



Avoiding the serpent's tooth: predator–prey interactions between free-ranging sidewinder rattlesnakes and desert kangaroo rats



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Many species perform complex antipredator displays that deter attacks by informing predators that continued attempts at prey capture will be costly. However, because of the difficulties in studying the behaviour of free-ranging predators, we have a limited understanding of how predators respond to those signals. Here, we took advantage of our ability to quantify predatory behaviours of free-ranging sidewinder rattlesnakes, *Crotalus cerastes*, to examine the influence of anti-snake behaviours performed by desert kangaroo rats, *Dipodomys deserti*. We recorded natural encounters and quantified the predator-deterrent behaviours displayed by the kangaroo rats, as well as any strikes performed by the rattlesnakes and whether the strikes were successful. We found that predator-deterrent signalling significantly reduced the probability that a rattlesnake would strike. This was most likely due to the ability of kangaroo rats to mobilize extremely rapid evasive leaps; even rats that appeared unaware of the snakes were almost always able to avoid rattlesnake strikes. The degree of effectiveness of this evasive leaping in countering rattlesnake predation was unexpected and indicates that this may be a rich system for exploring the biomechanics of extreme physical performance in a naturalistic context.

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Almost all animals have predators, and many species exhibit a robust suite of antipredator behaviours. Commonly, these antipredator behaviours aid animals in being difficult to detect (hiding), catch (flight) or subdue (fight). However, some species have evolved more proactive antipredator behaviours that can involve approaches towards a predator, conspicuous displays and active harassment. These antipredator behaviours are thought to function mainly as predator-deterrent signals (Bradbury & Vehrencamp, 2011). Predator-deterrent signals may work through several mechanisms: (1) informing the predator that it has been detected (Barbour & Clark, 2012; Cresswell, 1994; Zuberbühler, Jenny, & Bshary, 1999); (2) alerting the predator that the prey is in a heightened state of vigilance (Putman & Clark, 2015; Randler, 2006); (3) informing the predator of the physical health or vigour, and thus escape ability, of the displaying individual (FitzGibbon & Fanshawe, 1988); or (4) threatening direct physical harassment of the predator (Iwamoto, Mori, Kawai, & Bekele, 1996; Shields, 1984). This type of predator–prey communication can benefit both parties: the prey avoids energetic costs involved in

continued antipredator behaviour and the opportunity costs of forgoing other activities (e.g. foraging and mating), and the predator avoids opportunity, energetic and injury costs of launching an attack that is unlikely to be successful (Berger-tal, Mukherjee, Kotler, & Brown, 2009; Caro, 2005).

Few studies, however, have determined the actual effects that these predator-deterrent displays have on the predator, the recipient of the signal. As predators are typically difficult to study under natural conditions, and as the timing and location of interactions between predator and prey are largely unpredictable, many studies of predator-deterrent signalling use a human surrogate (Cooper, Perez-Mellado, Baird, Caldwell, & Vitt, 2003), a model predator (Leal & Rodríguez-Robles, 1997) or a restrained predator (Owings & Coss, 1977). Although these surrogate predators are useful for eliciting and studying prey behaviours, the response of the predator to prey behaviours cannot be examined, limiting our understanding of predator–prey communication. Therefore, it is necessary to study the interaction holistically by examining how predators alter their behaviour in response to displays, and whether they experience costs to not responding. The few studies that have examined predator responses have found that displays do often alter the behaviour of predators. FitzGibbon and Fanshawe (1988) found that African wild dogs,

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Lycaon pictus, preferentially pursued Thomson's gazelles, *Gazella thomsoni*, that stotted at slower rates, indicating that wild dogs used stotting as a means to detect less fit individual gazelles. Cresswell (1994) found that merlins, *Falco columbarius*, preferentially pursued skylarks, *Alauda arvensis*, that were not singing, seemingly because they were more successful at capturing them. Barbour and Clark (2012) found that tail-flagging by California ground squirrels, *Otospermophilus beecheyi*, towards northern Pacific rattlesnakes, *Crotalus oreganus*, both decreased the likelihood of the rattlesnakes striking and increased the probability of rattlesnakes abandoning ambush hunting sites in the vicinity of the signaller.

