Visual navigation in the Neotropical ant *Odontomachus hastatus* (Formicidae, Ponerinae), a predominantly nocturnal, canopy-dwelling predator of the Atlantic rainforest

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ABSTRACT

The arboreal ant *Odontomachus hastatus* nests among roots of epiphytic bromeliads in the sandy forest at Cardoso Island (Brazil). Crepuscular and nocturnal foragers travel up to 8 m to search for arthropod prey in the canopy, where silhouettes of leaves and branches potentially provide directional information. We investigated the relevance of visual cues (canopy, horizon patterns) during navigation in *O. hastatus*. Laboratory experiments using a captive ant colony and a round foraging arena revealed that an artificial canopy pattern above the ants and horizon visual marks are effective orientation cues for homing *O. hastatus*. On the other hand, foragers that were only given a tridimensional landmark (cylinder) or chemical marks were unable to home correctly. Navigation by visual cues in *O. hastatus* is in accordance with other diurnal arboreal ants. Nocturnal luminosity (moon, stars) is apparently sufficient to produce contrasting silhouettes from the canopy and surrounding vegetation, thus providing orientation cues. Contrary to the plain floor of the round arena, chemical cues may be important for marking bifurcated arboreal routes. This experimental demonstration of the use of visual cues by a predominantly nocturnal arboreal ant provides important information for comparative studies on the evolution of spatial orientation behavior in ants.

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1. Introduction

When an animal leaves its shelter or nest to search for food, it becomes exposed to many risks, including getting lost. In social insects, the survival of the colony depends heavily on the success of a subset of workers (foragers) in bringing food to be shared with nestmates. Some social insects are equipped with sophisticated navigation systems allowing them to travel tens to thousands of meters away from their nest and still find their way back, even in landmark-free habitats such as deserts (Wehner et al., 1996). The desert ant *Cataglyphis*, for instance, records direction and distance traveled while searching for food and integrates this information to form a homing vector with the shortest distance to the nest. This mechanism is known as path integration and involves the use of a compass based on celestial cues and an internal odometer for measuring distance (Müller and Wehner, 1988; Wehner, 2003; Wittlinger et al., 2007). Flying insects such as the honeybee (*Apis*) utilize similar navigational strategies, relying on optical flow for measuring distances traveled from the nest and visual cues such as horizon patterns and celestial cues as sources of directional information (Srinivasan et al., 2000; Wehner, 1992; Wolf, 2011). Insect navigation has been mostly investigated in diurnal insects such as desert ants and honeybees (Collett et al., 2013; Wehner, 1992). While foraging, these insects often face environments with a high degree of freedom of movement, in contrast to foraging in more constrained maze-like environments. In fact, we know very little about navigation in animals that are night-active or that live in environments with a lower degree of directional freedom (e.g., network of branches in tree canopies). By foraging in maze-like environments and with lower incidence of photons, insects face different navigational challenges and may therefore adopt different strategies. For instance, while traveling in the maze-like floor of Central Australia grasslands, the crepuscular desert ant *Melophorus bagoti* uses a route-based navigation system that is independent of path integration, unless they are displaced to unfamiliar terrain (Kohler and Wehner, 2005). Similarly to many

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diurnal ants, night-active ants may rely on chemical trails for guidance, as in *Formica nigricans* (Beugnon and Fourcassie, 1988) and *Camponotus pennsylvanicus* (Klotz, 1986). Some other night-active ants, however, are not capable of laying or using chemical trails and must use other sources of directional information. The bull ant *Myrmecia pyriformis*, for instance, uses polarized light for navigation if there is sufficient light (Reid et al., 2011). Peak foraging occurs at twilight (Narendra et al., 2010), but in dimming light *M. pyriformis* often gets lost (Narendra et al., 2013). In forests, dense plant cover compounds the problem of fading light at twilight. Moreover, when insects navigate under areas shaded by the canopy, the use of celestial cues for navigation and the use of polarized light becomes limited (Shashar et al., 1998). Low light conditions decrease the contrast of landmarks at the forest floor resulting in less salient cues for navigation, as in *Paraponera clavata* (Ehmer, 1999). Nonetheless, the canopy may still form patterns of high contrast that can serve as a reliable reference for guidance, even at night. This is the case not only for *P. clavata* (Baader, 1996; Ehmer, 1999), but it has also been suggested for many other night-active ants such as *Odontomachus bauri* (Oliveira and Hölldobler, 1989), *Nothomyrmecia macrops* (Hölldobler and Taylor, 1983), and *C. pennsylvanicus* (Klotz and Reid, 1993).

Few studies have been carried out on ants that forage in tree canopies, despite their great abundance and diversity (Davidson and Patrell-Kim, 1996). Tracking and manipulating foraging ants in the canopy to study their navigational abilities presents logistic challenges, especially if observations are made during the night. In addition, the field of canopy biology is relatively new and the standardization of methods is still a work in progress (e.g., Lowman et al., 2012; Moffett, 2000). Not surprisingly, there is a scarcity of studies involving navigational behavior of tree dwellers. Navigation in tree canopies, in contrast to navigation in terrestrial habitats, involves movement within a tridimensional habitat. It is likely, however, that the guidance systems used to navigate in a tridimensional maze include elements of the navigation systems of ground foragers. For instance, *Gigantiops destructor*, a formicine ant that forages both on the ground and on trees, is able to navigate through a maze by retrieving their motor memory on the sequences of turns needed to reach the other end of the maze (Macquart et al., 2008). An insect navigating in a tree may be also exposed to a high diversity of patterns from the horizon ("horizon patterns" from now on). For instance, workers of the tree and ground foraging ant *Formica japonica* use horizon cues when traveling back to the nest (Fukushi, 2001). Other local features such as small stones or vegetation can also serve as visual markers for foraging ants, as shown in *F. rufa* (Nicholson et al., 1999), *Cataglyphis* spp. (Wehner, 2003) and *M. bagoti* (Cheng et al., 2009). Graham et al. (2003) demonstrated that the routes traveled by the ant *F. rufa* can be also affected by tridimensional objects along the way, as shown by the placement of artificial landmarks such as cylinders. Ants are generally attracted to objects (beacons) en route, which segment their homing path in different points. This segmentation decreases the likelihood of an ant getting lost if slightly displaced from their homing path (Graham et al., 2003).

