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Behavior of Red Wood Ants (Hymenoptera, Formicidae) during Interaction with Different Symbiont Partners

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Abstract—A comparative analysis of the behavior of *Formica polyctena* Först during interaction with different symbionts (free-living aphids *Aphis grossulariae* Kalt. and hidden larvae of the sawfly *Blasticotoma filiceti* Klug) was carried out. Red wood ants demonstrate different levels of functional differentiation in relatively constant groups of foragers collecting honeydew. A deep "professional" specialization with clear division of a number of tasks among foragers was studied in groups of ants tending aphids. Four professional groups of foragers with different tasks were revealed: "shepherds," "guards," "transporters," and "scouts" (or "coordinators"). The groups of foragers caring for sawfly larvae mainly consist of unspecialized ants. Only few ants (about 5%) remain on duty on the fern plant near *B. filiceti* larvae and protect the food resource from competitors, especially from other ants. In addition, the ants demonstrate simpler behavior while collecting the larval excretion, resembling that at the sugar feeders. On the whole, the behavior of red wood ants is rather flexible. The level of functional differentiation in groups of foragers collecting honeydew is determined not only by the colony size and requirements but by the nature of their interaction with trophobionts, particularly, by the possibility of direct contact.

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Red wood ants, prevailing in multi-species communities, represent a unique object of ethological studies. They provide one of the most vivid examples of functional differentiation in the colony based on behavioral differences, varying from simple division of workers into functional groups (in-nest workers, hunters, honeydew collectors) to profound "professional" specialization within the groups collecting honeydew (Reznikova and Novgorodova, 1998a; Novgorodova, 2008). Red wood ants can be used to study behavioral patterns of different degrees of complexity, including the situations when coordinated actions are required. One of the most convenient model situations is interaction of ants with various insects producing honeydew (trophobionts).

Trophobiotic relations with various insects are common among ants and very important for them, since the diet of adult ants mostly consists of carbohydrates (Dlussky, 1967; Hölldobler and Wilson, 1990). This is especially true for red wood ants, living in large colonies that may number several millions of individuals (Oliver et al., 2008). These ants collect sugary excretions of the trophobionts and, in turn, actively protect them from various natural enemies, including other ants (Nixon, 1951; Gavrilyuk and Novgorodova, 2007). Trophobiotic relations have so far been observed between ants and representatives of three insect orders: Hemiptera, including both Homoptera (Sternorrhyncha, Auchenorrhyncha) (Nixon, 1951; Delabie, 2001) and Heteroptera (Gibernau and Dejean, 2001; Waldkircher et al., 2004), Lepidoptera (Maschwitz et al., 1987; Pierce et al., 2002), and Hymenoptera (Biryukova et al., 2006; Shcherbakov, 2006). Ants usually interact with free-living trophobionts, forming a symbiosis that involves a number of coadaptations (for reviews, see Mordvilko, 1901; Way, 1963; Dlussky, 1967; Novgorodova, 2004). Aphids (Hemiptera, Sternorrhyncha, Aphididae) represent one of the principal sources of carbohydrate food for ants. However, in the Altai in July–September, the ants actively visit not only aphids but also larvae of the fern sawfly *Blasticotoma filiceti* Klug, 1834 (Hymenoptera, Blasticotomidae) (Biryukova, 2007; Biryukova and Novgorodova, 2008).

Trophobiosis between ants and the larvae of *B. filiceti* is unique in that the sawfly larvae, unlike other trophobionts, remain almost permanently hidden from the ants (Fig. 1). They develop from eggs laid in the rachis of fern fronds (Verzhutskii, 1981; Shcherbakov, 2006). In the course of development, the larva of *B. filiceti* makes a hole in the frond for respiration and excretion. The hole gradually increases in diameter

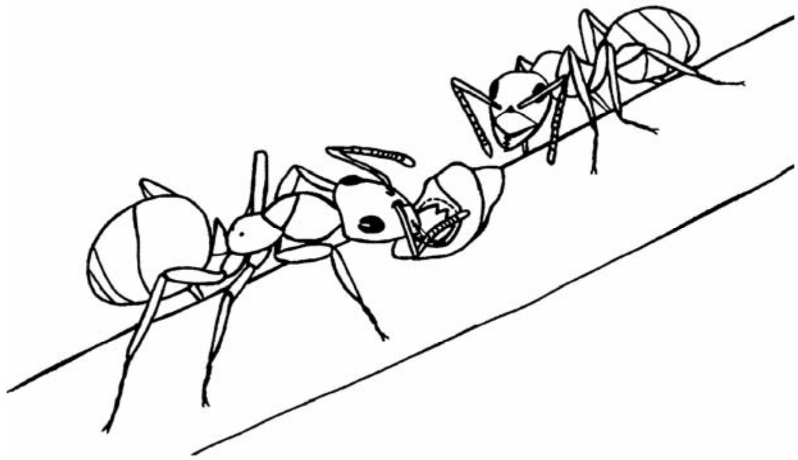

Fig. 1. Red wood ants collecting the excretions of *Blasticotoma filiceti* larvae on a fern frond.

