



Comparison of anti-snake displays in the sympatric desert rodents *Xerospermophilus tereticaudus* (round-tailed ground squirrels) and *Dipodomys deserti* (desert kangaroo rats)

RULON W. CLARK,* SCOTT W. DORR, MALACHI D. WHITFORD, GRACE A. FREYMILLER, AND STEVEN R. HEIN

Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182, USA (RWC, SWD, MDW, GAF)

Ecology Graduate Group, University of California, 1005 Wickson Hall, One Shields Avenue, Davis, CA 95616, USA (MDW)

Department of Biology, Miami University, 700 E High Street, Oxford, OH 45056, USA (SRH)

* Correspondent: rclark@mail.sdsu.edu

Several lineages of small mammals frequently preyed upon by snakes have evolved snake-specific signals and displays that they use in an attempt to deter predation. Although detailed studies have been conducted on the form and function of these behaviors in a few key species, limited work has been done that directly compares behaviors between species, and none that we know of between species of separate lineages. Representative species displaying these behaviors exhibit broad overlap in geographic range, and they often occur in sympatry with each other, where they are preyed upon by the same local guild of snakes. Thus, there is potential for these independently evolved signals to exhibit some degree of convergence in sympatry, reinforcing each other in a fashion similar to what has been documented for aposematic mimicry complexes. Here, we provide the 1st direct quantitative comparison of anti-snake signaling behavior in sympatric small mammals from separate lineages: *Dipodomys deserti* (Heteromyidae) and *Xerospermophilus tereticaudus* (Sciuridae). Although some aspects of the displays of squirrels and kangaroo rats were similar (e.g., use of foot drumming, time spent investigating snake), others were not (e.g., willingness to approach closely, tail flagging, sand kicking, jump back displays). Although further research will be necessary to test directly the possibility of convergence, the forms of the signals are disparate enough that it is unlikely that the displays represent an example of convergent mimicry. Our results highlight the potential for further comparative work regarding the evolution of form and function of anti-snake signaling in small mammals.

Key words: animal communication, antipredator signals, behavioral ecology, desert rodents, *Dipodomys*, predator–prey interactions, snake predation, *Xerospermophilus*

Almost all animals have predators, and thus they have evolved a variety of antipredator behaviors to help them avoid being killed and consumed. Although many of these strategies involve hiding from or avoiding predators, prey also actively approach, investigate, and display conspicuous signals toward predators. These antipredator displays can serve a variety of functions, including displays of physical vigor, signals of awareness, or incitement of conspecifics toward group mobbing (reviewed in Caro 2005).

Some of the most prominent research in the area of predator–prey communication involves rodents signaling to predatory snakes. Several lineages of rodents have evolved specialized anti-snake displays, including sciurids (Owings and Coss 1977;

Owings and Owings 1979; Phillips and Waterman 2013), heteromyids (Eisenberg 1963; Randall and Stevens 1987), murids (Randall et al. 2000), and cricetids (Richardson 1942). The most well-studied examples are ground squirrels (*Otospermophilus*) and kangaroo rats (*Dipodomys*); the anti-snake behaviors of several species of each of these genera have been characterized in detail (Goldthwaite et al. 1990; Randall et al. 1995; Randall 1997; Randall and Matocq 1997; Owings et al. 2001; Randall and King 2001; Owings and Coss 2008).

Although there are some similarities between the anti-snake displays of ground squirrels and kangaroo rats, in general, the displays do not resemble each other. Ground squirrels are diurnal, and their displays are largely visual and centered around a

conspicuous back-and-forth tail flag (Owings and Coss 1977). Kangaroo rats, on the other hand, are nocturnal, and the most significant component of their display is a vibrational signal made by thumping their large hind feet rapidly against the ground (Randall 2001). Despite these differences, there are several components of the respective anti-snake displays that the taxa have in common. Species in both genera repeatedly approach snakes, sometimes very closely, and occasionally kick sand or dirt toward snakes during displays.

Anti-snake displays of small mammals seem to be signals of unprofitability—signals that prey send to predators to reduce the probability predators will attempt to attack them (Randall and Matocq 1997; Barbour and Clark 2012; Putman and Clark 2015). Morphological and behavioral signals of unprofitability are common in many systems but have generally constituted different fields of investigation (Caro 2005). Morphological signals are often referred to as aposematic signals and typically involve bright or strongly contrasting markings. An extensive theoretical and experimental body of literature exists for aposematism (reviewed in Komárek 1998). In contrast, behavioral signals of unprofitability (usually referred to as pursuit-deterrent signals) have received comparatively little experimental work and almost no theoretical attention (Caro 2005, but see Vega-Redondo and Hasson 1993; Broom and Ruxton 2012). For example, one of the most robust evolutionary patterns for aposematic signals is mimicry—the convergence of signal form across unrelated lineages (Mallet and Joron 1999; Wang and Shaffer 2008). This convergence of signal form enhances the efficacy of predators learning to avoid unprofitable prey (Beatty et al. 2004). To our knowledge, investigations of mimicry in unprofitability signaling have been entirely restricted to aposematism, despite pursuit-deterrent signals being widespread and likely to occur across divergent sympatric lineages.

Behavioral signals of unprofitability in small mammals could represent an example of the evolution of mimicry in pursuit-deterrent signals. Although it is clear that anti-snake behaviors evolved independently in these divergent lineages, both ground squirrels and kangaroo rats are widespread and broadly sympatric in arid regions of North America. Because large snakes in these environments tend to be generalists and opportunistically consume whatever small mammals are available (e.g., Rodriguez-Robles 2002; Glaudas et al. 2008), it is likely that snakes are the recipients of antipredator displays from both sciurid and heteromyid species. Thus, it is possible that some elements of the displays have converged in sympatry in a way that may enhance the efficacy of signaling. If so, research on sympatric displays could lead to a deeper understanding of the general principles of the evolution of antipredator adaptations. Despite broad geographical overlap between these lineages and intensive research within them, there have been no studies to compare the antipredator displays of small mammals in areas where they are sympatric.

