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Experimental Investigation of Information Transmission in *Formica pratensis* (Hymenoptera, Formicidae) Using "Binary Tree" Maze

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Abstract—Organization of foraging and information transmission in the ant *Formica pratensis* were studied using the "binary tree" maze. The ants were shown to use distant homing. They were able to memorize and transmit up to four bits of information. The foraging mode was shown to depend on the colony size: an increase in the number of ants was accompanied by switching from solitary to group foraging. A relay mode of information transfer (an ant relays the information to several others, etc.) was revealed. The organization of work and information flows in the colonies of *Formica polyctena* and *F. pratensis* were found to be essentially different. The communicative systems in dominant ant species are variable and species-specific.

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The efficient organization of group activity and the information processes underlying it are among the most interesting and still poorly known aspects of the biology of social insects. Despite much effort, no clear concept of the informational basis of the functional structure of the colony of eusocial insects, and in particular ants, has been developed.

Ants are known to possess various means of communication, which can be switched at the colony level depending on the foraging conditions (Dlusskii *et al.*, 1978). The existence of distant homing in foraging ants, however, had long remained unconfirmed. The problem was solved by experiments in which the ants had to transmit a given amount of information concerning the way to food, which corresponded (in bits) to the number of turns in the "binary tree" maze. It was shown that red wood ants possessed a distant homing system, which was more complicated than the well-known "dance language" of honeybees (Lindauer, 1961; Frisch, 1965). Using the "binary tree" method, researchers were able for the first time to determine the rate of information transfer in ants (about 1 bit/min) and to reveal their ability of efficient "data compression" (Reznikova and Ryabko, 1986, 1990, 1994; Ryabko and Reznikova, 1996). In addition, the "binary tree" proved to be a convenient tool for studying the structural organization of the colony and the foraging activity of ants. In particular, it was found that the scouts shared information on the discovered food only with their own stable group of foragers.

The organization of activity of trophobionts collecting honeydew in the tree crowns was studied as a field model of the situation when ant workers act collectively to perform a specific task (Novgorodova and Reznikova, 1996). In this case, the task consisted in finding the aphid colony, informing other ants on the new food source, and organizing the honeydew collection and transportation.

Comparative studies of the ant behavior during trophobiosis have shown that the activity of trophobionts in the groups working in aphid colonies varies significantly between different ant species. The most complex variant of interaction with aphids, namely "professional specialization," is typical only of the dominant species with a high level of social organization (*Formica polyctena* Foerst. and *F. aquilonia* Yarr. in forest communities, and *F. pratensis* Retz. in steppe associations). Other members of the community use simpler schemes of interaction with aphids, which are based either on the activity of non-specialized trophobionts, or on partial segregation of duties in the groups (Novgorodova and Reznikova, 1996; Reznikova and Novgorodova, 1998a, 1998b). The work groups of red wood ants comprise individuals performing different tasks: the "milkers" collect honeydew droplets, the "guards" protect the aphid colony, the "transit work-

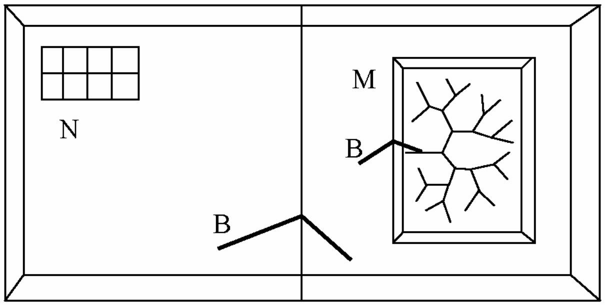

Fig. 1. Schematic view of the experimental area with the nest (N), the "binary tree" maze with four bifurcations (M), and the bridges (B) connecting different parts of the area.

ers" transport honeydew to the nest, and the "coordinators" ("scouts") look for new colonies (Reznikova and Novgorodova, 1998a, 1998b). Segregation allows the ants to protect their symbionts more effectively, increasing their survival rate (Novgorodova, 2000, 2005). By contrast, in *F. pratensis* we were able to distinguish between only two professional groups: "milkers" and "guards." These ants transport honeydew as well, since there are no specialized "transit workers." The functions of "coordinators" are performed by the "guards," whose behavior is characteristically multifunctional (Novgorodova, 2002). These findings suggest that the structural organization of the colony and the ways of information transfer may also vary between different ant species.

