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Interaction of Ants with Aphid Enemies: Do Inexperienced Ants Specializing in Honeydew Collection Recognize Aphidophages at Their First Contact?

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Abstract—Honeydew collectors of *Formica pratensis* taken from the nature (control) and laboratory-reared "naïve" ants, which had never met either "mature" workers or aphids and aphidophages, were observed during their interactions with various aphid enemies: adults and larvae of ladybirds and lacewings, and larvae of syrphid flies. The naïve ants were significantly more aggressive towards adults than towards larvae of aphidophages. More than 70% of the naïve ants treated ladybirds and lacewings as enemies at their first encounter and attacked them immediately without any prior antennation. The frequency of aggressive reactions (body jerking and bites) towards larvae was significantly higher in the control group, whereas the percentage of ants showing explorative behavior was significantly higher in the naïve ants. Overall, experience proved to be not important for displaying the key behavioral reactions towards adult ladybirds and lacewings underlying the protection of trophobionts from these natural enemies. However, accumulation of experience is assumed to play an important role in the recognition of aphidophage larvae and formation of aggressive behavior towards them.

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Trophobiont insects play an important role in the life of many ants. Their excreta (the honeydew) are rich in carbohydrates and form one of the main trophic resources for the ant colony (Dlussky, 1967; Delabie, 2001); therefore, protection of the trophobionts from various competitors is a fairly important task for ants. This is especially true of the species whose colonies include tens of thousands and more workers and require great amounts of carbohydrate food (Oliver et al., 2008). The efficiency of protection of trophobionts from their natural enemies varies significantly depending on the ant species (Itioka and Inoue, 1999; Gibernau and Dejean, 2001; Katayama and Suzuki, 2003; Novgorodova and Gavrilyuk, 2012). As a result, different representatives of the multi-species ant assemblage differently affect the survival of their symbionts (Addicott, 1978; Bristow, 1984; Buckley and Gullan, 1991). One of the key aspects of trophobiont protection by ants, and in particular protection of aphids from aphidophages, is recognition of these insects as potentially dangerous objects. The ability to distinguish between members of their own colony and "aliens" (representatives of other species or conspecific individuals from other colonies) forms the basis of the social life of ants (Zakharov, 1978; Hölldobler and Wilson, 1990). It is also known that ants of the genus *Formica* can differentiate their competitors, or at least some of them, from other objects that pose no threat to the ants or their resources. It was experimentally shown that foragers and guards of *Formica aquilonia* Yarr. were much more aggressive towards their topical competitors, the predatory ground beetles (Coleoptera, Carabidae), than towards mixo-phytophages (Dorosheva and Reznikova, 2006).

Honeydew collectors of the ant *Formica aserva* For. actively attacked adult ladybirds but almost completely ignored the non-predatory muscid flies (Phillips and Willis, 2005). However, it remains unknown how the honeydew collectors acquire their behavioral stereotypes underlying the protection of aphids from the natural enemies; in particular, whether the inexperienced honeydew collectors can recognize the aphidophage as an enemy and attack it at the first encounter.

Representatives of the genus *Formica*, living in large colonies (10^4–10^6 ind.) and dominating in multi-species ant associations, provide the most promising object for studying the interactions between ants and aphidophages. Species of this group are characterized by the highest level of "professional" specialization among the honeydew collectors (Reznikova and Novgorodova, 1998a; Novgorodova, 2008) and the highest level of aggression towards aphidophages (Novgorodova and Gavrilyuk, 2012). Due to these traits, they offer their symbionts the most efficient protection from natural enemies (Gavrilyuk and Novgorodova, 2007; Novgorodova and Gavrilyuk, 2012). In addition, the aggressive behavior of the honeydew collectors of these species towards aphidophages is to a greater extent related to protection of symbionts from potential competitors, rather than to simple predation. For example, as compared to ants with a simpler variant of honeydew collection (performed by non-specialized foragers with only partial division of labor), the honeydew collectors of ants of the subgenus *Formica* s. str., acting as obligatory dominants in multi-species ant assemblages, do not switch over to collecting proteinaceous food (Novgorodova, 2005a). They usually drive the aphidophage away or kill it but do not transport the dead or damaged insects into the nest.

