depends on successful feeding and defense (Davies et al., 2012) and, as such, an individual can employ a single behavior for both feeding and defensive activities or a different behavior for each activity. Avoiding predation while successfully feeding has major fitness consequences for the individuals involved (Dawkins and Krebs, 1979; LaDuc, 2002). An organism must be able to accurately and quickly identify a threat from a feeding opportunity and respond appropriately. Often, when animals encounter a feeding opportunity or are faced with a threat, their behaviors are markedly different in each scenario (Bowers et al., 1993; Davies et al., 2012). Therefore, differing situations may involve different levels of performance (LaDuc, 2002) or different behaviors entirely (Bowers et al., 1993). Some animals appear to use the same behavior but with varying levels of performance, making the behaviors quantitatively different (Avery et al., 1987). For example, the Viviparous Lizard (*Zootoca vivipara*) moves at speeds 2–7 times slower when foraging compared to when it is presented with a potential predator (Avery et al., 1987). *Anolis* lizards show markedly different levels of performance based on their surroundings and behavioral context (Irschick and Losos, 1998). Performance changes can also depend on the animal's maximum performance ability in relation to both lab and field environments (Irschick et al., 2005).

In animals with more simplified body forms, or that display rapid movements, or both (e.g., snakes), identifying and understanding potential differences between the behaviors used in both predation and defense has received less attention and requires technology beyond simple human observations (Young et al., 2001; LaDuc, 2002). However, given the major fitness consequences involved in these interactions, different levels of performance can be generally expected from organisms that appear to use the same behavior for both predation and defense. Snakes are capable of complex behaviors, such as feeding or defense, through the use of intricate musculature (Tingle, et al., 2017; Penning, 2018; Martins et al., 2019). A snake must strike rapidly over a variable and possibly changing distance to close in on its target. Snakes are unlike many other predatory vertebrates in that they first make contact with a target by thrusting their open mouths toward the individual while the inertia of the remaining body acts as an anchor (Cundall and Greene, 2000; Cundall et al., 2007). Striking behavior in snakes brings sensitive tissues into close contact with the target, which means that snakes are in danger of defensive countermeasures or predatory attacks when they strike (Moon et al., 2019). The target's response time is determined by their sensory system's ability to detect the snake strike and their nervous and motor abilities to respond rapidly (Davis, 1984; Yilmaz and Meister, 2013). Therefore, snakes likely benefit from striking in ways that enhance predatory and defensive success while reducing the potential for injury (Chiszar and Radcliffe, 1989; Young et al., 2001; LaDuc, 2002).

For many snakes, striking behavior is a defense tactic along with being a major avenue to securing food (Kardong, 1986; Lillywhite, 2014). Defensive strikes usually involve larger gape angles in which the teeth stab the offender and the head is quickly retracted (Cundall and Greene, 2000). From a predation perspective, early work revealed that some snakes may be able to modify their strike trajectories mid-strike to compensate for moving prey (Frazetta, 1966). More recent work indicates that many snake strikes are ballistic in nature and are not modified once initiated (Young and Kardong, 2007; Catania, 2009). Additionally, snakes have the ability to differentiate the head of predator or prey and can place a majority of their attacks at the appropriate location (Schmidt et al., 1993; Westhoff et al., 2010). Therefore, if snakes strike with a ballistic trajectory, they would benefit from reducing the time it takes to close the distance between themselves and their prey to prevent the prey from moving. Prey movement that occurs between the initiation of a strike and contact with the prey is likely to lead to inaccurate strike placement. Shorter strike distances or rapid strike speeds could also facilitate reaching prey faster, reducing the potential reaction time and countermeasures of the prey.

