



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.

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