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Sand scorpion home burrow navigation in the laboratory

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Summary

Many organisms can navigate their return to a previously experienced location. This ability is beneficial and often a necessary component of an organism's life strategy. Sand scorpions (*Paruroctonus utahensis*, Vaejovidae) typically leave their home burrows at night and subsequently return, suggesting navigational capabilities. Sand scorpions present an ideal system for navigational study in that they exist in ecologically simple dune environments, are abundant, are easily obtained, are easily maintained in the laboratory, and fluoresce under ultraviolet light. Additionally, behavior observed in the laboratory is generally consistent with that observed in the field, allowing comparable laboratory and field study. The work presented in this paper is a laboratory setup in which scorpions successfully navigate to their established home burrow. The ability to induce scorpion navigation in a laboratory setting will be useful in future study. Using this design, scorpion navigation can be assessed when navigational cues are present absent or manipulated.

Introduction

Navigation to a previously experienced location is an ability that has independently evolved throughout the zoological taxa. Convergent behavioral evolution across phylogenetically distinct taxa suggests an associated selective advantage. Undoubtedly, the ability to return to a desirable location such as a good food source, a successful mating location, or a site of refuge is advantageous.

Several different navigational mechanisms have been described in a variety of organisms. Many of these studies have focused on various arthropods owing to their large radiation and consequent, diversity of navigational abilities (for review see Wehner, 1992). Arthropods are model organisms for study in that they offer a variety of mechanisms to study in nearly every habitat.

Psammaphilic scorpions are ideal for navigational study in that they are abundant, easy to obtain, and easily maintained in the laboratory, and they live in environments which are comparatively ecologically simple. Among their most spectacular features is that they fluoresce under ultraviolet light, providing a built-in tracking mechanism for these nocturnal animals.

Although behavioral studies of scorpions are rare, the desert scorpion *Smeringurus mesaensis* (Stahnke, 1957) (Vaejovidae) occurring in the Mojave Desert of southern California has been the focus of several behavioral studies. These scorpions leave their home burrows at night to forage and subsequently return to the same burrow, suggesting navigational capabilities (Polis et al., 1985). Females and immature males use the same home burrow for long periods and may travel several meters away, although they typically remain within a meter of their burrow (Polis et al., 1985).

The sand scorpion *Paruroctonus utahensis* (Williams, 1968) (Vaejovidae) is a related species with a largely similar niche. These scorpions live in sandy burrows in shifting sand environments throughout Chihuahua (Mexico), northern Arizona, New Mexico, Utah, and western Texas (Sissom, 2000). Numerous field observations have indicated that *P. utahensis* scorpions exhibit similar homing behavior (Gaffin, pers. comm., pers. obs.). Following a disturbance, scorpions usually remain motionless for a brief period of time and then move short distances with intermittent pauses and frequent directional changes. This behavior occurs for a brief period of time (30 sec-5 min) and is followed by a rapid movement to the burrow with only minor deviations from a direct path. Complementing its homing ability, prior study of sand scorpion behavior has shown that behavior observed in the laboratory is generally consistent with that observed in the field, allowing comparable laboratory and field study (Gaffin & Brownell, 2001). These characteristics make *P. utahensis* a model organism for navigational study.

To understand how sand scorpions navigate to their home burrow, we must determine which environmental cue(s) they exploit for directional information in their home bound journey. We aim to design in a system in which scorpion navigation can be successfully induced in the laboratory. Once such a system is established, navigational ability can be reassessed with manipulated and/or deleted sensory cues. A loss of navigational ability in the absence or manipulation of a particular environmental cue will suggest dependence.

Methods

Scorpion collections and care

Paruroctonus utahensis specimens were collected from Winkler County Park northeast of Kermit, Texas, in fall of 2003 and summer of 2004. Scorpions were maintained in the laboratory with temperature ranging from 78-86°C with relative humidity ranging from 35%-45% and a light-dark phase of 2000-0700 h dark and 0700-2000 h light. Scorpions were housed in 3.8 L glass jars containing approximately 4 cm sand from their collection site and a broken piece of flowerpot clay. Scorpions were routinely fed crickets and given water in the form of a diffuse spray which lightly moistened the sand surface.

