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The Use of Spatial Cues for Structural Guideline Orientation in *Tapinoma sessile* and *Camponotus pennsylvanicus* (Hymenoptera: Formicidae)

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Camponotus pennsylvanicus *(DeGeer) and* Tapinoma sessile *(Say) exploit structural elements as guide-lines in their topographic orientation. This research documents the response of* T. sessile *and* C. pennsylvanicus *to a series of thigmotactic, gravitational, chemotactic, and phototactic cues while utilizing structural guidelines. Adherence to these guidelines is more pronounced on vertical than on horizontal surfaces and more pronounced in darkness than in daylight. Orientation switches from a crestline on the horizontal to a groove on the vertical. Light and odor trails serve an important role as distance cues in structural guideline orientation. The hierarchy of orientation cues and the adaptive significance of these ant's exploitation of structural guidelines are discussed.*

KEY WORDS: Insecta; *Camponotus pennsylvanicus; Tapinoma sessile;* structural guideline orientation; orientation cues.

INTRODUCTION

The black carpenter ant, *Camponotus pennsylvanicus* (DeGeer), and odorous house ant, *Tapinoma sessile* (Say), although belonging to different subfamilies (Formicinae and Dolichoderinae, respectively), have similar foraging behaviors. Both species tend aphids, forage both day and night, and rely on odor

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trails for orientation to resources (Hansen and Akre, 1990; Harada, 1990). More important to the purposes of our report, these ants display a common tendency to exploit structural features of the environment when foraging for resources.

We refer to this behavioral tendency as structural guideline orientation. Guideline orientation is one of four components of topographic orientation in ants and is defined as the following of preexisting edges, grooves, and crestlines or previously constructed tunnels and odor trails (Jander, 1977). The other three components are (1) landmark orientation, (2) distance orientation, and (3) directional orientation. Odor trails are an example of guideline orientation, and their importance to foraging behaviors in ants has been recognized since the late 18th century (Bonnet, 1779). The ant's odor trail is an important component in our study, since all observations were based on secondary, rather than primary, orientation (Jander and Daumer, 1974). In secondary orientation, new terrain has been explored and firmly established odor trails exist which the ants use for orientation. In primary orientation, scout ants are actively engaged in exploratory behavior without the guidance of odor trails.

In contrast to the use of odor trails, the tendency of ants to follow preexisting structural guidelines has received little attention (Jander and Daumer, 1974; Klotz *et al.*, 1985). We classify structural guidelines into four basic types (Fig. 1), and each type may be used differently by ants when they orient along their surfaces.

The focus of this paper is the topographic orientation of ants from their nest to a food source, and in this inquiry our purpose was twofold. First, we sought to describe and quantify the nature of structural guideline orientation on different types of structural elements. More importantly, through a series of experiments we hoped to determine the relative roles of orientation mechanisms

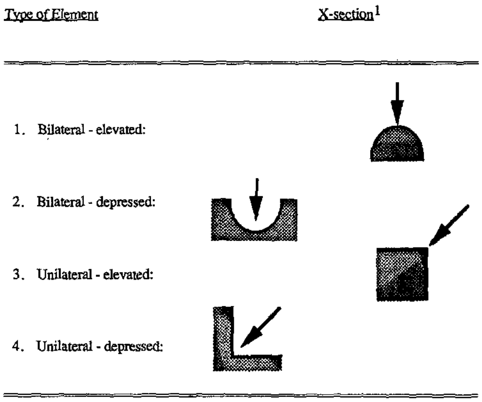


Fig. 1. Classification of structural guidelines. Arrows indicate the edge referenced when defining a guideline.

used by ants in mediating this behavior. Specifically, our mechanistic approach reveals the response of *T. sessile* and *C. pennsylvanicus* to a series of thigmotactic, gravitational, chemotactic, and phototactic cues while they are exploiting structural elements for guideline orientation.

MATERIALS AND METHODS

All experiments were conducted in the field with *T. sessile* and *C. pennsylvanicus* which coexisted in two abandoned trailers, where both nested in wall voids and were attracted to the same foods. To induce structural guideline orientation in free-foraging ants, baits were used to attract them to specific locations along structural elements. *Camponotus pennsylvanicus* was baited with a mixture of sugar and milk (1:1), while *T. sessile* was baited with a dab of honey. The methodologies and experimental apparati used in a series of experiments investigating guideline orientation along structural elements and the relative role of orientation cues are discussed separately.

