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GENERAL BIOLOGY

The Importance of Individual and Social Experience for Interaction between Ants and Symbiotic Aphids

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Trophobiosis with various Homoptera species that have a proboscis, such as aphids, is one of the most complex and, in many respects, mysterious types of behavior in ants. In an ant family, there is a group of trophobionts, which has a constant composition. The members of this group look after the symbionts, protect them from adverse conditions, and take them into the anthill for wintering. In return, the ants "milk" the aphids, whose sweet excretions are one of the main sources of carbohydrates for adult ants [1, 2]. Until recently, nothing was known about the roles of innate and acquired behavior in ant–symbiont interactions. We were the first to describe the division of labor among the trophobionts: "shepherds" only look after aphids and milk them, "guards" only guard the aphid colony and protect them from external factors, "transit" ants transfer the food to the nest, and "scouts" search for new colonies. This specialization increases the efficiency of trophobiosis. When we forced ants to change their roles, much food was lost. Such "professions" were only found in the most social species we studied, *Formica polyctena* Foerst. [3, 4]. Note that, in our experiments, ants of this species exhibited complex types of learning and communication, which required the ability to add and subtract small numbers when transmitting information within the nest on the location of food [5]. In this connection, it was especially interesting to assess the roles of innate and acquired behavior during the formation of trophobiosis in imaginal ontogeny of these species. We attempted to determine whether or not trophobiont ants recognize their symbionts at first contact and learn to milk aphids and what roles individual and social experience play in the division of labor.

To answer these questions, we studied how the types of behavior involved in looking after the aphids developed in the ant species *F. polyctena* that had grown up in the laboratory and had no contacts with either other ants or symbionts. Such deprivation experiments are routinely conducted in ethology [6]; however, we were the first to apply this method to ants [7]. The data obtained suggest that direct interaction with symbiotic aphids is based on so-called "innate recognition" [6], which is further complemented by more complex behavior, whereas the division of labor among trophobionts is determined by social experience.

Experimental. To form experimental laboratory families, ants were placed in artificial nests immediately after they came out of cocoons. The control families were obtained from the same anthills as the cocoons. We conducted the study on three experimental and three control families each comprising 2000 ants from 1994 until 1996. Ants lived in formicaria (10×20 cm) set on arenas (100×200 cm). Observations were preceded by three weeks of adaptation, when the ants received a carbohydrate diet (sugar syrup in open troughs). Note that three-week-old *F. polyctena* are physiologically mature and exhibit learning ability and the entire range of mature behavior, including trophallaxis, i.e., exchange of liquid food belched from the crop with other ants [7].

During the period of observation, the ants did not receive food. Instead, colonies of aphids *Chaitophorus albus* Mordv. were displayed in the arenas every two or three days. The aphids were placed on aspen shoots standing in jars of water. In order to find out whether or not ants kept to the same aphid colony, we simultaneously set two colonies 70 cm apart on the same arena. We timed the ants' behavior throughout the daily cycle of activity (a total of 60 ants were under observation for 130 h) and estimated the level of aggressiveness (for more detail, see [4]). We watched the behavior of the ants until the end of their seasonal activity (25–40 days). Each of the 230 trophobionts bore an individual label made of colored pyroxyline varnish.

Individual experience: Do ants learn to milk aphids? Under natural conditions, the behavior of a trophobiont during direct contact with an aphid is stereotypical and specific. The ant strokes the aphid's abdomen with its antennae, which are folded so that their ends are close to the ant's trophi. In this way, the ant "asks" for a drop of the sweet excretion; the ant immediately catches the drop and puts it into its crop [1]. During trophallaxis, the antennae are folded in a similar manner.

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Kloft [8] compared the aphid's abdomen to the head of an ant offering liquid food. The behavior of the aphids closely resembles that of ants during trophallaxis and apparently triggers the same behavioral stereotype in trophobionts. The behavior of an ant eating carbohydrate food from an open trough or encountering various objects is distinctly different. In these cases, the ant feels the objects with extended, almost straight antennae, with the frequency of tapping reflecting the degree of the ant's interest in the object; however, the position of the antennae themselves does not change.

