2020. Journal of Arachnology 48:1–25

REVIEW

Arachnid navigation – a review of classic and emerging models

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Abstract. Most arachnids are central-place foragers that return to retreats or burrows after excursions to hunt. In general, arachnids are relatively large and accessible to behavioral and physiological investigations, and in several cases the animals have special sensory structures that facilitate homing. Here we review the mechanisms used by non-arachnid walking animals to return to specific sites and compare them to what is known for several groups of arachnids. Much of what we know about path integration, in which an animal estimates the angle and distance of a homeward vector using information gathered during an outbound journey, has been gleaned through systematic behavioral experiments on spiders. We focus on the most heavily studied spider models, highlighting the methodology used to deduce various aspects of the path integration machinery. We also highlight some work being done on longer range spider navigators, and emerging work with other arachnid groups. We provide additional thoughts concerning the evolution of homing systems and suggest promising leads for further investigation.

Keywords: Homing, path integration, scene familiarity, sensory physiology, autonomous navigation

INTRODUCTION

Overview.—Arachnids are becoming important in understanding animal navigation due to their behavioral and physiological adaptations for returning to retreats and burrows. In this review, we first briefly cover why the study of animal navigation is important and argue for the importance of arachnids in this field. We then define terms to be used in the remainder of the review. We start our organismal focus with highlights of common navigational model systems such as birds and bees, but since arachnids do not fly, we subsequently focus on walking animals. Finally, we discuss in detail navigational work with arachnids, both their current and potential contributions to the study of navigation, along with some genetic and evolutionary considerations of homing.

Note that researchers in the broad field of navigation do not uniformly employ the same terminology for similar behaviors. Depending on the authors, most of the studies explored in this review might categorize certain behaviors not as navigation but as homing or another goal orientation behavior; this review generally uses the broader term *navigation* as an overall description of how animals "know" where to go as they move from one place to another.

Why is animal navigation important?—There is enormous and growing interest in technologies that allow robots, drones, cars and people to navigate to a given point. Indeed, the size of the global autonomous vehicle private ownership market is expected to grow from about $8 billion in 2020 to over $60 billion by 2030 (Frost & Sullivan 2018). Robots and drones are increasingly used in recovery missions in disaster situations (Floreano & Wood 2015; Arokiasami et al. 2016; Jorge et al. 2019), and augmented sensory technologies are being developed to assist visually impaired individuals navigate safely and efficiently both indoors (Kacorri et al. 2018) and outdoors (Lin et al. 2018). Efficient navigation strategies will also be crucial for reconnaissance in novel environments (such as unexplored planets) where local features are not yet mapped, GPS systems are not in place, and rovers must accurately return to a given point for refueling and transmitting information (Fink et al. 2017).

Most, if not all, of these emerging navigational technologies have been inspired either directly or indirectly by studies of animal models (Floreano & Wood 2015; Giakos et al. 2018; van Dalen et al. 2018). While learning the intricacies of animal navigation has obvious translational benefits, it is also crucial for filling in gaps in our understanding of animal biology and evolution. While prokaryotes and eukaryotes other than animals are capable of movement through ciliary action (Witman 1990), plasmodial extensions (Preston & King 2005), tissue growth (Liscum et al. 2014), and various propagules (Kinlan et al. 2005), it is in Kingdom Animalia that we find specialized contractile tissues (muscle) and networks of communication cells (neurons) that enable adaptive, longer-ranged, whole-body movements that are integrated with fast acquisition and processing of environmental information. With increased movement, the ability to return to a given point or area has clear selective advantage. Animals of all sorts build nests (Heyman et al. 2019), dig burrows (Zeil 1998; Hemmi & Zeil 2003), or use various retreats or common areas to rear their young, ambush prey, elude predators, and maintain appropriate physiological conditions.

Why arachnids?—Much has been learned about the specific mechanisms used by animals to return to a point, and arthropods have contributed mightily to this wealth of information. In fact, in his eminently readable, though somewhat critical, chapter in the book *Animal Homing*, Wehner (1992) highlights examples from across the phylum. Among the 74 species of homing animals that he noted were 51 insects and 16 crustaceans (13 of which were decapods), but only seven arachnids. Furthermore, of the insects, all but three were hymenopterans. The exceptional navigational feats of bees and ants have been scrutinized for centuries and much has been deduced about how they use both self-centered

(egocentric) and habitat-centered (geocentric) sources of information to return to critical locations (Wittlinger et al. 2006; Müller & Wehner 2010). However, significant controversy remains about the specifics; see, for example, the pointed discussions in *The Proceedings of the National Academy of Sciences* (Cheeseman et al. 2014; Cheung et al. 2014).

While bees and ants have been useful, they do have severe limitations. Their small size and fast movements make tracking and physiological investigations difficult. In contrast, many arachnids are large and long-lived. They don't fly; they walk, and not too far, which facilitates precise spatial-temporal mappings of their movements. Some groups, such as amblypygids (Hebets et al. 2014b; Bingman et al. 2017), tarantulas (Janowski-Bell & Horner 1999), and larger scorpion species (e.g., *Pandinus* Thorell, 1876, *Hadrurus* Thorell, 1876, or *Centruroides* Marx, 1890: Bibbs et al. 2014a, b), can wear harness transmitters without overtly affecting their movements. Scorpions even have the special property of fluorescence under ultraviolet light (Stachel et al. 1999), which allows for easy collection and tracking of activity. Almost all arachnids are terrestrial, which is of obvious advantage to human investigators; some decapod crustaceans have exceptional navigational and sensory abilities (Boles & Lohmann 2003; Kamran et al. 2019), but their aquatic habitats hinder observation and manipulation. Many arachnids adapt well to captivity and are amenable to laboratory behavioral investigations. Furthermore, some arachnids are equipped with not only exceptional visual capabilities (notably, jumping spiders and wolf spiders), but also ornate specialized organs that transduce information in the chemical (gustatory) and mechanical (tactile) domains. Among the most impressive examples of the sensory organs are the specialized first legs of amblypygids (Foelix 1975; Igelmund 1987; Hebets & Chapman 2000) and uropygids (Moro & Geethabali 1985; Geethabali & Ramamohan 1989), the pectines of scorpions (Foelix & Müller-Vorholt 1983; Gaffin & Brownell 1997a; Kladt et al. 2007), and the malleoli of solpugids (Brownell & Farley 1974; Sombke et al. 2019). Some of these systems have been traced morphologically to the brain (Brownell & Farley 1974; Igelmund 1987; Wolf 2008; Wiegmann et al. 2016), and because of the ease and stability of some of these preparations to electrophysiological recording, are yielding useful functional information (Knowlton & Gaffin 2011) that is difficult to acquire in other animal systems. With increased awareness, the number of arachnid navigational models is likely to increase significantly compared to those noted in Wehner's 1992 account.

Clarifying the navigation and homing vocabulary.—It is important to have a consistent set of terms to help us describe and understand various homing/navigation phenomena. Unfortunately, there is still considerable disagreement about the exact mechanisms that animals use to return to a goal, and this leads to confusion over terms. Papi (1992) classifies homing based on six categories, which we have summarized in Table 1: (1) random or systematic search, (2) genetically based orientation, (3) trail following, (4) route-based orientation, (5) pilotage, and (6) true navigation.

Of these six categories, three are not relevant to this review. Genetically based navigation relies on directional information passed through the generations (e.g., G_1 going east and G_2 going west in Table 1), such as demonstrated for migratory birds (Liedvogel et al. 2011) and does not appear pertinent to the short-range movements of arachnids. Trail-following involves retracing a physical trail left during an outbound journey. Although many spiders follow draglines back to a point, that simple form of navigation is not included in this review. Pilotage involves the concept of a mental or cognitive map and can be demonstrated by return to a goal after displacement (symbolized by "d" in Table 1) to unfamiliar territory. This form of homing occurs in vertebrates but has not been conclusively demonstrated in arthropods, including arachnids (Wehner 1992; Collett 2019).

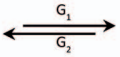
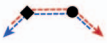
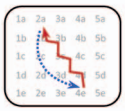
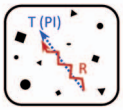
The remaining three categories – random/systematic searches, route-based orientation, and true navigation – occur in arachnids and deserve additional explanation. Random/systematic searches involve alternating movements in turns and straight lines, forming ever-widening circles that might intersect with the goal (Wehner & Srinivasan 1981). Animals that are confused will revert to this strategy even if they also use other navigation strategies. Later sections of this review describe several examples of this innate search strategy.

Route-based orientation includes three subcategories, as shown in Table 1. Route reversal implies the use of landmarks learned during an outbound journey to return to a goal. Vertebrates do it but its use is debated in arthropods. Course reversal involves simply reversing the animal's outbound direction, whereas path integration incorporates both distance and direction back to a point as acquired through the outbound journey. Path integration is explored in more detail in the next section of this review; it is well studied and prevalent in arachnids.

True navigation is subdivided into grid-based and map-based navigation. Grid-based navigation, which relies on physical or chemical gradients, may occur in large-scale movements of vertebrates but seems unlikely to be useful in the short-range movements of arachnids. In map-based navigation, the images in an original training path (T in Table 1) are acquired via path integration (PI). These images are subsequently retraced (R) when the animal returns to its original location. This type of navigation is pertinent to arachnids, especially if the definition of "map" is expanded beyond the day-to-day sense of the word to include matrices of information of various sources, including visual, chemical, and textural cues. Readers may notice some overlap between route-based orientation and true navigation. Papi's use of these terms is not always consistent with current hypotheses explaining arthropod navigation. In particular, navigation by scene familiarity contains elements of both categories. The considerations in deciding where scene familiarity best fits and some thoughts related to the term "landmark" are explored along with the description of this navigation strategy in the subsection entitled "Scene familiarity versus landmarks" below.

Untangling path integration.—Many animals can home by dead reckoning, in which rotational and distance information gathered during an outbound journey is used to chart a course back to the start. Path integration can be thought of as the mechanisms used by the animal to account for the phenomenon of dead reckoning (Wehner 1992). We mainly use the term *path integration* in this review. Two crucial ingredients are needed for path integration. The first is the comparison and updating of the animal's own bearing to a remote, often

Table 1.—Summary of navigation-related terms. Abbreviations are summarized in text. (Adapted from Papi 1992.)

Category	Schematic	Information source
Random or systematic search		Innate
Genetically based orientation		Innate (genetic)
Trail following		Sensory (trail from previous journey)
Route-based orientation		
-- Route based reversal		Memory (retracing outward landmark series)
-- Course reversal		Memory (reversing outward direction)
-- Path integration		Memory (integrating distance and direction of each outward leg)
Pilotage		Sensory / memory (acquired cognitive map without compass)
True navigation		
-- Grid-based		Physical or chemical gradients
-- Map-based (includes navigation by familiarity)		Directly or indirectly acquired mosaic of local cues

global, external reference, such as Earth's geomagnetic field, starlight patterns, or polarized scattering of sunlight. The second is an estimate of the distance traveled as gleaned from some measure of the animal's own movement. A nice analogy is provided by Etienne et al. (in Healy 1998) in an explanation of early transoceanic navigation. The explorers used star patterns to update their boat's relative direction and gathered incremental velocity readings (judged by comparing their movement to a piece of tethered wood dropped overboard over a given time interval) to estimate their current position relative to their point of departure. A main question is: How do animals navigate back to a point without such detailed record keeping?

Scene familiarity versus landmarks.—The best-known early research on the use of landmarks in navigation in animals is Tinbergen's famous account of the digger wasp, *Philanthus* (highlighted in various sources, including Collett 1992). Tinbergen arranged pine cones around the insect's nest and displaced them while the animal was foraging. Upon its return, the insect searched around the pine cones instead of its nest. Subsequently, many laboratory-based studies have used prominent, strategically placed objects in clean-walled rooms to deduce insect guidance mechanisms (Cartwright & Collett 1987; Wehner 1992). The animal's search behaviors among the objects ("landmarks") have suggested navigational algorithms such as minimizing retinal mismatch between current views and memorized retinal snapshots of objects as viewed near the nest (Cartwright & Collett 1982, 1987). This idea of landmark recognition has been expanded to ideas on longer range navigation, somewhat similar to following landmarks by route reversal as described by Papi (1992).

