### = GENERAL BIOLOGY =

# The Ontogeny of Hunting Behavior in Ants: Experimental Study

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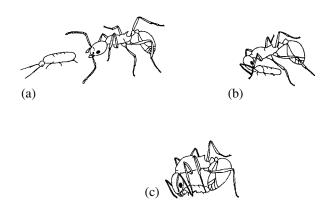
The ontogenetic development of complex behaviors is one of the most interesting and the least studied biological problems and is a constant focus of attention of ethologists, ecologists, and evolutionists. The role of individual and social experience in the scenarios of predatory behavior has been determined thus far for only a few species of vertebrates [1]. Most researchers still believe that invertebrates merely perform speciesspecific repertoires of behavioral reactions that are almost entirely determined by strict inherited patterns. In recent years, the methodology of deprivation experiments based on rearing naive (lacking experience) animals that is used with vertebrates has been applied to the behavior of invertebrates. The role of learning in the interaction with a potential prey appeared to be unimportant in larvae of dragonflies, spiders, and some other invertebrates [2–4]. Ants exhibits the most flexible behavior among insects, including catching a moving prey and even hunting in groups; however, the ontogeny of hunting behavior has not been studied in them. A few studies were performed at a colony level. For example, young and mature families of Myrmiacaria opaciventris have been demonstrated to differ in hunting strategy under natural conditions [5].

Earlier, we described the technique of individual hunting of ants from the genus *Myrmica* for jumping springtails (Collembola) as a mass prey and found a fixed action pattern (FAP) of catching the prey [6]. These results laid the basis for an original procedure of experiments on the ontogeny of the response to a potential prey in ants. We used this procedure to discover the scenario of the development of hunting behavior in ants.

The experiments were performed from July to September 2003. We used the ant *Myrmica rubra*, a mass species in the litter–soil layer. We compared the hunting behavior of the base family (about 500 workers and several females) and four naive families raised from pupae in separate laboratory nests and deprived of the experience of communication with adult ants (except for females, which permanently stayed in the nest

together with the brood) as well as with potential preys. To observe the interaction of the ants with active prey, we put live jumping springtails Tomocerus sibiricus into glass containers 6 cm in diameter and 12 cm in height (30 animals per container). The containers had a gypsum bottom covered with a "splints" made out of plastic bottles (this substrate mimicked forest litter but was transparent). Ants were put into containers individually, transferring them with a small brush. Their responses to the prey were timed and video recorded; the records were then viewed in the slow-motion mode, fixing and drawing in detail individual frames (Fig. 1). In the experimental family, 123 individually labeled ants were tested 2, 7, 14, 30, and 60 days after the pupae turned into imagoes. It was earlier demonstrated that ants exhibited the entire diversity of their behavioral reactions by the imaginal age (30 days) [1]. Testing sessions lasted for 15 min, because our earlier observations of natural families showed that ants caught a jumping springtail within 5 min after they were put into a container [6]. "Adult" members of the base family for used for control experiments. The total observation time was 80 h.

We scanned the array of test sessions recorded and selected 209 sessions during which ants actively moved in the containers. These records were used to analyze the behavior of naive ants. All active ants behaved in the



**Fig. 1.** Elements of the FAP in the ants *M. rubra* hunting for jumping spring tails (Collembola) (drawings of video frames): (a) an ant approaches a springtail; (b) the ant grasps the prey from above at the front part of the body; (c) the ant kills the prey using the stinger.

same way at different ages. Their behavior was distinctly exploratory. We observed numerous antennal contacts of ants with springtails; i.e., ants responded to springtails as to conspecific animals rather than potential prey. If the springtail made occasional jerks, the ant jumped aside. For six ants, we performed, in addition to 15-min tests, the sessions during which each ant stayed in the container containing springtails for one day. The pattern of the interaction with a potential prey did not change in these ants. Only 8 of the 209 sessions ended in catching the prey. In control experiments with the members of the base family, 116 of 214 tests ended in catching the prey; in the remaining tests, ants also responded to the springtails aggressively.

Those 7 out of 123 naive ants that were able to catch the prey (one of them had done it twice) are of special interest. All of them exhibited an "at once and entirely" FAP during the final act of the hunt and had no noticeable differences from the adults (Fig. 1). One of them caught the prey at an age of seven days and the others, at an age of 14 days (during the third test). In contrast to the control ants, they, however, stayed with their prey on the laboratory arena instead of transporting it to the nest. If we transferred them, together with their prey, to the nest by means of a brush, they left the springtail near the brood. Having found the killed prey, the members of the naive family that stayed in the nest carried it to the remote part of the nest, far away from the brood, and did not use it to feed the larvae. Our observations showed that the broods of the naive families fed on fodder eggs laid by adult worker ants. Thus, the hunting in the young families "ran idle"; i.e., the prey was not used for its intended purpose.

The "at once and entirely" FAP of ants hunting for a jumping springtail, which is so difficult to catch, indicates that the specific stereotype of hunting behavior may be expressed as an integrated set of inherited reactions. However, the expression of this stereotype is variable within a family. Only in a small proportion of ants (less than 10%) was hunting behavior expressed at an early imaginal stage. For comparison, note that the formation of such a complex behavioral pattern as asking symbiotic aphids for honeydew was observed in all naive ants within 60–90 min after the first contact with a drop of honeydew [7]. In contrast, the formation of the specific stereotype of interaction with the difficultto-handle prey requires a multistage completion for many days [8]. In fact, the hunting behavior requires maturation rather than learning. However, we may assume that the hunting behavior forms as socialization occurs and experience is accumulated. The maturation period may also include wintering in the nest. Observations performed under field conditions, immediately after the wintering was finished and Myrmica went out of the nests. Field experiments using containers showed that the hunting of overwintering ants for springtails was as efficient as in other seasons [6]. It is also possible, that the ants that began hunting at earlier ages accumulate experience and spread it among other members of the family on the basis of the so-called social facilitation, which is known to be the simplest form of social learning in vertebrates [1]: the presence of animals performing a stereotypic set of acts favors the "release" of the set of behavioral patterns in conspecific observers. The dependence of the activity of hunting for springtails on their abundance in the feeding area that we discovered earlier [6] suggests that the frequency of hunter-prey encounters also affects the formation of the stereotype. In general, the scenario of the formation of hunting behavior in ants is based on the multistage maturation and completion of the species-specific FAP, which probably includes elements of social learning.

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