

Managing predators: The influence of kangaroo rat antipredator displays on sidewinder rattlesnake hunting behavior

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Abstract

Upon sensing predators in their vicinity, many prey species perform antipredator displays that are thought to provide information to the predator that deters it from attacking (predator-deterrent signals). These displays can be complex, incorporating a variety of signaling elements as well as direct physical harassment of the predator. Although the display behaviors in these communication systems are often well characterized, evidence of the efficacy of these displays in deterring predators is limited due to the challenges associated with studying free-ranging predators. Here, we examine how the anti-snake signals of the desert kangaroo rat (*Dipodomys deserti*) influence the ambush hunting behaviors of sidewinder rattlesnakes (*Crotalus cerastes*). We found that, although desert kangaroo rats incorporate a number of signal elements into their antipredator display, only sand kicking behavior was a significant factor in motivating sidewinder rattlesnakes to cease hunting: high rates of sand kicking led to early abandonment of ambush coils. These results indicate that anti-snake displays of small mammals may be especially effective at mitigating the threat posed by rattlesnakes when those displays incorporate physical harassment as well as signaling.

KEYWORDS

animal communication, predator-deterrent signal, predator-prey

1 | INTRODUCTION

Predation imposes significant selection pressures on most organisms (Crawley, 1992) and frequently gives rise to coevolution (reciprocal counter adaptation) between predator and prey (Dawkins & Krebs, 1979). Consequently, many species have evolved a variety of physiological (Geffeney, Brodie, Ruben, & Brodie, 2002), morphological (Webster, 1962), and behavioral traits (Catania, 2009) that increase their likelihood of surviving a predatory encounter. Predator-prey interactions are inherently dynamic events shaped by the proximity of the two parties, the information either has about the other, and their behavioral responses to each other. To fully understand how predation shapes the diversity in form and function observed

in nature, it is critical to examine predator-prey interactions holistically, quantifying the behaviors of both parties across different stages of an interaction.

Most predator-prey interactions can be discretized into the following stages, with an interaction either ending or progressing to the next stage depending on how the two parties interact: (a) searching for cues, (b) evaluation, (c) attack/evade, (d) capture/escape, and (e) consumption (Bradbury & Vehrencamp, 2011; Caro, 2005; Hasson, 1991; Kramer, 2001; Lima & Dill, 1990). During the search stage, predators and prey are unaware of one another but are searching the environment for cues of the other. Evaluation occurs after the predator and/or prey have detected the other party and integrate information from their sensory systems to either evaluate the

suitability of the prey as a food resource and the potential for injury associated with capturing the prey or evaluate the attack risk posed by the predator. During this evaluation stage, prey may influence the predator's behavior via predator-deterrent signals, communication displays that are thought to decrease the probability that a predator will attack.

Predator-deterrent signals are largely thought to function by providing the predator with information. This can be information that conveys the signaler is in a heightened state of vigilance (Putman & Clark, 2015), the signaler has detected the predator (Cresswell, 1994), the signaler has the physical capabilities necessary to evade an attack (FitzGibbon & Fanshawe, 1988), or some combination of these. Although these displays signal to the predator that the probability of a successful attack is low (Godin & Davis, 1995), they are still thought to be beneficial to both predator and prey. Both parties benefit by avoiding a predation attempt that is unlikely to succeed; the prey avoids potential death and the energetic and injury costs associated with evading an attack, while the predator avoids the energetic, injury, and opportunity costs of attempting to capture prey when the probability of success is low (Berger-Tal, Mukherjee, Kotler, & Brown, 2009; Caro, 2005).

Our ability to understand the function of specific predator-deterrent signals is complicated by the fact that many prey species perform complex, multicomponent displays (Rowe, 1999). Individual elements within a display can encode information in numerous ways, including redundancy (same signal performed multiple times), degeneracy (multiple signals encoding identical information), or pluripotency (one signal encoding different information depending on context); signal elements can also interact to alter the intensity of the receiver's response or to provide emergent information (Hebets et al., 2016; Partan & Marler, 2005; Rowe & Guilford, 1999). Additionally, predators can respond to prey signaling in a variety of ways, including reduced overall probability of initiating an attack (Whitford, Freymiller, & Clark, 2017), targeting individuals of low physical quality (FitzGibbon & Fanshawe, 1988), or by abandoning pursuit and moving to a new hunting location (Barbour & Clark, 2012).

