

ARE THE ANTS CAPABLE TO LEARN THE NEST-BUILDING
ACTIVITY ATYPICAL TO THE SPECIES? (A STUDY OF
FORMICA CINEREA MAYR.)

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Abstract. *Formica cinerea* ants are the species digging their nests in the ground, so they never handle thicker building materials. Under conditions unfavorable to their normal existence, brought about by several years of continued meteorological disturbances, one colony of ants established itself in an atypical and unique in this species mound-shaped nest, similar to the nests of the hill-building species of *Formica*. On the basis of observations of individual building workers it was determined that most of the *F. cinerea* ants failed, during the whole summer, to achieve improvement in the technique of carrying building material. Moreover, they all used to drop it loosely, which is done only by the naive individuals of the hill-building species of *Formica*. It is suggested that the deficiency in manipulatory learning in *F. cinerea* is due to the lack of hereditary elements of hill-building behavior.

INTRODUCTION

Our earlier works dealt with the problem of learning by the ants to perform under natural conditions an activity which belonged to their species-specific pattern of behavior. The quick and efficient manipulatory learning, observed in the ants by Dobrzański (2) and confirmed in later works (1, 5) refers to functions belonging to the behavioral pattern of the given species, i.e., those activities which have a genetic

basis. Dobrzański described the process of learning by the hill-building species of *Formica* of the three basic stages of building activity: (1) seizing the building material, (2) carrying it to construction site and (3) incorporating it in the mound. Each of these stages contains innate elements which are performed without hesitation by naive individuals. Among these elements are: (1) in the first stage — seizing the building material and attempting to lift it, (2) in the second stage — carrying the material onto the mound, and (3) in the third stage — depositing it in a position parallel to the mound surface. As the workers are intent on performing those innate elements of behavior under the influence of a powerful drive, they quickly improve their efficiency by trials and errors. A few individuals gifted with higher manipulatory capabilities and possibly also with a better memory and ability for associations, relatively soon achieve a perfect workmanship. Individual differences in the quality of execution of a given activity are most distinct in the third stage. In that stage the innate element is the placing of the building material parallel to the mound surface, so the naive workers simply put down their material loosely on the mound. But it will not stay so for long, because more experienced workers will take notice of loose twigs under their feet, even if brought by someone else, and incorporate them in the structure. It happens that the position of an already inserted twig is corrected by another, more experienced worker. Thus, the quality of the complex action of building depends on the level of learning and on individual aptitude. Everything in this activity contributes to the durability of the mound surface and determines its final shape.

The *Formica cinerea* ants described in this study build their nests directly in the ground, without any kind of structure erected above the surface, always on the dry and sunny outskirts of the forest, and preferably on sandy dunes. Building activities in that species are limited to digging in the ground, which is manifested outside by ants carrying single grains of sand from underground onto the surface. The action seems so simple that there is no chance to investigate whether individual learning process is taking place. The observer is unable to state objectively if one method of handling sand grains is more or less efficient than another, or whether individual ants improve their performance with time. So far, therefore, it remains unknown if in *F. cinerea* workers there takes place, through learning, the process of perfecting that natural function.

However, owing to exceptional circumstances, it was possible to investigate whether the ants are capable of learning a function that is not typical to them, but which they are self-driven to undertake

under the pressure of natural conditions. A third successive summer (1980) in Poland with unusually abundant rainfall created unfavorable conditions of existence for ants like *Formica cinerea*, that need a warm and dry environment. The earth was wet through to the depth of dozens of centimeters. In an attempt to escape from dampness one colony of ants made a nest unusual in *F. cinerea*, and similar to the nest of *F. rufa*, a species inhabiting shaded and damp biotops. For the foundation of the nest the ants used a stump, around which they raised the mound using various building materials. Remarkably, in the neighborhood of that atypical nest, under identical biotopic conditions, there were dozens of *F. cinerea* colonies which kept to the traditional type of ground nest.

Observation of behavior of the mound-building *F. cinerea* ants provided a unique opportunity to investigate how they perform a self-imposed activity which is atypical to the species, difficult, and requires learning even in those species where it is genetically programmed.