1.1. The trap-jaw Odontomachus ants (Ponerinae)

Odontomachus ants are found in Central to South America, tropical Asia, Australia, and Africa, but are especially abundant in the Neotropics where many species occur from semi-arid to rainforest environments (Brown, 2000). Commonly known as trap-jaw ants, *Odontomachus* species have large, powerful mandibles that open 180° and snap shut on a broad variety of invertebrate prey (e.g., Dejean and Bashingwa, 1985; Ehmer and Hölldobler, 1995; Raimundo et al., 2009). Depending on the species, *Odontomachus* foragers may search for food on the ground and/or vegetation,

and can also consume plant-derived food such as sweet exudates (Blüthgen et al., 2003; Souza and Francini, 2010) and nutritious fleshy seeds and fruits (Passos and Oliveira, 2004; Christianini and Oliveira, 2010).

Odontomachus hastatus, an ant species inhabiting forests of Central and South America (Kempf, 1972), brings together features that makes it a great model for research in spatial orientation. This species is a crepuscular-nocturnal ant that concentrates its foraging in treetops, without chemical trails, in a habitat spatially similar to a maze (Jander, 1990). In the sandy plain forest of Cardoso Island (Brazil) specifically, *O. hastatus* is exclusively arboreal, with nests located among roots of large epiphytic bromeliads (Fig. 1; Oliveira et al., 2011; in French Guiana the ant nests on the ground, see Gibernau et al., 2007). These ants are solitary foragers and their foraging activity typically increases after sunset (around 17:30 h) and decreases after sunrise (around 5:30 h) (Camargo and Oliveira, 2012). On Cardoso Island, foragers of *O. hastatus* always move away from their nest towards the canopy and nearby plants, where they search for a variety of arthropod prey (Camargo and Oliveira, 2012; personal observation). No *O. hastatus* foragers were recorded in an extensive sampling of ground-dwelling ants in the same area (Passos and Oliveira, 2003).

This study investigates the mechanisms of spatial orientation in *O. hastatus* through field observations and laboratory experiments. First, we determined how far workers of *O. hastatus* forage in the field. Then, we hypothesized possible navigational cues based on these observations and the literature pertaining to insect navigation. Workers navigating in the tree canopy are exposed to visual patterns such as the silhouettes formed by the canopy vegetation and the succession of branches and bifurcations, which can provide directional information during foraging (Fig. 1D and E; see Hölldobler, 1980; Oliveira and Hölldobler, 1989). We tested the importance of the canopy, horizon patterns and branches as visual cues during navigation of *O. hastatus*. There are no known records of chemical trail use in the genus *Odontomachus*. However, the related species *O. bauri* and *O. troglodytes* have been reported to use feces markings as a cue for finding the nest at close range (Dejean et al., 1984; Jaffé and Marcuse, 1983). We have observed that *O. hastatus* tends to deposit fecal spots around the nest. Based on these observations, we also tested the importance of chemical marking during homing behavior in *O. hastatus*.

2. Material and methods

2.1. Field observations

Field work was carried out in 2008, in the sandy plain forest ("restinga" forest) of the Parque Estadual da Ilha do Cardoso (hereafter PEIC) (25°03′ S, 47°53′ W), a 22,500 ha island (altitude 0–800 m a.s.l.) located off the coast of São Paulo State, southeast Brazil. Sandy plain forests are part of the Atlantic forest domain, from which they differ by having an open canopy, dominant low stature trees and abundant epiphytes (Oliveira-Filho and Fontes, 2000). The sandy forest at PEIC consists of 5–15-m-tall trees forming an open canopy (Fig. 1), with abundant bromeliads on the ground (Barros et al., 1991).

Two easily accessible colonies of *O. hastatus*, 30 m apart from one another, were chosen for the nocturnal observations. Both focal colonies were relatively large (each containing 300–500 workers) and nested among roots of clumped epiphytic bromeliads *Vriesea altodaserrae* (L. B. Smith) (Bromeliaceae), ca. 2 m above ground (Fig. 1A). No other colony of *O. hastatus* was found within 10 m around each focal colony. Observations took place during the peak of foraging activity, which in the summer occurs between 22:00 and 02:00 h (see Camargo and Oliveira, 2012). The ants' main foraging
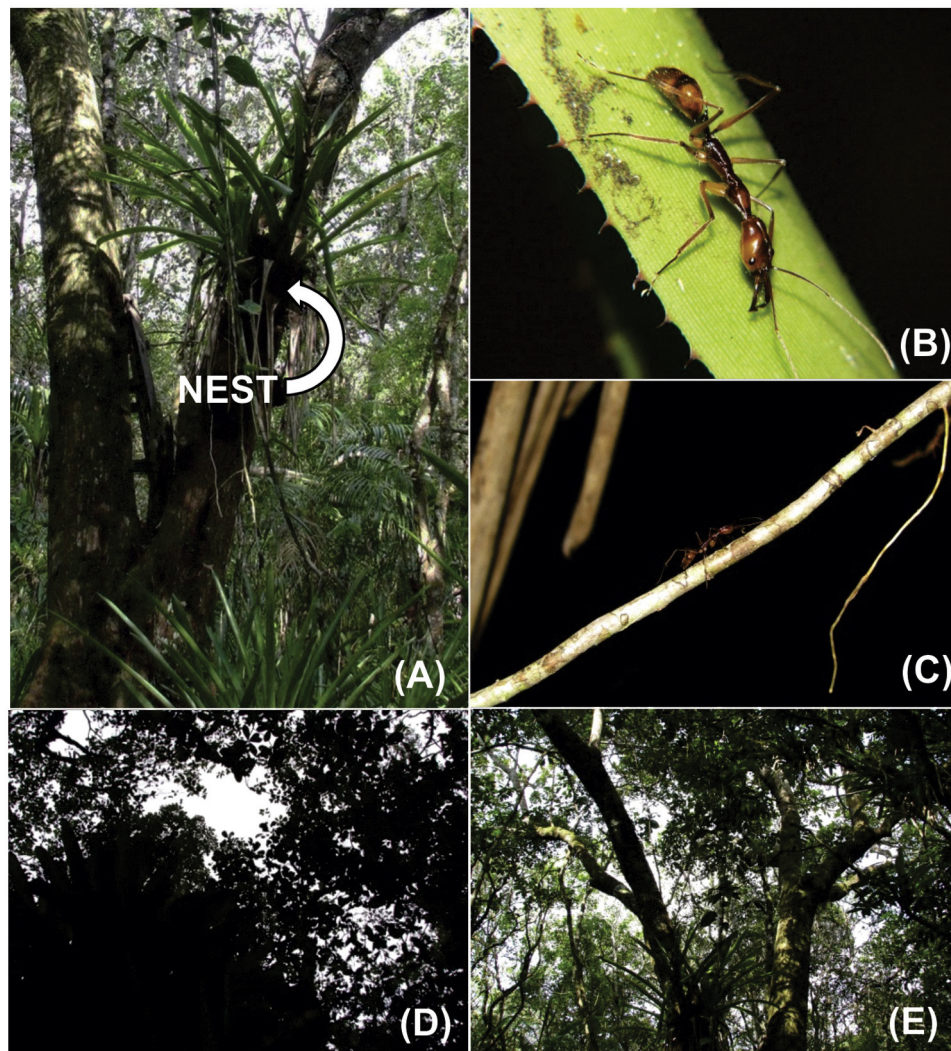
Fig. 1. Typical habitat and nest of *Odontomachus hastatus* in the sandy plain forest of Cardoso Island (Brazil). (A) General view of grouped epiphytic bromeliads (*Vriesea*); colonies of *O. hastatus* use the root mass as nesting site. (B) Worker walking on the nest bromeliad (photograph courtesy of E.R. Pereira). (C) A forager uses a climbing liana as bridge to return to its nest with a recently captured termite. Canopy patterns directly above (D) and in the surroundings (E) of the foraging area of *O. hastatus* at Cardoso Island. See also Fig. 3.

