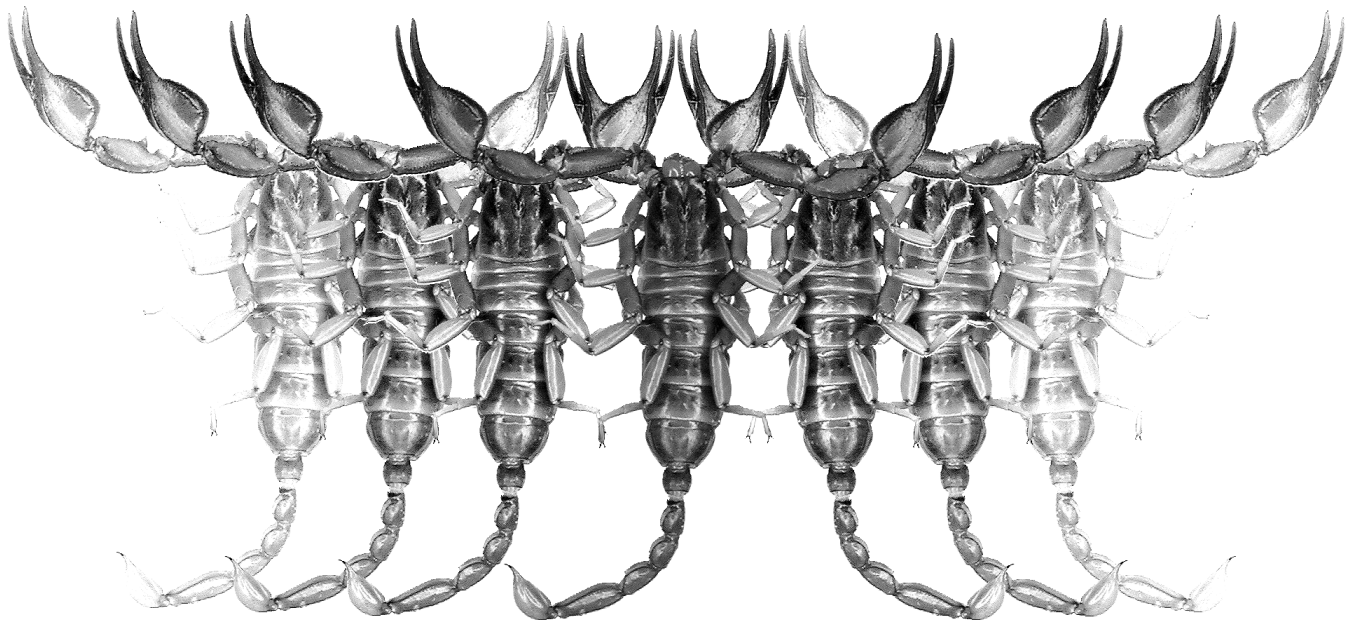


Euscorpium

Occasional Publications in Scorpiology



Scorpions 2011

John L. Cloudsley-Thompson 90th Birthday Commemorative Volume

***In situ* Infrared Videography of Sand Scorpion
Nighttime Surface Activity**

Douglas D. Gaffin

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Euscorpius

Occasional Publications in Scorpiology

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***In situ* infrared videography of sand scorpion nighttime surface activity**

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Summary

Sand scorpions make burrows from which they emerge at night to seek mates and prey. Previous ecological studies have documented scorpion activities on the sand surface. Few studies, however, have videotaped scorpion movements in the context of understanding their sensory neurobiology. Our objective is to understand which signals guide scorpions as they emerge from and return to their burrows. Candidate stimuli include chemical trails, footsteps, celestial patterns, geomagnetic cues, humidity and/or temperature gradients, distinctive scents from the burrow, seismic echolocation, memory, or landmark orientation. We videotaped scorpions to learn whether they return to their burrows by the same path they use as they exit, or whether they use a different route. The answer to this question could help eliminate some of the candidate stimuli from consideration. We used pole-mounted infrared surveillance cameras that relayed images to a digital recorder to monitor and record the movements of sand scorpions (*Paruroctonus utahensis*) near Monahans, Texas. Two-hour recording blocks of two animals on two consecutive nights revealed that the animals spent most of their time at the thresholds of their burrows, usually emerging briefly after an arthropod walked by. In each case, the scorpions took a looping path that did not retrace the route by which they exited their burrows. In additional experiments we used small lures to seismically entice scorpions from their burrows and monitored their movements as they returned to their burrows. These studies and other observations suggest that many of these sand scorpions do not spend much time on the sand surface; instead, they wait at the threshold of their burrows and ambush prey that wanders nearby.

Introduction

Previous ecological studies have documented scorpion activities on the surface at night (Bradley, 1988; Kaltsas et al., 2008; Polis, 1979, 1980; Shachak & Brand, 1983). In general, it appears that for most of the year, sand scorpions live solitary lives, emerging from their burrows soon after sunset, and settling into a sit-and-wait behavior until a potential prey item walks nearby. Some time later, they return to their home burrows. However, studies of the precise spatio-temporal movements that scorpions make in the context of understanding their sensory neurobiology are lacking. Furthermore, many of the previous studies used ultraviolet light and the scorpion's natural fluorescence to document animal position and movement. Since scorpion eyes are sensitive to UV light (Fleissner & Fleissner, 2001), this method probably influences the animal's behavior. The main question I ask here is: how do scorpions find their way home?

Scorpions have many sensory structures that could be useful for guiding them to their burrows (Fig. 1a). For example, scorpions have lateral and medial eyes that are physiologically sensitive to starlight levels (Fleissner & Fleissner, 2001) and photoreceptive elements in their tail

(Rao & Rao, 1973; Zwicky, 1970) allowing the potential for direct vision of their burrow or orientation to local landmarks or star patterns. They have elaborate mid-ventral chemosensory organs called pectines (Cloudsley-Thompson, 1955; Foelix & Müller-Vorholt, 1983; Gaffin & Brownell, 1997, 2001; Wolf, 2008) and multiple taste hairs on their leg tarsi (Foelix & Schabronath, 1983; Gaffin et al., 1992), either or both of which could be used to track self-made chemical trails back to their burrows (Melville et al., 2003). In addition, various other sensilla can transduce mechanical energy. Mechanosensory hairs on the tarsi (Foelix & Schabronath, 1983) could identify footstep patterns that lead back to the burrow. Trichobothria (Hoffmann, 1967; Messlinger, 1987) on the pedipalps are sensitive to minor air currents and perhaps even subtle pressure changes around a burrow entrance. Scorpions use basitarsal compound slit sensilla on their legs to detect the seismic disturbances of small arthropods in sand up to a half-meter away (Brownell, 1977). This opens the possibility that a scorpion could detect its own vibrations reflecting off of rocks and other objects, with the absence of a return cue signifying its burrow (Stephens, 2000). Scorpions also have humidity-sensitive tarsal organs (Gaffin et al., 1992) and putative thermo-

sensitive constellation arrays on their pedipalps (Fet et al., 2006), which could track temperature and/or humidity gradients radiating from their cool, moist burrows (Bradley, 1988).

There are still more ways to find home. Geomagnetic information could be used to find a burrow; however, no study suggests scorpions detect magnetic fields. Path integration based on memory of number of footsteps and turns, as shown for some ant species (Müller & Wehner, 1988; Wittlinger et al., 2006), is another possibility. Finally, an innate turning tendency could set an animal on an inward spiral leading to interception with its burrow, not unlike the orientation behaviors of displaced slugs (McFarume, 1980) or the slow search flights of disoriented bees (Menzel et al., 2005).

