Importance of the Antenniform Legs, but not Vision, for Homing by the Neotropical Whip Spider, *Paraphrynus laevifrons*

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Summary statement

Tropical amblypygids inhabit structurally complex habitats, yet navigate home in the dark after a night hunting prey. What sensory cues might they use to navigate? Olfaction appears important.

ABSTRACT

Amplypygids, or whip spiders, are nocturnal, predatory arthropods that display a robust ability to navigate to their home refuge. Prior field observations and displacement studies in amblypygids demonstrated an ability to home from distances as far away as 10 meters. In the current study, micro-transmitters were used to take morning position fixes of individual *Paraphrynus laevifrons* following an experimental displacement of 10 m from their home refuge. The intent was to assess the relative importance of vision compared to sensory input acquired from the antenniform legs for navigation as well as other aspects of their spatial behavior. Displaced individuals were randomly assigned to three treatment groups : (i) control individuals-C, (ii) vision deprived individuals-VD, and (iii) individuals with sensory input from the tips of their antenniform legs compromised-AD. C and VD subjects were generally sucessful in returning home, and the direction of their movement on the first night following displacement was homeward oriented. By contrast, AD subjects experienced a complete loss of navigational ability, and movement on their first night indicated no hint of homeward orientation. The data strongly support the hypothesis that sensory input from the tips of the antenniform legs is necessary for successful homing in amblypygids following displacement to an unfamiliar location, and we hypothesize an essential role of olfaction for this navigational ability.

INTRODUCTION

When one considers the remarkable navigational abilities of animals, what often comes first to mind are the long-distance migrations of birds, sea turtles and salmon, or the homing behavior of pigeons. However, what is becoming increasingly apparent is that despite relatively small brains and generally shorter distances traveled, the monarch butterfly (*Danaus plexippus*) not withstanding (Mouritsen et al., 2013), many arthropod species also display an impressive navigational ability (Cheng, 2012; Collett and Graham, 2004; Boles and Lohmann, 2003; Layne et al., 2003). Indeed, both honey bees (*Apis mellifera*; Menzel et al., 2005) and an Australian ant species (*Myrmecia croslandi*; Narendra et al., 2013) have been shown to be able to return to their nests even after experimental displacements to locations where they have never been before suggesting a cognitively rich navigational capacity. Arachnids too display impressive navigational abilities. For example, after searching for females, males of the Namib Desert spider, *Leucorchestris arenicola*, successfully return to their home burrows from as far away as 40 m (Henschel, 2002; Nørgaard, 2005).

Species of the Order Amblypygi (Class Arachnida), colloquially referred to as whip spiders or tailless whip scorpions, inhabit tropical and subtropical regions around the globe where they are often found in dense rain forest (Wegoldt, 2000). Beck and Görke (1974) were the first to report that tropical amblypygids are unexpectedly good at navigating to their home refuge shortly before dawn after having spent the night typically hunting on the vertical surfaces of tree trunks. Even after an artificial displacement of 10 m, one whip spider successfully returned to its home refuge. Building on the observations of Beck and Görke (1974), Hebets et al. (2014a) displaced individuals of *Phrynus pseudoparvulus* up to 4.5 m onto the opposite side of their home refuge tree and found that they were able to home successfully. They additionally used radio telemetry to track the navigational behavior of the amblypygid, *Paraphrynus laevifrons* (though this second species was not identified as such in Hebets et al., 2014a), and found that individuals routinely return to their home tree after experimental displacements of up to 8 meters. The routes that the displaced *Paraphrynus laevifrons* took were not necessarily straight and the journey home often took more than one night to be completed.

Amblypygids are excellent navigators, and although their homing success following displacement may not match the visually guided performance of diurnally active honey bees and

some ants, one needs to consider that tropical amblypygids are nocturnally active and live in a structurally complex environment of a cluttered and uneven ground surface, dense vegetation depriving the animals of any distal panorama of terrestrial stimuli and a dense canopy that offers little access to celestial cues or variation in light intensity. In other words, many of the sensory and behavioral mechanisms that guide the spatial behavior of bees, ants, and even other studied nocturnal navigating arthropods (Warrant and Dacke, 2016) are likely inaccessible to navigating amplypygids. The fascinating question then is what enables amplypygids to be such successful navigators, with the first order challenge being the identification of the sensory cues that guide their homing behavior.

Probably the most notable morphological feature of amblypygids are their elegantly articulating antenniform legs (thus the "whip" in whip spiders). The antenniform legs, and in particular the distal tarsus, are covered with a rich array of sensory receptors (Santer and Hebets, 2011; Wiegmann et al., 2016). Among the numerous receptor types are multiporous sensilla that respond to olfactory cues (Hebets and Chapman, 2000). Unlike the other receptor types, these multiporous sensilla are only found on the distal tips of the antenniform legs (Foelix et al., 1975; Igelmund, 1987). Amblypygids also possess eight eyes composed of a pair of medial eyes and a bilateral set of three eyes positioned more laterally (Weygoldt, 2000). Given their nocturnal activity and the light-impoverished nature of tropical amblypygd habitat, vision would seem to be an unlikely sensory channel to control navigation. Many nocturnal arthropods, however, are remarkably adept at using vision to guide their spatial behavior (Warrant and Dacke, 2016), opening up the real possibility that amblypygids could similarly rely on vision.