owing to the activity of both the larva and the ants which gnaw at the fern tissues from the outside (Biryukova and Novgorodova, 2008). The larvae appear to feed mostly on the fern sap, since their excretions largely consist of a liquid fraction that attracts various insects, including ants.

Studies of trophobiosis between ants and aphids revealed various schemes of interaction with the trophobionts, from activity of unspecialized foragers to "professional specialization" in groups (Reznikova and Novgorodova, 1998a; Novgorodova, 2004, 2008). Profound functional differentiation was observed only in ants of the group *Formica* s. str. with a high level of social organization, including the red wood ants.

Division of labor in social insects is known to be largely dependent on the colony size (Anderson and McShea, 2001). By the examples of various insects, including wasps (Karsai and Wenzel, 1998) and ants (Thomas and Elgar, 2003; Mailleux et al., 2003) it was shown that large colonies were characterized by the highest level of division of labor. The degree of specialization in the groups of honeydew collectors is also to a considerable extent determined by the size of the colony and its carbohydrate requirements (Novgorodova, 2003, 2007). A question arises in this connection, whether the ants' behavior is strictly determined by these factors, and in particular, whether ants from different colonies will behave differently under the same conditions. In order to answer this question, we performed comparative analysis of behavior of red wood ants during trophobiosis with aphids, living openly in colonies, and with sawfly larvae concealed in fern fronds.

MATERIALS AND METHODS

The work was carried out in fir–pine forests of Northeast Altai, near Artybash (51°48′N, 87°17′E), in July–September 2007–2008. For a detailed study, we selected a colony of *Formica polyctena* Förster, 1850 (nest measurements: d/D = 170/230 cm, h/H = 80/100 cm) with a vast defended foraging territory of about 5000 m^2 and a well-developed network of foraging trails (10 trails from 14 to 65 m long).

In order to reveal trophobiotic relations between ants and other insects, all the plants within the foraging area of the colony were carefully examined. The sawfly larvae were found by previously established attributes, such as morphological changes of the fronds (dark spots, holes), larval excretions, and the presence of ants (Biryukova and Novgorodova, 2008). The number of symbiotic partners simultaneously present on the plant (ants and aphids in aphid colonies, ants and sawfly larvae on fern plants and individual fronds) was recorded. The insects were fixed in 70% alcohol, after which the aphids and ants visiting the trophobionts were identified to species.

The behavior of ants and work organization in groups of honeydew collectors were studied: (*a*) in five colonies of *Aphis grossulariae* Kaltenbach, 1843 located on different branches of the same currant bush, (*b*) on fronds of five ferns *Athyrium filix-femina* (L.) Roth, inhabited by the larvae of *B. filiceti*. The ferns were located 2–8 m apart.

For behavior analysis, we selected 12 elements that could be most easily distinguished and at the same time reflected different aspects of interaction between ants and trophobionts. (1) Honeydew collection: tapping of the trophobionts with antennae folded in a specific way (with the scapus and flagellum positioned at an acute angle and the tips of antennae brought close to the mandibles) and collecting their excretions. (2) Standing still: immobile posture with periodical movements of the antennae from one side to another. (3) Grooming. (4) Trophallaxis: transfer of liquid food from one ant to the other. (5) Antennal contact between two ants. (6) Alert posture: immobile posture with mandibles open and antennae directed towards the stimulant. (7) Aggression posture: posture with abdomen bent, ready to spray a portion of acid. (8) Body jerking and hit-and-run attacks at irritative objects: quick movements towards the irritant with open mandibles. (9) Abrupt runs across the aphid colony or along the fern frond. (10) Exploratory behavior: exploration and repeated exploration of different parts of the host-plant of trophobionts (stem, leaves, fronds, etc.) with almost straight antennae, also when moving onto other aphid colonies or infested fronds on the same food plant. (11) Departure of the ant laden with honeydew from the plant. (12) Return of the ant to the plant with the trophobionts. During comparative analysis of time budgets of honeydew collectors from different "professional" groups, elements 6–9 were grouped together as manifestations of aggressive behavior.