In order to find out whether inexperienced honeydew collectors recognize aphidophages at the first contact, I have studied the behavior of the black-backed meadow ant, a dominant species in the meadow and steppe ant communities, during interaction with various enemies of aphids. Analysis of the behavior of inexperienced ("naïve") ants, which have never met either mature conspecific workers or aphids and aphidophages, in comparison with the behavior of honeydew collectors taken from the nature, which can use both their own experience and the experience of other nestmates, would reveal the role of social and individual experience in the formation of the behavioral stereotypes underlying the protection of trophobionts from their natural enemies.

MATERIALS AND METHODS

The behavioral reactions of ants encountering aphidophages were studied during a deprivation experiment with the black-backed meadow ant *Formica pratensis* Retz. in 2009 and 2012. I compared the behavior of honeydew collectors taken from the nature (the control) with that of "naïve" ants reared from pupae, which had no experience of interaction with mature workers, ants, or aphidophages. Two colonies of naïve ants were used in the experiments: one 7–8 weeks old (2009), the other more than one year old (13–15 months; 2012). By the moment of experiments, the naïve colonies counted about 2000 and about 1200 ind., respectively. Each colony also included the queen and brood. It should be noted that under the laboratory conditions, foraging activity in ants of the genus *Formica* starts at an age of about 3–5 weeks (Reznikova and Novgorodova, 1998a). Naïve ants were kept in plastic artificial nests (25 × 15 × 2 cm) placed in arenas (60 × 40 ×20 cm). Carbohydrate food was provided in feeders with sugar syrup; proteinaceous food was given in the form of larvae of the mealworm beetle *Tenebrio molitor* L. and minced boiled eggs.

The experiments were carried out by pairwise presentation tests of ants with aphidophages. In 2009, naïve ants at an age of 7–8 weeks and the control group were tested with five different types of aphidophages: larvae and adults of the ladybirds *Coccinella septempunctata* L. and *Harmonia axyridis* Pall., larvae and adults of the lacewings *Chrysopa perla* L. and *Chrysotropia ciliata* (Wesm.), and larvae of the syrphid *Syrphus ribesii* (L.). Since conspecific adults and larvae of ladybirds and lacewings could not be found in the nature in the needed quantities, the experimental groups of aphidophages were composed of individuals of two species, in the 1 : 1 ratio. During a preliminary study, no significant differences were observed in the behavior of ants with respect to different species of aphidophages in each of the four mixed groups (Fisher's exact test, $p > 0.05$). To eliminate the effect of the larva size on ants' behavior, larvae of only one size group (about 12–14 mm) were used in the experiments.

To determine the possible effect of age on the formation of aggressive reactions in naïve ants, such ants at an age of over one year were additionally tested in 2012 with adults of the ladybird *Harmonia axyridis* and larvae of the syrphid *Syrphus ribesii*.

The aphidophages and "natural" honeydew collectors of *F. pratensis* were collected in the recreational forest zone of Novosibirsk, 2–3 days before the experiments and kept in plastic containers with aphid-infested plants. The aphidophages were collected from various plants, and the ants, from colonies of the aphid *Symydobius oblongus* (Heyd.) on birch trees. Among the naïve ants, only those workers which regularly visited carbohydrate feeders were selected for tests; preliminary studies showed that it was such workers that usually became honeydew collectors.

Experiments on ant–aphidophage pairwise interactions were carried out in plastic containers measuring 14 × 14 × 5 cm in 2009, and in Petri dishes 10 cm in diameter in 2012. After adaptation of the ant in the container or Petri dish during 5–10 min, single aphidophages of the five different types described above (2009) or adult ladybirds and syrphid larvae (2012) were consecutively placed in the container, with intervals of 10–15 min between the tests. Preliminary observations in the nature showed that the outcome of the contact (i.e., whether the aphidophage would be able to attack aphids) was usually determined by the first reaction of the ants to the aphidophage, regardless of its species. Correspondingly, observations were carried out until the first contact of the two insects, but for no longer than 15 min.

