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Research article

The significance of visual landmarks for navigation of the giant tropical ant, *Paraponera clavata* (Formicidae, Ponerinae)

A. P. Baader

Department of Zoology, University of Zürich, Winterthurer Strasse 190, CH-8057 Zürich, Switzerland

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Summary

Workers of the giant tropical ant, *Paraponera clavata*, use trail pheromones for orientation and recruitment of nestmates. However, chemical markings may not always be sufficient for successful navigation in complex three-dimensional terrain, and additional orientation cues may be required. Behavioral field experiments were performed to investigate the significance of visual landmarks for homing foragers. Animals which were prevented from seeing the canopy were unable to navigate back to the nest, even though trail pheromones were still present. In contrast, foragers found their way back to the nest after their trail pheromones had been abolished but their visual scenes remained unchanged. This emphasizes the important role of visual landmarks during spatial orientation in homing *P. clavata* foragers. Individually foraging scouts were discovered in the understory of the forest floor up to 30 m away from their nest. They were rewarded, and displaced between 0.8 m and 13.6 m. Fifteen out of 16 animals had no difficulties in finding the nest entrance despite the altered appearance of local and distant landmarks at the release site. Apparently the scouts were able to recognize the visual scenes at the release site, and used them for reference to locate the nest entrance. In contrast, ants displaced from their nest to sites around 4 m away had more difficulties to re-find the nest.

Introduction

Many insects make use of different orientation cues to successfully navigate within their foraging territory. The kinds of sensory cues used depend on availability, and are often selected in a hierarchical order. Desert ants and honey bees take advantage of celestial cues, such as the polarization patterns of the sky and the position of the sun (for reviews see Rossel, 1993; Wehner, 1994). Path integration is then used to navigate back to the nest. This strategy is the major component of an egocentric reference system: the animals collect information as they travel away from the nest, and use this information to compute their position with respect to the nest. When celestial cues are not available, or when the animals are approaching their nest sites, they switch to visual image detection. Whether insects make additional use of a geocentric navigation system is still subject of an ongoing debate (Gould, 1986; Wehner and Menzel, 1990). A geocentric reference system implies that the animals possess an internal representation of their outside world. Such a cognitive map (Tolman, 1948; Gallistel, 1990) would enable them to obtain position information independently from the course they chose from the nest. Hard proof data that such a mechanism is used by insects are still missing.

Most ants employ trail pheromones as their primary orientation system (Carthy, 1950; Sudd, 1959). Among these is the ponerine ant, *Paraponera clavata.* This species lives in tropical forests where it builds underground nests at the base of trees, on which the adults forage. Extended foraging excursions include the forest floor, the foliage of the understory and the forest canopy where the animals collect nectar from extra-floral nectaries (Bennett and Breed, 1985) or hunt for arthropod prey (Young and Hermann, 1980). Foraging trails can lead from one tree to another (Breed and Bennett, 1985), hence spanning an immense three-dimensional territory. Foragers of *P. clavata* use chemical signals to mark their trails and to recruit nest mates to food sources (Breed et al., 1987). Trail pheromones, however, do not indicate the inbound- or outbound direction of a path (Wilson, 1962; Oliveira and Hölldobler, 1989), and by themselves do not ensure that individuals find the nest on extended excursions. Moreover, single *P. clavata* scouts have been observed foraging 60 m away from the nest (Young and Hermann, 1980), using different routes for foraging and homing. This suggests that additional cues must be involved in the spatial orientation of these animals. The only evidence to date for the utilization of visual landmarks by *P. clavata* is a report that experienced foragers preferentially used local landmarks to relocate a food source, while recruited naive nest mates relied primarily on trail scents (Harrison et al., 1989).

The aim of the present study was to investigate to what extent homing *P. clavata* foragers require visual information to locate their nest. It will be demonstrated that the images of the visual scenes provide essential information for successful homing, having an even higher priority than chemical cues. Moreover, individually hunting foragers were capable of finding their way back to the nest after being displaced into a different area within the surroundings of their nest site. The results will be discussed in the context of spatial orientation in a complex three-dimensional space.

Methods

Location

The experiments were performed during July 1994 at the La Selva Field Station of the Organization for Tropical Studies (OTS), Puerto Viejo, Province Heredia, Costa Rica. Several *P. clavata* colonies inhabited the arboretum, an area of disturbed primary rain forest adjacent to the station. In this area most of the scrub has been removed, leaving the trees and an understory composed of grass and bushes. The forest canopy of the arboretum was mostly dense but it also contained patches of skylight. Many colonies had their nests located underground at the base of *Pentaclethra macroloba* (Leguminosae) trees. While most foragers ascended their tree trunk, and usually returned carrying a drop of nectar, a small arthropod, or some plant material between the mandibles, occasionally single *P. clavata* were spotted on the forest floor, sometimes tens of meters away from their nest.

The temporal pattern of foraging frequencies in individual Paraponera colonies can vary greatly. Both diurnal and nocturnal peak activities have been observed (Hermann, 1975; Young and Hermann, 1980), sometimes considerably influenced by weather conditions. After an initial survey two diurnally active colonies were chosen for the experiments. Both colonies had their peak foraging activities during the gaps between the extended periods of heavy rains which are common at this time of the year.

