

**Nocturnal orientation in the black carpenter ant
Camponotus pennsylvanicus (DeGeer)
(Hymenoptera: Formicidae)**

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Summary

The black carpenter ant *Camponotus pennsylvanicus* (DeGeer), a predominantly nocturnal Formicine ant, responds to a hierarchy of visual and tactile cues when orienting along odor trails at night. Under illumination from moonlight or artificial light, workers rely upon these beacons to mediate phototactic orientation. In the absence of moonlight or artificial lights, ants were able to orient visually to terrestrial landmarks. In the absence of all landmarks, save for overhanging tree branches, ants could negotiate shortcuts or make directional changes in response to visual landmarks presented within the tree canopy on a moonless night. When experimental manipulations placed the ants in total darkness, they could no longer negotiate shortcuts and would resort to thigmotactic orientation along structural guidelines to reach a food source. The hierarchical organization of these diverse cues in a foraging strategy is discussed, as well as their adaptive significance to *C. pennsylvanicus*.

Introduction

Cyclic foraging patterns, whether driven by circadian rhythms or environmental stimuli such as temperature, are common for all ants (Hölldobler and Wilson, 1990). Nocturnal activity may provide an escape from intolerable temperature and humidity conditions, a mechanism for avoiding predators, or a release from interference competition with sympatric species at food resources. Although these and other benefits may accrue to nocturnal species, orientation to resources at night presents these ants with a considerable challenge. While a large body of literature exists concerning the home-range orientation of ants (reviewed in Hölldobler and Wilson, 1990), this information, including most of our insights into orientation

behavior in general, has been learned principally through studies on diurnal species. Visual orientation in diurnal ants has been most thoroughly studied in *Cataglyphis bicolor*. A desert species that forages individually in the absence of odor trails, *C. bicolor* responds to a hierarchy of cues for home-range orientation (Wehner, 1972) consisting of a combination of vector orientation and landmark orientation (Wehner and Flatt, 1972; Wehner and Raber, 1979; Wehner et al., 1983; Collett et al., 1992).

Due to the complications inherent to nighttime research, relatively little is known about those ant species that are primarily nocturnal, nor for predominantly diurnal species when they forage at night. In the cases thus far investigated, it appears that the moon or artificial light sources, terrestrial landmarks, odor trails, and structural guidelines, either alone or in combination, may serve as cues for nocturnal orientation. Lunar orientation has been documented in three cases. Santchi (1923) observed that workers of *Monomorium* sp. became disoriented and lost their bearing when clouds obscured the moon. Jander (1957) demonstrated that when the position of the moon was reversed with a mirror, *Formica polyctena*, in response, reversed its directional orientation. After sunset, workers of the diurnal *C. bicolor* that have not returned to the nest will orient homeward through anemomenotaxis and a tropotactic orientation toward the azimuth of the moon (Wehner and Duelli, 1971; Duelli, 1972). When moonlight is absent, or under conditions offering only dim light, some ants are still able to successfully orient. While primarily diurnal, *Formica polyctena* exhibited a considerable amount of nocturnal foraging (DeBruyn and Kruk-DeBruin, 1972; Rosengren, 1977a). Rosengren (1977b) showed that while diurnal route fidelity in *F. polyctena* was based on visual cues, workers maintained spatial route fidelity on moonless, overcast nights by reliance on olfactory cues. A similar result was found in *F. nigricans*, where visual landmark cues were primarily used during the day, and chemical cues at night (Beugnon and Fourcassie, 1988). However, in another species of the *F. rufa* group, terrestrial landmarks have been shown to function as orientation cues at night (Kaul and Kopteva, 1982). Hölldobler and Taylor (1983) strongly implicated visual landmarks within tree canopies serving as cues in nocturnal orientation by *Nothomyrmecia macrops*, which was the first nocturnal demonstration of the "canopy orientation" originally described by Hölldobler (1980) in *Paltothyreus tarsatus*. In the absence of visual cues, in a simulation of total darkness, we have demonstrated that *Tapinoma sessile* can successfully locate resources by relying in thigmotactic orientation along structural guidelines (Klotz and Reid, 1992).

