Oriented Mound Building in the Ant, *Trachymyrmex septentrionalis*[1]

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ABSTRACT

The soil excavated from nest chambers of *Trachymyrmex septentrionalis* McCook is placed in crescent-shaped heaps to one side of the entrance hole. The crescents occupy a mean arc of about 75° (but this increases somewhat with time) at a mean distance of 8.0 cm from the hole; a new mound is built at the same orientation and distance if the original mound is removed. The immediate orientational cue which the excavating ants use is a visual image, perhaps landmarks, but not simply a positive or negative phototaxis. If the local slope is altered the mound will be gradually reoriented to a downslope direction over a period of many days. Mound orientation is highly individualistic for each nest, and the compass orientations often appear to be random among nests of a local population.

To the observant naturalist peering at the north Florida ground, among the most persistent and conspicuous features are the peculiar crescent-shaped mounds in which the fungus-gardening ants, *Trachymyrmex septentrionalis* McCook, pile the soil excavated from their chambers (Fig. 1a). Their conspicuousness is often increased by the contrasting orange or red color of the deeper soil of the mound which rests on the white surface sand. There may be hundreds of such nests per acre. Species of at least 4 genera of attine ants are known to deposit mounds that are assymmetrical with respect to the nest entrance (Wheeler 1907, Weber 1969, 1972). Those of some *Sericomyrmex* and *Trachymyrmex* species are crescentic, like an incomplete crater, while some *Acromyrmex* species build conical heaps to one side of the entrance hole. *Apterostigma* is reported occasionally to form lunate mounds as well (Weber 1969). Weber (1972) noted that the mounds of *Trachymyrmex septentionalis* at a Florida site were oriented to random compass points. We began this study to verify an observation that if the crescent is removed the ants will continue to deposit soil pellets in the same location and thus rebuild a crescent with the same orientation.

Materials and Methods

Nests of *Trachymyrmex septentrionalis* McCook at 3 different sites in or near Tallahassee, Florida, were used. The first site was a level, cleared lot with large patches of open ground separating grassy and weedy areas. The second was an open woodlot with a slight eastward slope and practically no vegetative ground cover, and the third a level, young pine forest with a sparse ground cover of wiregrass, herbs, and other grasses. The soil of the first 2 sites was clayey-sand while the third was almost pure sand.

All measurements of compass direction were made with the nest entrance as the origin using a Boy Scout mapping compass which allowed reproducible determination within less than 5°. The highest part of the crescent as well as the extremes of its horns were measured, and the former measurement (which was usually midway between the latter two) was taken as the direction of the mound. The direction of slopes is that of the downslope vector. Computations were made on a Linc-8 Biomedical computer. The orientation of mounds is usually expressed either as relative orientation (orientation 1 minus orientation 2) which can have positive or negative values, or as the absolute difference in orientation (absolute value of orientation 1 minus orientation 2). Student's *t-test* was used to compare orientations.

Experiments and Results

In mid-May, 1973, 24 nests were numbered, the directions of the crescents measured, the crescents removed, and the directions of the subsequent crescents produced before the next day were measured. The orientation of the subsequent mound relative to the original mound for the 18 nests which rebuilt the crescent was 3.2° (SD = 27°) indicating that the ants are orienting rather accurately during deposition of the excavated dirt. The mean distance from the entrance to the mound crest is 8.0 cm (SD = 2.1, $n = 52$), and this distance is also retained upon rebuilding (mean = 8.2 cm; SD = 2.5; N.S.). A recently built mound occupies a mean angle of about 75° of arc (SD = 42°, $n = 25$) and this does not change significantly upon rebuilding (mean = 67°, SD = 29°), though there is a tendency for the arc to increase somewhat with time.

This experiment was repeated with similar results after we cleared circular areas around each entrance hole of all vegetation and obstacles. A number of nests rebuilt the crescent in the same direction 3 or 4 times.

Two trials of a turntable experiment indicated the orientational cue was neither a pheromonal trail nor was it in the immediate vicinity of the entrance hole. A circular piece of light cardboard with a 2-cm hole in the center was placed over a cleared colony so that the entrance hole was centered within the hole in the cardboard circle. The ants then deposited a mound in the pre-turntable direction. When this turntable was then rotated 180° without disturbing

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the mound on it, the ants built still another mound with the original compass direction, 180° from the mound already on the turntable.