Home burrow navigation experiments

Experimental arenas: Experiments were conducted using 15 individual circular arenas, each with a diameter of 76 cm and a height of 30.5 cm. Arena bottoms were constructed of medium density fiberboard, and the sides were composed of translucent acrylic. Each arena floor was covered with 4 cm sand from the collection site. A hanging 20-watt 120-volt halogen light was positioned 60 cm above the center of each arena. The lights were set to a light-dark phase of 1700-0400 h dark and 0400-1700 h light. A cylinder (15 cm diameter and 8 cm tall) was positioned at random along the outer wall of each arena (Fig. 1). These cylinders were used to confine scorpions to a small portion of the larger arena. A broken piece of flowerpot was placed in the middle of each cylinder to encourage scorpion burrow formation.

Experimental preparations: Six days prior to each experimental trial, a recently fed scorpion was placed inside each home cylinder and allowed to form a home burrow. Two days prior to each trial, the cylinders were removed, allowing the scorpion to explore the remainder of each arena at will. Each afternoon before the burrow lights turned off, the sand within each burrow arena was lightly sprayed with water, providing the surface texture conductive to burrow formation.

Experimental procedure: Experiments occurred in the laboratory at the University of Oklahoma in summer of 2004. Prior to trial, scorpions were removed from each arena and placed individually in black film canisters.

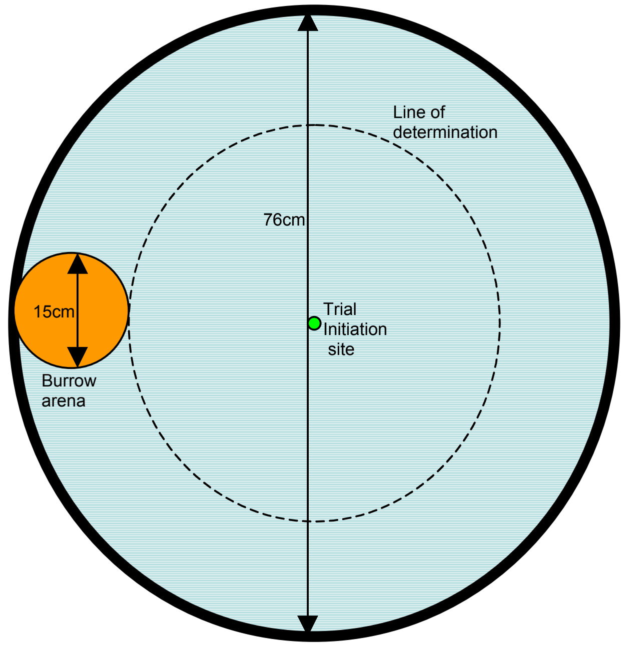

Fig. 1: Circular test arena including the removable burrow arena, site of trial initiation, and line of determination marking directional choice.

Each canister was rotated 360° five times and placed in the middle of each respective arena for at least 5 minutes. Arena sand was not disturbed, allowing any potential visual or chemical cues to remain, but arena lights were dimmed to encourage scorpion movement. Trials began immediately after film canisters were removed, leaving scorpions in the center of each arena. Scorpion activity was videotaped using a Sony Digital Video Camera Recorder (DCR-TRV 120) suspended from the ceiling on a rope pulley system in nine separate filming sessions, each session filming the activity in one or two arenas at a time. The camera's infrared Night Shot capability was used during recording due to the dim lighting. The camera was connected to a color television monitor in the adjacent room for immediate viewing by the experimenters. Scorpion directional choice was observed when the animal crossed an imaginary line delimiting a circle, 46 cm in diameter, in the center of each arena (Fig. 1). Trials ended as this line was crossed.

Analysis: Scorpion directional choice was quantified using a Batschelet test for circular uniformity (Zar, 1999). This test was used to determine if the initial chosen walking direction was uniform about the arena or if there was a bias in the mean walking direction in relation to the home burrow. Direction was quantified by comparing the center of the cylinder area (normalized to 0°) with the position that the scorpion crossed the circular line of determination. Scorpions that crossed the line of determination within 22.5° of the cylinder area center (1/8 of the total arena circumference) were considered to be within the burrow area.

Results

Thirteen of fifteen scorpions formed burrows within the cylinders (or within the area of the cylinders after day four after cylinder removal) during the six allotted days prior to trial. These observations were made each afternoon while spraying the cylinder areas with water (arena lights were on). Scorpions that did not form burrows were consistently found on top of the piece of flowerpot in the cylinder area throughout the six-day period. Two days prior to trial, all scorpions were found within the burrow-cylinder area, including those that did not form burrows.