The following patterns of ant behavior were recorded: (1) *contact avoidance*: an abrupt change in the direction of movement on approaching the aphidophage; (2) *neutral reaction*: ignoring the aphidophage; (3) *exploratory behavior*: exploration of the aphidophage by the antennae; (4) *aggression poses*: "alert pose," an almost immobile posture with mandibles open and antennae raised and directed towards the aphidophage, and "aggression pose," a pose with abdomen bent, ready to discharge a portion of acid; (5) *body jerking*: quick movements toward the aphidophage with open mandibles, without actual contact; (6) *hit-and-run attacks*: quick movements with open mandibles, ending in contact with the aphidophage; (7) *bites*: bites or series of bites (< 10 s); (8) *death grip*: grasping the aphidophage with mandibles and legs (> 10 s), with bending of the abdomen and spraying the enemy with acid. The ant reactions were split into two groups by the degree of aggression: "non-aggressive" (1–4) and "aggressive" ones (5–8). If the ant demonstrated a spectrum of reactions in rapid succession, the most aggressive reaction was used in the analysis. The following main behavioral tactics of the aphidophages approached or contacted by the ant were recorded: (1) *avoidance*: an abrupt change in the direction of movement; (2) *freezing*: cessation of movements, with appendages retracted or pressed to the body; (3) *active chemical defense*: the use of various compounds for defense against the attacking ants. The behavioral tactics of aphidophages during contacts with different ants, including the different variants of chemical defense, were considered earlier (Novgorodova and Gavrilyuk, 2013). All the insects were tested only once. After every series of tests, the containers and instruments were thoroughly cleaned with alcohol. For species identification, the larvae of aphidophages were reared until the adult stage in separate containers. Altogether, 100 naïve and control ants were tested: 30 ind. in each group in 2009, and 20 ind. in each group in 2012. A total of 150 tests were carried out with each group of ants in 2009, and 40 tests in 2012; 30 and 20 tests were performed with each type of aphidophages, respectively.

The effect of different factors on the behavior of ants towards aphidophages (the ratio of "aggressive" and "non-aggressive" reactions) and the choice of behavioral tactics by aphidophages were analyzed using generalized linear/nonlinear models (GLZ) within the STATISTICA software package.

To reveal the specific behavioral traits of the honeydew collectors taken from nature and the naïve ants, the ratio of "aggressive" and "non-aggressive" reactions to aphidophages was estimated, and occurrence of different variants of reactions (the percentage of individuals showing the given variant) was determined. For aphidophages, the percentage of different tactics upon contact with ants from different groups was estimated. Comparative analysis in all the cases was carried out using Fisher's exact two-tailed test, with the Bonferroni correction in case of multiple comparison of the fractions of aggressive and non-aggressive reactions. Statistical data processing was performed with STATISTICA and Microsoft Excel software packages.

RESULTS

Aphidophages had a significant influence on the behavior of ants (table). Ants were much more aggressive toward adults than to larvae of aphidophages. The ant experience, both by itself and in combination with the type of aphidophage, also significantly affected the ratio of aggressive and non-aggressive reactions during the first contact (table). Comparative analysis of ant behavior showed that the control individuals of *F. pratensis* had a fairly high level of aggression toward aphidophages: they were aggressive to practically all the insects used in the tests. No significant differences in their reactions to different aphidophages were observed (Fisher's exact test with Bonferroni correction, $p > 0.005$), though at the trend level they were less aggressive toward syrphid larvae than toward adult ladybirds ($p = 0.017 > 0.005$, Bonferroni correction) (Fig. 1). The group of naïve workers revealed significant differences in their interaction with adult and larval aphidophages. Naïve ants responded more aggressively to adults than to larvae (Fig. 1).