A preliminary, mark-recapture field investigation into the relative importance of the tips of the antenniform legs, and by inference olfaction, and vision in the amblypygid *Phrynus pseudoparvulus* revealed that displaced animals deprived of sensory input from the tips of their antenniform legs were never re-located on their home tree (Hebets et al., 2014b). The behavior of the vision deprived animals suggested perhaps a modest loss of navigational ability. The goal of the current study was to expand on this previous work in a distinct species, *Paraphrynus laevifrons,* using miniature-radio transmitters to reconstruct nightly movements following an experimental displacement of 10 m from the home tree. In particular, we investigated more thoroughly the spatial behavior of amblypygids when visual information and sensory information

from the distal tips of the annteniform legs were impaired, with the intent of reaching a better understanding of the sensory basis of their navigational ability.

MATERIALS AND METHODS

Subjects

During the end of June and early July 2014 (N= 19) and 2015 (N=11), 30 *Paraphrynus laevifrons* were captured in second growth rain forest at the La Suerte Biological Field Station (83° 46' 15" W, 10° 26' 30" N) near Cariari, Costa Rica in the Caribbean lowlands. The animals were captured at night after they emerged from their home refuges and, with the exception of two control animals (see below), were fitted with Advanced Telemetry Systems A2414 radio transmitters. The transmitters were affixed with a cyanoacrylate adhesive to the posterior prosoma (cephalothorax) of all individuals and transmitter antennae were trimmed to 2.5 cm. The widths of each individual's prosoma can be found in Table 1, but in general, they were large with typical prosoma widths of 15 mm or more. Individuals were then divided into three treatment groups: (i) control (C), (ii) vision deprived (VD) and (iii) tip of antenniform legs deprived (AD) groups (see below). We also made an attempt to sex each individual in the field, but because many of the individuals defied our best efforts to confidently sex them, we have chosen not to present our "best guesses" on sex. No gravid females were used in the experiment.

Sensory Deprivation Treatments and Displacement

Control (C) animals tested during 2014 consisted of seven animals with attached transmitters and two animals that had colored markings placed on the dorsal surface of their prosomas behind the eyes using DecoColor paint markers. The two animals with colored markings were tested as mark-recaptures in the absence of any in-transit, positional data. To control for the application of black nail polish (424 Black Crème; Wet 'n' Wild, USA) to the sensory deprived animals (see below), all 9 C amblypygids had the proximal segment of their fourth pair of walking legs covered with the black nail polish. One C amblypygid's transmitter stopped transmitting after the first morning; its first night orientation and distance data are included in the results, but this animal was not included in the homing success analysis. The

vision deprived animals (VD, N=5) had all eight eyes painted over with the nail polish. Antenniform leg deprived animals (AD, N=6) had the distal tips of the antenniform legs painted with black nail polish. The nail polish covered the entire tarsus. We chose black so that we could clearly see whether the targeted portion of the leg was indeed fully covered insuring that all receptors were rendered dysfunctional.

In 2015 we did not test any control animals because results from 2014 and our earlier studies revealed a consistent pattern of behavior of sensory intact animals (Hebets et al., 2014a,b). The VD subjects (N=6) were subjected to the same deprivation treatment as in 2014, having all eight eyes painted over with the black nail polish. Instead of using nail polish, the AD animals (N=5) had the ends of their antenniform legs cut with small surgical scissors at a distance of about 11-12 mm from the tips. The different AD treatments of nail polish (2014) and scissor cut (2015) did not result in any detectable differences in behavior (see Table 1) and the data from all AD individuals were pooled for all analyses.

All captures and displacements occurred within four hours after sunset after the amblypygids emerged from their diurnal refuges, which were located in the crevices of tree buttresses or under logs. Upon capture, an animal was held by hand, underwent its nail polish or cutting treatment and then was walked to its release point. The displacement distance for all animals was 10 m, and the direction of displacement was haphazardly scattered across individuals (Table 1) We originally intended to carry out systematic displacements to the cardinal directions, but this proved unfeasible as much of the understory vegetation was simply too thick to reliably move through in any predetermined direction. The 10 m displacements were far enough to prevent the use of home-tree buttresses as navigational guides, i.e., beyond what one could call the *catchment zone* of the home tree. By catchment zone we mean that once an animal is within the enveloping buttresses of a tree, the geometry of the buttresses could literally funnel an animal toward the tree's trunk and presumably closer to its home refuge.