However, in contrast with landmark recognition hypotheses — both at the goal and during route following — recent papers have explored the possibility of homeward guidance through localized movements towards familiar, pixelated, matrix-like scenes (similar to QR codes) acquired during initial homeward journeys via path integration (Collett & Zeil 1998; Webb 2019). In one model, deemed the *Navigation by Scene Familiarity Hypothesis* (NSFH) and proposed for long-distance homing in ants (Baddeley et al. 2011, 2012), pixelated panoramic scenes are stored as memories during goal-directed ventures, such as toward a feeding site or home. The initial set of goal-directed views is acquired through path integration. Then to recapitulate the original path, the animal scans left and right and moves in the direction of the most familiar panoramic scene to retrace its path back to a goal (Baddeley et al. 2012). Some interesting experiments have tested the relative use of panoramic scenes and distinct landmarks on the homing behavior of ants (Graham & Cheng 2009; Wystrach et al. 2011). In summary, the animals' searching behavior under a variety of tests argued against the use of distinct landmarks and more for the use of the panorama as a whole (of which landmarks are components).

CLASSIC MODELS

Overview.—We now briefly summarize the contributions of common model organisms in the study of navigation. We start

by comparing the suitability of various taxa for specific navigational questions. We then follow up with findings from commonly used taxa. This approach allows us to elaborate on the advantages and progress made using arachnids in the following section on arachnid models.

How navigational cues are used, in general, is divided between vertebrates and invertebrates; use of path integration occurs in both groups but evidence for cognitive maps is only convincing in vertebrates. Pigeons (summarized in Papi & Wallraff 1992; Wiltschko 1997) and rats (Thinus-Blanc 1996; Schenk et al. 1997) use maps in homing and navigation but little evidence exists for the use of maps in invertebrates. Bees, wasps, and ants use path integration (Wehner 1992; Collett 2019) and scene familiarity (Collett & Zeil 1997; Lehrer 1997; Baddeley et al. 2011, 2012). Invertebrate model systems such as these will be more comparable to arachnids and perhaps more useful in robotic algorithms because of their fast acquisition of environmental information for long-range navigation.

Each animal taxon offers its own advantages for navigational study depending on its natural history. Water striders, for example, are easy to rotate in experimental settings (Collett & Zeil 1998), but they lack homing to a goal, only use orientation cues, and exist on a two-dimensional surface instead of three-dimensional terrain. Pigeons are excellent study systems for homing locally, and other avian species' migratory behaviors have been useful to researchers seeking to understand long-distance navigation cues (reviewed in Rozhok 2008:55–57). Maps are used in some birds (Kamil et al. 2001) and mammals (Collett et al. 1986) that cache food, but not all species share these traits as their life histories do not require such skills. However, many bird navigation feats can be difficult to study in the lab, typically require institutional approval for vertebrate studies as well as national and local regulations, and indeed often cross international boundaries (BBC News 2019).

Animals use a variety of cues in navigation often via multiple mechanisms. For example, many organisms use polarized light as a compass, but mechanisms of polarized light vision are not uniform among taxa (Wehner 2001). Similarly, vertebrates use the magnetic field's inclination; invertebrates instead use its polarity to orient their compasses (Walker 1997, p. 203). Cue importance can vary with age and learned experience. For example, pigeons rely on path integration earlier in life as shown by passive displacement experiments (Papi & Wallraff 1992; Rozhok 2008:123), but switch to maps (Rozhok 2008:123) and to a lesser extent visual landmarks (Papi & Wallraff 1992) with experience (Guilford et al. 1998). Similarly, the magnetic field can be used by older alligators (Rodda 1984), but they use dead reckoning earlier in life (Rodda 1985). In contrast, roaches use kinesthetic path integration at all ages, although the ability to use visual cues takes a few days to develop (Dabouineau & Rivault 1995). Bees learn the sequence of scenes (Chittka et al. 1995) so that they use cues at the appropriate place in their route.

As arachnids are unlikely to evolve flight before publication of this article (excluding their navigation-free silk ballooning), we will restrict the remainder of this section to walking animals capable of returning to a central point. Additionally, flying animals are difficult for human observers to track (Wehner 1992). We briefly summarize navigation and homing in walking animals by expanding on rodents and ants and by providing more details of work on amphibians (Amphibia) and fiddler crabs (Malacostraca, Decapoda, Ocypodidae, *Uca*). The taxa are presented in order of abundance of studies, i.e., the bulk of navigation work has been done on rodents, followed by ants, then amphibians, and we found the least literature on fiddler crab navigation. We will cover each taxon's advantages and disadvantages as a model system, compare it to arachnids, and address its known cues and mechanisms in navigation.

Rodents.—Rodents are a diverse group with many established systems in the laboratory (McKay & Persinger 2005) and in the field (Fisler 1962; Fluharty et al. 1976). Many species are large enough to be tracked with devices to determine the actual homing routes in the field (Bovet 1992). Genomes of 253 rodents have been sequenced (taxon search for Rodentia and genome in Benson et al. 2012), including the mouse (Mouse Genome Sequencing Consortium et al. 2002) which should aid understanding the genetic basis of navigational abilities.

Compared to arachnids, rodents evolved relatively recently, diversifying in the Tertiary after the origin of placental mammals in the Cretaceous (Douzery et al. 2003). Arachnids diversified at least a hundred million years earlier, in the Paleozoic (Jeyaprakash & Hoy 2009), providing a different timescale on which to evaluate evolution of navigational abilities.

Cues used by rodents are the magnetic field (mole rats: Kimchi et al. 2004; rats: McKay & Persinger 2005; reviewed in Rozhok 2008); landmarks or beacons (Joslin 1977; Alyan & Jander 1997) and celestial positions as visual cues (Kavaliers & Galea 1994); and kinesthetic cues (Etienne et al. 1993; Moghaddam et al. 1996). Many taxa can choose from multiple cues based on environmental and spatial conditions (Etienne et al. 1988; Séguinot et al. 1993; Alyan & Jander 1997; Deutschlander et al. 2003; Skinner et al. 2010). Studies of rodents have found that relative cue importance can vary by population and environmental heterogeneity (Etienne et al. 1993; Biegler & Morris 1996).

How homing occurs appears to vary by taxa. Most simply, deer mice and voles search for their goal via random walking (Bovet 1992:345) and thus do not use cues. Path integration is common in other rodents (Mittelstaedt & Mittelstaedt 1980; Etienne et al. 1988; summarized in Rozhok 2008:108–109), but abilities within path integration vary. Gerbils cannot account for passive displacement, but can account for disruptions to their route (Mittelstaedt & Glasauer 1991). Hamsters, gerbils, and mice can use landmarks (Teroni et al. 1987; Alyan & Jander 1997; Cheng & Spetch 1998). Rats use both landmarks and maps (Save et al. 1998; Cook & Tauro 1999) and can evaluate relational space in navigating (Thinus-Blanc 1996:28).

Ants.—Ants fly at the reproductive stage, but here we will discuss only non-volant stages in their life cycles. Ants are conveniently abundant and tractable in the lab and field, although they are too small to track individually with electronic devices currently available. Software in development may allow tracking of individuals by video in the lab (Dornhaus, no date). Several species of ants have genomes

sequenced (Smith et al. 2011a, b; Wurm et al. 2011), which have already provided insights into other, non-navigational behaviors (Bonasio et al. 2010; Suen et al. 2011). These results suggest that more work with ants on the genetic basis of navigation would be fruitful.

Ants have been used to model navigation but not all ant taxa may be suitable. The modeled behavior of *Cataglyphis* Förster, 1850 matches error patterns found in navigational tracks of other animals (Müller & Wehner 1988, 1994; Wehner & Wehner 1990) and has been adapted to tests with robots programmed with navigation models based on their behavior (Lambrinos et al. 1997). The eusociality of many ants provides a distinct aspect to their navigation relative to arachnids (in particular their use of pheromone track following), but a main model system, the desert ant (*Cataglyphis*), forages solitarily.

Cues used by ants are varied. Chemical trails (reviewed in Wehner 1992:69–77) are well known for ant navigation. Their use of visual cues (Ronacher & Wehner 1995) includes spectral gradients (Wehner 1997:152) and polarized light (Duelli & Wehner 1973; Wehner 1997) detected by specialized areas of their compound eyes (Wehner 1997:169). The geomagnetic field can be used in place of visual cues in at least one species (Fleischmann et al. 2018). Kinesthetic cues for distance in path integration can be motor (Wittlinger et al. 2006) or optic (Ronacher & Wehner 1995; Collett & Collett 2017). Finally, gravity may be used in uneven terrain (Wohlgemuth et al. 2001, 2002; Grah et al. 2005). Some species can switch from chemical to visual cues with experience (Harrison et al. 1989), from light to chemical cues (Hölldobler 1971), and among types of visual cues (Wehner 1997).

Like bees, ants use path integration as part of their navigational toolbox (Müller & Wehner 1988), as well as landmarks (Collett et al. 1992) via matching multiple scenes retinotopically (Judd & Collett 1998). The use of cognitive maps is considered unlikely (Wehner 1992). Ants show some sophistication, incorporating scene familiarity (Wehner 1992:74) in their homing, especially near the nest (Wehner et al. 1996; Collett & Zeil 1998); matching skylines for long-distance navigation (Wehner et al. 1996); and ignoring landmarks that appear in the wrong place relative to their route (Wehner et al. 1996).

Amphibians.—As a model system, amphibians provide advantages in understanding habitat relationships to navigation abilities. In particular, what cues and mechanisms are needed to successfully navigate in the narrow environmental conditions (such as high humidity or moisture to prevent desiccation) often required by amphibians?

Occasionally, however, the semi-aquatic nature of these organisms can be inconvenient for the human investigators. Traditional amphibian tracking methods are passive and visual (Sapsford et al. 2014), although passive integrated transponder (PIT) tags now allow tracking of individuals remotely with large antennae (Ousterhout & Semlitsch 2014; Le Chevalier et al. 2017). Embedding the tags requires anesthesia and surgery, and ca. 15% of individuals expelled the tags from their bodies in one study (Weber et al. 2019). Many amphibians are restricted to high moisture habitats, which exist in limited areas on the landscape, restricting the paths they can take across the landscape.

Urodeles (newts and salamanders) can use polarized light (Phillips & Borland 1994; summarized in Rozhok 2008:65–66), the geomagnetic field (Sinsch 1992, 2006; Fischer et al. 2001), the direction of the shore (Rozhok 2008:34), acoustic cues (Sinsch 2006), chemical or olfactory cues (Sinsch 1992; Jaeger et al. 1993), and celestial cues (Diego-Rasilla & Luengo 2002). Some work suggests map use in amphibians (Phillips et al. 1995, 2002; Fischer et al. 2001; Sinsch 2006; Liu et al. 2019) and experience or learning of a familiar area is suggested to be critical for newts (Sinsch & Kirst 2016). Because amphibians use so many cues, more experimental work on mechanisms and their relative importance would be useful (Sinsch 1992).

Fiddler crabs.—Fiddler crabs are small enough for easy experimentation (Layne et al. 2003), while being large enough to attach tracking devices. They can be studied in their natural habitats (Layne et al. 2003), with multiple related species for comparison (Cannicci et al. 1999). The mitochondrial genome (Wang et al. 2020) has been sequenced, but not the nuclear genome, which is potentially unique (McClintock & Derby 2006; Stillman et al. 2008; Benson et al. 2012).

Fiddler crabs are distinguished from the taxa we have discussed so far in that some species build their own landmarks (Kim et al. 2010) as visual cues (Wehner 1992:66; Vannini & Cannicci 1995), although not all do (Zeil 1998). They also use an idiothetic (i.e., kinesthetic, tracking their own body movements) step counter (summarized in Vannini & Cannicci 1995; Walls & Layne 2009a, b) based on kinesthetic feedback (Layne et al. 2003). They combine these cues in path integration (Zeil 1998; Hemmi & Zeil 2003; Layne et al. 2003; Walls & Layne 2009b) and learn the area around their burrows on outward journeys (Cannicci et al. 1999).

ARACHNID MODELS

Overview.—Here we will focus on the contributions that arachnids have made to our understanding of navigation. We begin with spiders, where the most navigational work has been done, and finish with scorpions and amblypygids, highlighting their special sensory adaptations (pectines and antenniform legs) related to homing. Throughout, we pay particular attention to the special features of the animals that have made them useful subjects for navigational research while also highlighting the experimental approaches used to deduce various homing mechanisms.

Our tour starts by highlighting four spider species that have the most complete literature relative to deducing navigational mechanisms. We move from a web-obligate animal (*Agelena labyrinthica* (Clerck, 1757), Agelenidae) to those much less dependent on web-based cues (*Cupiennius salei* (Keyserling, 1877), Trechaleidae; *Lycosa tarantula* (Linnaeus, 1758), Lycosidae) and finally to an animal that ventures hundreds of meters from its burrow and back in a single night (*Leucorchestris arenicola* Lawrence, 1962, Sparassidae; syn. *L. kochi* Lawrence, 1965).