Visual blocking experiments

Foragers of one of the nests used a 1.2 m wide concrete walkway for more than 30 m as a convenient trail for foraging and homing. Homing foragers, dragging their gasters along the ground to release trail pheromones (Breed and Bennett, 1985) were often observed on this trail. Some of them returned from a *P. macroloba* tree 33 m away from the nest site where they had caught stingless bees (*Trigona*). During the period of this experiment (one week) between 1 to 5 animals per day, depending on the weather, regularly visited the bee hive at this tree. The trajectory of successful foragers (i.e. those carrying bee prey) was recorded along a 13 m-long portion of their homing path (between "A" and "B" in Fig. 1). Experimental animals were marked with a small drop of enamel. For the visual blocking tests, a square horizontal blind (42×42 cm) was kept centered approximately 20 cm above the walking ant. This blind covered about 90° of the animal's overhead view leaving a lateral field of view of 45°. It consisted of a wooden frame (1 cm diameter) containing a screen. Three types of screen were used: (1) A plastic transparency film to test whether the shape of the blind itself or the presence of the experimenter holding the blind affected the ants' homing behavior. (2) A white, partially translucent film was transmitting visible light and some UV ($\geq$380 nm). This screen reduced the light intensity (as measured with a lux-meter) by 30%. Its diffusing characteristics blurred the sharp edges of the visual surroundings, but very bright points (e.g., patches of sky) were still visible. (3) A red Plexiglass square (3 mm thick) with a cut-off wave length at 600 nm. It reduced the light intensity to 50%, and blocked virtually all visual overhead information for the ant while it enabled the experimenter to observe the walking ant through the blind, and to center it above the animal. Each blind was suspended from a 1 m long wooden pole held by the experimenter. It was removed either when the ant had reached the end of the test distance or after 10 minutes, whichever occurred first.

Chemical blocking experiments

Foragers were baited from the nest entrance. A 10-ml-vial filled with sucrose solution (1 Mol) served as feeding station. A cotton thread was led through a small hole in the lid of the vial. It was placed within a cube-shaped translucent plastic housing (13.5 cm edge length) which had a door at one side. The forest floor in front of the nest entrance was covered with a folded plastic tarpaulin extending an area of 4 m×1.5 m. Starting at the nest entrance, the housing was slowly moved along the plastic sheet 4 m away from the nest, while the foragers collected the sugar water from the feeder, and recruited nest mates. Ants were color coded by applying small drops of enamel to thorax and abdomen. When the housing was at its final distance, and about 5 to 15 foragers had visited the feeder at least five times each the housing door was closed, trapping all ants which happened to be inside the housing. Then all other animals on the tarpaulin were removed, and the tarpaulin was turned over. For the test, individual foragers were released by opening the door briefly, and their homing paths were registered. To force active orientation the plastic box was positioned with its door opposite to the nest direction. By further unfolding the tarpaulin, consecutive animals always walked on unscented areas of the tarpaulin. The rewarded foragers waited in the box with the sugar water drop between the mandibles, until they were allowed to start homing. Homing paths were recorded from the time when the animals left the box until they had reached the edge of the sheet next to the nest entrance. All animals which attempted to return from the nest to the food source were prevented from entering the tarpaulin, and removed.

Transfer experiments

The forest floor and the understory in the surroundings of a nest were carefully surveyed for individually hunting scouts. The term scout is used here for singly foraging individuals without implying that these animals necessarily recruited other nest mates once they had discovered booty. When an animal had been spotted, it was baited using the sucrose-filled vial (see above). The feeder was placed on a square plastic platform (9.5×9.5 cm) which was brought into close proximity to the scout. When the animals climbed onto the board and started to collect the sugar water it was marked with a drop of enamel, carefully lifted and moved quickly to a different site. This procedure had two advantages: the animals remained quiet since they were not directly mechanically manipulated, and after collecting the bait the foragers were highly motivated to return home.

Registration and evaluation of data

The terrain around a nest (11 m×11 m) was marked out with a 1 m^2 grid of nylon strings. Depending on the weather the homing paths of the observed foragers were recorded by using one or two of the following three methods: (1) the paths and times were registered on protocol sheets which had a 100:1 reduction of the grid; (2) the position of the animal and the time were voice recorded on a cassette recorder; (3) a second observer recorded characteristics of the animal's locomotor behavior on video tape.

Results

The role of overhead landmarks for homing foragers

Ants which return to the nest on a regularly used and apparently marked trail have at least two sensory modalities available for orientation, namely pheromone signals and the image patterns of the visual surroundings. To determine to what degree the latter may be important for finding the nest entrance, foragers were partially blinded. Twenty booty carrying foragers were divided into three groups, and tested on the 13 m long stretch along their trail (between A and B in Fig. 1). The control animals were covered with the transparent screen when they passed the A-line, and this was removed only when they had arrived at the B-line. Their actual pathlength was 13.3 ± 0.2 m (mean ± S.E.M, $n = 5$) for the distance of 13 m between A and B, i.e. the animals followed a reasonably direct homing course. The straightness was not different from the course of untreated homing foragers (13.2 ± 0.1 m, $n = 3$, paths not shown) which indicates that the ants did not seem to feel disturbed by the experimental arrangement (e.g. the moving frame of the screen, the strings, the pole, or the nearby walking experimenter).