Our research sought to expand the understanding of nocturnal cues in spatial orientation by focusing on the black carpenter ant *Camponotus pennsylvanicus* (DeGeer), which is a predominantly nocturnal Formicine species typically inhabiting woodland habitats in the eastern Nearctic region (Pricer, 1908; Klotz, 1984). This species relies heavily on olfactory cues, a trail pheromone originating from the hindgut (Traniello, 1977). We performed a series of manipulations with workers from field colonies to determine which cues are important to this species in nocturnal orientation along odor trails. Our results provide evidence of their reliance on the moon, artificial lights, and terrestrial landmarks as visual cues and for the role of structural guidelines as tactile cues in home-range orientation at night. The

hierarchical assembly of cues is considered from the perspective of foraging strategies in *C. pennsylvanicus*, as well as the adaptive significance of these cues.

Methods

All experiments were conducted in the field, between 2100 and 0100 local time. Displacement tests were conducted by the senior author in Johnson County, Kansas in 1984. One colony was nesting in a mature honey locust (*Gleditsia triacanthos*), and a second colony was nesting in the woodwork of a farmhouse. Arena tests were conducted in Tippecanoe County, Indiana in 1991 with colonies that were found nesting in mature oaks (*Quercus* spp.) or maples (*Acer* spp.). To facilitate our experimental manipulations, each nest was outfitted with a series of 3-cm diameter wooden poles arranged in a horizontal "runway" approximately 50 cm above the ground; these were connected end to end, 5–20 m in combined length away from the tree (or house). To train ants to travel on the poles, a 150 cm² feeding station was first set up on the pole closest to the nest and supplied with a bait mixture (whole milk and raw sugar, 2:1). After the ants had discovered the food source, and recruitment had begun, the station was gradually moved outward along the poles, thereby luring the ants to forage further and further from the nest. Ants were trained to use the entire length of this pole runway within 1 to 2 hours, and two types of experiments, displacement tests and arena tests, were then performed to examine visual cues (artificial light, moonlight, and landmarks).

Displacement Tests

These tests examined the role visual cues play in regulating directional changes by foragers as they travel along an odor trail, and our design involved displacing individual ants returning from the feeding station to a new location on the runway closer to the nest (Fig. 1 b), or to a T-maze fashioned from the same 3-cm diameter poles and located parallel to the main pole runway (Fig. 1 c). Poles in the T-maze had previously been used as runways and thus had an odor trail on their upper surface. When displacing individuals, ants leaving the feeding station were forced to congregate at the terminus of a pole section near the feeding station. This was accomplished by removing the inwardly adjacent section (Fig. 1 a), thus "stranding" these nestbound ants at the pole terminus. These ants were then displaced one at a time to the new location by gently moving the section of pole on which they were stranded. Since *C. pennsylvanicus* workers walk almost exclusively on the upper surface of horizontally oriented poles (Klotz, 1985), we handled pole sections only on the underside to reduce the influence of our hand odors on the ants' behavior. At the new location, or on the T-maze, ants were forced to make a binary directional choice to turn either to the left or to the right; a turn was defined as an ant's sideways rotation of at least 90°. To control for any intrinsic turning bias, the ants were alternately tested on either side of the pole runway. To control for extrinsic biasing from odor trail pheromones (freshly laid down by the ants being tested), each