The purpose of this work was to study the communication system (the process of information transfer and distribution) in *F. pratensis*, and to perform comparative analysis of the organization of foraging in *F. pratensis* and *F. polyctena*.

MATERIALS AND METHODS

The study was performed under laboratory conditions in June–August 2003.

Owing to a number of specific ecological and ethological features, the ant *Formica pratensis* Retz. represents a promising object for studying the specific aspects of information systems and their analysis in comparison with the previously obtained data for the red wood ants. In particular, various foraging strategies have been described for *F. pratensis*. The principal method of communication is via the scent trail. In medium-sized monocalic monogynous colonies, the scouts usually mobilize passive foragers from the roads subdivided into zones. As the colony grows, the foraging strategy becomes more similar to that of the red wood ants (Reznikova, 1979).

Maintenance conditions and experiment design. The experiment was performed using the "binary tree" method (Reznikova and Ryabko, 1986, 1990). A colony of *F. pratensis* (about 1500 individuals with the queen and brood) was placed in an experimental area of 180×60 cm and kept in a transparent plastic nest (20×12 cm), which allowed the contacts between ants to be observed. Later, the colony size was increased to 2500–3000 individuals by adding working ants (about 1500) and cocoons (about 400) taken from the same initial nest. Carbohydrate food (sugar syrup) was provided every third day.

After an adaptation period of two weeks, the area was divided into two parts: the living part containing the nest (Fig. 1N) and the experimental part in which a plastic "binary tree" maze (Fig. 1M) was installed. The maze had four bifurcations and, correspondingly, 16 end branches. During the seven-day preparation period, sugar syrup was given to the ants every other day and only in the maze. Identical feeders were located in each of the 16 branches; one feeder was filled with sugar syrup, and the rest, with water. The position of the food was changed constantly. Every ant which appeared in the experimental part was marked with nitrodope (in all, 457 individuals). This allowed us to reveal potential scouts (those ants which found the exit from the maze on their own, interacted with other ants in the area, and returned to the food).

The task. In order to obtain food, the ants had to transfer a certain amount of information, i.e., the sequence of turns on the way to the feeder. The number of bits of information which must be transferred to other individuals equals the number of turns. Therefore, if the feeder is located in one of the 16 branches of a maze with four bifurcations, the ant must transfer 4 bits of information. The sequence of turns was selected randomly (by the coin toss).

Sequence of actions. The potential scouts were placed individually on the feeder containing sugar syrup, after which they were allowed to find the way out of the maze on their own. While the scout was on the feeder, the bridge connecting the experimental area with the maze was removed so as to prevent other individuals from getting into the maze.

In the experimental area, the scouts contacted other ants, some of which were later able to find the way to the feeder. To exclude the possibility of ants using scent trail, the maze was always replaced by an identical copy in the absence of the scout; for this purpose, several interchangeable mazes of the same design were prepared. After the scout left the feeder with sugar syrup, it was replaced by an identical feeder with water, to exclude the possible influence on the food scent. The ants which appeared in the correct branch got their reward as the syrup feeder was placed back in.

Fifteen trials were made with ant colonies of each size category. In all, 22 potential scouts were tested in the colonies with 800–1500 individuals, and 47 scouts, in the colonies with 2500–3000 individuals. Of these, 3 and 5 ants did not return to the maze, respectively.