Although this experiment indicated the orientational cue was not in the immediate vicinity of the nest entrance, it did not eliminate the entrance itself as a cue. About 85% of all nests had entrance tunnels that deviated significantly from the vertical and often emerged onto the surface at angles as small as 30° from the horizontal, giving these entrances an inherent directionality. The orientation of the mounds and entrance tunnels of 60 nests was measured. The mean relative orientation (mound orientation minus entrance orientation) was found to be −7.9° (SD = 62°). Most of the mounds do not deviate more than 50 or 60° from the direction imposed by the oriented entrance.

At the sloped site, there appeared to be an additional correlation between the mound orientation and the downslope direction. While the general slope was eastward, the important slope seemed to be that immediately around the nest.

Such correlation between the slope and entrance directions and the mound orientation does not necessarily indicate either factor is the cause of the mound's orientation. Causal relationship was thus tested in the following experiments. The mound orientation and the local slope were found to correspond generally (Fig. 2A). By using a small trowel to scrape and pile the soil, we changed the local slope around the entrances to one of 4 directions (N, E, S, W) so that for each nest a large absolute difference between the original mound orientation and the new downslope resulted (Fig. 2B). After such slope alteration, the ants rebuilt the mounds with much the same orientation as the original mound (mean relative orientation −1.9° SD = 27°; $n = 8$), but when these first subsequent mounds were removed 4 days later, the 2nd subsequent mounds differed significantly more from the original than did the first subsequent mounds (mean absolute differences: first vs. original was 21°, SD = 15°, $n = 8$; second vs. original was 53°, SD = 23°, $n = 9$; $P < 0.001$). The same trends can be seen in the relationship of the mound orientations to the original and altered slope. Thus, the original mound deviates most from the altered slope (Fig. 2B), the first subsequent mound deviates less (Fig. 2C) and the 2nd subsequent mound less still (Fig. 2D). The relationship of the second subsequent mound to the altered slope does not differ significantly from that of the original mound to the original slope (Fig. 2A and 2D, Student's *t-test*). Furthermore, in the course of 4 days there is a significant change ($P < 0.05$) in the relationship of the mound to the altered slope (compare Fig. 2B, 2C and 2D).

It thus appears as if the ants are gradually readjusting the orientation of the crescent to coincide with the downslope direction. Three of these colonies were still active after about 20 days, and in all 3, the mound orientation was identical with the altered slope direction. This indicates that while the slope provides the ultimate orientational feature to which the nest adjusts over a long period, it is not the immediate cue to which the outward-bound excavating ants orient.

Since the experiment on the effect of slope had left the entrance orientation unchanged, it seemed possible that the latter provided the directional cue. We marked 15 nests, measured the mound and entrance orientation, and, using a small trowel, leveled the area centering around the entrance. A nail was then inserted into the entrance as far as it would easily go (usually ca. 10–15 cm) and pushed to one of 4 orientations (N, E, S, W) at an angle of about 30° from the horizontal. The soil was packed around it and smoothed before withdrawal. The mean change in entrance orientation was 123° (SD = 35°, $n = 14$). The ants used these reoriented entrances for many days without making any alterations.

From Table 1 it is apparent that changing the entrance orientation (in the absence of a slope) has no effect on the mound orientation, for the relative orientations of the original and subsequent mounds

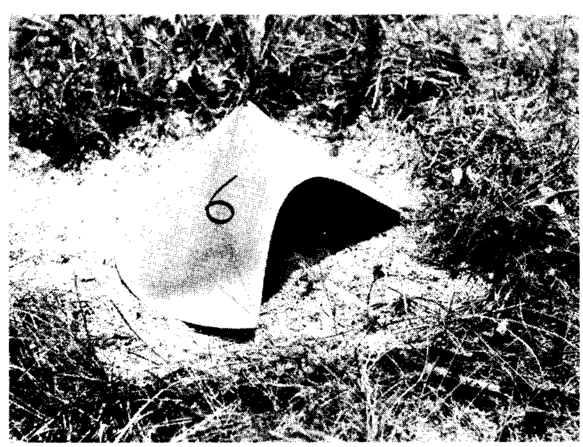

FIG. 1.—A. Normal mound of *Trachymyrmex septentrionalis*. Arrow indicates nest entrance. B. A "landmark-hat" covering a cleared nest-site. Note the mound visible under the arch.