Here, we present results from a series of experiments designed to compare the anti-snake displays of a kangaroo rat (the desert kangaroo rat, *Dipodomys deserti*) and a ground squirrel (the round-tailed ground squirrel, *Xerospermophilus*

tereticaudus), which are sympatric in the Mohave desert and are both preyed upon by sidewinder rattlesnakes (*Crotalus cerastes*—Funk 1965). Although the anti-snake behavior of desert kangaroo rats has been characterized in detail (Randall 1997; Randall and King 2001), these experiments involved presentations toward nonvenomous gopher snakes (*Pituophis catenifer*) and rubber snake models. Despite studies of ground squirrels indicating that small mammals can behave differently toward gopher snakes and rattlesnakes (Hennessy and Owings 1978), no past studies have presented desert kangaroo rats with rattlesnakes. Additionally, no past studies have characterized the anti-snake behavior of round-tailed ground squirrels.

Our experiments were stimulated by field observations of sidewinder foraging behavior. We opportunistically recorded several natural anti-snake displays of round-tailed ground squirrels and noted that these displays incorporated a foot drumming component, which is a display modality that is typically associated only with heteromyids (Randall 2001). Thus, we designed experiments to test the hypothesis that sympatric desert kangaroo rats and round-tailed ground squirrels would exhibit similar anti-snake displays, indicating possible evolutionary convergence of signal form. In particular, we predicted that the foot drumming component of anti-snake displays would be similar, and that both species would exhibit similarities in sand kicks, jump backs, and proximity of approaches. However, we predicted only ground squirrels would incorporate tail flagging into displays, as this behavior is not known to occur in heteromyid rodents.

MATERIALS AND METHODS

Study site.—Our study took place in the Mohave Desert approximately 3 km south of the Desert Studies Center in San Bernardino County, California. This area is characterized by a mixture of loose wind-blown sand, alkali sink vegetation, and creosote bush scrub. Both desert kangaroo rats and round-tailed ground squirrels were abundant at this site, digging extensive burrow systems in the margins of clumps of vegetation. These 2 species were by far the most commonly trapped small mammals at our site, representing over 90% of captures for nocturnal (*D. deserti*) and diurnal (*X. tereticaudus*) trapping sessions, respectively.

Trapping and marking.—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) and followed guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016). We trapped both species using Sherman live traps baited with black oil sunflower seed and placed in the vicinity of active burrow systems. Once captured, mammals were gently restrained with gloved hands by 1 researcher while another measured and marked the individual, which we then released at the site of capture. We marked the pelage of all mammals using Nyanzol dye for short-term visual identification. Each individual received a distinct combination of marks on the back, shoulder, or rump to provide individually unique markings. We

used ear tags (mouse ear tags 1005-1, National Band and Tag, Newport, Kentucky) with unique numbers for long-term identification. We recorded the sex, snout-to-anus length, tail length, hind foot length, and weight of each individual.

Collection and housing of rattlesnakes.—Although sidewinders are a relatively small species of rattlesnake, they are documented predators of both desert kangaroo rats and round-tailed ground squirrels (Funk 1965; Klauber 1972). We collected and housed 8 adult sidewinder rattlesnakes from nearby populations to use during tethering experiments (size range 49–65 cm body length, 120–190 g mass). Sidewinders were housed for up to 60 days in captivity at the Desert Studies Center field station. Each snake was housed individually in a secured cage with a sand substrate, provided with water and cover, and fed a lizard approximately every 2 weeks. Snakes were not used for tethering experiments for at least 7 days following feeding to allow sufficient time for the tethering process to not interfere with digestion. We also did not use the same individual on successive days, to avoid over-stressing any individual snake.

Experimental procedure.—We identified home burrow locations of mammals that we had trapped and marked, and then habituated these individuals to feed at a specific location by repeatedly placing small amounts of black oil sunflower seed at that location over the course of at least 2 days (hereafter called a feeding station). Because round-tailed ground squirrels are exclusively diurnal, we also constructed shade structures at squirrel feeding stations to provide shelter for tethered snakes. Shade structures consisted of a 60 × 120 cm plywood board held upright by long metal stakes sunk into the sand and oriented to provide shade from the morning sun. Shades were erected prior to baiting and maintained for the duration of the experiments. We conducted all squirrel trials between the hours of 0500 and 2300 h. Desert kangaroo rats are exclusively nocturnal and did not require shade structures. We conducted all kangaroo rat trials between the hours of 2100 and 0400 h.

We began a trial by verifying habituation to feeding stations (i.e., marked individual would visit feeding stations every 1–2 h during its active period). We then placed a tethered rattlesnake in position within 20 cm of the feeding station. We tethered snakes using a modified version of the technique described by Randall and Stevens (1987). Snakes were coaxed into elongate plastic tubes and held gently in place for restraint while the posterior two-thirds of the body was tethered. Four sand-colored

rubberized metal ties were used to hold the body of the snake in 4 locations against the grate so that it could not crawl forward or backward. We tethered snakes so their bodies were in a coiled position on top of a 10 × 10 cm section of metal hardware cloth. This method was chosen so that tethered snakes mimicked the stereotyped ambush coil of rattlesnakes (Reinert et al. 2011); small mammals encounter snakes in this position in natural observations and sidewinders generally remain completely immobile during encounters (Clark et al., 2016). Although the snakes could move the front 1/3 of their body slightly, they generally remained still during encounters and their overall movement was limited by the tethers. Tethered snakes were placed at feeding stations to elicit anti-snake behaviors of mammals and 2 ice packs were buried in the sand beneath the tethered snake to further protect snakes against overheating. Following the completion of trials, snakes were removed from tethers and replaced in cages.

We recorded the response of mammals to tethered snakes using pan/tilt/zoom security cameras (SNC-RX25N, Sony, Tokyo, Japan) connected to a laptop computer via wireless network radios (Nanostation M2, Ubiquiti Networks, San Jose, California). This allowed us to monitor and record trials remotely, from a central monitoring station hundreds of meters from feeding stations. We used small geophones (General Electromagnetic P496, Randolph, New Jersey) connected to cameras to record substrate vibrations during trials. Geophones were placed approximately 30 cm from tethered snakes. Trials commenced as soon as mammals approached snakes and exhibited any anti-snake behavior (Table 1) and ended when mammals stopped exhibiting anti-snake behavior and left the vicinity of the snake (within ~ 1 m of snake) for longer than 60 s. We conducted only 1 trial per individual, so we did not collect data on marked individuals after ending trials.