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Studies on snake-strike kinematics have largely focused on viperid and boid or pythonid snakes (Kardong and Bels, 1998; Cundall and Deufel, 1999; Cundall et al., 2007; Ryerson, 2020). However, few studies have investigated strike performance in the diverse and speciose Colubridae (Greenwald, 1974, 1978; Alfaro, 2002; Smith et al., 2002; Penning et al., 2019). Early work focused on various aspects of snake strike behavior including the impacts of body temperature, body orientation, and size; but how snakes strike at different types of targets remains unknown. The quantification of the differences between snake strikes at predators and strikes at prey have produced conflicting results. For instance, for Western Diamondback Rattlesnakes (*Crotalus atrox*), it was reported that snakes strike from a greater distance when striking at prey when compared to a perceived threat (Young et al., 2001), while LaDuc (2002) found that snakes strike from a greater distance at a perceived threat relative to strikes at a prey item. Because of a positive correlation between strike distance and velocity (Herrel et al., 2011; Penning et al., 2019), contrasting results were also found for strike velocity between the two studies. To our knowledge, studies that evaluate differences between defensive and predatory strike performance do not exist for snake species other than *C. atrox* (Young et al., 2001; LaDuc, 2002). Furthermore, snake strikes are currently considered to be an all-or-nothing response to both defensive and offensive signals (Penning et al., 2016; Higham et al., 2017; Ryerson and Tan, 2017). For example, Penning et al. (2016) stated that the defensive strike performances from ratsnakes (*Pantherophis obsoletus*) were similar to the offensive strikes of rattlesnakes. Higham et al. (2017) compared rattlesnake data (predatory strikes) to previously published data collected on observations of defensive strikes (Penning et al., 2016), and Ryerson and Tan (2017) argued that comparisons between the two strike types are valid and should represent maximum performance. Here, we provide evidence that defensive and offensive striking behaviors are quantitatively distinct and should be considered unique and separate behavioral traits. We address the discrepancies in the current literature and, to better describe striking in colubrid snakes, we quantified the effects of target type (predator vs. prey) on strike performance in Western Ratsnakes (*Pantherophis obsoletus*).

Materials and Methods

We used a total of 11 juvenile Western Ratsnakes (*Pantherophis obsoletus*; 99.8 ± 49.9 g; 70.1 ± 10.2 cm snout–vent length [SVL]) in our study; our sample size was similar to, or larger than, prior work on snake-strike kinematics (LaDuc, 2002; Ryerson and Tan, 2017). The 11 test snakes were obtained from 11 clutches that were collected from either captive or wild-caught females in order to avoid any potential maternal effects. All snakes were housed individually in opaque cages (Freedom Breeder®, Venomous 1133) and provided with a thermal gradient and a water source.

Prior to a trial, each snake was given a fasting period of 1 wk, regardless of target type being presented. For both strike types (defensive and offensive), each snake was measured three separate times on three separate days for a total of six different strike encounters. The order of encounters was randomized for each snake. We did not control for body temperature but took pre- and poststrike temperature measurements. There was no significant difference in body temperatures of snakes when striking during defensive (mean = 24.2 ± 0.22°C) or offensive (23.8 ± 0.26°C) scenarios ($t_{df\,=\,10} = 1.48$, $P > 0.17$).

To elicit defensive strikes, we presented snakes with a gloved human hand that served as a simulated threat for all snakes. Simulating a threat involved tapping the substrate and waving above and around the snake. Each trial started with the hand from the greatest distance possible. We then systematically moved forward to prevent a decrease in strike distance caused by the abrupt placement of the hand near each snake. To elicit predatory strikes, we presented each snake with a warmed cadaveric mouse on the end of long forceps. Each mouse was kept in the same plane as the snake and was slowly moved toward each snake until a strike occurred. Prey size (approximately 10% relative prey mass) was held constant across trials and did not differ across the three feeding events ($F_{df\,=\,2,\,30} = 1.48$, $P > 0.25$). We interpreted all strikes at the glove as defensive behaviors because no snake that struck at the glove stayed attached or attempted to constrict. Furthermore, we interpreted all strikes at rodents as predatory because all snakes remained in contact with the prey and proceeded to constrict and consume it. During weeks where defensive strikes were tested, snakes were fed in their home cages to keep hunger levels similar between trials and snakes. Feeding occurred after defensive strike tests.