This study provides clues about what stimuli scorpions might use to relocate their burrows. As portrayed in Fig. 1b, different paths back to the burrow would argue for the use of different cues. We used infrared videography to record the movements of two female desert sand scorpions, *Paruroctonus utahensis* (Vaejovidae) for two-hour blocks on two consecutive nights as they emerged from and returned to their native burrows. I found that these scorpions did not return to their burrows on the same path that they emerged, suggesting they may use stimuli other than chemical or footprint trails. I also found that scorpions waited in the thresholds of their burrows, emerging for brief surface excursions only after insects walked nearby. I corroborated this idea by enticing scorpions from their burrows using simple seismic lures. This observation prompted a review of our scorpion collection data from a previous year and offered the possibility that the traditional method of using UV light to find and collect scorpions may affect their behavior and bias our perspective of scorpion surface ecology.

Methods

2009 Videotaping

I used pole-mounted infrared surveillance cameras wirelessly connected to a DVD recorder to monitor and record the evening activity of two female sand scorpions (*Paruroctonus utahensis*) on the evenings of March 20 and 21, 2009 in Monahans Sand Hills State Park (near Monahans, Texas). I used portable UV LED flashlights (Streamlight Flashlights) to locate the animals, which were within 50 meters and to the west of my research trailer (Scamp trailer) parked at campsite number 21 (Fig. 2a). I found the scorpions inside their burrow entrances about 30 min after sunset (sunset was 20:03 on March 20 and 20:04 on March 21). The burrows were on slight slopes ($< 5^\circ$) and in open sand, but within a meter of vegetation.

I mounted two Swann Wireless NightHawk Day/Night Security Cameras on 3.05 m long, 2.54 cm diameter, galvanized metal poles (Fig 2b,c). I inserted one end of the hollow pole about 0.5 m into the sand and downhill from the burrow for support, and angled the pole to a height of about 1.5 m above the scorpion burrow. I powered the cameras using heavy-duty extension cords connected to 120 V outlets at the base campsite. The cameras transmitted video (and audio) wirelessly to a receiver unit (Swann) mounted on the outside of the Scamp trailer (Fig. 2d). The receiver, which toggled between the two cameras every four seconds, was connected to a DVD recorder (Magnavox ZC320MW8) inside the trailer and to a small video monitor (Fig. 2e). The video produced a 90 cm diameter field of view centered on the scorpion burrow (Fig. 2f). Recordings began at 20:50 on March 20 and 20:35 on March 21.

Once the cameras were set, I moved away from the area and did not disturb the burrows or the area, except for one instance, near the end of the second night of filming. At this time, an assistant placed a freshly caught cricket near the burrow of scorpion 1 to see if this would entice the animal from its burrow. It did, and I have included these movements in the set of excursions described in Fig. 4.

Weather conditions based on recordings from sensors posted within the park (US Climate Reference Network: TX Monahans 6 ENE - Sandhills State Park) were as follows. On March 20, air temperature ranged from a low of 12.6°C at 4:10 to a high of 26.4°C at 15:10, surface temperature ranged from a low of 10.4°C at 4:00 to a high of 32.6°C at 17:00, and average hourly wind speed ranged from 2.19 to 6.52 m/s. At the time of recording (21:00), the air temperature was 20.1°C, surface temperature was 17.1°C, and wind speed averaged 4.56 m/s, gusting to a maximum of 7.82 m/s. On March 21, air temperature ranged from a low of 15.0°C at 7:45 to a high of 26.9°C at 15:35, surface temperature ranged from a low of 13.0°C at 8:00 to a high of 35.4°C at 14:00, and average hourly wind speed ranged from 1.70 to 6.33 m/s. At the time of recording (21:00), the air temperature was 20.1°C, surface temperature was 16.8°C, and wind speed averaged 5.13 m/s, gusting to a maximum of 8.24 m/s. There was no precipitation on either day. The moon was a waning crescent (32% on March 20, 23% on March 21) but set well before nightfall (14:37, March 20; 15:34, March 21).

To plot the movements of each scorpion and all intruding animals, I captured frames from the recordings at one-second intervals. Since the cameras toggled every four seconds, I had to extrapolate animal positions between views; the movements were slow and deliberate enough that I am confident I captured the correct tra-

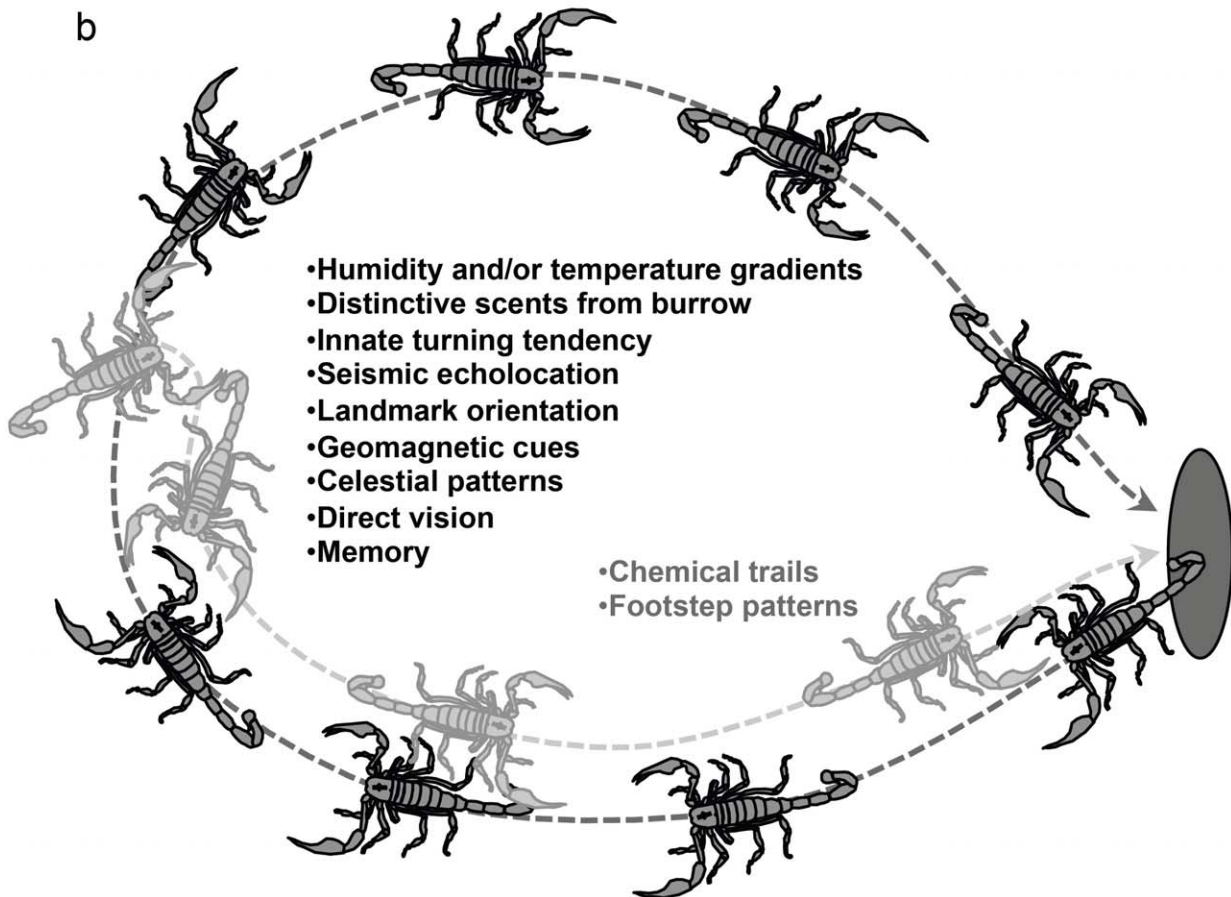
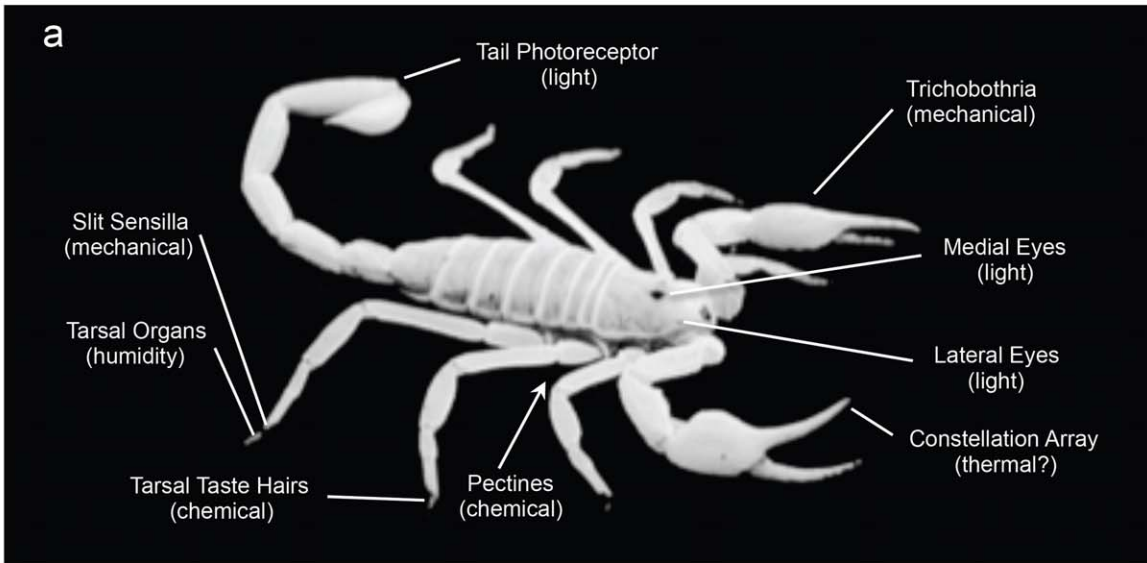