In addition to conducting trials with tethered snakes, we included 15 control trials (5 kangaroo rat and 10 ground squirrel) with a non-snake novel object, a dark-colored, 5-cm-diameter, solid polyethylene sphere. These trials were included to be sure that behaviors exhibited towards snakes were actually specific to snakes and were not displayed toward all new objects placed at a location where they had been foraging.

Behavioral measurements.—We quantified a number of distinct anti-snake behaviors of squirrels and kangaroo rats (Table 1). These behaviors included foot drums, tail flags (squirrels only), sand kicks, jump backs, and nose touches.

Table 1.—Ethogram of mammal behaviors quantified during tethering trials with rattlesnakes.

Behavior	Definition
Foot drum	Mammal repeatedly strikes ground with hind foot. <i>Dipodomys deserti</i> typically uses same foot throughout foot drumming bout, whereas <i>Xerospermophilus tereticaudus</i> alternates hind feet between strikes. <i>D. deserti</i> occasionally punctuates foot drumming with foot rolling, a very rapid (~ 14 foot drums per second) series of strikes made by alternating hind feet.
Tail flag	Mammal raises tail at least 45 degrees off ground and moves tail in side-to-side motion at rate of approximately 1–3 Hz. Only <i>X. tereticaudus</i> was observed to tail flag.
Sand kick	Mammal uses feet to kick sand toward snake. <i>X. tereticaudus</i> was always seen to use forefeet for sand kicking, and <i>D. deserti</i> always used hind feet.
Jump back	While approaching snake, mammal leaps abruptly into the air with all four feet off the ground, jumping away from snake.
Nose touch	Mammal approaches snake and touches its nose against the head or body of the coiled snake.

Foot drums, tail flags, and sand kicks were all counted in bouts, whereas jump backs and nose touches were counted individually. A bout of foot drumming was defined as a series of foot drums uninterrupted by locomotion or other behaviors. A bout of tail flagging was defined as a series of tail flags with no pause between flags longer than 5 s. A bout of sand kicking was defined as a series of sand kicks uninterrupted by locomotion with no pause between kicks longer than 5 s.

We quantified the total duration of the initial encounter with the snake in seconds for all trials. Most trials ended within 5 min or less, but occasionally individuals continued to interact with snakes for very long periods. Although we recorded the total interaction time for these trials, we only quantified rates of specific snake behaviors for the initial 5-min period for all trials (or less, if trial ended in less than 5 min). For this period, we estimated the closest proximity of the mammal to the snake in centimeter by using the hind foot of the mammal as a size reference. We accomplished this by exporting the video frame containing the closest approach and used ImageJ software to estimate distances in the digitized frame using the hind foot of the mammal to scale the image (Abramoff et al. 2004). Because of the inherent imprecision in this estimate due to differing camera placement and angles, we rounded distances to the nearest 5 cm.

In order to quantify foot drum signals, we imported the audio component of the video recordings into Audacity 2.1.0 and used the waveform display to measure the total duration of each foot drumming bout, as well as the number of distinct foot strikes in that bout. We imported representative audio files into Syrinx 2.6 to generate sample waveforms.

Statistical analyses.—We used a general linear model (GLM) framework implemented in R for statistical analysis. To analyze overdispersed count data (with variance much larger than mean), we used negative binomial GLMs implemented in the MASS package. Because our comparisons of foot drumming bouts involved multiple foot drums from the same individuals, we used both linear and generalized linear mixed-effect models (LMMs and GLMMs, respectively) implemented in the lme4 package for these comparisons and included individual identity as a random factor. We used LMMs to compare length of bouts and frequency of foot strikes and assessed significance by comparing models with and without mammal species as a fixed factor using the Kenward–Roger correction in the pbkrtest package. We used lognormal Poisson GLMMs incorporating an additional observation-level random effect (Elston et al. 2001; Bolker et al. 2009) for comparing number of foot strikes during foot drumming bouts. We used linear models to compare body size and mass between the 2 species. All values are given as mean \pm SE.

RESULTS

We completed experimental trials on 19 kangaroo rats and 16 ground squirrels. We conducted control presentations with an additional 5 kangaroo rats and 10 ground squirrels, for a total sample of 24 kangaroo rats and 26 ground squirrels. Kangaroo rats and ground squirrels were similar in both snout-to-anus length (kangaroo rats = 13.6 ± 0.26 cm, squirrels = 13.4 ± 0.52 cm,

$t = 0.5$, $P = 0.62$) and body mass (kangaroo rats = 109 ± 5 g, squirrels = 93 ± 12 g, $t = 1.6$, $P = 0.13$). As in natural encounters, both kangaroo rats and ground squirrels in experimental trials spent prolonged periods of time investigating and exhibiting stereotyped displays toward rattlesnakes.

Investigation time and proximity.—Both species varied widely across individuals in the amount of time they spent interacting with snakes and did not differ from each other significantly in this regard (kangaroo rats = 339 ± 48 s, squirrels = 443 ± 127 s, $z = 0.92$, $P = 0.36$). Kangaroo rats were more willing to approach snakes closely, with an average closest approach to the snake significantly lower than that of squirrels (closest proximity of kangaroo rats = 4 ± 3 cm, squirrels = 28 ± 2 cm, $z = 3.0$, $P = 0.002$). Kangaroo rats were frequently willing to contact snakes physically during interactions, and they exhibited an average of 2.9 ± 0.7 nose touches, whereas no squirrels came closer than 15 cm to snakes (Fig. 1).

Foot drums.—Both kangaroo rats and squirrels regularly foot drummed during encounters with snakes, at approximately equal rates (average number of foot drum bouts, kangaroo rats = 9.4 ± 2.0 , squirrels = 9.4 ± 2.4 , $z = 0.01$, $P = 0.99$). Although the number of foot drumming bouts was similar, the structure and form of the signal differed between the species (Fig. 2). Kangaroo rats mainly foot drummed by repeatedly striking the substrate with a single hind foot at a rate of approximately 4–5 drums per second (dps; average = 4.5 ± 0.1 dps). The average length of a kangaroo rat foot drumming bout was 3.4 ± 0.8 s, and individual bouts ranged from 0.5 to 18.1 s.

