

Sand Pile Formation in *Dorymyrmex* Ants

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We studied circular sand pile formation by two colonies of Brazilian Dorymyrmex ants, in which workers dumped sand excavated from their underground nest around the nest entrance hole. In most cases a worker dumped its load just beyond the ridge of the pile. Each dumped piece either stayed where it was deposited (81.9% in colony A and 73.0% in colony B) or rolled down the outer slope of the sand pile away from the entrance (17.9% in colony A and 27.0% in colony B). Ants almost never dumped in a way that resulted in the load rolling back to the entrance. When one side of the sand pile was experimentally removed, ants preferentially dumped soil on the now flat side, thereby restoring the original circular shape.

KEY WORDS: sand pile; nest excavation; self-organization; *Dorymyrmex*.

INTRODUCTION

During the enlargement or maintenance of an underground nest worker ants frequently remove soil, which they carry in their mandibles and deposit around the nest entrance (Sudd, 1969). The particles can accumulate into a mound containing nest chambers (Cassill *et al.*, 2002) or pile consisting only of excavated material (Sudd, 1977). The piles can be irregular, semicircular (crescentic) or circular. Circular sand piles are often crater-shaped with regular inner and outer slopes (Wheeler, 1910; Wehner, 1970). Ant colonies are able to build circular sand piles with regular slopes even

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though it is unlikely that individual workers are centrally controlled or supervised. The organization of work in an ant colony with thousands of individuals is potentially a very complex task. However, simple rules applied by individuals can solve complex colony-level problems. This is often called self-organization (Bonabeau *et al.*, 1997; Camazine *et al.*, 2001).

Self organization allows ants to work efficiently and to a common purpose without central control. Nest excavation can require a significant amount of effort and if it is well organized can help the colony function efficiently. For example, it is important that the loads of excavated material are deposited in a suitable way. Loads deposited on the inner slopes of the sand pile may roll back into the entrance. Random deposition would not be a good strategy, except in very small colonies, because some loads would roll down the inner slope back into the entrance tunnel. A better strategy would be to release soil particles in places from which they do not roll back.

The aim of this paper is to describe the natural history of sand pile formation in *Dorymyrmex*. We recorded the positions at which ants deposited their loads before and after experimental flattening of half of the sand pile. Our results show that ants did not dump the excavated sand at random but near the top of the pile and on its outer slopes from which the loads would not roll back into the nest. In addition, after one side of the sand pile had been flattened most dumping was on the lowered side thereby restoring the pile's original circular shape.

MATERIAL AND METHODS

Pile formation around nest entrances of *Dorymyrmex sp.* colonies was studied in September, 2002 in a sugar cane field with sandy soil at Fazenda Aretuzinha, São Simão, state of São Paulo, Brazil. Heavy rain following a dry period had resulted in extensive excavation, perhaps because the wet soil was softer or because the rain had caused internal collapsing. We photographed the sand piles of 64 colonies in order to determine their size. Two of the colonies were studied in greater detail by video recording (using a Sony DCR-TRV16E digital camcorder; frame size 720 × 576 pixels, 25 frames per second). After 20 minutes recording of an undisturbed nest entrance, half of the sand pile was experimentally removed and the recording was continued for another 20 min. Because of technical problems the first 12.5 min of the recording (before flattening) could not be analysed for one colony. However, the remaining 27.5 min provided enough data for statistical analysis.

After downloading to a computer hard drive, the footage was analysed using VideoPoint software (Lenox Softworks, <http://www.lsw.com/videooint/>). Frame by frame observations allowed us to determine both

the time and place of deposition of each load. For depositions before manipulation we also determined if the load stayed where it was dumped, or rolled either towards or away from the entrance.

RESULTS

General Information

Ants transporting soil from their nests built circular sand piles around the nest entrances. The radius of the sand piles, measured from the nest entrance to the outer margin was 3.63 ± 0.97 cm (mean \pm SD, range 1.67–6.58 cm, $N = 64$, Fig. 1). The radii of the sand piles around colonies A and B, which we studied in greater detail, were 3.76 and 4.62 cm, respectively.