routes were initially determined by following foragers exiting the nest to hunt in the surrounding vegetation. In two different nights (one night/colony), the number of ant foragers in the surroundings of each focal nest was recorded through visual scans at increasing distances towards the canopy, neighboring trees, and along lianas connected to the tree hosting the nest bromeliads. Two observers scanned different routes at the same time, each using a ladder and headlamps. The maximum distance from the nest achieved by foragers was determined with a measuring tape based on landmarks of the canopy environment, and was limited by how far the observers could observe with accuracy ants moving away from the nest. At each section of their routes, ants were exposed to light for no more than 10 s and a complete scan took no more than 3 min. To minimize interference on ant foraging behavior, 10-min intervals were taken between each scan of the vegetation around focal nests.

2.2. Laboratory experiments

The colony of *O. hastatus* used in the orientation experiments was collected at PEIC and transported to the laboratory at the Universidade Estadual de Campinas, where it was cultured under controlled temperature (25° C), humidity (60% RH), and light (12:12 h photoperiod). By April 2008, at the beginning of our observations, the colony consisted of one mated queen, approximately 300 workers, a few pupae and eggs. The colony was housed in seven test tubes (diameter 2 cm × 15 cm) containing water trapped by a cotton plug. All test tubes were placed in a nest box (30 cm × 20 cm; see Fig. 2) which was connected to different types of foraging arenas, depending on the experimental arrangements (see below). Ants were fed *ad libitum* with sucrose solution (40%), *Drosophila* flies, and artificial diet (Bhatkar and Whitcomb, 1970).

The experimental design was adapted from Oliveira and Hölldobler (1989) and consisted of a circular arena (70 cm diameter) connected to the nest (Fig. 2A). The internal walls of the arena (40 cm high) were completely painted in white, to prevent visual cues. A 3 cm × 1 cm wood stripe bridge at 0° connected the arena to the entrance tube of the nest box; identical control bridges that led to cotton-plugged tubes were placed around the circumference at 90°, 180°, and 270° (Fig. 2A). Therefore the correct homing direction in the arena was toward 0°. Neon lights from above were diffused by a translucent plexiglass plate (2 m × 2 m) suspended 40 cm above the arena. The floor of the arena was lined with a circular piece of paper (60 cm diameter).
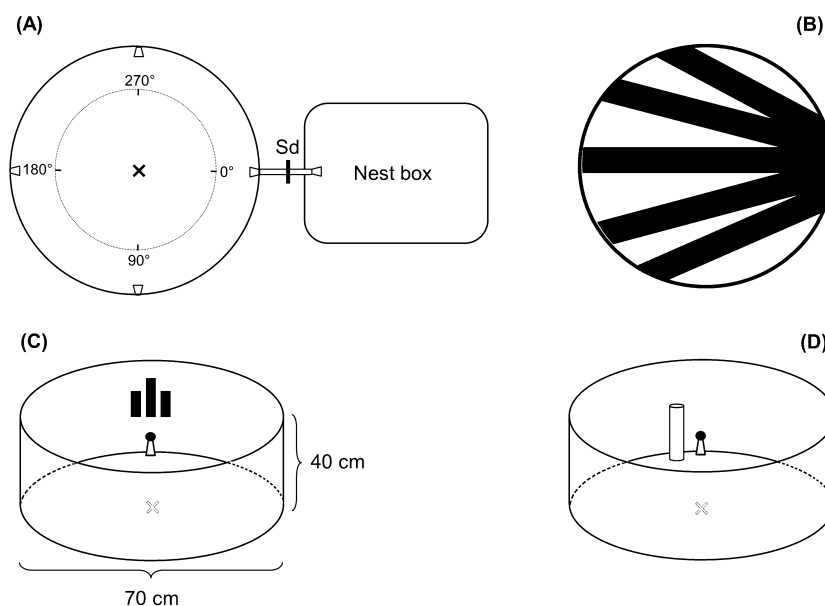
Fig. 2. Artificial setting for the orientation experiments with *Odontomachus hastatus*. (A) Top view of the round foraging arena and the artificial nest; ant traffic through the connecting tube was controlled by a sliding door (Sd); the food source was placed at the center of the arena ("X"); the nest bridge is shown at 0°, and control bridges at 90°, 180°, and 270°; (B) artificial canopy pattern (five cardboard stripes), which was placed on the top of the arena at varying positions, depending on the experimental procedure; (C) lateral view of the round arena, showing the horizon marks located above the nest bridge at 0° (control bridges not shown), and (D) the cylinder (vertical tridimensional landmark) at 350°, next to the nest bridge at 0° (control bridges not shown). See text for further details.