In addition to this slower drumming, kangaroo rats would occasionally exhibit very rapid foot drums by striking the ground with both hind feet in an alternate pattern (termed “foot rolls” by

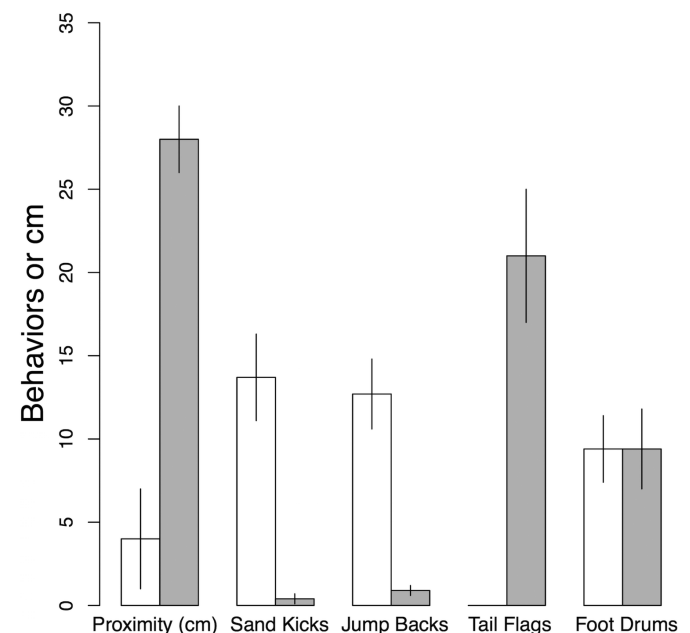


Fig. 1.—Comparisons of mean \pm SE values for key behavioral traits of kangaroo rats (*Dipodomys deserti*; open bars) and ground squirrels (*Xerospemophilus tereticaudus*; shaded bars) interacting with sidewinder rattlesnakes (*Crotalus cerastes*). Values on y-axis indicate centimeters for proximity, and counts of occurrence for other behaviors.

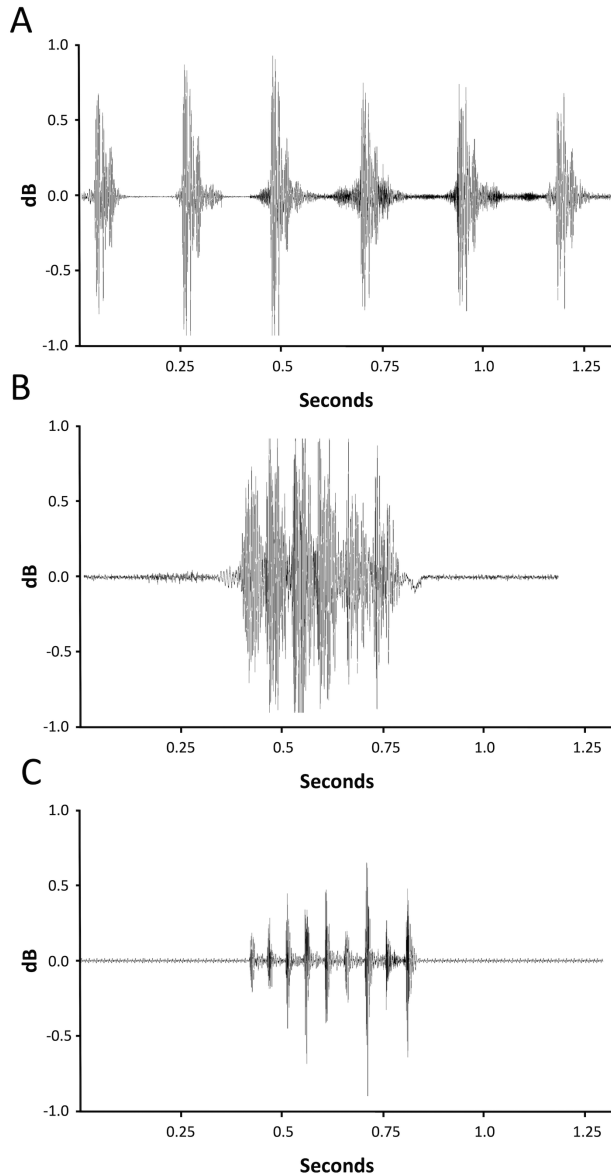


Fig. 2.—Waveforms of typical foot-strike signals for *Dipodomys deserti* and *Xerospemophilus tereticaudus*. A) Foot drumming of *D. deserti*, B) foot drumming of *X. tereticaudus*, C) foot roll of *D. deserti*.

Randall 1997). Foot rolls were an average of 0.32 ± 0.02 s, and foot strikes during foot rolls occurred at a rate of 16.7 ± 0.6 dps. Foot rolls almost always occurred either just after (26% of cases), just before (47% of cases), or in the midst (18%) of foot drums, and 27% of foot drum bouts were associated with foot rolls.

Ground squirrels appeared to foot drum by rapidly striking both hind feet in an alternate pattern, creating a “fluttering” signature of approximately 20 dps (average rate = 20.9 ± 0.5 dps). Ground squirrel foot drum bouts were 0.59 ± 0.09 s, with individual bouts ranging only from 0.21 to 1.35 s. Kangaroo rat foot drumming bouts were significantly longer than ground squirrel foot drumming bouts ($F_{9,1} = 21.7$, $P = 0.001$), but because of the higher strike rate of ground squirrels, both species had a similar number of foot strikes per bout ($z = 1.3$, $P = 0.19$). Although kangaroo rat foot rolls were more similar in structure to ground

squirrel foot drums, ground squirrel foot strikes still occurred at a higher rate (squirrel foot drums = 20.9 ± 0.5 dps, kangaroo rat foot rolls = 16.7 ± 20.6 dps, $F_{6,1} = 13.7$, $P = 0.01$; Fig. 1).