METHODS

In our previous studies on acquiring building skills by individual ants we marked young individuals, which have not so far performed any outside functions, and were therefore naive with regard to building activities. In the observed *F. cinerea* nest, however, either the young perished owing to unfavourable weather conditions, or these conditions prevented them from leaving the nest. For that or other reason, individuals sufficiently young to be recognized by coloring failed to emerge on the surface. That forced us to use a more time-consuming method of determining the level of building skill in individual ants. The method consisted in a prolonged individual observation of each worker (previously marked with paint) performing a building activity, in order to determine the skill it showed during the first and, eventually, the second stage, i.e., in seizing and carrying building materials. Only after the level of the skill had been ascertained, the ant was permanently marked with a wire ring and subjected to further observation. We had therefore no knowledge how long it had performed a building function; we only knew, by observation of its behavior, whether the ant learned the function or not. The ants were marked on the legs and on a given day they all received wire rings on the same part (tarsus or tibia) of the specified leg. In that way we knew, on the next encounter with the marked worker, on which day it has been marked and, in consequence, how many days ago it showed inefficiency in building activities. As each ant had to be under a long observation before being marked

(and it could escape and hide itself in the meantime or during capture, which made our observation work useless), we managed to mark only a few specimens during the day. Of the total of 37 marked ants, only 15 have been encountered again at a later time, and there were never more than 2 ants with similar markings showing they had been marked on the same day. As it is always possible to distinguish between 2 similarly marked ants owing to a slightly different placing of a wire ring, we were able to identify individual ants.

The observation was conducted from the middle of July to the middle of October.

OBSERVATIONS

Seizing and carrying building material

A minute observation of building individuals showed, already in the first building stage, an important difference of behavior between *F. cinerea* workers and hill-building species. The ants' mandibles are so constructed that to seize a long object the ant has to position itself along its axis. Therefore, a typical error committed by every beginner in building activities is standing upon the twig it is trying to seize. As we said before, ants of the hill-building species soon eliminate such inadequate behavior through learning by trials and errors. Due to their persistence and patience in manipulating the seized material, they create conditions where, by the association of a correct grasp with a positive result, faulty elements of behavior get eliminated. In contrast, the *F. cinerea* ants lacked such perseverance: they abandoned immediately every resisting piece of material and tried to seize another one. If that, too, could not be lifted because it was too heavy, or immobilized in the substratum, or mostly because the ant was standing upon it, it was abandoned again for the next one. So, contrary to the workers of the hill-building species of *Formica*, the *F. cinerea* workers quickly relinquished all resisting building materials; consequently, they selected only such materials that yielded easily and could be moved at the first go. Therefore the activity of most building workers was limited to carrying small and light-weight materials. Larger items were carried only if, accidentally, they had been grasped correctly at the first attempt. That observation applies to the whole mass of the building ants, marked or unmarked. So that our first general impression was that for the most part, unidentified building ants failed, through the entire summer season, to acquire skill in the technique of seizing and carrying larger pieces of building material.

We managed to observe again only 15 ants from among the 37 which we had marked. Some of them, however, showed highly significant behavior, permitting certain conclusions. Most observations confirm the general impression of inefficiency of these ants in building activities. For instance, the worker marked "RM" (Right-Middle leg) on the fifth day of observation would stand upon the twig it was trying to seize and then abandon it, exactly like it did on the day it was marked. Another worker — "RH-1" (Right-Hind), encountered as late as ten days after the first observation, still has not learnt to seize long twigs. Possibly it was due to the individual character of this ant, marked by slowness and a weak work drive. After each action it either cleaned itself, or walked idly for some minutes.

However, we also made other observations. One day after marking the worker "LHT" (Left-Hind-Tibia) several times correctly seized the twigs by the ends. It also could pull the twigs walking backwards. On the fourth and fifth day it grasped in the right way and carried even very long objects. The same ant was encountered three more times: on the 7th, 9th and 18th day, but it was not engaged in building and seemed to be walking idly.

When "RFT" (Right-Fore-Tibia) ant was marked, it showed a typical inefficiency in seizing. It would stand upon twigs and abandon them after a short time. Observed again after 5 days, it showed a marked change of behavior. It started work that day with carrying mostly small objects, but after 20 min it switched to increasingly larger items and carried them correctly, regardless of difficulties. It did not let go the carried twig even when it fell from the hill, tumbling down over its head. Further down we shall explain the reason of such accidents, frequent on *F. cinerea* mounds.

The worker "P" (Petiolus) was marked individually, as the only one who already during the first observation displayed atypical skill in carrying building materials. Observed again after 7 days, it showed carrying skill comparable to that of an experienced *F. rufa* worker. It happened once that "P" abandoned a twig that would not move because "P" was standing upon it. But otherwise this ant showed an unusual skill in carrying, as well as another extraordinary feature — mobility associated with exceptional activity in building, which singled it out from all its nestmates. It never made an unnecessary step and always moved with a purpose. Its working speed and skill and its quick and purposeful movements enabled us to distinguish it at a glance from the distance of 1 to 1.5 m. Also, "P" showed a machine-like endurance. It was so distinct, that when after 90 min of incessant activity it carried

the load up and loitered for some time before leaving it on top of the mound, we judged it as a symptom of exhaustion and predicted that the ant would make not more than one additional trip. We were proved right. We observed "P" on two more occasions, on the 9th and 10th day, but it was not engaged in building and did not appear as active as formerly.

