

Determinants of predation success: How to survive an attack from a rattlesnake

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Abstract

1. The selection pressures that arise from capturing prey and avoiding predators are some of the strongest biotic forces shaping animal form and function. Examining how performance (i.e., athletic ability) affects the outcomes of encounters between free-ranging predators and prey is essential for understanding the determinants of predation success rates and broad scale predator–prey dynamics, but quantifying these encounters in natural situations is logistically challenging.
2. The goal of our study was to examine how various metrics of predator/prey performance determine predation success by studying natural predator–prey interactions in the field with minimal manipulation of the study subjects.
3. We used high-speed video recordings of free-ranging sidewinder rattlesnakes (predator, *Crotalus cerastes*) and desert kangaroo rats (prey, *Dipodomys deserti*) to study how performance at various stages of their encounters alters the outcome of their interactions.
4. We found that predation success depends on (a) whether the rattlesnake struck accurately, (b) if the rattlesnake strike was accurate, the reaction time and escape manoeuvres of the kangaroo rat, and (c) if the kangaroo rat was bitten, the ability of the kangaroo rat to use defensive manoeuvres to avoid subjugation by the snake.
5. The results of our study suggest that the role of performance in predator–prey interactions is complex, and the determinants of predation success are altered by both predator and prey at multiple stages of an interaction in ways that may not be apparent in many experimental contexts.

KEYWORDS

biomechanics, escape manoeuvres, kangaroo rat, performance, predator–prey

1 | INTRODUCTION

Catching prey and avoiding predators are central to the reproductive success of animals in nature and a major focus of evolutionary research in biomechanics and locomotion (Higham et al., 2016). Predation is an inherently dynamic interaction that proceeds through a sequence of events (typically termed detection, evaluation, pursuit,

subjugation; Curio, 1976, Endler, 1986) that result in either the capture or escape of the prey. Although popular media often focus on cases where predators successfully kill and consume prey, detailed field studies indicate that prey are usually successful in evading attacks (reviewed in Vermeij, 1982), with rates of predator success in many systems as low as 1%–5%. Because most prey appear to escape predators by rapidly moving away from them, researchers

studying the biomechanics of predator–prey interactions have focused extensively on speed: work on both predators and prey has emphasized maximal velocity (Husak, 2006; Law & Blake, 1996; Meager, Domenici, Shingles, & Utne-Palm, 2006; Miles, 2004; Pruitt, 2010; Walker, Ghalambor, Griset, McKenney, & Reznick, 2005). The focus on speed can mask the importance of other factors that may be more important in determining the outcome of encounters in natural systems (Clemente & Wilson, 2016).

In nature, the outcome of a predatory attack is largely determined by the interaction between the predator's physical performance and any evasive or escape manoeuvres initiated by the prey (Clemente & Wilson, 2016; Combes, Rundle, Iwasaki, & Crall, 2012; Moore & Biewener, 2015; Moore, Cooper, Biewener, & Vasudevan, 2017), and these attributes generally differ based on the hunting mode of the predator (Moore & Biewener, 2015). Generally, active-pursuit predators (e.g., wolves) rely on speed and endurance (Liebenberg, 2006; Young & Goldman, 1944), sit-and-pursue predators (e.g., cheetah) rely on speed and manoeuvrability (Wilson et al., 2018), and sit-and-wait predators (e.g., mantis shrimp, alligators, boas and vipers) rely on stealth and strike speed to circumvent the prey's capabilities for detection and evasion (deVries, Murphy, & Patek, 2012; Groot & Leeuwen, 2004; Huey & Pianka, 1981; Pruitt, 2010; Wainwright, Kraklau, & Bennett, 1991).

These strategies depend on different elements of performance. Predators that pursue prey (either sit-and-pursue or active pursuit) must adapt to the direction, speed and the manoeuvrability of the fleeing prey for a successful capture (Combes, Salcedo, Pandit, & Iwasaki, 2013; Moore & Biewener, 2015), and research on pursuit interactions tends to directly compare athletic performance between predators and prey (Wilson et al., 2018). Because sit-and-wait predators capture prey via rapid surprise attacks that minimize the probability of prey initiating a timely evasive response (Huey, Bennett, John-Alder, & Nagy, 1984), ambush strategies putatively favour high predator acceleration and velocity to quickly close the gap between predator and prey. Prey that are ambushed should be under selection to respond to and evade attacks as quickly as possible. Thus, effective evasion is constrained by the morphology and physiology of the musculoskeletal system, and by the information processing and response time of the sensory systems involved in detection (Dangles, Casas, & Coolen, 2006; Eaton & Emlerley, 1991). As a result, prey response latency (i.e., reaction time), predator attack accuracy and the time that it takes the predator to reach the prey (i.e., relative velocity of two parties) should interact to determine the outcome of the encounters. Little is known, however, about how these performance metrics alter the outcome of actual predation attempts. Sit-and-wait systems are characterized by infrequent, unpredictable predation that can occur much too rapidly to be quantified in any detail by human observers, or even traditional video recording systems, and few studies can examine detailed performance of both predator and prey in nature.