Before Manipulation

Loads were deposited almost entirely in places in which they stayed in place (81.9%, $N = 2787$ in colony A; 73.0%, $N = 434$ in colony B). Almost all loads that rolled (99.8%, $N = 505$ in colony A; 100%, $N = 117$ in colony B) did so away from the entrance and down the outer slope of the pile. Only one of the 3221 loads rolled towards the nest entrance (Fig. 2). The number of loads deposited on both sides of the sand pile were similar

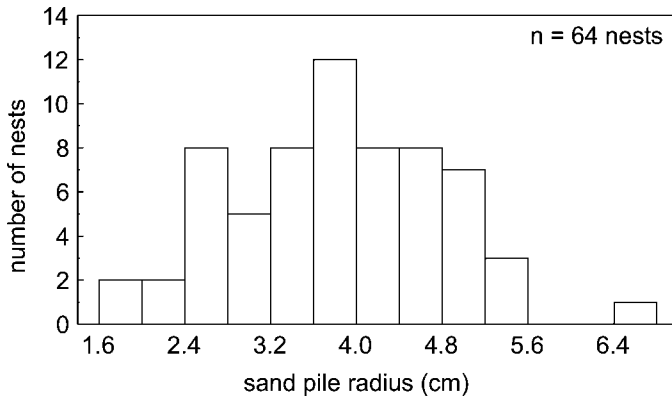


Fig. 1. Distribution of radius lengths of crater shaped sand piles built by *Dorymyrmex* ants. Distances were measured from the centrally positioned nest entrance to the outer margin of the pile.

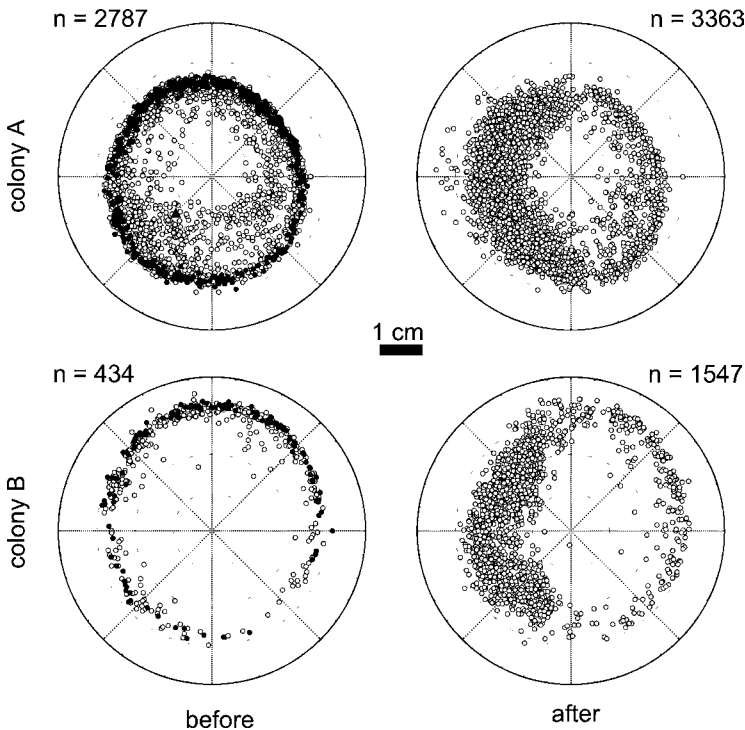


Fig. 2. Nest entrances of the two study colonies showing the positions where loads were deposited before and after flattening the left half of the sand pile. In the “before” flattening figures loads which did not roll after deposition are shown as open circles and loads which rolled towards the outer margin of the sand pile as closed circles. The single load which rolled towards the nest entrance is marked with a triangle. The entrance holes are represented by the centres of the circles. In the “after” flattening figures we only recorded the position that the loads were deposited.

and approximately circularly symmetrical. The proportion of loads on the side that was later flattened was 54.5% in colony A and 57.1% in colony B (Fig. 3). The distributions of distances at which ants deposited loads were skewed to the left and significantly different from a normal distribution in both colonies (Kolmogorov-Smirnov test: colony A, $d = 0.13$, $N = 2787$, $P < 0.01$; colony B, $d = 0.09$, $N = 434$, $P < 0.01$, Fig. 4). The maxima of the distributions occurred immediately beyond the top of the sand pile (Fig. 4). There was no significant relationship between time and distance of deposition in both colonies (Spearman test: colony A, $r = 0.02$, $N = 2787$, $P = 0.44$; colony B, $r = -0.01$, $N = 434$, $P = 0.84$).