Parameters recorded. All the contacts made by the scout after visiting the maze were recorded. The time required to find the correct feeder (from the moment of entering the maze), as well as the duration of the information contact with the scout was determined using a stop watch. For the purpose of this study, all antennal contacts between the scout and other individuals, including the trophallactic interactions, were regarded as information contacts.

In the cases when, after a contact with the scout, not a single ant appeared at the feeder, the position of the feeder was not changed so as to allow the scout to make several trips. Every time, the scout's errors in finding the feeder and the duration of contacts with other individuals were recorded. Data for the last contacts that resulted in the foragers entering the maze were used in the subsequent calculations.

Food seeking by "informed" and "uninformed" ants. In order to make sure that it is during the antennal contact with the scout that the ants obtain the information needed to find food, the following experiment was carried out. The potentially "informed" ants (after a contact with the scout) and "uninformed" ones were placed at the beginning of the binary maze, and the time required for finding the feeder was recorded. The "uninformed" individuals had previously visited the maze and were therefore "familiar" with its structure and the task at hand. The ants were observed during 30 minutes; if no attempts at finding the feeder were recorded within this period, the result was discarded. The results were compared using a nonparametric Wilcoxon test.

RESULTS

The use of the "binary tree" maze allowed us to study in detail the distant homing process which had previously been unknown for the species in question. Information sharing and the organization of foraging in *F. pratensis* depend on the colony size. We have considered colonies differing in this parameter.

Experiments with the Colony Comprising about 800–1500 Individuals

Nearly all the ants stay in the nest; only 6–8 individuals watch the open area, usually keeping to the corners of the living territory (1 or 2 ants in each).

Distant homing. During 20 days (15 trials), 22 potential scouts were placed on the feeder; 3 of them did not return to the maze. Five individuals had difficulties finding the feeder on their way from the nest and made up to 8 errors in the process (on the average 5.8 ± 1.48, $n = 5$). They did not attract other ants and could hardly learn to find the feeder again if it was relocated during the trial, but instead returned each time to its initial position. The remaining 14 individuals worked actively in the maze. They memorized the way to the feeder from the first time and found it without errors. Moreover, they re-learned much more easily when the way was changed during the trial. During their first independent trip to the feeder, they made no more than two errors (on the average 0.7 ± 0.63, $n = 23$), and made no errors at all afterwards (Fig. 2). These individuals were regarded as potential scouts.

As a result of each trial, up to two ants visited the feeder on their own (i.e., without the scout). On the whole, the time required for finding the feeder was 15.7 ± 5.65 seconds ($n = 47$). In 29 cases out of 47 both the duration of contact with the scout and the duration of food seeking was recorded. The average values were 33.1 ± 14.79 and 16.44 ± 5.53 ($n = 29$) seconds, respectively (Fig. 3). Correlation between these parameters was non-significant.

In 18 cases out of 47, information contact was not recorded; however, we can state with certainty that these contacts were not primary ones (i.e., they were not made directly with the scout). This fact suggests that information is not distorted in the sequence of transfer events.

Information distribution pattern. The scouts went to the nest immediately after visiting the feeder. The number of contacts observed in the experimental area was 1–2 (0.86 ± 0.68, $n = 42$), and in the nest, 6–12 (7.76 ± 2.08, $n = 42$). The group of ants contacting with the scout in the nest was relatively constant. Six individuals almost always interacted with the re-