An Advanced Telemetry Systems R410 receiver with a Yagi three element antenna was used to relocate individuals. Each morning following displacement, the position of each individual was recorded as the distance and direction from the release site for the first morning or its last known position on subsequent mornings (if not back at the home tree). The data were collected during daylight hours, while individuals were sheltering in their tree or log refuges, to ensure that our activities did not interfere with their behavior. We are confident that our ability to

relocate animals with the telemetry was accurate as the positions of some subjects were visually verified during the day and every marked animal we saw at night was at the location indicated by telemetry during the morning of the next day. With few exceptions, all animals were relocated for at least five consecutive mornings following displacement and all animals were re-located at least three sampled mornings in a row at the same location; i.e., positon fixes of individuals at their morning locations were taken until they seemed to cease to move from their current refuge. Some animals were re-located as long as ten mornings following displacement. Importantly, all distances reported are the beeline distances from where an animal was found on a given morning and where it was on the previous morning (or its displacement location). Thus, distances reported are minimum distances, and if animals took indirect paths during nightly movements, the actual distances covered would have been longer than those reported.

Statistical analysis

The first-order dependent measure was homing success, which was the proportion of animals that eventually returned to the home refuge within each of the VD, AD and C groups. Of additional interest were the direction of movement on the first night in relation to the refuge tree, the distance travelled on the first night, the total distance a subject travelled and the distance to the home tree from the last recorded position for each of the subjects. A Fisher Exact Test, modified for three groups, was used to test for group differences in homing success, followed by pair-wise tests (Freeman and Halton, 1951); circular statistics were used to analyze the orientation of the animals on the first night (Batschelet, 1981); and one-way ANOVA was used for all other between group comparisons (Sokal and Rohlf, 2011).

RESULTS

The transmitter of one C subject stopped transmitting after the first morning and only its orientation and distance data for the night on which it was displaced could be utilized for analyses. All the individual data used in the analyses are summarized in Table 1.

Homing Success

Presented in Figure 1 are some sample paths recorded from animals in the three treatment groups. With respect to homing success, application of the Fisher Exact Test revealed a significant difference across the three treatment groups (p=0.006). Examination of Figure 2 shows that whereas 6/8 C animals and 6/10 VD animals successfully homed (no group difference, p=0.64), only 1 of 11 AD amblypygids homed, a performance deficit that significantly differed from both the VD (p=0.02) and C (0.006) groups.

Associated with the homing success data were some noteworthy behavioral observations. First, it was not unusual for successfully homing animals to initially move farther away from their home refuge, and then return back to eventually reach their refuge (Figure 1). The four transmitter-carrying C animals that homed took between two and five nights to return to their refuge, and two of those four travelled a minimum distance of more than 20 m before reaching home. The six VD animals that homed took between 1 and 4 nights to return to their refuge, with three of the animals returning on the morning following displacement! In summary, depriving whip spiders of sensory input from the distal tips of their annteniform legs completely disrupted their navigational ability.

Initial Orientation

Summarized in Figure 3 is the orientation of the subjects' movement on the night of displacement. Using the direction to the refuge as the predicted direction, both the C (N = 7, mean = 10°, mean vector length = 0.50, V = 0.49, p = 0.03) and VD (N = 10, mean 319°, mean vector length = 0.46, V = 0.46, p = 0.02) animals were significantly oriented with mean directions whose 95% confidence intervals included the direction to the home refuge. By contrast, the AD amblypgids were disoriented (N = 11, mean vector length = 0.20, V = 0.19, p =

0.19). Despite the presumptive conflicting motivations of escaping from capture and returning to the home refuge, both the C and VD animals already displayed an ability to orient homeward on the first night. No such ability was detected in the AD animals.

Distance Travelled

The interpretation of the AD animals' inability to return home arising as a failure to navigate is confounded by the possibility that disrupting the tips of the antenniform legs eliminated the motivation to return. To partially untangle a navigational from a motivational effect, we were particularly interested in how far the animals moved after they were displaced (Figure 1). Figure 4 summarizes the minimum distance moved on the first night after displacement and the minimum total distance travelled across all nights among the animals in the three treatment groups. No between group differences were found in either the distance travelled on the first night ($F(25,2) = 0.62$, $p = 0.56$; C, mean 5.0 m, SE +/- 0.73 m; VD, 5.8, +/- 1.02; AD, 4.5, +/- 0.72) or the cumulative distance travelled across nights ($F(24,2) = 0.71$, $p = 0.50$; C, 17.4, +/- 3.55; VD 11.9, +/- 1.63; AD 14.0, +/- 3.48). A curiosity was one AD subject that covered a minimum total distance of 44.6 m during its nightly wanderings. Despite moving as far as the C and VD amblypygids, the mean distance away from the home refuge of the AD animals at the end of sampling was 10 meters (SE +/- 1.5m); as a group, the AD animals made no progress toward their home refuge following displacement. Sensory deprivation to the tips of the antenniform legs did not inhibit the AD animals from moving around (cutting the tips of the antenniform legs similarly does not interfere with the tendency to move in *Phrynus marginemaculatus* tested in a laboratory arena, personal observation), rendering more probable that the behavioral effects of antenniform leg disruption was principally a result of a navigational rather than motivational impairment.