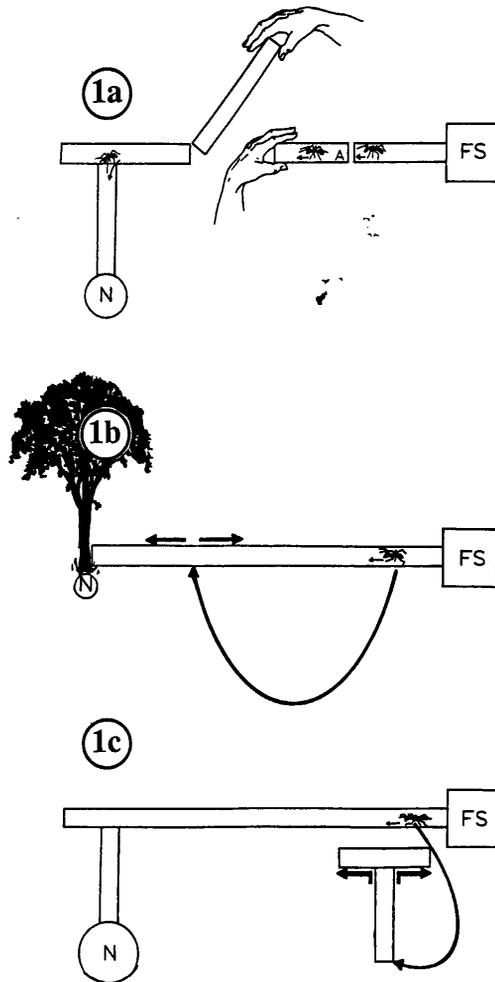


Figure 1. Schematics of the materials and methods in the displacement tests. After removing a pole section to strand ants returning to the nest (N) from the feeding station (FS), one ant is picked up on pole A (1 a). The ant on pole A is then transported to new location farther along the runway toward the nest (1 b), or to a T-maze located parallel to the runway (1 c), where it is forced to make a directional decision before continuing its return to the nest.

individual ant was tested at a different location along a 15 cm section of the runway. Equivalent precautionary steps were taken in the T-maze test.

Arena Tests

Whereas displacement tests examined the role that visual cues play in secondary orientation by individual ants along extant odor trails, arena tests were designed to

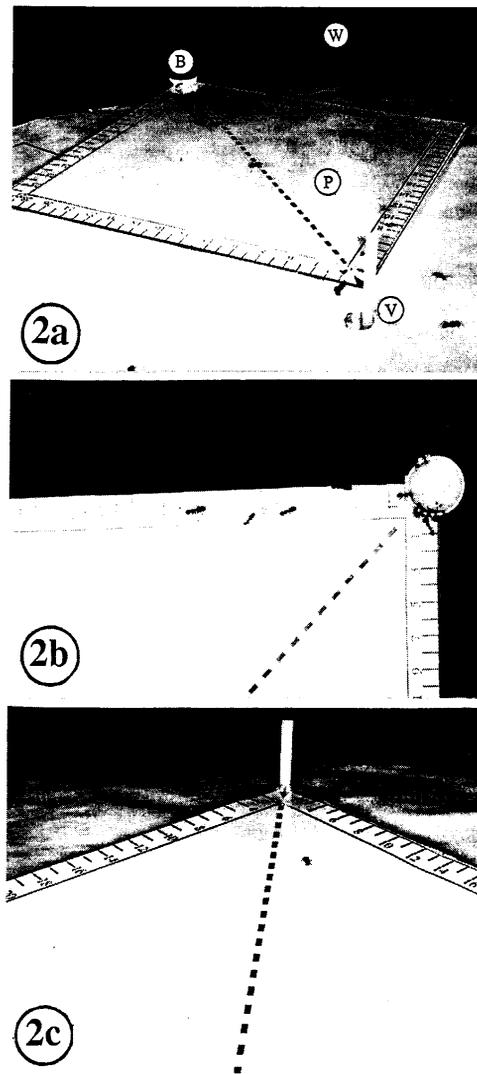


Figure 2. Materials and their configuration in the arena tests (2a). Ants travelling along the runway enter the arena on a vertical pole (V) that contacts the glass plate (P) at a corner opposite from the bait dish (B); the 90-cm diam. arena was delimited by a 10-cm high arena wall (W) atop the table (1 m²). Whenever ants travelled within 2 cm of the edge (see printed underlay) they were considered to be orienting to thigmotactic cues (2 b), and when not following the edge they were considered to be orienting to visual cues (2c).

