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NEST BUILDING BEHAVIOUR OF THE TERMITE *ZOOTERMOPSIS NEVADENSIS* (HAGEN)

by P. E. Howse (*),
Abteilung für Zoophysiologie,
Zoologisches Institut der Universität, Bern (1).

Zootermopsis nevadensis is a relatively primitive termite from the american Pacific coast, and builds no highly organized nest in nature. The nest building behaviour of this insect was studied in the laboratory to find what sensory factors were involved, what was the nature of co-operation between individuals, and what was the nature of the sequence of reactions involved. In this way it was hoped to find some general principles that might help to explain the apparently complex building behaviour of the higher termites.

GENERAL FEATURES OF NEST BUILDING

Termite colonies were kept in 2 litre jars. They built crusts and ledges of wood and faecal particles over the wood in which they were living, which ultimately resulted in a complete roof being built across inside the jar. When termites were kept in 10 × 3 cm. specimen tubes each with a central cardboard partition they were found to build at the top of the partition, and in the course of time the tubes were each sealed by ledges built across to the glass walls of the tube. This building activity, however, took place only in conditions of high humidity.

In experiments with partitions of differing shapes in glass tubes it was found that building took place :

a) on upwardly directed edges;

b) where there were gaps in a partition;

c) sometimes 1-2 cm. above the bottom of the partition;

d) where particles were already present so that ledges were built out horizontally.

(*) The work described here will be published elsewhere in greater detail. It was carried out in the department of Prof. M. Lüscher, to whom I am indebted for his help and hospitality, during the tenure of a DSIR/NATO Research Fellowship.

(1) Present address : Dpt. of Zoology, University College, Cardiff, G.-B.

In other experiments with controls it was shown that building took place more often :

a) where there was most air movement ($P < .001$);

b) where light entered ($P \leqslant .001$), and

c) where particles had recently been deposited ($P < .001$).

There is good evidence that this tendency is correlated with the accumulation of odour trails.

THE ROLE OF AIR MOVEMENTS

Emerson (1956) considering the building behaviour of *Z. angusticollis*, and in particular the tendency to seal off air spaces and plug up holes, suggests that the stimuli involved may be gradients of oxygen, carbon-dioxide, or humidity. But in conditions of low humidity (35 % and 56 % R.H.) the building behaviour of *Z. nevadensis* was found by the writer to be inhibited after about the first 24 hours, although above 90 % R.H. building continued at an undiminished rate*.

When termites were placed in an open glass tube with a long partition reaching right out of the tube, they immediately began to climb the partition but at some level showed an avoidance reaction and turned back. These avoidance reactions must be assumed to be responses to air movements, since in the few seconds taken to set up this experiment there was no possibility for gradients of humidity, CO_2 etc. to be set up. The avoidance reactions occur with increasing frequency towards the upper end of the tube (*fig.* 1). The termites soon began to build on the partition, and there is a highly significant degree of correlation between the distribution of building particles and the frequency with which avoidance reactions occur at different levels ($P < .001$).

Air movements inside the tube were measured by recording the movement of a very fine hair under a binoclar microscope. They were found to increase in a logarithmic fashion from the bottom of the tube towards the open end. Up to the level of the top of the tube there was a very significant correlation between the amplitude of air movements and the number of avoidance reactions at different levels ($P < .001$ for *Z. nevadensis* and $P < .0001$ for *Z. angusticollis*). There is therefore very good evidence that air movements are very important stimuli in building behaviour. Responses to puffs of air directed on to the antennae have been detected in electrophysiological preparations.

(*) This is not necessarily in contradiction to the findings of Grassé & Noirot (1958, pp. 9-10) on *Calotermes flavicollis*, since a drop in relative humidity may initially stimulate building activity, but a current of air would constitute a very stromg diturbing stimulus and prevent it.

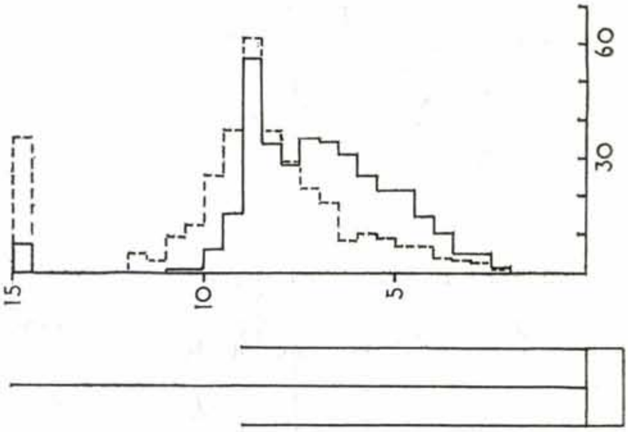

FIG. 1. — Avoidance reactions of termites climbing a partition 15 cm. high placed in a glass tube. Abscissa : number of avoidance reactions. Ordinate : height in cm. above the bottom of the tube. The continuous line refers to *Z. nevadensis*, the broken line to *Z. angusticollis*.

THE SEQUENCE OF REACTIONS

Nest building behaviour in *Z. nevadensis* involves a series of actions (*fig.* 2 top) :

1. During a phase of exploratory behaviour a termite stops at some point and makes repeated probing movements with its antennae (a), and then turns and goes downwards (e). The termite grasps a particle between its mandibles and returns, in the vast majority of cases, to its point of departure following an odour trail (b). It now reverses through 180° bringing the tip of its abdomen into the place previously occupied by the head with an oscillatory movement of the abdomen in the long axis expells a droplet of 'cement' from the anus (c). The cement appears to be a liquid suspension of minute wood particles. The termite then turns again through 180° to its its original position and makes palpating movements with its antennae which become quicker the nearer they become to the droplet of cement. When the antennae touch the cement the particle is pressed into it with a side to side rocking movement of the head (d). At intervals, the particle is released by the mandibles and held loosely between the palps. If it does not move, the termite releases it, turns, and goes downwards (e) guided by odour trail and gravitational stimuli.