We studied the effects of the predator-deterrent behaviours expressed by desert kangaroo rats, *Dipodomys deserti*, on the attack (striking and envenomating) behaviours of sidewinder rattlesnakes, *Crotalus cerastes*. Kangaroo rats (*Dipodomys* spp.) are semifossorial heteromyid rodents common throughout the arid regions of western North America. Many species are known to perform a variety of predator-deterrent signals when encountering snake predators (Bouskila, 1995; Randall & Boltas King, 2001) and will spend a substantial amount of time in the vicinity of snakes, often within striking distance (Clark, Dorr, Whitford, Freymiller, & Hein, 2016; Randall, Hatch, & Hekkala, 1995). A typical desert kangaroo rat predator-deterrent display may include a combination of sand kicks, foot drums, foot rolls, inspections (close approach to the predator) and jump backs (see Table 1 for descriptions of predator-deterrent behaviours; Randall & Boltas King, 2001). Like many snakes, sidewinder rattlesnakes are ambush predators, relying on crypsis via camouflage or self-burial to effect a close encounter with potential prey, whereby they can attack with a rapid envenomating strike (Clark, Dorr, Whitford, Freymiller, & Putman, 2016).

We recorded the behaviours of free-ranging sidewinders and desert kangaroo rats to test the hypothesis that predator-deterrent signalling would reduce the likelihood of a predator attacking. We predicted that some combination of the elements of the anti-snake displays of desert kangaroo rats would decrease the probability that a sidewinder would strike. We also attempted to determine the outcome of snake strikes and used a high-speed camera (120 frames/s) to record two strikes and anecdotally describe the corresponding evasive manoeuvres of the kangaroo rat.

Table 1
Ethogram of desert kangaroo rat and sidewinder behaviours

Behaviour	Description
Kangaroo rat	
Foot drum bout	Repeated drumming of the hindfoot (Video 1)
Foot roll	Rapid drumming of both hindfeet (Video 1)
Jump back	A jumping motion in which the individual first approaches the snake and then rapidly leaps into the air away from the snake (Videos 1 and 2)
Sand kick	The use of the hindfeet to kick substrate towards the snake (Videos 1 and 2)
Sidewinder	
No strike	No strikes occurred during the interaction
Strike	Snake struck at prey
Miss	Strike did not make contact
Apparent contact	Contact was made, but the degree of contact was uncertain
Bite	Strike resulted in contact for more than one frame

URLs for videos are given in Table 2.

METHODS

Study Site

Our study took place at a dune system south of the California State University Desert Studies Center in San Bernardino County, CA, U.S.A. (35° 7'7.16"N, 116° 7'5.01"W). The site consisted of low-lying, wind-blown sand dunes with interspersed mesquite patches (*Prosopis glandulosa*) and was bordered by desert scrub dominated by creosote (*Larrea tridentata*) and galleta grass (*Hilaria rigida*). The site was chosen because it contained high concentrations of both sidewinder rattlesnakes and desert kangaroo rats. We collected data from mid-May through 1 August in 2013 and 2014, with additional observations included from several weeks during the summers (June – August) of 2011 and 2012. All trials and observations were conducted between sunset and sunrise as both species are nocturnal during the summer months due to the extremely high daytime temperatures.

Study Animals

We used visual searching and hand-tracking to locate and catch sidewinder rattlesnakes, which were then surgically implanted with a temperature-sensitive radiotransmitter (AVM G3 and ATS R1630) following the methods of Reinert and Cundall (1982). The transmitter was always less than 5 % of the snake's body mass. Following surgery, each snake remained in captivity until normal behaviour (rapid tongue flicking, maintaining an upright position and showing coordinated movements) was resumed (typically within 24 h), at which point the snake was released at the site of capture. Once released, we tracked the snakes at least once per night using radiotelemetry, and we recorded the general behaviour (moving, in a burrow, or in ambush), body position (ambush coil or elongate) and spatial location (via GPS) of the snake.

Desert kangaroo rats were trapped using Sherman live small mammal traps baited with black oil sunflower seed throughout the study. We measured kangaroo rat body mass (g), tail length (mm), hindfoot length (mm), sex, body condition (healthy appearance or scarred and unkempt) and reproductive state (presence of enlarged or swollen testes or teats). We marked each individual with a numbered eartag, and we used Nyanzol fur dye to create a unique fur dye mark that allowed us to identify marked individuals on video recordings.