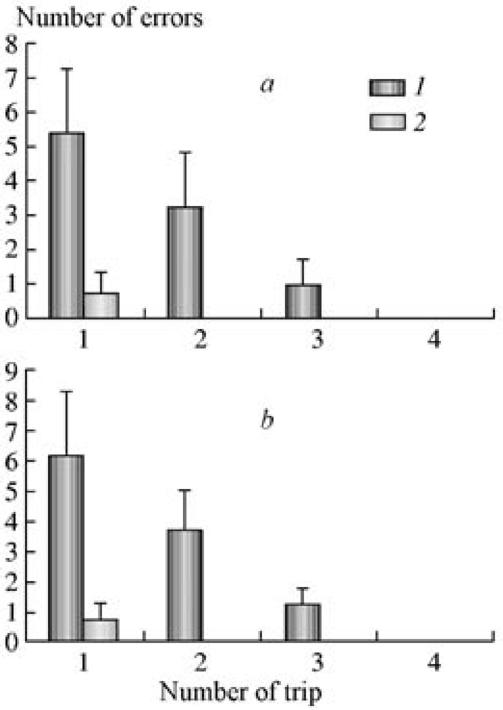

Fig. 2. Number of errors made by the foragers (*1*) and the scouts (*2*) after the food source was relocated during the trial. Colonies with 800–1500 individuals (*n* = 5 and 23, respectively) (*a*) and 2500–3000 individuals (*n* = 7 and 35, respectively) (*b*).

turning scouts (97.62 ± 3.01%), after which they made active contacts with other ants, transferring food and information. Two ants of this group immediately after contacts with the scout went to the open area and visited all the ants watching the living territory. Contacts with the remaining six individuals appeared to be random (14.68 ± 6.97%). The scouts visited the feeder up to five times an hour. Foraging was solitary (see Fig. 5). The number of ants working in the maze simultaneously never exceeded three.

Experiments with the Colony Comprising about 2500–3000 Individuals

The feeding territory is clearly subdivided into zones "patrolled" by constant groups of ants (4–9 individuals in each zone). A total of eight such groups were recorded, positioned in the corners and near the bridge leading to the maze.

Distant homing. During 30 days (15 trials), 47 ants were placed on the feeder. Five of them did not return to the maze, and not all of the remaining individuals memorized the right way at the first attempt. Some ants (7 individuals) were able to find the feeder without error and transfer the information to other ants only after 2–3 trips (Fig. 2). The remaining 35 ants remembered the sequence of turns during their first trip to the nest. Before leaving the maze, these ants made 2–4 runs along the binary tree segment, i.e., from the feeder to the bridge connecting the maze with the experimental area.

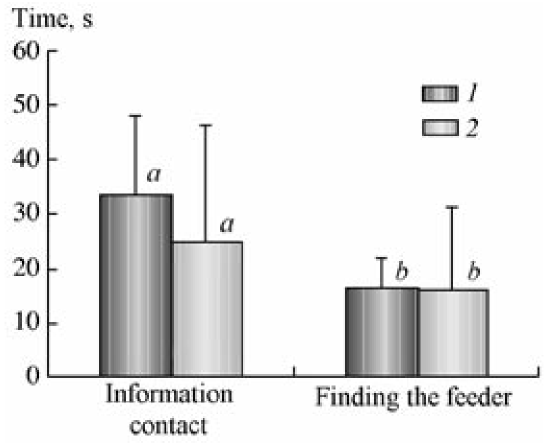

Fig. 3. Duration of information contacts and the time required for finding the feeder in the "binary tree" maze by *F. pratensis* ants from colonies with 800–1500 individuals (*n* = 29) (*1*) and 2500–3000 individuals (*n* = 76) (*2*). The pairs of values marked with *a* and *b* are significantly different (Wilcoxon test, $p < 0.05$).

The duration of information contacts and the time required for finding the feeder differed non-significantly from the values obtained for smaller colonies (Fig. 3). After an information contact (duration, 24.81 ± 21.30 s) with the scout, it takes on the average 16.09 ± 15.1 s for the forager to locate the feeder with sugar syrup ($n = 76$). The correlation between the time taken by the contact and the time required for finding the feeder in the maze is non-significant ($r = -0.1375$, $n = 76$).

Comparison of "informed" and "uninformed" ants showed that the former spent considerably less time finding the feeder, regardless of its position (Fig. 4). This confirms the hypothesis that the most probable channel of information transfer is the "antennal code" (Wassmann, 1899).