DISCUSSION

The present study demonstrates that, despite their nocturnal behavior and the structurally complex and light diminished nature of their natural habitat, individual *Paraphrynus laevifrons* are remarkably capable navigators that routinely return to their home refuge following experimental displacements of 10 m (see also Hebets et al., 2014a). Indeed, displacements carried out in other subjects, which were not part of the current experiment, yielded evidence for successful navigation from distances as far as 25 m (Wiegmann et al., In prep). Amblypygids are not the only arthropods that have proven to be successful nocturnal navigators (Warrant and Dacke, 2016), and their homing ability may not be as good as in, for example, bull ants (*Myrmecia pyriformis*, Reid et al., 2011). However, most of the documented examples of successful navigation in nocturnal arthropods occur in species that live in relatively open spaces with easily accessible visual information and where retinal adaptations that increase the gain of a visual signal have evolved (Warrant and Dacke, 2016). What is remarkable about *P. laevifrons* is not so much that they are nocturnal, but that they are able to successfully navigate in an environment of seemingly overwhelming structural complexity and minimal reliable sensory guide posts.

Animals rarely organize their movements in space randomly, but the apex of spatial ability is generally considered to be the capacity to navigate to a goal following experimental (or any) displacement to an unfamiliar location (Wiener et al., 2011). In arthropods, this capacity to re-orient following displacement has been documented in a number of species including honey bees (Menzel et al., 2005), a species of diurnal ant (Narendra et al., 2013), the nocturnal bull ant (Reid et al., 2011) and spiny lobsters (*Panulirus argus*, Boles and Lohmann, 2003). Amblypygids can now be confidently added to this list. Having said that, we acknowledge that we cannot be certain that every displaced individual was unfamiliar with its release site given that amblyppygids, particularly larger, older ones like those used in the current study, move considerable distances and change home trees (Hebets, 2002). However, the general success of the C and VD subjects to return to their home refuge, and more importantly the fact they were released on the ground, indicates that amblypygids can characteristically return to their home refuge following experimental displacements to unfamiliar locations. Finally, it is worth noting that despite the impressive distance of their migration, monarch butterflies do not count among

the arthropod species that can re-orient following displacement, at least during migration (Mouritsen et al., 2013).

The principal goal of the present study was to determine the extent to which vision and sensory information from the tips of the antenniform legs is necessary for successful navigation. The results reveal a complete loss of navigational ability following disruption of the antenniform leg tips while there was no detectable effect of depriving the animals of visual input; results consistent with preliminary mark-recapture findings of Beck and Görke (1974) and Hebets et al. (2014b), who studied *Heterophrynus batesii* and *Phrynus pseudoparvulus*, respectively. However, one cautionary note is warranted regarding vision. Our sample sizes were on the order of 10 animals per group, and therefore we acknowledge the possibility that a larger sample size could have revealed a navigational deficit (modest) following visual deprivation. However, the impression we had in the field is that, if anything, the VD animals were perhaps even better at homing compared to the C animals (but see the *P. pseudoparvulus* of Hebets et al. (2014b)), and clearly any eventual effect of visual deprivation would be modest compared to the devastating effect on homing from lost information derived from the tips of the antenniform legs.

Depriving whip spiders of sensory input from the distal tips of their annteniform legs completely disrupted their navigational ability. It is noteworthy, however, that one did return home and did so in one night. However, that one animal was displaced and released at close to the same time and location as a VD animal, which was captured from the same tree and also homed that same night. This admittedly anecdotal observation strikes us as extraordinary, and in our view, raises the real possibility that social interactions between animals can occur during nightly forays, social interactions that may have navigational consequences even in animals deprived of sensory inputs to their antenniform leg tips.

Given the necessary role of the antenniform leg tips in enabling navigation in *P. laevifrons*, the important question that arises is which stimulus or combination of stimuli detected by the antenniform legs is essential in supporting navigation. The antenniform legs are elegantly articulated and possess chemosensory, mechanosensory and possibly humidity sensing sensilla (Santer and Hebets, 2011; Wiegmann et al., 2016). However, whereas mechano-, contact chemo- and humidity-sensing receptors are found along most of the entire length of the antenniform leg, multiporous, olfactory sensilla are limited to the distal tarsus. Therefore, by disrupting only the tips of the antenniform legs of our experimental subjects, it logically follows

that the detection of olfactory cues would be most seriously impaired. This consideration lends strong support to the hypothesis that much of the navigational behavior of *P. laevifrons* is based on olfactory information (see also Beck and Görke (1974) and Hebets et al. (2014b)). Indeed, olfaction as a navigational guide is not unusual in arthropods, particularly in ants (Steck, 2012; Buehlmann et al., 2015).