Field Videography

When a snake was found in a stereotypical ambush hunting coil (as described by Reinert, MacGregor, Bushar, & Zappalorti, 2011), a battery-operated video recording system was positioned to record the snake and any interactions that took place (cameras were ~2 m from the snake; Clark, 2006). From 2011 to 2013, we used network security cameras (Sony SNC-RZ25N) with pan/tilt/zoom functionality along with network radios (Ubiquiti Nanostation M2) that communicated with a single base station (Ubiquiti Powerstation P5-EXT) located on a 10 m aluminium tower in the centre of the field site. Laptop computers were connected to the base station to allow for constant monitoring and recording of multiple video feeds simultaneously. In 2014, we used Sony video cameras (models SR-65 and SR-300), which recorded to internal memory. When a snake moved out of the camera frame, the snake was located via radiotelemetry and, if found to be hunting, the camera was repositioned to continue video recording. All cameras were also equipped with a geophone (General Electromagnetic P496) to record the occurrence of kangaroo rat foot drums and foot rolls.

Although we recorded some initial encounters between rattlesnakes and kangaroo rats, in order to obtain a statistically viable sample size we also increased the probability of interactions occurring by increasing the foraging activity of rats in the vicinity of snakes. When snakes were found to be hunting near marked rat burrow systems, we scattered black oil sunflower seeds in the vicinity of the snakes to increase kangaroo rat foraging movements in that area, thus increasing the probability of an encounter and interaction.

We defined an encounter as any instance when a kangaroo rat approached within 30 cm of the rattlesnake (the approximate effective strike range of the snake). Encounters became interactions when either the kangaroo rat, the snake, or both performed a behaviour illustrating recognition of the other animal. We defined the start of an interaction as when the kangaroo rat exhibited any of the predator-deterrent behaviours listed in Table 1, or when the snake struck towards the kangaroo rat or changed the direction of its ambush coil to face a kangaroo rat. Rattlesnakes frequently change the direction of ambush (moving their head by $>45^\circ$ from its original position) when they locate a kangaroo rat in the vicinity. Under these definitions, all interactions occur within encounters, but not all encounters include interactions. Interactions ended when one of the following criteria was met: (1) a period of 5 min passed with no obvious predator/prey behaviours being exhibited by either the snake or the kangaroo rat, or (2) the snake moved out of the field of view of the camera. During each interaction, we recorded the number of times the kangaroo rat exhibited each of the four primary predator-deterrent behaviours and summed the behaviours across all interactions (Table 1). For six of the interactions, we were unable to discern foot drums and foot rolls due to malfunction of geophones; for these interactions, we excluded foot drums and foot rolls from analyses. Videos showing typical examples of the behaviours that we recorded are viewable online through URLs listed in Table 2.

Strike Occurrence

For each encounter (all instances where kangaroo rats came within 30 cm of snakes), we recorded whether the snake attempted to strike the kangaroo rat and the time of day for any strikes. We also recorded the minimum approach distance of the animals, which we defined as follows: (1) the closest kangaroo rat approach during the entire encounter, if a strike did not occur, or (2) the distance between the snake and kangaroo rat when the snake initiated a strike, if a strike occurred. We estimated distances following the technique of Clark, Dorr, Whitford, Freymiller, & Putman (2016). Briefly, camera angle and the position of the kangaroo rat relative to the snake prevented us from measuring distances precisely. Thus, we made general distance estimates by using the hindfoot of the kangaroo rat (measured during animal processing) as a size standard to estimate the distance from the closest part of the kangaroo rat's hindfeet to the closest part of the snake's body, rounded to the nearest 5 cm. In Clark, Dorr, Whitford, Freymiller, & Putman (2016), an analysis of confidence intervals generated from multiple independent estimates of distance using this approach demonstrated that 5 cm distance classes represented an appropriate level of precision. All distances were estimated using digitized video frames imported into ImageJ software (Abràmoff, Magalhães, & Ram, 2004). For encounters and interactions with unidentified kangaroo rats, we used the average foot length of captured adult rats (mean \pm SD = 4.9 ± 0.39 cm). All kangaroo rats involved in a recorded encounter were adults (i.e. body mass >83 g; Best, Hildreth, & Jones, 1989).