investigate the importance of visual cues by describing the trail followed by ants after a period of undisturbed foraging. The runway leading from the nest was diverted onto a vertically-positioned wooden dowel (1 cm diam.) which led ants into a 90-cm circular arena through a 1.5 cm hole cut in the arena's floor (Fig. 2a). Upon entering the arena, this dowel was in contact with one corner of a horizontal glass plate (30.5 × 30.5 cm), raised by a central pedestal 3 cm off of the arena floor. Sugar/milk

bait had been placed at the opposing corner of the plate. After bait placement, ants were allowed 1 to 2 hours to establish an odor trail on the glass plate. This trail was determined by watching ants going to or coming from the bait, and recording the path taken. Our arena method tests for thigmotaxis by evaluating the ants' adherence to the glass plate's edge, which was defined as a 2-cm wide boundary around the glass plate; a printed underlay facilitated data collection (Fig. 2b and 2c). These observations were quantified as "edge fidelity", defined as the distance traveled along the glass plate's edge as a percentage of the total distance (55 cm along the inner boundary) to the bait along the glass plate's edge. New glass plates were used in each of the experiments to prevent any previous trace of odor trails from obscuring results in new trials.

Data Analysis

In both types of experiments, we observed a total of 40, or 50, ants. Our manipulations of orientation cues performed in each experiment are presented with the results of each experiment. In the displacement tests, χ^2 tests ($\alpha = 0.05$) were used to ascertain whether the distribution of the turns was significantly different from random or from the distribution of turns in another test. Data from the arena tests were analyzed in paired comparisons of two experiments using a Kruskal-Wallis rank sums test (Hollander and Wolfe, 1973), with a single degree of freedom ($\alpha = 0.05$). SAS procedures were used to generate the test statistics (SAS Institute, 1990).

Results

Displacement Tests

Nocturnal orientation to artificial light. To test whether foraging ants responded to an artificial light source as a directional cue when orienting on a moonless night, a kerosene lantern was placed alongside, and 2 m away from, the runway to the feeding station and 3-hour training period then ensued. Nestbound ants were then displaced to a new location further along their route, where they could turn either toward or away from the nest; we found that 37 of 40 (93%) ants turned homeward ($\chi^2 = 28.9$, $p < 0.001$). The lantern was then moved to the opposite side of the runway, and the displacement experiment was repeated. Results of this test proved to be opposite to the one described previously, as we found that 34 of the 40 (85%) displaced, homebound ants turned in the direction away from the nest ($\chi^2 = 19.6$, $p < 0.001$). Thus, it was concluded that an artificial light source can serve as a very strong nocturnal directional cue for *C. pennsylvanicus*.

Lunar orientation. Lunar orientation was tested under full-moon illumination after ants had foraged undisturbed for 3 hours. Homebound ants were picked up from the runway at a point where the moon's azimuth was perpendicular to the runway and

displaced to the test location, which also was perpendicular to the moon's azimuth. When given the choice of turning toward or away from home, 37 of 40 (93%) ants turned homeward ($\chi^2 = 28.9$, $p < 0.001$). In the next experiment, ants were displaced to the same location as above, but direct light from the moon was blocked with a piece of cardboard, and a mirror (930 cm²) was used to redirect moonlight from the opposite side of the runway. Twenty-four of 40 (60%) homebound ants turned in the direction of the feeding station. This distribution was significant ($\chi^2 = 22.4$, $p < 0.001$) and the turning direction of these ants was reversed from the previous experiment in response to the reversed directional information in the redirected moonlight. Thus, as we have shown with the artificial light, moonlight can also serve as a directional cue.