In the context of the proposed olfactory hypothesis, there are three considerations worth elaboration. First, several of the AD animals were later seen again after treatment and one of those animals had dropped both its entire antenniform leg tarsi presumably as a result of our experimental manipulation. In the lab, cutting the tip of the antenniform legs in *P. marginemaculatus* results in the dropping of an entire antenniform leg tarsus in about 10% of the cases (personal observation). We acknowledge that more than one of the AD subjects may have dropped the entirety of both of its antenniform leg tarsi, consequently losing much more sensory ability than just olfaction. However, only one of the AD animals observed after treatment dropped an entire antenniform leg tarsus and we remind the reader that just one of the AD subjects ever returned to its home refuge, and that one animal likely followed a VD subject.

Second, following from the olfactory hypothesis, the temptation is to assume that each home refuge was characterized by some unique olfactory signature that could be detected by the displaced animals. However, it is noteworthy that the vast majority of the home refuges were associated with *Pentaclethra sp.* trees. Whatever olfactory information the animals may have used to discriminate their home refuge from alternative sites, it is unlikely to be based on a signal unique to the species of tree associated with the home refuge. It is important to point out here that the successful navigation of the C and VD animals also could not have resulted from the simple strategy of "find a *Pentaclethra* tree". Many of the animals that successfully homed were closer to alternative *Pentaclethra* trees than their home refuge when released. Also, in one anecdotal case, we displaced a marked, unmanipulated subject from one *Pentaclethra* tree on to the trunk of a nearby (5 m) *Pentaclethra* only to see the animal on its home, capture tree a few nights later.

Finally, probably what was most striking about the successful homing of *P. laevifrons* is that it would routinely take more than one night for the animals to return to their home refuge with the subjects taking routes that often deviated substantially from the beeline route between release site and home refuge (an observation that also speaks against the unlikely use of path

integration by the displaced subjects). Indeed, subjects that eventually homed could even increase their distance to the home refuge on the night of displacement (see also Hebets et al. 2014a). If the olfactory hypothesis can explain, at least in part, the successful navigation of amblypygids following displacement, then the typically multiple night, less direct paths taken by *P. laevifrons* could provide hints as to both the chemical nature of the signals, how those signals are distributed in the environment and how the olfactory information is processed and represented in the brains of *P. laevifrons*. For example, at night a few individuals were observed on the trunks of non-home trees prior to eventually returning to the home tree, suggesting the possibility that climbing trees could be a behavioral mechanism that facilitates detection of olfactory cues hypothetically useful for navigation.

In our view, the challenge now is to experimentally test the validity of the olfactory hypothesis and investigate the behavioral and neural implementation of an eventual "olfactory map" under controlled laboratory conditions while remaining cognizant that olfaction may be only one element in the navigational tool box of amblypygids that enables their impressive homing ability (Wiegmann et al., 2016).

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Competing Interests

The authors declare no competing or financial interests.

Author Contribution

V.P.B., J.M.G., E.A.H. and D.D.W. designed the study, V.P.B., J.M.G. and D.D.W. conducted the experiments, V.P.B. and D.D.W. analyzed the data, and V.P.B. wrote the manuscript with contributions from E.A.H. and D.D.W.