Table 2

Video files referenced in the text that illustrate anti-snake behaviours of desert kangaroo rats

Video	URL	Description
Video 1	https://youtu.be/cLfy-M9NWbl	Typical anti-snake display showing repeated approaches, foot drums, foot rolls and sand kicks
Video 2	https://youtu.be/Yc-qc6wFRKs	Anti-snake display illustrating jump back behaviour
Video 3	https://youtu.be/YeesFjACFJo	Video illustrating evasive leap of kangaroo rat. First sequence recorded at 30 frames/s shows a free-ranging sidewinder strike at a kangaroo rat, but the animals move too quickly for movements to be seen. Second sequence is the same strike recorded at 120 frames/s and played back at 10% speed to demonstrate how the force of the rat's leap physically knocks the striking snake out of the way before the snake can embed fangs and envenomate the rat
Video 4	https://youtu.be/a0QJvmuANfQ	Video illustrating kangaroo rat kicking away striking snake. First sequence recorded at 30 frames/s shows a free-ranging sidewinder strike at a kangaroo rat, but the animals move too quickly for movements to be seen. Second sequence is the same strike recorded at 120 frames/s and played back at 10% speed to demonstrate how the kangaroo rat swings its legs around in midair and kicks the snake away to prevent envenomation

Videos are viewable on the video-sharing site YouTube.

Strike Outcome

To determine the outcome of a strike, we examined each strike video frame by frame. Strikes were separated into four categories (see Videos 3 and 4 for examples of strikes; URLs for videos are given in Table 2). First, if it was clear from the video that no contact occurred, the strike was termed a 'miss'. Second, if it appeared that contact occurred, but the extent of contact was ambiguous (due to either blurred motion or contact lasting only a single frame), the strike was termed an 'apparent contact'. Third, if the recording showed the head of the snake in contact with the kangaroo rat for more than one video frame the strike was termed a 'bite'. Lastly, strikes that could not be scored due to video quality and/or camera angle are reported as 'unknown'. As the sample size for bites was too low for statistical testing ($N = 1$), we grouped them with apparent contacts for all statistical tests. Because kangaroo rat and snake movements were often too rapid to record effectively at standard frame rates (30 frames/s), we recorded two strike and avoidance interactions at 120 frames/s using Sony video cameras (model SR 300). We analysed behaviours frame by frame in these recordings to provide qualitative descriptions of kangaroo rat and snake manoeuvres during the strike (see Videos 3 and 4; URLs for videos are given in Table 2).

Statistical Analyses

We used R version 3.2.0 for all analyses. We used a logistic regression in the logistf package to examine the influence of

kangaroo rat predator-deterrent behaviours on snake strike occurrence during encounters (a binary response variable; Ploner, Dunkler, Southworth, & Heinz, 2010). We included minimum approach distance as a predictor variable, as well as whether predator-deterrent behaviours were exhibited during the entire encounter (a binary predictor variable: 'yes' if predator-deterrent behaviours were exhibited, 'no' if predator-deterrent behaviours were not exhibited). In our analysis, we did not include kangaroo rat predator-deterrent behaviours that were exhibited post-strike. To ensure that all encounters scored involved a unique pair of individuals, we removed any subsequent encounters between the same snake and kangaroo rat from analyses. If the encounter was with a kangaroo rat that was not marked, as a conservative measure, we excluded all further encounters with unidentified kangaroo rats within 62 m of the initial encounter, which represents the estimated radius of the home range for the average mass of the captured kangaroo rat (Garland, 1983; Harestad & Bunnell, 1979). There is a small possibility that repeated encounters may have occurred if the first encounter took place near the periphery of the unknown kangaroo rat's home range; however, given the large abundance of kangaroo rats throughout the site and the high levels of territoriality between individuals (Best et al., 1989; M. D. Whitford, personal observation), it is unlikely that the same individual kangaroo rat was filmed twice at this distance. In addition, to test whether strike outcome was influenced by minimum approach distance, a Poisson regression was conducted with strike outcome as the binary response variable (miss or apparent contact), and minimum approach distance as a fixed predictor variable. Reported values are means \pm SE.