For each event, snakes were placed on a flat, white surface (61 × 91 cm). We recorded each strike with a pair of linked Edgertronic SC1 (Sanstreak Corp.) high-speed color cameras set to 500 frames per second and with a shutter speed of 1,000 frames per second. The cameras were synchronized to one another through an electronic trigger that simultaneously operated both cameras (potential initiation variation of ±1 μs). The strike stage was illuminated with three high-output light-emitting diode (LED) units. To measure the strike variables, all strikes were calibrated using a calibration cube built from Lego® pieces (Bartoni et al., 2010; McElroy et al., 2012) that encompassed the volume of the strike location (Higham et al., 2017). For each strike at a target, we measured five strike variables: time to start mouth gape, strike distance, strike duration, velocity, and acceleration. We used only peak performance variables in all analyses (longest distance, shortest duration, highest instantaneous velocity, and instantaneous acceleration). Videos were recorded in movie (MOV) format and then converted into audio video interleaved of (AVI) format using TEMPLO analysis software (version 2017.0.452, Contemplas, Deutschland). We digitized videos using VICON MOTUS 10 (version 10.0.01, Contemplas, Deutschland). To digitize the videos, we placed a digital landmark point on the snout of each snake as it moved during each strike. Coordinates in the x, y, and z dimensions were calculated for both camera positions to create a digital trace of each snake's movements through three-dimensional space. A quintic spline function was used to smooth the displacement data prior to the calculation of kinematic variables (Anderson, 2016; Higham et al., 2017).

To avoid pseudoreplication and to follow previous methods, we used only the single best performance value for each of the strike variables from each individual snake for each target type. Therefore, peak performance variables are likely to derive from different strikes (Herrel et al., 2011). We also quantified average performance for each strike variable from each snake and, in this case, we defined an average performance value as the mean value of all peak performance values across strikes at each target. For example, the average strike velocity for a snake would be the mean value of the highest instantaneous velocity values from each strike at a particular target. We defined the time to start mouth gape as the elapsed time from the start of the strike to the first moment of jaw depression. For each strike performance variable, we tested for differences between strike types using paired *t*-tests. In cases where test assumptions were violated (data normality), we used Wilcoxon sign-rank tests. Means are followed by ±1 SE.

Results

During defensive strikes, snakes would readily strike at their targets. During offensive strikes, snakes paused prior to striking, seemingly focusing intently on the target before striking. On occasion, a snake would not complete a strike trial; however, each snake is represented by multiple strikes. All snakes completed all six strike trials except one subject that struck defensively only twice.

When snakes were presented with a gloved hand, they typically responded in one of two ways. Snakes either attempted to flee the strike arena or remained in place with their mouth open while rapidly shaking their tail. For snakes that attempted to flee, we increased the simulated aggression until we elicited a defensive strike (Fig. 1). For the offensive strikes, snakes often used one of two methods to get close to the prey. Many snakes remained in place and simply waited for the prey to get close to them (Fig. 1), while a smaller group slowly crawled toward their prey before striking.

