ISSN 0012-4966, Doklady Biological Sciences, 2008, Vol. 418, pp. 56–58. © Pleiades Publishing, Ltd., 2008.
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GENERAL BIOLOGY

Development of Aggression as a Possible Basis of "Professional" Specialization in Ants

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Presented by Academician V.K. Shumnyi August 28, 2007

Received August 28, 2007

DOI: 10.1134/S0012496608010195

Division of labor among working individuals in families of social insects is a classical example of adaptive variation in populations. Situations where the fulfillment of specific functions is ensured by caste morphological variation (specific mandible and head shapes and substantial differences in sizes) have been sufficiently studied in ants [1]. In many species of ants, however, there are no morphological differences between functional groups, and the division of labor is based on behavioral differences alone [2]. The relative roles of hereditary and acquired structural and functional parameters of division of labor in ants, as well as in other social insects, long remained unclear. A possible cause of the failure to estimate them is the methodological approach based on studying "depersonalized" functional groups of the family (aphid milkers, hunters, guards, nurses, and workers). On the other hand, studies at the individual level revealed a system of "professional" division of labor within a specialized functional group of *Formica*: shepherds, guards, scouts, and transfer ants. We also found that the age of the ants did not substantially affect their choice of "profession" [3]. It is conceivable that professional specialization of ants occurs in the course of ontogeny on the basis of the combination of cognitive and psychophysiological characteristics, such as the intensity and number of aggressive reactions, the ability to learn how to avoid danger or solve searching problems.

To test this hypothesis experimentally, we first studied the appearance and early ontogeny of aggressive behavior in red wood ants *Formica aquilonia* Yarrow. The scheme of experiments was based on the notion of a species-typical "images of the enemies" developed by Tinbergen [4] with the use of birds as an example. It was earlier found that one of the images of the enemies for red wood ants is predatory carabids, their natural competitors. In experiments, they were successfully substituted with artificial models reproducing characteristic features of carabids. Testing representative of different functional groups showed that guards attacked the enemies, whereas aphid milkers avoid contacts with dangerous objects [5]. This allowed us to use carabids as a test object for determining the professional characteristics of ants. We assumed that guards are recruited among the ants that have the clearest species-typical image of the enemy (or a set of such images) and are characterized by a high level of aggressiveness expressed early in imaginal ontogeny.

Organization and results of experiments. Reactions towards enemies were compared in two pairs of laboratory families of equal sizes: a basic (natural) family and a "naive one," which consisted of ants that came out of cocoons in the laboratory and were reared in isolation. The ants were tested individually in 15 × 15 cm arenas, where they were presented with a live beetle or an artificial model, which was tied to a thread and moved at a speed of 6–7 cm/s by pulling the thread. Hypotheses on differences between reaction of ants to different objects were tested using Fisher's equation for comparison of two sampling proportions of variants: the χ^2 test and Wilcoxon's test [6]. In the first, preliminary series of experiments, four groups of seven ants each were used: guards, hunters, and aphid milkers from a basic family and naive ants about two weeks of age. Guards were collected from the lid of the formicarium by passing a needle above them and selecting the ants that attacked it most aggressively. Hunters were selected according to the reaction to a potential prey in the habitation arena. To identify aphid milkers, aspen shoots with aphid colonies on them were put onto the arena. A total of 140 tests were performed with 28 ants. These experiments showed that guards and hunters from the basic family aggressively reacted towards not only a beetle, but also an artificial model of the enemy, whereas naive ants substantially more often reacted to a live beetle ($p < 0.05$, Fisher's equation). This suggests

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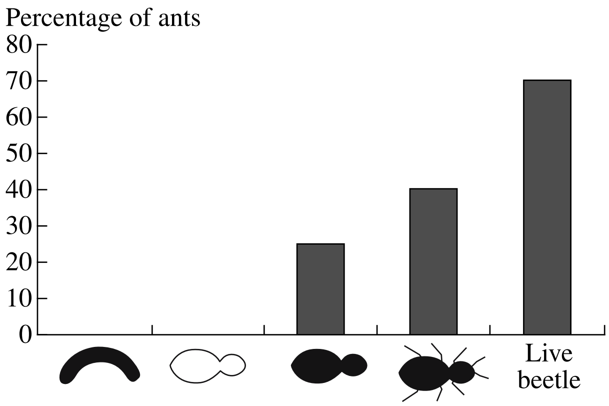

Fig. 1. The proportion of ants from the guard group of a basic family displaying prolonged bites in tests with artificial models and a beetle.

that the ability to grasp the key features of the enemy requires further completion [7]. According to preliminary estimations, naive ants and aphid milkers behaved towards the enemy the least aggressively, whereas guards and hunters displayed stronger aggression and differed little from each other in this respect.

In the second series of experiments, we used two groups of 20 ants each from other two families: an undifferentiated group of three- to five-week-old ants from the other naive family and a group of guards from the other basic family. The ants were put onto an arena together with a live beetle for 15 min. Five to 15 min later, the ants were tested on artificial models, which were presented for 15 min each in a random order. We performed a total of 200 presentations and recorded the sequence and number of behavioral reactions in 40 ants. The following reactions towards artificial models and live beetles were observed (in order of increasing aggressiveness): (1) opening the mandibles; (2) a thrust with the mandibles opened; (3) a short bite (shorter than 5 s); (4) a prolonged bite (longer than 5 s); (5) a death grip; (6) chasing the object of aggression while making thrusts and short bites; (7) the ant's falling on its back and trying to seize the beetle's legs with the mandibles. This last reaction was observed only in naive ants and only towards a live enemy. The ranges of behavioral reactions of ants from the two naive and two basic families towards beetles and their models were similar, which suggests a considerable contribution of the hereditary component into their aggressive behavior. We found two essential differences: (1) naive ants never exercised a death grip, whereas 20% of ants from basic families displayed this reaction; (2) 65% of naive ants, having failed to seize the prey with their mandibles, fell on their backs, whereas ants from the basic families never responded in this way. These differences are related to the formation of a death grip as a final act of aggressive behavior, which apparently requires completion through accumulating experience.