Agelena labyrinthica.—While the phenomenon of kinesthetic (or idiothetic) orientation has been reported for various animals across many clades (Papi 1992), our earliest understanding comes from work with spiders. Research on the funnel web spider, *Agelena labyrinthica* (Bartels 1929; Görner 1966, 1988; Moller 1970) provided some of the first insights into how animals could return to a point using information

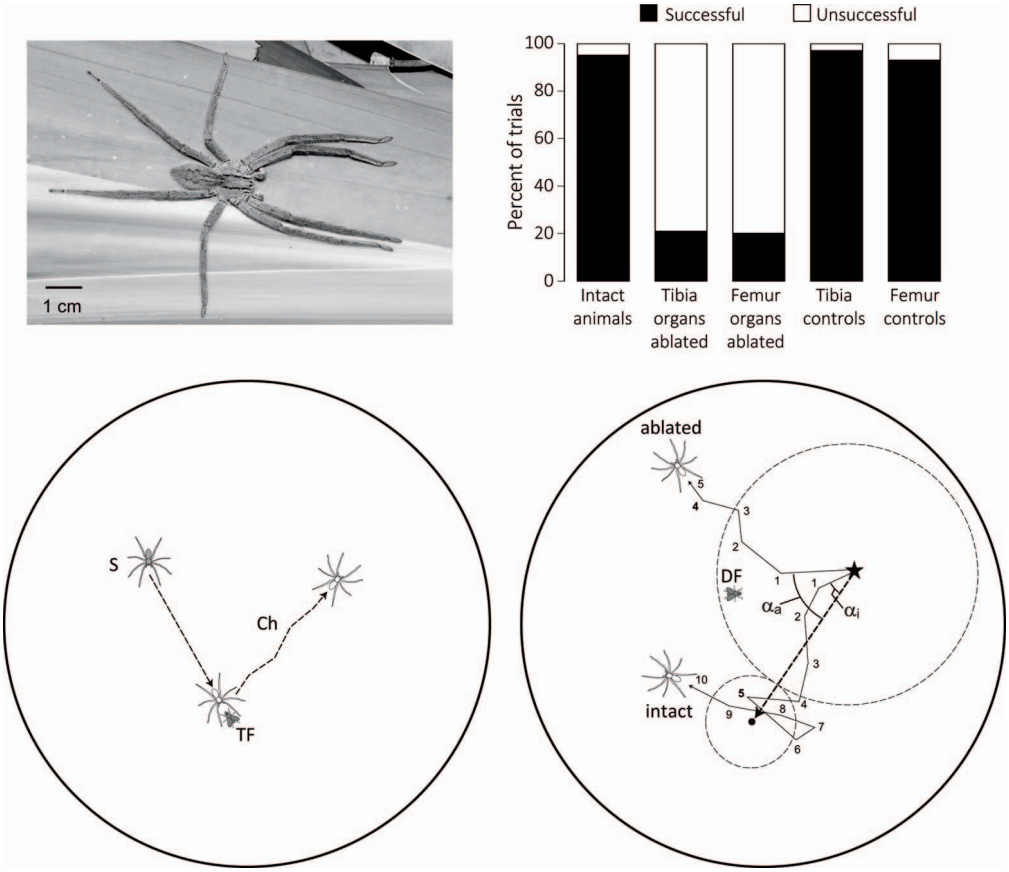


Figure 1.—Early demonstration of kinesthetic (idiothetic) orientation in spiders. Upper left: *C. salei* male atop a banana leaf (*Cupiennius salei*, adult male © Stuart J. Longhorn used under a CC BY-SA; Online at https://upload.wikimedia.org/wikipedia/commons/c/cf/Cupiennius_salei%2C_Adult_Male.JPG Lower left: In a circular laboratory arena (80 cm diam), an individual *C. salei* is lured from its starting position (S) to the humming of a tethered fly (TF). After catching, a voltage applied to the fly induces the spider to release it and an investigator uses a brush to chase (Ch) the spider about 25 cm away. Lower right: After displacement, the now dead fly (DF) is positioned nearer to the displaced spider (star) than previous capture position (filled circle) and each segment of the spider's movements are recorded. The angle of the spider's first movement relative to a direct path (dashed arrow) back to the capture site is calculated. An excursion is deemed successful if it comes within 10 cm of the capture site (indicated by smaller dashed circle; e.g., point 5 for the intact spider example). Unsuccessful excursions are labeled once the spider has moved beyond a radius of the distance to the capture site minus 10 cm (larger dashed circle; e.g., point 4 for the ablated spider example). Upper right: The percent successful and unsuccessful trials for all trial conditions (see text). Adapted from Seyfarth & Barth 1972.

gained on their outbound journeys. *Agelena labyrinthica* build horizontal webs with tube-like retreats from which they emerge to catch insects snared by their webs (Bartels 1929; Görner & Claas 1985). They return to the retreat to consume their prey. In laboratory tests, spiders were allowed to build a web in a square or circular frame and then lured from the retreat to capture a fly. Beyond the frame, two lights were positioned at a slight angle above the horizon and perpendicular to each other relative to the center of the web. During training trials, with one of the lights on, each spider captured a fly and returned directly to its retreat. Then, in a test situation, after capturing the fly, the first light was turned off and the second light turned on. The spider's return journey was then altered – not by 90 degrees as predicted by the change in light angle, but by about 60 degrees. Apparently, the spider is using some combination of optical and idiothetic information to deduce a homeward bearing. Additional experiments showed that the spider's return movements are influenced by both internal and external cues, including the plane of polarized light (Görner 1962), gravity, and web-based information (Görner & Claas 1985; Mittelstaedt 1985; Görner 1988; Moller & Görner 1994), including tension as shown for bowl and doily spiders (Suter 1984).

Cupiennius salei.—While much has been learned about path integration from studies of web-building spiders such as *A. labyrinthica*, other researchers have focused on spiders that do not use any directional information gleaned from web-based cues. One such subject is the trachaleid spider, *Cupiennius salei*, from Central America. These spiders are nocturnal predators that hunt on solid surfaces, often banana leaves on the tree or in leaf litter. The spiders use the base of the leaves for retreats but do not add webs for their shelters or to capture prey. The spiders hunt for several hours and consume prey at the site of capture before returning to their retreats (Barth & Seyfarth 1979).

In a classic set of laboratory experiments, blinded spiders were tested for their ability to return to a point of prey capture after being displaced (Barth & Seyfarth 1971; Seyfarth & Barth 1972). The testing protocol is depicted in Fig. 1. The tests were conducted in a circular arena atop a PVC floor. The

spider was lured by the humming of a fly suspended above the floor on a probe. A voltage pulse induced the spider to release the fly immediately after capture, after which a brush was used to chase the spider about 25 cm from the capture site. Meanwhile, the captured (now dead) fly was moved so that it was nearer to the spider than the spider to the site of capture, controlling for potential olfactory cues from the fly. Nearly all of the blinded spiders returned successfully to the previous capture site.

To determine which internal cues the spiders could be using, the researchers looked to special cuticular strain gauges called slit sensilla that riddle the exoskeleton of arachnids. Of the approximately 3300 slit sensilla on the body of *C. salei*, 86% are on the legs (Barth & Lirera 1970; Barth 2013). Slit sensilla are arranged in various configurations from isolated slits to ornate, parallel groupings called lyriform organs (owing to their resemblance to a lyre, an ancient Greek stringed instrument), which have up to 30 slits. *C salei* has 144 lyriform organs, with the majority occurring on its legs near joints (Barth & Lirera 1970).

The return paths of intact animals and animals whose lyriform organs had been mechanically destroyed on their femur or tibia leg segments, as well as control animals with holes poked in the femur or tibia cuticle were compared. The animals were scored based on number of successful returns to within 10 cm of the fly capture site, as well as other measures of accuracy, including the angle of the initial movement relative to the most direct route and a measure of cumulative error during the return excursion. The percent of successful returns was significantly greater for the intact and sham controls compared to those with lyriform organs ablated (Fig. 1); the angle of the initial return movement and cumulative error along the return path were also significantly different. The spiders also seemed to estimate the distance of displacement, since searching behavior in many animals increased dramatically when the intact and sham control spiders reached the fictive area of the captured fly (such as shown for the intact animal in Fig. 1). Return accuracy also fell with increasing chase distance. All intact animals that were chased 20 cm returned to the target region, whereas only 55% of ablated animals did. When chased 40 cm, 70% of intact animals were successful, compared to only 15% of the ablated animals (Seyfarth et al. 1982). In additional experiments, intact spiders chased through a curved hallway returned successfully and on straight line paths to the site of fly capture while ablated spiders did not (Seyfarth et al. 1982).

An important outcome of these studies was the identification of potential sensory organs involved in idiothetic monitoring and assessing of the angle and distance of the outbound journey to estimate the vector of a return path. The spiders in these studies were vision deprived. Of continued interest will be understanding how visual and other sensory input modifies path integration behavior, both to a dislodged prey item and back to the retreat. Also, *C. salei* have been shown to raise their front two legs in "antennae-like" fashion when deprived of all light (Schmid 2014), which may suggest detection of air currents or olfactory cues, further adding to the possible sensory milieu. Although there may be some change in behavior of *C. salei* under complete darkness, kinesthetic information gathered from the lyriform organs is paramount for path integration in this nocturnal species.

Lycosa tarentula.—In contrast to *C. salei*, many spiders are diurnal and have exceptional visual capabilities. Furthermore, many spiders are capable of detecting the plane of polarized light, including funnel web spiders (Görner 1958; Görner & Claas 1985) and wolf spiders (Papi 1955; Papi & Syrjamaki 1963; Magni et al. 1964, 1965; Melamed & Trujillo-Cenóz 1966; Kovoor et al. 1993), and perhaps use polarized light as a global reference system for calibrating their outbound turns — much as earlier navigators did relative to star patterns.

Some of the most complete work on how vision and polarized light are used for path integration and homing in spiders has been conducted on the tarantula wolf spider *L. tarantula* from southern Europe (Fig. 2A). These spiders dig small burrows (about 20 cm deep) in the dirt, from which they emerge to chase prey (Ortega-Escobar & Muñoz-Cuevas 1999). Such chases can take the spiders on meandering outbound paths up to 40 cm away from their burrow, to which they return on a straight line (Ortega-Escobar & Muñoz-Cuevas 1999; Ortega-Escobar 2002). Through several clever behavioral experiments, coupled with systematic covering of specific sets of eyes, many of the details of how vision plays into the path integration abilities of *L. tarantula* have been deduced.

In the first set of experiments, conducted under open sky, spiders were assessed for their ability to detect and use polarized sunlight (Ortega-Escobar & Muñoz-Cuevas 1999). Individual spiders were allowed to acclimate inside a rectangular, soil-filled terrarium (30 × 60 cm) in which a pre-formed burrow was created along the middle of one of the long walls (Fig. 2B). In tests, animals were gently chased away from their burrow, along the wall, around the first corner to one of the two corners across from the burrow. The terrarium was angled relative to north such that the hypotenuse back to the burrow formed a 30° or 300° topographic angle, depending on which corner the spider was chased to. The spider was then captured in a glass cup and moved to the center of a larger circular arena (90 cm diam.), and its movements were monitored until it neared a wall, where its bearing relative to the arena center was recorded. Animals were tested under clear sky, overcast sky, or a plastic cover that changed the patterns of light polarization from parallel to elliptical (Fig. 2C, left three plots); in all cases, a small shield blocked the spiders' direct view of the sun. Under these conditions, animals walked the correct, burrow-directed path (along the 30° or 300° hypotenuse) only under clear sky; there was also no orientation relative to any other visual patterns in the test environment. Taken together, the data strongly suggest the animals were updating their angular position on their rectilinear outbound path relative to the pattern of polarized light in the clear sky. It is interesting too that some of the animals chased to the 300° corner oriented 180° opposite to the predicted inbound path. These animals were likely confused by the symmetrical solar-antisolar e-vector pattern that occurs at sunrise and noon — the times the trials were conducted (Ortega-Escobar & Muñoz-Cuevas 1999).