Consequently, most biomechanical studies of ambush predation rely heavily on either a laboratory context or simulations of predator or prey. Such studies are critical to provide the control necessary

for examining performance under experimental conditions (Herrera, Casas, Dangles, & Pincebourde, 2018; LaDuc, 2002; Zamora-Camacho, Rubino-Hispan, Reguera, & Moreno-Rueda, 2015), but can be complemented by studies that retain the full natural context in which both parties are free-ranging (Moore & Biewener, 2015). In natural encounters between predator and prey, the outcome and the locomotor performance achieved by both parties are highly context dependent (VanHooydonck & Van Damme, 2003) and variable (Higham, Clark, Collins, Whitford, & Freymiller, 2017). The ability of either party to overcome the other can be influenced by numerous biotic (Freymiller, Whitford, Higham, & Clark, 2017) and abiotic factors (Higham, Stewart, & Wainwright, 2015; Tudorache, Blust, & De Boeck, 2008). However, even though field-based studies can capture the context in which the two parties evolved, the spatial and temporal unpredictability of predator–prey interactions has made it difficult to tie this dynamic performance to predation outcome in nature.

Many snakes are sit-and-wait predators that may be particularly amenable to field observations in this context due to their tractability in radiotracking and field videography (reviewed in Clark, 2016); such species could serve as a model system for understanding factors that affect the dynamics of sit-and-wait predator–prey interactions. Rattlesnakes (*Crotalus* spp.) are classic ambush predators that hunt by remaining nearly motionless in hiding for prolonged periods (Reinert, Cundall, & Bushar, 1984; Reinert, MacGregor, Esch, Bushar, & Zappalorti, 2011). Rattlesnakes occasionally consume kangaroo rats (*Dipodomys* spp.), common desert-dwelling mammals renowned for their explosive antipredator jumping ability (Biewener & Blickhan, 1988; Webster, 1962). Interactions between rattlesnakes and kangaroo rats follow the typical pattern of sit-and-wait predation: a snake waits in ambush to strike at prey that gets too close, at which point the prey either is struck or initiates a successful evasive manoeuvre.

As with most predator–prey encounters, the outcome of the interaction can potentially be altered by a suite of factors at multiple timepoints (as in Higham et al., 2017). For example, a large body of literature has shown that kangaroo rats can use predator-deterrent signals (e.g., foot drumming, sand kicking) during the evaluation stage of the interaction to dissuade snakes from attacking (Whitford Freymiller, & Clark, 2017, 2019). If the encounter does proceed to the attack stage, an ambush predator must not only accurately target prey, but also attempt to time the strike such that it can reach the prey without being detected (Casas & Steinmann, 2014); therefore, both strike accuracy and speed are critical factors in determining the outcome of the interaction (Clark, Tangco, & Barbour, 2012). Snake strikes are renowned for their rapidity, and a large body of kinematic literature emphasizes the high degree of speed and acceleration achieved during the strike (Herrel, Huyghe, Okovic, Lisić, & Tadić, 2011; Penning, Sawvel, & Moon, 2016). The unique morphology and sensory capability of kangaroo rats appears to be an adaptation for countering such attacks: kangaroo rats have enlarged auditory bullae that endow them with highly sensitive hearing to detect sudden surprise attacks (Webster, 1962; Webster & Webster, 1971) and their large hindlimb muscles allow for rapid vertical leaps (Biewener,

Alexander, & Heglund, 1981; Biewener & Blickhan, 1988; Biewener, Blickhan, Perry, Heglund, & Taylor, 1988). Free-ranging kangaroo rats in at least one population avoided the majority of predatory strikes from sidewinder rattlesnakes, indicating that kangaroo rats are well-equipped to detect and avoid snake strikes (Whitford, Freymiller, & Clark, 2017).

Furthermore, although ambush and rapid-pursuit predators typically move through these stages very quickly, a successful attack must be followed by successful subjugation for the predator to obtain a meal. Current biomechanical studies on high-speed predation largely do not consider subjugation (Casas & Steinmann, 2014; Combes et al., 2012; Domenici & Blake, 1997; Ilany & Eilam, 2007; Moore et al., 2017; Nair, Nguyen, & Mchenry, 2017; Wilson et al., 2018), leading to an implicit assumption that predator success hinges solely on the predator making contact during the attack. Our system provides an example where attack and subjugation can be considered independently. If a rattlesnake manages to embed its fangs into prey, it must then subjugate prey by maintaining fang penetration long enough to inject a sufficient quantity of venom. The quantity of venom injected correlates with the likelihood of the snake successfully obtaining a meal, as rattlesnakes typically avoid retaliation by releasing prey directly following envenomation, and then relocate the prey carcass using chemosensory cues (Hayes, 1992). Prey injected with larger doses of venom are immobilized more quickly, so whether a kangaroo rat dies after being bit may be influenced by the ability of the kangaroo rat to actively reduce the duration of fang penetration. Our previous work found anecdotal evidence that kangaroo rats may actively attempt to avoid subjugation by kicking snakes after a bite occurs, but the frame rate of these recordings was not sufficient for detailed analysis (Whitford et al., 2017).

