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Nocturnal homing in the tropical amblypygid *Phrynus pseudoparvulus* (Class Arachnida, Order Amblypygi)

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Abstract

Arthropods are renowned for their navigational capabilities, with numerous examples known from insects and crustaceans. Early studies of amblypygids (Class Arachnida, Order Amblypygi) also suggest complex nocturnal navigation, despite their apparent lack of visual adaptations to the low-light conditions of a tropical understory. In a series of two studies, we use the tropical amblypygid, *Phrynus pseudoparvulus*, to assess their nocturnal homing ability. Our first experiment displaced and tracked resident and nonresident individuals. Resident individuals, displaced up to 4.5 m from their home refuges and released onto their home tree, were more likely to return to their previously occupied refuge than were nonresident individuals that were collected from trees outside the study area and released at the same locations. In a follow-up study, we displaced amblypygids longer distances (6–8.7 m) from their home trees and tracked them by telemetry. These individuals returned to home trees, typically within 1–3 nights, often via indirect paths. Taken together, our results provide evidence that P. p*seudoparvulus* are able to navigate home, often taking indirect routes, and can do so through a mechanism other than path integration.

Keywords: Navigation, Spatial cognition, Spatial orientation, Telemetry

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Introduction

The navigational abilities of arthropods are extraordinary (reviewed in Cheng 2012). Desert ants can travel hundreds of meters from their nest and often follow nearly straight paths home (reviewed in Wehner and Wehner 1990). Male wandering spiders in Namibia similarly travel hundreds of meters in search of females and return to their home burrows with minimal retracing of the outward path (Nørgaard et al. 2007). Fiddler crabs are capable of quick returns to their burrow, facilitated by their maintenance of a fixed angle between the position of their transverse body axis and their home (Land and Layne 1995 ; Zeil 1998 ; Layne et al. 2003a , b). The ability of these animals to successfully navigate their way to and from their home (i.e., homing), and the mechanism(s) underlying this ability, have been, and continue to be, the focus of much research.

Here, we examine the homing ability of the neotropical amblypygid *Phrynus pseudoparvulus* (previously misidentified as *P. parvulus* ; see de-Armas and Viquez 2001), a highly mobile nocturnal arachnid whose visual

capabilities are unknown (reviewed in Santer and Hebets 2011). During the day, amblypygids hide in tree crevices, behind bark, under rocky outcrops, or in abandoned burrows of small mammals (Weygoldt 2000). At dusk, they venture out into the rainforest understory to forage, returning to their home refuge by dawn. Field studies of Heterophrynus and Phrynus species reveal a high fidelity for their home refuge, with single individuals residing in the same location for weeks or even months (Beck and Go¨rke 1974 ; Weygoldt 1977 ; Hebets 2002). An earlier mark–recapture study indicated that P. p*seudoparvulus* can travel more than 36 m in linear distance, spread over the course of several weeks, sometimes returning to the tree upon which they were originally observed (Hebets 2002). Such observations led to the suggestion that P. p*seudoparvulus* may have home ranges that include multiple large, buttressed trees spaced tens of meters apart. Given the complexity of the intervening habitat, the previously observed distances traveled, and the potential for large territories, this species seems ideal for studying how nocturnal arthropods navigate complex, low-light, three-dimensional habitats. Here, our goals are to use P. p*seudoparvulus* to: (1) document their homing ability and (2) use telemetry to gain snapshots into return routes when displaced longer distances ([6 m) from a home refuge.

Preliminary background studies

In an early study of amblypygid homing, Beck and Görke (1974) displaced a small number of *Heterophrynus batesii* (as cited in Weygoldt 2000) (n = 9) B 7.5 m from their home tree and found that the majority returned one night after displacements (a single individual displaced 10 mtook\ 5nights to return). This pioneering study, however, did not control for potential attractive, beacon-like qualities of resident trees/ crevices, and data on return paths were not reported.

We conducted a similar preliminary study on P. p*seudoparvulus* in Sarapiqui Province, Costa Rica (January 2000) to establish a protocol for our following experiments. Nine males and three females were captured at dusk as they emerged from their home refuges. Each individual was displaced (see Experiment Procedures) to the opposite side of the tree on which it was collected. Six males and one female were re-sighted at their home refuge over the subsequent three nights (i.e., 58 % returned). Four additional individuals were displaced 3 m from the tree on which they resided, where they were placed on the forest floor. The nearest tree was not always their home tree. Three of these individuals returned to their home refuge within three nights (i.e., 75 % returned). These preliminary results provided the foundation and incentive for the following studies.