Nine animals were blinded by the white screen (Fig. 1, partial block) when they passed the A-line. The animals continued their straight paths for some distances, but then started to deviate and walked in circles. The length of their route was 24.4 ± 3.1 m, but 8 of the 9 animals reached the B-line within 10 min. When blinded by the red screen (Fig. 1, complete block) none of the six test animals reached the B-line. The animals walked in many circles and stopped frequently. Their actual

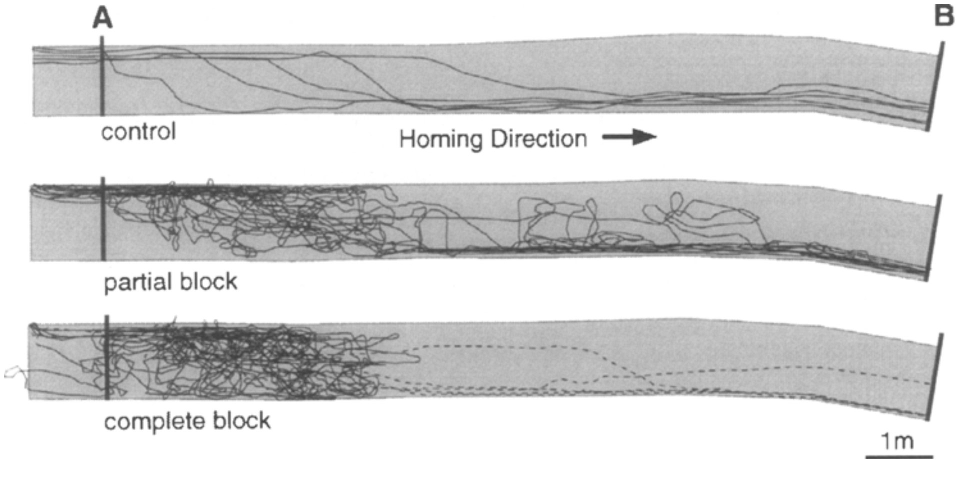

Figure 1. Trajectories of rewarded foragers which homed on a concrete footpath (shaded in gray). When the animals entered the 13 m-test-distance (between A and B) different overhead screens were applied. Control animals ($n = 5$) were blinded with a transparent screen. Experimental animals were covered with a white, partially transparent ($n = 9$, partial block) or a red ($n = 6$, complete block) overhead screen. Stippled lines in the third group (complete block) indicate homing paths after removal of the red screen (after $t = 10$ min)

path length during the 10 min-test was 30.6 ± 2.3 m. When the screen was removed after 10 min their average position was only 4.1 ± 1.2 m closer to the nest than before their view had been blocked. Five of 6 animals turned around immediately and homed (dashed lines in Fig. 1). One animal returned to the initial departure point. These results show that pheromone information alone is not sufficient for successful homing when visual information is at least partially blocked.

Visual orientation after blocking of chemical information

How do homing *P. clavata* foragers perform after a complete removal of any pheromone markings but with unchanged visual inputs? When traveling on the tarpaulin from the feeding station to the nest the foragers marked their trails along the tarpaulin by dragging the abdomen. Regularly animals were observed to use their individual trails during their homing runs. Figure 2 shows the homing routes of two animals which were released from the feeding station 4 m away from their nest tree after the marked portion of the tarpaulin had been replaced by a clean one. Animal a 1 turned after it had left the housing, and reached the edge of the tarpaulin at the nest site after 22 s. It was the fasted animal observed during these experiments. A similar behavior was displayed by animal b1 although its speed was slower: its homing path was looped, and it arrived after 78 s. Figure 3 compares the cumulative homing times of 11 experimental animals with 11 control animals which had pheromone information available on the scented tarpaulin. There was no significant difference between the two groups ($p = 0.85$, single-factor Anova). This means that chemical information is used by *P. clavata* foragers when present. But it is not necessary as long as the animals have visual cues, such as the canopy and/or the

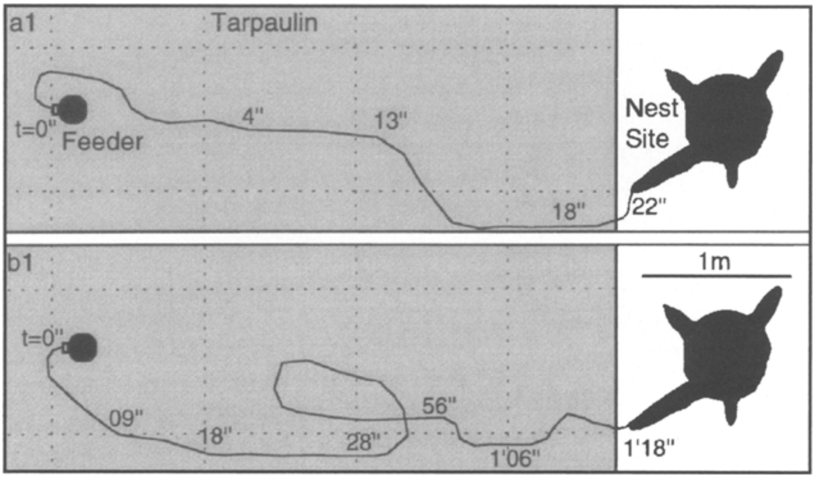

Figure 2. Two foragers (a 1, b 1) homing on a plastic tarpaulin (gray area) which contained no pheromone traces. Foragers were baited to the feeder and tested after the scented tarpaulin had been turned over. Nest tree with buttresses is drawn to scale at floor level