Study 1. To quantify structural guideline orientation and how it is influenced by the type of structural element and the orientation of that element, experiments were performed with *T. sessile* on two different elements on both a horizontal and a vertical plane. The two structural elements examined were (Fig. 2) an elevated unilateral edge and an element which presented both an elevated bilateral edge (crest-line) and a depressed bilateral (or grooved) edge.

An arena (90-cm diameter) was set up adjacent to a nest inside a mobile

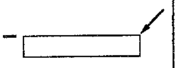
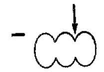
	Orientation			
	Horizontal		Vertical	
Element[2]	time[3]	fidelity[4]	time	fidelity
	15.7 ± 0.7	51.8 ± 2.1	37.5 ± 1.9	91.9 ± 1.5
	19.8 ± 0.8	27.5 ± 3.1	14.0 ± 0.5	100.0 ± 0.0

Fig. 2. Influence of structural elements and gravitational stimuli on guideline orientation of *T. sessile* workers. Data presented are means (±SE) taken from 20 individual workers (10 going to and 10 coming from the bait). Notes: (2) Cross sections of elements (scale: 0.5×)—arrow denotes edge referenced when determining guideline fidelity, and reference bar denotes the relative size of the worker ants; (3) time (s) required for workers to traverse the 50-cm length of the structural element in a given orientation; (4) percentage of time spent on the edge while workers traversed the structural element in a given orientation.

home. A 1.5-cm hole, drilled in the center of the arena floor, was connected to the nest by a series of wood dowels (1-cm diameter). The structural element being tested was attached to a dowel which led up through the arena floor. Ants were entrained to follow the dowels into the arena and to the bait situated at the end of each structural element (50-cm length of wooden molding). The structural element was oriented either vertically or horizontally. Twenty ants were observed on each element in each orientation (horizontal or vertical plane), 10 ants coming to the bait and 10 returning from the bait. Once an ant stepped on the structural element, and until it reached the bait, the time on and off the reference edge was recorded with a stopwatch. Similar measures were made for the 10 ants returning from the bait. These data were then converted to the percentage of time spent along the reference edge while traversing the element's length, which we refer to as edge fidelity.

Study 2. To determine if light has an influence on edge orientation, we performed experiments with *T. sessile*. The arena described for Study 1 was modified so the dowel entering the arena was connected to one corner of a horizontally positioned glass plate (30.5 × 30.5 cm). Bait to attract the ants was placed at the opposing corner of the glass plate. These experiments were conducted in natural daylight and total darkness. In the latter, visual cues were obviated by placing a cylindrical hood of black cloth over the arena. After bait placement, the ants were allowed 12 h (in the light or dark) to establish a trail on the glass plate. At this time, the resulting trail was determined by watching 50 ants (25 going to and 25 coming from the bait); in all cases the ants used the same trail when going to or from the bait. After recording this path, the ants were left undisturbed for another 12 h in the alternative condition (either light or dark), at the end of which time the new trail was measured. These observations were quantified as edge fidelity, or the total distance traveled along the edge as a percentage of the total distance to the bait along the edge. New glass plates were used for each experiment, to prevent any previous trace of odor trails. Three replicate experiments were run, with the initial exposure being in the light followed by dark and three starting in the dark followed by light.

Study 3. To address the role of intrinsic and extrinsic orientation cues in edge orientation, the next two studies compared the relative use of visible stimuli and odor trails as cues for *C. pennsylvanicus*; this first study focused primarily upon visual cues. The ants were trained to travel along a glass divider to a feeding station within an arena with a sand floor (Fig. 3). The training period lasted for 2 weeks to train the ants thoroughly. A light source (flood lamp on a portable ring stand) was located 10 cm beyond the end of the training divider to serve as the orientation cue. In each of four experiments, the training divider was replaced by a longer glass test divider marked off in centimeters and then the distance at which an ant attempted to cross the divider for the habitual U-turn was recorded; a total of 50 ants was observed for each experi-

