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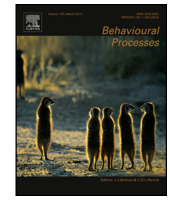

# Multimodal sensory reliance in the nocturnal homing of the amblypygid *Phrynus pseudoparvulus* (Class Arachnida, Order Amblypygi)?

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ABSTRACT

Like many other nocturnal arthropods, the amblypygid *Phrynus pseudoparvulus* is capable of homing. The environment through which these predators navigate is a dense and heterogeneous tropical forest understory and the mechanism(s) underlying their putatively complex navigational abilities are presently unknown. This study explores the sensory inputs that might facilitate nocturnal navigation in the amblypygid *P. pseudoparvulus*. Specifically, we use sensory system manipulations in conjunction with field displacements to examine the potential involvement of multimodal – olfactory and visual – stimuli in *P. pseudoparvulus*' homing behavior. In a first experiment, we deprived individuals of their olfactory capacity and displaced them to the opposite side of their home trees (<5 m). We found that olfaction-intact individuals were more likely to be re-sighted in their home refuges than olfaction-deprived individuals. In a second experiment, we independently manipulated both olfactory and visual sensory capacities in conjunction with longer-distance displacements (8 m) from home trees. We found that sensory-intact individuals tended to be re-sighted on their home tree more often than sensory-deprived individuals, with a stronger effect of olfactory deprivation than visual deprivation. Comparing across sensory modality manipulations, olfaction-manipulated individuals took longer to return to their home trees than vision-manipulated individuals. Together, our results indicate that olfaction is important in the nocturnal navigation of *P. pseudoparvulus* and suggest that vision may also play a more minor role.



## 1. Introduction

Arthropods are known to rely both on idiothetic (internal) and allothetic (external) cues to navigate both short and long distances. For example, path integration, or the assimilation of information that an animal derives from its own movements with its memory of a past position (Mittelstaedt and Mittelstaedt, 1980, 1982), often abetted by visual cues, is known to be an important internal mechanism in successful arthropod homing behavior (reviewed in Wehner and Srinivasan, 2003; Cheng, 2012). Such a mechanism is likely during 'learning walks' in new environments, where animals locate landmarks and produce mental snapshots of their placement (Graham et al., 2010; Muller and Wehner, 2010). Navigation by path integration has been documented in ants (Cheng et al.,

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2009; Wehner and Srinivasan, 1981, 2003; Wehner and Wehner, 1986, 1990), bees (Von Frisch, 1967), spiders (Moller and Gorner, 1994), roaches (Rivault and Durier, 2004), and fiddler crabs (Cheng, 2012; Zeil, 1998), and remains a primary focus of many studies of terrestrial arthropod navigation.

In combination with idiothetic cues, many arthropod taxa simultaneously rely on allothetic (e.g., visual, chemical) cues. For example, despite the assumed difficulty of vision in low light environments, numerous studies confirm the role of visual input in the navigation of nocturnally active arthropods (Cheng, 2012). In fact, Warrant and Dacke (2010) suggest that visual, landmark-based homing (the ability of an individual to return to its preferred retreat) is an essential mechanism of navigation in nocturnal environments (Warrant and Dacke, 2010). Even species with presumably poor eyesight have been shown to rely on visual cues for nocturnal homing. For example, the wandering spider, *Drassodes curpeus*, uses polarized moonlight to find its way back to a silk nest (Dacke et al., 1999) and nocturnal Dancing White Lady spiders in the Namibian desert, *Leucorchestris arenicola*, require only visual cues to return to home burrows (Norgaard, 2005; Norgaard et al., 2003, 2007, 2008). Similarly, African dung beetles, *Scarabaeus zambesianus*, navigate using celestial polarization and other night sky features, including the Milky Way (Byrne et al., 2003; Dacke et al., 2003a,b, 2004, 2011, 2013). Ultimately, reliance on a diverse set of visual cues is widespread among arthropods, even among those that navigate in low light conditions.