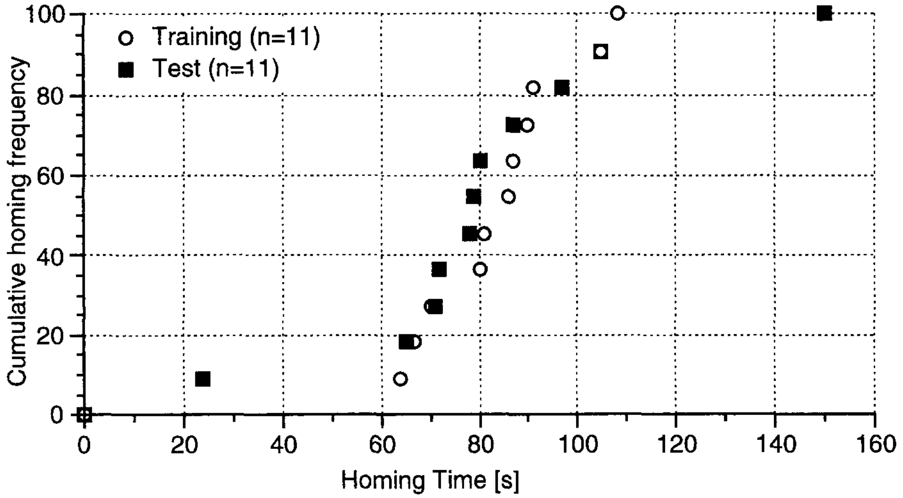

Figure 3. Cumulative homing times of 11 training animals (open circles) which traveled in the presence of trail pheromones 4 m back to the nest, and of 11 test animals (black squares) which homed on clean parts of the tarpaulin, as shown in Fig. 2

home tree still available. Presumably, the visual information was acquired when the animals were repeatedly traveling between feeder and nest.

Navigation with changed visual and chemical inputs

Pheromone signals vanish with time and are less reliable markers than visual landmarks. Scouts which explore and forage in territory far away from the nest may be unable to derive enough information from solely chemical markings, to find their way back to the nest once they have caught a prey. On circuitous excursions other navigation mechanisms must take over. The animals could use a route integration system based on celestial cues or they could match visual landmarks which they had sequentially stored during their outbound course. To test these hypotheses 16 animals which were discovered on the forest floor within a radius of 15 m around their nest were displaced laterally or in the direction towards or away from the nest. None of the animals carried booty indicating that they were not on their way home to the nest when they were transferred. If the ants navigated by route integration they would have chosen a course which normally should have led them back to the nest. When relying on sequential image matching techniques or on pheromone signals alone they should have been confused, unable to determine the correct course. A displacement in an overall direction towards or away from the nest should test the possibility that the animals use internal references for position information by means of computing their distance to the nest idiothetically.

A typical example of a displacement is illustrated in Fig. 4. The scout was spotted and baited on the footpath, and transferred into the understory about 6 m away. It was moved as fast as possible, but no attempt was made to block its pan-

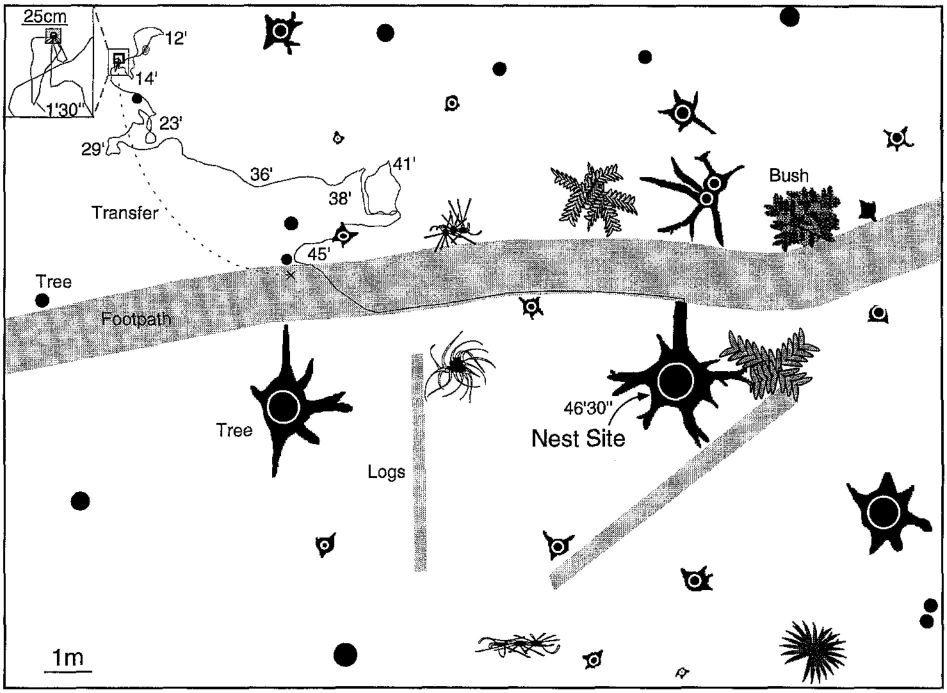

Figure 4. Homing route of a displaced *P. clavata* forager. The course of the animal was recorded on a 100:1 protocol sheet; simultaneously position data, times and major events were voice recorded (see Methods). Only the two-dimensinal portion of the route (i.e. along the forest floor was recorded and drawn. Major tree trunks (black circles), bushes and rotten logs are drawn to scale. Some trees are shown with main buttresses. The animal was spotted on a foot path (X) while traveling in outbound direction. It was rewarded and transferred 6 m away (open square). The home tree was not visible at the release site. Inset shows initial orientation loops. The animal arrived after 46′30″ min at the nest site