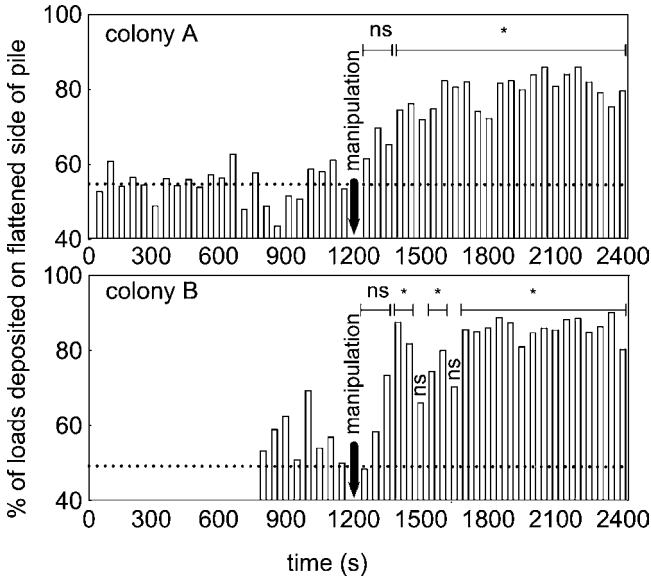


Fig. 3. Proportions of loads deposited on the flattened sides of the sand pile before and after flattening. G-test of goodness of fit was used to compare the proportions of load deposited on the left side before and after manipulation (NS: $P > 0.05$, * $P < 0.01$). The dotted line is the proportion of loads deposited on the side that was later flattened.

After Manipulation

More loads were deposited on the flattened side of the sand pile (colony A, 79.5%, $N = 3363$; colony B, 82.8%, $N = 1547$, Fig. 3) than on the unmanipulated side. Flattening significantly affected the proportion of loads deposited on the manipulated side of the sand pile in both colonies (G test of independence: colony A, $G = 440$, $P < 0.001$; colony B, $G = 115$, $P < 0.001$).

However, ants did not immediately start to favour the flattened side, but took approximately 2.5 minutes to do so in both colonies (Fig. 3). The distributions of the distances at which loads were deposited on the flattened side were not significantly different from a normal distribution in either colony (Kolmogorov-Smirnov test: colony A, $d = 0.03$, $N = 2674$, $P > 0.05$; colony B, $d = 0.04$, $N = 1281$, $P > 0.05$, Fig. 4). On the unmanipulated side of the pile the distributions remained skewed to the left (Fig. 4). However, only the distribution in colony A differed significantly from a normal distribution (Kolmogorov-Smirnov test, colony A, $d = 0.06$,

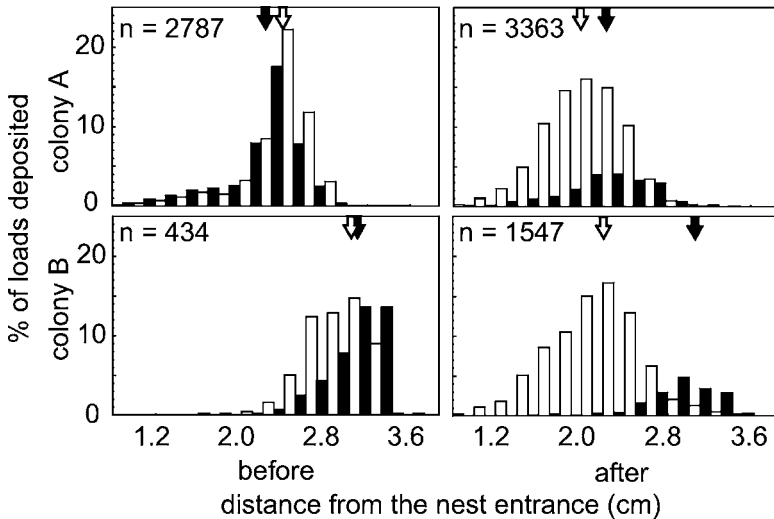


Fig. 4. Distributions of distances from the nest entrance at which loads were deposited around the entrances of the two colonies before and after flattening of the left half of the sand pile. Arrows indicate the top of the sand pile. The empty arrows and bars correspond to the manipulated (flattened) side of the sand pile and the black arrows and bars correspond to the unmanipulated side of the pile.

$N = 689$, $P < 0.05$; colony B, $d = 0.08$, $N = 266$, $P > 0.05$). The distance at which ants deposited their loads on the flattened side of the pile increased with time after manipulation in both colonies (Spearman test: colony A, $r = 0.50$, $N = 2674$, $P < 0.001$; colony B, $r = 0.29$, $N = 1281$, $P < 0.001$).

DISCUSSION

Our data show clearly that ants did not deposit their loads at random locations. Rather, they dumped near the top of the sand pile and on its outer slopes. The loads deposited in those places almost never rolled back into the entrance but either stayed where they were deposited or rolled towards the outer margin of the sand pile. Similar behaviour, depositing loads near the top of a sand pile, was observed in *Myrmica ruginodis* and *Camponotus compressus* (Sudd, 1977). However, it was not quantified.