Landmark orientation at night. To allow observation under the dim light of a moonless night, the dorsal abdominal surface of numerous ants was painted with luminescent paint. This paint was activated to glow when ants passed beneath a 150-watt flood lamp during a 3-hour training period; once activated, paint marks continued to be visible in the dark for 1 hour. During tests, the floodlight was switched off, so that the only light came from the starlight overhead and distant city lights on the horizon (this light intensity was measured as 0.025 lux with a light meter fitted with a 5 × 5 cm silicon photocell (Archer) calibrated against a commercial light meter with a cadmium sulfide photocell). To determine if ants could visually orient in such dim light, foragers returning from the feeding station were displaced to a T-maze located alongside, and 15 cm away from, the observation runway; 38 of 50 (75%) ants tested turned towards the nest in the dim light ($\chi^2 = 13.5$, $p < 0.001$). To determine if the directional cue(s) responded to by ants that continued in a homeward bearing was visual, the test was repeated while a large umbrella was held over the T-maze to obstruct the ants' overhead view. In this test, only 28 of 50 (56%) ants turned homeward, a distribution which is not significant ($\chi^2 = 0.7$, $p < 0.5$). Nevertheless, this result was significantly different from the preceding test where the ants' view of possible landmark cues were not obstructed ($\chi^2 = 4.5$, $p < 0.05$). These results suggest that visual landmarks, and specifically overhead landmarks (the contrast of trees or man-made structures against the night sky), were being used as directional cues under conditions devoid of light sources (e.g., the moon, streetlights, etc.).

Arena Tests

Orientation without visual cues. Two experiments examined ant orientation in the absence of visual cues. To simulate total darkness, all visual cues were obviated by placing a 1-m high, cylindrical hood of black cloth over the arena. Intermittent observations, aided by a red-filtered flashlight, were made through a portal in the side of the hood, which was cloaked by a section of black cloth to cover the observer's head and the portal opening. Under these conditions (= no cues), the 50 ants that were observed traveled a mean \pm SEM of $91.8 \pm 1.7\%$ of the total distance (55 cm) within 2 cm of the edge of the glass plate (e.g., Fig. 2b). In a second experiment,

where the arena was located in a clearing 15 m from the tree trunk, the arena walls were extended to a height of 1 m by a cardboard chimney. This barrier was high enough to block the ants' view of both the moon and landmarks, so that the only view available would be the cloudless night sky visible directly above the arena. Intermittent observations, again aided by a red-filtered flashlight, were made through a portal cut into the chimney and cloaked by a section of black cloth. In this test, the 50 ants were observed traveled a mean \pm SEM of $93.4 \pm 1.9\%$ of the total distance along the edge of the glass plate. The high edge fidelity evident in the paths being followed by ants in both of these experiments were not significantly different ($\chi^2 = 1.75$, $p = 0.19$) from each other, and the ants' thigmotactic adherence to the edge in the second test suggests that the overhead view of the clear night sky offered no cues that ants could use to negotiate the shorter diagonal path to the bait.

Landmark orientation. To examine the role of landmarks in nocturnal orientation by *C. pennsylvanicus*, the arena was surrounded by a 10-cm high steel ring; overall height of this visual obstruction was just 5 cm higher than the surface of the glass plate. The experiment was conducted on a moonless night with the arena located 5 m away from the trunk, and directly beneath the canopy, of the oak tree containing the nest. On this moonless night, as in the analogous displacement test, the only light sources were starlight and distant city lights. Under these test conditions, the 50 ants we observed traveled a mean \pm SEM of $10.8 \pm 1.4\%$ of the total distance along the edge of the glass plate. This path was significantly different ($\chi^2 = 76.08$, $p < 0.0001$) from that followed by ants in the first arena test (= no cues) discussed above. Our observations of the trail following were that the ants quickly left the edge and followed a shorter, more diagonal route to the bait (e.g., Fig. 2c). This result suggested to us that the ants were using visible landmarks to negotiate the more direct route. In an attempt to determine what role the tree canopy immediately above the arena may have played in mediating the observed orientation, the 10-cm steel ring was removed and the ants' overhead view was obstructed with a 1×1 m sheet of plywood supported over the entire arena at a height of 10 cm above the glass plate. On a similar moonless night, and with only a lateral view provided, the 50 ants we observed traveled a mean \pm SEM of $89.8 \pm 3.0\%$ of the total distance along the edge of the glass plate. This path was significantly different ($\chi^2 = 78.97$, $p < 0.0001$) from that followed by ants provided with a canopy view in the preceding experiment, while the ant's thigmotactic adherence to the edge was not significantly different ($\chi^2 = 1.94$, $p = 0.16$) from that displayed by ants in the no-cues experiment discussed earlier. These results, which we confirmed in one additional test series on other colonies, strongly implicated the tree canopy as providing useful visual cues that *C. pennsylvanicus* workers can exploit in nocturnal orientation on moonless nights.