Once the polarized light behavior was established, the search was on for which eyes were responsible. Morphological studies implicated the anterior medial eyes (AME) because of

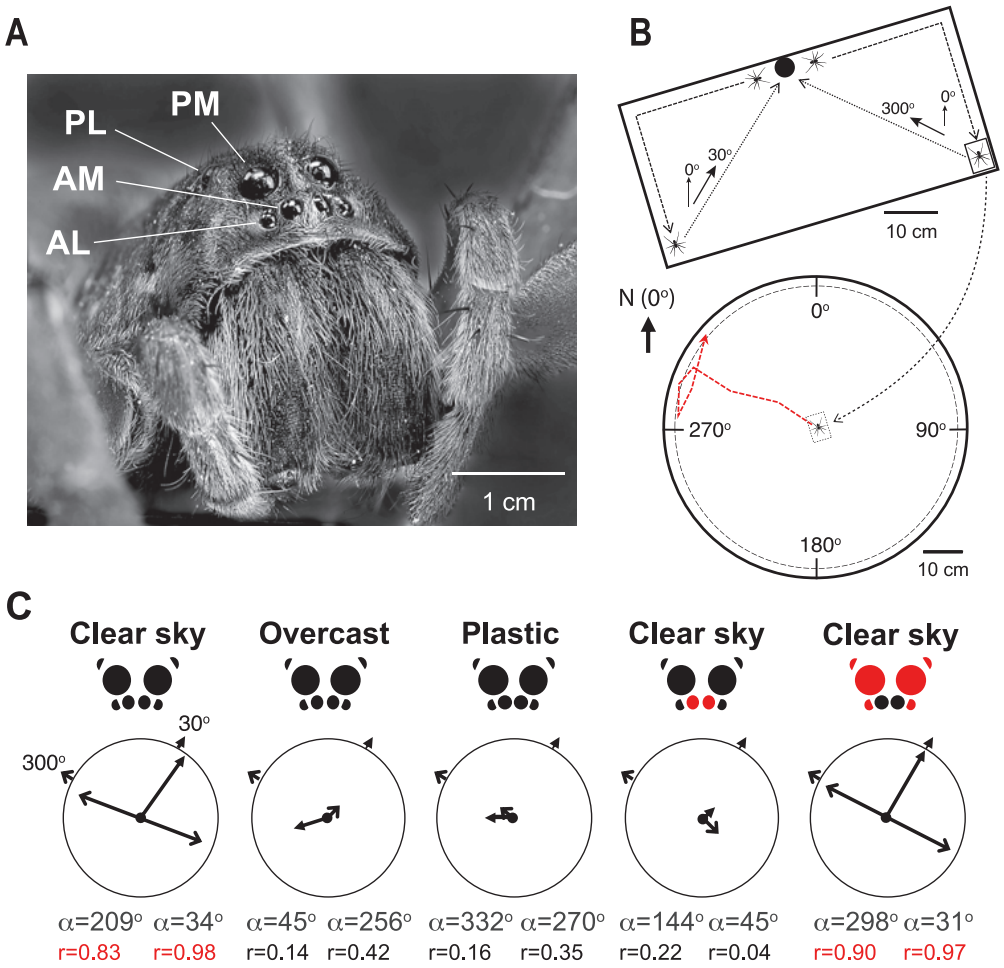


Figure 2.—Use of polarized sunlight in path integration in *L. tarantula*. (A) Photo of an adult male showing position of eyes (PL=posterior lateral; PM=posterior medial; AM=anterior medial; AL=anterior lateral; online at https://www.publicdomainpictures.net/ru/view-image.php?image=3186&picture=wolf-spider (B) Test spiders were housed individually for three days in a terrarium (60 × 30 × 35 cm) filled to a depth of 15 cm with soil (upper drawing). An artificial burrow was dug near the wall of one of the long sides (filled black circle). A test animal was chased from the burrow along the walls to an opposite corner of the terrarium where it was captured in a transparent glass container and transferred in the same orientation to the middle of a circular, 90 cm diam arena with 48 cm walls (lower drawing). The angle of the direction of the animal relative to the center was scored once it had moved 40 cm away from the center (dashed circle; a fictitious example is shown in red). (C) The animals were tested under clear sky, overcast sky, or a plastic cover that changed the polarized light patterns from parallel to elliptical; a shield blocked direct view of the sun. In two of the tests, spiders either had their AM eyes masked or all eyes except AM eyes masked (red indicates masking). The primary vectors are given for each test (based on circular statistics). Only the tests of animals under clear sky with all eyes unmasked or with only AM eyes unmasked showed significant movement (*r* values highlighted in red) in the direction of the fictive burrow (which would have been either 30° or 300° depending on which corner they were captured). Adapted from Ortega-Escobar & Munoz-Cuevas 1999.

the sky-directed orientation of their ventral photoreceptors that also have orthogonally arranged lines of rhabdoms (Kovoor et al. 1993), which is characteristic of other polarization detectors. The other sets of *L. tarantula* eyes do not show these characteristics. Furthermore, electroretinograms of *L. tarantula* AME showed a neurological response to the plane of polarized light (Ortega-Escobar & Muñoz-Cuevas 1999). As such, another set of behavioral tests were run under clear sky for animals with only their AME covered or with all eyes (ALE, PLE, PME) except AME covered (see Fig. 2A for eye arrangement and labeling). Only the animals with their AME uncovered oriented in the same manner as the intact animals (Fig. 2C, right two plots). So, based on morphological, physiological, and behavioral evidence, the AMEs appear to transduce the polarization information these wolf spiders use for path integration (Ortega-Escobar & Muñoz-Cuevas 1999).

Beyond using polarized light patterns, *L. tarantula* may update its homeward vector by using additional sources of visual information. In tests under artificial light, in a similar rectilinear testing situation as described above (Ortega-Escobar 2002), animals were chased to a corner of the terrarium that would have put the topographic direction of their burrow at 350° – which also meant the spider would need to turn 135° to the left from its final direction (Fig. 3). At the corner, the spider was captured in a glass cup and moved

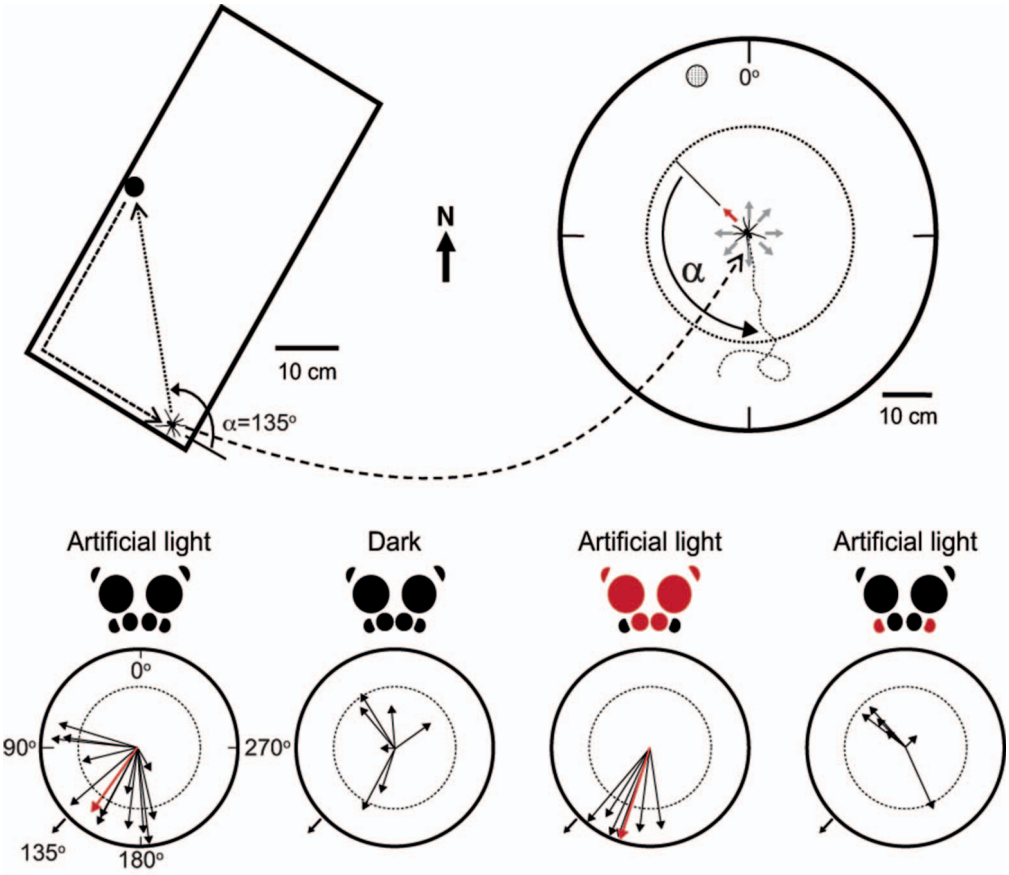


Figure 3.—Tests of path integration in *L. tarantula* under artificial light. In these tests, animals were chased to a corner where the direct line back to the burrow was topographically 350° (upper left). To make this angle, the animal would need to turn counter-clockwise (to their left) 135° (α). Each animal was tested in the larger circular arena (upper right) after being transferred in a clear container and placed facing in one of eight directions (shown by small arrows). The example shown was placed in a direction offset counterclockwise 45° from north (0°); the direction of the fictive burrow is shown by the dot-filled circle. In these experiments, the animals were scored once they had moved 20 cm from the center (dashed circle). The angle α was calculated for each animal by subtracting the angle that the animal was placed from the animal's response angle. In initial trials, animals were tested with lights on or in the dark (lower left two plots). In subsequent tests, animals with all eyes except ALE covered or with only their ALE covered were tested in the light (lower right two plots). Only trials under artificial light with intact animals or with AL eyes only uncovered showed significant directionality towards the predicted 135° turn angle (indicated by red mean vector arrows). No topographic significance was seen in any of the trials. Adapted from Ortega-Escobar 2002 and 2006.

again to the center of the large circular arena and placed in one of eight directions. In these tests, the bearings of the animals were noted once they moved 20 cm from the arena center. Plots of these bearings showed no directionality. When the angle that the animal was placed was subtracted from the animal's chosen bearing, however, the directionality was significant and in the 135° direction of the fictive burrow (Fig. 3, lower plots). No such directionality was observed in darkness. Animals with only their ALEs uncovered behaved similarly to intact animals, while those with their ALEs covered did not turn in the 135° burrow direction (Ortega-Escobar 2006). The ALEs are directed forward and down to the side and may acquire visual flow information used to assess outbound rotational information, such as when the animal turned the corner of the arena. The animal can then use this information to estimate the angle required to turn back to its burrow.

The tests in which animals were chased around corners in a rectangular terrarium were useful for understanding how vision plays into updating the spider's angular component of its outbound journey. However, that experimental design is not as useful for assessing the other component of path integration: distance estimation. To do this, a different behavioral approach was used, one that has proven its worth in several insect odometry studies (Kirchner & Srinivasan 1989; Wittlinger et al. 2007; Schwarz et al. 2012). In this design, a spider is maintained in a long, narrow plastic housing chamber with an artificial burrow formed near one end (Reyes-Alcubilla et al. 2009; Ortega-Escobar & Ruiz 2014, 2017). In the tests, a spider is chased some distance, captured, and placed in an adjacent, but burrow-less chamber (Fig. 4, upper diagram). The spider's movements are followed with particular attention paid to turning points and back-and-forth movements that suggest systematic searches (Wehner & Srinivasan 1981) for a fictive burrow.