In the current study, we used high-speed cameras to record the outcome of predator-prey interactions between free-ranging sidewinder rattlesnakes and kangaroo rats in order to assemble a dataset that could explore the relationship between interaction outcome and predator/prey performance at each stage of a rapid predatory attack. By quantifying these natural interactions in detail, we addressed the following questions: (a) What is the relative influence of snake performance and kangaroo rat performance on the outcome of the interactions? and (b) What are the specific mechanisms by which kangaroo rats reduce the risk of mortality during an encounter? We predicted the dominant factors influencing the outcome would include the ability of the snakes to strike accurately (strike accuracy), the speed of the strike (strike performance), the time for kangaroo rats to respond to a strike movement (reaction time) and the manoeuvrability of kangaroo rats during envenomation attempts (evasion performance).

2 | MATERIALS AND METHODS

2.1 | Field site, study animals and radio telemetry

We conducted this study in the summer of 2016 from mid-May to August 1st on the Barry M. Goldwater Range (32°25'17.0"N

114°22'55.1"W) operated by the Marine Corps Air Station in Yuma, AZ (USA). The site was at the intergrade of windblown sand dunes and creosote scrub (Malusa & Sundt, 2015). At the beginning of the research period, we visually searched for sidewinder rattlesnakes for radiotransmitter implantation. Once captured, we collected morphological data for each snake and implanted a temperature-sensitive radiotransmitter (Reinert & Cundall, 1982). Following surgery, we released snakes once normal behaviour was resumed (typically <24 hr) and removed transmitters at the end of the study. Throughout the study period, we trapped desert kangaroo rats using Sherman live small mammal traps baited with sterilized black oil sunflower seed. We collected morphological data on trapped kangaroo rats and marked their fur in a unique pattern using Nyanzol dye to allow for identification of individuals on video recordings. However, despite marking numerous individuals, we often recorded unmarked kangaroo rats because of the high densities at our field site. For this reason, we used a combination of approaches to ensure no kangaroo rat-snake pair was recorded more than once; we used any readily discernable natural variation in pelage and morphology to identify unique individuals; we attempted to capture and mark kangaroo rats immediately after a trial; and, if these failed, we waited until snakes moved well out of the home range (i.e., >50 m) of unmarked kangaroo rats before recording additional observations.

2.2 | Videography and data collection

As both species are strictly nocturnal during the summer, we tracked radio-implanted rattlesnakes each evening beginning at approximately sundown and again periodically throughout the night. When a snake was found to be hunting on the surface in the vicinity of active kangaroo rat burrows, as evident by the stereotypical ambush position used by rattlesnakes (Reinert et al., 2011), we positioned two synchronized Edgertronic high-speed cameras (model SC1) recording at 500 Hz and a shutter speed of 1/500 of a second, with 4–6 infrared lights above the hunting snake. The camera arrangement changed depending on the ambush site chosen by the snake but, in general, one camera was positioned low (~0.5 m from the ground) and perpendicular to the anticipated strike direction, and the other camera was positioned high (~1.8 m from the ground) and in line with the anticipated strike direction. An onsite observer with 2 laptop computers (one tethered to each camera) sat ~30 m away from the snake and triggered the cameras to save the previous 10 s of video recording if a strike occurred. We encouraged the above-ground movements of kangaroo rats at our site by sprinkling small amounts of black oil sunflower seed (5–10 g), thereby increasing kangaroo rat foraging activity in the area. Although the reliance on radiotelemetry meant we had only a limited number of individual rattlesnakes to record, we only recorded each snake in a maximum of 3 interactions to ensure no individual was over-represented in our data; snake ID was also included as a random factor in statistical analyses to control for repeated observations on individual snakes. Additionally, no interactions were recorded with the same snake and kangaroo rat combination that had been recorded previously. Once

a strike occurred and the cameras had been triggered, the onsite observer visually monitored the status of the snake and the kangaroo rat to discern signs of envenomation. Envenomated kangaroo rats were never observed to enter burrows following envenomation, making it possible to accurately record their fate. After recording an encounter, we positioned a custom-built, rigid metal three-dimensional calibration object in the exact location of the snake strike and recorded it with both cameras to allow for post hoc calibration of the video frames. The calibration object encompassed a volume of 90 cm wide × 93.5 cm long × 89.6 cm tall and contained 69 points scattered throughout the volume that we measured to the nearest millimetre.

2.3 | Video analysis

From the videos, we extracted multiple variables that correspond to the performance of both the kangaroo rat and rattlesnake. First, we measured reaction time as the time from strike initiation (first visible movement of the strike) to the first visible movement of the kangaroo rat's evasive jump. Second, we recorded the time from strike initiation to contact with the kangaroo rat (i.e., the duration of the extend stage of the strike; Kardong & Bels, 1998) or, when a strike did not result in contact, the time from strike initiation until the snake would have made contact had the kangaroo rat not moved. Lastly, we measured strike distance as the distance from the tip of the snake's rostrum to the part of the kangaroo rat's body (excluding the tail) closest to the snake when the strike was initiated.

