ORIENTATION OF THE HARVESTING TERMITE HODOTERMES MOSSAMBICUS (Hagen)[1, 2]

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Termites are commonly known as "white ants". This characterizes the general appearance of the poorly pigmented and eyeless worker caste of most termites, which are adapted to their concealed life permanently protected from light and fresh air. They either nest in their food substrate, which they never leave, or they build protecting galleries above or underground, which lead to the food sources they haunt by following their pheromone trails. An outstanding exception to this rule is the harvester termites of the subfamily Hodotermitinae (Coaton 1958). Hodotermes mossambicus represents this type in arid grassland and thorn-tree regions of Kenya. Our studies were performed in the Great Rift Valley 50 km S.E. of Nairobi on a flat terrain with sparse grass vegetation. Nothing on the surface gives evidence of the underground nest site and the vast network of galleries, except a few fresh dumps of excavated loose soil or grass and the hardly visible plugged foraging holes distributed over the colony's territory.

Harvesting takes place once a day or less, for periods of 60 to 180 minutes, starting at well-defined times both during day or night hours. Troupes of the dark-pigmented and eyed workers emerge from the foraging holes. They first scout at random around the holes, then, within 15 minutes, establish a strict foraging direction from each hole to a determined harvesting area which is at a maximum distance of 3m. The harvesting workers climb tufts of grass and cut off parts of the plant in pieces 2 to 6 cm long, preferably from dead leaves. They carry these back to the hole, deposit them at a point from which other nest mates transport them underground, and then run back to the harvesting place. This above-ground activity resembles more closely the foraging activity of some formicine ants than the trail-submissive behaviour of most termites. We have demonstrated that the principles of orientation evolved in this outstanding group of termites are comparable with those in social Hymenoptera. Menotaxis or "orientation to a constant light angle" and distance-memory have for the first time been proved in termites. All experiments were performed in the field employing the following methods:-

(a) Displacement of foragers. The termites are trained to a cluster of grass baits. While they are in the process of chewing bits off, the bait is displaced to an unknown terrain. With this technique the orientation of homing workers under different light conditions was analysed: sunshine, sun covered with scattered clouds, sky heavily overcast,

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1 A detailed report of this work is published elsewhere: Leuthold R.H., Bruinsma O. and van Huis A. 1973.

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night with moonlight, and night with artificial light source.
(b) Turntable experiments. Foragers were trained to a feeding place over a turntable (a wooden disc 88 cm in diameter, mounted in a frame). To test those going out from the nest the foraging hole was arranged in the centre of the disc and the food bait was located at the edge of the frame. The opposite arrangement was made to test those returning to the nest. This method, by shifting the established walking path through a certain angle, proved the existence of chemical trails and allowed an analysis to be made of its relative significance in competition with optical orientation under different light conditions.
(c) Mirror experiments. By means of a mirror and simultaneous shading of the sun, the angle of light incidence of the foraging area was deflected by about 90° from the original direction. This procedure allowed an analysis to be made of the significance of sun orientation relative to other cues in determining the original direction on a natural foraging ground.
(d) Recording of walking patterns. The running patterns in all the experiments were recorded on a perspex plate, installed 8 cm above the runway. The paths of single workers were followed with ink-markers on the plate and from there drafted on to paper sheets.
(e) Statistical analysis of the recorded running patterns was worked out following the statistical methods for circular distributions proposed by Batschelet (1965).

SUMMARY OF THE RESULTS.

1. Menotaxis proved to be a significant major factor for the above-ground orientation of outgoing and returning workers during harvesting activity, if optical conditions are suitable. Optimal conditions are provided by sunshine, moonlight, or artificial light (e.g. lantern) at night.
2. Pheromone trails are established by outcomers. Trail-dependent chemical orientation is essential when optical cues are lacking (e.g. overcast sky or moonless night), as proved in turntable experiments by shifting the trail through an angle of 90°. By using extracts from different tissues it was demonstrated that the sternal gland produces the trail active substance. This was expected from work on other termites. The trail-following behaviour, however, differs from the conventional type. Whereas in other termites that have been studied, a trail is perceived on rather close contact and followed tropotactically as a firm line, in Hodotermes it acts as a gradient chemical zone within the boundaries of which the termites vaguely keep on course. This principle explains the more scattered distribution of foraging workers on overcast days compared with the rather bundled pattern when menotactic orientation takes over.
3. If the direction of the chemical trail is well separated (e.g. by an angle of 90°) from the trained azimuth, a 100% menotactic orientation is observed when there is a central light source (turntable and mirror experiments), whereas trail orientation is performed when the sky is overcast. When clouds cover the sun, but blue patches of sky are visible, the outcomers follow the azimuth of the trained direction (whether the pattern of polarized sky is the cue for orientation is a matter for further

investigation). If the trail is shifted only a little from the trained direction (22^{o}), the termites leaving the nest in full sunshine first pursue the chemical trail and then change over to sun orientation. The returning termites first keep an intermediate course and then run according to sun orientation.

Summarising these results the following statements can be made:-

(a) Optical orientation dominates over chemical orientation in clearly segregated alternative situations.

(b) Chemical trails influence the orientation, if their active area overlaps with the path determined by optical cues.

(c) With decreasing strength of the optical stimulus, the chemical means of orientation gains increasing dominance.

(d) Termites going out from the nest tend to use pheromone-orientation more readily than returning termites. (This is probably due to both motivational differences and higher pheromone concentration in the vicinity of the hole).

4. Memory for the homing-distance has been proved by means of displacement-experiments. Returning foragers displaced from food-baits far from home (100cm) walk significantly further before they stop orientating than do those displaced from foodbaits near home (40 cm).

REFERENCES

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