oramic view during the transfer. The animal's final distance from the nest was 13.6 m. After the animal had collected the sugar water it started to walk around along the edges of the platform without leaving it. This behavior was frequently alternated with returns to the top of the feeder. When walking along the edges, the animal intensively sampled the substrate outside the platform with the antennae. This behavior could take several minutes, before the ant walked onto the forest floor for the first time. In general, the animals walked one or several orientation loops, which led them back to the feeder (see inset of Fig. 4), before they finally traced their way along the forest floor. The animal in Fig. 4 frequently deviated from a theoretically possible direct course, but maintained on overall direction towards the nest site. When it arrived at the walkway it walked straight along it (see Discussion), and reached the nest entrance after 46.5 min.

Figure 5 maps the positions of all original sites (where the animals were discovered, x) and of the transfer sites (to which the animals were displaced, black squares) relative to the nest site, and indicates major landmarks, such as trees (black circles), bushes and rotten logs. The average transfer distance was 3.7 ± 2.6 m

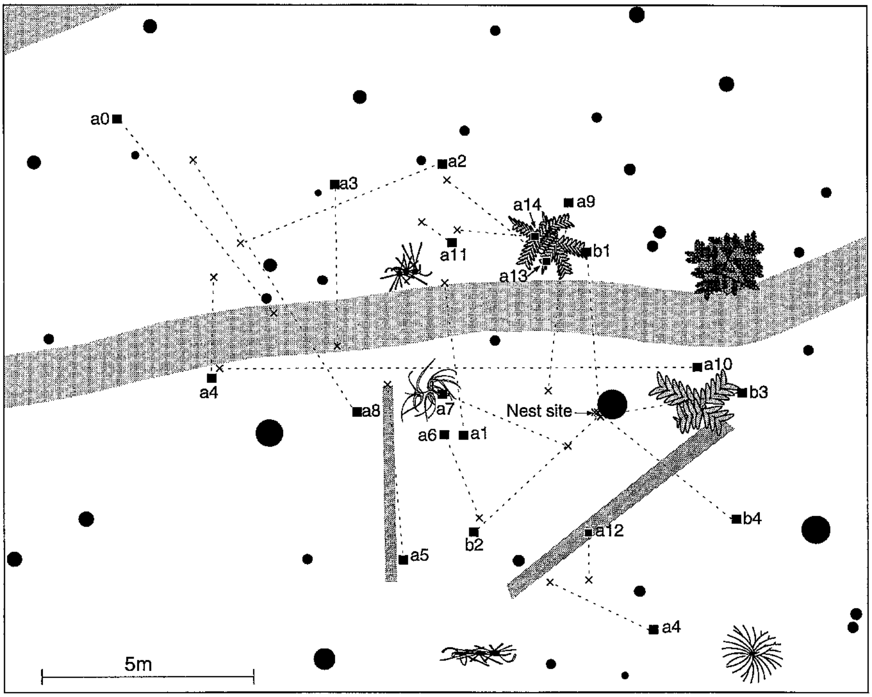

Figure 5. Original sites (X) and transfer sites (black squares) of 19 displaced foragers. Animals were displaced either within the surroundings of the nest site (a 0 – a 14) or from the nest entrance away (b 1 – b 4). For explanation of landmarks see Fig. 4

(mean ± S.D.). The distance between the original site where the animals were found and the nest was 5.9 ± 2.6 m (mean ± S.D.). Animals a 0 to a 14 were discovered in the surroundings of the nest and transferred either more laterally with respect to the nest (a 1 – a 6) or in an overall direction towards or away from the nest (a 0, a 7 – a 14). The course of forager a 0 is depicted in Fig. 4. Animals b 1 to b 4 were baited at the nest entrance. In 82 % of 17 evaluated cases the initial direction of the departure was contained in a 90° arc centered on the nest. Figure 6 shows the decreasing distances of animals a 1 – a 14 from the nest as they travel from the feeder. The individual dynamics of their homing courses varied (see e. g. animals a 1, a 9 or a 10), but all except animal a 8, homed within 30 min.

For comparison, 5 animals were baited at the nest entrance and transferred for 3.7 ± 0.3 m (mean ± S.D.) away. The example of Fig. 7 displays the course of a forager which was baited from the tree trunk above the nest entrance and transferred 4 m away. The animal performed several orientation loops, always returning to the feeder, but did not make any progress towards the nest. It was only after the animal had been displaced close to the nest that it found its way home. Similar search patterns were observed from animals which were displaced to release sites several hundreds of meters away from the nest (data not shown). Out of the 5 tested animals which were baited at the nest three failed to locate the nest entrance (Fig. 8).