For peak performance, snakes defensively struck from significantly greater distances (mean = 15.1 ± 1.7 cm) than when they struck at prey (mean = 4.3 ± 0.6 cm; $t_{df\,=\,10} = 6.3$, $P < 0.0001$; Fig. 2). The defensive strike distances equated to an average of 23.27 ± 6.3% of each snake's body length, while the offensive strikes equated to 6.03 ± 2.7%. Defensive strikes also had significantly longer durations (mean = 122 ± 13 ms) compared to predatory strikes (mean = 49 ± 5 ms; $t_{df\,=\,10} = 6.6$, $P < 0.001$; Fig. 2). While strike durations were different, the time to start mouth gape did not differ between strike types (Wilcoxon test, $P > 0.16$). Snakes struck with high velocities, with defensive strikes having significantly higher strike velocities (mean = 1.80 ± 0.11 ms^{-1}) than did offensive strikes (mean = 1.06 ± 0.10 ms^{-1}; $t_{df\,=\,10} = 5.9$, $P < 0.001$; Fig. 2). Both defensive (mean = 101.4 ± 15.2 ms^{-2}) and offensive (mean = 81.4 ± 18.9 ms^{-2}) strikes had high accelerations. Defensive strikes had higher accelerations than did offensive strikes ($t_{df\,=\,10} = 3.3$, $P < 0.01$; Fig, 2).

The results for average performance measures were similar to the peak performance measures. Average strike distance was significantly greater in defensive strikes (mean = 13.1 ± 1.3 cm) compared to offensive strikes (mean = 2.9 ± 0.4 cm; $t_{df\,=\,10} = 8.2$, $P < 0.0001$; Fig. 2). The defensive strike distances averaged 20.35 ± 4.2% of each snake's body length, while the offensive strikes equated to 4.16 ± 1.4%. Defensive strikes also had significantly longer average durations (142 ± 14 ms) compared to predatory strikes (77 ± 6 ms; $t_{df\,=\,10} = 5.4$, $P < 0.0001$; Fig. 2). The average start of mouth gape did not differ between strike types ($t_{df\,=\,10} = 1.0$, $P > 0.33$). Defensive strikes had significantly higher average strike velocities (1.66 ± 0.09 ms^{-1}) than did offensive strikes (mean = 0.74 ± 0.07 ms^{-1}; $t_{df\,=\,10} = 10.3$, $P < 0.001$; Fig. 2). Both defensive (mean = 75.0 ± 13.1 ms^{-2}) and offensive (mean = 44.0 ± 6.3 ms^{-2}) strikes had high average accelerations. Defensive strikes had higher average accelerations than did offensive strikes ($t_{df\,=\,10} = 7.0$, $P < 0.001$; Fig. 2).

Discussion

Snakes delayed the initiation of a predatory strike until predators and prey were in close proximity, but quickly initiated strikes from relatively large distances from targets that could represent a physical threat. Striking defensively over greater distances at targets that pose a threat would allow snakes to maintain a greater space barrier between themselves and their aggressor, thus offering more space to fight, flee, or both. Furthermore, using a defensive strike from a ranged position allows the snake to eventually retract back to a safer position. During offensive strikes, the snakes did not retract after the strike but instead stayed engaged with the prey until we released it. We observed a much smaller strike distance when the snakes were offered food. In the maximum performance data, defensive strike distance was approximately three times that of the offensive strike distance. Snakes maintained a greater distance barrier between themselves and a threat but minimized the distance barrier when prey was involved. Our observed differences in strike distance are congruent with the life-dinner principle that predicts major differences in behavior and effort between offensive and defensive scenarios (Dawkins and Krebs, 1979).

In general, greater defensive strike distances should cause greater durations simply because the snakes must cover a greater distance over time. Defensive strikes required almost 2.5 times the amount of time to reach their target when compared to offensive strikes. In defensive scenarios, many of the potential threats to snakes are mammals (Ernst and Ernst, 2003). However, although the durations were almost double, all strike durations were still quite rapid compared to recorded mammalian reaction times (Caffier et al., 2003; Yilmaz and Meister, 2013). Therefore, even if snakes modulate strike distance, there still might be selection against some longer strikes if it causes the duration of the strike to put the snake at risk of predatory reactions. Understanding the selection pressures on specific performance traits in differing behavioral scenarios has proven to be a fruitful field of study in lizards (Irschick and Losos, 1998; Irschick et al., 2005) and provides a conceptual framework to further explore in strike behavior.