Figure 1: Cue clues. **a.** Major scorpion sensory organs and the modalities to which they respond. **b.** Different return routes suggest the use of different stimuli.

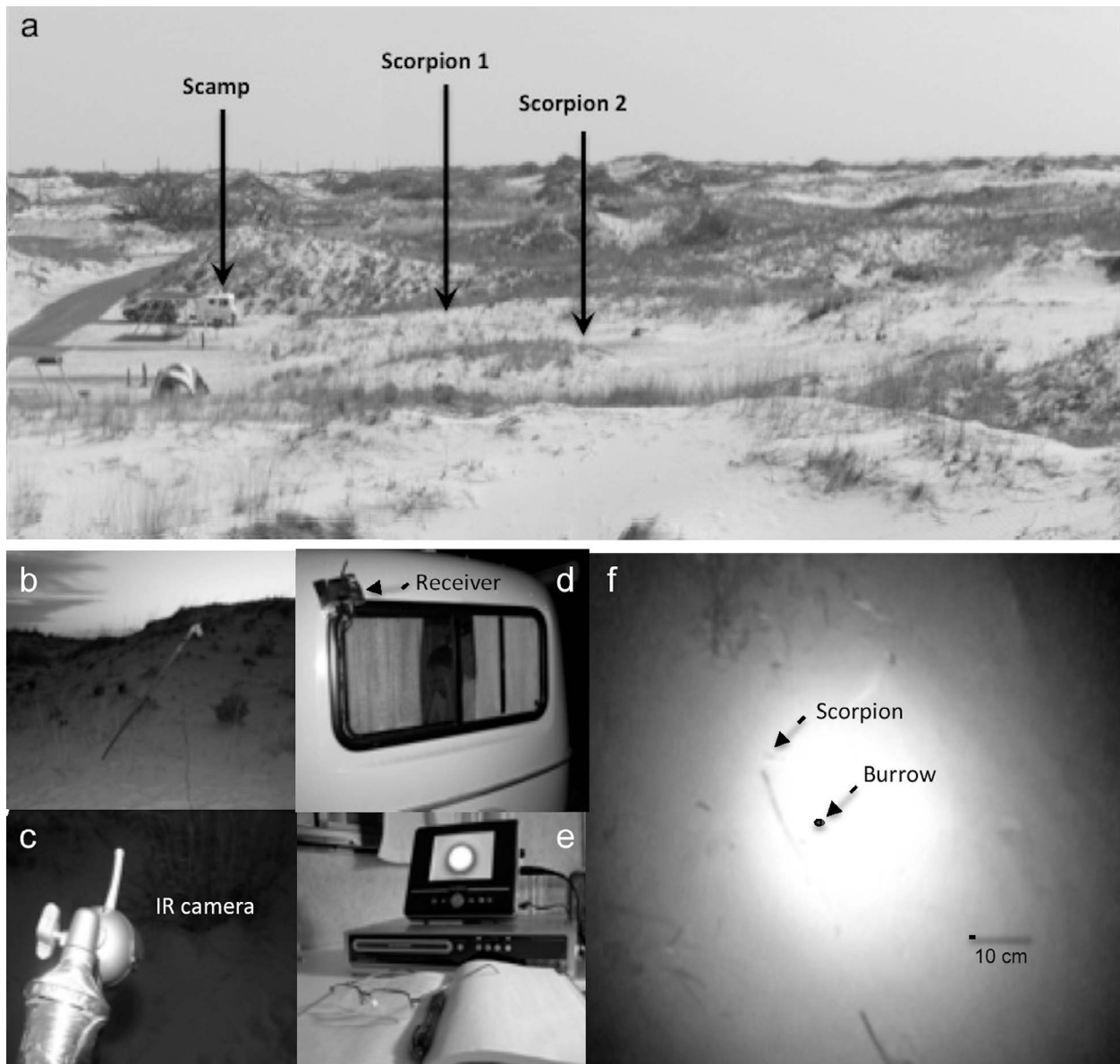


Figure 2: *In situ* videotaping of scorpions. **a.** The relative positions of the Scamp base trailer and the two scorpion burrows. **b.** IR camera mounted on metal pole inserted in sand and positioned above burrow. **c.** Close-up of IR camera. **d.** Video receiver mounted on back of base trailer. **e.** Inside trailer showing video monitor and DVD recorder. **f.** Still frame of IR video of scorpion outside of its burrow.

jectories and that this extrapolation had little to no effect on the analysis.

2011 Videotaping

In these experiments, conducted on March 13 and 15, 2011, I videotaped scorpions from above while coaxing them from their burrows using a small lure. The lure was simply a small 2 x 2 cm piece of duct tape folded across the end of a meter-long strand of dental floss. As before, I located animals at the threshold of

their burrows soon after sunset and carefully positioned a video camera over the area, centered on the burrow. In this set of filmings I used a Defender SP301-C infrared video recording system. The cameras were connected via coaxial cable to the recording unit and the image did not toggle between views, as did the Swann system used in 2009. To improve the image resolution, I covered the IR lights on the video capture camera with duct tape and used the IR lights from a second camera to flood the field of view from a side angle at a distance of about 3 meters. Videos were played back frame-by-frame and