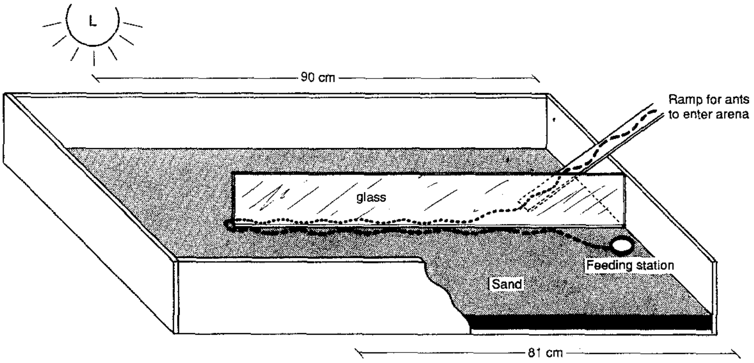


Fig. 3. Experimental arena, with front wall removed, showing sand floor, removable glass training divider, ant entryway and feeding station. A flood lamp (L) served as an orientation cue; during training, L was 90 cm from the entryway.

ment. This distance was easily determined since, up to this point, the ants would travel smoothly along the divider and then abruptly turn sideways, bump into the glass with their heads, and eventually turn around and head back to the nest. To prevent an accumulation of ants along the test divider during an experiment, which disturbed any oncoming ants, the test divider was periodically replaced with the training divider.

In the first experiment, which served as a control, no changes were made from the training condition except for the training divider being replaced by the test divider. In the second experiment, the light was moved to 30 cm beyond its position during training, and the odor trail in the sand, which was established during training, was destroyed by scattering the sand. In the third experiment, the light was again moved to 30 cm beyond its position during training but the odor trail was left intact. In the fourth experiment, the light was moved backward along the odor trail to a point 30 cm before its position during training.

Study 4. This study, like study 3, was designed to investigate the role of intrinsic and extrinsic cues, however, this time the guideline used was a crestline of a pole rather than the bilateral depressed edge of study 3. To determine the relative importance of the odor trail of *C. pennsylvanicus* with respect to visual cues, ants were trained to travel along a pole-maze to a feeding station (Fig. 4). A flood lamp alongside the configuration of poles served as a visual orientation cue. To specify the odor trail's length, pole A was marked in centimeters so that the odor trail could be lengthened or shortened by sliding the pole forward or backward along pole B. Prior to experimentation, ants were trained for 2 weeks to travel to the feeding station atop pole D. In each experiment, a duplicate of pole A, with an odor trail, was substituted for pole C and pole D was removed. The turning point along the duplicate of pole A was based

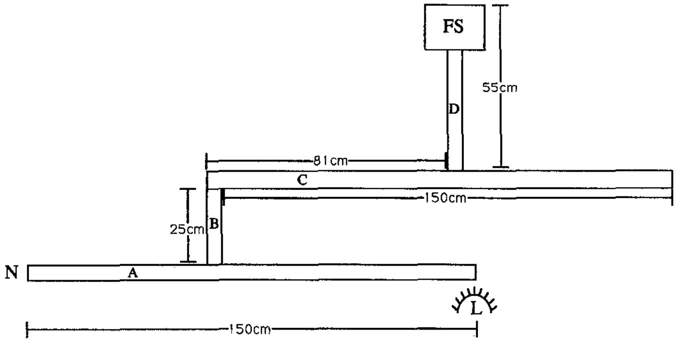


Fig. 4. Configuration of poles (3-cm diameter) connecting the nest (N) to a feeding station (FS). A flood lamp (L) served as an orientation cue.

on the point at which an ant attempted to turn toward the feeding station; a turn was defined as an ant's sideways rotation of at least 90°. The mean turning point for each experiment was determined from a total of 50 ants. During each experiment, pole D was periodically replaced to prevent a buildup of stranded ants at the turning point. In the first experiment, which was the control, no changes were made from the training condition except for the removal of pole D with the feeding station. In the second and third experiments, the odor trail on the duplicate of pole A was either shortened or lengthened, respectively, by 30 cm. In the fourth experiment, the trail was again lengthened by 30 cm and the training light was moved along pole C, 30 cm farther from pole B.

Statistics. Owing to their nonnormal distribution and severe variance inequality, these data were analyzed with nonparametric statistics. In each study there was either a binary test of two conditions or a control test to which comparisons with other tests were made. For these analyses, the paired comparison of two samples was conducted using a Kruskal-Wallis rank sums test (Hollander and Wolfe, 1973), with a single degree of freedom and the acceptable Type I error rate set at 5%. SAS software and the PROC NPAR1WAY procedure were used to generate the test statistics (SAS Institute, 1990).