2.2.1. General experimental procedure

Each experimental series consisted of two phases: habituation and tests. The habituation phase was one-week long, during which the ants had free access to the arena and were exposed to visual and/or chemical cues. In the first four days of the habituation phase, the ants were fed daily with freshly killed *Drosophila* flies at the center of the arena (Fig. 2A). In the following three days, ants were starved to encourage foraging during tests. Orientation tests always consisted of two experimental procedures (control and treatment), and up to 40 ants were tested in each experimental group. Ants were tested individually and the access of each "focal ant" to the foraging arena was controlled by a sliding door at the entrance located at 0°. Upon entering the arena, each focal ant was allowed to search for *Drosophila* flies at the center. The time spent to find and retrieve prey was recorded, and the homing direction was registered as the tested ant crossed a dashed line (30 cm radius) drawn around the periphery of arena's paper floor (Fig. 2A). The time taken by each laden homing ant to select a given exit bridge in the round arena was also recorded.

Although *O. hastatus* ants are more active during the night, their activity during the day is not null (see Camargo and Oliveira, 2012). For the purpose of this investigation, we assume that these ants should be able to employ their navigational skills regardless of the time of the day. Experimental sessions were intermittent and lasted no longer than 3 h, between 09:00 and 18:00 h. Only focal ants successfully finding and capturing prey within a 10 min period were considered in the analyses; those dropping prey while homing were discarded. No individual ant was used more than once during an experimental session; tested individuals were kept isolated until the end of each experimental session. Manipulations in each experimental series were performed while the focal ant inspected prey at the center of the arena, which typically lasted 10–15 s. To eliminate possible olfactory cues, the paper floor and the bridges were replaced by new ones after every five ants had been tested, at which time the inner wall of the arena was also cleaned. This procedure, however, was altered for the experiments involving chemical cues (see below). The position of the observer around the arena was shifted constantly to control for possible cues to homing ants.

In addition, the arena itself was rotated 180° prior to every test phase in order to avoid possible uncontrolled orientation cues for the ants. Further methodological details are given below with the description of the individual experimental series.

2.2.2. Visual cues: canopy

We placed on the top of the round foraging arena a glass plate onto which we provided an artificial canopy consisting of five black cardboard stripes (10 cm × 70 cm each) converging toward the nest entrance at 0° (Fig. 2B). This arrangement was kept for a week to allow the ants to habituate with the canopy pattern. We tested canopy orientation during homing in *O. hastatus* by manipulating the canopy pattern as follows. In the control series (N = 37 ants), while the focal ant inspected prey, the canopy was rotated for 45° and immediately placed back in its original position (to control for possible interference on ant behavior due to dragging the canopy over the arena). In the treatment series (N = 40 ants), the canopy was rotated for 90° during prey inspection by the focal ant at the center of the arena. In either experimental situation homing decisions by focal ants were recorded as they crossed the dashed circle at the periphery of arena (Fig. 2A and B).

2.2.3. Head-raising behavior

Forest-dwelling ants that use the canopy as a visual clue tend to frequently look up and raise their heads while homing, as reported for the African *Pachycondyla* (=*Paltothyreus*) *tarsata* (Hölldobler, 1980) and the neotropical *O. bauri* (Oliveira and Hölldobler, 1989). Indeed, *O. hastatus* also exhibits head-raising behavior (Camargo, 2002) but at a lower frequency than that registered for *O. bauri* (Oliveira and Hölldobler, 1989). Here, we investigated if this behavior in *O. hastatus* is associated with changes in the canopy pattern with which they had become familiar during the habituation phase (i.e., stripes converging toward 0°, see Fig. 2A and B). To do so we counted the number of times homing ants raised their heads in control (canopy unaltered) and treatment (canopy rotated for 90°) experimental series. It is expected that ants homing under a rotated canopy pattern would scan the visual field above them more frequently than those returning under a familiar canopy pattern.
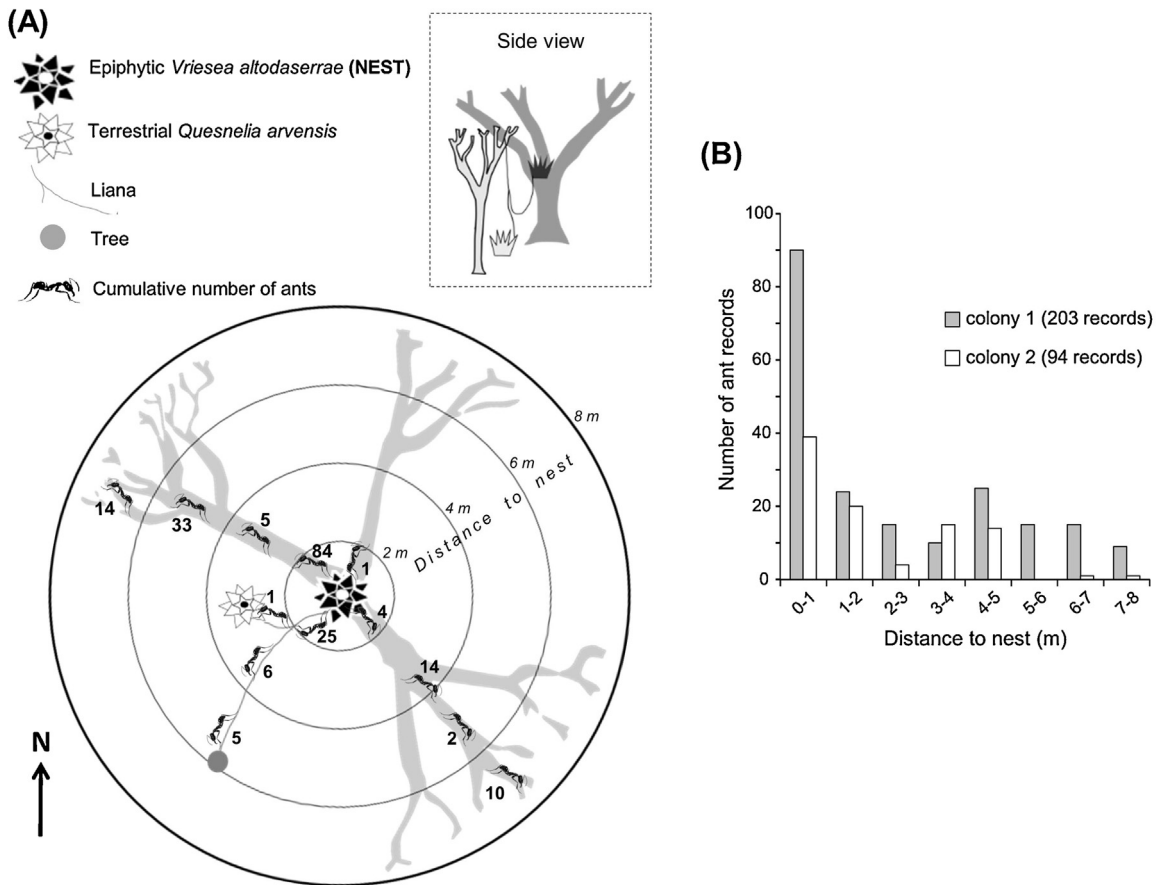
Fig. 3. Spatial distribution of foraging activity by *Odontomachus hastatus*, in the forest canopy at Cardoso Island (Brazil). (A) Topographic view from above of the host tree and the epiphytic nest bromeliad hosting "colony 1", and details of nearby foraging places (inset diagram shows a side view). The nest is located in the bromeliad at the center of the diagram (black), which is directly connected to three ramifications of the tree, and to one liana leading to a terrestrial bromeliad (white) and a nearby tree. Quantity of foragers at increasing distances from the nest is given next to ant symbols along concentric circles (2 m intervals) in the canopy, up to 8 m away from the nest. (B) Frequency distribution of ant foragers at 1 m intervals from the nest, for focal colonies #1 and #2. See also Fig. 1.