Mound building

Already at the first glance the *F. cinerea* mound differed in appearance from the structures erected by hill-building *Formica* species. Its base was covered with thicker pieces of material, mostly twigs. The top changed its aspect depending on the weather. On windless days — rare that summer — the top grew in height, being strewn chaotically with sticks and twigs. But the first breeze would blow down most of the thicker sticks, while smaller bits held to the irregularities of the surface, giving it smoothness. Individual observation of the working ants revealed the reason of the mound's instability. They are illustrated in the following descriptions.

The "RFT" ant described earlier, which carried so bravely even the longest twigs, lifted one of them up the stump wall and "put it down", i.e., it put the twig on the vertical wall and then let it go. The twig fell down and the ant, unperturbed, went to fetch the next one. It repeated the procedure with four successive twigs. The spot where the ant chose to deposit the twigs was in addition situated directly above the opening leading to a tunnel inside the stump. So the twigs, hauled up with such effort, blocked the entrance opening when they inevitably fell down. Other workers passing through the entrance pulled the obstacles away, but the new ones kept falling down upon them. That absurd "cooperation" continued for some time: the "RFT" busily pulled thick twigs up the wall, and its nestmates below were forced to clear the entrance over and over again. After the lapse of two days (on the 7th day after marking) the "RFT" ant still continued to "put down" the carried building material on the vertical wall.

The ant "P", the most hard-working and efficient of them all, tried even to deposit the material from below upon the ceiling of the tunnel leading inside the stump. The fact that the twig fell down upon its head and blocked the entrance had no effect on the ant's behavior — the twig was left on the spot where it had fallen and the ant ran to fetch another one.

In several cases the workers, both marked and unmarked, put the sticks upright against the stump wall. The cases described above were

the extreme ones. But all observed workers followed one general rule: it was to drop at random the carried material without any attempt to organize it. Workers not observed by us presumably behaved in the same manner, for the erected mound bore no likeness to permanent structures raised by workers belonging to hill-building species. The shape and texture of those structures is resistant to gusts of wind, and the ants can walk freely upon their surface, whereas the *F. cinerea* workers always had difficulties in moving on the sliding and unsteady surface of their mound. Frequently a loose twig would give way under a load-carrying ant and both would fall down together, as happened to the "RFT" worker. Such accidents happened mostly to ants pulling heavy pieces of material, which required walking backwards. In doing so, the ant climbing on the mound clings to the surface with its hind legs and pulls itself up by their strength. When the surface gives no sufficient support and slides, the ant tumbles down and frequently not one stick, but an avalanche of sticks falls upon it. No similar scenes are observed in the hill-building species.

The next (1981) season was favorable for the existence of the *F. cinerea* and our colony move from the investigated atypical nest in the tree stump. The attempts of finding this colony between a lot of ground nests of this species were without results.

DISCUSSION

If we admit that the process of manipulatory learning of building activities occurred in *F. cinerea* workers, that process followed a different course than in the hill-building species, both in quality and in quantity. Already the first stage (seizing building material) could not be mastered by all individuals. As to the workers successful in mastering that stage, our incomplete findings suggest that they needed a much longer time to do it than ants belonging to hill-building species. However, some — though few — *F. cinerea* workers achieved a high level of perfection in both the first and second (carrying building material up the mound) stages. Still, we have failed to find even a single case where the worker of that species would make any attempt at performing the third stage, which can be named "mound building proper". Even the condition of placing the build-material parallel to the mound surface, which is the innate element in hill-building species of *Formica*, was not met. The entire building activity of *F. cinerea* was reduced to carrying the material to the base of the stump inhabited by the colony. What resulted from such work was a simple stack of loosely shaped-on twigs and bits of material.

In consequence, the colony failed to gain through the whole summer, the skill accessible to other species of the same genus, and by some individuals mastered to perfection.