The first tests assessed both the effect of active and passive movement of the spider during the outbound journey (Reyes-Alcubilla et al. 2009). Spiders were either chased 20 cm from

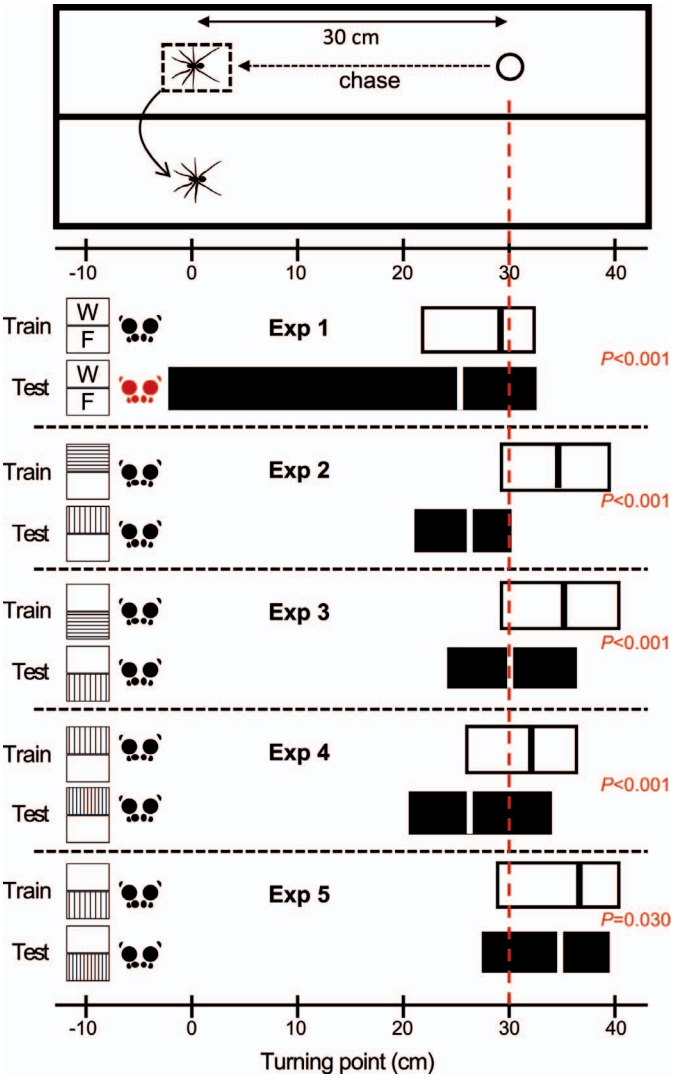


Figure 4.—Channel displacement studies of path integration in *L. tarantula*. Spiders were housed in rectangular plastic chambers 52 cm long, 9.5 cm wide, 10 cm tall. An artificial burrow (open circle) was place in the middle of the floor, 12 cm from one of the end walls. To test, spiders were gently chased 30 cm away from their burrows, captured in a clear glass and moved to the same relative location in an adjacent test arena, which did not contain a burrow. The spiders' movements were monitored until they made their first turn; each animal was tested multiple times. The patterns on the walls and floor varied among experiments as indicated by the key to the left of each of the graphs. The upper box indicates the pattern on the walls (W) and the lower box the pattern on the floor (F). For each experiment, eight females were used, and 10 trials were conducted under the training conditions followed by 10 trials under the test condition. The housing chamber of the animals was always patterned the same as in the training trials. The line in each graph is the median and the rectangle indicates the interquartile range (25%–75%). Significance level between the two conditions is shown at right. The eyes of the test animals were masked in Experiment 1 (indicated by red); the animals' eyes were uncovered in all other trials. Adapted from Ortega-Escobar & Ruiz 2014.

their burrow into a glass cup (active movement) or captured in a glass cup at their burrow and manually displaced 20 cm (passive movement). The spiders were then transferred to the test chamber and placed in the same relative position, 20 cm from their fictive burrow. The active spiders that walked the 20 cm outbound journey returned to beyond their fictive burrow position a few cm before making a U-turn, while the passively displaced spiders searched near their release points, suggesting a role for proprioceptive information for judging distance similar to *C salei*. In subsequent tests of active locomotion, markings were added to the walls near the burrow in the animal's housing chamber. The test chamber either had similar markings at the fictive burrow position, 10 cm beyond the burrow position, or no markings at all. The markings had no effect on the spider's search behavior, indicating that landmark visual information was not used to locate the burrow position (Reyes-Alcubilla et al. 2009).

Similar linear chambers were used to explore visual effects on the spider's estimate of distance (Ortega-Escobar & Ruiz 2014, 2017). In the experiments shown in Fig. 4, spiders were chased 30 cm from their burrow in their housing chamber, captured and moved to an adjacent test chamber and their responses monitored. In the initial experiment (Exp 1), spiders were tested with their eyes covered or uncovered in pure white chambers. Whereas even blinded spiders showed some tendency to return toward the burrow before turning, the intact spiders were significantly better and quite accurate in judging the distance. Subsequent tests (Fig. 4, Exp 2–5) were used to assess the effect of varying the orientation and spacing of grating patterns on the walls and floor of the chambers on the spiders' estimate of distance. Animals underestimated the distance to the burrow when the direction of stripes on the floor or wall was changed during test trials (Exp 2 & 3). Increasing the frequency of vertical lines in test trials compared to training runs also caused the animals to undershoot the target (Exp 4) and seemed to have a greater effect than when the line spacing differences occurred on the floor (Exp 5). This result suggests that the PLE, which are directed more toward the side, may have a larger effect on distance estimation compared to the downward directed ALE.

Taken together, this set of experiments paints a fairly comprehensive picture as to how vision is used in estimating the homeward vector in path integration for *L. tarantula*. However, some questions remain. For example, why is directionality so pronounced under laboratory conditions under artificial light with ALE uncovered (Fig. 3), but not outdoors under overcast skies (Fig. 2C)? Also, the effect of visual information on the floor and the role of the ALE does not appear as pronounced in the behavioral configuration shown in Fig. 4 (Exp 5) as it was under different conditions in a very different behavioral assay (Ortega-Escobar 2011). This difference needs to be explored.

Leucorchestris arenicola.—Perhaps due to their limited foraging distances, which allow for highly controlled, laboratory-based behavioral assays, the spiders (*A. labyrinthica, C. salei, L. tarantula*) highlighted above have been extremely useful for deducing various path integration components. However, in looking for arachnid examples that push navigational possibilities beyond near-range path integration, there may be no better animal than the wandering desert

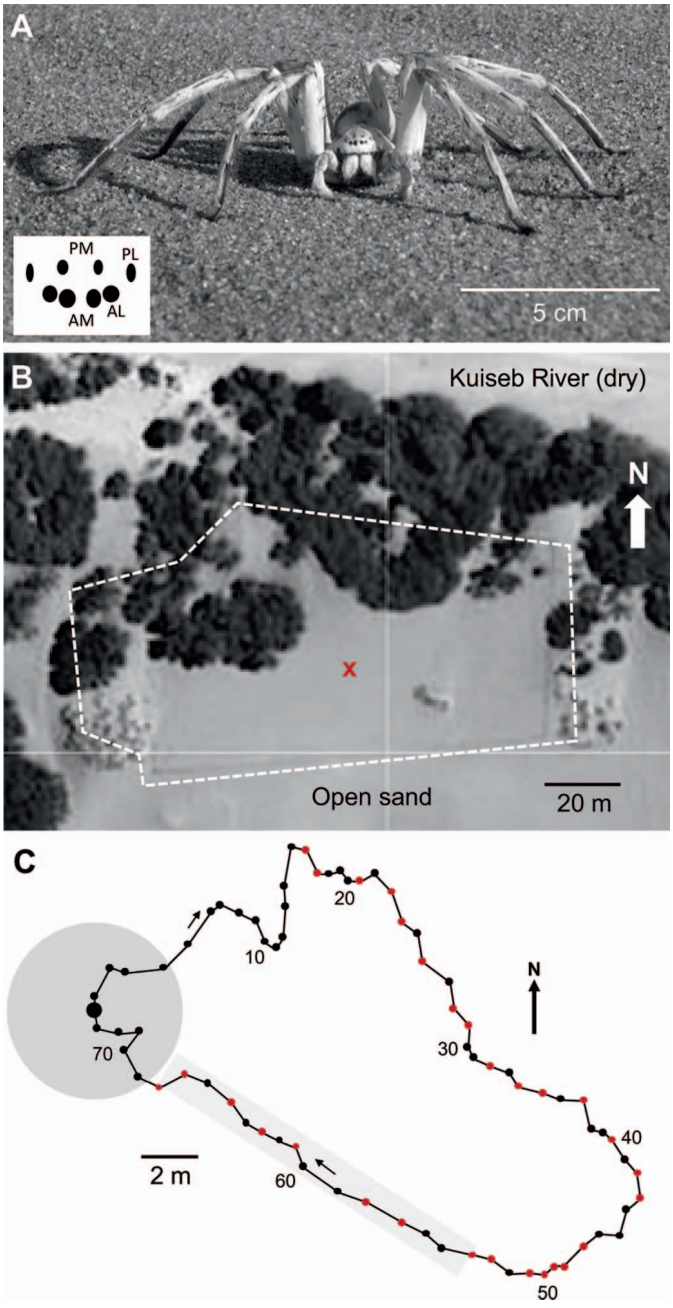


Figure 5.—Homing in the wandering Namib spider *L. arenicola*. (A) Adult male (photo online at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0049263); inset shows pattern of eight eyes (key as in Fig. 2A). (B) Principle Namib study site. The main site is located inside a fenced area (white dashed line) south of a shrub area that borders the ephemeral riverbed of the Kuiseb River, about 0.5 km SW of the *Gobabeb Training and Research Centre* on the north edge of the Namib Desert, Namibia. The red x indicates the location of a 360° survey of the surrounding visual horizon as depicted in Fig. 6A (aerial photo online at https://earthexplorer.usgs.gov/ centered at 23° 33′ 37” S, 015° 02′ 25” E). (C) An example of a nighttime round-trip excursion by an adult male recreated the following day by mapping the animal's footstep imprints in the sand. The dark circle is the spider's burrow and the larger gray circle an approximation of the spider's main hunting territory. Each black dot marks where the spider made a turn that moved it more than a body width outside its previous direction. The red dots indicate positions of

spider, *L. arenicola* (Fig. 5A). These large nocturnal spiders (males can weigh up to 4 g with leg-spans greater than 10 cm) are long-lived (2+ years) and endemic to the sand dunes of the Namib Desert on the Atlantic coast of Namibia (Henschel 1990; Nørgaard et al. 2006) (Fig. 5B). They are faithful to long (30–40 cm), silk-lined burrows that they dig at a 30-degree angle into the bases of dunes (Henschel 1990) and cover with trapdoors (Nørgaard et al. 2003). The animals are most active on the surface during periods of new moon (Nørgaard et al. 2006) and they aggressively defend territories 3–4 meters in radius around their burrow (Henschel 1990).

Although both males and females venture at night from their burrows to hunt and mate, the distance covered by the males is the most impressive. Male mate-seeking journeys range far beyond their defended territories and across the dunes (Fig. 5C); some journeys have been measured at more than 800 meters round trip (Nørgaard 2005). The mean journey distance for a population of males was $40.92 + 6.64$ m (mean + SE) with a mean maximum distance to the burrow of $13.13 + 2.23$ m (Nørgaard et al. 2003). In fact, the navigational feats of these spiders draw comparisons to the long-range navigational abilities of the heavily studied bees and ants (von Frisch 1967; Wehner 1992; Beekman & Ratnieks 2000), yet they have added benefits of large size, longevity, and trackability. The animals are heavy enough to leave clear markings of their footsteps in the sand, which can be tracked to map their journeys (Henschel 1997, 2002; Nørgaard et al. 2003). Temporary records of other behaviors, such as male drumming, are also impressed in the sand and wiped clean with the winds of the next day (Henschel 2002). The outbound journeys of the males are more meandering compared to inbound journeys, which often have long, burrow-directed segments. The return paths do not retrace the outbound paths; in fact, inbound paths near the animals' territories deviated 65° (median) from their outbound paths (Henschel 2002) (for example, see the difference in the angle of departure and return in Fig. 5C). The spiders also engage in search-like behavior within their territories if they miss their burrow position on their initial return (Henschel 2002; Nørgaard et al. 2007).

How do these spiders find their way back from such long distances? One possibility is that they are proficient at idiothetic path integration (Warrant & Dacke 2010), monitoring their own body movements (as in *C. salei*). However, the Namib spider's range is orders of magnitude larger, and the cumulative error incurred over long excursions makes this possibility highly unlikely. In fact, the researchers themselves, in retracing the spider's movements, more or less demonstrated this by the errors they incurred by taking compass directions at every turn the spider made along the way (Nørgaard et al. 2003; Nørgaard 2005). A more likely possibility is that the spiders use a fixed reference or external cue to recalibrate their bearings along the way. The slope of

←
communicative drumming, which are conspicuous by their impressions (Henschel 2002). The numbers mark every 10 points of the path and small arrows indicate direction of movement. The gray rectangle highlights a long and relatively straight portion of the homeward path. Adapted from Nørgaard et al. 2003.