Observations of individual ants that left the plant with a load of honeydew showed that all of them moved to the nest and returned already without their load. Therefore, the time passing between the ant leaving the plant with a load and its returning to the plant was regarded as "transportation costs" in the time budget.

The observations were accompanied by group or individual marking of ants and timing of their behavior. In all, about 1500 ants were marked. Behavior during trophobiosis with aphids was studied in detail for 62 *F. polyctena* ants, and during interaction with sawfly larvae, for 73 ants. The total time of observation was about 340 h: 140 for aphid colonies and 200 for *B. filiceti* larvae. The time of observation of individual aphid colonies or fern plants was 20–40 h.

The aggressiveness of ants was assessed by their response to an artificial stimulant in the form of a preparatory needle brought to the distance of about 1 cm to an initially undisturbed insect. The aggressiveness was estimated using the standard 9-point scale (Novgorodova, 2009).

Statistical data processing was performed using STATISTICA 5.5 and Microsoft Excel 2003 software packages. The similarity between the time budgets of individual ants was determined by hierarchical cluster analysis (total linkage method, with 1 – Pearson r as the similarity metric). The behavior of ants from different groups was compared by calculating Spearman's rank correlation coefficients (r_s) between averaged time budgets of ants from different groups (Urbakh, 1964), and also the duration of individual behavioral elements related to the total time spent on the plant with trophobionts (the means and standard deviation). Comparison of the shares of time spent on the plant with trophobionts by honeydew collectors from different professional groups, and also their aggressiveness was performed using Mann-Whitney test.

RESULTS

Composition and Size of Groups of Honeydew Collectors

Our observations of marked ants showed that individual fern plants with *B. filiceti* larvae, as well as individual aphid colonies were "tended" by relatively constant groups of *F. polyctena* ants. Occasional movements of ants were observed only between aphid colonies located on the same branch less than 50 cm apart, and also between fern plants positioned less than 1 m apart. If an aphid colony disappeared, the ants switched to tending neighboring colonies within the same currant bush. In addition, after the larvae of *B. filiceti* migrated from the fronds into the soil, the honeydew collectors moved onto the neighboring fern plant located 1 m from the original one along the same foraging trail.

The size of the group of honeydew collectors in *F. polyctena* was found to depend on the number of trophobionts: aphids in the colony or *B. filiceti* larvae in the fern fronds. The group of *F. polyctena* foragers on a frond with several sawfly larvae may include up to 20 ants. Calculation of the symbiotic partners simultaneously present in aphid colonies or on fern fronds revealed a significant correlation between the number of the ants *F. polyctena* and the aphids *A. grossulariae* ($r = 0.955$, $n = 45$, $p < 0.01$), and also the ants and the larvae of *B. filiceti* ($r = 0.48$, $n = 353$, $p < 0.01$).

Functional Differentiation in the Groups of Honeydew Collectors

Cluster analysis of time budgets of individual honeydew collectors allowed us to build dendrograms in which the ants with the most similar time budgets