Resident versus nonresident displacements

We displaced residents (n = 17) and nonresidents (n = 17) to test (a) whether P. p*seudoparvulus* can successfully navigate back to their home refuge and (b) whether a previously occupied refuge acts as an attractive beacon for a wandering amblypygid. This experiment was conducted in the arboretum at La Selva Biological Station in Sarapiqui Province, Costa Rica on 1–12 January 2007.

Amblypygids

Phrynus pseudoparvulus were captured at dusk as they emerged from home refuges in trees. Individuals were placed in ziplock bags to restrain their movements while cephalothorax widths (mm) were measured with digital calipers. Their cephalothoraxes were marked with a unique pattern of two-colored paint dots using DecoColor paint markers. We determined and recorded the sex and developmental stage (male, female, or juvenile) of each individual. Individuals were then transferred to a large, opaque plastic snap-cap vial (which precluded visual feedback) for transport to displacement sites. The entire process from initial capture to displacement generally took less than 10 min. A total of 34 individuals were used in displacement trials.
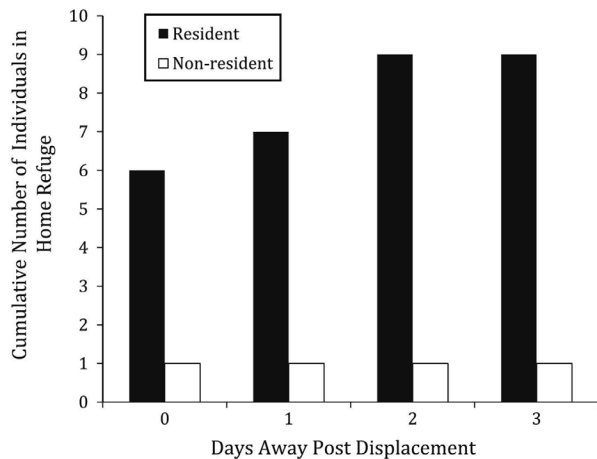
Fig. 1 Relationship between time post-displacement and the cumulative number of individuals relocated in resident refuges. Black bars represent residents (n = 17) and white bars represent nonresidents (n = 17)

Procedures

Residents were located exiting their home refuge at dusk. We marked home refuges using plastic flagging tape and subsequently measured their heights. Residents were transported to a displacement site on the opposite side of the tree and released onto the tree at the height of their home refuges.

Nonresidents were collected from trees that were at least 50 m from the residents' trees and were released at the exact same displacement sites as residents. Nonresidents and residents were matched based on sex and body size (cephalothorax width). Our expectation was that a nonresident would be similarly attracted to a home refuge if the refuges are particularly attractive (i.e., are general beacons). If previously occupied residences are not attractive beacons, we expected only residents to return to the home refuge. Residents were always tested before nonresidents so that they could be removed from their refuges when nonresidents were tested, but residents and nonresidents were otherwise captured and handled identically.

The focal tree for each resident/nonresident pair was searched at dusk and for 2 h afterward on each of the four nights fol-

Fig. 2 Photograph of P. pseudoparvulus fitted with a radio transmitter

lowing displacements. Because P. p*seudoparvulus* typically emerge from their refuges at dusk and do not initially move far from their entrance, we were able to determine the refuge occupied by a displaced individual (if it remained on the focal tree). In particular, we recorded whether the home refuge of the resident was occupied by a marked individual. If a subject could not be relocated on the focal tree, the nearest tree in each of the cardinal directions was also surveyed.

The circumference (C) of focal resident trees at the height of home refuge was measured (cm) after the experiment was completed to approximate the linear distance, namely ½ C, between displacement sites and home refuges.

Results

Three females, ten males, and four juvenile residents and nonresidents were displaced at distances of 50–450 cm (mean ± SD = 198 ± 128 cm) from their home refuges. Nine residents (53 %)—two females, six males, and one juvenile—returned to the home refuge (Fig. 1). An additional three males and one juvenile resident were seen on nearby trees. Only one nonresident (6 %), a male, was ever observed in the refuge of its paired resident, while eight nonresidents (six males, one juvenile, and one female) were re-sighted on nearby trees. Indeed, displaced residents were relocated in their

Table 1 Summary of telemetry data for displaced individuals

| Individual | Displacement site to home tree | | | | |
	Distance (m)	Catchment (m)	Angle (degrees)	Days away	Travel distance (m)[a]
First displacement					
A	6.1	2.2	0	0	6.1 (6.1)
B	8.2	3.5	328	0	8.2 (8.2)
C	6.8	3.2	298	0	6.8 (6.8)
D	6.0	3.9	72	3	23.4 (13.4)
E	6.5	3.2	94	2	12.8 (8.4)
Second displacement					
A	8.7	4.1	108	0	8.7 (8.7)
B[b]	7.5	4.8	132	≥3	≥38.8 (≥17.8)
C	8.5	5.4	349	1	11.1 (8.5)