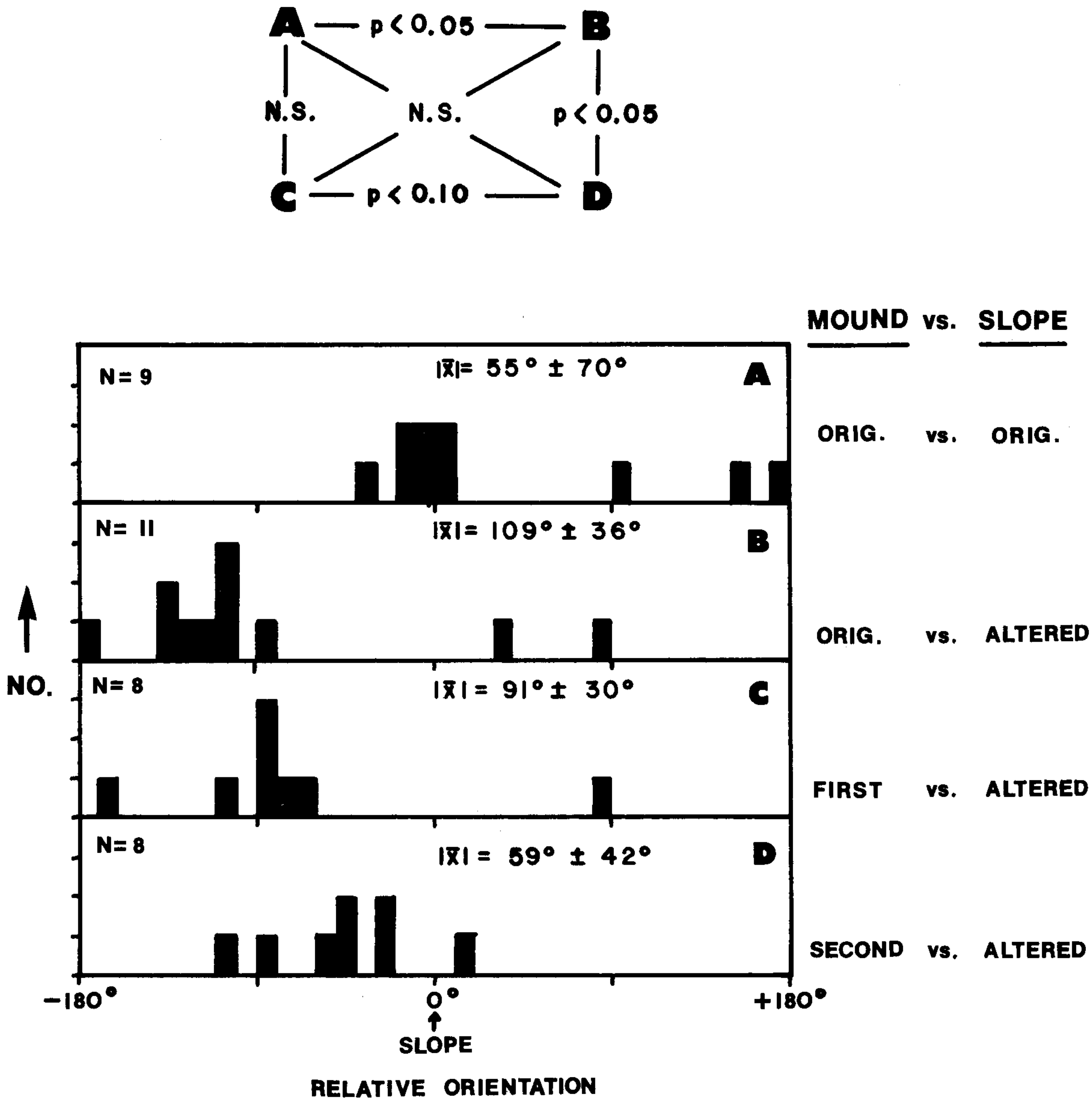

FIG. 2.—The effect of local slope alteration on the orientation of the mound. Slope and mound conditions are indicated to the right of each histogram. The absolute magnitudes of the differences in orientation are indicated in each histogram. The *P* values in the diagram at the top indicate the significant differences between all pairs.