Information distribution pattern. After visiting the feeder with sugar syrup, the scout leaves the maze and moves into the experimental area, where it participates in primary contacts with individuals from different groups. After this, information is relayed from one forager to another in the sequence of secondary, tertiary etc. contacts (Fig. 5). Since every ant usually interacts with several individuals, the information is spread rather quickly among the colony members. The scout usually makes from 1 to 7 contacts before returning to the maze (3.16 ± 1.68, $n = 31$). The greatest number of interactions was recorded right near the bridge leading to the maze (2.19 ± 0.83, $n = 31$). The ants located in this part of the experimental area appear to act as “messengers.” In other words, they serve as a link responsible for relaying information from the scout to the groups of passive foragers located both in the open area and in the nest. Unlike the passive foragers, these ants make contacts with individuals from different groups “patrolling” the area before going to the maze. Only 4 out of 35 scouts returned directly to the nest; in other cases, it was the “messenger” that ran there.

Observations of the contacts made by the “messengers” showed that only 32 out of 117 ants (27.4%) left their positions after such contacts and went to the maze. Of these, 26 individuals (81.3%) made no errors. This confirms our assumption that the relayed information is not distorted.

Thus, we have shown that *F. pratensis* are capable of transferring information on the location of food in a “binary tree” maze with 4 bifurcations by distant homing. This information is spread by relaying.

DISCUSSION

Functioning of the colony of social insects as a coordinated whole largely depends on the organization of the group activity, which is based on the processes of communication. Different communication systems can be used to attract ant foragers to the food source: kinopsis (response to the scout’s excited movements), acoustic signals, scent trail, tandems, and antennal code (Wilson, 1971; Reznikova, 1975, 1982, 1983; Zabelin, 1979; Hölldobler and Wilson, 1990). Experiments with a “binary tree” maze revealed the fact of information transfer by distant homing. The results of comparative studies indicate that this variant is likely to occur in a small number of species characterized by a high level of social organization, in particular, the red wood ant (Reznikova and Ryabko, 1990, 1995, 1999, 2003). The flexible communicative systems allow some ant species to use different foraging systems, depending on the colony size, as well as the nature and quantity of trophic resources (Zakharov, 1972; Reznikova, 1983; Dlusskii, 1984). The amount of data concerning this ability is growing. For example, it was found that, depending on the available quantity of carbohydrate food, *Paraponera clavata* Fabr. (Ponerinae) and *Polyrhachis laboriosa* F. (Formicinae) could switch from individual foraging to mass recruitment of workers (Fewell *et al.*, 1992; Mercier and Lenoir, 1999). In *Formica cunicularia glauca* Ruzs., coordination of trophobiont activity may change according to the needs of the colony, from solitary activity of individual insects to professional specialization in small groups tending separate aphid colonies (Novgorodova, 2003).

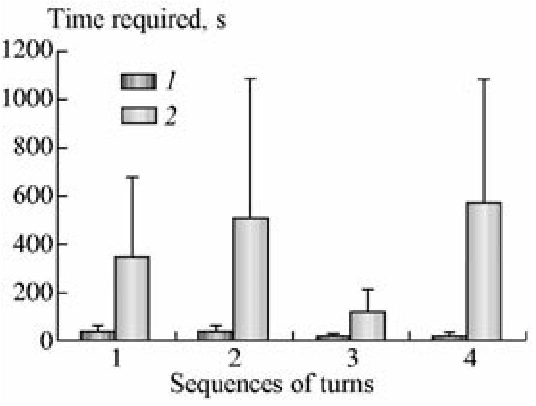

Fig. 4. Time required for finding the feeder in the “binary tree” maze with 4 bifurcations, by “informed” ants (after a contact with the scout) (*1*) and “uninformed” ones (having no contact with the scout) (*2*). The following sequences of left (L) and right (R) turns on the way to the feeder were tested: RRRR (*1*, $n = 9$), LLLL (*2*, $n = 8$), LRRL (*3*, $n = 7$), and RLLR (*4*, $n = 7$). The values in pairs are significantly different (Wilcoxon test, $p < 0.05$).