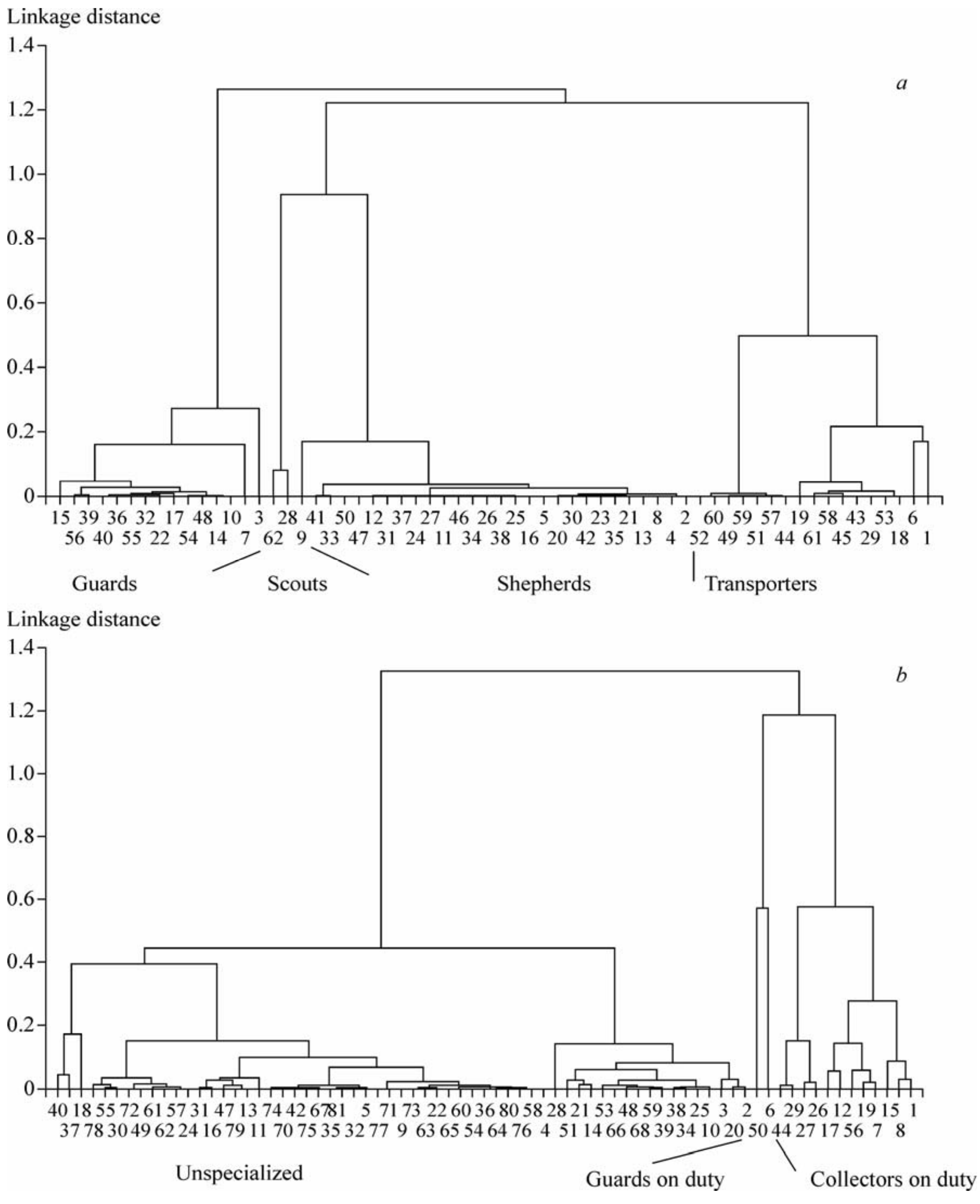

Fig. 2. Similarity dendrograms of workers of *Formica polyctena* Först. collecting honeydew from the aphids *Aphis grossulariae* Kalt. (*a*) and from the larvae of *Blasticotoma filiceti* Klug (*b*). Abscissa: record numbers of foragers.

were grouped together (Fig. 2). Analysis of averaged time budgets of ants from different “professional” groups revealed their principal functions, according to which the groups were named.

Interaction of ants with aphids. The groups of honeydew collectors tending individual aphid colonies consist of four “professional” groups of ants with similar functions: “shepherds,” “guards,” “transporters,” and “scouts” (or “coordinators”) (Fig. 2). The “shepherds” ($X \pm SD$: 31.14 ± 3.00%, $n = 5$) and “guards” (16.75 ± 1.45%, $n = 5$) together comprise about half the group (47.89 ± 3.59%; $n = 5$). Foragers of these groups are almost permanently present on the plant (Fig. 3). The “shepherds” spend about 80% of their

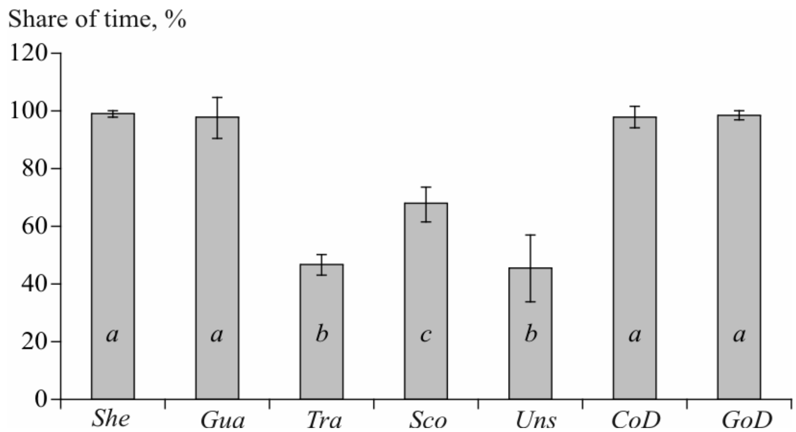

Fig. 3. Fraction of time spent on the plant with trophobionts by different "professional" groups of honeydew collectors. The groups: *She*, shepherds, *Gua*, guards, *Tra*, transporters, *Sco*, scouts, *Uns*, unspecialized foragers, *CoD*, collectors on duty, *GoD*, guards on duty. The difference between the values marked with different letters is statistically significant (Mann-Whitney test, $p < 0.01$).