Lunar orientation. A final experiment examined directional orientation in response to the moon. An arena, cloaked with a cardboard chimney, was established in a clearing 20 m from the colony's tree and a 930-cm² mirror was suspended just outside and above the 1-m high chimney wall to reflect moonlight down onto the glass plate. In this test, the ants' direct view of the moon and landmarks was obstructed, so that the only cues available were in the image of the moon reflected in the mirror or the sky

visible directly above the arena. In this test, the 50 ants that were observed traveled a mean \pm SEM of $58.7 \pm 3.3\%$ of the total distance along the edge of the glass plate. While this path was significantly different ($\chi^2 = 45.83$, $p < 0.0001$) from that followed by ants in the first chimney experiment, the deviation away from edge fidelity was significantly less ($\chi^2 = 69.35$, $p < 0.0001$) than that observed in the path followed by ants provided with an unobstructed view of the canopy. Reflected moonlight seemingly provided an adequate reference point to allow the foraging ants to deviate away from the glass plate's edge, but the directional information presented by moonlight was not as strong as that presented by the tree canopy.

Discussion

Our studies have shown that in *C. pennsylvanicus* a relatively bright point source of light, such as the moon or a floodlight, can serve as a directional cue for orientation at night along odor trails. In the carpenter ant *C. modoc*, a bright light from a parking lot was shown to be the primary directional cue when the ants were observed to reverse walking direction along the odor trail in response to a 180° change in the position of the artificial light source (David and Wood, 1980). In our experiments, the dimmer moonlight, compared to the brighter lantern light, was seemingly not as strong a cue. The turning response of ants in the displacement experiment with redirected moonlight (60% turned homeward) was significant, but weaker than the response to the repositioned artificial light (85% turned homeward). A similar result was seen in the arena test with redirected moonlight, where the deviation away from thigmotaxis along the edge of the glass plate was not as strong as when ants were afforded a view of landmarks.

Terrestrial landmarks are important cues in nocturnal orientation by *C. pennsylvanicus*. Our experiments suggest that *C. pennsylvanicus* responds to landmarks within tree canopies as nocturnal orientation cues, as similarly reported for *Paltothyreus tarsatus* (Hölldobler, 1980) and *Odontomachus bauri* (Oliveira and Hölldobler, 1989). Canopy orientation was strongly implicated in the nocturnal orientation of *Nothomyrmecia macrops* by Hölldobler and Taylor (1983), and our results represent an additional case where this type of landmark orientation is responded to by a nocturnal species. Kaul and Kopteva (1982) point out that nocturnal orientation to landmarks is more dependent on sufficient contrast of the landmark against the background than it is on levels of illumination. Given this assertion and Hölldobler's (1980) argument for canopy orientation being well suited to restrictive lighting conditions in tropical forests, response to canopy landmarks by *C. pennsylvanicus* under the low light conditions during our studies is understandable. A special condition to be considered is the effect of urbanization of the levels of illumination in the night sky. The contrast of landmarks against the night sky will vary as a function of their proximity to urban centers and thus the reliance on these landmarks for nocturnal orientation may also vary.

Considering that *C. pennsylvanicus* typically nests within trees, the species' adoption of canopy landmarks as orientation cues may be an adaptation that increases the likelihood of workers returning to the tree, and thus the nest, after foraging

sorties. The ability of *C. pennsylvanicus* foragers to carry over visual information for 24 h, as demonstrated in the laboratory by Hartwick et al. (1977), would be facilitative in this regard. Fourcassie (1991) reported an analogous finding when he concluded that *F. lugubris* foragers associated their nest's location with the position of trees having the highest apparent size above the horizon.