are quite close and the absolute difference in orientation is small (line 2). Therefore, the differences between the subsequent mound and the new entrance orientation are large (line 3) and differ significantly ($P < 0.001$) from the relationship of the original mound to the original entrance (line 1). Thus, the orientation of the entrance tunnel is not the immediate cause of oriented mound-building in *T. septentrionalis.*

Having thus eliminated the nest entrance and the immediate nest vicinity as the primary orienting cues, we thought it reasonable to test the effects of light and visual images. Visual cues were thus completely eliminated by covering 30 leveled nest sites with large cans (about 25 cm diam) so that the nest entrance, which had been given a vertical orientation, lay at the center of the circle and the interior of the can was completely dark. The ants were reluctant to deposit dirt pellets at all under these conditions, and a large number simply ceased all excavation. Figure 3 shows the effects of this treatment on the 9 colonies which did deposit some dirt before ceasing activity. It is apparent that in complete darkness the ants are generally disoriented both with respect to direction and distance, for they drop their burdens all around, frequently nearer the nest entrance. This results in the formation of low turrets around the entrance when deposition con-

Table 1.—Effect of alteration of the entrance tunnel orientation on the orientation of the subsequent mound.

Orientation of	Relative to	N	Mean relative orient. ± SD	P		Mean absolute difference ± SD	P	
1. Original mound	original entrance	30	−7.9°±61	N.S. (1 vs 2)	0.05 (1 vs 3)	41°±46°	N.S. (1 vs 2)	0.001 (1 vs 3)
2. Original mound	subsequent mound	15	−7.0°±44	0.1 (2 vs 3)		27°±34°	0.001 (2 vs 3)	
3. Subsequent mound	altered entrance	15	−57°±93			105°±51°		

tinues long enough (e.g., nos. 2 and 5, in Fig. 3). Usually deposition ceased after only a thin scattering of dirt had resulted. In 4 cases, deposition showed some orientation (no. 4, 7, 8 and 9). In the case of number 8, this was probably due to a light leak under the rim of the can at 190° where the ants had dug an exit, but in numbers 4 and 7 the orienting cues are not known.

Nest 9 was given a 20% downslope and an entrance orientation toward 90° before it was covered with the can. Under these conditions, it seems the slope and entrance direction are moderate orienting stimuli, for most of the dirt was deposited downslope at 90°. When the can was removed the ants once more deposited their dirt at 270°. This line of experimentation was not followed further and the relative importance of these effects are not known.

The drawbacks of the previous experiment are obvious and it seemed desirable to implicate visual orientation without affecting the deposition of the dirt. The following rationale was thus applied: if the ants really orient to landmarks or visual images, it may be possible to accustom them to a new, possibly stronger, and movable image whose orientation could then be changed. We therefore fashioned 48 posterboard cones ("landmark-hats"), each with an arch cut out of one side subtending about 40° of arc (Fig. 1B). The bottom diameter of the cones was about 35 cm and the rim rested flat on a horizontal surface.

Nest sites were prepared (in area 3, a young pine forest) by clearing ca 40–50 cm circle around the nest entrance of all vegetation and smoothing the ground. When a mound was rebuilt in this cleared area, its direction was recorded, the mound was removed, and a "landmark-hat" was placed over the nest site so the center of the arch had the same orientation as the mound which had just been removed, and the apex of the cone was directly above the entrance (Fig. 4). After ca. 24 h, the orientation of the subsequently rebuilt mound was recorded, this mound was also removed, and the "landmark-