time spent in the aphid colony collecting honeydew. They continuously stimulate the aphids to excrete honeydew by tapping them with their antennae ("milking") and collect the droplets produced (Fig. 4). The "guards" protect the aphid colonies from competitors. They spend most of the time (about 78%) standing still near the aphids and respond instantly to any irritating factor. Ants of this group show aggressive responses several times more frequently than other individuals tending aphids (Fig. 4). The "transporters," constituting nearly half of the forager group (46.26 ± 4.65%, $n = 5$), deliver the collected honeydew to the nest. Antennal contacts with other ants and trophallaxis make up about 74% of their time in the aphid colony (Fig. 4). The "scouts" ("coordinators") find new aphid colonies and to a certain extent coordinate the activity of foragers in the groups. This group is the smallest (5.85 ± 1.57% of the total group size, $n = 5$); we observed only two individuals performing such functions, each controlling several aphid colonies. Exploratory behavior, i.e., regular repeated examination of a particular part of the plant, make up about 64% of their time on the plant with trophobionts. The ants from the distinguished "professional" groups differ significantly in their average time budgets (table). According to the tests, the "guards" proved to be much more aggressive than ants from other groups (Fig. 5). Not a single individual of *F. polyctena* changed its "profession" during the period of observation.

Interaction of ants with sawfly larvae. As a result of cluster analysis, the ants collecting honeydew from sawfly larvae could be clearly subdivided into three groups: unspecialized foragers, "collectors on duty," and "guards on duty" (Fig. 2). The average time budgets of the ants from these groups were significantly different (table). However, the results of the aggressiveness test showed no significant differences between the groups (Fig. 5).

The unspecialized foragers constitute about 95% of the party ($X \pm SD$: 96.85 ± 3.74%, $n = 5$). These ants move constantly between the infested fern plant and the nest, resembling the "transporters" in this respect. However, unlike the "transporters," each forager collects honeydew and transports it to the nest on its own, with almost no contacts with other ants from this or other groups (Fig. 4). The antennal contacts and trophallaxis made up only about 0.05 and 1.50% of the time spent on the fern frond, respectively. Collecting the excretions of the sawfly larvae accounts for the most of the time (about 76.50%). The time budgets of unspecialized foragers and "transporters" are different (table).

The "collectors on duty" and "guards on duty" together comprise about 5% of the group. These ants are almost permanently present on the fern plant with sawfly larvae, spending significantly more time there as compared to unspecialized foragers (Fig. 3). They seldom leave their posts and usually transfer the collected excretions to unspecialized foragers. The "collectors on duty" spend most of their time on the frond collecting honeydew (35.5%) and exploring the plant (43.4%) (Fig. 4). They make regular rounds, systematically examining all the holes with the larvae.

The "guards on duty" seem to protect the source of carbohydrate food from the possible competitors. The percentage of time of aggressive behavior of these ants