Sand kicking.—Although both species were seen to kick sand at snakes, squirrels did this rarely, whereas sand kicking was a major component of kangaroo rat displays (average number of sand kicks, kangaroo rat = 13.7 ± 2.0 , squirrel = 0.4 ± 0.3 , $z = 7.8$, $P < 0.001$). The form of sand kicking differed between the 2 species. Kangaroo rats always kicked sand by turning so their posterior was oriented toward the snake and then vigorously kicking sand behind them with their hind legs, causing relatively large amounts of sand to fly 10–20 cm through the air toward the snake, often physically contacting the snake. When squirrels sand kicked, they remained with their head facing snakes and used their forelegs to shovel relatively small amounts of sand only 1–2 cm in front of their heads, never physically touching the snake with the sand (Fig. 1).

Jump backs.—Both species exhibited jump backs away from the snake, but as with sand kicking, this was seen frequently in kangaroo rats and rarely in squirrels (average number of jump backs, kangaroo rats = 12.7 ± 2.1 , squirrels = 0.9 ± 0.3 , $z = 7.76$, $P < 0.001$). Kangaroo rat jump backs were also more vigorous, typically launching rats several body lengths vertically into the air away from snakes, whereas squirrel jump backs typically moved squirrels less than a body length in a more horizontal plane (Fig. 1).

Tail flags.—Only ground squirrels were seen to tail flag. Ground squirrels consistently exhibited tail flagging bouts when approaching and inspecting snakes. Squirrels exhibited an average of 21 ± 4 tail flags during interactions, resulting in an average rate of 5.9 ± 0.8 tail flags per minute. All squirrels except 1 (15 out of 16) tail flagged during interactions (Fig. 1).

Control trials.—The behaviors we documented in experimental trials were snake-specific—in control trials, both species would approach and sniff the novel object (polystyrene sphere), but rarely or never exhibited foot drumming, sand kicking, tail flagging, or jump backs.

Statistically, when compared to control objects, kangaroo rats exposed to snakes exhibited longer interaction times (snake 339 ± 48 s, control 56 ± 9 s, $z = 6.2$, $P < 0.001$), more foot drums (snake 9.4 ± 2.0 , control 0.2 ± 0.2 , $z = 3.5$, $P < 0.001$), more jump backs (snake 12.7 ± 2.1 , control 0.2 ± 0.2 , $z = 3.9$, $P < 0.001$), and more sand kicks (snake 13.7 ± 2.0 , control 0.4 ± 0.4 , $z = 4.5$, $P < 0.001$). However, kangaroo rats exhibited a similar number of nose touches in snake and control trials, indicating they were as likely to physically contact snakes as they were control objects (snake 2.9 ± 0.7 , control 2.4 ± 1.0 , $z = 0.41$, $P = 0.69$).

Ground squirrels also exhibited longer interaction times (snake 443 ± 127 s, control 191 ± 39 s, $z = 2.2$, $P = 0.03$) during trials with snakes. Ground squirrels exhibited no foot drums, sand kicks, jump backs, or tail flags during control trails (thus rendering them unsuitable for quantitative statistical analysis). However, unlike kangaroo rats, ground squirrels stayed further away from snakes than control objects (snake 28 ± 2 cm, control 1 ± 0.6 cm, $z = 10.1$, $P < 0.001$).

DISCUSSION

We found that both desert kangaroo rats (*D. deserti*) and round-tailed ground squirrels (*X. tereticaudus*) readily engaged sidewinder rattlesnakes in a series of antipredator displays. Both species exhibited these behaviors only to rattlesnakes, and not to nonpredator novel objects that were placed near feeding stations in control trials. Some elements of the displays (amount of time spent investigating snakes, rate of foot drumming bouts) were similar between the species, whereas others (willingness to contact snake, structure of foot drumming signal, frequency and structure of sand kicking and jump backs) were very different. Overall, given the differences we observed in the structure of the displays, our results did not offer strong support for the hypothesis that these displays represent the evolution of convergent forms of pursuit-deterrent signals in disparate lineages.

Foot drumming.—Both species interacted with snakes and foot drummed for periods of about 5–10 min (but occasionally for much longer) before moving away from the scene. However, the foot drumming of the 2 species differed in execution and length. Desert kangaroo rats typically drummed in 4-s bouts of individual foot strikes at a rate of 4–5 strikes per second, with occasional foot rolls of 4–5 foot strikes at a rate of 17 per second. Ground squirrel drumming bouts lasted only about 1 s and consisted of a rapid sequence of foot strikes at a rate of 20 per second by alternately striking the ground with both feet.

Only the occasional foot rolls of the desert kangaroo rats converge with the drumming pattern of the round-tailed ground squirrels. This convergence in pattern likely does not involve mimicry and may be more related to the intensity of the interaction between the kangaroo rat and snake and to the foot drumming patterns of kangaroo rats in general. The 2 other kangaroo rat species (*D. spectabilis* and *D. ingens*) that foot drum when interacting with predators use foot roll-style displays and not single thumps; however, the geographic range and habitat preferences of *X. tereticaudus* overlaps extensively only with *D. deserti*. Both *X. tereticaudus* and *D. deserti* are associated with loose sand and dune microhabitats, a soil type that is particularly effective for transducing vibrations (Brownell and van Hemmen 2001). Thus, it may be that both displays evolved independently as a component of anti-snake signaling in an environment where such vibrational signals would be particularly effective. Nevertheless, future studies could investigate the possible convergence of *D. deserti* foot rolls and *X. tereticaudus* foot drums by comparing the structure of the signals across a geographic mosaic. Such a study could reveal if the signals are more convergent when the 2 mammals exist in sympatry compared to allopatry.

Proximity and jump backs.—Kangaroo rats approached snakes much more closely than ground squirrels, frequently contacting them physically during displays. Although the initial approach distances could be influenced by ambient light and the modality of predator detection (kangaroo rats are exclusively nocturnal and may rely more on olfaction for preliminary predator detection), kangaroo rats continue to closely approach, touch snakes, and jump back from them even after it is clear that they have located them spatially. Thus, it seems

as if close approaches and jump backs are components of the display, rather than unintended consequences of signaling in the dark.