To extract the kinematic variables of interest from the video recordings, we calibrated the videos and digitized the movements of the snake and kangaroo rat in MATLAB (R2016b) using DltDataviewer version 5 (Hedrick, 2008). We digitized the back of the neck in line with the posterior end of both venom glands on the snake and the back of the head between the ears of the kangaroo rat. The XYZ coordinates were then imported into *Rstudio* for further analysis. The point-to-point displacements values were filtered using a zero-lag Butterworth filter with a cut-off frequency of 50 Hz (Herrel et al., 2011; Penning et al., 2016) using the *signal* package; velocity and acceleration values were then calculated from the filtered data.

2.4 | Strike outcome

We quantified the spatial accuracy of strikes and, if they contacted prey, the duration of fang penetration. Strikes were categorized as "accurate" if the strike contacted or would have contacted the kangaroo rat (had the kangaroo rat remained in place); otherwise, strikes were categorized as inaccurate. We further categorized accurate strikes as "bites" when fang penetration was observed, or "misses" when we observed no fang penetration. We then noted the duration of fang penetration (in ms), and whether bitten rats survived envenomation.

Previous work suggested that kangaroo rats attempt to reduce the amount of time the snake can maintain fang penetration

by kicking and/or rapidly rotating their body, thereby decreasing the likelihood of envenomation during a bite (i.e., whether the prey effectively avoided subjugation following a successful attack; Whitford et al., 2017). To reflect these behaviours, we further categorized bites according to how the fangs were withdrawn from the kangaroo rat. We categorized a bite as "released" if the snake withdrew its fangs (i.e., snake released and/or retracted), or "removed" if the kangaroo rat through kicking or rapidly rotating its body forcibly removed the fangs.

2.5 | Statistical analysis

To assess the degree to which the rattlesnakes' strike performance and/or the kangaroo rats' evasion performance influenced the outcome of a strike, we implemented a mixed logistic regression in R (version 3.3.1) using the package "lme4." We modelled "strike success" as a dichotomous dependent variable ("0" for a miss or "1" for a bite) and included snake ID as a random effect. Due to the sample size of our dataset, we limited our model to three predictor variables and only included variables that were highly likely to influence strike outcome: average velocity of the snake strike, kangaroo rat reaction time and the distance between the snake and kangaroo rat at strike initiation. Additionally, metrics of snake performance show a high degree of collinearity, indicating that average strike velocity is a reasonable proxy for overall snake performance (Supporting Information Table S1). We then performed a bootstrapping procedure using the package *boot* on the final model to generate confidence intervals for the estimated coefficients (Canty & Ripley, 2017). We opted to not include acceleration of the snake strikes in our statistical model as second-derivative calculations can be heavily influenced by noisy data, acceleration and velocity are correlated (Supporting Information Table S1), and our estimates of strike acceleration are lower than the acceleration values reported in other rattlesnake strike studies (Higham et al., 2017; LaDuc, 2002). It is unclear whether our estimates of strike acceleration are lower due to the introduction of digitizing error resulting from filming strikes in the field, or whether the small body size of sidewinder rattlesnakes results in reduced accelerative abilities compared with other, larger rattlesnake species; our ongoing experiments in a laboratory setting on *C. cerastes* and *C. scutulatus* will provide more detailed information on the interspecific differences in accelerative ability. Summary statistics are provided for variables not included in our model. Because most strikes did not result in bites, we have limited data on the role of fang penetration and present only descriptive statistics for this analysis.

3 | RESULTS

3.1 | Summary of strikes and strike accuracy

A total of 32 strikes were recorded from 13 snakes (1–3 per snake, median = 3 observations/snake), 15 of which resulted in bites

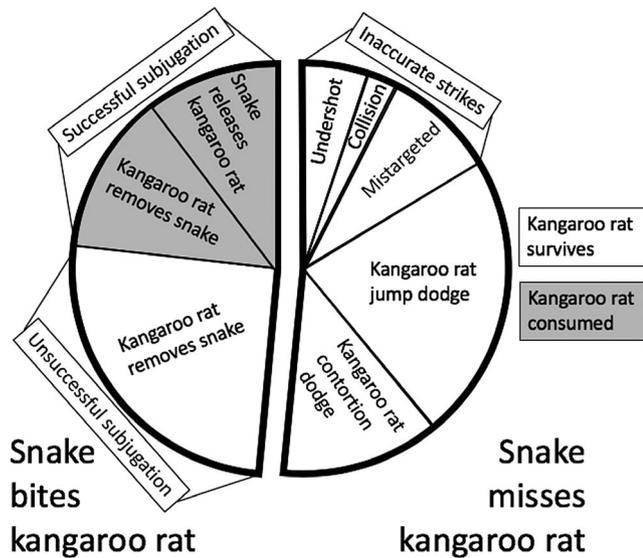


FIGURE 1 Relative frequencies of all possible outcomes from rattlesnake predatory strikes at kangaroo rats ($n = 32$ total strikes). Approximately 81% of strikes were accurate, but only 47% of strikes resulted in the snake biting the kangaroo rat, and only 22% resulted in the kangaroo rat being killed and consumed (shaded portions). See text for additional details