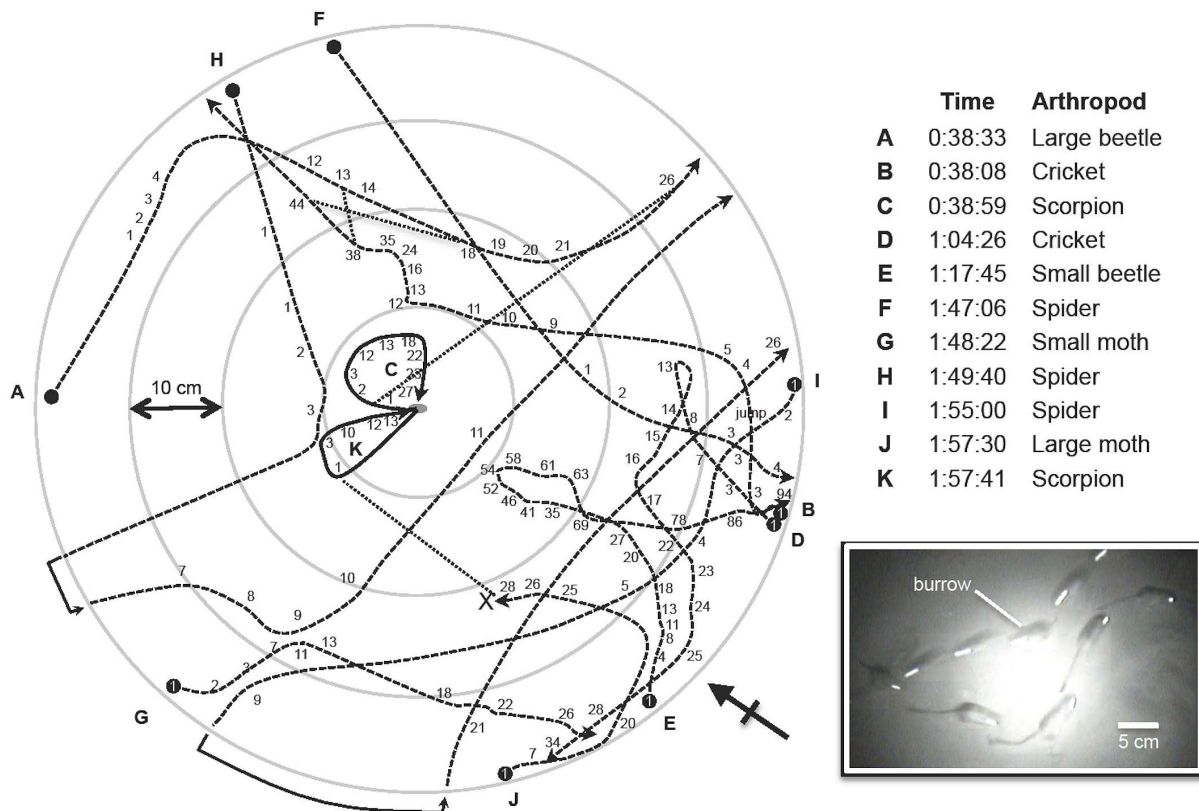


Figure 3: Scorpion emergence relative to traffic around the burrow. Shown are tracings of paths taken by all animals moving within 40 cm of scorpion 2's burrow during the 2 hr surveillance on night 1. The key shows the beginning time of each animal's path. The small numbers on the paths indicate time, in seconds, after the beginning of the movement into the region. Scorpion 2 emerged from its burrow twice (excursions C and K). The fine dotted lines indicate the time and location of other animals at the moment of scorpion emergence. The inset shows a composite photo of a kangaroo rat's movements near scorpion 2's burrow on the second night of filming; the top path occurred about 35 minutes into the filming, the lower path 82 minutes later. Each path took less than 2 seconds to complete. Both arrows are 10 cm long; the direction arrow points north. Upslope is toward the top of figure.

the movements of the lure and the scorpions were plotted every few seconds.

2008 Collecting Trip

On March 15, 2008, I participated in a collecting trip with three lab members shortly after sunset. We collected from an area 24 km SE of Monahans, in the same dune system as Monahans State Park. Three of us walked a broad swath searching for adult animals with our LED UV flashlights (Streamlight), while the fourth recorded the GPS coordinates of each animal detected using a handheld GPS unit (Garmin). The weather conditions for March 15, 2008 (based on recordings from the Monahans State Park sensors) were as follows. Air temperature ranged from a low of 7.7°C at 7:00 to a high of 27.5°C at 16:30, surface temperature ranged from a low of 5.0°C at 7:00 to a high of 42.9°C at 15:00, and

average hourly wind speed ranged from 1.86 to 5.65 m/s. At the time of collecting (21:00), the air temperature was 21.9°C, surface temperature was 17.2°C, and wind speed averaged 5.13 m/s, gusting to a maximum of 10.09 m/s. There was no precipitation that day. Sunset was at 20:00. The moon was waxing and 64% illuminated; moonrise was at 14:04 and moonset was at 4:04 the next morning.

Results

2009 Videotaping

A lot of activity occurs on the sand surface around a scorpion burrow. Fig. 3 shows the paths of all animals that walked within 40 cm of scorpion 2's burrow during the two-hour block on the night of March 20. Scorpion 2 emerged twice during this 2-hour block (excursions C