The influence of different factors on the behavior of ants and aphidophages during contacts

Dependent variable	Distribution	Factors	d.f.	χ^2	*p*
First reaction to aphidophage (“aggressive”/“non-aggressive”)	Binomial	Aphidophage	4	57.20	< 0.001
		Ant experience	1	12.91	< 0.001
		Aphidophage × Ant experience	4	31.69	< 0.001
First reaction to aphidophage by honeydew collectors from nature	Binomial	Aphidophage	1	11.16	< 0.001
		Year	1	0.26	0.061
		Aphidophage × Year	1	0.01	0.938
First reaction to aphidophage by naïve ants	Binomial	Aphidophage	1	63.56	< 0.001
		Ant age	1	0.69	0.405
		Aphidophage × Ant age	1	0.08	0.775
Aphidophage behavior (choice of tactics)	Polynomial	Aphidophage	8	180.31	< 0.001
		Ant experience	2	38.21	< 0.001
		Aphidophage × Ant experience	6	15.94	0.014
		Ant aggressiveness	12	122.97	< 0.001

Comparative analysis of the behavior of naïve ants and honeydew collectors taken from the nature revealed a number of considerable differences. For example, in tests with aphidophage larvae the naïve ants demonstrated aggressive reactions much less frequently than the ants from the control group (Fig. 2). On the contrary, during tests with adult lacewings the naïve ants had aggressive reactions more frequently than the honeydew collectors from the nature. The differences between the two groups of ants were non-significant only in the tests with adult ladybirds (Fig. 2).

A detailed analysis of the frequency of separate behavioral reactions of ants from different groups (Fig. 3) revealed significant differences only in the tests with larvae of aphidophages. The naïve ants much more frequently antennated the larvae, regardless of their taxonomic identity (Fisher’s exact test, $p < 0.0001$). Ants from the nature (control) more frequently showed aggressive reactions: body jerking and bites upon contact with lacewing larvae ($p < 0.05$ and $p < 0.01$, respectively), and bites upon contact with syrphid larvae ($p < 0.01$).

The year of the experiment had no significant influence on the behavior of honeydew collectors from the control groups in the experiments of 2009 and 2012 (table). The behavior of these ants depended only on

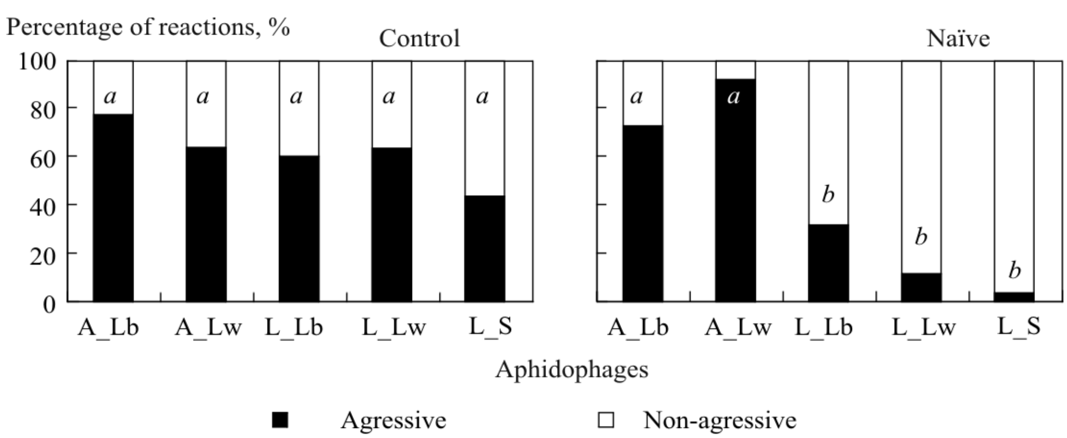

Fig. 1. Ratios of aggressive and non-aggressive reactions in *Formica pratensis* ants from the control and “naïve” groups toward adults and larvae of aphidophages in the experiments on ant–aphidophage pairwise interactions. Aphidophages: A_Lb, adult ladybirds; A_Lw, adult lacewings; L_Lb, larvae of ladybirds; L_Lw, larvae of lacewings; L_S, larvae of syrphid flies. “Aggressive” reactions: body jerking, hit-and-run attacks, bites, and death grip; “non-aggressive” reactions: avoidance, neutral reaction, exploratory activity, and aggression poses. The values marked with *a* and *b* are significantly different (Fisher’s exact test with Bonferroni correction, $p < 0.005$).