[a] The minimum (linear) distance a subject traveled to return from its displacement site to its home tree and, in parentheses, the farthest distance a subject was observed away from its home tree before it returned

[b] This individual did not return within the 3 days of monitoring, but was seen at its original location 17 days later (20 days after initial displacement)

home refuges more often than their matched nonresidents (Fisher Exact Test, p = 0.0066), indicating that previously occupied refuges did not act as attractive beacons. The cephalothorax width of residents (mean ± SD = 6.97 ± 3.15 mm) and nonresidents (mean ± SD = 7.14 ± 3.34 mm) was similar (Paired t Test, t = - 0.18; p = 0.7168).

Displacements and telemetry

We used telemetry to follow up our experiment and explore, for the first time, the return paths of P. pseudoparvulus when displaced long distances ([6 m) from their home tree. This study was conducted at La Suerte Research Station (83° 46′15″ W, 10° 26′ 30″ N) on May 25–31, 2012.

Amblypygids

Phrynus pseudoparvulus were captured on their home trees at night after they emerged from their refuges and were fitted with radio transmitters (Fig. 2). Advanced Telemetry Systems A2414 transmitters (with 2.5 cm antennae) were affixed with a cyanoacrylate adhesive to the posterior prosoma (cephalothorax) of six individuals (identified by the letters A–F).

Procedures
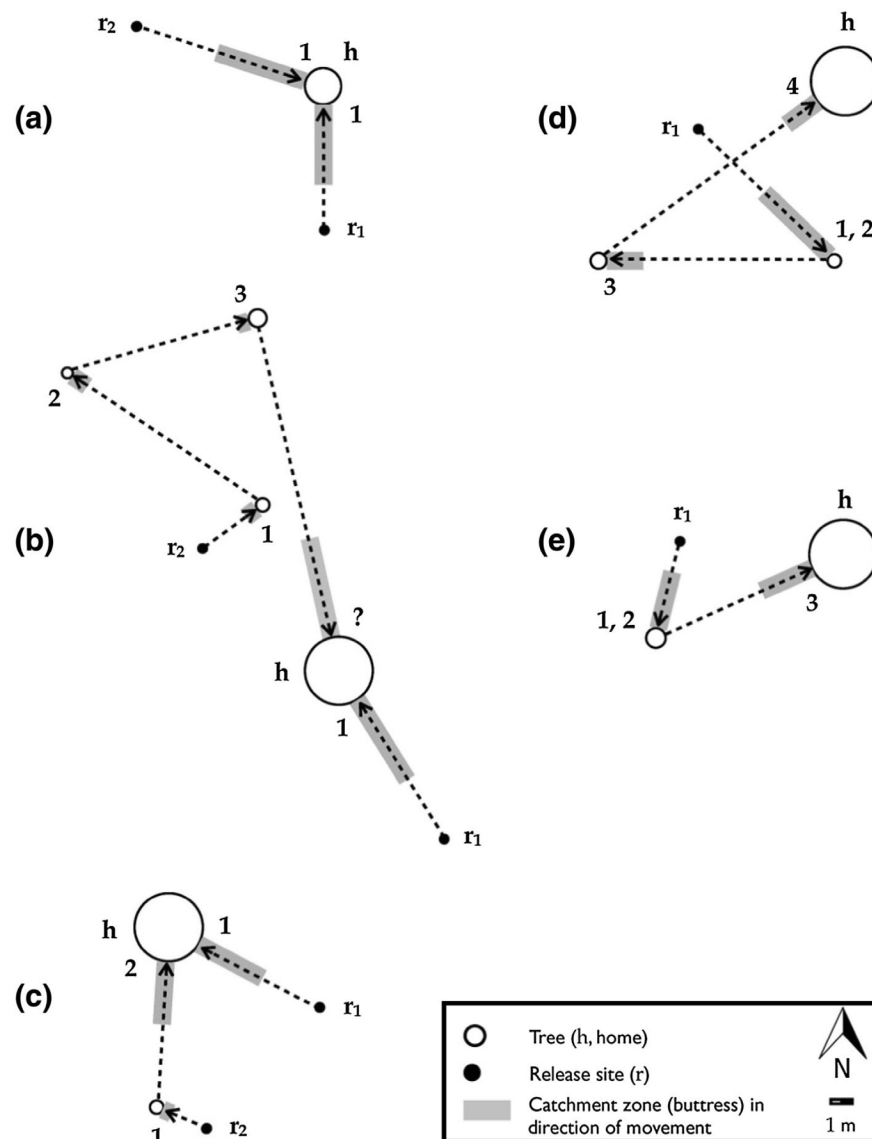
Five of the individuals (A–E) were displaced