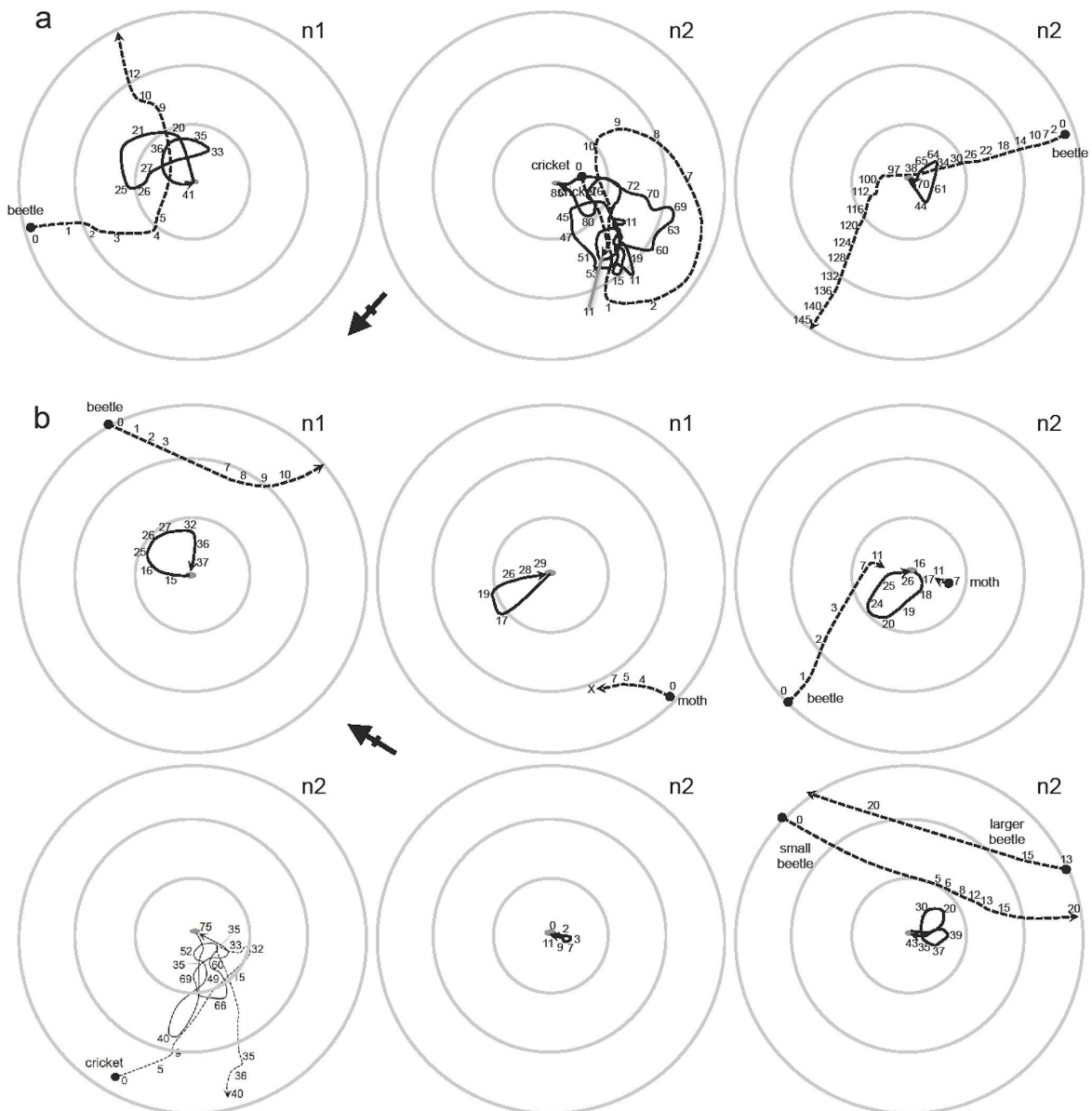


Figure 4: Scorpion excursions. **a.** Scorpion 1 excursions. **b.** Scorpion 2 excursions. n1 = night 1 excursions; n2 = night 2 excursions. Arrows are 10 cm long and point north. Upslope is toward the top of the figures. All scorpion 1 and 2 excursions, except scorpion 2's third excursion on night 2, occurred within seconds of an arthropod passing. A cricket, placed near the burrow of scorpion 1, elicited excursion 1 on night 2.

and K). Excursion C was apparently induced by either a large beetle (path A) or cricket (path B). Excursion K was apparently induced by a large moth walking toward the burrow. The moth flew (indicated by "X" at end of plot J) soon before the scorpion emerged. Not all arthropods induced the scorpion to emerge from its burrow. For example, scorpions did not emerge for spiders (paths F, H, I), which moved considerably faster than the other arthropods. Scorpion 2 did not emerge after a kangaroo rat hopped over its burrow twice on night 2 (Fig. 3, inset).

In all, the scorpions emerged from their burrows nine times during the 8 hours of filming (Fig. 4). Scorpion 1 emerged once on night 1 and twice on night 2. Scorpion 2 emerged twice on night 1 and four times on night 2. Eight of the nine scorpion excursions occurred shortly after an arthropod passed by on the surface (emergence latency: mean 7.1 s; standard deviation 5.3 s; median 7.0 s; range 0-13 s). For the eight arthropods that elicited scorpion emergence, the closest approach was an average of 9.1 cm from the burrow (standard deviation 6.9 cm; median 6.5 cm; range 2-21

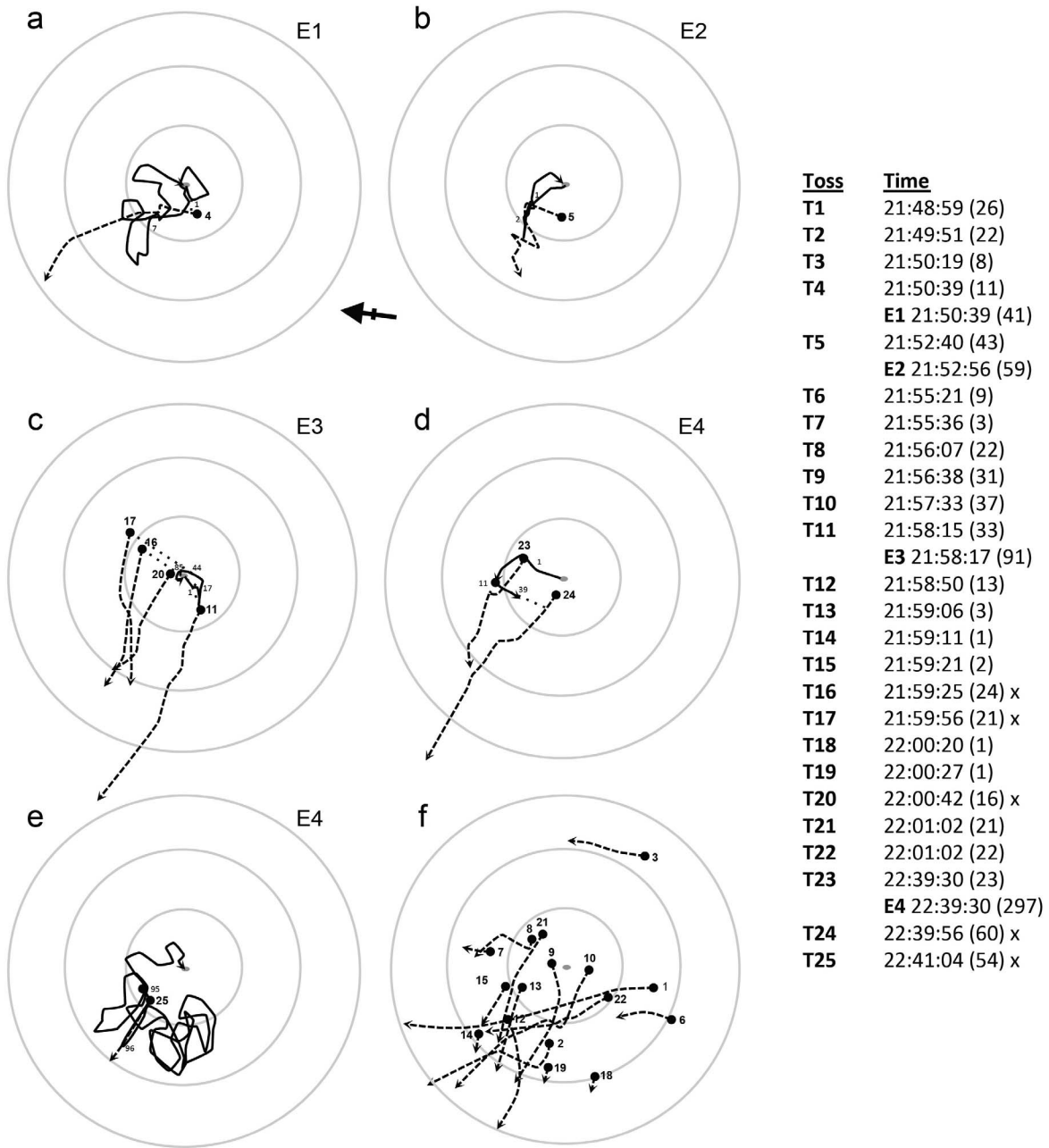


Figure 5: Lured excursions. Twenty-five tosses of a small lure were made across the span of about an hour; times of tosses are indicated at right and the movement of the lure after each toss is shown in the figures at left. The duration of the dragging of the lure is indicated in parentheses next to the time. The arrowhead at the end of each tracing indicates the point where the lure was lifted from the sand surface. The scorpion was coaxed from its burrow on four separate occasions. These excursions are depicted in parts a-e and indicated as E1-E4 in the time list at right. Part f shows all tosses that did not induce scorpion movement. Sometimes the animal reacted to subsequent tosses while away from its burrow; these tosses are indicated with an “x” next to its time and the interaction between the movement of the lure and the movement of the animal is indicated by fine dotted lines on figures c-e (the very small numbers indicate the time in seconds of the excursion at which the interaction occurred). The arrow is 10 cm long and points north; upslope is toward the top of the figures.

cm). None of the excursions resulted in prey capture. Each scorpion returned quickly to its burrow (excursion durations: mean 26.2 s; standard deviation 20.0 s; me-

dian 23 s; range 10-74 s). The total duration of scorpion excursions was 242 s, which represents only 0.8% of the 8-hour observation period. In each case, the scorpions