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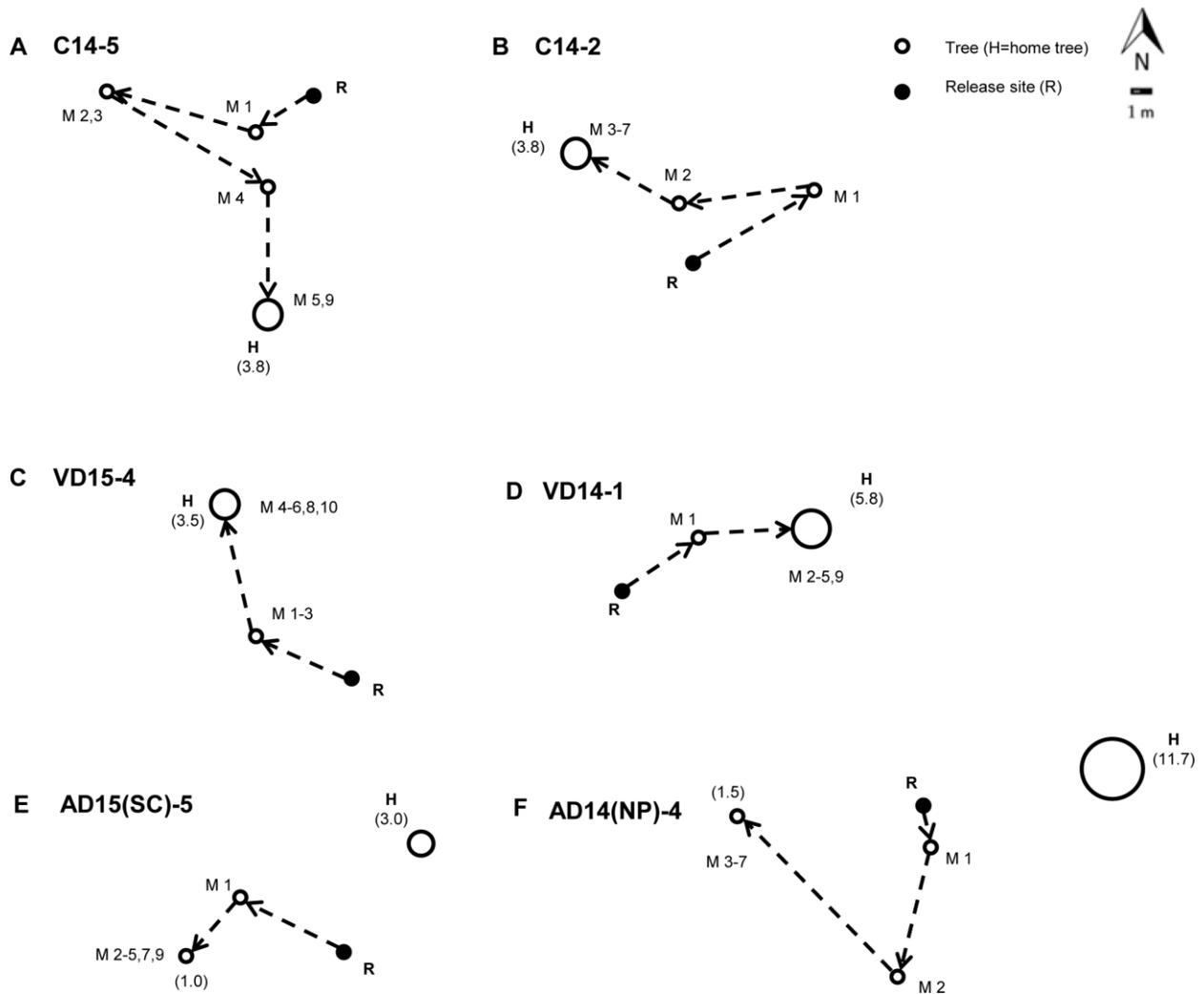
Figures

Figure 1. Representative tracks of two control (A,B), two vision deprived (C,D) and two tips of antenniform legs deprived (E,F) *Paraphrynus laevifrons*. R associated with a filled circle identifies the release site of an individual with the home tree, H, identified as an open circle, the circumference of which, in m, is found in parentheses (not drawn to scale). M#, associated with an open circle, identifies the locations where animals were re-located on mornings following release; the numbers associated with the Ms identify the morning after

release. (Because weather did not permit us to search for subjects on each day, the daily locations are incomplete for some subjects.) For AD animals E and F, the circumference of the tree they eventually adopted as their new home can be read in the parentheses of their last recorded location. Direction north and scale bar can be found on the upper right. All displacements were 10 m.
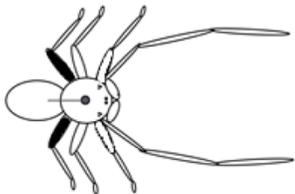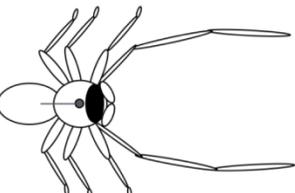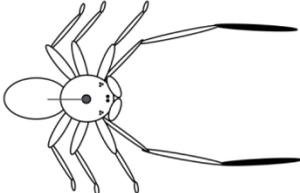
	Home (+)	Home (-)
C	6	2
VD	6	4
AD	1	10