at least once, while three (A–C) were displaced twice. Individual F served as a procedural control. It was affixed with a radio transmitter and placed back in its home refuge to insure that the procedure did not instigate wandering or other abnormal behavior. All displacements occurred between 20:00 and 01:00 h. We displaced individuals far enough to prevent their use of buttresses as guides (i.e., beyond what we call the catchment zone) back to their home tree and we chose sites that did not force individuals to cross a trail to return to the tree from which they were collected (for details, see Table 1).

An Advanced Telemetry Systems R410 receiver with a Yagi three-element antenna was used to relocate individuals. Each morning following displacements, the position of each individual was recorded, as was the distance and direction between its release site (or its last known position if an individual took more than one night to return) and its current location. These data were collected in daylight hours, while individuals were sheltering within tree crevices, to ensure that our activities did not interfere with their behavior.

Results

Table 1 summarizes displacement locations and

Fig. 3 Snapshots of movement patterns of displaced individuals (a–e) tracked with telemetry. Dashed arrows indicate the direction of movement from the release site (r) or a stopover tree and the number(s) at the end of arrows indicate the morning(s), after displacement, on which an individual was observed at a particular location. The shaded spokes of arrows show the catchment zone, the extension of tree buttresses in the direction an individual moved. Snapshots of routes are shown for the three individuals (a–c) displaced twice (indicated by subscripts on r), and the two (d, e) individuals displaced only once. The diameter of trees (open circles) was measured at approximately 1 m and is indicated by circle size. The question mark on the final arm of the route used by individual b represents an unknown time to return as its movements were

the movements of individuals after they were displaced. All displaced individuals eventually returned to their home tree, but many (4 different individuals) spent a day or two at 1–3 different stopover trees while in transit (Fig. 3). The nondisplaced individual (F) remained in its home refuge, and no displaced individuals were observed to leave their home tree after they returned. The farthest an individual traveled was more than 38 m during its return trip and the shortest possible distance traveled was 6.1 m (Table 1). Prior work on P. p*seudoparvulus*

has demonstrated site fidelity (Hebets 2002). Individual B was observed on its home tree 20 days after displacement and individual E was observed on its home tree 19 days following its return home, which suggests that at least some individuals remain in their home refuge following homing.

Discussion

This study verifies that the neotropical ambly-pygid, *Phrynus pseudoparvulus* , is capable of nocturnal homing in the tropical forest under-

story. Results of our experiment confirm that individuals find their way back to their refuges when they are artificially displaced to a distant location on their home tree and that residences (i.e., previously occupied tree crevices) do not exhibit general attractive beacon-like qualities. The possibility that resident refuges act as a repellent to nonresidents requires further study, but preliminary olfactometer trials indicate that individuals are attracted to, not repelled by, conspecifics (unpublished data). Furthermore, their ability to navigate cannot be attributed—at least not entirely—to path integration, as individuals were not allowed to conduct their own outward journey. These results are consistent with both our preliminary observations as well as with results of Beck and Görke (1974), who similarly displaced a small number of *Heterophrynus batesii* (as cited in Weygoldt 2000), but did not control for potential beacon-like qualities of refuges.

The mechanism(s) by which P. p*seudoparvulus* navigate through the complex rainforest understory has yet to be studied systematically. Sensory manipulations of a single individual by Beck and Görke (1974) suggest a role of olfaction, but this has yet to be confirmed. Our telemetry results reveal that displaced individuals often take an indirect path home. At least four of our displaced individuals stopped at alternative trees on subsequent nights prior to returning to their home refuge. This pattern of movement is consistent with systematic search, or systematic search followed by goal-directed navigation from within a 'catchment area,' which may or may not be delineated by the extent of the home tree buttresses. Additional studies are necessary to tease apart these, and other, alternative explanations.

In conclusion, the results of our study unequivocally add amblypygids to the growing list of arthropods capable of nocturnal homing. Amblypygids are an obscure and understudied group of arachnids, but our work, in combination with knowledge gained from previous studies (reviewed in Santer and Hebets 2011), highlights their potential to provide novel insights into how habitat characteristics and sensory capabilities interactively shape navigation systems.

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