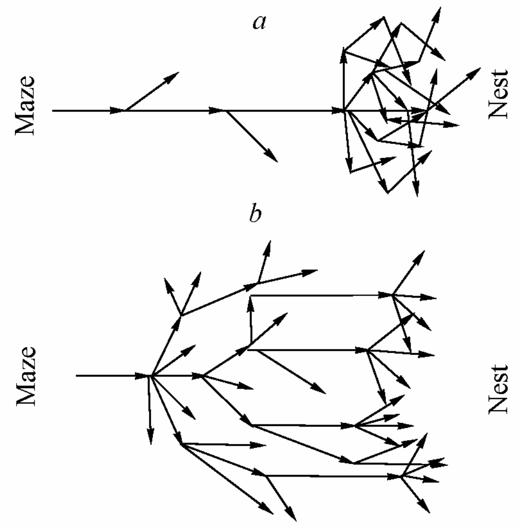

Fig. 5. Diagrams of information transfer by *F. pratensis* ants in the colonies with 800–1500 individuals (*a*) and 2500–3000 individuals (*b*). Arrows show the succession and directions of movements.

The level of structural and informational organization of an ant colony is closely related to its size. For some species of the genus *Formica* it was experimentally shown that increase in the colony size resulted in establishment of a higher level of the spatial and ethological population structure. For example, *F. cunicu-*

laria glauca and *Formica picea* Nyl. start to guard their feeding areas and to implement secondary subdivision of the territory. The ants *F. pratensis* switch from monocalic colonies with a specific system of forager recruitment from the segmented pathways, to polycalic settlements and colonies, their recruitment and territorial behavior changing completely in the process (Reznikova, 1979, 1999).

Our laboratory experiments showed the modes of foraging in *F. pratensis* to be related to the colony size. Increasing the number of ants allowed us to observe switching from solitary to group foraging. Moreover, the information distribution pattern and the mode of recruitment of foragers were found to be significantly different from the variants previously described for the red wood ant (Reznikova and Ryabko, 1990). In the latter species, information about the location of food is transferred in a strictly linear pattern (from the scout to the members of its “team”); whereas in *F. pratensis* the information is relaid (each ant contacts several individuals, which, in their turn, also relay information to several ants, and so on). The specialized group of messengers, working as intermediates between the scout and the passive foragers patrolling specific zones of the feeding area, quickly spreads the information over the entire colony and allows recruitment of the ants to the food source.

The relay pattern is widely used by social insects, including ants, for transporting proteinaceous and carbohydrate food, building materials, leaves etc. (review: Ratnieks and Anderson, 1999; Hart and Ratnieks, 2001). In some cases this pattern becomes evident only in large colonies; this was observed in the wasps *Vespula* (Jeanne, 1986) and some ants (Schatz *et al*., 1996). In our study, not only the transport of liquid food but also the transfer of information about the location of food in the maze was observed.

As concerns the information transfer rate, our data cannot be compared with those obtained for the red wood ant, because they depend on the experiment design, the pattern of information transfer in a particular species, and the choice of parameters observed. For example, the information transfer rate in the red wood ant was found to be about 1 bits/min (Reznikova and Ryabko, 1990). In *F. pratensis*, foragers were able to find the feeder in a maze with 4 bifurcations even after a short (8 s) contact with the scout. However, previous experiments (Reznikova and Ryabko, 1990, 1995) showed that after finding the food source, the scout mobilized all members of its team (6–8 individuals) which moved to the maze simultaneously. Because of this, the duration of an information contact was measured from the first touch of the scout to the moment when the first two foragers left the nest. In *F. pratensis*, each forager moves to the maze separately after a contact with the scout or the messenger. Because of the relay mode of information transfer, we determined the length of an information contact as the total duration of all antennal interactions with an “informed” ant.