RESULTS

Study 1. On the unilateral edge, the ants displayed moderate fidelity (ca. 50%) to the edge while traveling on the horizontal plane (Fig. 2). However, on the vertical plane they spent about 90% of the time on the edge, significantly ($\chi^2 = 29.4$; $P < 0.01$) more than when on the horizontal. On the element with both crestline and groove, evidence was again seen for a gravitational influence on guideline orientation. In the horizontal plane, the ants spent less than 30% of their time along the groove (= reference edge; Fig. 2); rather, they spent nearly 75% of their time traversing the 50-cm span along the elevated crestline. However, in a vertical plane this pattern was reversed in dramatic fashion, as the ants spent the entirety of the time traveling along the grooved edge, significantly ($\chi^2 = 33.4$; $P < 0.01$) different from the horizontal plane.

The significance of gravitational stimuli along the unilateral edge was a result of the greater amplitude observed in the ants' stereotypic sinusoidal movements along the horizontally oriented edge, relative to the vertically oriented edge. In the case of the combined element, the increased thigmotaxis (i.e., following the groove) on the vertical, as opposed to crestline trailing on the horizontal, may provide an ant a better purchase of the substrate and reduce the likelihood of an ant falling off.

Study 2. This set of experiments examined the role visual cues play when ants establish foraging trails. In the first test series, where the ants were allowed to establish the trail in total darkness, they displayed a pronounced fidelity toward the unilateral edge, traveling 90.3 ± 3.5% of the total distance (61 cm) to the bait along the edge. However, when the ants were allowed to continue foraging in the daylight, the foraging trail changed significantly ($\chi^2 = 3.9$; $P < 0.05$) and followed the edge for only 22.9 ± 15.4% of the total distance along the unilateral edge. In the reverse series, when ants were allowed to establish the foraging trail in the light, they displayed little fidelity toward the unilateral edge, traveling along the edge for only 11.8 ± 6.2% of the total distance. This same pattern (11.8 ± 6.2% of the total distance) persisted when the ants continued foraging at the bait in darkness; there was no significant difference ($\chi^2 = 0.0$; $P = 0.99$). Thus, the odor trail, established in the daylight, remained the primary cue for orientation in the dark.

These experiments show that when these ants were deprived of visual cues, they rely extensively on tactile stimuli when orienting to resources. However, when provided with visual cues they readily deviate from the edge-following behavior. Thus, while tactile cues are certainly a component of topographic orientation, they are not the primary cue in guiding foraging activities. The next two studies expand our examination on the role of extrinsic factors (specifically, light and odor trails) as cues for ants.

Study 3. This set of four tests examined the role of light as an extrinsic cue enabling *C. pennsylvanicus* to locate a feeding station. The first test determined where ants attempted to turn along the test divider under undisturbed visual and chemical conditions (Fig. 3) and serves as the control against which subsequent tests were compared. The mean turning point under training conditions was ca. 83 cm (Table I). As the training divider was just 81 cm long, ants were attempting to cross where previous experience during the training regime dictated the divider should have ended.

The ants may have determined this location by intrinsic factors (i.e., quantifying motor output) or extrinsic factors (i.e., light or odor trails). To examine

Table I. Intrinsic Orientation and Extrinsic Distance Cues in *C. pennsylvanicus* Workers

Study 3: The role of the light as a distance cue

Test Condition[a]	Distance of light source (cm)	Mean ± SE turning point	Control comparison[b]		
			χ^2	df	*P* value
Training conditions	90	82.9 ± 1.0	—	—	—
Light source further + odor trail destroyed	120	96.4 ± 3.3	28.9	1	<0.0001
Light source further	120	84.3 ± 1.1	4.3×10^{-4}	1	0.9834
Light source closer	60	51.1 ± 1.9	69.5	1	<0.0001

Study 4: The role of the odor trail as a distance cue

Test condition[a]	Length of order trail (cm)	Mean ± SE turning point	Control comparison[b]		
			χ^2	df	*P* value
Training conditions	81	82.7 ± 0.2	—	—	—
Shortened odor trail	51	56.9 ± 0.9	69.5	1	<0.0001
Lengthened odor trail	111	94.5 ± 2.6	17.8	1	<0.0001
Lengthened odor trail + light source moved	111	111.7 ± 0.2	75.0	1	<0.0001

[a] A more complete description of test conditions is presented in the text.