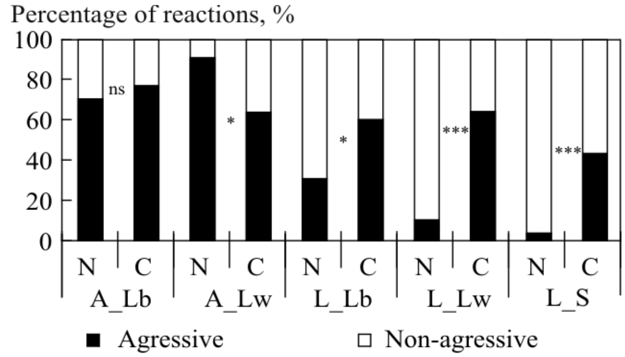

Fig. 2. The difference in the reactions of honeydew collectors taken from the nature (C) and naïve workers (N) of *Formica pratensis* with respect toward adults and larvae of aphidophages. The aphidophages are designated as in Fig. 1. Significance of the differences (Fisher's exact test): * $p < 0.02$; *** $p < 0.001$; ns $p > 0.05$.

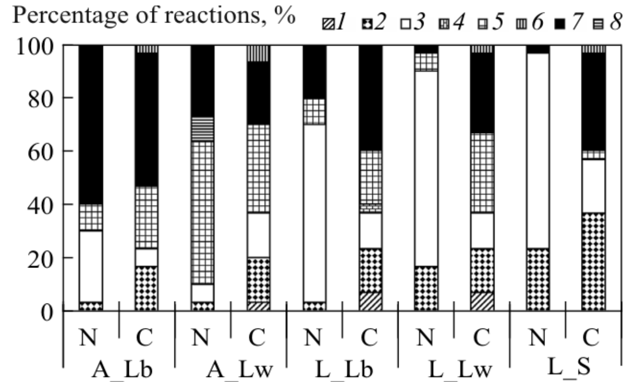

Fig. 3. The occurrence of different reactions of honeydew collectors taken from the nature (C) and naïve workers (N) of *Formica pratensis* with respect to adults and larvae of aphidophages in experiments on ant–aphidophage pairwise interaction. Reactions: (*1*) avoidance of contacts; (*2*) neutral reactions; (*3*) exploratory activity; (*4*) aggression poses; (*5*) body jerking; (*6*) hit-and-run attacks; (*7*) bites; (*8*) death grip. The aphidophages are designated as in Fig. 1.

the type of aphidophage. Analysis of the data for naïve ants of different age variants (7–8 weeks and over one year) showed that the type of aphidophage was the only factor significantly affecting the ant behavior (table). The ants responded much more aggressively to adult ladybirds than to syrphid larvae, the percentage of aggressive reactions being over 70% and about 5%, respectively. The age of worker ants did not affect the ratio of aggressive and non-aggressive reactions in their behavior, both by itself and in combination with the type of aphidophage (table; Fig. 4).

The behavior of aphidophages to a great extent depended on the type of aphidophage, the levels of aggression and experience of the ant, and also on the combination of ant's experience and the type of aphidophage (table). Adult aphidophages more frequently avoided contact with ants, whereas larvae often demonstrated the freezing tactics and active chemical defense. The effect of experience was largely determined by the much more aggressive behavior of the control honeydew collectors towards the larvae of aphidophages (Fig. 2). In response to more aggressive behavior of the ants, the larvae much more frequently used the avoidance tactics. Significant differences were observed between the larvae of ladybirds and lacewings. When interacting with naïve ants these aphidophages more frequently use the freezing tactics, whereas in the tests with honeydew collectors from the nature, the prevalent tactics was that of contact avoidance (Fig. 5).

