<u>Excavation of nests by ants.</u>

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The excavation behaviour of ants can be studied in the laboratory by placing worker ants in moist sand. The way that they dig and the sort of excavations they make, can be to some extent related to the sort of nest they dig in the field.

1. The method of excavation in moist sand.

As the movements of excavation are described in some detail elsewhere[1] only the most important points and their consequences need be mentioned here. First, the method by which ants dig is more or less uniform from species to species, at least in seven common species from Northern England and nine from Nigeria. Even ants of unusual form like <u>Odontomachus</u> and <u>Cataulacus</u> show very slight modification of digging behaviour. The arboreal species of <u>Crematogaster</u> hardly dug at all, but a soil-nesting <u>Crematogaster</u> dug in the ordinary. (<u>Oecophylla longinoda</u> also dug though with little effect.)

The digging movements (at least in moist sand) have three components:-

1) The GRAB in which the ant pulls a sand grain or grains from the soil with its mandibles. A large grain is carried away at once, smaller ones are placed on the ground between the ants front feet;

2) The RAKE in which the fore-legs are used to rake deposited grains into a heap;

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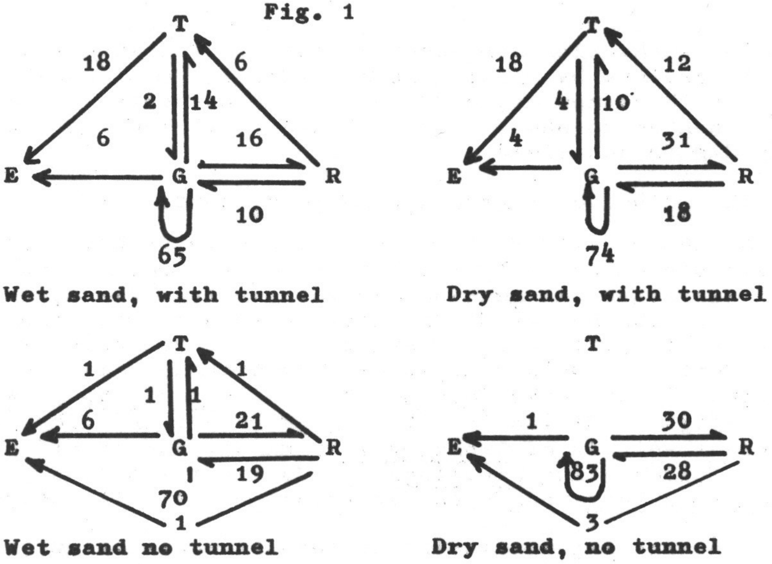
[1] <u>Sudd, J.H. 1969 Zeits Tierpsychol. in press.</u>

3) **TRANSPORT** in which the ant carries sand from its heap in its jaws to the end of its tunnel.

Fig. 1



Analysis of the sequences of these three components shewed that only 3 out of 353 rakes did not follow a grab, though if rakes had occurred at random about 30 would have followed transport and 51 would have begun a bout of digging (fig. 1). Clearly raking is merely a method of handling materials removed by a grab and not, as has sometimes been suggested, a method of digging in its own right. In short tunnels raking suffices to remove sand especially if it is dry, and this may be why Formica fusca has been said to dig with its fore-legs.

It follows that the form of tunnels depends on the location of grab acts, each of which is a separate event, often separated from other grabs by a transport phase.

2. The form of natural nests.

It is relatively well established that different species of ant build nests which differ in form, though these differences may be hard to define. In extreme cases it is clear that ants of dry soils (e.g.

Prenolepis imparis[1]) and of deserts and perhaps ants that need a high degree of environmental control (e.g. *Atta* sp.[2]) dig nest of great average depth with many vertical shafts; other ants may build much shallower nests with many horizontal passages. It is impossible at present to say how far these differences are due to innate differences in behaviour, and how far to responses (perhaps innate) to characteristics of the soils in which that species nests. The fact that *Formica cunicularis* digs its nest deeper in winter[3] seems to argue that local responses are important in determining nest form. Perhaps as important as form is "texture", a combination of tunnel size, convolution and particle size.

3. The tunnels of isolated ants.

Although an ants' nest is the product of communal work over a considerable period of time, tunnels dug in the laboratory by single ants in 24 hours show some specific differences which can be to some extent related to what little we know of the natural nests of those species. Unfortunately they also show a good deal of variation within the species, with some ants digging tunnels of a specific form and others digging tunnels which might have been dug by other species. On a superficial inspection the tunnels dug by single *Lasius niger* workers are much convoluted so that they work a large proportion of the available soil, have many horizontal sections, often branch and anastomose and may be dug in an upward direction. The tunnels dug in similar conditions by *Formica fusca* and *F. lemani* are relatively straight, and in our conditions often nearly vertical. They hardly ever branch or anastomose below the surface, though a single ant may dig 2 or 3 unconnected tunnels.

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[1]Talbot, M. 1943 Ecology 24, 31 - 45.

