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GENERAL BIOLOGY

Efficiency of Aphid Protection from Enthomophages by Ants of Various Species

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Trophobiotic relationships have been found between ants and representatives of four insect orders: Homoptera (families Aphididae, Coccidae, Pseudococcidae, Membracidae, Cicadellidae, and Aleyrodidae), Lepidoptera (Lycaenidae), Heteroptera (Plataspidae, Coreidae, and Pentatomidae), and Hymenoptera (Blasticotomidae) [8, 12, 13]. In exchange for the sweet egesta (honeydew) of insect symbionts, ants protect them from enemies [9, 15]. Homopterans (Aphididae), in particular aphids, is one of the major supplyers of carbohydrate food for ants. Ant-visited (myrmecophilous) aphids make up 60% of the world fauna of this group [14]. The ant–aphid relationships can be used as a convenient model for studying the mechanism of trophobiotic interactions that develop in multispecies animal communities; in particular, the coadaptive potential of symbiont protection by ants could be estimated. Evidence obtained by now suggests a wide spectrum of transitional forms of interaction between these insects, from mutualism to exploitation [11]. Comparative analysis of aphid fecundity, size, and deathrate of their colonies in the presence and absence of ants showed that the myrmecophilous aphid prosperity depends on the symbiont species [6, 7]. However, the degree of influence of various ant communities on the survival of myrmecophilous aphids remains unknown. This study is the first attempt at comparing the efficiency of aphid protection from aphidophages by ants of various species in a multispecies community.

MATERIALS AND METHODS

Our studies were conducted in pine–birch and birch–aspen forests of Novosibirsk oblast in 2006. We examined colonies of myrmecophilous aphids on the aboveground organs and roots of plants along a 44-km transect 3 m in width and in five test plots located in associations of different plants (150–200 m^2 each). Aphidophages were detected in the aphid colonies and on the fodder plants. Both ants and aphids were fixed in 70% alcohol. In total, 518 aphid colonies were examined. Aphidophage imagoes were collected by hand and with a net. Larvae of predators and parasitoids (in mummified aphids) were put into individual containers and grown in the laboratory until the imaginal stage. Insect behavior during their interaction was studied in nature directly on plants inhabited by aphids. In the area examined, 12 ant species with different systems of territorial organization proved to have trophobiotic relationships with aphids. Data on ants of the same genus and type of the feeding territory organization were pooled. A vast protected territory with a well-developed network of foraging roads and secondary division between steady forager groups was characteristic of *Formica* s. str. (*F. rufa* L., *F. lugubris* Zett., *F. polyctena* Först., *F. pratensis* Retz.); a partially protected territory was typical of *Camponotus* (*C. saxatilis* Ruzs., *C. herculeanus* Ruzs.) and *Lasius* (*L. niger* L.); an unprotected territory was characteristic of *Serviformica* (*F. fusca* L., *F. cunicularia glauca* Ruzs.) and *Myrmica* (*M. rubra* L., *M. ruginodis* Nyl., *M. schencki* Emery) [3].

The following representatives of eight aphidophage families were identified in the aphid colonies: Aphididae; Aphelinidae; both larvae and imagoes of the Coccinellidae; larvae of Chrysopidae, Syrphidae, and Cecidomyiidae; and some bugs (Nabidae and Anthocoridae).

Aphidophage abundance in ant-visited aphid colonies was compared using one-way ANOVA and the two-sample *t* test with different variances. The data obtained were processed using the Excel software package.

RESULTS AND DISCUSSION

Comparative analysis of different aphid colonies visited by ants of various species showed that the proportion of colonies containing aphidophages varied considerably (one-way ANOVA: $F_{real} = 29.08 > F_{critical} =$

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Comparative analysis of the number of aphid colonies with and without aphidophages among the colonies visited by various ants ($t_{real}/t_{critical}$)

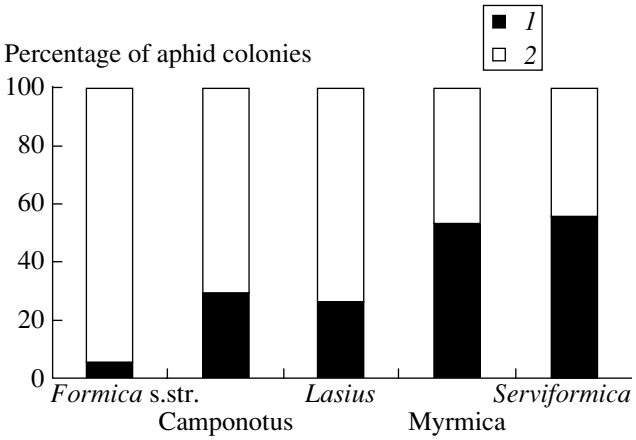
Ants	Number of colonies		t_{real}	$t_{critical}$	p
	examined	with aphidophages			
Formica s.str./Camponotus	249/48	13/14	3.53	2.40	**
Formica s.str./Lasius	249/140	13/37	5.30	2.34	**
Formica s.str./Myrmica	249/68	13/36	7.62	2.37	**
Formica s.str./Serviformica	249/16	13/9	3.95	2.60	**
Camponotus/Lasius	48/140	14/37	0.35	2.37	ns
Camponotus/Myrmica	48/68	14/36	2.63	2.36	**
Camponotus/Serviformica	48/16	14/9	1.87	1.71	*
Lasius/Myrmica	140/68	37/36	3.70	2.61	**
Lasius/Serviformica	140/16	37/9	2.23	1.73	*
Myrmica/Serviformica	68/16	36/9	0.23	2.50	ns