Trials were run to elicit home burrow navigation after displacement to the center of the arena. Upon trial initiation, most scorpions remained motionless in the center of their arena for one minute to two hours. Two scorpions quickly ran to the side of the arenas as soon as the film canisters were lifted. These trials were removed from the analysis because the rapid movement was a presumed panic response and not a reliable measure of directed movement. Two scorpions did not move after two hours and were also removed from the analysis. Upon the initiation of movement, the remaining scorpions crossed the line of determination within 43 s. Two basic movement patterns were observed (Fig. 2). Some scorpions initiated a series of turns and pauses before making a more directed movement across the line of determination, whereas others initiated movement with one directed movement that took them across the line of determination.

Eleven legitimate trials yielded five scorpions that crossed the line of determination within 22.5° of the cylinder center (0°, the center of the home cylinder). Batschelet test for circular uniformity indicated that directional choice is not uniformly distributed about the circle and that it is concentrated around 0° (V=0.007, (n=11) (Fig. 3).

Discussion

This design evolved from several preliminary experiments. Initially, directional choice was obtained using rectangular choice chambers. Trials were initiated by placing the scorpion in the center of the rectangular chamber and observing their directional choice, toward or away from the side with their given burrow. The series of turns and pauses associated with movement onset coupled with the thigmotaxic nature of the scorpion rendered inconclusive directional choice. Scorpions commonly hit the arena wall while turning and followed the edge to the corner.

In preliminary tests using circular arenas with a diameter of 76 cm, scorpions were able to make multiple turns in the center of the arenas without hitting the walls. Consequently, scorpions commonly moved toward their burrow after a series of uninterrupted turns and pauses. Additionally, behavior observed during preliminary tests suggested that scorpions may be more loyal to their burrow if they are self-made rather than provided. It was also determined that the burrow forming cylinder must be clear and at least ten cm in diameter, otherwise

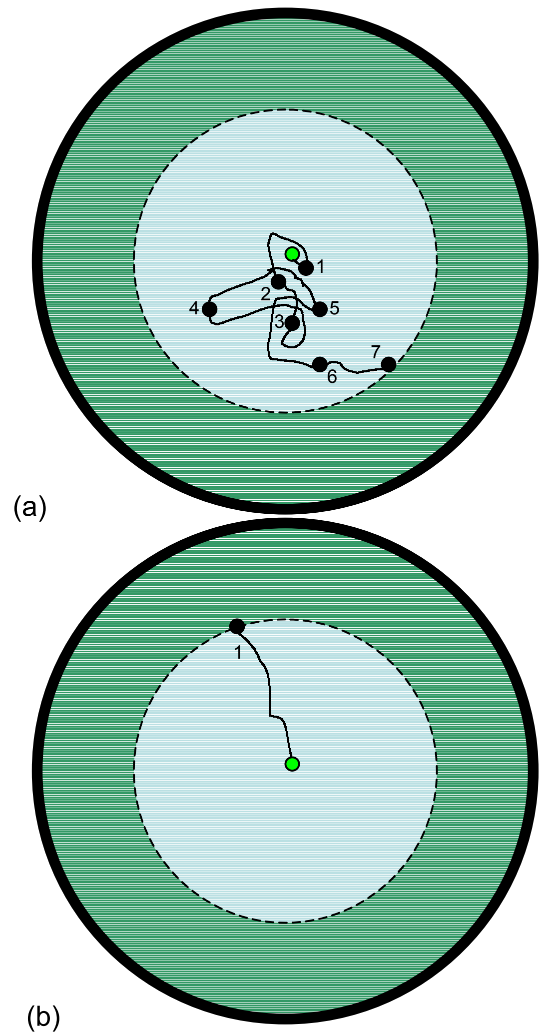

Fig. 2: Typical scorpion movements during trials. Black dots represent scorpion position at five-second intervals. (a) A series of turning and pausing before a seemingly directed movement across the line of determination (b) An initial seemingly directed movement across the line of determination.

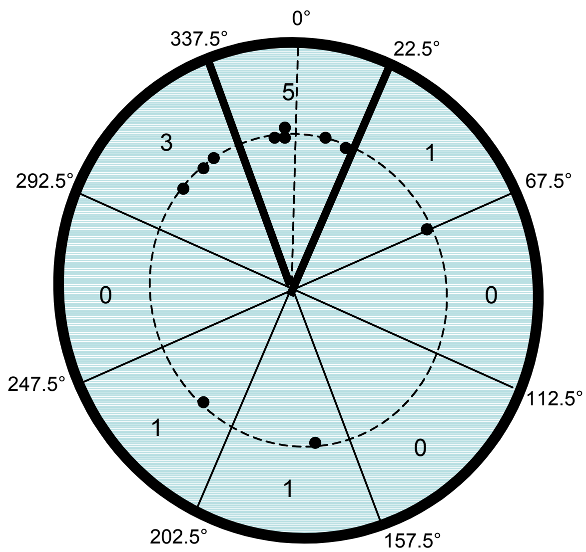

Fig. 3: Circular test arena divided into 45° sections with the burrow cylinder section outlined. The black dots indicate the positions where scorpions crossed the line of determination during experimental trials. The number in each section represents the frequency of scorpion crossing. Note that five of the eleven tested scorpions crossed the line of determination in the section containing the burrow and four additional scorpions crossed in adjacent sections.

most scorpions were not stimulated to form their own burrow.