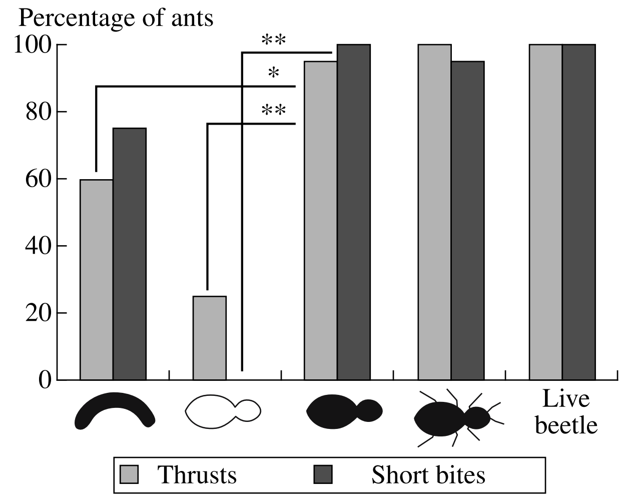

Fig. 2. The proportion of ants from a naive family displaying aggressive thrusts in tests with artificial models and a beetle. Significant differences: * $p < 0.05$, ** $p < 0.01$ (the χ^2 test).

Comparing the reactions towards carabids and their artificial models in representatives of different functional groups, we found the following tendencies. Guards displayed the most aggressive reactions when interacting with live carabids. They also responded aggressively to all models, including those that had only one key feature. The models that were the closest to the original in external appearance caused the strongest aggression (Fig. 1). Note that, in both naive ants and ants from the basic families, a white color of the model entirely suppressed aggressive reactions (thrusts and short bites) and an asymmetric shape of the model decreased their intensity (Fig. 2; see also [5]). This suggests that naive beetles use the same visual characters for recognizing enemies as adult ants do.

Although behavioral patterns were compared at the individual level in only in small samples, the obtained results allow us to assume that the distribution of ants among functional groups is based on essential differences in aggressive behavior. Indeed, three out of 27 naive ants from both families displayed both a prolonged bite and chasing in tests with carabids. These ants were comparable with adult guards with respect to the number of aggressive reactions towards live beetles. We may assume that future guards and hunters are recruited among such ants displaying strong aggression at early stages of ontogeny. Probably, aggressive ants are hereditarily incapable of learning to avoid danger, which is a natural behavior in others. This, in turn, may be related to cognitive specialization [8]: facilitation of the formation of some associative links is combined with disabling the formation of others. This hypothesis requires testing. To date, our data suggest that a combination of psychophysiological characteristics plays the main role in the "professional" specialization of ants. Guards and hunters are characterized by a high level of aggression; they display reactions to combinations of the features of the enemy early in ontogeny. The ability to grasp the key features and effectively attack the enemy requires completion through accumulation of individual experience and, possibly, simple forms of social learning, as it was earlier demonstrated for hunting behavior of ants [9].

ACKNOWLEDGMENTS

We are grateful to Corresponding Member of the RAS V.I. Evsikov for fruitful discussion of and valuable comment on our study.

This study was supported by the Russian Foundation for Basic Research (project no. 05-04-48104), Russian Federation Presidential Council for Grants (project no. NSh-1038.2006.4d), and program of the Presidium of the Russian Academy of Sciences "The Origin and Evolution of the Biosphere."

REFERENCES

1. Hölldobler, B. and Wilson, E.O., *The Ants*, Harvard: Belknap Press of Harvard Univ. Press, 1990.
2. Dobrzanska, J., *Acta biol. Exp.*, 1958, vol. 18, pp. 55–67.
3. Reznikova, Zh.I. and Novgorodova, T.A., *Dokl. Biol. Sci.*, 1998, vol. 359, no. 4, pp. 173–175 [*Dokl. Akad. Nauk*, 1998, vol. 359, no. 4, pp. 572–574].
4. Tinbergen, N., *The Study of Instinct,* Oxford: Clarendon, 1951.
5. Dorosheva, E.A. and Reznikova, Zh.I., *Zool. Zh.,* 2006, vol. 85, no. 2, pp. 183–191.
6. Urbakh, V.Yu., *Biometricheskie metody* (Methods in Biometry), Moscow: Nauka, 1975.
7. Lobashev, M.E., in *Issledovaniya po genetike* (Genetic Studies), Leningrad: Leningr. Gos. Univ., 1961, vol. 1, pp. 1–11.
8. Reznikova, Zh., *Animal Intelligence: From Individual to Social Cognition*, Cambridge: Cambridge Univ. Press, 2007.
9. Reznikova, Zh.I. and Panteleeva, S.N., *Dokl. Biol. Sci.*, 2005, vol. 401, no. 1, pp. 110–111 [*Dokl. Akad. Nauk,* 2005, vol. 401, no. 1, pp. 139–144].