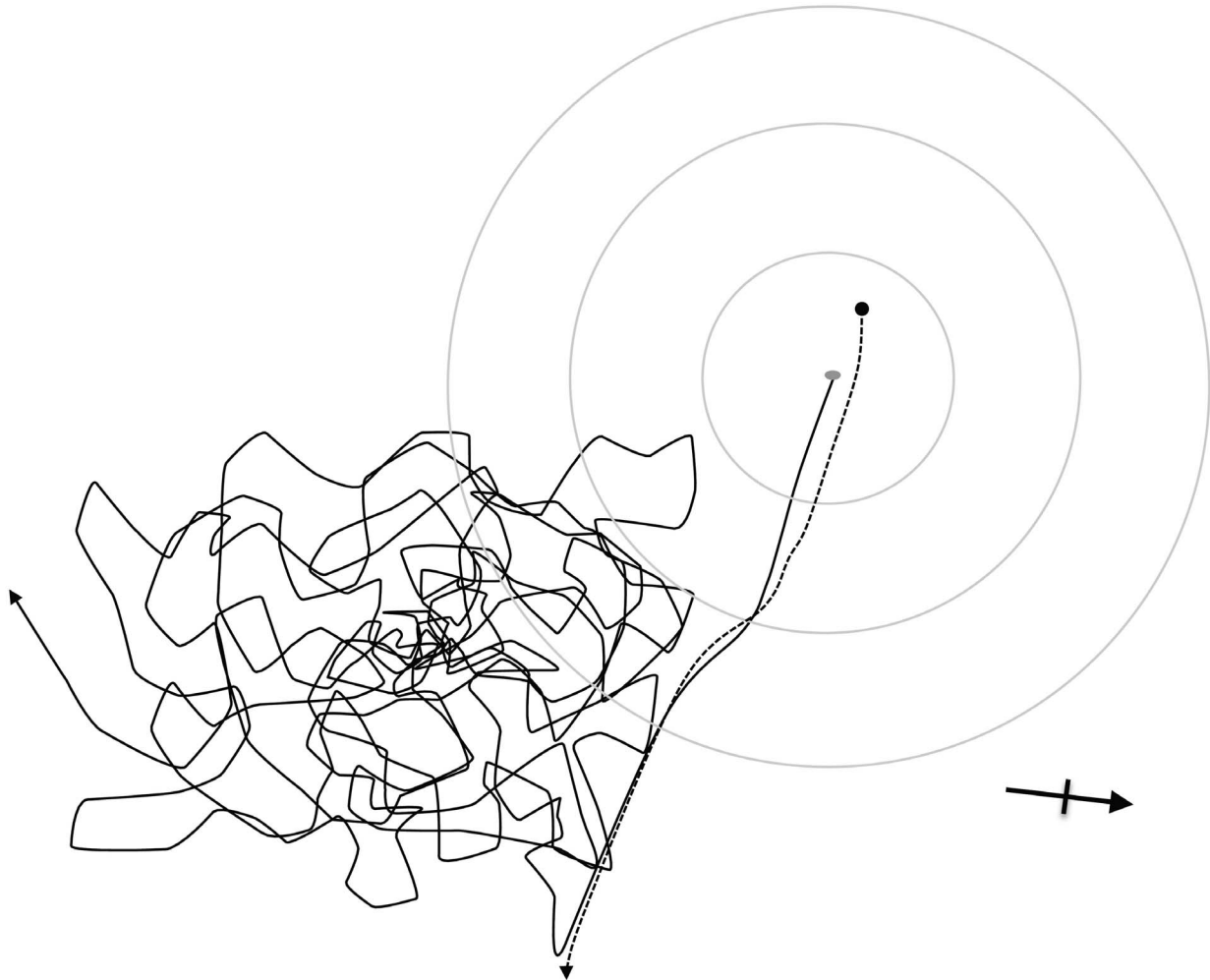


Figure 6: Scorpion movement after being displaced from its burrow. The scorpion in this lured experiment grabbed the floss as it moved past its burrow and was dragged about 50 cm away from its burrow in the direction of 7 o'clock. The excursion began at 21:14:12 and lasted almost 32 minutes. The scorpion did not relocate its burrow and walked off the screen to the left as indicated by the arrowhead. The arrow is 10 cm long and points north; upslope is toward the top of the figure.

took looping paths that did not appear to retrace the route by which they exited their burrows.

Two of the excursions deserve special mention. The first excursion of night 2 for scorpion 1 (which was in the final 10 minutes of the 2-hour film block) occurred after we placed a cricket near the animal's burrow. The cricket walked in a loop around the area, and on the second pass, the scorpion quickly emerged and nearly caught the cricket. Their tussle carried the two about 20 cm from the burrow within the first second of struggle (between seconds 10 and 11 of the moth's excursion). In addition, the third excursion of night 2 for scorpion 2 was notable in that it was not preceded by any apparent arthropod surface activity. This excursion lasted 11 seconds and took the animal only 5 cm from its burrow.

2011 Videotaping

Animals can be enticed from their burrows with small lures dragged near their burrows to create a small seismic disturbance that presumably mimics a small arthropod walking nearby. Figure 5 shows the result of several tosses of a small lure near to a scorpion waiting at the threshold of its burrow. Of the twenty-five tosses, the animal was drawn out on four distinct occasions. The proximity of the toss appears correlated with animal emergence, with tosses within 10 cm being most effective. Once emerged, this scorpion again tended to take looping versus direct routes back to its burrow. The only emergences observed were immediately following the passing of the lure; no emergences were seen in the