In this study, *P. utahensis* scorpions exhibited nonrandom directional choice. Furthermore, directional choice was concentrated near the region of the established home burrow. Available cues including light, the Earth's magnetic field, chemical gradients, and humidity gradients may have influenced directional choice. These cues were provided to aid scorpion navigation in attempt to establish a system where it can be observed in the laboratory. These data suggest that scorpions were able to orient themselves in their arenas and navigate towards their home burrows using one or more sensory cues available in the laboratory. These data do not imply that any specific cue or cues present facilitate navigation.

The mechanisms underlying scorpion navigation are currently in the beginning stages of study, thus hypotheses must be formed from information obtained from taxonomically close organisms and from what is known about scorpion sensory systems.

Vision is a likely sensory mechanism used in navigation. Scorpions may use vision to observe landmarks, follow footsteps to retrace their outbound journey, or to potentially use light polarization patterns in navigation. The median and lateral eyes are ocelli bearing a single lens with a few photoreceptors (Locket, 2001). Ocelli are effective in determining light intensity but less capable of allowing shape determination, especially at greater distances. Thus, scorpions may be able to use nearby landmarks or visual cues such as footprints in navigation, but the use of distant landmarks is unlikely. Many arthropods are able to detect light polarization patterns, most notably bees and ants (for review see Wehner, 1997). It has been observed that the microvilli within the rhabdoms are arranged uniformly, and some rhabdomeres occur with differential microvilliar orientation (Locket, 2001). These structures may allow scorpions to exploit polarized light as a navigational tool (Brownell, 2001).

Scorpions possess several sensory structures receptive to chemosensory stimuli, most notably the pectines, which hold many pore-tipped peg sensilla (Gaffin & Brownell, 2001). The ventromedial position of these pectines facilitates contact, and therefore direct chemoreception, between the sensilla and the substrate. Additional chemoreceptive pore-tipped sensilla are common to the mouthparts, chelicerae and distal regions of appendages in arachnids (Foelix, 1985). Contact chemoreception of female chemical deposits has been observed in males of scorpion *Centruroides vittatus* (Buthidae) (Krapf, 1986; Gaffin & Brownell, 1992; Steinmetz et al., 2004). Perhaps similar detection of chemical deposits laid in the sand substrate on the outbound journey provide a chemical trail that the scorpion can follow home.

Detection of moisture and humidity is crucial to desert dwelling sand scorpions. Gaffin et al. (1992) provided evidence that chemoreceptive tarsal hairs detect substrate moisture. Additionally, Abushama (1964) concluded that organs on scorpion tarsi detect humidity. This humidity detection has been associated with the tarsal organ of scorpions, similar to the spider tarsal organ (Foelix & Schabronath, 1983). Prior to experimental trials, scorpion burrows areas were sprayed with water daily. The burrows were sprayed for the last time 24 hours before trial initiation. After trial completion, a HOBO Pro Series device was placed in the burrow area to monitor the level of humidity about the burrow. The HOBO was placed in the burrow for 24 hours, sprayed with the normal amount of water, and removed 24 hours later. Data recorded from the HOBO indicated that relative humidity about the burrow area returned to the initial burrow area humidity (42% RH) within three hours of spraying water (97% RH). These data indicate that a potential humidity gradient established from burrow area moistening had dissipated well before trial initiation, thus it is unlikely that scorpions followed a humidity gradient to their burrows.

It is possible that scorpions are using other environmental cues, including the Earth’s magnetic field, which may aid path integration. Evidence exists for magnetic orientation in several arthropod species, although it has not been shown to be a useful cue in path integration (Nørgaard et al., 2003).

The laboratory design presented here provides a controlled system that can be used to isolate and manipulate potential navigational cues. For instance, controlling the presence, intensity, polarization and wavelength of available light, or providing a fresh sand substrate, or locally disrupting the magnetic field in future trials will provide evidence for the use (or lack thereof) of specific environmental cues in navigation.

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