(Figure 1). Of the 15 bitten kangaroo rats, 8 avoided subjugation (survived without apparent effect of envenomation) and 7 died from envenomation and were consumed by snakes. Of the 17 misses, 6 were inaccurate strikes and 11 were accurate strikes that missed due to the kangaroo rat moving out of the way prior to the snake being able to embed its fangs (Table 1, Video 1, Figure 1). Of the 6 inaccurate strikes, 3 were inaccurate because the snake would not have contacted the kangaroo rat even if the kangaroo rat had not moved (Table 1, Video 2), 2 were inaccurate due to the snake's forward movement ceasing before reaching the kangaroo rats position, and 1 was inaccurate due to the snake colliding with a branch shortly after strike initiation. Of the 11 strikes that were unsuccessful due to the kangaroo rat moving out of the way, 7 kangaroo rats leaped out of the way (Figure 2a), and in the remaining

4, the kangaroo rat contorted its body such that the snake did not make contact. Interestingly, kangaroo rats exhibited a substantial amount of variability in the manner that they manoeuvred out of the way of the snake's path: 2 retracted their head, 1 kangaroo rat flipped upside down (Table 1, Video 3), and 1 swung its hindquarters away from the snake. The kangaroo rats were moving rapidly in only 2 interactions when the snake initiated the strike (i.e., movement that exceeds the slow walking and short hops characteristic of kangaroo rat foraging): 1 was bitten while running directly towards that snake, and the other was running perpendicular to the strike trajectory, resulting in an inaccurate strike. For the remaining analyses, we excluded the 6 interactions with inaccurate strikes. Additionally, 3 interactions resulting in bites could not be analysed quantitatively due to low-quality calibrations resulting in poor estimates of kinematic variables.

3.2 | The effects of performance on strike outcome

A total of 23 strikes from 12 snakes (median = 2 strikes per snake, 12 bites and 11 missed strikes) were included in our analysis of strike outcome. From the logistic regression, kangaroo rat reaction time significantly influenced strike outcome (Coef = 0.06, SE = 0.03, $z = 2.41$, $p = 0.02$, bootstrapped CI = 0.03–33.32), while distance (Coef = -0.11, SE = 0.15, $z = -0.74$, $p = 0.46$, bootstrapped CI = -80.97–4.47) and average strike velocity (Coef = 1.81, SE = 2.05, $z = 0.88$, $p = 0.38$, bootstrapped CI = -92.37–1,795.75) were both nonsignificant factors. The odds ratio for reaction time (odds ratio = 1.06) indicates that an 11.3 ms increase in reaction time doubles the probability of being struck (Figure 3). The random effect of snake ID was not a substantial source of variation in the model (variance ≈ 0 , $SD \approx 0$). Summary statistics for variables included in the logistic regression and for variables that were excluded from our model due to sample size limitations are provided in Table 2. Additionally, to facilitate comparisons with past studies, we report results of univariate logistic regression models for all these performance variables as Supporting Information (Table S2); these models also show that only reaction time had a significant effect on outcome.

TABLE 1 Example videos illustrating various components of the recorded interactions

Video	URL	Description
Video 1	https://youtu.be/WPqgr6v2iTI	A kangaroo rat evading a rattlesnake strike by rapidly detecting, reacting and evasively leaping out of the strike trajectory
Video 2	https://youtu.be/eQeqCztvao4	An inaccurate strike due to the snake strike achieving full extension before reaching the kangaroo rat
Video 3	https://youtu.be/svz9MPebQRw	A kangaroo rat evading a snake strike by rapid manoeuvring its body out of the strike path and using its hindlegs to kick the snake away
Video 4	https://youtu.be/4xJyxo5MJp0	A successful snake strike that results in the kangaroo rat using its hindlegs to kick the snake, thereby forcibly removing the snake's fangs