Although snakes covered a greater distance over a longer time, they still had higher strike velocities and accelerations when striking defensively. Looking at these variables in combination, defensive strikes were initiated from greater distances and with higher accelerations. High accelerations over greater distances will produce higher velocities. Further confirming our findings, the maximum performance data and the average performance data show the same support for our hypotheses. In both maximum and average performance data, strike distance, duration, velocity, and acceleration were greater for defensive strikes than for offensive strikes.

The determinants of strike success are complicated by the possible outcomes of each scenario. For example, in a defensive situation, a snake would have the lowest risk of injury or death (greatest success) if they avoid physical contact with the threat. Therefore, target contact and strike accuracy may not be nearly as important in defensive scenarios when compared to predatory strikes (Whitford et al., 2019). Given the dynamic nature of a snake strike, further experimentation and analysis is needed from multiple snake species to

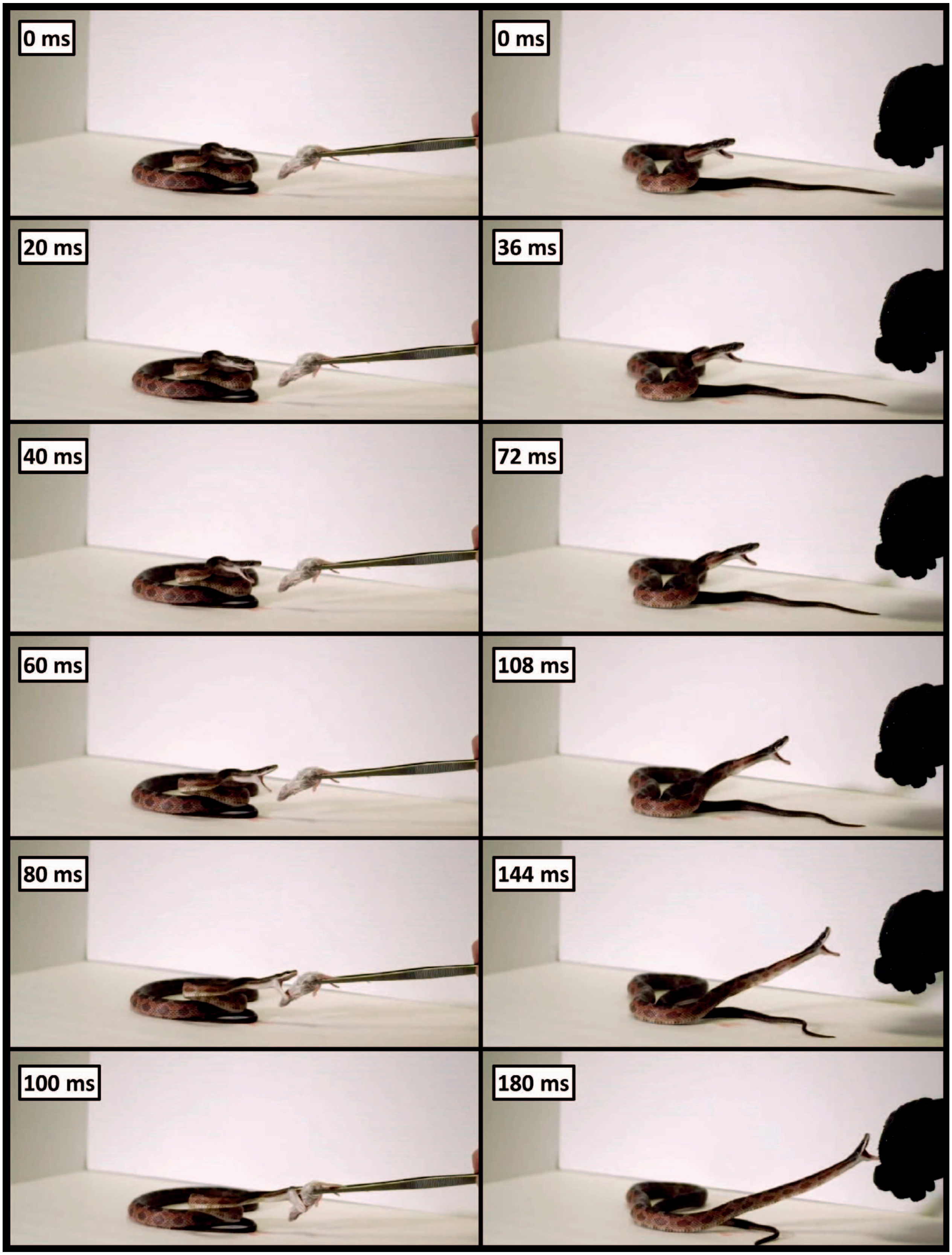

FIG. 1. Still-frame images of an offensive (left) and defensive (right) strike from a juvenile Western Ratsnake (*Pantherophis obsoletus*). The text boxes denote the elapsed time (in milliseconds) from the onset of the strike until first contact with the target.