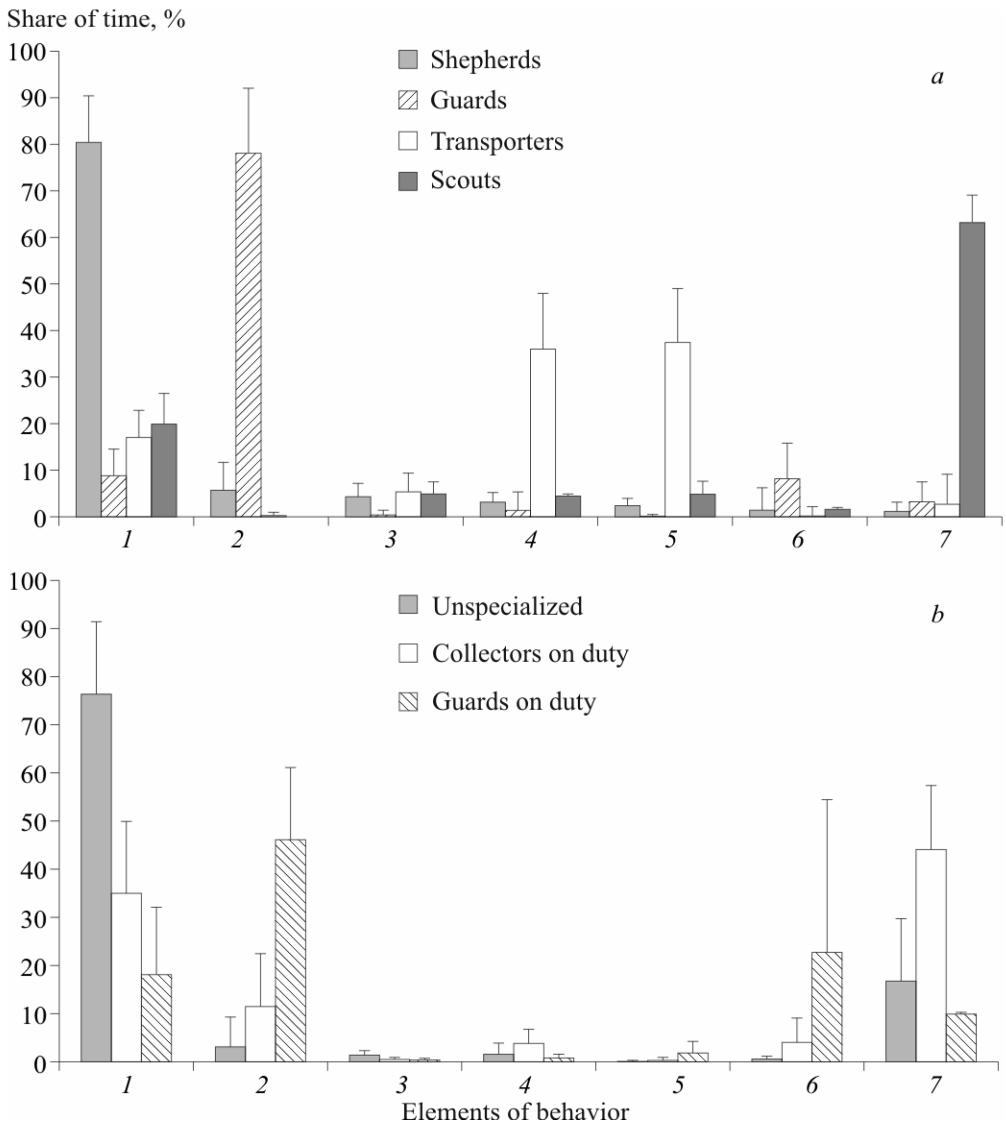

Fig. 4. Fraction of time devoted by ants of different "professions" to different behavioral elements during interaction with aphids (*a*) and sawfly larvae (*b*): honeydew collection (*1*), standing still (*2*), grooming (*3*), trophallaxis (*4*), antennal contact (*5*), aggressive behavior (*6*), and exploratory behavior (*7*).

is several times greater than in other foragers, whereas the share of honeydew collection in their time budget is considerably smaller (Fig. 4). Unlike the representatives of other groups, the "guards on duty" spend most of the time (45.4%) standing still near the sawfly larvae and respond instantly to any external stimulus (movement, wind, other insects, etc.). However, this "professional" group was the smallest, including only 2 ants in our material. The ants with such behavior were observed only on 2 out of the 5 examined fern plants.

The "collectors on duty" and "guards on duty" are almost constantly present on the plant with sawfly larvae and perform functions similar to those of the "shepherds" and "guards" tending aphids. However, only "guards on duty" and "guards" proved to have similar time budgets (table). The difference between the time budgets of "collectors on duty" and "shepherds" seems to be determined by the way of life of the sawfly larvae. The primary reason is that an aphid colony is compact, whereas the tunnels of the sawfly larvae are positioned a certain distance apart (4–25 cm). The "collectors on duty" have to move constantly over the fern frond from one larva to another, checking the openings for honeydew; direct interaction with the larvae and actual "milking" are virtually absent.

Observations of ants on one of the fern plants infested with sawfly larvae (no. 5) were carried out in