Ethical Note

All research with live animals in our study was approved by the Institutional Animal Care and Use Committee of San Diego State University (APF 13-08-015C). The mass of the transmitters used to track the rattlesnakes was 2.1 g (percentage of body weight: mean = 2.5%, range 1.2–3.9%). Transmitters were removed at the end of the study each year following the same methods described above. Although the rattlesnakes commonly spent several days post-surgery in burrows, once the rattlesnakes surfaced and began hunting there appeared to be few, if any, effects from the transmitters. Traps for kangaroo rats were set shortly after sundown and were checked after 3–4 h. There were no indications that the trapping, processing or dye markings had any adverse effects on the kangaroo rats.

RESULTS

Strike Occurrence

We recorded 40 encounters between 15 snakes, 21 identified kangaroo rats and 17 unidentified kangaroo rats. Kangaroo rats exhibited predator-deterrent displays in 13 of the 40 encounters, and no displays in the remaining 27 encounters. Snakes struck at kangaroo rats in 23 of the 27 encounters in which kangaroo rats did not display, and 0 of the 13 encounters with displays (Fig. 1). Statistically, predator-deterrent displays significantly decreased the likelihood of a strike (19 snakes, $N = 39$ encounters; likelihood ratio test: -6.99 , $df = 3$, 95% CI = -16.07 to -2.81 , $\chi^2 = 7.42$, $P = 0.01$). However, strike probability was not affected by minimum approach distance (likelihood ratio test: -0.116 , $df = 3$, 95% CI = -0.26 to 0.01 , $\chi^2 = 0.353$, $P = 0.06$) or the interaction between strike distance and predator-deterrent behaviour (likelihood ratio test: 0.23 , $df = 3$, 95% CI = -0.27 to 0.75 , $\chi^2 = 0.143$, $P = 0.23$).

Although no antipredator behaviours were exhibited prior to any of the 23 strikes (i.e. snakes either struck before antipredator behaviours or not at all), after most strikes (19 of 23) kangaroo rats frequently remained in the area and displayed antipredator signals. Of the 17 encounters in which no strike occurred, 13 were classified as interactions (see above) and the remaining four encounters did not result in an interaction (i.e. kangaroo rats came within 30 cm of snakes, but neither party overtly responded to the other).

Strike Outcome

Of the 23 recorded strikes, 13 missed (56.5%), seven (30.4%) were apparent contacts, one (4.4%) was a bite and two (8.7%) were categorized as unknown due to vegetation blocking the camera view. None of these strikes resulted in the death of kangaroo rat as all kangaroo rats involved in strikes were later observed alive and in good health during the study. Only a single kangaroo rat (the individual categorized above as a 'bite') displayed signs of envenomation (i.e. rubbing of the bite site on the substrate), but this individual also survived. Furthermore, strike outcome was not affected by minimum approach distance (minimum approach distance for apparent contacts/bites: 12.5 ± 2.3 cm; no contacts: 10 ± 1.3 cm; Poisson regression: $Z = 0.83$, $P = 0.41$).

From the two high frame-rate recordings, we determined that one rattlesnake made contact with the kangaroo rat but was unable to successfully embed its fangs, while the other rattlesnake successfully embedded its fangs in the kangaroo rat (this interaction was not included in statistical analyses as the rattlesnake had previously interacted with the struck kangaroo rat); however, neither kangaroo rat exhibited envenomation symptoms following the interaction, and both were later seen alive and exhibited normal behaviour. In the interaction that did not result in a bite, the kangaroo rat began to react (first sign of evasive movement) within eight frames (~ 66 ms after the onset of the strike), the snake made contact with the rat by frame 12 (~ 100 ms), and by frame 14 (116 ms) the kangaroo rat began a powerful leap that propelled its body into the air, pushing the head and anterior body of the snake out of the path of the jump. In the interaction that resulted in a bite, the kangaroo rat began to respond by frame 6 (~ 50 ms), then by frame 7 (~ 58 ms) the rattlesnake's head contacted the kangaroo rat and the kangaroo rat began to leap. By frame 26 (~ 217 ms) the kangaroo rat extended one of its hindlegs while in the air and kicked the snake's head away from the kangaroo rat's body. In both interactions, the rapid jumping and kicking movements of the kangaroo rat appeared to prevent a successful envenomation by the