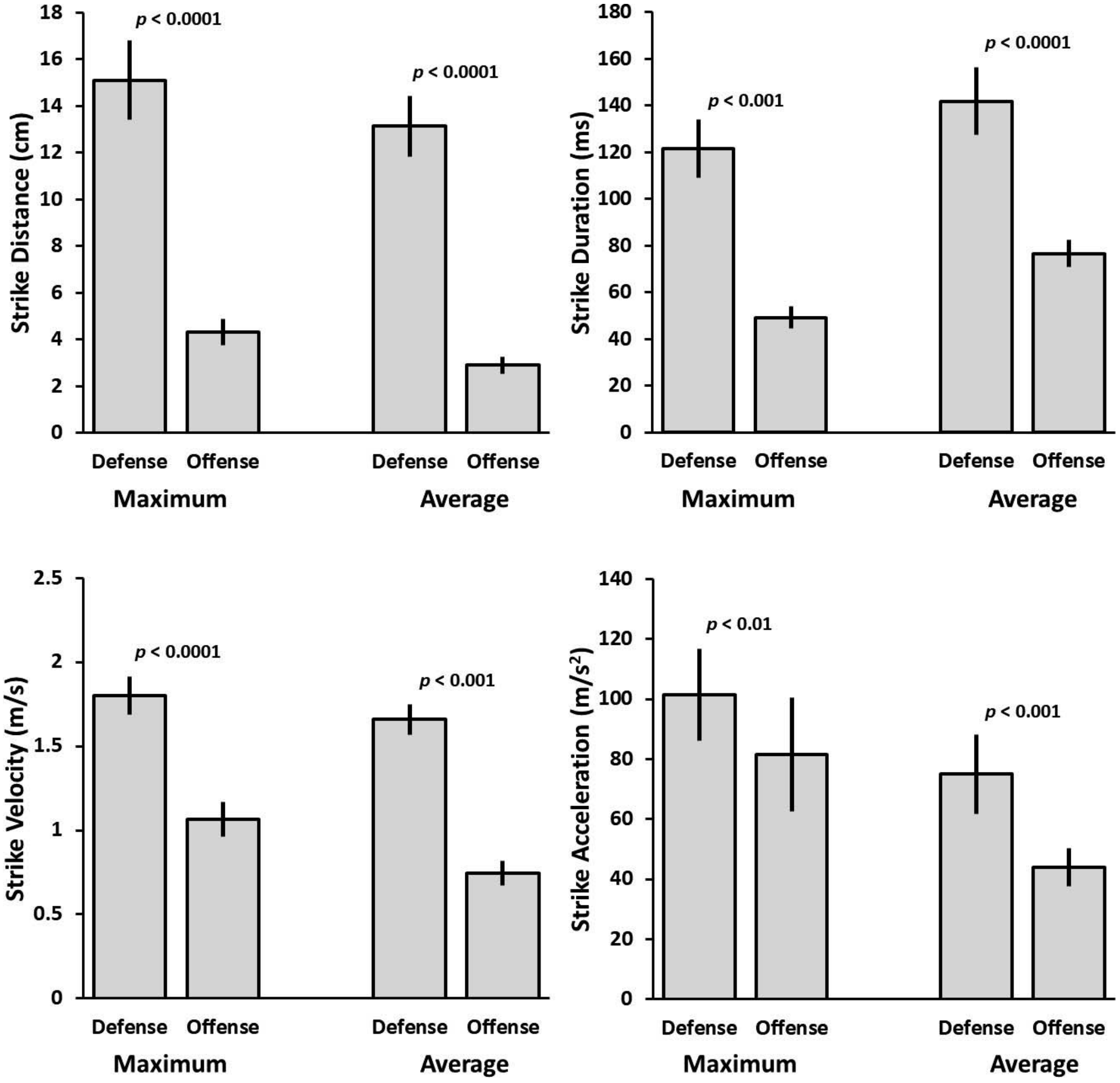

FIG. 2. Maximum and average strike performance (average ± SE) for strike distance, duration, velocity, and acceleration for 11 trials in each category (defensive and offensive) for 11 individual juvenile Western Ratsnakes (*Pantherophis obsoletus*).

understand predator–prey dynamics across the diversity of snakes. Many strike performance variables derive from changes in time and distance, which are likely to be the two most important variables to both predator and prey. For example, strike success was significantly higher in rattlesnakes that struck over short distances when compared to strikes from a greater distance (Clark et al., 2012). Furthermore, predatory strike failure appears partially dependent on the reaction time of the prey (Whitford et al., 2019). Complicating this is the high degree of correlation between strike performance variables (Herrel et al., 2011; Penning et al., 2019; Whitford et al., 2019). Regardless of which performance variable best predicts strike success, what is not clear is how much of the strike is being actively controlled by the snake. Clearly, a snake can control strike distance but whether or not other aspects of the strike can be modulated during movement remains to be determined. Further, we used cadaveric rodents in our study. Prior work investigating snake predation performance has used both living and dead prey (Young et al., 2001; LaDuc, 2002), but it is worth noting this as a potential confounding factor that future work could address.

LaDuc (2002) and Young et al. (2001) conducted similar experiments with rattlesnakes and found contrasting results. Young et al. (2001) found a greater strike distance between the snake and its prey compared to strikes at threats. Although our findings generally support LaDuc (2002), we also found