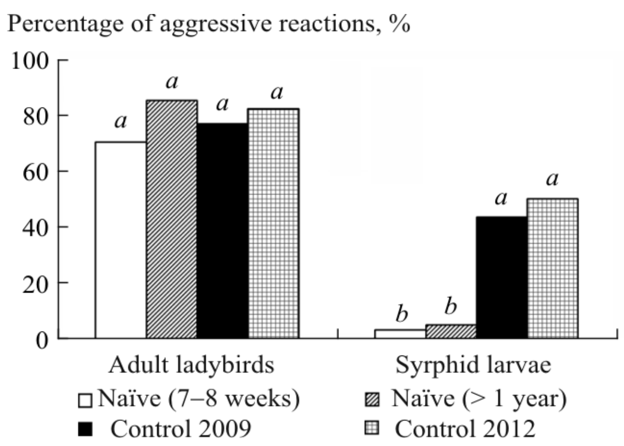

Fig. 4. The percentage of aggressive reactions towards different aphidophages in the behavior of naïve ants of different age (7–8 weeks and more than 1 year) and honeydew collectors of *Formica pratensis* taken from the nature (control). The values (separately for adults and larvae) marked with *a* and *b* are significantly different (Fisher's exact test with Bonferroni correction, $p < 0.008$).

DISCUSSION

It was repeatedly shown in experiments that isolation of colonies of myrmecophilous aphids from the visiting ants led to an abrupt decrease in abundance and even to disappearance of the trophobionts (Karhu, 1998; Shingleton and Foster, 2000; Novgorodova, 2005a), mostly due to the increasing negative influence of aphidophages (Bishop and Bristow, 2003; Tilles and Wood, 1982; Fischer et al., 2001; Nagy et al., 2007). As the result of constant interaction between ants, aphids, and aphidophages the insects have acquired specific behavioral mechanisms aimed at the highest benefit. Myrmecophilous aphids possess a variety of behavioral adaptations for attracting ants (Mordvilko, 1901; Way, 1963; Douglas and Sudd,

1980) while ants improve their skills of collecting honeydew and defending the symbionts from various competitors, including aphidophages (Mordvilko, 1901; Nixon, 1951; Way, 1963; Novgorodova and Reznikova, 1996; Novgorodova, 2008). In their turn, aphidophages actively expand the repertoire of behavioral tactics aimed at avoiding contacts with ants or at reducing their aggression (Rotheray, 1986; Szentkirályi, 2001; Majerus et al., 2007; Novgorodova and Gavrilyuk, 2013). During such close interactions, the insects have to distinguish each other's signals. The efficiency of defense from natural enemies which ants provide for their symbionts largely depends on the ability of honeydew collectors to recognize their competitors and attack them immediately.

It is known that aggressive behavioral reactions are established gradually in the individual development of ants; these reactions have to "mature," rather than improve (Yakovlev, 2010). It was previously shown by laboratory experiments that active foraging in ants of the genus *Formica* started at an age of 3–5 weeks (Reznikova and Novgorodova, 1998a). Some individuals may start visiting aphid colonies even earlier, at an age of 1 week, but formation or "maturation" of aggressive behavior takes a much longer time, from 5 to 8 weeks (Yakovlev, 2010). At an age of 7–11 weeks ants already demonstrate the complete range of aggressive reactions typical of the obligate dominants of the genus *Formica*, and also have the level of aggression comparable to that of the guards (Yakovlev, 2010). In order to reduce the possible effect of age on the behavior of ants in this research, only "mature" individuals at an age of 7 weeks and more were used in the tests. In addition, comparative analysis of behavior of naïve ants at an age of 7–8 weeks and more than 1 year was performed. The naïve ants of different ages were tested in different years; the tests were carried out in containers in 2009 and in Petri dishes in 2012. Therefore, the possible influence of the year of experiment on the behavior of control individuals had to be preliminarily estimated. No differences in the ant behavior were observed between the two years of experiment, therefore the effect of age of naïve ants on their behavior towards aphidophages could be adequately assessed. In this case, the age of naïve ants had no significant influence on the behavior during the first encounter with an aphidophage.