While visual cues play a well-characterized role in nocturnal arthropod navigation, the potential role of olfactory cues remains understudied. Past work has largely focused on the role of olfaction in tracking pheromone trails over short distances (Rosengren, 1977; Beugnon and Fourcassie, 1988), but there is evidence that non-pheromonal olfactory cues can also facilitate navigation. For example, the desert ant, *Cataglyphis fortis*, which was previously thought to rely solely on path integration and visual cues to navigate and find their nests, was recently found to use odor landmarks as well (Steck et al., 2009, 2011). Additionally, German cockroaches, *Blattella germanica*, use path integration, visual landmarks, and olfactory cues to indicate the end of their path (Rivault and Durier, 2004). Examples of navigation based upon non-visual sensory modalities, such as olfaction, are none-the-less relatively uncommon. The relative paucity of multisensory navigation studies likely relates to the tradition of navigation research focusing predominantly on a small subset of taxa using modality-specific approaches. We suggest that advancing navigation research necessitates the integrated investigation of multimodality, complex navigation, and a diversity of taxa. Such an approach can not only advance our understanding of the mechanisms underlying navigation, but can contribute to our general understanding of the sensory control of complex behavior. Navigation is a tangible manifestation of complex behavior, and its study requires the identification of model species that successfully navigate in structurally complex environments. To that end, this study explores multimodal sensory reliance, olfaction and vision, during nocturnal navigation in the amblypygid *Phrynus pseudoparvulus* (previously misidentified as *P. parvulus*; see de Armas and Viquez, 2001).

*P. pseudoparvulus* are capable of nocturnal homing through complex tropical understory habitats (Hebets et al., 2014). These nocturnally active predators can travel more than 36 m in linear distance over the course of several weeks (Hebets, 2002). Prior field displacement studies demonstrate that established individuals can return home without the use of path integration and that they may take indirect return routes, which incorporate stopovers at non-home trees during homeward journeys (Hebets et al., 2014). These previous studies paint a picture of a central place forager that retains some degree of site-fidelity, but also navigates around a home territory (of unknown dimensions) that may encompass multiple trees. The mechanism(s) of their putatively complex navigational capacities are currently unknown, but a prior observation of a single displaced individual whose olfactory perception was compromised and did not return home hints towards a role of olfactory reliance (Beck and Gorke, 1974). Additionally, amblypygids possess unique sensory structures that can enable multisensory (including olfactory) perception as well as enlarged brain processing centers (i.e., mushroom bodies) that may provide neural substrates for complex behavior such as navigation.

Amblypygids possess extraordinary sensory appendages that earned them the common name ‘whip spider’. They walk on only six legs (as opposed to the typical eight), and their thin and elongate first pair of legs (frequently measuring 2.5 times the length of the walking legs or longer) are no longer used for walking (Igelmund, 1987). These “antenniform legs” are highly articulated and covered with thousands of sensory hairs that have mechanosensory and chemosensory functions (Igelmund, 1987; Beck et al., 1977; Foelix, 1975; Santer and Hebets, 2011). The multiporous sensilla, located on the distal ~1 cm of the antenniform legs (reviewed in Santer and Hebets, 2011; Weygoldt, 2000), are confirmed to have an olfactory function (Hebets and Chapman, 2000). The visual capacity of amblypygids, in contrast, is thought to be considerably less impressive, facilitated by eight relatively small, single-lens eyes (reviewed in Santer and Hebets, 2011). The sensory structures of amblypygids cast doubt on the importance of visual cues in nocturnal navigation, but raise the distinct possibility that olfaction may be crucial. None-the-less, the predominance of vision in the navigation of other arthropods with purportedly poor sight makes this modality worthy of careful examination. Our goals here were to use the amblypygid *P. pseudoparvulus* to examine the roles of olfactory and visual input in nocturnal homing. We explored this in the field by displacing individuals with manipulated olfactory and visual capacities.

## 2. Materials and methods

### 2.1. Animals

*P. pseudoparvulus* were captured between 1800 and 2100 from the trunks of trees upon which they were residing. Given that most individuals were collected within 3 h of sunset, it is highly likely that they were collected on the tree possessing their prior night’s refuge – likely their home refuge (for details of site fidelity see Hebets, 2002). Individuals were immediately placed in a Ziplock bag to restrain their movements, and their cephalothorax widths (mm) were measured with digital calipers. Their cephalothoraxes (or sometimes abdomens) were then marked with a unique pattern of two (in one instance, three) colored paint dots using DecoColor paint markers (Uchida of America Corporation, USA; Fig. 1). The variation in the number and placement of paint dots was due to us exhausting potential unique color patterns based upon the paint markers available to us in the field. We determined and recorded each individual’s sex and developmental stage (male, female or juvenile) and assigned it to a sensory manipulation treatment (sensory-intact vs. sensory-deprived) detailed in specific experiments. Following manipulations, individuals were transferred to a large, opaque plastic snap-cap vial (which precluded visual feedback) for transport to displacement sites.

### 2.2. Experiment 1 – olfaction manipulation (home tree displacement)

This experiment was conducted in the Arboretum at La Selva Biological Station in Heredia Province, Costa Rica on 8–21 January 2007.