We used the tractable predator-prey interactions that occur between sidewinder rattlesnakes (*Crotalus cerastes*) and desert kangaroo rats (*Dipodomys deserti*) to determine how different elements of the kangaroo rat antipredator display affected the hunting behaviors of rattlesnakes. Rattlesnakes are ambush predators that hunt by remaining motionless in a coiled position for extended durations, waiting for prey to mistakenly approach within striking distance (Clark, 2016; see Reinert, MacGregor, Esch, Bushar, & Zappalorti, 2011 for a detailed description and visual examples of ambush coils). The coiled ambush position of rattlesnakes also acts as a clear indicator that a snake is prepared and motivated to capture any potential prey, as rattlesnakes that are not actively hunting typically either retreat to cover or adopt a loosely coiled position (Reinert, Cundall, & Bushar, 1984; Reinert et al., 2011). Tight coiling is critical for effective prey capture as it allows for the posterior body portion of a snake to act as an anchor while the anterior body of the snake is rapidly propelled

forward during a strike (Cundall, 2002; Lillywhite, Delva, & Noonan, 1998, 2002).

When desert kangaroo rats discover snake predators, they typically perform a series of multimodal, multicomponent predator-deterrent displays, including repeated approaches toward the snake followed by acrobatic jumps, rapid drumming of the feet against the ground, and kicking sand in the direction of the snake (Clark, Dorr, Whitford, Freymiller, & Hein, 2016; Randall & Matocq, 1997; Randall & Stevens, 1987). In a previous study, we showed that any anti-snake displays given by kangaroo rats suppressed predatory attacks from sidewinders, likely because alert kangaroo rats are very effective at leaping out of the way of snake strikes (Freymiller, Whitford, Higham, & Clark, 2017; Whitford et al., 2017). Here, we used the same field-based videography to quantify various specific signaling elements of the kangaroo rat displays to determine how they impacted the subsequent ambush hunting behaviors of rattlesnakes; in other words, to determine how long snakes would persist in hunting at that same location after receiving kangaroo rat signals. Due to the nature of the various predator-deterrent signals, we predicted that one particularly aggressive behavior, sand kicking, would be directly associated with causing the snake to cease hunting activity.

2 | METHODS

2.1 | Study site and study animals

The study was conducted near the California State University Desert Studies Center in San Bernardino County, CA, USA (35°7'7.16"N, 116°7'5.01"W). The study took place on a dune system heavily populated with both sidewinder rattlesnakes and desert kangaroo rats. The majority of the data were collected from May to August of 2013 and 2014, but we included some field recordings from 2011 and 2012. Due to the nocturnal nature of both species during the summer, all data were collected between sunset and sunrise.

Sidewinders were located by visual searching and following their unique tracks in the sand and, once located, adult individuals were implanted with a temperature-sensitive radio transmitter (AVM G3 and ATS R1630 transmitters; see Reinert & Cundall, 1982). Transmitters were only implanted if they weighed less than 5% of snakes' body mass. Following transmitter implantation, snakes were released at their capture site once they resumed normal behavior (typically within 24 hr). We used radio telemetry to track implanted snakes each night (often multiple times per night) and recorded whether they were hunting, moving, or in a burrow.

We trapped desert kangaroo rats throughout the study period with Sherman live traps and measured a variety of morphological traits for every individual, including: body mass (g), tail length (mm), hind foot length (mm), sex, body condition (healthy appearance or scarred and unkempt), and reproductive state (noted presence of enlarged or swollen testes or teats). Each kangaroo rat was given a numbered ear tag and an individual-specific fur dye pattern using Nyanzol dye prior to release. The fur dye pattern was used to discern kangaroo rat identity from the video recordings.

TABLE 1 Transition frequency table describing the probability that a given predator-deterrent signal was followed by another behavior. Data used in the table is from 10 interactions (5 min per interaction) with a cumulative total of 400 transitions between predator-deterrent signals. Values shown are proportion of transitions, with total number of transitions observed in parenthesis. Rows = initial behavior, columns = subsequent behavior

Behaviors	Sand kicks	Jump backs	Foot drum	Foot roll
Sand kicks	0.48 (82)	0.16 (28)	0.23 (40)	0.12 (21)
Jump backs	0.48 (32)	0.33 (22)	0.15 (10)	0.03 (2)
Foot drum	0.39 (46)	0.1 (12)	0.34 (41)	0.17 (20)
Foot roll	0.2 (9)	0.05 (2)	0.75 (33)	0 (0)