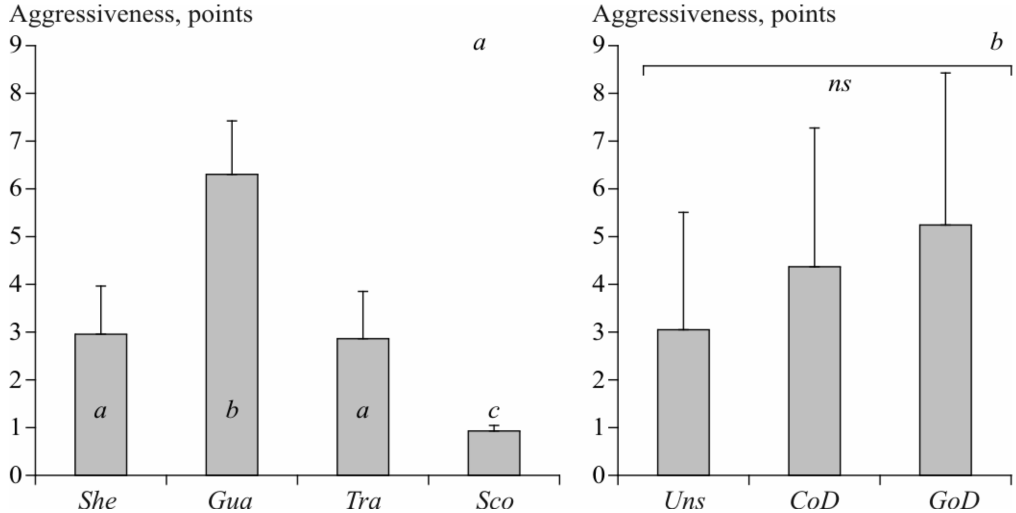

Fig. 5. Aggressiveness of ants from different "professional" groups of honeydew collectors during trophobiosis with aphids (*a*) and sawfly larvae (*b*). The abbreviations are the same as in Fig. 3. The difference between the values marked with different letters is statistically significant (Mann-Whitney test, $p < 0.01$); *ns* means that the pairwise differences are non-significant.

September. The party of honeydew collectors in this case consisted entirely of unspecialized foragers; the "collectors on duty" and "guards on duty" were absent.

DISCUSSION

It is known that behavior of ants, in particular the choice of foraging strategy and division of labor, is closely related to the size of the colony (Anderson and McShea, 2001; Thomas and Elgar, 2003; Mailleux et al., 2003). This relation can be observed at both interspecific and intraspecific levels. As the colony grows, its requirements and the number of tasks to be performed by its members change, affecting in turn the functional differentiation in the colony (Jeanson et al., 2007). In order to understand whether the behavior of ants is flexible or strictly determined by these factors, we have excluded the influence of the colony size and requirements. Our material included one colony of red wood ants, and observations of behavior of ants during their interaction with free-living aphids and hidden larvae of *B. filiceti* were carried out simultaneously.

The organization of work in the relatively constant groups of honeydew collectors was found to depend on the trophobiont; the schemes of interaction of ants with aphids and sawfly larvae are essentially different. In case of interaction with aphids the ants demonstrate deep "professional" specialization with clear division of functions: collection of honeydew ("shepherds"), protection of the symbionts ("guards"), transfer of honeydew to the nest ("transporters"), and also discovery of new aphid colonies and coordination of activities within the team ("scouts" or "coordinators"). Similar data were previously obtained for other representatives of *Formica* s. str. (Reznikova and Novgorodova, 1998a; Novgorodova, 2008).

During trophobiosis with the larvae of *B. filiceti* the ants display a simpler scheme of interaction. The core of the group is formed by unspecialized foragers that

Pairwise comparison of averaged time budgets of ants from different "professional" groups involved in collecting the excretions of aphids (shepherds, guards, scouts, and transporters) and sawfly larvae (unspecialized, collectors on duty, and guards on duty)

Professional groups of ants	r_s
Shepherds vs guards	0.595
Shepherds vs transporters	–0.310
Shepherds vs scouts	0.048
Guards vs transporters	–0.810
Guards vs scouts	–0.048
Transporters vs scouts	0.143
Unspecialized vs collectors on duty	0.523
Unspecialized vs guards on duty	0.071
Collectors on duty vs guards on duty	0.619
Unspecialized vs transporters	0.167
Collectors on duty vs shepherds	0.143
Guards on duty vs guards	0.786*

Note: * The similarity was significant ($r_s > r_{s\,0.05} = 0.72$, $n = 8$).

work on their own with almost no contacts with other ants, moving constantly between the fern plant and the nest. At the same time, some ants (about 5% of the entire group) stay almost permanently on the fronds with the larvae and seem to protect the trophic resource from competitors. These ants can be subdivided into "collectors on duty," which examine the larval tunnels for honeydew, and "guards on duty," which respond most actively to all external stimuli. The presence of a special category of foragers that remain at their "posts" and control the life and exploitation of the trophobionts, and further subdivision of this category into "collectors on duty" and "guards on duty" is likely to represent an initial stage of functional differentiation in the groups of honeydew collectors.

The interaction between ants and trophobionts includes not only organization of activities of foragers (the presence and degree of functional differentiation), but also the very process of obtaining honeydew (the complex of actions required to get the "reward").