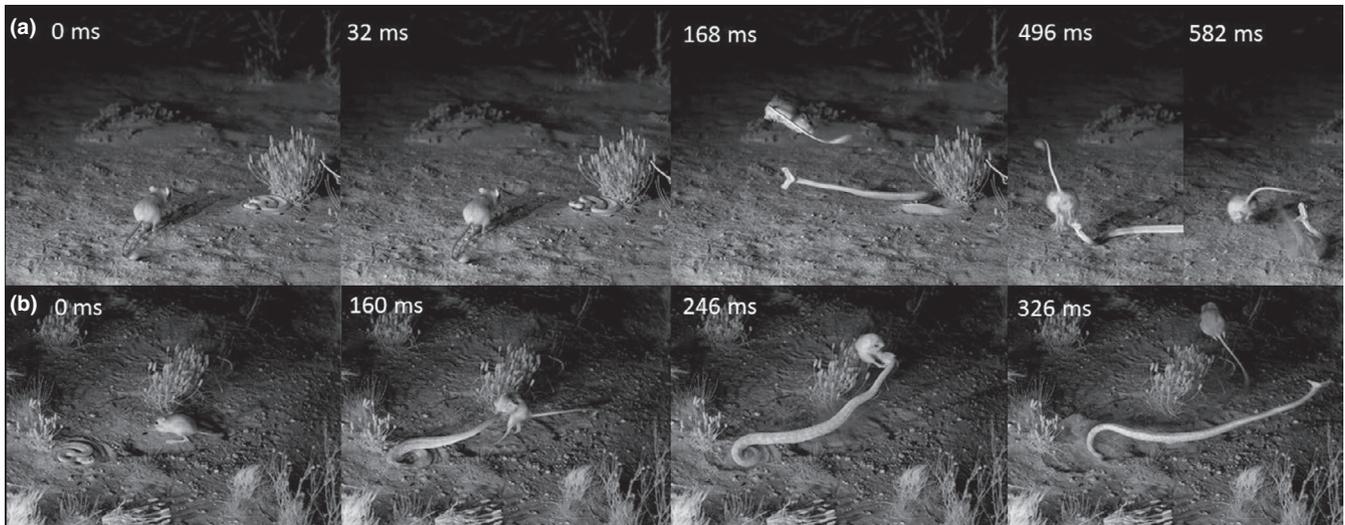


FIGURE 2 Series of images taken from a missed strike (a) and a bite where the kangaroo rat forcibly removed the snake's fangs (b). In the unsuccessful strike, the images correspond to the moment of strike initiation (0 ms), first frame of the kangaroo rat response (32 ms), kangaroo rat's leap (168 ms), kangaroo rat landing on the snake (496 ms), and the kangaroo rat running away (582 ms). In the bite, the images correspond to strike initiation (0 ms), first contact with kangaroo rat (160 ms), kangaroo rat kicking the snake (246 ms), and the snake being propelled away by the kangaroo rat's kick (326 ms)

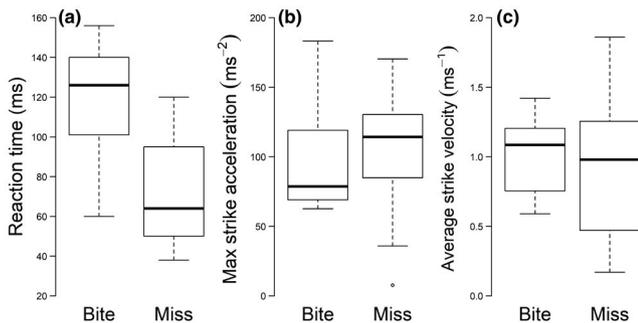


FIGURE 3 Boxplots of kangaroo rat reaction times (a), max strike acceleration (b) and average strike velocity (c) in missed strikes ($N = 11$, 8 snakes, 1–3 strikes per snake) and strikes resulting in a bite ($N = 12$, 8 snakes, 1–3 strikes per snake). Lower reaction times indicate faster responses by the kangaroo rat. Whiskers indicate maximum and minimum values, box indicates interquartile range, and black lines indicate the median

3.3 | Bite survivability

Of the 15 strikes that resulted in bites (12 strikes that were included in the logistic regression and 3 that were removed due to low-quality calibrations), 7 of the kangaroo rats died from envenomation (Figure 1). In only 3 of the bites did the snake release its fangs, and in all these cases the kangaroo rat died. Of the 12 bites where the snake was forcibly removed, the kangaroo rat kicked the snake off in 9 (Figure 2b) and rotated to the point that the snake was forced to release in 3 (Table 1, Video 4), resulting in death for 1 that rotated and 3 that kicked that snake off. The duration of fang penetration for all bites where snakes released kangaroo rats (mean = 734.67 ms, min = 726 ms, max = 746 ms) was greater than all bites where kangaroo rats removed snakes (mean = 200.67, min = 60 ms, max = 516 ms;

Figure 4). Three of the kangaroo rats that died after removing snakes (i.e., that died after a relatively short duration of fang penetration) were bitten by the same large female snake, indicating some of this variation may be due to individual differences in the injected quantity or chemistry of rattlesnake venom.

4 | DISCUSSION

Capturing prey and escaping predators are major determinants of reproductive success, and meeting these challenges has resulted in the evolution of extreme athletic ability throughout the animal kingdom. Understanding how relative athletic ability of free-ranging animals influences the outcome of predator–prey interactions is logistically challenging, but also essential for understanding how selection has shaped natural communities. By studying predator–prey interactions in nature and comparing how the level of performance achieved by both parties influences the outcome of the interaction, we illustrate that the most important determinates do not necessarily correspond with performance attributes that are most well studied (e.g., velocity, acceleration).

4.1 | Predator performance

Snakes increased the likelihood of successful predation in two ways: (a) strike accuracy and (b) biting prey long enough to inject sufficient venom for subjugation. A substantial portion (5 of 32) of snake strikes missed simply due to the snake having either misjudged the distance to the kangaroo rat and/or having struck at a location other than the space occupied by the kangaroo rat at the time of strike initiation. If the strike was accurate, velocity and distance of the snake

TABLE 2 Descriptive statistics for interactions that resulted in bites (bite) and those that did not result in bites (miss) for variables included in the logistic regression model and those that were excluded

	Bite (N = 12, 8 snakes, 1–3 strikes per snake)	Miss (N = 11, 8 snakes, 1–3 strikes per snake)
Included in logistic regression		
Average strike velocity (m/s)	1.01 (0.59–1.42)	0.89 (0.17–1.86)
Distance (cm)	17.43 (8.03–25.79)	13.37 (3.73–24.05)
K-rat reaction time (ms)	119.83 (60–156)	71.64 (38–120)
Not included in logistic regression		
Strike extend duration (ms)	133.84 (54–180)	142 (82–308)
Maximum strike acceleration (m/s ²)	97.81 (62.60–183.22)	103.62 (7.66–170.30)
Maximum strike velocity (m/s)	2.56 (1.43–3.47)	2.35 (0.63–3.97)