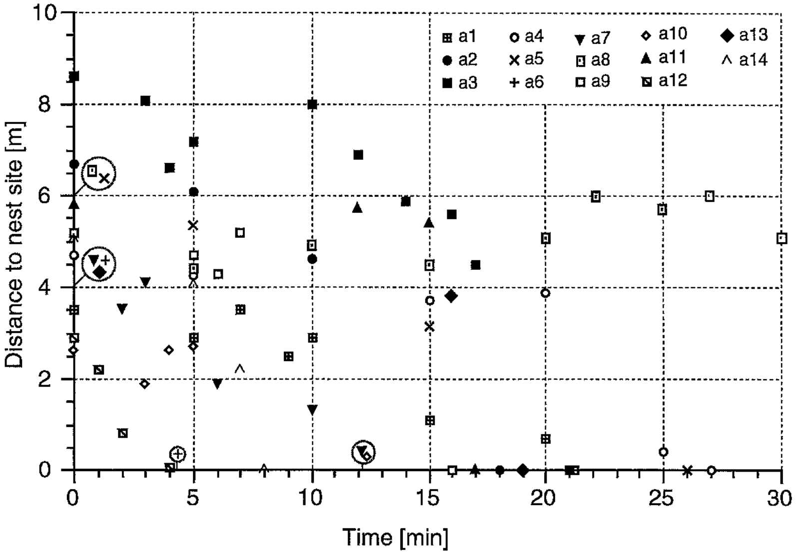

Figure 6. Data of 14 displaced foragers discovered in the surroundings of their nest. Positions (i.e. distances to the nest site) were registered at different times during their homing runs. The values for $t = 0$ correspond to the distances between the release sites and the nest site

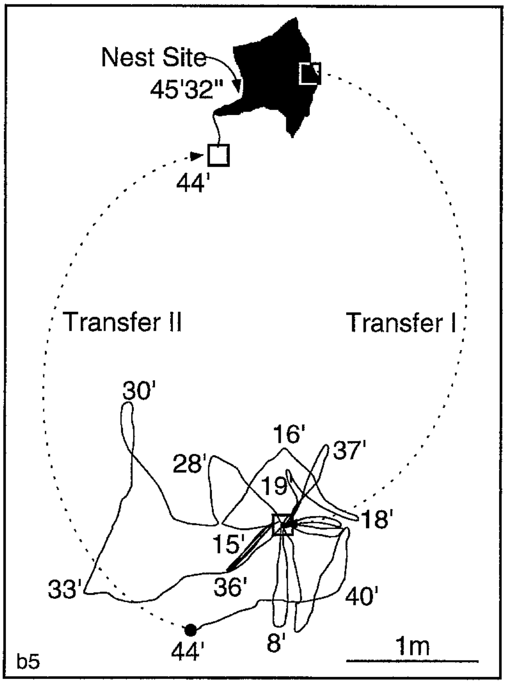

Figure 7. Example of a forager (b 5) which was displaced from above the nest entrance (different nest than in Fig. 5) 4 m away when it intended to ascend its home tree (Transfer I). It was transferred again after 44 min (black dot) to a place closer to the nest (Transfer II) from where it found the nest entrance

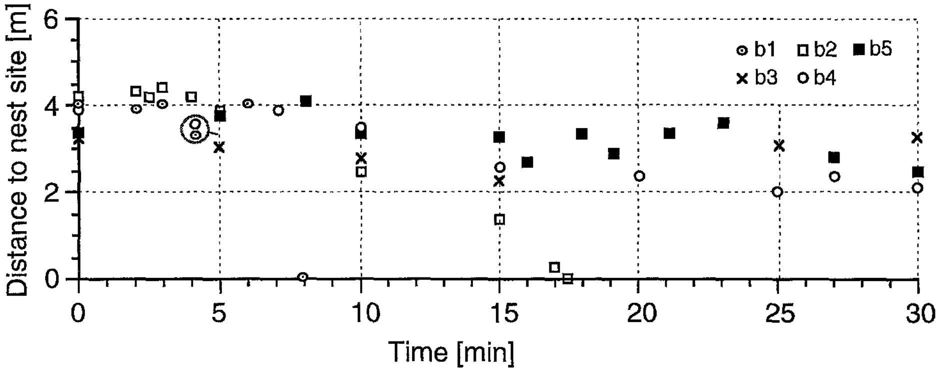

Figure 8. Distance of 5 animals which were displaced from their home tree as a function of time. Two of the 5 animals (b 1, b 2) homed, while 3 animals (including b 5 from Fig. 7) were unable to approach the nest site

To what extend find displaced *P. clavata* foragers their nest? In general the displaced ants did not re-appear at the nest entrance again once they had found their way back home. This made it impossible to transfer them to yet another place even further away. There was only one case where a forager (animal a 15) was displaced several times consecutively (Fig. 9). After the first displacement it found the nest entrance without difficulties. It returned to the feeder after it had delivered the bait. It was then transferred for another 2 m laterally to the nest (Fig. 9a), homed again and returned to the feeding site. Only the third transfer caused the animal to walk in circles, having more difficulties in finding the nest entrance, which it did after 30 minutes (Fig. 9b). It did not appear again outside the nest.