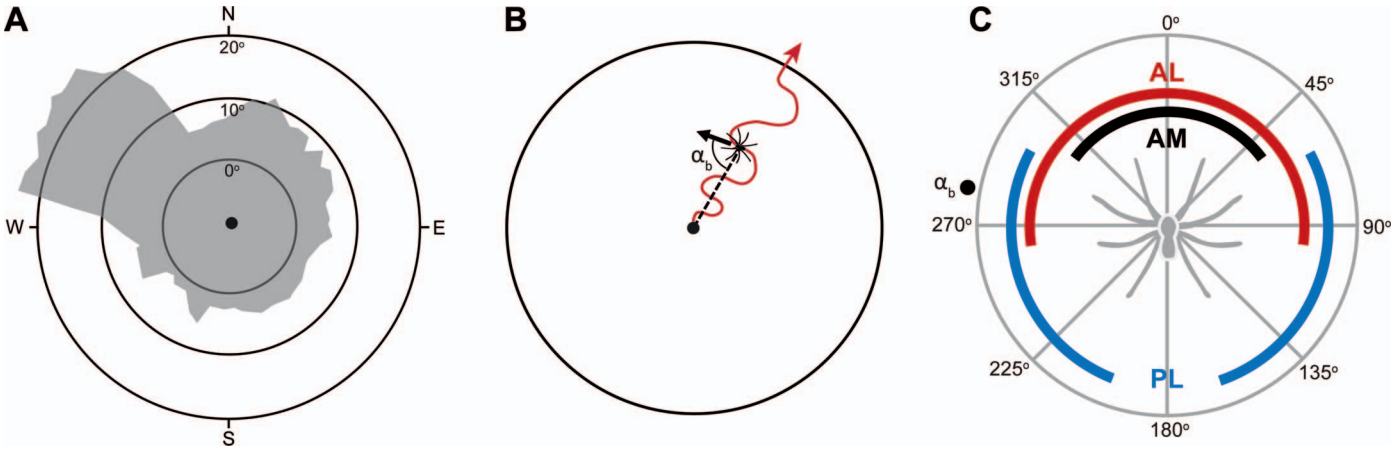


Figure 6.—Deducing homing mechanisms in the wandering Namib spider *L. arenicola*. (A) Contour of the horizon skyline in degrees as measured from spider height at position "x" shown in Fig 5B (adapted from Nørgaard et al. 2006). (B) An example of a sinusoidal walk of an initial outbound path conducted by a naïve spider caught kilometers away and induced to make a new burrow at this new location (the circle is 2 m in radius and indicates the detectable area of the IR camera). The angle of the burrow relative to the animal's direction is indicated by α_b. (C) Measured horizontal fields of view for adult *L. arenicola* for three sets of eyes: AL (red), AM (black), and AL (blue). The black dot on the left side of the circle indicates the burrow angle (α_b) as shown in B. Parts B and C adapted from Nørgaard et al. 2012.

the dunes might serve as one cue, but the information available was deemed unreliable for this type of navigation (Nørgaard et al. 2003). Celestial cues (polarized patterns of light from the sun or moon) and light intensity and/or hue gradients across the sky are used by many animals (Horváth 2014) and could serve as a global reference for the spiders. However, these spiders appear on the surface only during the darkest times of night, avoiding dusk/dawn, and periods when the moon is in the sky at all (Nørgaard et al. 2006), precluding any possibility of a role of the sun or moon. Star patterns might act as reference points, and they have yet to be ruled out. Wind direction is too variable (Nørgaard et al. 2003; Nørgaard 2005), and displacement experiments have shown that olfactory cues do not play a significant role (Nørgaard et al. 2007). The spiders are extremely vibration sensitive and they use vibrations to hunt and find mates (Henschel 1990; Birkhofer et al. 2006), so they might use the audio landscape around their burrows. In one experiment, two speakers were placed in contact with the sand and emitted tones that carried through the sand at least 20 m. The speakers were placed 5 m and 10 m away from spider burrows. The 5 m speaker was on while the spiders left on their excursions; while away, the 5 m speaker was switched off and the 10 m speaker was switched on. The change in the acoustic profile had no effect on the spiders' ability to relocate their home burrows (Nørgaard 2005). Another homing mechanism could be true navigation where geocentric information such as geomagnetic cues away from the burrow are assessed relative to intensity and inclination angle learned while at the burrow. While the distances these spiders traverse are impressive, the scale of their movements is still too limited to suggest this is possible (Nørgaard et al. 2003; Nørgaard 2005). However, the use of magnetic bearings as a global reference for recalibrating idiothetic directional bearings during path integration (Fleischmann et al. 2018) has yet to be ruled out.

The role of vision in *L. arenicola* was explored by testing the navigation success of animals with various groups of eyes disabled. Homing was critically diminished when all eyes were covered; further, spiders could navigate using only their lateral eyes (ALE and PLE) or AME (Nørgaard et al. 2008). Electroretinogram recordings indicated that only bright stars would be detectable through instantaneous glimpses. However, the locomotory activity of *L. arenicola* is punctuated by prolonged stances that correlate with the amount of available light (Nørgaard et al. 2008). As such, it is possible that temporal summation during such poses could yield additional visual information to detect star patterns or coarse landscape features, including the contour of the horizon skyline (Nørgaard et al. 2006) (see Fig. 6A). Surrounding skyline information is also suggested in studies where burrows were displaced a few meters while males were on excursions. Upon return, the spiders searched at the site of the original, not at the displaced burrow (Nørgaard et al. 2007). This result also negates the importance of burrow olfactory cues. Interestingly, 10 of 12 males displaced an average of ~30 m during their excursions returned home. Some of the tracks hint at path integration and searching at a fictive burrow site (had the animal not been displaced) followed by meandering paths to the actual burrow (Nørgaard et al. 2007). It needs to be noted that these spiders are long-lived and range widely across the habitat. Homebound visual information (perhaps the horizon contour) could therefore accumulate with successive excursions and be used to guide animals to familiar areas, similar to navigation by scene familiarity suggested for ants (Baddeley et al. 2011, 2012).

Visual information is further implicated by the finding that naïve *L. arenicola* males perform something akin to learning walks during their initial outbound journeys (Nørgaard et al. 2012). Learning walks and flights, well documented for various hymenopterans (Collett 1995; Zeil et al. 1996; Wehner et al. 2004; Fleischmann et al. 2016), are innate behaviors thought to enable learning of visual information around the hive or nest, essentially broadening the target for returns from subsequent journeys. The sinusoidal paths (one of which is shown in Fig. 6B) decrease in amplitude with subsequent exits (Nørgaard et al. 2012) and the burrow position in the spider's

field of view during the walks falls mainly in that covered by the ALE and PLE (Fig. 6B,C). However, the notion that the image of the cryptic burrow is being learned during these walks seems unlikely, especially given the very low light levels during which they occur. Also, the behavior seems somewhat different from that of bees and ants, which turn more completely in the direction of the nest or hive during their learning flights or walks. It seems more likely that glimpses of the surrounding horizon (Fig. 6A) are acquired and learned from multiple points near the burrow and that the animal may use this information during searches on return journeys. The spiders are probably not coupling scenes to the walking direction experienced during the outbound acquisition phase, since the incoming information would fall on the eyes on the wrong side of the animal (barring discovery of a complicated anatomical commissural system for horizontally inverting visual information). Instead, the spiders may gather near 360° horizon scenes from multiple points in their territory and re-experience these with increasing frequency as they meander near their burrows during returns from excursions.

Jumping spiders.—Jumping spiders are perhaps the most visual of all arachnids. They do not use prey-capture webs, and they are highly mobile. Some, such as those in the genus *Portia* (Karsch, 1878) are renowned for their complex hunting behaviors that include irregular gaits that disguise their movements as background noise, calculation of complex detour paths to a prey item, and vibration mimicry of the mating signals of other species (Cheng 2006; Tarsitano 2006). However, what is of most interest here is behavior that allows the spider to return accurately to a previous location. Other jumping spiders, such as *Phidippus sp*., have been shown to remember their initial positions even after detouring significantly and out of direct line of sight with a goal (Hill 1979). An interesting study of *Phidippus clarus* Keyserling, 1885 showed that spiders can learn and use beacons to navigate back to their nests. Further, the spiders could also discriminate the color of a nest-associated beacon from similarly shaped, differently colored beacons (Hoefler & Jakob 2006). Still, much more research is needed to fully assess and deconstruct the special navigation mechanisms of these animals.

Scorpions.—Increasing attention is being paid to the homing skills of some other arachnid groups, especially those that venture some distance from their homes. For example, considerable work has been done on the ecology and natural history of desert sand scorpions, such as *Smeringurus mesaensis* (formerly *Paruroctonus mesaensis*) (Stahnke, 1957) (Scorpionida, Vaejovidae) found in sand dunes and hummocks in California, Nevada, Arizona, Sonora, and Baja California (Brownell 2001). These long-lived animals are faithful to self-built burrows (Polis & Farley 1979b, 1980; Polis 1980) from which they emerge at night to hunt by vibrations (Brownell 1977; Brownell & Farley 1979). Both females and males maintain territories of a couple square meters (Polis et al. 1985); females are faithful to their territories year-round, but males wander in the late summer mating season in search of mates (Polis & Farley 1979a) that they detect via pheromone deposits (Gaffin & Brownell 1992). *Paruroctonus utahensis* (Williams, 1968) (Scorpionida, Vaejovidae) is another dune inhabitant that is native to the sands of southeastern Utah, Arizona, New Mexico and western Texas

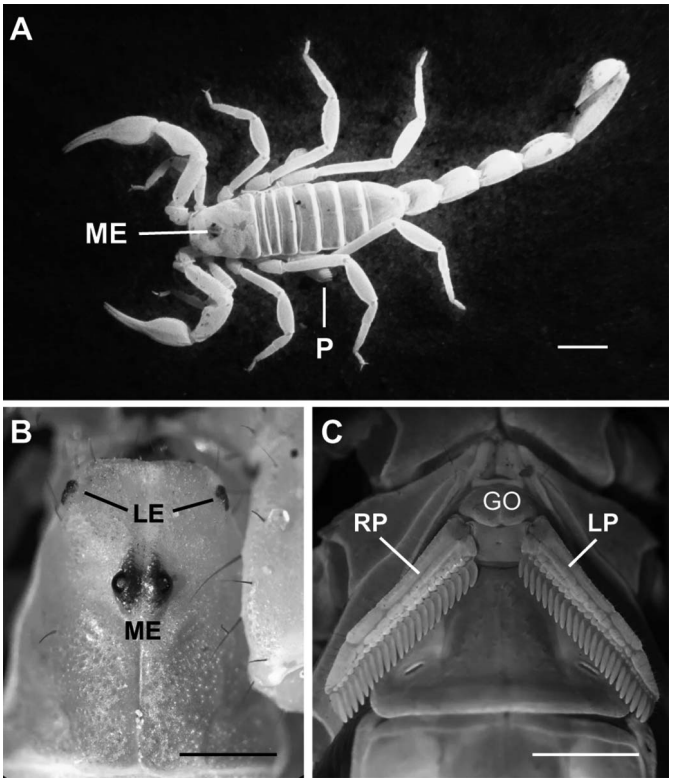


Figure 7.—Sensory systems related to scorpion navigation. (A) Top view of *P. utahensis* male showing medial eyes (ME) and pectines (P). Photo taken under UV light atop sand; scale bar 1 cm. (B) View of *P. utahensis* prosoma showing median (ME) and lateral eyes (LE); scale bar 0.5 cm. (C) Ventral view of female *P. utahensis* pectines (RP = right pecten, LP = left pecten, GO = genital operculum); scale bar 0.5 cm. All photos by K. Ashford.

that has similar life history traits (Bradley 1982, 1984, 1986, 1988) to *S. mesaensis,* including mating behavior mediated by putative sex pheromones (Taylor et al. 2012). Both of these species are amenable to physiological and behavioral lab investigations and can be induced to form homes and display typical cyclical nocturnal behaviors (Vinnedge & Gaffin 2015).

Scorpion bodies are replete with sensory structures, but two systems are particularly relevant to navigation: the median eyes and the pectines (Fig. 7A). Scorpions have two median eyes and a variable number of lateral eyes (2–5 on each corner of the anterior prosoma). All of the eyes have lenses, but those of the median eyes are particularly large and well-formed; a vitreous layer also exists between the lens and retina of the median eyes (Locket 2001). The median eyes are positioned on an ocular tubercle on the midline of the dorsal prosoma (Fig. 7B) and have a 360° view of the horizon and a 40° degree region of binocular vision above the animal (Locket 2001). While considerable information exists concerning the neuronal organization of circadian rhythmicity among the lateral and medial eyes (Fleissner 1977a, b; Fleissner & Fleissner 2001a, b) and morphological work is resolving some questions about central connections and relationships among the optic neuropils (Lehmann & Melzer 2013), very little is known about how vision plays into homing. The median eyes have high acuity, and both sets of eyes are sensitive to very low

light. In fact, physiological measurements indicate that dark-adapted scorpion eyes can detect light on overcast moonless nights, in the range of 10^{-6} to 10^{-7} irradians (Fleissner 1977b, c). This means that navigational cues such as star patterns and features of the ground and surrounding horizon are discriminable during their nighttime surface activity (Fleissner & Fleissner 2001c; Kaltsas & Mylonas 2010 Freas et al. 2017). Also, trans-illumination with polarized light of median eye lenses shows a darkened cross pattern that changes with the orientation of the polarizer (Locket 2001). This pattern is characteristic of birefringent spherical lenses (Locket 2001) and could account for the polarization sensitivity of scorpions (Horváth & Varjú 2004). Low level polarized light induces directional walking of scorpions atop a locomotory compensator, which was abolished under diffuse, uniform light or by covering the median but not the lateral eyes (Brownell 2001).