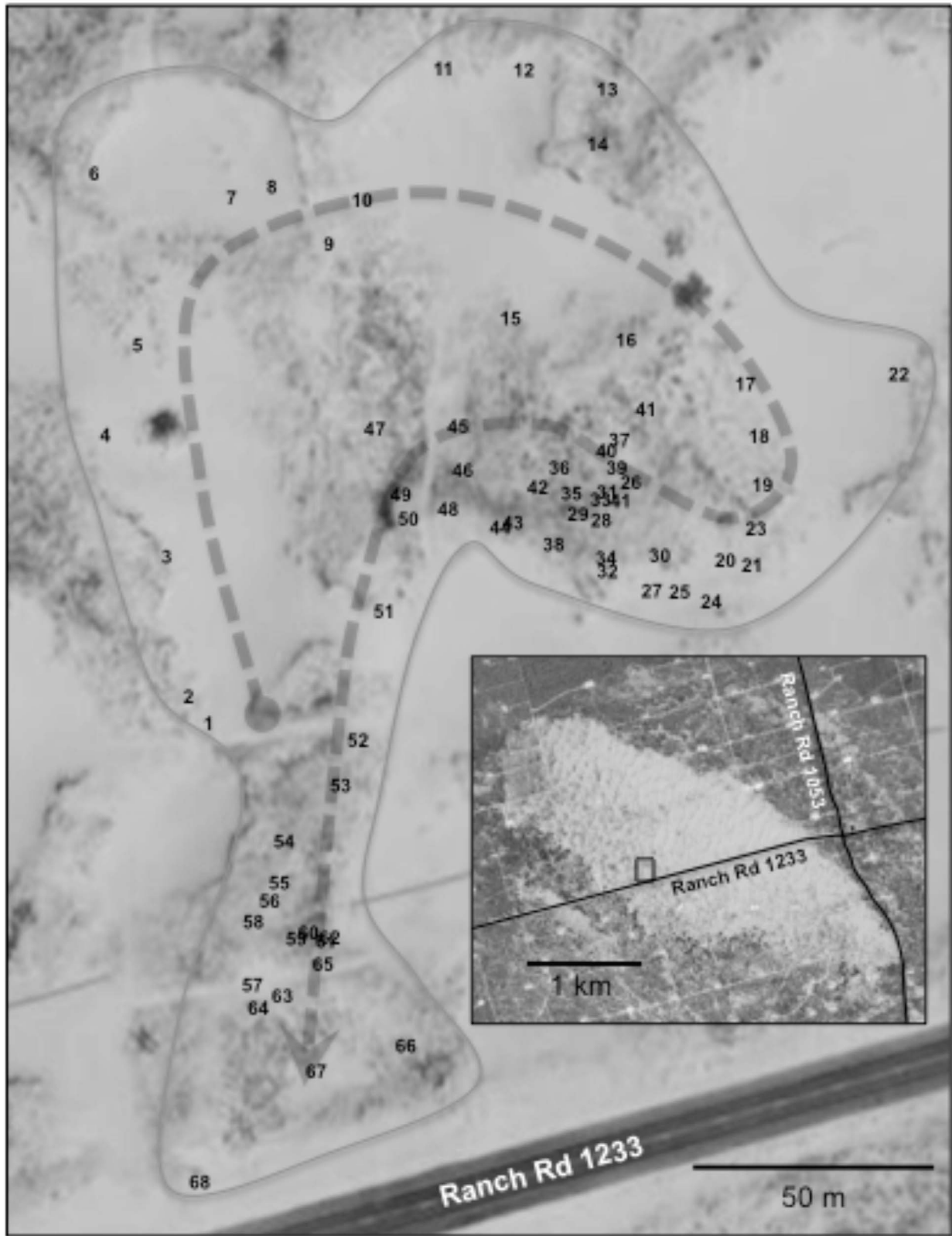


Figure 7: *P. utahensis* collected on March 15, 2008 from sandy area about 24 km SE of Monahans, TX. Three people collected for 1.5 hr and GPS coordinates were taken for each adult located (animal captures are indicated by numbers on photo). The first animal was found at 2030. A total of 68 adults were found; the area of coverage was approximately 2.26 hectares. Total adult scorpion surface density was approximately 30.1 scorpions/ha. The dashed line indicates the general path of the survey crew.



Figure 8: Scorpion at burrow threshold. A female *P. utahensis* near the Scamp trailer is photographed at the opening of her burrow under UV light on March 21, 2009.

45 minutes following the sequence of tosses, even though one insect walked within 10 cm of the burrow.

In another filming an animal grabbed the string lure and was quickly pulled approximately 50 cm away from its burrow (Fig. 6). The locomotory path of the animal after releasing the lure is interesting. It made tight looping tracks centered on an area about 20 cm uphill and slightly to the left of its release point. The loopings became more spread out with time until the animal eventually walked completely out of the screen to the left. After about 20 minutes I relocated the animal a few meters to the left of the field of view and placed it about 10 cm immediately below its burrow. It remained motionless for about five minutes and then walked directly to and entered its burrow.

2008 Collecting Trip

The tendency for these animals to wait in the threshold of their burrows and make short excursions in pursuit of prey prompted me to examine the results of a previous spring collecting trip within the same dune system. Fig. 7 shows the locations of the animals caught during this survey. In all, we found 68 adult animals in 1.5 hours while covering an estimated 2.26 ha; this

equates to about 30.1 adult *P. utahensis* per hectare detected on the sand surface.

Discussion

The videos suggest that scorpions may rely on cues other than self-produced chemical trails or footstep patterns to guide their near-range return to their burrows. Also, the videos and other unrecorded observations suggest that these scorpions may not spend much time on the sand surface. While unsuccessful in prey capture, the scorpions in these recordings waited in the threshold of their burrows in ambush of prey that happens to wander nearby. I presume the scorpions are using seismic cues (Brownell, 1977, 2001) to detect walking arthropods and discerning the vibration patterns of potential prey (beetles, crickets, moths) from other animals (spiders, kangaroo rats).

If scorpions aren't retracing their footsteps or deposits, how do they get home? While there are several possibilities, temperature/humidity gradients and vision seem to be the most plausible hypotheses, based on known sensory structures. Scorpions have sensitive humidity detectors (tarsal organs) on the dorsal side of

each of their eight tarsi (Foelix & Schabronath, 1983; Gaffin, et al., 1992). Furthermore, they have constellation arrays at the tips of their pedipalps (Fet et al., 2006) that appear sensitive to slight changes in temperature (Gaffin, unpublished data). These sets of organs are ideally situated to sample and discriminate subtle gradients in temperature and/or humidity. *P. utahensis* live in areas where the sand surface can reach $>50^{\circ}\text{C}$ during the day. However these scorpions make deep, spiral burrows where the microclimate remains cool and moist below the surface (Bradley, 1988). Subtle humidity and temperature gradients therefore must radiate from the burrow. Since the sand surface is usually drier than the burrow, humidity should decrease with horizontal distance from the burrow. The direction of temperature flux would change depending on time of day. Although the burrow is cooler than the sand surface by day, the temperatures invert through the night. Bradley (1988) found that the mean burrow temperature was 30°C in midsummer and varied in amplitude only $7\text{--}10^{\circ}\text{C}$ through 24 hrs while the mean nocturnal surface temperature was 20°C in midsummer but varied in amplitude by 20°C . This means that immediately after sunset, the surface temperature is higher than that of the burrow, but as the surface cools with nightfall, the burrow becomes warmer relative to the surface. The resulting temperature gradient would diminish with distance from the burrow. Taken together, in the normal active time of *P. utahensis*, both temperature and humidity gradients fall with distance from the burrow. Furthermore, the amplitude of temperature fall and temperature-induced airflow should intensify as the night progresses.

In addition, vision may help guide a scorpion to its burrow. In the sandy, sparsely vegetated dune habitat, few obstructions block a scorpion's ability to see the entrance to its home burrow. The medial and lateral eyes of scorpions are sensitive to the intensity and wavelengths of starlight (Fleissner & Fleissner, 2001). Moreover, the location of the medial eyes at the top of the prosoma would seem to suggest a panoramic view of the surroundings. Knowledge of scorpion vision, however, remains sparse. The few existing studies on scorpion visual orientation have been carried out in laboratories. Abushama (1964) found that scorpions avoid light and have poor vision, but the study conditions did not mimic the scorpions' natural habitat. In other behavioral studies, scorpions tended to move toward darkened walls of arenas (Camp & Gaffin, 1999) and avoided some wavelengths more than others (Blass & Gaffin, 2008). No published studies, however, address the question of whether scorpions use vision in homing. The displaced scorpion shown in Fig. 6 tends to argue against the use of direct vision to locate the burrow. For example, in one foray the animal moved within 12 cm, and in direct line sight of its burrow, only to turn away

and return to the area of its previous erroneous search. This observation suggests the animals may employ an innate turning tendency search strategy in conjunction with some means of burrow identification.

During the two nights of the 2009 recordings, as well as the nights leading up to the filmings, my crew and I witnessed many scorpions waiting in the thresholds of their burrows. Figure 8 is a picture of one of these scorpions, which was within 3 meters of our trailer. We learned that we could easily entice this animal from its burrow by disturbing the nearby sand with a small stick to simulate an insect. In the 2011 season I found I could readily coax animals from their burrows using small lures. This threshold-waiting behavior seems to be a fairly common strategy for this population of scorpions, at least during this time of year.

From various accounts of sand scorpion ecology, the general impression is that these animals are mainly "sit-and-wait" predators that move some distance from their burrows, spread their legs out, and wait (perhaps for hours) for prey to betray themselves with their footsteps (Brownell, 1977; Polis, 1979, 1980). Moreover, nearly every *P. utahensis* I have collected in the field with a UV light has been motionless and away from its burrow. A few summers ago, however, I tried something different. When I located a motionless scorpion with my UV flashlight, I quickly turned off my light and turned on a video camera equipped with IR night vision. In each case, the animal remained motionless for about a minute under the IR, but then started moving. Most found a burrow within 30 seconds (Gaffin, unpublished data). Because scorpion eyes are sensitive to UV light (Fleissner & Fleissner, 2001), it is possible that the intense luminance of my UV flashlight temporarily inhibited the locomotion of these dark-adapted animals. Alternatively, these animals may have been still before I arrived and my intense light switched them into "go home" mode once the danger passed.