2.2 | Field videography

When a snake was found in a stereotypical ambush hunting coil (Reinert et al., 2011), we positioned an infrared light and video camera powered by a 12-volt battery to record the ambush hunting snake and all subsequent interactions (Clark, 2006). From 2011–2013, we used network security cameras (Sony SNC-RZ25N) paired with network radios (Ubiquiti Nanostation M2) that allowed for wireless communication to a base station (Ubiquiti Powerstation P5-EXT) mounted in the center of the field site. The base station was connected to laptop computers that allowed for the continuous monitoring of multiple camera feeds. In 2014, we used Sony video cameras (models SR-65 and SR-300) recording to an internal memory. If a snake moved out of the camera view, they were relocated and, if found to be hunting, the cameras were repositioned to continue recording the activity of the snake. All cameras were also paired with a geophone (General Electromagnetic P496) to record kangaroo rats' foot drumming behavior. Because kangaroo rats and sidewinders live in a low productivity habitat at a relatively sparse population density, we increased the foraging activity of kangaroo rats and the probability of encounters by scattering small amounts of black oil sunflower seed in locations where snakes were also actively foraging.

2.3 | Ambush coil abandonment

An "ambush coil" was defined as the specific location in which a snake coiled in a stereotypical ambush position. Ambush coil abandonment occurred when a snake uncoiled and moved out of the area occupied by its body when it was coiled. In other words, if a snake uncoiled and moved even a short distance, we classified the movement as an ambush coil abandonment. For each ambush coil, we recorded the time that the snake was first found in that coil and the time that snake abandoned the coil. As in Clark et al. (2016), extreme daytime temperature prevented snakes from exhibiting surface activity from a few hours after sunrise to shortly before sunset, circumscribing the time in which a snake could remain in any given ambush coil. Thus, snakes always exhibited ambush coil abandonment at least once for each night they were actively ambush hunting.

For each ambush coil, we recorded the number of kangaroo rats the snake interacted with, the number of interactions that occurred, and the cumulative number of each predator-deterrent behavior performed by kangaroo rats. We defined the start of an interaction as when the kangaroo rat exhibited any predator-deterrent behaviors or when the snake struck at or reoriented toward a nearby kangaroo rat, indicating the snake was aware of the kangaroo rat's presence. The predator-deterrent behaviors included sand kicks (using the hindlegs to kick sand at the snake), jump backs (a close approach to the snake followed by rapid vertical leap away from the snake), foot drums (drumming of one hind foot), and foot rolls (rapid drumming of both hind feet)—video examples of the predator-deterrent behaviors can be found in Whitford et al. (2017). Kangaroo rats would often interact with a snake and then leave without returning for some time—for this reason, we defined an interaction as ending when 5 min had passed without any observable predator/prey behaviors or, if a snake abandoned during an interaction, the time of the abandonment behavior. For each interaction, the total number of each predator-deterrent behavior was recorded. Due to technological issues with the geophones, foot drums and foot rolls could not be measured for six of the recordings.

2.4 | Statistical analyses

In order to provide a graphical summary of the order in which predator-deterrent signals are performed by kangaroo rats, we sampled 10 interactions from our dataset and generated a sequential list of the predator-deterrent signals that were performed for a 5-min period. We then created a transition frequency matrix by counting the number of times each predator-deterrent signal was followed by another, and then divided each transition count total by the cumulative total number of times a given signal was followed by any another.

We used a survival analysis to examine the effect of kangaroo rat anti-snake behaviors on the abandonment behavior of snakes. We used the *survival* package in R (version 1.0.136) to perform a Cox proportional hazards regression (PHREG) with time until abandonment as the response variable (Cox, 1972; Therneau & Crowson, 2013). We included the cumulative numbers of each antipredator behavior as time-dependent covariates, and included snake identity in the model to account for multiple observations involving the same individual snake. We reduced collinearity in our predictor variables by only including antipredator behaviors that were not highly correlated. We tested the proportional hazards assumption of Cox PHREG and found that no variables deviated from these assumptions (all variables: $p > 0.05$). Reported values are means \pm SE.

3 | RESULTS

From the transition frequency table describing the order of predator-deterrent signals, sand kicks were the most likely behavior to follow any signal with the exception of foot rolls, which were more

most likely to be followed by a foot drum (Table 1, Figure 1). The order of behaviors was highly variable with 13/16 possible transitions having a probability equal to or greater than 10%. Notably, foot rolls were never performed sequentially, but were highly likely to be followed by a foot drum—foot drums had a 75% probability of following a foot roll and is the highest observed transition frequency.