[b] Each test condition was compared to training conditions (control) with a Kruskal-Wallis rank sums, two-sample test (Hollander and Wolfe, 1973).

intrinsic cues, manipulations were made to nullify the training conditions for both extrinsic cues by moving the light 30 cm farther from the end of the divider (to a new distance of 120 cm) and destroying the odor trail by scattering the sand. Under these conditions, the mean turning point was about 96 cm (Table I), which was significantly farther from the turning point in the control study. However, since the ants did not travel the additional 30 cm toward the light source, this indicates that they might also be relying on some intrinsic information on distance, provided that their usual references to visual and chemical cues are obscured or contradictory.

The next two tests examined the ants' reference to visual cues by moving the position of the light, while leaving the chemical trail intact. In the first test, the light was again moved 30 cm farther from the end of the divider, which resulted in a mean turning point of about 84 cm (Table I). This distance was not significantly different from the turning point of the control study, suggesting that, compared with the previous experiment where the odor trail was disturbed, the termination of the odor trail is the primary cue for turning. To ascertain further the role of light as an extrinsic cue, the light source was next moved 30 cm backward along the odor trail. This resulted in a mean turning point of about

51 cm (Table I), which was both dramatically reduced and significantly different from that in the control study. This result demonstrates that the light served as a primary cue for turning and can override extrinsic cues provided by an odor trail.

These results indicate that *C. pennsylvanicus* used the odor trail, in conjunction with visual cues (light source), to guide them around the glass divider toward the food source. In the experiment where the light was moved closer, visual cues took precedence over the odor trail and served as the primary cue for turning. But in the trial where the light was moved farther from the end of the divider, travel beyond the end of the previously established odor trail was reduced. Therefore, light cues were not as strong a distance cue as was the end of the odor trail.

Study 4. These tests were conducted to determine the relative importance of the odor trail for *C. pennsylvanicus* with respect to visual cues. In the undisturbed setup, akin to training conditions (Fig. 4), ants attempted the turn onto the pole (D) supporting the feeding station (removed in the study) at a mean distance of about 83 cm (Table I), very close to pole D's location during training (81 cm). To determine whether the odor trail by itself was sufficient to initiate turning, the setup was manipulated by shortening or lengthening the odor trail. When the odor trail was shortened to 51 cm, ants attempted to turn at a point about 57 cm (Table I) down the pole. As this was about 24 cm sooner than, and significantly different from, the turning point during training, it once again demonstrates that odor trails serve as the primary cue for determining distance. However, when the odor trail was lengthened to 111 cm, ants attempted to turn at a distance of about 95 cm (Table I). While significantly different from the turning point during training conditions, this was only 12 cm beyond the turning point during training and did not extend the full 111 cm where the odor trail ended. This again shows the importance of the light over chemical cues, as ants never followed the odor trail to its end when visual cues indicate otherwise.

In the final experiment, both the light cue and the odor trail were manipulated simultaneously by lengthening the odor trail to 111 cm and moving the light source 30 cm farther down the runway—the lengthened odor trail and light were in the same relative position as they were during training. In this setup ants attempted the turn at a mean distance of about 111 cm (Table I), about 32 cm farther than, and significantly different from, the turning point during training. This demonstrates that when both extrinsic cues (odor trail and light source) are in agreement with previous experience, the ants will continue to follow the odor trail to its terminus.

Taken together, the last two studies demonstrate that the odor trail is a powerful distance cue due to reduced travel onto fresh substrate. This appears to explain why ants turn prematurely on the shorter trail even when the light cue conflicts. However, the light did serve as an auxiliary distance cue in experiments when the odor trail was lengthened; the ants did not continue along a lengthened odor trail beyond the light source. In the last experiment, simultaneous changes in the light and odor trail were sufficient to confuse the ants and they reverted to responding to the odor trail as the primary cue for determining distance.

DISCUSSION

Guideline orientation in ants, other than odor trails, has been descriptively reported in just a few cases (Jander, 1957, 1977; Burns, 1973). Only one experimental study so far has addressed structural guideline orientation in any depth (Klotz *et al.*, 1985), but this investigated orientation only along bilateral elevated structural elements (crestlines). Here we address orientation along structural elements from two perspectives: (1) the mechanisms of structural guideline orientation and (2) its adaptive significance.

Mechanisms for Structural Guideline Orientation. When locating resources within their home range, ants could use any of a number of potential external and internal cues. The present experiments have investigated four extrinsic cues: (1) tactile—structural guidelines; (2) visual—point source of light; (3) chemical—odor trails; and (4) gravity—vertical versus horizontal surfaces. One intrinsic cue, distance, was also examined.