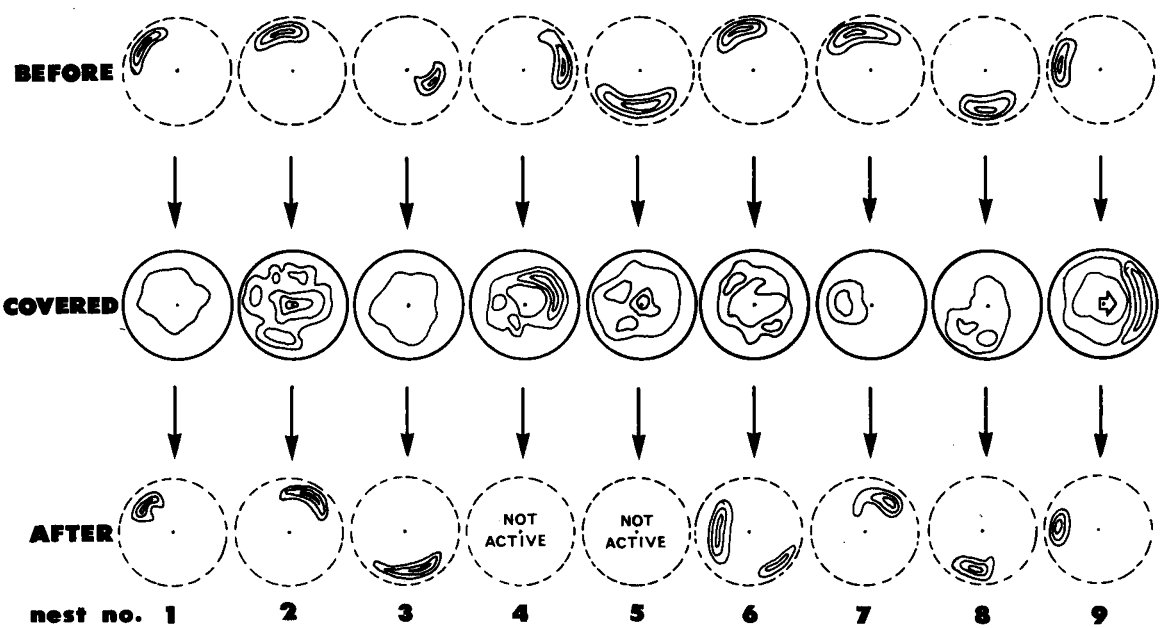

FIG. 3.—The effects of complete darkness on orientation during mound building. The top row shows the position of the mound of each of the 9 nests before removal and covering, the center is the mound built while covered with a can, and the bottom row shows the mound rebuilt after uncovering. Heights of the piled-up dirt are indicated by contours. Top of the figure is north (0°).