To analyze snake behavior, we used ambush coil abandonment data from 23 snakes. We collected data on 150 ambush coils, and snakes interacted with a kangaroo rat in 43 (29%) ambush coils, 39 of which involved kangaroo rat signaling (see Table 2 for a summary of kangaroo rat behaviors). The average amount of time a snake stayed within an ambush coil was 442 ± 197 min. From our recordings of snakes in ambush, we observed a total of 32 strikes from 15 snakes directed toward kangaroo rats; however, snakes never struck toward kangaroo rats that had performed any predator-deterrent signals; all snake strikes occurred prior to any kangaroo rat signaling (strike behavior analyzed in Whitford et al., 2017). As snakes typically recoiled into their original ambush site after a strike and kangaroo rats would return and display toward the snakes, ambush coils involving strike attempts were retained in our analysis. On occasion, snakes would react defensively to the predator-deterrent displays of kangaroo rats by taking a defensive posture (nine occurrences from seven interactions), enlarging their body (two occurrences from two interactions), or moving to avoid kicked substrate (15 occurrences from eight interactions; rattling and tongue flicking could not be observed reliably on video recordings and are therefore not included despite being common defensive behaviors of rattlesnakes).

In our interaction data, we found that foot drums were highly correlated with foot rolls ($r = 0.76$) and jump backs were highly correlated with sand kicks ($r = 0.87$). To remove collinearity, we summed

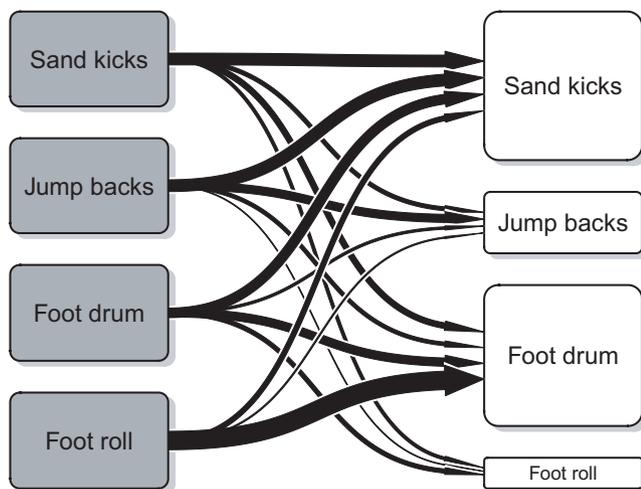


FIGURE 1 The sequence of predator-deterrent signals as calculated from the transition frequency table. Behaviors on the left (gray boxes) are the initial behaviors and on the right are the behaviors that immediately followed (white boxes). Line thickness is scaled to indicate the probability of occurrence, and the boxes of the subsequent behaviors are scaled according to the cumulative proportion of instances in which they followed any behavior

foot drums and foot rolls into a foot signals variable, and due to a priori predictions of the role sand kicks may play as a harassment mechanism, we retained sand kicks in the model and removed jump backs. Our PHREG model then tested for the effects of sand kicks and foot signals on the time of ambush abandonment, by analyzing whether snakes that experienced foot signals and/or sand kicks remained in ambush for shorter durations. Sand kicks were found to significantly increase the likelihood of ambush coil abandonment (coefficient = 0.012, robust standard error = 0.006, $z = 1.98$, $p = 0.047$; robust standard errors are reported as a conservative measure and to account for heteroskedasticity; Box-Steffensmeier & Boef, 2006), with each sand kick increasing the probability of coil abandonment at a given time by a factor of 1.01 relative to a snake that experienced one fewer sand kicks (hazard ratio = 1.01, Figure 2). Foot signals, however, was not a significant predictor of ambush abandonment time (coefficient = 0.007, robust standard error = 0.01, $z = 0.68$, $p = 0.50$). Because sidewinders experienced an average of 26 ± 4 sand kicks while in an ambush coil, sand kicking typically increased the likelihood of a sidewinder abandoning an ambush coil by 1.38 ($\sim 1.01^{26}$) times the baseline hazard rate (Kleinbaum & Klein, 2005).