2.2.4. Visual cues: horizon

To test the importance of the horizon in the homing orientation of *O. hastatus*, a white cardboard plate with three black stripes (two lateral 4 cm × 9 cm stripes and one central 4 cm × 25 cm stripe) was placed on the arena's wall, above the exit located at 0° (Fig. 2C). Ants were allowed to familiarize with the visual marks for one week before tests; no canopy pattern was provided. The orientation tests consisted of manipulating the position of the horizon marks while ants were inspecting prey at the center of the arena. In the control series (N = 40 ants), the plate was lifted 5 cm and immediately placed back to its original position at 0°. In the treatment series (N = 40 ants), the position of the horizon marks was shifted to 90°.

2.2.5. Visual cues: vertical tridimensional landmark

In this experiment, the vertical landmark consisted of a brown cylinder (15 cm high, 4 cm diameter) that was placed 10 cm away from the wall of the arena. For one week the ants were allowed to familiarize with the presence of the cylinder at 350° (Fig. 2D); no canopy pattern was provided. In the control series (N = 40 ants), while the focal ant inspected prey at the center of the arena, the cylinder was shifted to 35° and immediately placed back in its original location at 350°. In the treatment series (N = 40 ants), the location of the cylinder was shifted to 80° while the focal ant inspected prey at the center of the arena.

2.2.6. Chemical cues

The effect of odor cues on the orientation of *O. hastatus* was tested by comparing the homing behavior of foragers on a 7 day-old

paper floor with that on a new one. During the habituation phase, ants were allowed for one week to familiarize with the canopy pattern converging toward the nest entrance at 0° (Fig. 2A and B). During both the control and treatment series (N = 40 ants each), the canopy was removed while the focal ant was handling the prey at the center of the arena. In this situation, since visual cues would no longer be available, the ants were expected to use other available cues when homing. In the control series, the ants were tested over a new paper floor, which was replaced together with the bridges after every five ants had been tested, at which time the inner wall of the arena was also cleaned. During the treatment series, we kept the 7 day-old paper floor and the bridges in all trials as a possible source of chemical cues for homing, and the inner wall of the arena was not cleaned. In this experimental design one cannot rule out the possibility that ants entering the arena might mark the floor with chemical homing cues. The only difference between new (control) and old (treatment) paper floors would then be the degree of marking.

2.3. Statistical analyses

For each experimental series, the presence of a significant direction was determined using the Rayleigh test (Batschelet, 1965). We also tested if directions taken by ants corresponded with the expected direction by using the V-test and the mean vector 95% confidence interval (CI). In all experiments, the time to return to the nest between homing ants in control and treatment groups was assessed using the Mann–Whitney *U*-test. The

Table 1

Number of *Odontomachus hastatus* ants climbing on different exit bridges while homing, during experimental series using different types of cues in a round foraging arena (see Figs. 4 and 5). *N* = 40 ants for each group in each experimental series. A true exit bridge at 0° connected the arena to the entrance tube of the nest box; identical control bridges that did not lead to the nest were located at 90°, 180° and 270° (see Fig. 3). The expected directional vector in each experimental group is given in parentheses. Statistical comparisons in each experimental series were made through *G*-tests. See text for further details.

Ants climbing on bridge at	Type of cues							
	Canopy		Horizon		Vertical marks		Chemical marks	
	Control (0°)	Treatment (90°)	Control (0°)	Treatment (90°)	Control (0°)	Treatment (90°)	Control (0°)	Treatment (0°)
0°	25	8	30	10	18	7	17	10
90°	7	18	5	25	9	16	5	6
180°	2	12	3	4	11	7	7	12
270°	6	2	2	1	2	10	11	12
P value	<0.05		<0.05		<0.05		>0.05	

frequency of head-raising behavior between experimental groups was compared with a χ^2-test. The selection of bridges around the arena (at 0°, 90°, 180° and 270°) by homing ants in each group were analyzed using a *G*-test. All tests were performed according to Zar (1999) with a significance level of 5%. Circular statistics was performed using the software PAST (v. 1.81) (Hammer et al., 2001) and Oriana (v. 4) (Kovach, 2011); other tests were performed in Bioestat (v. 5.0) (Ayres et al., 2007).

3. Results

3.1. Field observations

O. hastatus foragers typically leave the nest independently at night, and travel up to 8 m away from the nest to hunt for arthropod prey in the canopy; greatest traffic of ants occurs within 2 m of the nest bromeliad (Fig. 3A and B) because foragers arriving from different parts of the canopy are brought together to common branches close to the nest. In the search for arboreal prey, workers may also use twigs, foliage and vines as bridges between the host tree and neighboring vegetation, which may include terrestrial bromeliads (Figs. 1B and C, 3A).