One characteristic common to *C. pennsylvanicus* and nocturnally foraging *Formica* spp. is the importance of odor trail guidelines in their spatial orientation. *C. pennsylvanicus* (Traniello, 1977) and *F. polyctena* (Rosengreen, 1971) use trunk routes to guide foragers travelling to permanent food sources. Olfactory cues in the odor trail would be important backups, given the very low light conditions under which nocturnally active ants sometimes forage. However, eventually the individual forager deviates away from the trunk trail in searching for resources and it is here that visual cues would become increasingly important. In a series of experiments, David and Wood (1980) explored the role visual cues (lights and landmarks) play in maintaining correct bearing along odor trails in *C. modoc*. The importance of visual cues to nocturnal orientation was amply demonstrated in an experiment where visual cues and the odor trail were made to conflict with previous experience, by perpendicular displacement of the odor trail in litter. Fifty-eight of the 100 ants tested became disoriented when the odor trail turned away from its original route, and 15 of these ants went on to travel down the original route in response to the visual cues and thereby deviated away from the conflicting odor trail. We, too, have shown a similar dependence on visual cues in *C. pennsylvanicus* (Klotz and Reid, 1992). When an odor trail on a pole was lengthened, by manipulating the relative position of the elements in a pole-maze, and the light source held constant to the training conditions, the ants tested would invariably make their turns at a point coincident with the position of the light source despite the continuance of the odor trail.

Structural guidelines (e.g., grooves, crestlines, edges, etc.; Klotz and Reid, 1992) which serve as tactile cues are an important pre-existing guideline used as a backup by *C. pennsylvanicus*. The importance of tactile cues for nocturnal orientation has been reported in the army ant *Neivamyrmex nigrescens* where physical objects served as a backup for chemotactic orientation (Topoff and Lawson, 1979) and in *Tapinoma sessile* where workers followed edges to food sources when visual cues were obviated (Klotz and Reid, 1992). Whenever landmarks or light cues were available, these ants switched over to vector orientation, integrating visual cues to take a shorter, more direct route to a food source. In our postulated hierarchy, tactile cues were the lowest cues we investigated, as *C. pennsylvanicus* only resorted to thigmotactic orientation along the edge of the glass plate in total darkness, or when the visible landmarks were obstructed.

Despite being a predominantly nocturnal species (Pricer, 1908; Fowler and Roberts, 1980; Klotz, 1984), *C. pennsylvanicus* will occasionally forage during daylight. Since *C. pennsylvanicus* live in a habitat rich with trees and shrubs, it relies on these conspicuous objects as landmarks during both diurnal (Klotz, 1986) and nocturnal home-range orientation. The tree canopy, and presumably other vegetative (or geologic) features in the landscape, would seem to serve the primary role in their orientation. This undoubtedly arises as a consequence of the native, woodland habitat of the species. However, light sources, whether natural or artificial, could

provide directional information to foraging workers. Under the dimly lit conditions at night beneath a forest canopy, the strong odor trail of *C. pennsylvanicus* is a fundamentally important navigational aid. In addition to this olfactory guideline, foraging ants could also rely on pre-existing structural guidelines (crevices in tree bark, vines climbing tree trunks, and limbs or branches lying on the forest floor) that provide tactile cues with which to traverse complex terrain. Within this assembly of orientation cues there is a built-in redundancy, in that foraging ants show a dependence on more than one orientation cue; e.g., their concurrent use of an odor guideline and a light source. As a consequence, however, this hierarchy of cues provides the ants a series of backup cues with which they could continue to successfully orient to and from food resources in the absence of any one particular class of orientation cues. This arrangement empowers *C. pennsylvanicus* with the skills essential to foraging under the limited sensory environment associated with their nocturnal existence. Comparable studies with other predominantly nocturnal ant species, or comparative studies with diurnal and nocturnal sympatric ant species, would yield valuable insight into the nocturnal orientation of ants.

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