4 | DISCUSSION

Our study illustrates that the predator-deterrent displays performed by kangaroo rats influence the ambush coil abandonment behaviors of sidewinder rattlesnakes. The sand kicking behavior of desert kangaroo rats was found to be highly influential in motivating sidewinder rattlesnakes to leave their ambush coils. However, due to the colinearity between sand kicks and jump backs, it is possible that jump backs also increase the likelihood of ambush coil abandonment. Experimental setups mimicking these signals in a controlled fashion would be necessary to discriminate between them.

4.1 | Predator harassment

In contrast to many other predator-prey signaling systems, interactions between desert kangaroo rats and sidewinder rattlesnakes involve frequent aversive physical elements. For example, Barbour

TABLE 2 Summary of the number of interactions between snakes and kangaroo rats and the number of predator-deterrent behaviors performed by kangaroo rats toward snakes per ambush coil (ambush coils that did not involve an interaction are not included). Min values for all variables are 0 or 1

	\bar{x}	Median	Max
Number of interactions	1.33	1.00	5.00
Number of kangaroo rats	1.19	1.00	4.00
Jump backs	12.98	4.00	57.00
Sand kicks	19.79	6.00	91.00
Foot signals	12.56	0.00	67.00
Cumulative behaviors	45.44	33.00	160.00

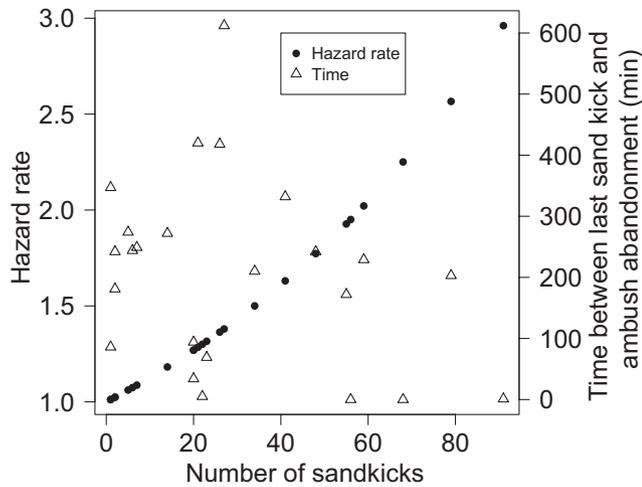


FIGURE 2 Scatterplot illustrating the relationship between sand kicks, hazard rate, and ambush coil abandonment. Hazard rate increases with sandkicks, and the time between the last sandkick and coil abandonment decreases with sandkicks. Black dots represent the hazard rate associated with a given number of sand kicks. Triangles represent the amount the time between the last sand kick a snake received and when they abandoned their ambush coil. Increased sand kicks and hazard rates are associated with more rapid abandonment. See text for details of survival model

and Clark (2012) found that California ground squirrels only incorporated some type of physical harassment in 5% of interactions with free-ranging rattlesnakes, while desert kangaroo rats sand kicked in 32/36 (89%) interactions. This propensity for desert kangaroo rats to kick sand may be driven both by the abundance of sand in the desert kangaroo rats' preferred habitat and the powerful hindlimbs kangaroo rats use to both avoid snake strikes with propulsive jumps (Whitford et al., 2017) and kick snakes away in mid-air to prevent envenomation (Whitford et al., 2019). Kangaroo rats can kick sand with their hindlimbs from 20–30 cm away, outside of the effective strike range of sidewinders (Clark et al., 2016). This harassment mechanism is likely effective because sand could compromise the sensory organs of rattlesnakes. Repeatedly striking the rattlesnake with sand may cause irritation and impairment to the snake's eyes, nostrils, and/or pit organs. Additionally, sand piled in front of the snake from multiple kicks may act as a physical barrier to the snake, further increasing the likelihood snakes will abandon to a location where it can hide again.

Sidewinders often do not abandon their ambush coils immediately following an aversive stimulus but will rather wait for some time prior to abandoning (e.g., snakes will often leave ~30 min after an observer gets too close to the snake while radio tracking or setting up a camera; M. D. Whitford, G. A. Freymiller, R. W. Clark, personal observation). Thus, even though snakes often remained in ambush up to several hours following an interaction, this is not unusual for ambush hunting snakes (reviewed in Clark, 2016) and any reduction in the time spent in ambush would result in an overall reduction in total risk posed to a kangaroo rat. Secondly, snakes may only abandon if kangaroo rats are persistent in their harassment. If sand kicking