This is not the only possible sequence of activities : there are 4 main sequences (*fig.* 2) and an analysis of the sensory stimuli involved at each stage in the behaviour has made it possible to recognize that the components (a-b-c-d & e) are unitary ones.

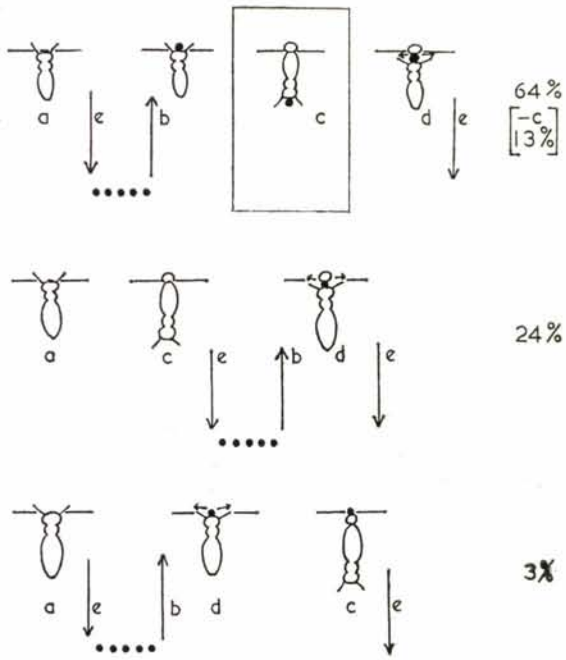

Fig. 2. — A diagram illustrating the sequences of actions observed in the building behaviour of *Z. nevadensis*. The percentage occurrence of the different patterns are given. Further explanation in the text.

If a particle is dropped during (b), (c) or (d) the behaviour will not continue until another particle has been fetched or one nearby has been grasped. If cement is not expelled from the anus during (c) the termite will continue turning back and turning again until this occurs. In (d), if the particle moves against the palps when released by the mandibles the rocking movements will be continued. This evidence suggests that each component of the behaviour has sensory feed-back mechanisms — the termite must receive specific sensory information indicating that one component is complete before another can continue. Once it has been completed, the same component never occurs again in the same sequence.

It can be seen from figure 2 that there is a basic common sequence pattern a-e-b-d-e, with (c), the component involving deposition of cement, linked in the series in differing positions. This suggests that two originally separate behaviour patterns have become joined during the course of evolution. Namely, (a) the removal of particles resulting from the excavation of galleries and (b) the tendency to defaecate at the ends of galleries and thereby plug up holes. *Z. angusticollis* larvae have been observed to expell semi-liquid faecal particles during building behaviour.

THE MECHANISM OF THE BEHAVIOUR

It appears, from the investigations briefly described here, that once the sequence of actions has started it will continue of its own accord even if the stimulus situation is suddenly changed. This suggests that there may be nervous centres for each component of the behaviour linked by what may be thought of as excitatory pathways. For instance, if an insect is knocked on to the floor while it is depositing cement the normal sequence of actions will continue. If the cement is removed with a brush from the tip of the abdomen the behaviour will also continue, although the rocking movements are unusually weak.

On the other hand, particles are sometimes fixed into droplets of moisture or the cement of another termite, and this may even occur during (c) when an insect is making a 180° turn. Evidence such as this suggests that specific sign stimuli may control the sequence of activities, to some extent at least.

It may be suggested that specific stimuli can set off each component in the sequence, but that the motor or premotor centres are linked by excitatory pathways so that the activation of one lowers the threshold for the activation of another. There would thus be a chain of activation a-e-b-d-e with (c), physiologically nearer to (b), included at some point. The *in vacuo* sequence would then be a-e-b-c-d-e, with the activity of each motor or premotor centre being partly controlled by feedback mechanisms.

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Intervention de M. NOIROT.

Au sujet du dépôt de « trail pheromone », avez-vous effectivement constaté le dépôt d'une telle trace au moment où le Termite se retourne?

En effet, *Cubitermes fungifaber* présente une séquence de comportement analogue (mais pas dans le même ordre), mais le retournement de 180° de l'ouvrier paraît indépendant de stimuli olfactifs. En effet, si un ouvrier est bousculé par un congénère, il s'en va sans achever la séquence : il faut que la rotation se fasse sur place.

Réponse de M. HOWSE.

Il est certain qu'au début du comportement de construction chez *Zootermopsis* il y a déposition d'une trace odorante. J'ai pu constater ceci dans deux expériences différentes. Mais il semble qu'après quelque temps, il y a beaucoup de traces odorantes sur toutes les surfaces. En ce cas, il est probable qu'il n'y a pas d'autres traces déposées. Il faut dire en tous cas, qu'au moment du retour, les traces odorantes ainsi que le geotropisme dirigent le termite.

Intervention de M. LINDAUER.

Liegt eine Analyse darüber vor, welche physiologischen Faktoren (qualitativer und quantitativer Art) die Reibenfolge der einzelnen Bauhandlungen bestimmen?

Réponse de M. HOWSE.

Ja, ich habe eine Analyse vorbereitet. Es gibt leider Keine Zeit diese Frage ausführlich zu erklären. Ich darf sagen, dass die Reinhenfolge durch ein Reizwechsel versuchsweise modifiziert werden Kann.