It may be that close approaches and jump backs are elements of the kangaroo rat display that specifically advertise their ability to avoid snake strikes. Kangaroo rats are known to employ a high-speed evasive jump to avoid rattlesnake strikes (Bartholomew and Caswell 1951; Webster 1962); indeed, this ability may be primarily responsible for the disproportionately enlarged hind leg muscles that give the clade its unique look and name (Biewener et al. 1981). In our examination of foraging behaviors of free-ranging sidewinders, we documented kangaroo rats avoiding sidewinder rattlesnakes via evasive jump backs (Clark et al., 2016), indicating that this behavior is an important element of snake avoidance in natural encounters.

Sand kicking.—Although both species dig extensive burrow systems, sand kicking was a frequent and important element of kangaroo rat displays but was virtually absent in ground squirrels. Kangaroo rats used their powerful hind legs to kick sand relatively long distances, frequently hitting snakes, whereas squirrels only very occasionally made small shoveling motions in the sand with their forelegs. Data from natural encounters indicate that sand kicking is an important element of *D. deserti* signaling to free-ranging sidewinders (Clark et al., 2016).

Given its efficacy in managing snakes, it is somewhat mysterious that sand kicking in ground squirrels is virtually absent. The displays of round-tailed ground squirrels are similar to those of other ground squirrel species in that they involve repeated close approaches, inspection, tail flagging, and occasionally substrate kicking with the forelimbs (Owings and Coss 1977; Towers and Coss 1991; Owings et al. 2001; Phillips and Waterman 2013). Although California ground squirrels (*Otospermophilus beecheyi*) can behave aggressively toward snakes that are anesthetized, caged, tethered to the ground, or elongated (reviewed in Owings and Coss 2008), they almost never kick substrate or aggressively mob free-ranging rattlesnakes that are coiled in a ready-to-strike posture (Barbour and Clark 2012). Qualitatively, the substrate throwing exhibited by ground squirrels of any species is not as robust as the sand kicking displayed by *D. deserti*. For example, Owings and Coss (1977) reported that the most aggressive ground squirrels kicked sand toward rattlesnakes at an average rate of 0.3 bouts of sand kicking per minute, whereas in our study desert kangaroo rats sand kicked at an average rate of 2.7 kicks per minute.

Sand kicking by kangaroo rats is not only more frequent, but it is also more effective, resulting in large amounts of sand physically contacting snakes. In our experiment, sand kicks by *D. deserti* were typically directed toward the snake's head, where it may be especially aversive to sensitive sensory organs (eyes, pits, and nostrils). Sand kicking by both round-tailed ground squirrels and California ground squirrels is frequently cursory, resulting in small amounts of substrate being moved in the direction of the snake, but not contacting the snake (R. W. Clark, pers. obs.). This difference may have to do with the specialized hind limb morphology of the kangaroo rats. Although the disproportionately enlarged hind limb muscles,

tendons, and bones of kangaroo rats most likely evolved to support evasive antipredator jumping maneuvers, they also aid in digging. Kangaroo rats dig burrows by loosening soil with their front feet, and then using strong kicks of the hind feet to send soil flying backward (Culbertson 1946; Eisenberg 1963; Reichman and Smith 1990). Thus, their disproportionately stronger hind limbs may endow them with the ability to kick sand at snakes more effectively than other rodent species that engage in anti-snake behavior. However, the incorporation of sand kicking specifically by *D. deserti* probably also relies on the physical characteristics of sandy microhabitats. *D. deserti* is the only kangaroo rat known to kick substrate at snakes. Other large species such as *D. spectabilis* and *D. ingens* also confront snakes with displays and have equally strong hind limbs, but occupy arid grasslands with compact soils (Randall 1997; Randall and King 2001; J. A. Randall, San Francisco State University, pers. comm.). Thus, the evolution of sand kicking in *D. deserti* is likely predicated on their specialized microhabitat.

Other taxonomic comparisons.—Previous research has documented the responses of *D. deserti* to gopher snakes (Randall and King 2001), as well as the details of foot drumming in a territorial context (Randall 1997). Randall and others have also documented and compared the anti-snake behavior of several *Dipodomys* congeners (Randall et al. 1995; Randall 2001; Randall and King 2001). The responses of desert kangaroo rats to sidewinder rattlesnakes we describe here incorporate very similar behaviors. However, the rate of these behaviors seems to differ when encountering rattlesnakes. Kangaroo rats exhibited 2.5 ± 1.7 jump backs per minute when interacting with rattlesnakes, and only 0.1 ± 0.03 jump backs per minute when interacting with gopher snakes (Randall and King 2001). Kangaroo rats exhibited similarly high rates of foot drumming ($10.7 \pm 9.6\%$ of interaction time spent foot drumming) and sand kicking (2.7 ± 1.7 sand kicks per minute) when interacting with sidewinder rattlesnakes compared to gopher snakes (approximately $6.7 \pm 2.3\%$ of interaction time spent foot drumming and 1.4 ± 0.4 sand kicks per minute for gopher snake trials). Like California ground squirrels (Hennessy and Owings 1978), desert kangaroo rats may be able to discriminate among gopher snakes and rattlesnakes and exhibit different levels anti-snake behaviors to the 2 predators; future experiments should investigate this possibility.

One element of desert kangaroo rat displays that does not seem to differ between sidewinder rattlesnakes and gopher snakes is the willingness of *D. deserti* to repeatedly approach snakes closely. Although direct comparisons are difficult because of differing ways close approaches were quantified, in both this study and Randall and King's (2001), kangaroo rats repeatedly came within strike range, and occasionally physically contacted snakes with their nose before jumping back. Although kangaroo rats do not appear to have innate venom resistance (Randall and King 2001; Biardi 2008), their remarkable evasive leaps appear to offer sufficient protection to allow these close approaches and inspections.

As with desert kangaroo rats, several related sciurid species exhibit anti-snake behaviors that are similar to *X. tereticaudus*.