Of these five, tactile cues are probably the most ancestral (Schone, 1984). Hierarchically, tactile cues were also the lowest of cues we investigated, as the ants relied on this sense in total darkness (study 2). Similarly, for a nocturnal army ant, *Neivamyrmex nigrescens*, tactile cues are an important backup for chemical orientation (Topoff and Lawson, 1979).

Our findings again confirm the importance of visual cues in an ant's orientation (studies 2–4). Whether they be landmarks or pinpoint sources of light, foraging ants used visual cues for both directional and distance information and for navigating shortcuts to a food source. These capabilities have been previously investigated and documented in *Formica rufa* (Jander, 1957).

For *T. sessile* the odor trail was secondary in importance to visual cues which, when present, enabled test ants to take the shortest route to a food source (study 2). However, when these cues were manipulated to be in conflict, as in our experiments on *C. pennsylvanicus*, the odor trail became the primary orientation cue, overriding visual cues (studies 3–4).

Gravity is an important cue in ant orientation, as, for example, when ants forage for honeydew in trees. On a vertical plane, edge orientation was more pronounced, possibly due to the ants' switching off their visual orientation (study 1). On the horizontal, when visual cues are present, ants tended to leave the edge and took a shorter route to the resources (study 2).

Camponotus pennsylvanicus used both extrinsic and intrinsic cues for distance orientation. When reference to any visual cues was made difficult or contradictory, ants appeared to possess some measure of the distance traveled (study 3). How this is accomplished, whether by energy expenditure or number of steps taken, is unknown. The odor trail was used in conjunction with the light as a distance cue. In one instance, light served as the primary cue so long as an odor trail was present (studies 3–4). However, light was not as strong a distance cue as the end of the odor trail, as evidenced by reduced crossover onto fresh substrate (studies 3–4).

Adaptive Significance. We have observed several species of ants following naturally existing guidelines: *C. pennsylvanicus* and *F. subsericea* exhibiting crestline trailing on branches lying on the forest floor, or following ridges and grooves in the bark of tree trunks, and *Crematogaster* spp. using vine stems to orient up and down along a tree's trunk. These naturally existing guidelines provide quick and easy access for traversing territory that otherwise might obstruct an ant's progress, resulting in the ant's following the path of least resistance and thus in conserving energy. However, fidelity to these guidelines diminishes as the detour away from, and thus the total distance to, the final destination increases. These guidelines might also confer a measure of safety from predators or inclement weather, relative to crossing open and exposed surfaces. In the case of crestline orientation, orientation to gravity keeps ants atop the structural element (Klotz *et al.*, 1985), thereby avoiding the underside where they are prone to falling off (Jander, 1990).

Hints as to the adaptive significance of structural guideline orientation may be found by looking to other invertebrate and vertebrate organisms exhibiting this behavior. Cockroaches are thigmotactic (Bell and Adiyodi, 1981; Berthold and Wilson, 1967) and, thus, gain harborage within cracks and crevices and travel along unilateral edges. An in-depth study of guideline orientation (Jander and Daumer, 1974) in the genera *Macrotermes* and *Hospitalitermes* demonstrated the importance of crestline orientation to these blind, open-air foraging termites. We have also noted a tendency in a subterranean termite, *Reticulitermes flavipes*, for building mud shelter-tubes along edges.

Because they are primarily nocturnal, rodents, too, rely upon tactile orientation by utilizing their vibrissae and guard hairs to contact with vertical surfaces along their runways. Further, mice often exhibit a "corner response," in that they gravitate toward corners, which enables their guard hairs to have contact with two adjacent walls while they feed or rest (R. M. Corrigan, personal communication).

A restricted use of vision for orientation behaviors is a common thread in each of these examples of using structural elements in orientation. In our study, one of the ants, *C. pennsylvanicus*, is primarily nocturnal (Klotz, 1984) and relies less on visual than on chemical cues compared to diurnal ants, such as

Formica subsericea (Klotz, 1986). For blind organisms, such as termites or some army ants, or nocturnal organisms where vision is restricted (e.g., rats, mice, cockroaches, and many ants), tactile cues would be important stimuli for their topographic orientation. In all such organisms structural guideline orientation behavior would be an integral component of their spatial orientation repertoire.

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