significant differences in strike acceleration between the two strike types. LaDuc (2002) posited that nonsignificant differences among maximum accelerations in *C. atrox* are because of this performance being completely maximized, regardless of target type. While perhaps the case for *C. atrox*, *P. obsoletus* may experience different selection on other strike components. Given that the life-dinner principle predicts that snakes should strike from greater distances when threatened compared to how they strike at prey, we expected to corroborate many of the findings of LaDuc (2002). Based on the differences in acceleration that we found, it is likely that some snakes are recruiting different muscles, groups of muscles, or are modulating muscle activity prior to or during the strike that is resulting in differences in strike acceleration. To date, however, very little work has been done on active muscle use during striking (Young, 2010).

Based on the prestrike behaviors, snakes showed marked behavioral differences in the way they interacted with both targets. Tail shaking occurred before defensive strikes but not before predatory strikes (Garland, 1988). Slow locomotory advancement toward a target occurred only in predatory strikes and not in defensive strikes. Snakes can use sensory information about what they are presented with and are capable of different prestrike, strike, and poststrike behaviors. Our results show that snakes can, and do, modulate many portions of their behavior in response to different potential targets, including various aspects of their striking behavior. Therefore, both offensive and defensive striking behaviors, while perceived as similar in real time, are quantitatively distinct and should be considered separate performance variables.

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