Note: Significant differences: * $p < 0.05$; ** $p < 0.01$; ns, nonsignificant difference, $p < 0.05$.

3.36, $p < 0.01$). Ants with different systems of colony territorial organization provided different degrees of protection for the symbiotic aphid colonies, which resulted in different abundances of aphidophages in these colonies (table). Only nonsignificant differences were found between the species groups with the same type of organization of feeding territories: partially protected (*Camponotus* vs. *Lasius*) and unprotected (*Myrmica* vs. *Serviformica*).

In aphid colonies associated with *Formica* s. str. protecting their territories, natural enemies (aphidophages, including predators and parasitoids) were five to six and ten to eleven times less frequent than in colonies visited by ants that partially protected (*Camponotus* and *Lasius*) or not protected at all (*Serviformica* and *Myrmica*) their feeding territories, respectively (figure). Insect behavior in the communities suggested that the dominating *Formica* s. str. protect aphid actively from both mobile (mostly imago) and slowly moving (larvae) aphidophages. Mobile entomophages (including Aphidiidae and Aphelinidae) that appear in aphid colonies induce a wide spectrum of aggressive responses in ants. Apparently, there were a few aphid mummies (the result of attacks of Aphidiidae and Aphelinidae) in the aphid colonies and on neighboring branches (2%; n = 147 for *F. rufa* and 2.4%; n = 85 for *F. pratensis*) because the parasitoid infection occurred far away from the ant-protected colony during usual migration of aphids within a host plant. Ants with partially protected feeding territories (*L. niger, C. saxatilis*, and *C. herculeanus*) protected aphids efficiently mainly from mobile aphidophages, whereas larvae did not provoke aggression in ants. The ants attack imago actively until the predator leaves the plant inhabited by aphids. *Camponotus* ants scare away mobile aphidophages (including the parasitoids Aphidiidae and Aphelinidae) by quick runs on the plant; very few mummies were found in the colonies protected by these ants (*C. saxatilis*: 6.5%; n = 46). *L. niger* ants fail to protect aphid colonies from aphidophages. In this case, the number of colonies with mummified aphids was considerbale (10.2%), and the number of parasitoid imagoes was 0.7% (n = 137). The ants of unprotected territories (*Myrmica* and *Serviformica*) displayed a neutral response to every aphidophage.

Aphidophages proved to display three behavioral strategies in response to ant attack: avoidance, freezing, and active defense. Mobile entomophages mostly avoided interaction with ants (they changed the direction of movement). Freezing was characteristic of all aphidophages: they crossed extremities, pressed themselves tightly to the substrate, and did not move until the ants lost interest in them. Larvae of Syrfidae displayed an active defense. In response to attacks (stings) of ants, viscous substance has been excreted from the



Aphidophage occurrence in aphid colonies visited by various ants: *1,* colonies with aphidophages; *2,* colonies without aphidophages.

larval mouth to render ant motionless for a time (this substance stuck ant mandibles, antennae, and extremities). The same substance is usually used to capture aphids [1].

Thus, the presence of aphidophages in myrmecophilous aphid colonies depends on the ant species that look after the colony. *Formica* s. str., which have large colonies and vast protected territories [2], displayed the most efficient protection of the symbionts. The degree of aphid protection seems to depend on the organization of work and behavior of honeydew pickers, i.e., the ants that permanently look after the aphids. In multispecies ant communities, the degree of specialization among the groups of workers looking after the aphid colonies differed significantly in various species [10]. Complex schemes of interaction have been observed—from nonspecialized forager activity to "professional" specialization with a distinct division of functions, such as honeydew collection and aphid protection. The latter scheme is the most complex, and it was observed only in *Formica* s. str. with a high degree of social organization [4, 5]. The groups of red forest ants looking after the aphids were composed of the working ants that fulfill different functions: "shepherds" (collecting honeydew), "guards" (protecting aphids), "transporters" (transferring honeydew to the nest), and "coordinators" (searching for new colonies and coordinating group activity) [5]. In the aphid colonies associated with these ants, aphidophages were almost absent.

In general, our results suggest that *Formica* s. str., dominating the communities, have the most important influence on symbiont survival and prosperity, because of the high level of their social organization and because of functional differentiation in the groups of working ants that look after the aphids; the remaining ants partially used the results of the mutualistic relationships of *Formica* s. str.

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