The implication is that our traditional method of observing and collecting scorpions in the field with UV lights may greatly affect scorpion behavior and ultimately our interpretation of their surface activity. Some "back of the envelope" calculations are in order. If the amount of time spent on the surface for the two animals videotaped in this study is typical for the population at large, then the 30.1 adults per hectare we found in our 2008 trip may be a gross underestimate of the actual surface activity that evening. Let us assume that all of the animals we detected during the 2008 survey were interrupted during one of their brief pre-chasing excursions and were "frozen" by our lights. Dividing the 30.1 adults per hectare by 0.008 (from the 0.8% surface time calculated above) suggests 3,763 total adults per hectare. It is interesting that Polis (1990) estimates community-wide scorpion density in arid ecosystems averages more than 3,200 individuals/ha. In

our survey, however, we ignored juveniles, which would have further increased our overall population estimate. On the other hand, our survey was not a single snapshot of the density, but rather spanned 1.5 hours and involved non-random movements by three collectors. Further, the very nature of casting our lights with the intention of finding animals probably biases our numbers upward.

Nevertheless, it is provocative to think that our experimental methods might jade our view of these animals. One simple way to test the hypothesis that our UV collecting lights are suspending animal movements during their brief excursions is to retrace a given area several times rather than move to new areas as we typically do during our collections. The prediction would be that the number of animals caught would not diminish significantly with each pass. The idea is that each pass freezes animals in the midst of a prey-chasing excursion. With each new pass, a new batch of animals would be caught during their prey-chasing excursions. If the animals were already sitting on the sand when we passed with our lights, then, after removing these animals, subsequent passes should yield far fewer animals.

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References

ABUSHAMA, F. T. 1964. On the behavior and sensory physiology of the scorpion *Leiurus quinquestriatus*. *Animal Behavior*, 12: 140–153.

BLASS, G. R. C & D. D. GAFFIN. 2008. Light wavelength biases of scorpions. *Animal Behaviour*, 76: 365–373.

BRADLEY, R. A. 1988. The influence of weather and biotic factors on the behavior of the scorpion (*Paruroctonus utahensis*). *Journal of Animal Ecology*, 57: 533–551.

BROWNELL, P. H. 1977. Compressional and surface waves in sand: used by desert scorpions to locate prey. *Science*, 197: 479–482.

BROWNELL, P. H. 2001. Sensory ecology and orientational behaviors. Pp. 159–183 in Brownell, P. H. & G.A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

CAMP, E. A. & D. D. GAFFIN. 1999. Escape behavior mediated by negative phototaxis in the scorpion *Paruroctonus utahensis* (Scorpiones, Vaejovidae). *Journal of Arachnology*, 27: 679–684.

CLOUDSLEY-THOMPSON, J. L. 1955. On the function of the pectines of scorpions. *Annals & Magazine of Natural History*, 8: 556–560.

FET, V., M. E. SOLEGLAD, M. S. BREWER, D. P. A. NEFF & M. L. NORTON. 2006. Constellation array in scorpion genera *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis* (Scorpiones: Vaejovidae). *Euscorpius*, 41: 1–15.

FLEISSNER, G. & G. FLEISSNER. 2001. Night vision in desert scorpions. Pp. 317–324 in Fet, V. & P. A. Selden, eds.). *Scorpions 2001; In Memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.

FOELIX, R. F. & G. MÜLLER-VORHOLT. 1983. The fine structure of scorpion sensory organs. II. Pecten sensilla. *Bulletin of the British Arachnological Society*, 6: 68–74.

FOELIX, R. F. & J. SCHABRONATH. 1983. The fine structure of scorpion sensory organs. I. Tarsal sensilla. *Bulletin of the British Arachnological Society*, 6: 53–67.

GAFFIN, D. D. & P. H. BROWNELL. 1997. Response properties of chemosensory peg sensilla on the pectines of scorpions. *Journal of Comparative Physiology A*, 181: 291–300.

GAFFIN, D. D. & P. H. BROWNELL. 2001. Chemosensory behavior and physiology. Pp. 184–203 in Brownell, P. H. & G.A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

- GAFFIN, D. D., K. L. WENNSTROM & P. H. BROWNELL. 1992. Water detection in the desert sand scorpion *Paruroctonus mesaensis* (Scorpionida, Vejovidae). *Journal of Comparative Physiology A*, 170: 623–629.
- HOFFMANN, C. 1967. Bau und Funktion der Trichobothrien von *Euscorpius carpathicus* L. *Zeitschrift für vergleichende Physiologie*, 54: 290–352.
- KALTSAS, D., I. STATHI & M. MYLONAS. 2008. The foraging activity of *Mesobuthus gibbosus* (Scorpiones: Buthidae) in central and south Aegean archipelago. *Journal of Natural History*, 42: 513–527.
- McFARUUME, I. D. 1980. Trail-following and trail-searching behavior in homing of the intertidal gastropod mollusc, *Onchidium verruculatum*. *Marine and Freshwater Behaviour and Physiology*, 7: 95–108.
- MELVILLE, J. M., S. K. TALLAROVIC & P. H. BROWNELL. 2003. Evidence of mate trailing in the giant hairy desert scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae). *Journal of Insect Behavior*, 16: 97–115.
- MENZEL, R., U. GREGGERS, A. SMITH, S. BERGER, R. BRANDT, S. BRUNKE, G. BUNDRÖCK, S. HÜLSE, T. PLÜMPE, F. SCHAUPP, E. SCHÜTTLER, S. STACH, J. STINDT, N. STOLLOFF & S. WATZL. 2005. Honey bees navigate according to a map-like spatial memory. *PNAS*, 102: 3040–3045.
- MESSLINGER, K. 1987. Fine structure of scorpion trichobothria (Arachnida, Scorpiones). *Zoomorphology*, 107:49–57.
- MÜLLER, M. & R. WEHNER. 1988. Path integration in desert ants, *Cataglyphis fortis*. *PNAS*, 85: 5287–5290.
- POLIS, G. A. 1979. Prey and feeding phenology of the desert sand scorpion *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *Journal of Zoology*, 188: 333–346.
- POLIS, G. A. 1980. Seasonal patterns and age-specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. *Journal of Animal Ecology*, 49:1–18.
- POLIS, G. A. 1990. Ecology. Pp. 247–293 in Polis, G.A. (ed.). *The Biology of Scorpions*. Stanford, California: Stanford University Press.
- RAO, G. & K. P. RAO. 1973. A metasomatic neural photoreceptor in the scorpion. *Journal of Experimental Biology*, 58: 189–196.
- SHACHAK, M. & S. BRAND. 1983. The relationship between sit and wait foraging strategy and dispersal in the desert scorpion, *Scorpio maurus palmatus*. *Oecologia*, 60: 371–377.
- STEPHENS, A. V. 2000. *Seismic echolocation: do scorpions use this novel method of orientation to aid in locomotion?* Undergraduate Honors Thesis, University of Oklahoma.
- WITTLINGER, M., R. WEHNER & H. WOLF. 2006. The ant odometer: stepping on stilts and stumps. *Science*, 312: 1965–1967.
- WOLF, H. 2008. The pectine organs of the scorpion, *Vaejovis spinigerus*: structure and (glomerular) central projections. *Arthropod Structure & Development*, 37: 67–80.
- ZWICKY, K.T. 1970. Behavioral aspects of the extraocular light sense of *Urodacus*, a scorpion. *Experientia*, 26: 747–748.