Notes. Values are average (min–max). Bolded rows indicate significant variables ($p < 0.05$). K-rat: kangaroo rat.

strike were not statistically related to outcome. This result was unexpected, due to the overwhelming emphasis on maximum velocity in the biomechanical and kinematic literature on ambush predation in general, and snake strikes in particular (LaDuc, 2002; Ryerson & Tan, 2017; Young, 2010; Young, Phelan, Jagers, & Neiman, 2001). Our study illustrates that the outcome of predator–prey interactions involving high-speed attack and evasion behaviours can be driven by intricate, system-specific dynamics (e.g., attack accuracy, prey reaction time, forced fang removal), and may be heavily influenced by context. Experiments attempting to capture these behaviours in a controlled setting may require considerable modifications to capture the important elements of the natural context for both predator and prey.

Although predatory snakes certainly rely extensively on strike speed, the possibility exists that there is still some sort of trade-off between attack speed and detectability, similar to what Casas and Steinmann (2014) have shown for spiders attacking crickets. As with crickets running at spiders, increased snake strike speed

could possibly elicit faster reaction times of kangaroo rats though increased air disturbances or a more rapidly expanding looming stimulus. Interestingly, Freymiller et al. (2017) found desert kangaroo rats reacted to an artificial “strike” (a mechanical spring uncoiling at the approximate velocity of a snake strike) much more rapidly than reaction times we report here to an actual snake: kangaroo rats reacted to the spring within 20–50 ms, whereas reaction times to rattlesnakes spanned from 40–160 ms. It is possible that this drastic difference in reaction times results from snakes using strike movements that minimize sound or air disturbance, resulting in a more delayed reaction when compared to a less “camouflaged” rapid attack. More empirical work is necessary to address this hypothesis experimentally.

Our findings also highlight the capacity for predator hunting mode to shape performance characteristics of the prey. Prey co-evolving with pursuit predators typically exhibit physical characteristics that increase sprint speed, endurance and turning radius while fleeing (Bro-Jørgensen, 2013; Howland, 1974; Wilson et al., 2018). However, sprint speed, endurance and the ability to turn sharply while running are irrelevant to the time-scale at which many ambush predators attack (snake attacks spanned <308 ms in our study). As a result, the prey of sit-and-wait and ambush predators evolve different physical characteristics to avoid capture. For example, African herbivores commonly hunted by more ambush-reliant predators have slower sprint speeds but increased defensive morphologies (e.g., African buffalo, *Syncerus caffer*) when compared to sympatric prey species more commonly hunted by pursuit-style predators (e.g., springbok, *Antidorcas marsupialis*; Caro, 2005; Bro-Jørgensen, 2013). Similarly, kangaroo rats have multiple specialized sensory and motor adaptations that allow them to avoid ambush attacks by employing rapid and powerful leaps (Biewener & Blickhan, 1988; Biewener et al., 1988; Webster, 1962).

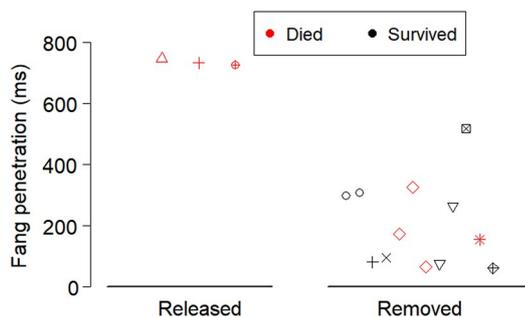


FIGURE 4 A plot of the duration of fang penetration for each bite relative to whether the snake released the kangaroo rat (released, $N = 3$, 3 snakes) or the kangaroo rat forcibly removed the fangs (removed, $N = 12$, 8 snakes). Red points indicate the kangaroo rat died due to envenomation, and black points indicate the kangaroo rat survived. Each plotting symbol corresponds to a different individual snake (i.e., snake identity). All points are jittered along the x-axis within their respective categories to increase the visibility of overlapping points

4.2 | Prey performance

Kangaroo rats have specialized, enlarged auditory bullae which greatly enhance their ability to perceive the quiet, low-frequency

sound of a snake or owl attacking from ambush (Webster, 1962). Experimental work has even demonstrated empirically that deafened kangaroo rats are much more susceptible to rattlesnake predation in a captive context (Webster, 1961,1962). Additionally, the hindlimbs of kangaroo rats appear to be specialized for explosive leaps that can rapidly propel them out of the attack trajectory of a predator (Biewener & Blickhan, 1988; Biewener et al., 1988; Rankin, Doney, & McGowan, 2018). Our recordings demonstrate not only the effectiveness of these defensive jumps, but also reveal that body manoeuvrability while jumping is an important attribute of effectively avoiding subjugation.