Figure 2. Homing success summary for the three treatment groups. Top, C; middle, VD; bottom, AD subjects.
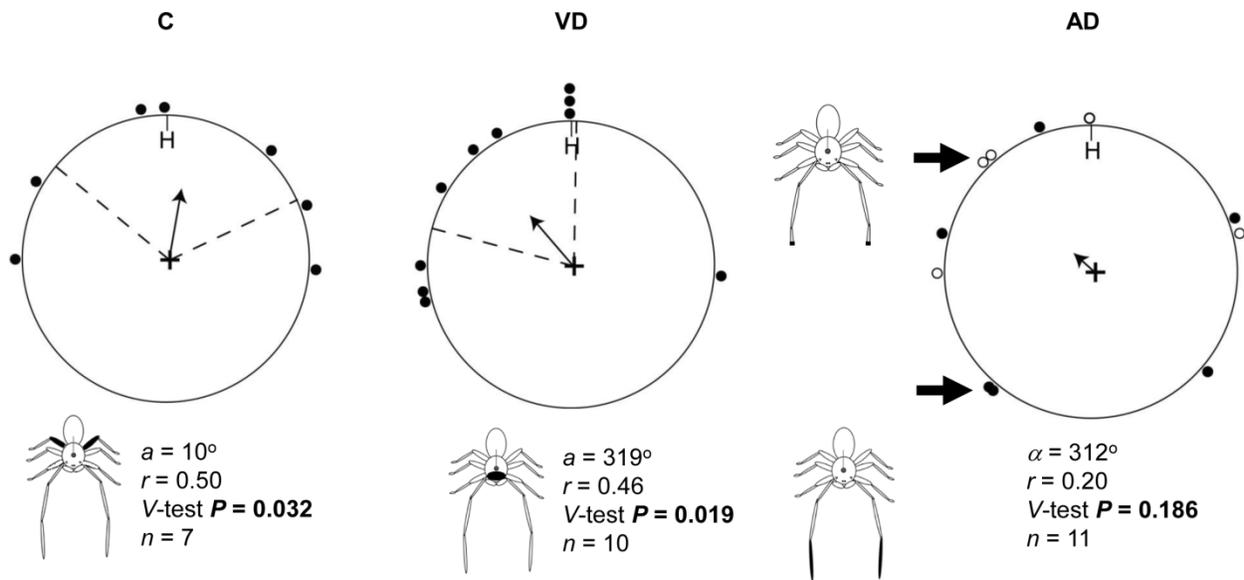
Figure 3. Orientation of the first night movement across the three treatment groups. Dots on the outside of each circle identify the direction of movement of one individual (for the AD animals represented in the right circular diagram, filled dots are nail polish subjects and open dots are scissor-clipped subjects). Arrows at the center of each circle identify the groups' mean vectors, whose lengths are proportional to the mean vector length (r, with an arrow equal to the radius of a circle indicating a mean vector length of 1.0). Directions are plotted with respect to home (H) located at the top of each diagram. α, mean direction; r, mean vector length.
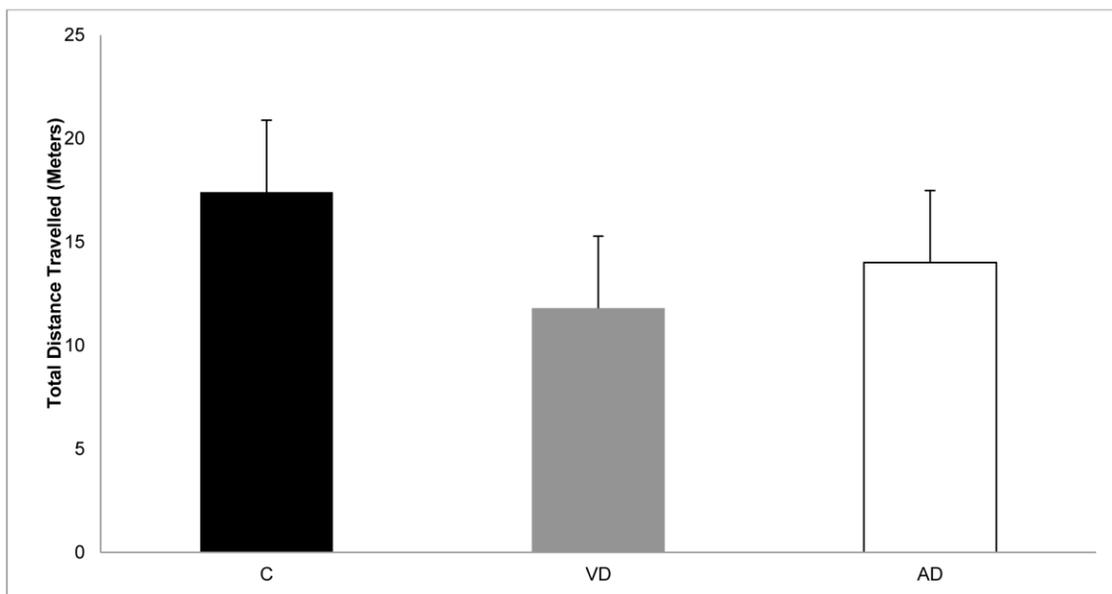
A
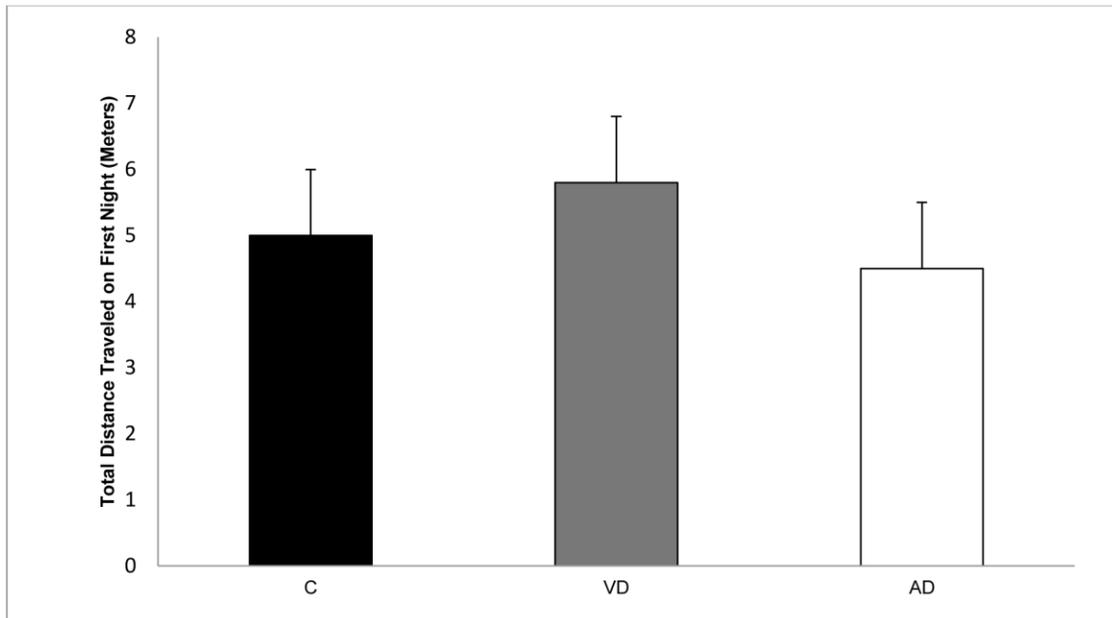
B