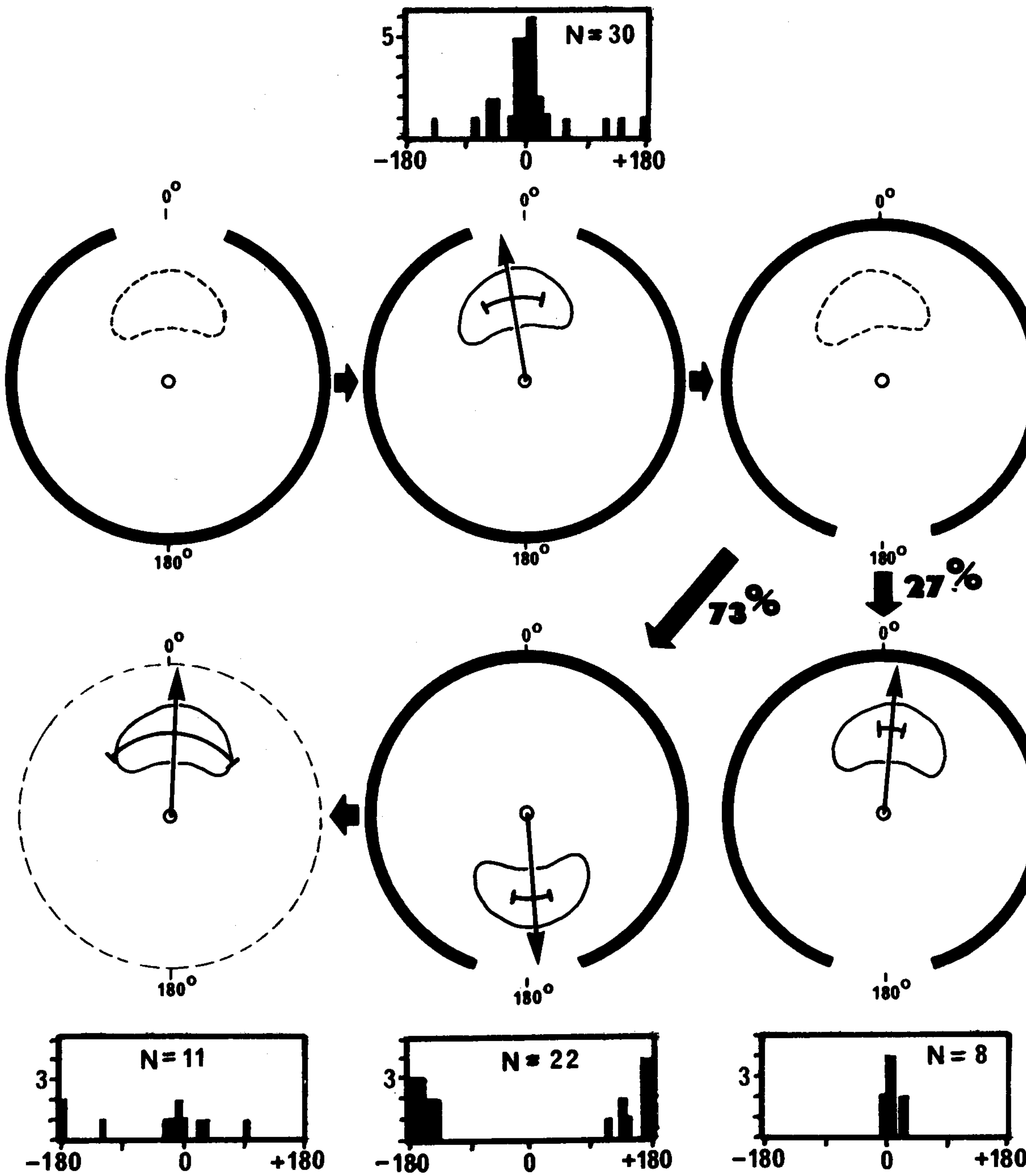

FIG. 4.—The "landmark-hat" experiment. Mean orientations (arrows) relative to the original mound and arch of the hat. Arc crossing the arrow indicates ± 2 S.E. Histograms indicate frequency distributions of the relative mound orientations. Upon reorienting the "hat" by 180°, 73% of the colonies reoriented the mound by the same amount (see text). When the mounds and hats of the reorienting nests were removed, the mounds were rebuilt with a mean orientation similar to the original mound, but with more scatter (bottom left).

hat" was rotated so that the arch was now oriented 180° from the first orientation. After another 12–36 h, the orientation of the subsequent mound was recorded. Under these conditions, 22 out of 30 nests changed the orientation of their mounds by approximately 180° when the arch orientation was changed through 180° (Fig. 4, bottom center) indicating that the ants oriented to the image formed by the bright arch. In 3 instances, the ants did not reorient the first time the cone was rotated, but they did when the experiment was repeated. Nevertheless, 8 out of 30 nests did not reorient the mounds under these conditions. In 2 cases, the experiment was repeated 6 times, but the ants retained the same mound direction no matter what the arch's orientation was. It is not possible to say to what cues the ants of these latter nests were orienting.

It is important that in several cases, the mound was not oriented within the bright sector of the arch but at some angle to it. Yet when these hats were turned 180°, the mounds were reoriented about 180°, once more bringing them into their original relationship to the arch, i.e., at some constant angle to its image and not directly toward it (Fig. 4 center, top and bottom histograms). Such observations support the hypothesis of orientation to a directional property of light other than positive phototaxis.

Most of the nests seemed to orient the mound roughly toward the center of the arch, but one nest, which made a slender radial mound rather than a crescent, seemed to be orienting toward one edge of the arch. When this arch was turned so that its center coincided with the mound, the ants formed a new mound in the direction of the arch edge once more. This was repeated 5 times without removing the mounds, resulting in a series of mounds arranged like the petals of a sunflower and spanning about 90° of arc.

In a few cases, the arches were reoriented other than 180° and the ants changed their mound orientations by about the same amount. In one case, a nest whose "landmark-hat" was carried through 4 different orientations (40°, 220°, 310°, and 130°) without removing the mounds, produced 4 mounds with orientations of, respectively, 38°, 245°, 340°, and 185°.