Although this behavior has been documented in detail for California ground squirrels, to our knowledge, all species of sciurids that have been studied in the context of snake predation exhibit some form of anti-snake behavior, including Colombian ground squirrels (*Urocitellus columbianus*), rock squirrels (*Otospermophilus variegatus*), Cape ground squirrels (*Xerus inauris*), gray squirrels (*Sciurus carolinensis*), eastern chipmunks (*Tamias striatus*), and black-tailed prairie dogs (*Cynomys ludovicianus*—Owings and Coss 1977; Owings and Owings 1979; Towers and Coss 1991; Owings et al. 2001; Clark 2005; Phillips and Waterman 2013).

Compared with California ground squirrels and rock squirrels, the anti-snake behavior of round-tailed ground squirrels appears to be more cautious. When confronting tethered rattlesnakes, rock squirrels and California ground squirrels approach repeatedly to within the effective strike range, kick substrate with their forelegs, and sometimes directly attack snakes (Owings and Coss 1977; Owings et al. 2001), whereas we observed very limited sand kicking, almost no approaches to within strike range, and no physical attacks on tethered sidewinder rattlesnakes. Smaller ground squirrel species may be more vulnerable to snakes, both due to their reduced physical ability to retaliate, and perhaps a lack of venom resistance. Although populations of rock squirrels and California ground squirrels that co-occur with rattlesnakes have evolved resistance to snake venom, the degree of resistance depends on body size, with smaller juveniles still susceptible to snake envenomation (Poran et al. 1987). To our knowledge, no studies have examined the potential for venom resistance in *X. tereticaudus* (reviewed in Biardi 2008), but if they exhibit the same trade-off with body size as other ground squirrels, it is unlikely that they have significant levels of venom resistance. Thus, their increased vulnerability to snake strikes could have resulted in the evolution of a more cautious set of anti-snake displays. However, the relationship between body size and venom resistance may only be relevant to intraspecific comparisons. For example, Biardi (2008) found that blood sera from white-tailed antelope ground squirrels (*Ammospermophilus leucurus*) exhibited high levels of venom neutralization. *A. leucurus* and *X. tereticaudus* are similar in body mass, so smaller sciurids can be highly resistant to snake venom. Clearly, more comparative research is needed to substantiate a possible relationship between the aggressiveness of anti-snake signaling and venom resistance.

In a broader sense, we believe our results highlight the potential for more in-depth comparative research both within and between heteromyid and sciurid rodent lineages. Although the anti-snake behaviors of ground squirrels and kangaroo rats have been studied in great detail, the bulk of this research is limited to just a few species (primarily *O. beecheyi* for Sciuridae and *D. spectabilis* for Heteromyidae). To date, the general assumption seems to be that the form and function of anti-snake displays is similar in the large number of other species within these families that are preyed on by snakes. However, it is likely that there are important differences driven by specific ecological and physiological constraints present for particular species.

The relatively simple 2-species comparison we present here already demonstrates some fundamental differences in displays that are likely driven by variation in the evolution of particular antipredator adaptations. It is likely that broader comparisons will continue to reveal co-evolved predator–prey adaptation.

ACKNOWLEDGMENTS

We would like to thank J. Randall and an anonymous reviewer, who both provided extensive comments that greatly improved this manuscript. For assistance with fieldwork, we thank K. Huang, C. Barnes, M. Herr, K. Stauffer, C. Brahm, and J. Tingle. For assistance with field logistics, we thank R. Fulton, J. Wallace, and the rest of the staff at California State University Desert Studies Center. For assistance with quantifying video data, we thank M. Shoya and E. Vazquez. Funding for this research was provided by San Diego State University, the National Science Foundation (DBI-0951010 to RWC), the California Desert Research Fund of the Community Foundation (SID 811996543 to SWD), and the Judith Presch Desert Research Scholarship (to SWD).