3.2. Visual cues: canopy

The canopy affected the spatial orientation of *O. hastatus* workers. In the control series (canopy unaltered), the direction taken by homing workers was significant ($\mu = 8.98°$, $r = 0.3935$, $p < 0.05$) and corresponded with the expected direction (0°) (V-test, $p < 0.001$; 95% CI = 342.68–35.28°) (Fig. 4A). In the experimental series (canopy rotated for 90°), the mean directional vector taken by homing ants was $\mu = 101.59°$ ($r = 0.5764$, $p < 0.05$), and within the expected direction at 90° (V-test, $p < 0.0001$; 95% CI = 78.15–125°) (Fig. 4B). There was no significant difference in the time taken by homing workers to select an exit bridge in the control and treatment series (mean ± SD control = 105.97 ± 96.69 s; treatment = 100.22 ± 59.34 s; $U = 735$, $p = 0.53$, $N = 40$). The exit bridge selected by homing workers, however, differed significantly between control and treatment ($G = 24.22$, df = 3, $p < 0.05$, $N = 40$); the true nest bridge at 0° was selected more frequently by ants in the control series, whereas the exit at 90° was chosen more often in the treatment series (Table 1).

3.3. Head-raising behavior

No difference was found in the number of workers raising their heads in the control and treatment series ($\chi^2 = 0.11$, df = 1 $p = 0.74$, $N = 31$). The frequency of head raisings per worker was also similar in both experimental groups (control: 5.19 ± 4.55, treatment: 5.55 ± 7.57; mean ± SD).

3.4. Visual cues: horizon

There was a clear association between the horizon position and the homing direction taken by *O. hastatus* workers. The mean direction taken by workers in the control series (horizon unaltered) was significant ($\mu = 1.29°$, $r = 0.69$, $p < 0.001$), and included the expected direction to the true nest exit at 0° (Fig. 4C) (V-test, $p < 0.0001$; 95% CI = 351–11.59°). When the position of the horizon marks was changed to 90°, the mean direction was also significant ($\mu = 80.53°$, $r = 0.618$, $p < 0.001$; Fig. 4D) and included the expected direction for the experimental situation at 90° (V-test, $p < 0.0001$; 95% CI = 60.71°–100.4°). The choice of the exit bridge by tested ants also supports these results. Homing ants differed significantly between control and treatment series ($G = 25.50$, df = 3, $p < 0.001$). In the control situation the exit most frequently chosen by homing ants was the true one at 0°, whereas in the treatment series they selected more often the bridge located at 90° (Table 1). Additionally, homing ants took longer to select an exit in the treatment compared to the control series (mean ± SD treatment = 99.92 ± 59.82 s; control = 62.92 ± 42.61 s; $U = 443.5$, $p < 0.001$, $N = 40$).

3.5. Visual cues: vertical tridimensional landmark

There was no significant direction taken by *O. hastatus* ants in the control ($\mu = 40.89°$, $r = 0.192$, $N = 40$, $p > 0.05$; V-test (0°), $p > 0.05$) or treatment series ($\mu = 121.54°$, $r = 0.089$, $N = 40$, $p > 0.05$; V-test (90°), $p > 0.05$; Fig. 4E and F). Nevertheless, tested ants were able to find the expected exit bridge in each experimental series. In the control series (cylinder at 350°), homing ants selected more frequently the true exit bridge located at 0°, whereas in the treatment situation (cylinder shifted to 80°) ants chose more often the bridge located at 90° (Table 1; $G = 13.71$, df = 3, $p < 0.01$). The time taken by ants to select a bridge did not differ between the experimental groups (mean ± SD control = 72.15 ± 34.16 s; treatment = 86.42 ± 51.45 s; $U = 706$, $p > 0.05$, $N = 40$).

3.6. Chemical cues

Chemical cues were not important in the navigation process of *O. hastatus* ants (no visual cues available). The mean direction taken by ants when chemical cues (7 day-old paper floor) were available was not significant ($\mu = 320.66°$, $r = 0.199$, $p = 0.205$, $N = 40$; V-test (0°), $p > 0.05$; Fig. 5A). Surprisingly, however, ants showed a significant homing direction when no chemical cues (new paper floor) were provided ($\mu = 329.64°$, $r = 0.298$, $N = 40$, $p = 0.03$), with 95% CI ranging from 298.8° to 9.4° and within the expected direction at 0° (V-test, $p = 0.01$) (Fig. 5B). Homing ants took longer to select an exit bridge on a 7 day-old paper floor
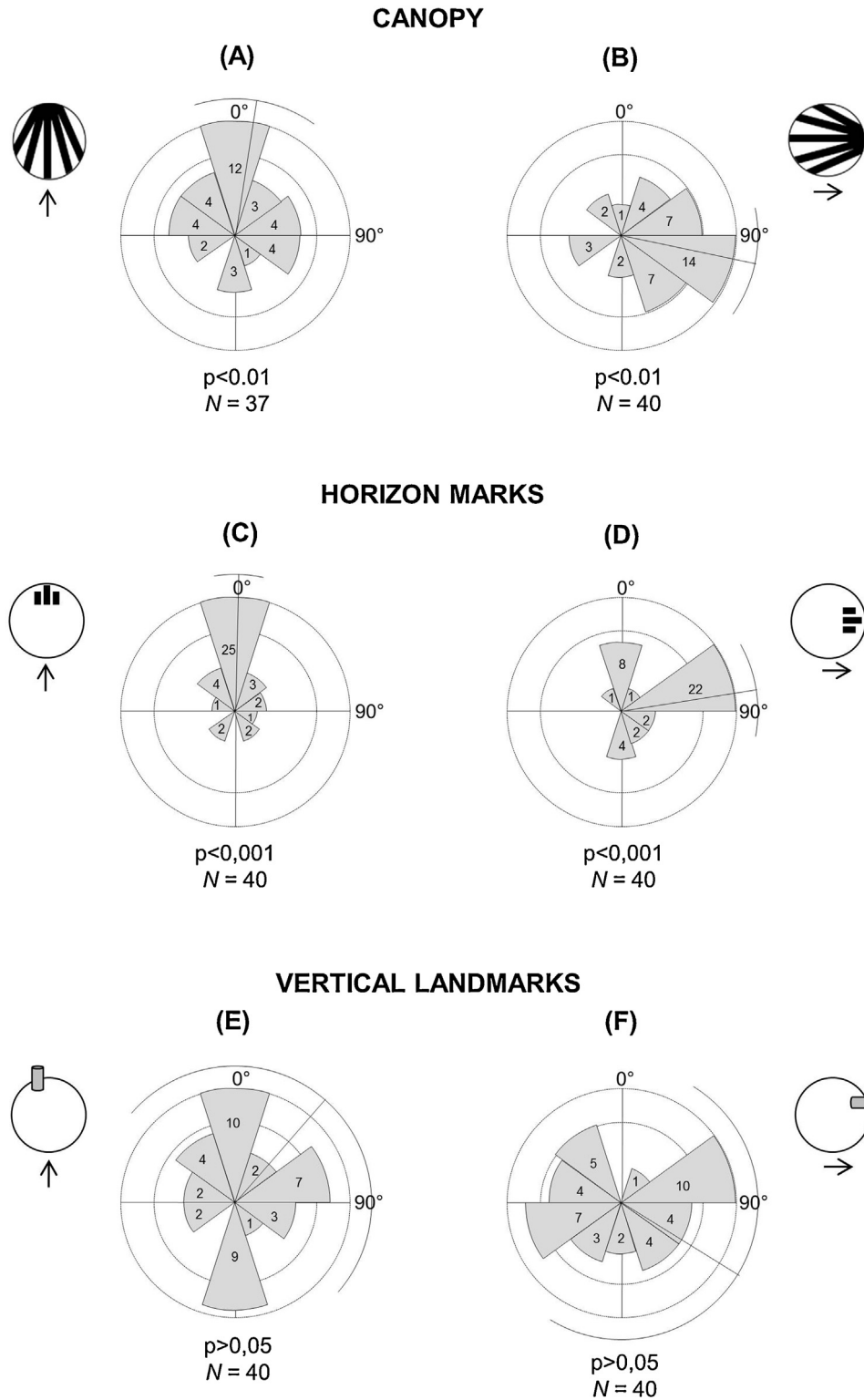
Fig. 4. Homing directions of foragers of *Odontomachus hastatus* during tests in a round foraging arena, involving different types of visual cues: (A and B) canopy, (C and D) horizon pattern, and (E and D) vertical landmarks. In each diagram, the numbers inside shaded triangles indicate the quantity of ants taking a direction within the angle covered by the shaded area. The mean directional vector is represented by a line originating at the center of the diagram; the arc at the end of each vector represents the 95% confidence interval. Small diagrams next to each major graph indicate the position of the visual cues in each experimental series; the small arrow shows the expected homing vector if ants use the visual cues being tested. *P* values <0.05 indicate that the mean vector represented in the figure is statistically different from random (Rayleigh test). See text for further details.