In conclusion, the experiments show that the primary, short-term orientation cue in the mound building of *Trachymyrmex septentrionalis* is visual. It is almost certainly not simply a phototactic movement toward the brightest light, for immediate neighbors may have very different orientations even though they certainly perceive almost the same visual images from their nest entrances. Thus, the directions of the mounds in an area of a few square meters cannot be predicted from any apparent environmental or visual features (except, to some degree, slope) and often seem random. Each nest, nevertheless, retains its peculiar orientation if the mound is removed and rebuilt, and indeed, the crescents may become very high if they are not flattened by rain. While the range of the crescent may increase, the orientation of its highest point remains much the same.

Discussion

Discrete, oriented refuse piles and "cemeteries" have been noted in several species of ants (McCook 1879, Wheeler *in* Réaumur 1926, Brown 1969, Rettenmeyer 1963, Wilson 1971). Unfortunately, with the exception of the fire ant, *Solenopsis invicta* Buren, almost no work on the orientational aspects of sanitation behavior exists. In the field, *S. invicta* workers bearing refuse or dead simply proceed on a random radius from the nest, though if slope is present, they tend to go downslope. Since they do not drop their burden at a fixed distance, this species does not normally produce discrete refuse piles (Howard 1974).[4] Nevertheless, each individual worker maintains its radial orientation by keeping a constant angle to some orientational reference, such as the sun or landmarks. In this respect, *S. invicta* resembles *T. septentrionalis.* It seems possible that, in those species producing discrete, oriented refuse piles, the nest behavior is fundamentally similar to oriented mound building in *T. septentrionalis.* In fact, as far as mechanism is concerned, it may be immaterial whether the ant is laden with a dirt pellet or refuse.

Inspection of nests on level sites that have been active over a period of several months often show the packed-down remains of mounds with very different, often opposing, orientations than the actively growing mound. Mound building results from excavation of underground chambers and appears to be determined by the cycles of brood rearing in the colony. During periods when no excavation is in progress and a brood is in the larval stage, the workers may close up the nest entrance a short distance below the surface (Creighton 1950, Tschinkel, personal observations). When they reopen the entrance, they may occasionally choose a new direction for the detritus deposit. How this direction is chosen is not known. Presumably, some type of learning is involved. Such factors as slope (and possibly entrance orientation) are the ultimate orientational cues but workers exiting with a burden of dirt do not respond primarily to these long-term cues, but rather to short-term visual cues associated with the long-term cues. How the reorientation to a downslope direction takes place in terms of individual workers is also not known.

The nature of the visual image to which the ants orient seems to be fairly complex, but its actual nature cannot even be guessed. It is possible they use the entire visual field on the one hand, or a portion of it on the other, or perhaps even simply a single landmark object. How all workers come to "agree" on the same orientational cue, or at least to orient in the same direction, is an intriguing question. When a colony of *T. septentrionalis* was transported into my lab (WRT) and set up in a vertical dirt nest with a vertical entrance, the ants built a completely circular crater mound. Thus, they were not able to orient in the new, unfamiliar surroundings.

In light of the fact that three-fourths of the colonies orient to visual cues, the one-fourth which did not reorient in the "landmark-hat" experiment are perplexing. No doubt some of these would eventually reorient if the experiment were repeated, or if they were given longer to accustom them to orient to the "landmark." But there is still a residue of cases which will not reorient even after extended time or numbers of repetitions and after we repeat-

[4] Howard, D. F. 1974. Nest sanitation and necrophoric behavior of the red imported fire ant, *Solenopsis invicta.* Unpubl. master's thesis, Fla. State Univ., Tallahassee.

edly cleared and smoothed the area under the landmark cone. To what cues these nests are orienting is not known, but it is possible they use cues other than landmarks, perhaps polarized light. On the other hand, if the ants had the capacity to remember the orientation of all objects in their visual field, and could orient with equal facility to any of them, they would still be able to retain their original orientation if only a small portion of their visual field were available to them.

An intriguing question is why such oriented mound building evolved in the first place. What could be the selective advantage of depositing all debris to one side of the entrance hole? Prevention of flooding can be ruled out since the mounds are generally downhill on slopes, and can thus have no effect on water running down the hill. Wherever the answer lies, the phenomenon seems to be anything but incidental, for the behavior embodies considerable sophistication with respect to the cues used for orientation and distance. We are continuing work on this fascinating and unimportant problem.

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