Biomechanists typically associate manoeuvrability in a predator–prey context with the ability to perform tight turns at speed, an effective means of escaping pursuit predators (Clemente & Wilson, 2016; Howland, 1974). Our high-speed recordings show manoeuvrability at finer temporal and spatial scales can also be integral to successful avoidance of ambush attacks. We found that kangaroo rats combined vertical leaps with body contortions and defensive kicks in unexpected ways. For example, in one instance, the kangaroo rat flipped onto its back, used its hindlegs to kick the rattlesnake's head away, and then rotated back upright and leaped away (Table 1, Video 3), all in under 250 ms. Although it is possible that this sequence of events may have resulted from undirected flailing and luck, our impression is that these are coordinated and directed defensive manoeuvres performed with extreme speed. If so, then these remarkable avoidance behaviours indicate that kangaroo rats are not only capable of perceiving an oncoming snake strike and responding rapidly but can also process enough information about the snake to use alternative defensive manoeuvre behaviours other than just leaping. On multiple occasions, kangaroo rats exhibited avoidance behaviours similar to the one described above; by either retracting their head from the snake's trajectory or swinging their haunches away from the snake, kangaroo rats could avoid a bite by incorporating these additional manoeuvres into their evasive leaps. The complexity and variability of these defensive movements was surprising, and our current study is not sufficient to analyse the underlying mechanisms—more experimental work is necessary to evaluate these locomotor abilities quantitatively. Even with only qualitative descriptions, we think it is worth highlighting these movements, as they appear to be a key component of successful evasion and are likely present in other prey species that must avoid rapid, short duration attacks from sit-and-wait predators.

Our results from kangaroo rats differ dramatically from other vertebrate escape responses, including the C-start of fishes. The latter is stereotyped and, therefore, potentially predictable by the predator. Indeed, tentacled snakes (*Erpeton tentaculatum*) have capitalized on this by anticipating future fish behaviour by striking where the fish would end up at the end of an escape response (Catania, 2009). In contrast, we found no evidence that snakes can anticipate the future location of a kangaroo rat following an escape initiation, which likely enhances the ability of kangaroo rats to escape

a strike. Among vertebrates, our system is ideal for examining the interactions of high-performing predators and prey with complex behaviours.

The mid-air manoeuvres and kicks of kangaroo rats were frequently effective at allowing them to avoid subjugation by venom even after they had been bitten by snakes. Even ambush predators that rely on rapid venom injection systems need some minimal amount of time to subjugate prey after orchestrating an effective attack. Past studies have emphasized that to subjugate relatively large rodents, venomous snakes must balance the need to inject a sufficient quantity of venom with the potential for injury from kicking, biting and clawing prey (Radcliffe, Chiszar, & O'Connell, 1980). As a result, venomous snakes have been consistently characterized as voluntarily releasing mammalian prey after an envenomating bite. In our system, snakes released only 3 of the 15 kangaroo rats. The other 12 kangaroo rats actively removed the snakes via kicking or contorting. This is the first direct evidence that some prey can remove snakes that have bitten them before lethal envenomation occurs, thereby increasing their likelihood of surviving a bite. The duration of fang penetration was drastically reduced in all instances where the kangaroo rats forced the removal of the snake's fangs relative to instances where the snake disengaged its fangs, resulting in higher survival prospects for kangaroo rats that removed the fangs (8/12 kangaroo rat survived) than for kangaroo rats that were not able to remove the fangs (0/3 kangaroo rats survived).

5 | CONCLUSIONS

Our study of rattlesnakes and kangaroo rats has several important implications for the general understanding of the biomechanics of predator–prey interactions. Our findings complement other systems that have examined these relationships in free-ranging animals in demonstrating that prey reaction time plays a central role in shaping outcome. Unlike many vertebrate systems, such as fishes, the prey in our study have a complex repertoire of escape manoeuvres and post-strike defensive behaviours (e.g., kicking) that could serve as a model for more complex predator–prey interactions. Future research in this area should continue to explore the sensorimotor constraints on reaction time. Conversely, successful ambush predators may not necessarily be the fastest, but rather the individuals that target prey in such a way that enhances the element of surprise. Our findings also highlight the importance of incorporating accuracy, as well as speed, into studies that aim to understand capture success among predatory vertebrates, as in Higham, Day, and Wainwright (2006) and Kane and Higham (2014). Lastly, our study illustrates the importance of complementing laboratory studies with observations of free-ranging individuals in nature: the ultimate outcome of interactions was influenced by predator attack accuracy, prey reaction time, prey manoeuvrability and the physical struggle between both parties to retain or remove fangs after the bite. Future studies can build on our results by examining how

performance and interaction success vary across populations and species that differ in relative success rates, as well as incorporating more environmental stochasticity (e.g., ambient temperature, light level, ambient noise level). We believe this system can ultimately serve as exemplar for understanding how predators and prey shape each other's behaviour and morphology over evolutionary time.

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CONFLICT OF INTERESTS

None.

AUTHORS' CONTRIBUTIONS

All authors designed the study. M.D.W., G.A.F. and R.W.C. collected the data. M.D.W. quantified recordings, ran statistical analyses and drafted the manuscript. All authors read, revised and approved the manuscript.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.18516pq> (Whitford, Freymiller, Higham, & Clark, 2019) and supplementary videos are available at YouTube.com (see Table 1 for URLs).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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