Discussion

Many hymenopterans learn and memorize visual landmarks when they depart from the nest site and at the food source, irrespective of whether celestial cues are available or not. Hölldobler (1980) showed that an African ponerine ant orients by learning the pattern of the canopy if it is sufficiently patterned. A similar strategy is employed by *P. clavata*. Direct evidence that these animals use the image of the canopy is their inability to maintain a straight homing route when 90° of their dorsal visual field was blocked (Fig. 1). This canopy information was essential for the animals although their lateral view up to an elevation of 45° was not impaired. In a small number of additional experiments ($n = 5$) with ants on the same test distance these 45° of the lateral field of view were blocked by an arena (40 cm×40 cm) leaving 90° of the canopy view free. The ants deviated from the straight course much in the same behavioral patterns that was exhibited by animals with blocked overhead view. They resumed their direct homing course when the arena was removed. Apparently the animals acquire an overall image of the visual scenes during their foraging excursions. When a sufficient portion of this image is missing they fail to navigate successfully. In a similar way, *Cataglyphis cursor* was found to use the

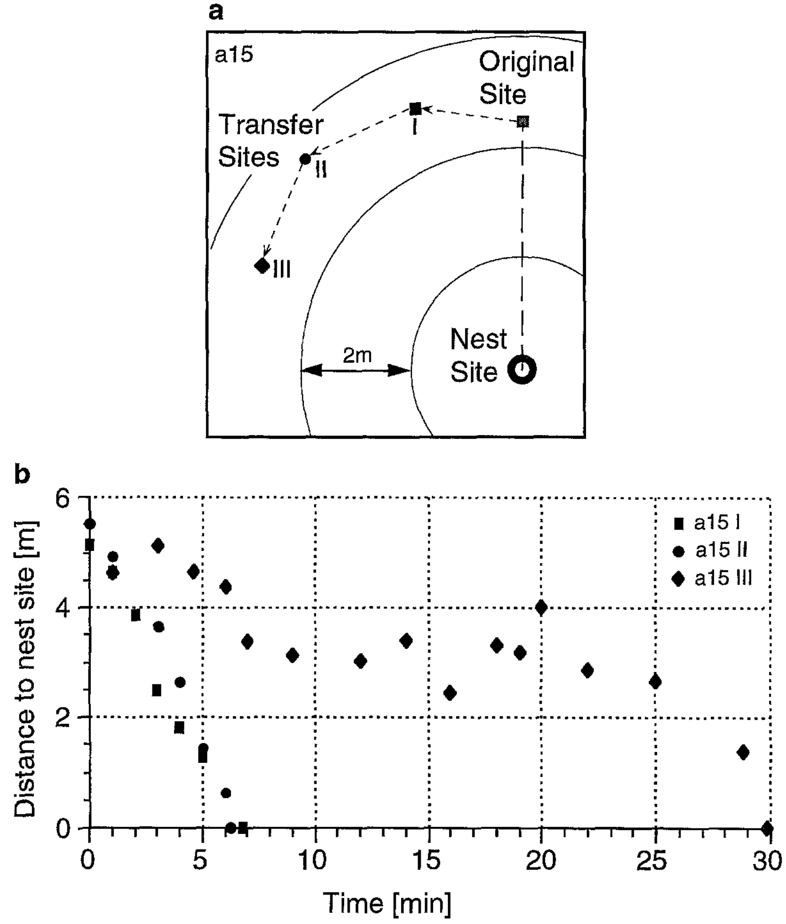

Figure 9. Homing behavior of an animal (a 15) which was displaced three times consecutively. a: Position of the original site and of the 3 transfer sites with respect to the nest site. The ant was transferred to I, from where it homed before it returned to I. It was than transferred to II, homed, returned to II, where it was transferred to III. From here it homed a third time. b: Distances of the animal to the nest at different times during the three homing runs

global arrangement of visual landmarks within the visual scenery for spatial orientation (Pastergue-Ruiz et al., 1995).

Blocking the pheromone inputs had less dramatic consequences for homing foragers as long as sufficient visual information was still available (Figs. 2–3). However, when the overhead view was blocked in addition to abolishing the pheromone signals the animals were unable to continue homing (pers. obs.). The experiments of Figs. 1 and 2 have in common that the ants had acquired both visual and pheromonal information during the training phase. The behavior of the visually blocked ants showed that chemical signals *per se* were not sufficient to guide them home. It is the information provided by all visual surroundings which is both necessary and sufficient when the scent trails had been completely removed. Red wood ants also navigate using visual and pheromone information on their excursions (Fourcassie and Beugnon, 1988). With a similarly three-dimensional foraging habitat both modalities help them finding food sources. But in contrast to the experiments described here (Fig. 3) the wood ants' foraging accuracy and traveling speed was diminished as soon as any one of the modalities was experimentally abolished, suggesting a complementary recruitment of the two external references. However, both ant species seemed to prefer the more reliable visual cues over pheromone cues, as shown in Figs. 1–3 for *P. clavata*, and as found for the wood ants in choice experiments for situations where the two modalities contained conflictual information (Beugnon and Fourcassie, 1988). This does not preclude that the animals use chemical cues when traveling at night, with no visual information available at all.