than on the new paper floor (mean ± SD control = 133.20 ± 101.14 s; treatment = 77.82 ± 46.84 s; $U = 517$, $p < 0.05$, $N = 40$). The choice of the exit bridge by tested ants did not differ between experimental groups ($G = 3.3$, df = 3, $p = 0.35$).

4. Discussion

The navigation system of *O. hastatus* is remarkable among crepuscular-nocturnal insects. Our field data support the previous
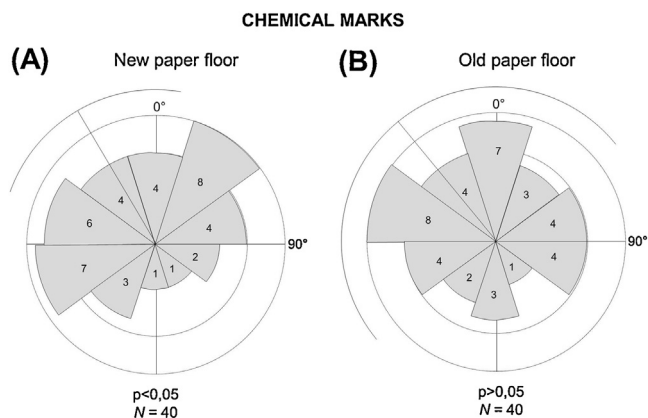
CHEMICAL MARKS

(A) New paper floor **(B)** Old paper floor

Fig. 5. Homing directions of foragers of *Odontornachus hastatus* during tests in a round foraging arena involving chemical cues, when no canopy or other visual marks are available. In the control series (A), the arena's paper floor was replaced by a new one after every five ants had been tested, at which time the true exit bridge (0°) and the control bridges (90°, 180° and 270°) were also replaced by new ones, and the inner wall of the arena was also cleaned. In the treatment series (B), ants were tested on a 7 day-old paper floor. Numbers inside shaded triangles indicate the quantity of ants taking a direction within the angle covered by the shaded area. The mean directional vector is represented by a line originating at the center of the diagram; the arc at the end of each vector represents the 95% confidence interval. Statistical significance of mean vectors evaluated by Rayleigh tests. See text for further details.

observations by Camargo and Oliveira (2012) suggesting that *O. hastatus* forages exclusively on the forest canopy. Workers were observed to use branches, leaves and vines to reach different plants and they often reached distances farther than 8 m from the nest (Fig. 3A and B). This foraging range is comparable to the ones recorded for ground-nesting neotropical ponerines such as *O. bauri* (Ehmer and Hölldobler, 1995), *Dinoponera gigantea* (Fourcassié and Oliveira, 2002), and *Pachycondyla striata* (Medeiros and Oliveira, 2009). In contrast, *Gnamptogenys moelleri* (Ectatomminae), an arboreal poneromorph found at the same site in Cardoso Island, restricts its foraging range within 2 m from nest bromeliads where many prey items are found (Cogni and Oliveira, 2004). Indeed, Camargo and Oliveira (2012) suggest that the abundant water tank of epiphytic bromeliads may work as a prey reservoir for *O. hastatus* colonies at Cardoso Island (see also Gibernau et al., 2007). Nonetheless, the larger foraging range of *O. hastatus* indicates that foragers must travel greater distances in order to retrieve sufficient prey to sustain their colonies.

Our results also show that despite their crepuscular-nocturnal habit, foragers of *O. hastatus* are capable of using visual cues when available (see also Hölldobler and Taylor, 1983). Light may become 11 times dimmer at night, but nocturnal insects, including hymenopterans such as solitary bees in the genus *Megalopta*, are usually able to navigate using visual cues (reviewed by Warrant and Dacke, 2011). The canopy provided effective cues for correct navigation, but *O. hastatus* was also able to use the horizon when navigating (Fig. 4A–D; Table 1). This pattern differs from the terrestrial congeneric species *O. bauri* (Oliveira and Hölldobler, 1989) and the poneromorph *P. clavata* (Ehmer, 1999), which are unable to use patterns from the horizon when light is dim. In the tree top, horizon marks are also part of the canopy and may exhibit higher contrast than the low-contrast visual marks on the forest floor (Fig. 1E; Ehmer, 1999). Moreover, the definition of cues as belonging to the horizon or the canopy is interchangeable: depending on the plan by which an ant is walking, the canopy pattern may be present above the worker's head, in front of it, or at any other angle (Fig. 1D and E; Hölldobler, 1980). Despite this exchange of roles, each visual cue is likely interpreted differently. According to Wehner (1994), cues such as the canopy are analogous to a visual compass – the directional information is given by a relatively static pattern over

the ant's head. In the case of the horizon pattern, visual information changes as the insect moves towards the horizon and decisions are made based on the matching between the pattern reaching the ant's retina and the expected pattern features as memorized by the ant (Wehner, 1994). This image-memory matching mechanism has been described in both ground- and canopy-foraging ants (Harris et al., 2007; Nicholson et al., 1999; Wehner et al., 1996).