Let us analyze the three stages of mound-building activity from the point of view of *F. cinerea* innate behaviors. The workers of all ant species are capable of seizing and carrying objects, as the stock of social behaviors of each independently living species includes carrying nestmates and brood during nest moving and bringing prey to the common nest. These activities must therefore have a genetic basis. Consequently, seizing and carrying building material should be practicable to every ant. However, the stereotyped way of carrying one another, hereditarily preserved in every ant species, is much simpler than seizing and carrying thick materials of various shapes. Also, the transport of prey does not require special abilities from *F. cinerea* workers, for those ants are not highly predatory and their prey is always small, easy to seize and carry. One might think that the ant, possessing a drive to seize, could direct it also to larger objects. But a deeper analysis shows that these actions are qualitatively different. First, the ant can seize a small object in any position, without having to step upon it. Refraining from the latter is the greatest difficulty in learning to seize larger objects. Second, being by nature prepared to carry only small objects, or objects seized in the typical way, the *F. cinerea* workers have not enough persistence in carrying on the started action and soon abandon any resisting objects. Whereas it is that drive-elicited persistence in jerking and pulling at the seized object which helps the ant to associate a correct grasping of the load with its moving from the spot and makes learning by trials and errors possible. We therefore arrive at the conclusion that *F. cinerea* workers have some predispositions necessary to learn the way of seizing the building material, but being devoid of a sufficiently strong drive, they are inferior with regard to the speed and quality of learning to workers of other *Formica* species. Hence only a few ants attempted to carry larger objects, and only some from among those few reached a higher level in the performance of that task.

As to the third stage — parallel placing of building materials and incorporating them in the structure — the *F. cinerea* ants seem to lack an appropriate genetic basis for its performance; such basis as is possessed by the hill-building species, apparent in their placing the building material parallel to the mound surface. It may be inferred from the facts of “laying” the material on a vertical wall that ants have no insight into a situation which is not genetically programmed.

There is, however, another possible way of thinking. Maybe learn-

ing a function can be quicker if from year to year there remain in the nest some experienced workers, which from the beginning of the season proceed to perform the activity in the proper way. The young ants, especially susceptible to learning, are exposed to their example directly upon leaving the nest. The process of adopting the patterns of behavior related to building activities can take place through *kynopsis* (according to Stäger (6), example set by experienced nestmates), as well as through *stigmeria* (according to Grassé (3), perception of correctly constructed elements of the nest). But in the nest of *F. cinerea* such models as properly working nestmates or correctly constructed parts of the nest are absent, which makes the process of social form of learning impossible.

Against that assumption could be the fact that *F. fusca* workers (species closely related to *F. cinerea*, also building only in the ground), being slave-ants of *F. sanguinea*, do not build as well, although they have the example of their nestmates and the model of construction available. They lack, however, the drive to build and the social drive: owing to a division of labor, the nest is built by *F. sanguinea* workers that possess innate predispositions for that work. So this fact is no evidence against the role of example in the building activity. This question might be clarified if the investigated colony were still staying in the same nest during the following summer. Unfortunately, they moved out.

In answer to the question formulated in the title, we can only state that when an activity not included in a wide notion of behavioral pattern of the species is required, the process of manipulatory learning is either absent, or its course is slower and, more important still, it shows wider individual differentiation than in the case of improving innate functions.

A separate question is whether the described change of behavior is of evolutionary importance to the species. A process of evolutionary nature can take place, if the modified behavior observed by us results from genetic changes (mutations), and if climatic disturbances have a permanent character, giving preference to mound over ground nests. Admittedly, however, it is not less probable that the described occurrence was a case of behavioral adaptability that happened but once. Individual differentiation of plasticity, considerable in ants, may comprise a wide range of adaptable behaviors. In the species of genus *Formica* the division of labor is based on an individual predisposition to perform a given function. Such mode of the division of labor is unprecedented in animals, and even in human societies. In ants the selection of individuals best fitted for a given function tends to increase

individual differences of behavior. That, in turn, leads to a pronounced increase of the plasticity of the colony as a whole. The existence within the colony of a certain number of individuals with extreme behavioral capacities ensures the ability to respond adequately to sudden and atypical circumstances. The manifestation of such extreme behaviors may create an illusory impression of a leap, of absolute novelty. It therefore cannot be excluded that nest-building performed in an atypical way and with atypical material, which we have observed, may well be within the limits of behavioral variability of the species. Such behavior, according to Lorenz's rule of social heredity (4), may continue for some time, being passed to succeeding generations in the colony through e.g., the mechanism of stigmeria and kynopsis. And although, without the appearance of hereditary mutations, such behavior will remain a temporary deviation, connected with the existence of one particular colony, it may provide that colony with an increased chance of survival during the period of climatic disturbances.

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