The experimental removal of half of the sand pile showed that the ants are able to adjust their behaviour in such a way as to re-establish the original circular structure of the pile by preferentially dumping on the flattened side of the pile. The change of behaviour of the ants after manipulation

was not immediate, even though it only took a few minutes. This suggests that individual ants do not acquire the information about shape of the sand pile every time they leave the nest entrance. Instead they probably learn to climb the pile in a particular direction and need some time before switching to a new direction. It is possible that ants memorize the steepness of slope during consecutive trips performed in different directions and choose directions associated with smallest slope. Instead of comparing the steepness directly ants can also observe the height of the horizon (Pratt *et al.*, 2001; Graham and Collett, 2002). It has been demonstrated that the orientation of crescentic sand piles in *Trachymyrmex septentrionalis* is adjusted to the local slope surrounding the nest entrance in such a way that loads are transported down the slope (Tschinkel and Bhatkar, 1974). In *Atta colombica* waste heaps are always located downhill from nest entrances (Hart and Ratnieks, 2002). Even ants that do not build sand piles or waste heaps, such as *Solenopsis invicta*, prefer to transport refuse downhill (Howard, 1974 cited by Tschinkel and Bhatkar, 1974).

The deposition of loads near the top of the sand pile can increase the efficiency of nest excavation. It is obvious that sand removed from the nest should not be deposited in places from which it rolls back in. It is also unnecessary to transport the load far beyond the top of the sand pile as the loads roll down the outer slope under gravity. Dumping of loads on the flattened side of a sand pile may also be more efficient because it is easier to climb less steep slopes and the risk of rolling of sand particles on the flattened side is lower. It is also possible that the circular sand pile around the nest entrance helps to defend the nest against intruders. The outer slopes of the pile are unstable and a potential intruder trying climb the pile initiates multiple avalanches. It was observed that ants of other, larger species had problems climbing the sand pile (FLWR personal observation) which collapsed under them.

Because the diameter of the sand pile increases with time and because the ants tend to deposit their loads at the top of the sand pile, we can expect that the mean distance at which ants deposit their load should grow in time. The rate of radial growth of a sand pile should decrease with its size because more pieces of soil are needed to fill the volume growing proportionally as the 3rd power of the radius. Therefore, no correlation was found between time and the distance of soil dumping before manipulation. However, after manipulation the sand pile on one side was initially not present and then growing rapidly. This gave a highly significant positive correlation between the distance of soil deposition and time.

Based on the data presented in this paper we hypothesize that a circular sand pile can be formed if the ants follow two simple rules. The first is for each ant to deposit its load at the top of the sand pile or at the outer

slope. The second is to climb the less steep slope. These two (hypothetical) rules could also maximise the efficiency of soil removal by minimizing both the risk of excavated material rolling back into the nest and the distance travelled. Further research is needed to determine whether the ants use the rules suggested here and the mechanism involved.

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REFERENCES

- Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S., and Camazine, S. (1997). Self-organization in social insects. *TREE* **12**: 188–193.
- Cassill, D., Tschinkel, W. R., and Vinson, S. B. (2002). Nest complexity, group size and brood rearing in the fire ant, *Solenopsis invicta*. *Ins. Soc.* **49**: 158–163.
- Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Theraulaz, G., and Bonabeau, E. (2001). *Self-organization in Biological Systems*, Princeton University Press, Princeton.
- Graham, P., and Collett, T. S. (2002). View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks. *J. Exp. Biol.* **205**: 2499–2509.
- Hart, A. G., and Ratnieks, F. L. W. (2002). Waste management in the leaf-cutting ant *Atta colombica*. *Behav. Ecol.* **13**: 224–231.
- Pratt, S. C., Brooks, S. E., and Franks, N. R. (2001). The use of edges in visual navigation by the ant *Leptothorax albipennis*. *Ethology* **107**: 1125–1136.
- Sudd, J. H. (1969). The excavation of soil by ants. *Zeits. Tierpsychol* **26**: 257–276.
- Sudd, J. H. (1977). Nest construction in ants. Proceedings of the 8 International Congress of the IUSSI, Wageningen, pp. 173–176.
- Tschinkel, W. R., and Bhatkar, A. (1974). Oriented mound building in the ant *Trachymyrmex septentrionalis*. *Environ. Entomol.* **3**: 667–673.
- Wheeler, W. M. (1910). *Ants: their structure, development and behaviour*, Columbia University Press, New York.
- Wehner, R. (1970). Etudes sur la construction des crateres au-dessus des nids de la fourmi *Cataglyphis bicolor*. *Ins. Soc.* **17**: 83–94.