Scorpion pectines are the other sensory organ that must be considered in the context of homing. These elaborate, chemotactile appendages (Fig. 7C), extend laterally from the ventral mesosoma of all scorpions. Each of the paired pectines is shaped like a comb with a flexible spine that supports a species-specific number of ground-directed teeth (Gaffin & Brownell 2001). On the distal face of each tooth are tens to hundreds of minute peg-shaped sensilla (i.e., "pegs"). Each peg is a double-walled cuticular paddle with an inner receptor lymph chamber into which extend the dendritic outer segments of several bipolar chemosensory neurons (Ivanov & Balashov 1979; Foelix & Müller-Vorholt 1983). Each sensillum is additionally supplied with a mechanoreceptor that terminates near the peg base (Foelix & Müller-Vorholt 1983). The peg tip has a slit-shaped terminal pore that opens to the receptor lymph and allows transference of environmental chemical stimulants to the sensory neurons (Ivanov & Balashov 1979; Foelix & Müller-Vorholt 1983). Electrophysiological investigations of peg sensilla show rich responses to a variety of chemo-stimulants (Gaffin & Brownell 1997a) including modulation of responses via unusual synaptic interactions among primary afferents (Gaffin & Brownell 1997b). Both males and females have pectines, but there is a pronounced dimorphism in pecten length and the number of teeth and peg sensilla (male pectines being longer, with more teeth and sensilla) in species, such as *S. mesaensis* and *P. uthaensis,* in which males wander and are guided to female pheromonal deposits (Gaffin & Brownell 2001). Nevertheless, female pectines are notably complex, even in the strongly dimorphic species.

The dense peg matrices conjure similarities to the ommatidial matrices of insect compound eyes. Together with other clues, including polarization and low-light sensitivity, and some interesting behavioral observations, parallels can be drawn with the Navigation by Scene Familiarity Hypothesis (Baddeley et al. 2011, 2012) described for ants above. Recall in NSFH that the initial set of goal-directed views are acquired through path integration while subsequent returns are guided by moving always in the direction of the most familiar scene. Could something akin to NSFH, namely navigation by chemo-textural familiarity, be happening in scorpions? Beyond path integration, additional requisites for NSFH include ample environmental and sensor complexity to avoid aliasing (confusing similar looking scenes from the wrong places).

A hint at path integration in a sand scorpion is shown in Fig. 8A. An animal is lured from its burrow to a position atop a platform submerged just beneath the sand surface. After the platform is displaced, the scorpion appears to move initially in the angle and distance of the fictive burrow. Such a homebound vector could be established through kinesthetic information from lyriform organs (as with *C. salei*) coupled with directional updates relative to polarization or star patterns, horizon information, or geomagnetic directional cues. Another interesting behavior noted during lab observations (Fig. 8B) are short, quick circular forays by animals around their burrows, suggestive of learning walks in ants (Wehner et al. 2004), potentially widening the burrow target area.

As to sensory capacity, the potential represented by the peg matrices is enormous (Fig. 8C). For example, the pectines of female *P. utahensis* have about 100 pegs per tooth (Gaffin & Walvoord 2004) and 20 teeth per pecten for roughly 4000 total pegs (100*2*20; note, males of some species have at least an order of magnitude more). Based on the kinetics of a pectinal sweep (Gaffin & Walvoord 2004) and the temporal response characteristics of individual pegs, it takes at least eight pegs working in concert to resolve two chemicals (Knowlton & Gaffin 2011). Dividing 4000 by 10 pegs (a conservative resolution estimate) yields 400 points across the pectinal area. The square root of this produces a square with sides of 20. Fig. 8D shows a catchment area that forms when an image of sand at this resolution (the image serves as a proxy for textural information) is compared with hundreds of neighboring images in memory (computed based on the sum of the absolute pixel-by-pixel image differences). The catchment plot shows that one image is a perfect match and all others have varying degrees of similarity. This shows that aliasing based on pectinal resolution is unlikely; furthermore, computer simulations have shown that navigation by familiarity is plausible based on the criteria outlined above (Gaffin & Brayfield 2017).

Computer simulations are suggestive, but additional experiments with live animals are necessary. In particular, we need to learn much more about path integration and learning walks. Also, it is important to determine an animal's reliance on vector information acquired through path integration vs. homeward environmental information transduced by the pectines and/or the median eyes. Well-designed behavioral assays are needed in which animals are confronted with conflicting information during homeward journeys. Tests need to be run on the response of experienced animals to altered chemo-tactile information by disrupting or rotating substrates while the animal is on a hunting foray while similar tests are run to independently assess the use of visual skyline information. In addition, a physiological approach would be to record from the scorpion subesophageal ganglion (SEG) to determine whether the unit of information is the pecten tooth or the peg as scorpions resolve cues in their habitat (Hughes & Gaffin 2019). SEG recordings might also help resolve the unusual occurrence of synaptic interactions among peg neurons (Gaffin & Brownell 1997b; Gaffin 2002). Ultimately, the goal would be to understand how the CNS processes information from the pectines (and other sensory organs)

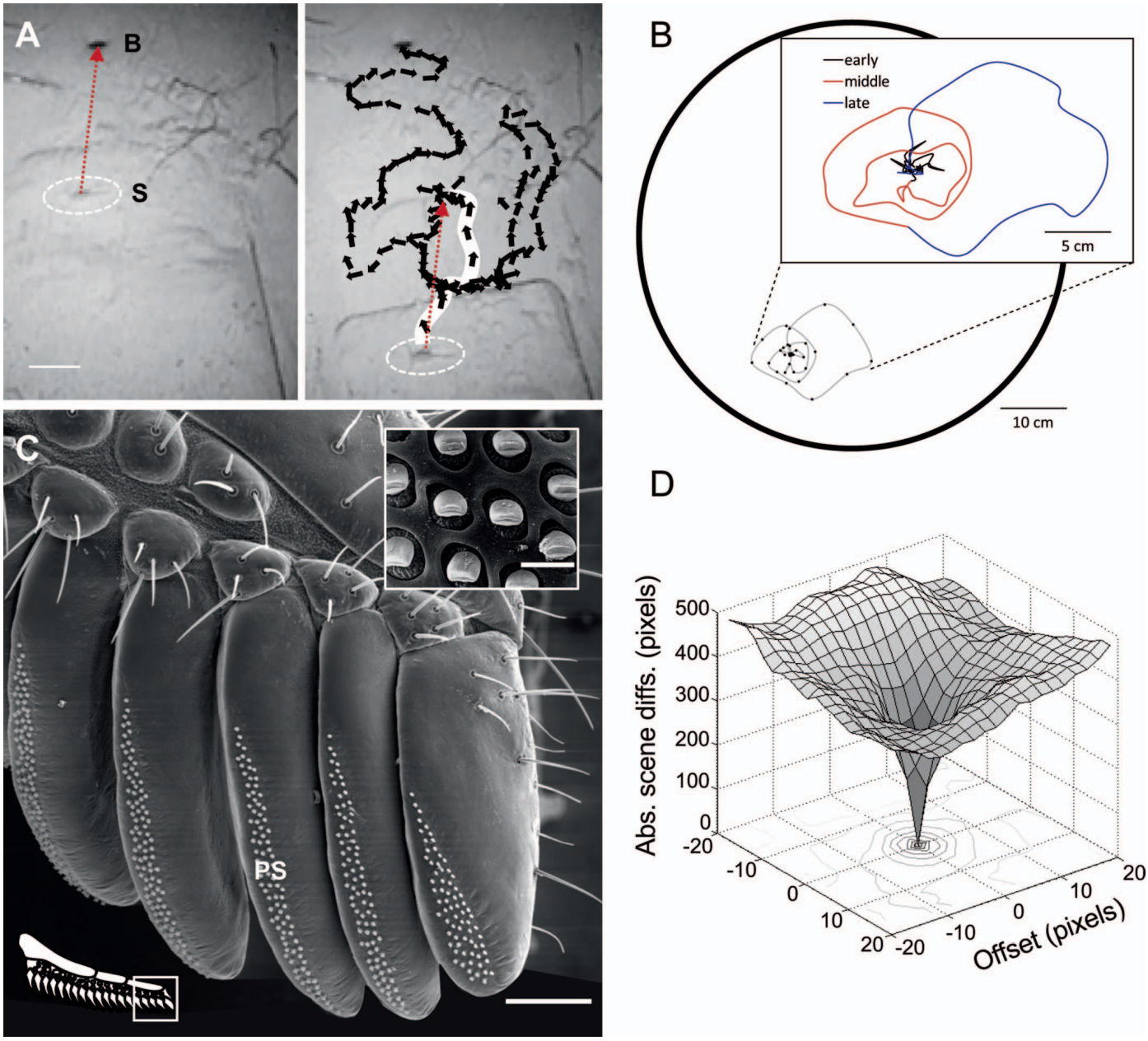


Figure 8.—Requirements for chemo-textural familiarity navigation. (A) Slip sand experiment hints at path integration. Right photo: a scorpion (S) was lured from its burrow (B) to a position atop a submerged cutting board (scale bar is 10 cm). Left photo: board with scorpion was then slid about 20 cm away from the burrow and the subsequent movements of the animal were tracked. Small black arrows indicate position and direction of the animal at roughly 1s intervals. Wide white line shows path of initial movements and thin red dashed arrows indicate distance and direction of the burrow before displacement. (B) A plot of a scorpion's movements immediately after emerging from its burrow in a laboratory study reveals putative learning walks (dots spaced at 8s). The inset shows three phases: initial tight movements next to the burrow (black), secondary movements a little bit farther away (red), and wider looping movements (blue). (C) SEM of distal teeth on left pecten of *P. utahensis* female (scale bar is 50 um); the teeth support dense matrices of chemo-tactile peg sensilla (PS) on their ground-directed faces (photo provided by E. Knowlton). Inset shows SEM of a patch of sensilla from *S. mesaensis* (scale bar is 5 um). (D) An image difference funnel forms when a focal scene is compared to all other scenes based on the sensory resolution of pectinal peg sensilla (see text and Gaffin & Brayfield 2017 for details).

and passes it on to motor centers that produce the appropriate behavior. Along these lines, it should be noted that tooth order is preserved in the neural projection to the subesophageal ganglion in what might be called a "pectinotopic" map (Brownell 1998, 2001; Wolf 2008).

Amblypygids.—The navigational abilities of the neotropical amblypygid *Phrynus pseudoparvulus* Armas & Víquez, 2002 (Amblypygi, Phrynidae) have received considerable attention. These long-lived, nocturnal animals live in dense, complicated rainforest habitats; they emerge from refuges in the crevices of

tree buttresses to hunt (Santer & Hebets 2011b; Chapman & Hebets 2016). They walk on leg pairs 2–4 (Fig. 9A) and use their extremely thin and elongated front legs to communicate with conspecifics (Santer & Hebets 2011a) and chemotactically detect their insect prey (Igelmund 1987; Hebets 2002; Santer and Hebets 2009a). These antenniform legs are up to 30 cm long and are covered with various types of chemo- and mechano-sensory sensilla (Fig. 9B) (Igelmund 1987; Foelix & Hebets 2001; Hebets 2002). Olfactory sensilla are densely concentrated at the antenniform leg tips, and mechanosensory bristles throughout the legs make extensive chemical synaptic contacts with giant axons that rapidly transmit information to the CNS (Foelix 1975; Foelix & Hebets 2001; Spence & Hebets 2007). These animals lend readily to physiological investigation, and the giant neuron action potentials are readily detected using recording electrodes in contact with electrode cream applied to the external leg cuticle (Igelmund & Wendler 1991; Santer & Hebets 2011b). Also, extracellular electrophysiological investigations of the antenniform legs show rich olfactory responses to a variety of organic molecules of different classes and chain length (Hebets & Chapman 2000).