Figure 4. Mean distance moved, in m, by each treatment group (C, black bars; VD, grey bars; AD white bars) on the first night after release (A) and accumulated over all nights (B). Standard error bars are shown.

Table 1. Summary of telemetry data for displaced individuals

Animal	P	$DR_{H/G}$	$DR_{N1/H}$	DS_{N1}(m)	DS_T(m)	DS_{THT}(m)	N_{HOMED}
C14-1	15.3	90°	70°	7.2	7.2	9.5	X
C14-2	18.7	315°	95°	7.7	20.7	0	3
C14-3	13.9	150°	360°	5.0	24.5	23.0	X
C14-4	14.3	360°	270°	2.5	12.7	0	2
C14-5	19.7	200°	45°	4.2	29.2	0	5
C14-6	16.7	360°	60°	3.2	-	-	-
C14-7	19.2	260°	350°	5.2	10.2	0	2
VD14-1	19.0	60°	330°	5.7	11.4	0	2
VD14-2	18.3	290°	95°	3.5	6.2	12.0	X
VD14-3	15.1	180°	360°	10.0	10.0	0	1
VD14-4	18.0	270°	360°	10.0	10.0	0	1
VD15-1	15.6	125°	260°	2.8	16.3	10.5	X
VD15-2	18.1	325°	320°	5.8	12.9	0	4
VD15-3	10.2	265°	255°	4.2	21.5	14.0	X
VD15-4	18.2	215°	360°	10.0	10.0	0	1
VD15-5	15.8	250°	300°	4.3	13.4	0	3
VD15-6	18.3	30°	270°	1.2	1.2	10.1	X
AD14(NP)-1	15.2	225°	285°	4.5	11.5	12.3	X
AD14(NP)-2	19.0	180°	220°	2.6	17.0	12.0	X
AD14(NP)-3	18.1	260°	340°	3.6	44.6	4.8	X
AD14(NP)-4	16.8	90°	70°	1.9	21.4	19.2	X
AD14(NP)-5	20.0	200°	130°	5.6	6.6	14.5	X
AD14(NP)-6	16.5	180°	220°	2.8	5.8	12.2	X
AD15(SC)-1	-	215°	360°	10	10	0	1
AD15(SC)-2	16.2	325°	320°	5.8	5.8	6.7	X
AD15(SC)-3	15.9	10°	75°	4.5	10.3	9.4	X
AD15(SC)-4	13.0	90°	315°	1.8	1.8	8.7	X
AD15(SC)-5	19.5	30°	270°	6.3	10.4	15.0	X

C, VD, AD(NP), and AD(SC) are control, vision deprived, tips of antenniform legs nail polished and tips of antenniform legs scissors cut subjects, respectively. P, individual prosoma widths in mm; $DR_{H/G}$, direction home from release location with geographic north set to 360°; $DR_{N1/H}$, direction moved during the first night after release with the home direction set to 360°; DS_{N1}, distance travelled on the first night after release in m; DS_T, total distance travelled across all recorded mornings in m; DS_{THT}, distance to the home refuge tree from the last recorded position in m; N_{HOMED}, number of nights taken to return home (X indicates the subject never returned home). Note, the transmitter for subject C14-6 stopped working after the first recorded morning position.