[2]Jacoby, M. 1953 Zeits angew. Entomol. 34, 145 - 169.

[3]Dlusskij, G. 1967 Ants of the genus *Formica* (in Russian) Izdatel'stvo "Nauka", Moscow.

Tunnels of Myrmica ruginodis are in general also deep, though much less straight than those of F. fusca, but the tunnels of M. scabrinodis are convoluted something like those of L. niger.

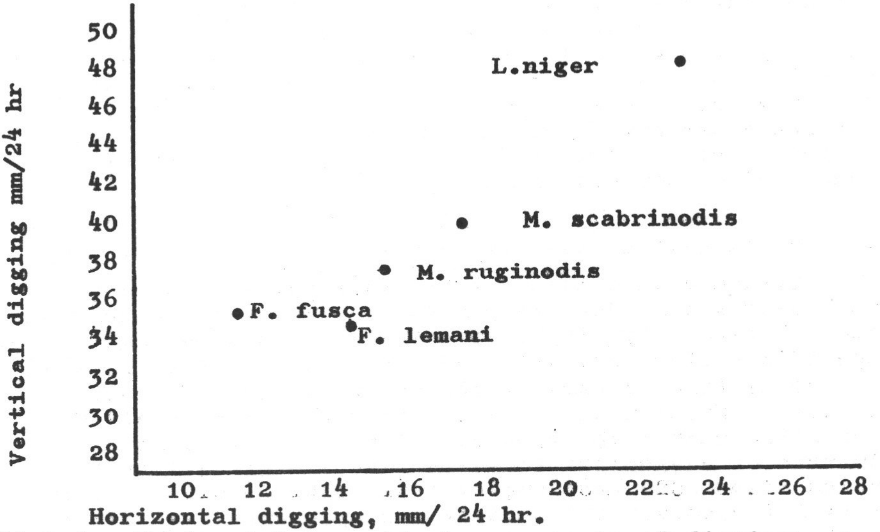

Fig. 2. Horizontal & vertical components of digging.

When the extension of the tunnel each hour (from time-lapse photography) is separated into its horizontal and vertical components this picture is more or less confirmed fig. 2. The relative proportions of horizontal and vertical components are similar in all species and tend towards the limits imposed unavoidably by the container. The tunnels of Lasius niger are significantly longer than those of other species, that is they are more tightly packed into the available space. (They are of course little more than half the diameter of a Formica lemani tunnel so that the volume or weight of sand brought to the surface is less.) The contrast of vertical tunnels in F. lemani and horizontal ones in L. niger was not fully confirmed by this analysis, though differences in horizontal components were more often significant than differences in vertical components.

4. Site and orientation of digging.

Tunnels are extended by distinct grabs and the extension is along more or less characteristic patterns. It should be possible, therefore, to derive the pattern of excavation from the location of the individual grabs which produce the tunnel. Unfortunately this is not so simple as one might hope. In the first place many grabs are sited well behind the end of the tunnel and so do not extend the tunnel; in the second place the actual location of a grab which does extend a tunnel has a large element of chance in it.

If an ant is placed in a tube of sand and digs, it is almost certain to dig against a wall of the tube or against a vertical object stuck in the surface of the sand. It can, however, be drawn to the centre of the container if a depression is made in the centre of the sand (this is in fact how we control the position of digging in experiments). Ants therefore are likely to dig in depressions and re-entrant corners; they also seem likely to pick up loose or projecting sand grains.

As an ant which is digging moves down its tunnel it may encounter a loose grain of sand - perhaps one it dislodged on its upward journey. It may grab the grain and carry it to the surface. It may on the other hand meet a recess on the tunnel wall and dig in this. The recess thus becomes enlarged and unlike the projecting grain, may attract more digging later. The ant may, in spite of all these temptations, reach the end of its tunnel. Even here it may clear up grains behind the work face of the tunnel, and it does not in any case deliberately choose certain grains. It will usually try several grains before it is able to dislodge one. It is hard to see how far the selection of grains might be affected by orientation to e.g. gravity.

We are now studying the locations of grabs in some detail. At present we have a little evidence that Lasius niger (whose tunnels often branch) is more likely to attack the walls of the tunnel away from the end than Formica lemani is. It is also noticeable that the tunnels of L. niger are less tidy than those of F. lemani. F. lemani seems to spend some time, especially after the first day, in lining its tunnel walls with medium size sand grains. Whether this is related to its tunnel pattern as a cause or as an effect, we cannot say. The greater convolution, or smaller scale, of L. niger tunnels is, I think, only partly explained by its smaller stature, but we do not yet know of any ethological differences.

It would be pleasant to think that this work would open the possibility of explaining, or perhaps simulating, how real ants' nests become the shape they are. But it is clear from our work that local influences (soil texture, soil structure and moisture characteristics for instance) have a very strong influence. We know very little of ants' responses to these. There is, I think, a real possibility that the finer structure (or "texture") of nests may be explained, however.