functions not just as harassment, but also to inform the snake that it has been detected and to motivate the snake to leave, the snake may abandon an ambush only if it is certain that the probability of future attack success at that site is low. Sand kicking is frequently inaccurate and misses the snake entirely, and kangaroo rats sometimes kick sand at objects that only vaguely resemble snakes (M. D. Whitford, G. A. Freymiller, R. W. Clark, personal observation); thus, sand kicking may provide imperfect information. As such, snakes may assess multiple, repeated signals prior to abandoning in order to ensure that the kangaroo rat has indeed detected the snake (Hebets et al., 2016) rather than abandon early and risk foregoing a potentially profitable encounter. Lastly, rattlesnakes are most vulnerable when elongated because they are not prepared to strike as they are when coiled (snakes strike by rapidly straightening the coils of their body); therefore, it is also possible that the rattlesnakes are choosing to remain in an ambush coil until they are certain the kangaroo rat has vacated the area and the snake can leave without being vulnerable to harassment.

Although we did not find a significant effect of foot drumming behaviors on ambush abandonment, it is likely that foot drumming is an important element of the kangaroo rat predator-deterrent display, but this effect is masked by the more powerful influence of kicking sand. Previous studies have reported that foot drumming functions to inform snakes that the displaying kangaroo rat has detected them (Randall & Matocq, 1997). The detection-advertisement function of foot drumming was also supported in our analysis of snake strikes (Whitford et al., 2017), as we found that any signaling behaviors greatly reduced the probability of a strike, as would be predicted for an ambush predator that relies on surprise to capture prey (Zuberbühler, Noe, & Seyfarth, 1997). It is also possible that foot drumming may act to warn conspecifics or nearby kin to the presence of a snake, thereby further reducing the ability of snakes to capture kangaroo rats in the vicinity; that said, the high degree of territoriality in desert kangaroo rats and large spatial separation between burrows seems to indicate that the display is directed toward the snakes and not conspecifics (Randall & Matocq, 1997). Additionally, each signal within the complex kangaroo rat display may perform similar functions, such as perception advertisement, to account for signaler and environment-induced variability (Hebets & Papaj, 2005; Patricelli, Krakauer, & Taff, 2016). For example, sand kicking would only be an effective signal when performed near the snake, when the snake is not blocked by vegetation, and when wind speeds are low. Foot drumming may then function as a backup signal to account for the inherent inaccuracy and variability associated with sand kicking. Similarly, as the vibrations of foot drumming can only be heard within some radial propagation distance of the kangaroo rat, it is an indirect signal and is not easily directed at any specific receiver. The signaling displays of kangaroo rats may then benefit by adding an additional display component that directs the display toward a specific snake. Jump backs appear to be an informational constrained index signal, as kangaroo rats frequently come nose-nose with snakes before jumping back, and a proximity signal, as kangaroo rats approach well within the strike range of the snake (Bradbury &

Vehrencamp, 2011). Thus, coupling foot drumming with jump backs may allow the kangaroo rats to signal predator detection from a safe distance, while periodically informing the snake that its location is known precisely, and the displaying individual is prepared to evade.

As this is the first study to examine rattlesnake ambush hunting decisions in response to kangaroo rat signaling, and as desert kangaroo rats are the only kangaroo rat species known to incorporate sand kicking into their predator-deterrent displays (Randall & Boltas King, 2001), we cannot separate the independent functions of each kangaroo rat signal. That said, it is likely that the addition of sand kicking to the kangaroo rat display acts to decrease the response time (time until abandonment) of rattlesnakes to the signaling displays. Future studies could further elucidate the role of different signal elements by examining how snakes respond to the displays of non-sand kicking kangaroo rats (Randall, Hatch, & Hekkala, 1995) and whether response times to such displays are longer.

5 | CONCLUSION

Due to logistical issues associated with following and recording the behaviors of free-ranging predators, studies on the behaviors of predators following signaling interactions with their prey remain sparse. Our study, when examined in conjunction with our analysis of snake strikes (Whitford et al., 2017), describes how predator-deterrent displays can alter the behaviors of predators in multiple ways by both lowering the probability of an attack and increasing the likelihood that the predator will cease pursuit of the displaying individual. The confirmation that sand kicks act as an aversive element of these predator-deterrent displays indicates that rattlesnakes, as predators, actively respond to the behaviors of their prey, and that kangaroo rats can successfully mitigate the threat imposed by rattlesnakes.

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CONFLICT OF INTEREST

We have no competing interests.

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