Collection of aphid excretions requires considerable effort and specific skills from the ant. The symbiotic partners have acquired a number of morphological and behavioral adaptations to trophobiosis (for reviews, see Hölldobler and Wilson, 1990; Novgorodova, 2004). One of such adaptations is the "milking" of aphids by ants. The ants move from one aphid to another and tap them with their antennae, stimulating the release of honeydew droplets. The aphid demonstrates its readiness to offer honeydew by characteristic movements of its extended hind legs, after which the ant carefully removes the droplet from the preanal setae of the aphid (Way, 1963; Novgorodova, 2002). This process requires certain skills from the ants; "unskilled" individuals may sometimes fail to collect the entire droplet. This was shown by deprivation experiments with "naive" *F. polyctena* ants that encountered aphids for the first time (Reznikova and Novgorodova, 1998b), and also by experiments in which the "shepherds" of *F. polyctena* were removed from aphid colonies, so that the "guards" had to collect honeydew themselves (Reznikova and Novgorodova, 1998a). A considerable loss of honeydew was observed in both cases. The droplets often got stuck to the antennae, mandibles, and clypeus of the ants, requiring long periods of grooming.

During trophobiosis with sawfly larvae there is almost no direct contact between the symbiotic partners, and the process of "milking" is absent as well. This can be explained by the biology of *B. filiceti* larvae, which live in short tunnels inside the frond rachis and remove their excretions through small holes (Verzhutskii, 1981; Shcherbakov, 2006). The honeydew of *B. filiceti* is usually collected by the ants at the moment of excretion. When the liquid appears in the tunnel, the ants gather around the hole and fill their crops. While waiting for the next excretion, the ants regularly examine the holes and scrape away the remains of sugary liquid around them. Actual interaction between the symbiotic partners takes place only after the larvae leave their tunnels on their way into the soil (Biryukova and Novgorodova, 2008). In this case the ants show the behavior resembling "milking" of aphids: the foragers tap the larva with their antennae folded in a specific way (the scapus and flagellum are positioned at an acute angle, so that the tips of antennae are brought close to the mandibles). However, since the larvae produce practically no honeydew in this period, the ants remove the remains of the sugary liquid from their bodies, rather than stimulate them to release new droplets. In general, when collecting honeydew from sawfly larvae that are hidden from direct contact, the ants show a simpler pattern of behavior, similar to that observed at carbohydrate feeders.

The extent of "professional" specialization in the teams of honeydew collectors appears to be closely related to the way of life of the trophobionts. The possibility of direct contact with aphids allows the ants to modify the quantity of honeydew collected. In particular, the ants actively stimulate the aphids to release more honeydew (Nixon, 1951; Way, 1963; Takeda et al., 1982). In addition, to avoid scraping the dry honeydew off the plant, the droplets should be collected at the moment of excretion. Therefore, the constant and abundant trophic resource requires not only protection but also training of "shepherds," specialized in "milking" aphids and collecting honeydew, and "transporters" that bring the honeydew to the nest. In case of interaction with *B. filiceti* larvae, the amount of excretions does not depend on the collectors' activity since there is virtually no contact between the symbionts. However, the larvae of *B. filiceti*, like aphids, represent a relatively stable and easily accessible source of carbohydrates that attracts various insects, including ants, wasps, and flies. Therefore the ants have to protect their resources from competitors, which leads to some foragers staying "on duty" on the fern fronds. Generally speaking, interaction with aphids sets more tasks than trophobiosis with *B. filiceti* larvae, leading to more extensive "professional" specialization in the foraging teams tending aphids. This conclusion agrees with the data of Jeanson and co-authors (2007), who showed that the number of tasks positively affected the division of labor between individuals.

It was previously shown that the degree of functional differentiation in groups of honeydew collectors depended on the carbohydrate requirements of the ant colony (Novgorodova, 2007). Deficiency of carbohydrates in the colony of *F. cunicularia glauca* Ruzs., resulting from either general trophic deficiency or colony growth, leads to considerable changes in the organization of honeydew collectors' activities, related to functional differentiation (Novgorodova, 2003). Division of tasks of honeydew collection and protection of the trophobionts occurs in the groups of unspecialized honeydew collectors. Some ants remain "on duty" in aphid colonies and actively protect them from any external influence. On the contrary, reduced carbohydrate requirements of the colony in autumn may result in the foragers' activity becoming less complex. For example, the group of foragers tending sawfly larvae in September included only unspecialized ants, with no individual remaining "on duty." The red wood ant groups tending aphids in autumn are also characterized by a smaller number of "professional" groups, namely the absence of "guards" and "scouts" (Novgorodova, 2008).

Thus, red wood ants with a high level of social organization have a rather flexible behavior. The organization of activity of their foragers, in particular honeydew collectors, can change quickly under the influence of various factors. The degree of functional differentiation in parties of honeydew collectors is determined not only by the colony size and its carbohydrate requirements, but also by the nature of their relations with the trophobionts, in particular the possibility of direct contact with them.

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