Strong initial evidence of homing in *P. pseudoparvulus* was demonstrated through short range displacement studies. Animals were displaced from their home refuges to the opposite side of their trees (distances ranged from 50 to 450 cm) and were compared to animals from different trees placed in the same release spots. Only one of the 17 non-residents found the resident's home refuge compared to nine of 17 residents (Hebets et al. 2014a). Near range refuge identification appears to be mediated in part by tactile learning (Santer & Hebets 2009b) and olfaction (Hebets & Chapman 2000; Hebets et al. 2014a). In a subsequent field study, animals that were deprived of olfaction by clipping the tips of their antenniform legs were less likely to return to their home refuges after displacement to the opposite side of their trees compared to intact animals (Hebets et al. 2014a). These results are supported by laboratory studies showing that self-derived chemical cues are important in amblypygid home burrow identification (Castro et al. 2019) and that removal of olfactory receptors on distal segments of the antenniform legs appear important for near-range burrow localization (Wiegmann et al. 2019).

Telemetry studies using fitted radio transmitters were used to test homing from longer range displacements (Hebets et al. 2014b). Animals were removed just after dark from their refuges, fitted with transmitters (Fig. 9A), and moved at least 6 m from their home tree (well beyond the tree buttresses). The positions of the animals were recorded each morning following release. All five of the animals tested returned to their home refuges following displacement, though a couple required multiple days. One of the animals moved in a meandering path that covered more than 23 m over three days before returning. Three of the animals that returned successfully on the first day following their displacement experienced a second displacement in a different direction from the first. Of these, one of the animals returned the following day and a second animal returned on the second day. However, the third did not return within the three days of monitoring (Fig. 9C) but was back at its home tree 20 days following release; tracking showed it had moved at least 38 m

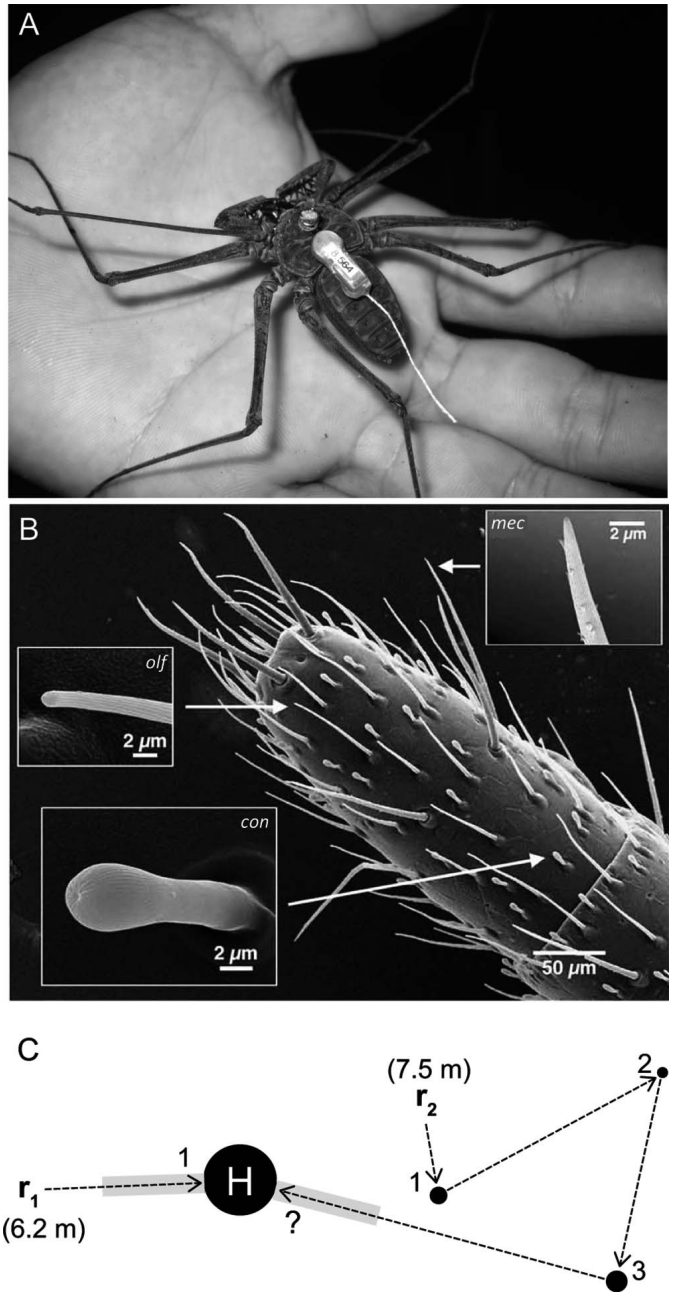


Figure 9.—Homing studies of amblypygids. (A) Photograph of *P. pseudoparvulus* equipped with radio transmitter (photo contributed by V. Bingman). (B) An SEM of the distal tip of an antenniform leg showing dense concentrations of contact chemosensory (con), olfactory (olf), and mechanosensory sensilla (mec) (image online at https://www.frontiersin.org/articles/10.3389/fnbeh.2016.00047/full) (C) Return paths following displacements of *P. pseudoparvulus* from its home tree (H). The animal returned directly to its home tree the following night after its first displacement to position r_1. However, after displacement to a different position (r_2) it meandered away from its home tree to smaller trees on nights 1–3. It was found at its home tree 20 days later after an indeterminate amount of roaming. Parenthetic numbers indicate displacement distances; shaded bars indicate home tree buttress area. Adapted from Hebets et al. 2014.

during its excursion. Additional studies compared homing ability of intact animals to animals with either their eyes or olfactory senses compromised. While both vision and olfaction appear to play a role in homing, olfaction had the greater effect (Bingman et al. 2017).

These tests do not reveal whether these animals are capable of path integration. The displacement was passive, so the animals could not access kinesthetic information gained from outbound journeys. Path integration could be tested by gently nudging the animals to their release points (such as in the *C. salei* and *L. tarantula* experiments above) or by capturing the animals while away from their trees and displacing to a distant, unfamiliar site to see if they move in a vector consistent with that to their home tree had they not been displaced (such as done in the classic ant displacement studies by Wehner 1992). Since amblypygids are long lived animals, it is also possible that the animals in the tests above were placed in familiar areas and followed familiar chemo, textural, and/or visual routes back to their home trees. Since amblypygids are highly sensitive to chemical cues (Hebets & Chapman 2000), it may be that they followed familiar chemical paths acquired during previous homebound journeys, such as shown for desert ants (Buehlmann et al. 2015).

The complex forest habitat, exquisite sensory structures, long-range navigational abilities, and conduciveness to laboratory behavioral and physiological investigations make amblypygids among the most exciting of all navigating arachnids. Furthermore, the higher order brain regions called mushroom bodies are considerably larger and more highly folded in amblypygids compared to insects, suggesting an important integrative role of spatial and multimodal sensory information (Wiegmann et al. 2016).

Other arachnid groups.—Several additional arachnids seem ripe for navigational studies. Tarantulas come to mind because of their size and longevity. Although males have been found to move hundreds of meters, the directionality of their excursions appear to be random and they do not circle back to a central place (Janowski-Bell & Horner 1999). More typically, animals remain at the threshold of their burrow and usually maintain contact with their silken retreat while ambushing prey. Occasionally, tarantulas venture tens of centimeters from their burrow, but they leave a silk dragline for return (Minch 1978; Shillington & Verrell 1997).

The elaborate chemoreceptive maleoli organs of solpugids (Sombke et al. 2019) draw analogies to scorpion pectines, and these animals are known to move extensively on the surface and reuse burrows for successive days (Gore & Cushing 1980). However, solpugids are elusive (Cushing & González-Santillán 2018) and do not lend well to laboratory studies, so very little has been gleaned about their homing mechanisms.

Vinegaroons or whip scorpions (Order Thelyphonida) are large, long-lived animals that thrive in captivity. They have antenniform first legs (Geethabali & Ramamohan 1989) similar to amblypygids, but very little ecological information exists, especially concerning their navigational abilities. This group is in need of further investigation.

Finally, displaced harvestmen nymphs were found to be able to return to a parental aggregation (Proud & Townsend Jr 2008) and surprisingly, displaced females were shown to use vision primarily and proprioception secondarily to return to nests (Silva et al. 2018). These animals are greatly in need of further study.

PHYLOGENETIC CONSIDERATIONS OF HOMING

Why homing has evolved, been lost, or retained across phylogenies can help us understand what navigational strategies and cue redundancies are necessary and sufficient in a given environment. According to Rozhok (2008:84), the "'ecology' of navigation is a field that has hardly been touched in scientific literature with proper scrutiny so far, and its future potential appears vast." Arachnids are excellent models for the ecology of navigation since not all groups have homing, and work has begun documenting the diversification times within the group (Jeyaprakash & Hoy 2009).

Work in other taxa suggests homing varies with environmental conditions. For example, stickleback fish from different habitats showed variation in landmark use (Odling-Smee & Braithwaite 2003) and cue learning (Bensky & Bell 2018). Rat work shows stability of landmarks (or scenes, in our terms here) to be important (Biegler & Morris 1996; Jeffery 1998). Sandhopper crustaceans vary in orientation behavior between populations (Scapini & Buiatti 1985). Reasons for homing (Braithwaite 1998) that vary between taxa or even populations could enlighten us as to the strategies and cues needed for different life histories (Behney et al. 2019). For example, the energetics of navigation varies between migratory populations in birds with different migratory routes (Toews et al. 2014).

Arachnids' taxonomic diversity will allow comparison of different populations within species, between species, and among broader taxonomic groups. In particular, already existing broad coverage of sequencing in arachnid mitochondria, because of the obvious connection to oxidative metabolism, provides fertile ground for energetics studies, made easier by arachnids' tractability in the lab. The taxa currently sequenced include amblypygids (Fahrein et al. 2009), spiders (Masta & Boore 2004; Liu et al. 2015), parasitic mites (Rider et al. 2015; Han & Min 2017), symbiotic mites (Ernsting et al. 2009), free-living mites (Yuan et al. 2010; Lee & Wang 2016; Xue et al. 2016; Schäffer et al. 2018), hooded tickspiders (Fahrein et al. 2007), ticks (Campbell & Barker 1998; Williams-Newkirk et al. 2015), scorpions (Dávila et al. 2005; Choi et al. 2007), pseudoscorpions (Ovchinnikov & Masta 2012), harvestmen (Masta 2010), and more (Jeyaprakash & Hoy 2009).

A notable behavioral research question to be addressed by genomic data is the broader basis for path integration in animals across phyla (Müller & Wehner 1988; Maurer & Séguinot 1995). The genetic and developmental pathways of behavioral traits (The Honeybee Genome Sequencing Consortium 2006; Suen et al. 2011; Schwager et al. 2015) are now in easier reach in the genomics era. Chelicerates, the taxon in which arachnids are nested, have a diversity of genomic architectures (Hoy et al. 2016), including whole genome duplications (Schwager et al. 2017), and different genomic architecture from the often-compared insects (Cao et al. 2013) and arthropods in general (Dermauw et al. 2010). Garb et al. (2018) highlight priority taxa for sequencing to give greater coverage within arachnids. It is plausible that unrelated species may conduct path integration similarly (Wehner 1992). These

genomic features, combined with the fact that some arachnid structures are not homologous to those in insects, such as the respiratory system (Sharma 2017), suggest that examination of path integration and its developmental origins should be studied across arthropods and indeed across Metazoa (Gissi et al. 2008). More specifically, arachnids may provide key variation in both genomic architecture and navigational abilities necessary to understand evolution of this complex set of traits.

CONCLUSIONS

Arachnids are an underused taxon in investigations of navigational behavior. We have reviewed their advantages and current state of knowledge for understanding several navigational systems. Arachnids, especially spiders, have proven to be tractable models for unlocking the mechanisms of near-range path integration. Because of their hardiness, longevity, and conduciveness to laboratory studies, many studies have documented their precise spatial-temporal movements through direct video monitoring, following animal-produced tracks, or remote telemetry. Several arachnid models hold promise for examining cues used during longer-range excursions and may help resolve disagreements over the use of cognitive maps, landmarks, or panoramic scene information during homeward journeys. Further, the special sensory organs of several arachnids, many of which have already proven to be physiologically approachable, will open doors to understanding navigational mechanism beyond vision and help generalize principles related to the matching of sensory resolution to environmental information. Finally, taxonomically broader studies are likely to focus on the evolutionary ecology of navigation and homing both within arachnids and within animals as a whole.

ACKNOWLEDGMENTS

First, we thank Mariëlle Hoefnagels and Wes Honeycutt for their outstanding critical review of this manuscript. We also thank Jen Waller for assistance with image permissions and copyright policies. Finally, we are greatly appreciative of the reviewers for their careful scrutiny of the manuscript and wonderful suggestions for improvement.

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Manuscript received 23 August 2019, revised 7 December 2019.