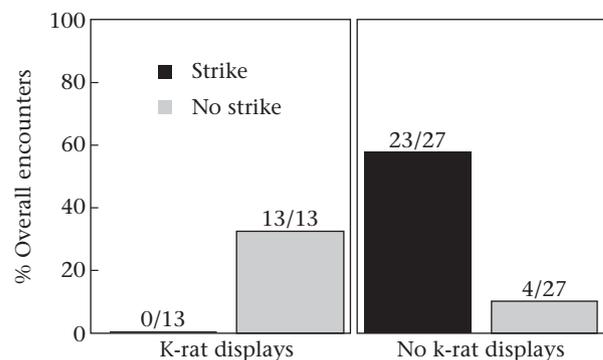


Figure 1. Bar plot of the number of encounters that did or did not include antipredator displays, and whether they involved a strike from a sidewinder rattlesnake towards a desert kangaroo rat (k-rat). Numbers above bars indicate the number of snake strikes out of the total number of encounters in that category (displays or no displays). The four encounters that resulted in no strikes and no displays were all instances where the kangaroo rat approached within 30 cm but did not interact with the snake.

snake, even when the snake was able to briefly bite the kangaroo rat.

DISCUSSION

Our results indicate that the antipredator behaviours of the desert kangaroo rat reduce the likelihood that sidewinders will attempt to strike. Because the rattlesnakes in our study never attempted to strike any kangaroo rats that had displayed any combination of antipredator behaviours, we were unable to determine whether specific elements of the display (i.e. foot drumming, jump backs or sand kicks) were responsible for this effect. It appears as if any indication of awareness on the part of the kangaroo rat dramatically reduced the likelihood that a snake would attempt to strike, even when the kangaroo rat repeatedly approached within strike range. These results corroborate those found in [Barbour and Clark \(2012\)](#), in that pursuit-deterrent signals by small mammals reduce the probability of a rattlesnake attempting to strike.

Perhaps more surprisingly, our study also revealed that *D. deserti* is almost always able to avoid sidewinder strikes and/or envenomation, even when apparently unaware of the presence of the snake prior to the strike. We only observed a single strike that definitively resulted in envenomation, as evident by the kangaroo rat's erratic behaviour and rubbing of the envenomation site on the substrate. Given that kangaroo rats are reported to not be physiologically resistant to rattlesnake venom ([Biardi, 2008](#)), it appears as if they are largely protected by their physical agility. The evasive jump exhibited by kangaroo rats is so rapid and forceful it appears to allow them to mostly avoid envenomation by sidewinder rattlesnakes, regardless of how close they accidentally come to a snake hidden in ambush. Below, we discuss the implications of each of these findings in turn.

Perception Advertisement

In our study, rattlesnakes never struck at kangaroo rats that exhibited any predator-deterrent signalling, even when kangaroo rats approached very closely. This result may be explained by the ability of the kangaroo rats to perform rapid evasive leaps ([Biewener & Blickhan, 1988](#)) that are capable of moving the kangaroo rats out of the trajectory of the snake strike extremely quickly, thereby greatly reducing the probability of the rattlesnake being able to successfully prey upon an aware kangaroo rat. As our high-speed videos illustrate, unaware kangaroo rats can initiate evasive leaps extremely rapidly and effectively, thus making strikes at aware kangaroo rats futile, as the reaction time of kangaroo rats is likely to increase with awareness of the snake's presence.