Our observations on head-raising behavior in arboreal *O. hastatus* did not follow the same pattern reported for ground-dwelling *O. bauri* (Oliveira and Hölldobler, 1989). In the latter species, homing ants increased the frequency of head-raising when the canopy arrangement differed from the pattern they had been habituated with. This suggests that *O. bauri* foragers that have lost their familiar canopy pattern need to scan the visual field above them more often in order to reorient themselves while homing (Oliveira and Hölldobler, 1989). In *O. hastatus*, however, the frequency of head-raising by homing ants did not change between unaltered and rotated canopy patterns. This behavioral difference between *O. hastatus* and *O. bauri* may result from their distinct lifestyles (i.e., *O. bauri* forages on the forest floor, meters away from the canopy). The degree to which ecological features related with foraging terrain (i.e., ground *versus* arboreal) can affect visual navigation in forest-dwelling ants awaits further investigation.

Our experiment with a tridimensional object (cylinder) had the goal of simulating a branch along the foraging route. Ants showed no directional preference for homing after capturing prey (Fig. 4E and F). Nonetheless, their first exit choice when homing was the closest to the cylinder, even when this landmark was positioned at a different exit than the one leading to the nest (Table 1). The cylinder was relatively thin in diameter and had a relatively low contrast (brown in color) compared to other visual cues that were tested (black in color). Therefore, the cylinder likely remained undetectable from the center of the arena by tested ants, although it could be easily seen at short range. Indeed, arboreal *P. clavata* foragers are significantly more successful in using visual cues colored in black against a white background (high contrast) compared to a similar pattern painted in gray (low contrast) (Ehmer, 1999). When no directional cue is available, ants begin a systematic search for the location of their nest, as also observed in other insects (Bell, 1991; Wehner, 1992). Wall-following behavior is a search pattern often observed in displaced ants (Dussutour et al., 2005; Graham and Collett, 2002). This behavior was frequently observed with homing workers of *O. hastatus*, during tests having the cylinder as the single visual cue available. Based on this observation, we hypothesize that workers of *O. hastatus* learned to find the exit bridge by following the arena's wall until the cylinder was at a short visual distance.

Lastly, our results did not support the hypothesis that chemical cues are relevant for the navigation of *O. hastatus*. When chemical cues were available, workers were disoriented and unable to find the correct exit bridge to the nest (Fig. 5B). However, in the absence of chemical and visual cues ants preferred to head to the correct exit (Fig. 5A). This pattern suggests that the chemically marked paper was negatively affecting the ability of workers to find their way back to the nest. *Odontomachus* ants are solitary foragers and navigation using chemical cues in this genus relies on the gradient of fecal spots deposited around nests (e.g., *O. troglodytes*; Dejean et al., 1984) rather than formation of chemical trails. Based on this information and in our results, we do not discard the possibility that *O. hastatus* may depend on chemical cues when navigating. We hypothesize that *O. hastatus* may not follow trails of odor but they might be able to use gradients of odor for navigation. In natural conditions, foragers walk through routes made up of branches and bifurcations, where odor concentration may indicate the most used branches for navigation, as in *Oecophylla longinoda* (Formicinae) (Dejean and Beugnon, 1991). In the flat and circular arena used in our experiments (Fig. 2), ants were observed to cover the whole floor surface

when foraging. Therefore, a gradient of chemical marking likely did not exist in this relatively small foraging range. Future research on chemical cues used by arboreal ants should take into consideration the forked paths commonly found in the canopy.

The fact that workers were able to home in the absence of visual and chemical cues is puzzling, and it is possible that *O. hastatus* is able to navigate using only their motor memory. For instance, desert ants are able to memorize distances traveled by monitoring the movement of their legs (Wittlinger et al., 2007). The spider *Cupiennius salei* (Ctenidae) is able to return to specific points in space by using their motor memory as recorded by mechanoreceptors located in the femur and tibia (Seyfarth and Barth, 1972). Learning a simple sequence of turns is another strategy found in ants such as the formicine *G. destructor* (Macquart et al., 2008). Whether mechanoreceptors contribute to navigation of ponerine ants is unknown. Alternatively, ants may use the Earth's magnetic field as a compass. Magnetic particles were found in the head capsule and abdomen of the ponerine ant *Pachycondyla marginata*, known to migrate along the north-south axis of the Earth's magnetic field (Acosta-Avalos et al., 1999). The ability to navigate using the Earth's magnetic field has been also observed in other ants (e.g., *Atta colombica*, Banks and Srygley, 2003; *Formica uralensis*, Çamlitepe and Stradling, 1995). In the hierarchy of directional cues, navigation by motor memory or by using a magnetic compass seems to be used only when no other cues are available. A fact that strengthens this idea is that the time to find the correct exit bridge of the arena was shorter in the situation where the lining of the arena's floor was frequently replaced compared to the situation where chemical cues were available. In this scenario, workers likely relied in the chemical marking for homing, but they took a longer time to choose one of the exits since these cues were not reliable. A similar pattern was observed when testing horizon patterns, i.e., the time taken to find the exit was shorter in the control than in the test situation, due to a possible conflict between the motor memory and the location of the exit as indicated by the visual cue.

This is the first experimental study investigating the navigation system of a crepuscular-nocturnal and exclusively arboreal ponerine ant. The navigation system of *O. hastatus* is remarkable and allows foragers to travel along the maze-like, complex canopy environment, most likely relying on visual cues when available. Future work on the eye structure of *O. hastatus* may shed light on how photons are collected in their retina during nocturnal navigation. This study adds important information to foster more comparative studies on the evolution of navigation systems in insects, which so far has relied mostly on investigation of diurnal and terrestrial insects.

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