In the deprivation experiment, when ants from all three experimental families encountered aphids for the first time, they perceived the aphids as any other unknown object: the ants felt the aphids with extended antennae and did not remain near them for long. An ant behaved in this manner until it accidentally touched a drop of an aphid's excretion and had to taste it when cleaning its antennae or legs. After this, the ant's behavior substantially changed: instead of tapping at the aphids, the ant began to stroke them with folded antennae, thus asking for the sweet excretion. This change was gradual. At first, the ant only slightly folded the antennae, so that they tapped the aphid's sides (in normal trophobiosis, ants pat aphids' backs); the movements of the antennae were uncoordinated. We observed this stage in the behavior of all "beginners." After successful contact with the first aphid, an ant began to perceive other aphids in the colony. The ant stopped them and tried to milk them, lengthening the contacts until a drop of excretion emerged. At this stage, the movements of the antennae were more coordinated; however, the ant was usually unable to catch the drop in time, and, hence, was compelled to clean itself continually. The development of trophobiotic behavior, including the stages of asking and waiting for the drop of excretion, was accomplished 60–90 min after the ants had faced aphids for the first time. The behavior of the experimental ants during their subsequent contacts with aphids did not differ from the behavior of the control trophobionts.

We think that, in this case, so-called innate recognition of the objects of the species-specific instinctive behavior occurred [6]. When the ants perceived the stimuli that came from the aphids, innate recognition was complemented with acquired reactions, and all behavioral elements formed an integral behavior. Apparently, imitative behavior was also involved in this process. This suggestion agrees with the fact that those ants that were the first to appear in the aphid colony took considerably more time to develop the behavior. In 1996, the first five ants that came to the aphid colony (within 30 min after these colonies were placed on the arena) showed an interest in the aphids, a response to aphids encountered beyond the colony, and the reaction of waiting for and catching the drop of excretion after 7–13, 8–20, and 17–37 min, respectively. In the next five ants, this took 0.3–0.5, 1–1.2, and 1.6–2.3 min, respectively.

Social experience: How is the division of labor formed in the trophobiont groups? While studying the control families, we found that permanent groups of trophobionts began coordinated work as early as 30–60 min after hungry ants were shown aphid colonies. Each group stayed with the colony that it initially chose and never moved to a neighboring colony; this is also typical of natural populations. The division of labor between the professional subgroups (shepherds, guards, and transit ants) was almost the same as in natural populations.

At first glance, the groups of trophobionts from the experimental families were no different from the control trophobionts. For the most part, both the composition and size of these groups were constant: on average, there were 14 ants per colony (one trophobiont per three aphids). In addition, the ants stayed with the aphid colony that they initially chose and never moved to another one. However, experimental and control families substantially differed from each other with respect to interactions and the division of functions between trophobionts. The groups lacking in social experience did not display a distinct division of labor. Instead, there were ants with average trophobiont characteristics, rather than representatives of different trophobiotic professions. As we noted above, direct interaction between these trophobionts and aphids did not differ from that observed under natural conditions. However, the general patterns of their behavior in an aphid colony were different. They were considerably more passive than control shepherds: "rest" periods, when they remained passive on the aspen branches, took over 60% of their time, whereas the control shepherds spent only about 8% of their time at rest and at least 70% on direct contacts with aphids. In contrast to the shepherds, the experimental trophobionts paid no attention to migration of aphids and did not try to return them to the colony. When comparing experimental trophobionts with control guards, we found that the former were four times less aggressive. The differences relating to the interaction between the ants themselves were especially marked. In contrast to the control ants, the experimental ants kept away from each other and did not enter into any contacts. It is clear that these groups faced difficulties when distributing the excretions obtained from aphids. We did not observe distinct transit functions in the experimental groups; i.e., there were no ants specializing in transportation of the aphid excretions and who made regular trips between the nest and the aphid colony. Instead of transit ants, there was a permanent group of 5–12 ants who kept close to the colony and passively waited for trophobionts to offer them food. When they received it, they offered it to the ants that they met on the arena instead of going to the nest immediately. Trophobionts also gave food to other ants, which apparently got hungry and came to the aphid colony (this is not characteristic of a natural population). While control trophobionts actively offered food to other ants, experimental trophobionts paid no attention to the ants that came to the colony and only gave them food after being energetically asked for it. This behavior was observed throughout the period of seasonal activity (note that this coincides with the natural life-span of many trophobionts). Apparently, the formation of fine mechanisms of interaction and division of labor in highly social ant species, including *F. polyctena*, requires specific social experience. Individual skills are not sufficient to develop this complex behavior. This species exhibits the phenomenon of imprinting [9]; therefore, we may suppose that an absence of contacts with "elder" ants within a certain sensitive period of imaginal ontogeny prevented the experimental trophobionts from developing professional specialization.

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