According to the results of laboratory experiments, during interaction with adult ladybirds and lacewings the demonstration of key behavioral reactions of ants underlying the defense of symbionts from their natural enemies did not depend on individual and social experience. More than 70% of naïve ants treated these insects as enemies. Similar to the honeydew collectors from the nature, they attacked the aphidophages immediately on the very first contact, without preliminary exploration. When encountering lacewings, the naïve ants were even more aggressive than the control ones. This fact suggests that ants may have an innate ability to recognize competitors by a certain set of cues triggering the aggressive reaction. Because of this ability, even inexperienced workers respond immediately to the appearance of adult aphidophages in the aphid colonies and drive them away before any harm is done to the aphids. Moreover, as shown by our research, the recognition of adult aphidophages by naïve ants proceeds even faster than the recognition of aphids themselves. In particular, the naïve workers of *Formica polyctena* Foerst. during their first contact with aphids paid no special attention to them until they had tasted their honeydew (Reznikova and Novgorodova, 1998b). It was at that moment that the specific behavioral stereotype of honeydew collectors (striking of aphids with the antennae folded in a particular way, and collection of honeydew droplets at the very moment of excretion) started to be formed. The completion of the stereotype took from 60 to 90 min (Reznikova and Novgorodova, 1998b). In the case of interaction with adult aphidophages, no additional cues were required for the naïve ants to display the complete spectrum of aggressive reactions.

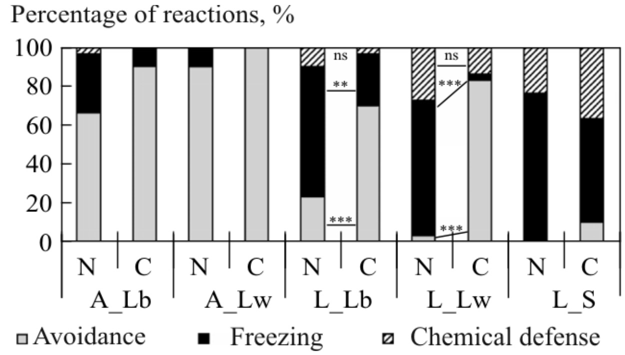

Fig. 5. The behavioral tactics of different aphidophages during contacts with naïve ants (N) and honeydew collectors of *Formica pratensis* taken from the nature (C). The aphidophages are designated as in Fig. 1. Significance of the differences (Fisher's exact test): ** $p < 0.01$; *** $p < 0.001$; ns $p > 0.05$.

The hypothesis postulating the existence of an innate "enemy template" in ants was first tested by observing the artificially arranged conflicts between the ants *Formica aquilonia* and predatory ground beetles (Dorosheva et al., 2011). The cited authors showed that experienced foragers recognized the beetles using a number of visual cues, such as movement, dark coloration, body symmetry, and the presence of appendages (legs and antennae), and that inexperienced (naïve) workers responded most aggressively to the complete "enemy image" (Dorosheva et al., 2011). Our results suggest that such cues may be universal, allowing the ants to recognize various potential competitors including adult aphidophages. Most of the naïve *F. pratensis* ants attacked adult lacewings and ladybirds without delay. A neutral reaction with respect to ladybirds was observed only in the cases when the beetles "clamped down," attaching firmly to the substrate and retracting their legs under the body. Along with contact avoidance, this is one of the commonest behavioral tactics, often employed by ladybirds to avoid ant aggression (Majerus et al., 2007; Novgorodova and Gavrilyuk, 2013). Movements and the presence of appendages seem to be among the most important visual cues facilitating object recognition by ants and responsible for triggering aggressive reactions. In some cases this mechanism may lead to errors, when honeydew collectors of *Formica* s. str. actively attack and drive away not only ladybirds but also various phytophagous beetles (for example, Curculionidae) which happen to be close to the aphid colony. Such situations can be quite often observed in the nature.