One side observation about homing *P. clavata* is worth mentioning. Foragers trained to walk on the plastic tarpaulin had apparently no difficulties with the texture of this substrate, even when scent markings were missing. They were usually even faster than on the forest ground. But when a 40-cm-portion of a frequently used trail on the forest floor was covered with a small tarpaulin of the same material, animals which had not experienced this substrate before, refused to cross this portion. They walked straight onto the sheet for several centimeters, in continuation of their original route. Then they stopped suddenly and ran in circles, unable to maintain their straight path. Apparently they were confused by the mismatch between the altered texture information and all other sensory modalities suggesting that the texture of the substrate surface was learned and utilized as an additional orientation cue.

How do transferred animals navigate?

Individually displaced animals found their way back to the nest. This raises several questions. First of all, what kind of sensory modality provided them with position information with respect to their nest? And what has guided them to trail through the vegetation towards the nest entrance? Any pheromone signals, known to be used by *P. clavata* (Breed and Bennett, 1985) were highly unlikey to be present at the release sites. In a related ponerine ant, *Megaponera foetens*, both short- and longer-persistence pheromones were described, with the latter inducing following responses in nest mates for up to 29 h (Hölldobler et al., 1994). In this study the animals were transferred into areas where no other ants had been spotted for hours or days before. Intensive search in an area greater than 200 m^2 revealed only some twenty individually foraging scouts over a period of five days. The probability of such a scout finding any familiar directional pheromone signal at the transfer site was therefore very low. Of course, the chance of chemical trail signals increased with decreasing distances from the nest entrance, and they could certainly not be excluded as a positive reinforcement for those ants which chose their last portion of the homing course on trails, such as the small concrete walkway (see Fig. 4). Another possibility to consider are airborne pheromones emitted from the nest entrance, although there is no evidence for the existence of any such signals in ants.

Pheromone streams would also be likely to be distorted by wind and rainfall, highly unlikely to provide directional information at distances of several meters away from the nest.

Magnetic compass information as used by bees (Martin and Lindauer, 1977; Collett and Baron, 1994) and ants (Anderson and Vander Meer, 1993; Camlitepe and Stradling, 1995) would not have enabled displaced ants to home. It provides only directional information, but does not reveal the absolute position.

Therefore, visual information must be used by *P. clavata* scouts on circuitous routes in remote, complex terrain. Celestial cues used by many insects, including ants (Hölldobler, 1971; Wehner, 1989) and bees (Wehner and Menzel, 1990) can clearly be ruled out. In the rain forest with its dense canopy and the long periods of overcast skies sun compass information is very unreliable. In addition to this, it codes only for course direction as in the case of magnetic cues, and should have led the displaced foragers to invariably miss the nest. At least for the initial determination of the homing direction another visual strategy, beacon orientation, is also unlikely to be used by *P. clavata*. The home tree was only partially or not at all visible from the transfer sites. Nearby trees of similar dimensions (see Fig. 4) appeared for the animal at similar visual angles, thus making it difficult to pinpoint the home tree from greater distances. Beacon orientation, however, could have become more important as the animals approached their nest tree.

The results lead to the following working hypothesis: foragers of *P. clavata* learn and memorize the visual landmarks of their surroundings. This information may be of limited importance, or not at all used while traveling on routes with less degrees of freedom, e.g. along branches and tree trunks marked with trail scents, or during nocturnal foraging excursions. It may be the essential orientation cue for scouts foraging far away from the nest. One possibility is that individually foraging scouts acquire the important parameters about their visual surroundings on their extended foraging trips. Such an acquisition of data without immediate reward has been described as latent learning in rats and mice (Thorpe, 1950; Rodrigues et al., 1993). The retrieval of the stored images would enable the animals to recognize the transfer site, to use it as the reference to determine its own position, and to locate the nest site. This does not exclude that familiar beacons at the transfer site may additionally serve as intermediate orientation cues. The spatial limits of such a task are shown in Fig. 9 where the animal had difficulty in locating the nest site after its third successive displacement. The information about the visual surroundings is presumably acquired as the foragers extend their excursion trips. Consequently, less experienced foragers or ants which serve as guards at the nest entrance should have more difficulties to re-find their nest after a displacement. The results of Figs. 7 and 8 support this hypothesis. Although the actual degree of experience of the animals collected from the nest site was unknown three of five displaced animals did not find their way back to the nest entrance.

Experimental limitations of displacement experiments

Unfortunately, the technique of displacing individual foragers to distinct areas in the field is subject to several limiting factors. The experiments depend essentially on the fact that there are single foragers around and that they can be found in the forest. The history of these animals is largely unknown. Animals could have been in the process of an exploring foraging trip, or they could have remained in distant foraging areas without returning to the nest (Fewell et al., 1992). Furthermore, it was sometimes not possible to follow displaced animals continuously on their way home, as they frequently disappeared in the scrub, e.g. when hiding from rain showers Finally, the successfully homing animals usually did not start new foraging excursions after the first displacement, but stayed within the nest (for an exception, see Fig. 9). Therefore, repeated experiments with the same individuals to determine the spatial limits of an individual's terrain, are difficult to conduct.

In conclusion, the data show that *P. clavata* foragers, besides pheromone trails, used the visual landmarks of their surroundings when returning to the nest. Some scouts were able to recognize their foraging habitat after displacement to a site which they had not visited immediately before, and returned to the nest. Future field experiments aim to investigate the mechanisms which enable these scouts to perform this site specific recognition in further detail, and to characterize the spatial borders of their foraging territories.

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