LITERATURE CITED

- ABRAMOFF, M. D., P. J. MAGALHAES, AND S. J. RAM. 2004. Image processing with ImageJ. *Biophotonics International* 11:36–42.
- BARBOUR, M. A., AND R. W. CLARK. 2012. Ground squirrel tail-flag displays alter both predatory strike and ambush site selection behaviours of rattlesnakes. *Proceedings of the Royal Society B-Biological Sciences* 279:3827–3833.
- BARTHOLOMEW, G. A., JR., AND H. H. CASWELL, JR. 1951. Locomotion in kangaroo rats and its adaptive significance. *Journal of Mammalogy* 32:155–169.
- BEATTY, C. D., K. BEIRINCKX, AND T. N. SHERRATT. 2004. The evolution of Müllerian mimicry in multispecies communities. *Nature* 431:63–67.
- BIARDI, J. E. 2008. The ecological and evolutionary context of mammalian resistance to rattlesnake venoms. Pp. 557–568 in *The biology of rattlesnakes* (W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush, eds.). Loma Linda Press, Loma Linda, California.
- BIEWENER, A., R. ALEXANDER, AND N. C. HEGLUND. 1981. Elastic energy storage in the hopping of kangaroo rats (*Dipodomys spectabilis*). *Journal of Zoology (London)* 195:369–383.
- BOLKER, B. M., ET AL. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- BROOM, M., AND G. D. RUXTON. 2012. Perceptual advertisement by the prey of stalking or ambushing predators. *Journal of Theoretical Biology* 315:9–16.
- BROWNELL, P. H., AND J. L. VAN HEMMEN. 2001. Vibration sensitivity and a computational theory for prey-localizing behavior in sand scorpions. *American Zoologist* 41:1229–1240.
- CARO, T. 2005. *Antipredator defenses in birds and mammals*. University of Chicago Press, Chicago, Illinois.
- CLARK, R. W. 2005. Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): the response of snakes to harassment displays. *Behavioral Ecology and Sociobiology* 59:258–261.
- CLARK, R. W., S. W. DORR, M. D. WHITFORD, G. A. FREYMILLER, AND B. J. PUTMAN. 2016. Activity cycles and foraging behaviors of free-ranging sidewinder rattlesnakes (*Crotalus cerastes*): the ontogeny of hunting in a precocial vertebrate. *Zoology* 119:196–206.
- CULBERTSON, A. E. 1946. Observations on the natural history of the Fresno kangaroo rat. *Journal of Mammalogy* 27:189–203.
- EISENBERG, J. 1963. *The behavior of heteromyid rodents*. University of California Publications in Zoology 69:1–100.
- ELSTON, D. A., R. MOSS, T. BOULINIER, C. ARROWSMITH, AND X. LAMBIN. 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology* 122:563–569.
- FUNK, R. S. 1965. Food of *Crotalus cerastes laterorepens* in Yuma County, Arizona. *Herpetologica* 21:15–17.
- GLAUDAS, X., T. JEZKOVA, AND J. A. RODRÍGUEZ-ROBLES. 2008. Feeding ecology of the Great Basin Rattlesnake (*Crotalus lutosus*, Viperidae). *Canadian Journal of Zoology* 86:723–734.
- GOLDTHWAITE, R., R. COSS, AND D. OWINGS. 1990. Evolutionary dissipation of an antisnake system: differential behavior by California and Arctic ground squirrels in above-and below-ground contexts. *Behaviour* 112:246–269.
- HENNESSY, D. F., AND D. H. OWINGS. 1978. Snake species discrimination and the role of olfactory cues in the snake-directed behavior of the California ground squirrel. *Behaviour* 65:115–124.
- KLAUBER, L. M. 1972. *Rattlesnakes: their habits, life histories, and influence on mankind*. 2nd ed. University of California Press, Berkeley.
- KOMÁREK, S. 1998. *Mimicry, aposematism and related phenomena: mimetism in animals and plants*. Vesmir Publishing House, Prague, Czech Republic.
- MALLET, J., AND M. JORON. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics* 30:201–233.
- OWINGS, D. H., AND R. COSS. 1977. Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behaviour* 62:50–69.
- OWINGS, D. H., AND R. G. COSS. 2008. Hunting California ground squirrels: constraints and opportunities for northern Pacific rattlesnakes. Pp. 155–168 in *The biology of rattlesnakes* (W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush, eds.). Loma Linda Press, Loma Linda, California.
- OWINGS, D. H., AND S. C. OWINGS. 1979. Snake-directed behavior by black-tailed prairie dogs (*Cynomys ludovicianus*). *Ethology* 49:35–54.
- OWINGS, D. H., R. G. COSS, D. MCKERNON, M. P. ROWE, AND P. C. ARROWOOD. 2001. Snake-directed antipredator behavior of rock squirrels (*Spermophilus variegatus*): population differences and snake-species discrimination. *Behaviour* 138:575–595.
- PHILLIPS, M. A., AND J. M. WATERMAN. 2013. Olfactory snake-predator discrimination in the cape ground squirrel. *Ethology* 119:278–285.
- PORAN, N. S., R. G. COSS, AND E. BENJAMINI. 1987. Resistance of California ground squirrels (*Spermophilus beecheyi*) to the venom of the northern Pacific rattlesnake (*Crotalus viridis oreganus*): a study of adaptive variation. *Toxicon* 25:767–777.
- PUTMAN, B. J., AND R. W. CLARK. 2015. The fear of unseen predators: ground squirrel tail flagging in the absence of snakes signals vigilance. *Behavioral Ecology* 26:185–193.
- RANDALL, J. A. 1997. Species-specific footdrumming in kangaroo rats: *Dipodomys ingens*, *D. deserti*, *D. spectabilis*. *Animal Behaviour* 54:1167–1175.
- RANDALL, J. A. 2001. Evolution and function of drumming as communication in mammals. *American Zoologist* 41:1143–1156.
- RANDALL, J., S. M. HATCH, AND E. R. HEKKALA. 1995. Interspecific variation in antipredator behavior in sympatric species of kangaroo rat. *Behavioral Ecology and Sociobiology* 36:243–250.

- RANDALL, J., AND D. KING. 2001. Assessment and defense of solitary kangaroo rats under risk of predation by snakes. *Animal Behaviour* 61:579–587.
- RANDALL, J., AND M. MATOCQ. 1997. Why do kangaroo rats (*Dipodomys spectabilis*) footdrum at snakes? *Behavioral Ecology* 8:404–413.
- RANDALL, J. A., K. A. ROGOVIN, AND D. M. SHIER. 2000. Antipredator behavior of a social desert rodent: footdrumming and alarm calling in the great gerbil, *Rhombomys opimus*. *Behavioral Ecology and Sociobiology* 48:110–118.
- RANDALL, J. A., AND C. M. STEVENS. 1987. Footdrumming and other anti-predator responses in the bannertail kangaroo rat (*Dipodomys spectabilis*). *Behavioral Ecology and Sociobiology* 20:187–194.
- REICHMAN, O. J., AND S. C. SMITH. 1990. Burrows and burrowing behavior by mammals. *Current Mammalogy* 2:197–244.
- REINERT, H. K., H. K. REINERT, G. A. MACGREGOR, L. M. BUSHAR, AND R. T. ZAPPALORTI. 2011. Foraging ecology of timber rattlesnakes, *Crotalus horridus*. *Copeia* 2011:430–442.
- RICHARDSON, W. B. 1942. Reaction toward snakes as shown by the wood rat, *Neotoma albigula*. *Journal of Comparative Psychology* 34:1.
- RODRIGUEZ-ROBLES, J. 2002. Feeding ecology of North American gopher snakes (*Pituophis catenifer*, Colubridae). *Biological Journal of the Linnean Society* 77:165–183.
- SIKES, R. S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- TOWERS, S. R., AND R. G. COSS. 1991. Antisnake behavior of Columbian ground squirrels (*Spermophilus columbianus*). *Journal of Mammalogy* 72:776–783.
- VEGA-REDONDO, F., AND O. HASSON. 1993. A game-theoretic model of predator-prey signaling. *Journal of Theoretical Biology* 162:309–319.
- WANG, I. J., AND H. B. SHAFFER. 2008. Rapid color evolution in an aposematic species: a phylogenetic analysis of color variation in the strikingly polymorphic strawberry poison-dart frog. *Evolution* 62:2742–2759.
- WEBSTER, D. B. 1962. A function of the enlarged middle-ear cavities of the kangaroo rat, *Dipodomys*. *Physiological Zoology* 35:248–255.

Submitted 17 November 2015. Accepted 2 August 2016.

Associate Editor was Tereza Jezkova.