Strike Avoidance

When sidewinders did strike at kangaroo rats, apparent envenomation resulted in only 1 of 23 strikes (4.3% of strikes), even though all strikes occurred towards kangaroo rats that exhibited no awareness of the snake prior to the onset of the strike. Even this one strike appeared to be only partially effective, as the kangaroo rat exhibited signs of envenomation but survived and recovered. Other studies quantifying strike success in free-ranging rattlesnakes have reported success rates around 50% ([Barbour & Clark, 2012](#); [Clark, Tangco, & Barbour, 2012](#); [Putman & Clark, 2015](#)). The discrepancy appears to be the result of the unique evasive leaping ability of kangaroo rats. Although strike and evasion movements were too rapid to examine in detail with standard video, our two high frame-rate recordings revealed at least three mechanisms that kangaroo rats employ to evade envenomation. First, kangaroo rats are able to perceive an oncoming strike and begin leaping very quickly (within

50 ms), which could frequently allow them to avoid all contact with the snake. Second, when kangaroo rats leap, they leap with enough force that they can physically push the snake out of their trajectory and avoid contact with the fangs. Lastly, even when the snake appears to have successfully embedded its fangs, kangaroo rats can kick forcefully with their hindlegs to dislodge the snake rapidly enough that envenomation is not effective.

Previous studies have also noted the remarkable evasive jumps of kangaroo rats. Research by [Webster \(1962\)](#) indicated that kangaroo rats may rely on subtle acoustical cues to detect sudden attacks from snakes and owls, and [Biewener and Blickhan \(1988\)](#) concluded from biomechanical studies that the disproportionate muscles and tendons in the hindlimbs of kangaroo rats represent an adaptation for high-speed avoidance of predators. However, prior to our study, it was unclear how effective this predator avoidance adaptation would be in a natural context. Indeed, a recent laboratory analysis of snake strikes concluded that many snakes accelerate so rapidly that they reach their target faster (within 50–90 ms) than known startle response times for most small mammals (60–395 ms) ([Penning, Sawvel, & Moon, 2016](#)). Because kangaroo rats in our study apparently responded more quickly (within 50 ms) than what has been seen for other small mammal species, further efforts are underway in our research programme to quantify in detail the timing and physical forces involved in these remarkable manoeuvres (e.g. [Higham, Clark, Collins, Whitford, & Freymiller, 2017](#)).

Despite the low strike success of sidewinder rattlesnakes we documented here, [Funk \(1965\)](#) reported that desert kangaroo rats comprise a significant portion (~10% by count, which would represent a much higher proportion by biomass given their relatively large body size) of the diet of Colorado desert sidewinders, *Crotalus cerastes laterorepens*. The discrepancy between the results of our study and [Funk \(1965\)](#) is puzzling but may be explained in several ways. (1) Although desert kangaroo rats were found in sidewinder stomach contents, we do not know how many strikes were made to obtain these meals; sidewinders may strike at many kangaroo rats and only kill a few. (2) We studied only adult kangaroo rats, and those consumed by sidewinders may have been more vulnerable juveniles. (3) Different relative population sizes of predators and prey could lead to variation in interactions. For instance, if the population studied by [Funk \(1965\)](#) was near or over its carrying capacity, the kangaroo rats may have been experiencing increased resource competition that caused them to be more vulnerable to predation by rattlesnakes. (4) There may be a high degree of interpopulational or interindividual variation in either rattlesnake or kangaroo rat physical morphology or performance, leading to some predator–prey combinations that result in much higher success rates for snakes at other sites.

Although our results showed that sidewinder rattlesnakes at one site are usually unsuccessful when attempting to strike desert kangaroo rats, other rattlesnake species may be capable of overcoming kangaroo rat antipredator defences more effectively. Previous studies have found that Mohave rattlesnakes, *Crotalus scutulatus*, consume adult Merriam's kangaroo rats, *Dipodomys merriami*, on a regular basis ([Reynolds & Scott, 1982](#)), even though Merriam's kangaroo rats seem to share the specialized evasive leaping ability we found in desert kangaroo rats ([Bartholomew & Caswell, 1951](#); [Webster, 1962](#)). More detailed recordings are needed to determine how kangaroo rats are able to avoid strikes and what attributes may make some rattlesnakes more efficient kangaroo rat predators. Future work using high-speed videography techniques to record kangaroo rat/rattlesnake interactions under natural conditions (as in [Higham et al., 2017](#)) would greatly enhance our understanding of how coevolution may have shaped the physical performance of both predator and prey in this system.

DATA ACCESSIBILITY

Data will be available at datadryad.org, and supplementary video files are available at youtube.com (see Table 2 for URLs).

COMPETING INTERESTS

We have no competing interests.

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