By contrast, recognition of the larval aphidophages was much less efficient in naïve ants. On average for three groups, less than 15% of naïve individuals showed aggressive reactions towards the larvae. The smallest fraction of aggressive reactions (3–5%) was observed during interaction of naïve ants with the larvae of *Syrphus ribesii*. The high level of ants' tolerance with respect to syrphid larvae seems to be determined by several factors, first of all by the specific traits of their morphology and behavior. The wormlike larvae of syrphid flies, unlike those of ladybirds and lacewings, lack appendages and eyes and move slowly and with caution. In particular, upon contact with an ant the syrphid larva usually freezes with its body pressed against the substrate, and remains motionless until it is left alone (Novgorodova and Gavrilyuk, 2013). Freezing is one of the behavioral tactics most commonly used by various insects and most efficient for avoiding danger (Hübner, 2000; Majerus et al., 2007; Gromysz-Kałkowska and Unkiewicz-Winiarczyk, 2011). The absence of activity (movement) in an object usually "switches off" the ant's exploratory activity. When studying the behavior of interacting ants and aphidophages, we repeatedly observed an ant abruptly losing interest in an object after it stopped moving (Novgorodova and Gavrilyuk, 2013). This mechanism works well even for adult ladybirds. If the beetle manages to freeze in time, with its body pressed to the substrate and its legs retracted, the ant usually does not attack it at all.

One more possible explanation of ants' tolerance towards syrphid larvae is chemical mimicry or chemical camouflage with specific cuticular carbohydrates, which may be synthesized by the larvae or obtained from aphids passively or actively (Hölldobler and Wilson, 1990; Akino, 2008). It was found that syrphid larvae might indeed use chemical mimicry to avoid ant attacks: the cuticular carbohydrates of *Syrphus ribesii* larvae were quite similar to those of aphids (Lohman et al., 2006). Earlier deprivation experiments showed that during their first contact with aphids, naïve honeydew collectors of *F. polyctena* explored them with straight antennae, as they did with any other unknown object (Reznikova and Novgorodova, 1998b). It may be assumed that ants have an innate ability to distinguish between "enemies" and "friends" using not only visual but also chemical cues. In order to form trophobiotic associations with aphids, which are of vital importance for ants, worker ants should be able to recognize the potential symbionts, or at least to avoid treating them as enemies. Ants may possess a certain innate mechanism blocking their aggression upon encounter with specific olfactory cues. In this case, their tolerance towards syrphid larvae, possessing cuticular carbohydrates similar to those of aphids, may reflect the action of the mechanism protecting the potential symbionts from aggression. This hypothesis, however, requires detailed further research.

On the whole, ants often use chemical cues to differentiate between objects: they easily distinguish "alien" individuals among their nestmates by the composition of cuticular carbohydrates (Lahav et al., 1999; d'Ettorre and Lenoir, 2010), while slaver ants recognize their slaves (Delattre et al., 2013). It is well known that many invertebrates can respond to universal chemical cues related to consumption of animal food, or the "predator scent" (Grostal and Dicke, 1999). It was experimentally shown that *F. aquilonia* workers taken from the nature also relied on olfaction to a considerable extent when recognizing their topical competitors, the ground beetles (Dorosheva et al., 2011). However, it is still unknown whether this ability is innate, and special studies are needed to answer this question.

The differences in the behavior of naïve ants and those taken from the nature were also reflected in the behavior of aphidophages. The choice of tactics by these insects upon contact with ants was largely dependent on the ant's aggressiveness. In response to more aggressive behavior, the larvae much more often used the avoidance tactics. In particular, ladybird and lacewing larvae preferred to avoid contacts with honeydew collectors from the nature, whereas during encounters with the less aggressive naïve ants they more often used the freezing tactics. The effect of the ant's experience on the behavior of aphidophages was mostly determined by the more aggressive behavior of the experienced honeydew collectors.

On the whole, the individual and social experience of the worker ants contacting adult ladybirds and lacewings proved to be of no significance for the manifestation of the key behavioral reactions underlying the defense of symbionts from natural enemies. At the same time, naïve ants do not recognize aphidophages at the larval stage and, as a rule, display no aggression towards them. There are grounds to believe that the presence of social experience and/or accumulation of individual experience play an important role both in recognizing the competitors at the larval stage and in development of aggressive behavior towards the larvae in honeydew collectors. Besides, the individual and social experience may significantly affect the establishment of specific behavioral tactics with respect to aphidophages. However, this hypothesis requires additional research.

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