To summarize, the “binary tree” method allowed us to reveal the distant homing process which was previously unknown for *F. pratensis*. As the colony grows, the solitary mode of foraging is replaced by group foraging. The relay mode of information transfer facilitates rapid dissemination of information and efficient recruitment of foragers to priority tasks. The considerable differences observed in the work coordination and the information flows in the colonies of *F. polyctena* and *F. pratensis* indicate that communication systems in the dominant ant species are variable and species-specific.

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REFERENCES

1. Dlusskii, G.M., “Family Organization in Social Insects,” in *Behavior of Insects* (Nauka, Moscow, 1984), pp. 3–25 [in Russian].
2. Dlusskii, G.M., Vol'tsit, O.V., and Sulkhanov, A.V., “Group Foraging in Ants of the Genus *Myrmica*,” Zool. Zh. **57** (1), 65–77 (1978).
3. Fewell, J.H., Harrison, J.F., Stiller, T.M., and Breed, M.D., “Distance Effects on Resource Profitability and Recruitment in the Giant Tropical Ant, *Paraponera clavata*,” Oecologia **92**, 542–547 (1992).
4. Frisch, K., *Tanzsprache und Orientierung der Bienen* (Springer-Verlag, Berlin etc., 1965).
5. Hart, A.G. and Ratnieks, F.L.W., “Why Do Honey-Bee (*Apis mellifera*) Foragers Transfer Nectar to Several Receivers? Information Improvement through Multiple

Sampling in a Biological System," Behav. Ecol. Sociobiol. **49**, 244–250 (2001).

6. Hölldobler, B. and Wilson, E.O., *The Ants* (The Belknap Press of Harvard Univ. Press, 1990).
7. Jeanne, R.L., "The Organization of Work in *Polybia occidentalis*: the Costs and Benefits of Specialization in a Social Wasp," Behav. Ecol. Sociobiol. **19**, 333–341 (1986).
8. Lindauer, M., *Communication among Social Bees* (Harvard Univ. Press., Cambridge, 1961).
9. Mercier, J.L. and Lenoir, A., "Individual Flexibility and Choice of Foraging Strategy in *Polyrhachis laboriosa* F. Smith (Hymenoptera, Formicidae)," Insec. Soc. **46**, 267–272 (1999).
10. Novgorodova, T.A., "Ants Impact on Species Diversity of Aphids," in *Proceedings of 1st International Conference "Biodiversity and Dynamics of Ecosystems in Northern Eurasia," Novosibirsk, Russia* (2000), Vol. 3, No. 2, pp. 264–267.
11. Novgorodova, T.A., "The Study of Behavior of the Ants *Formica pratensis* (Hymenoptera, Formicidae) in Aphid Colonies during Honeydew Collecting," in *Proceedings of XII Congress of the Russian Entomol. Society* (St. Petersburg, 2002), pp. 259–260.
12. Novgorodova, T.A., "Intraspecific Diversity of Behavioral Models in the Ants *Formica cunicularia glauca* during Trophobiosis," Uspekhi Sovrem. Biol. **123** (3), 229–233 (2003).
13. Novgorodova, T.A., "Relative Contribution of Members of a Multispecific Association of Ants in the Population Potentials of Shared Aphid Symbionts," Doklady Ross. Akad. Nauk **401** (6), 848–849 (2005).
14. Novgorodova, T.A. and Reznikova, Zh.I., "Ecological Aspects of Aphid and Ant Interaction in the Recreational Forest Zone of Akademgorodok (Novosibirsk)," Sibir. Ekol. Zh., Nos. 3–4, 239–245 (1996).
15. Ratnieks, F.L.W. and Anderson, C., "Task Partitioning in Insect Societies," Insectes Soc. **46**, 95–108 (1999).
16. Reznikova, Zh.I., "Recruitment and Interaction in Ants of the Dominant and Subdominant Species," in *Proceedings of V All-Russia Symposium "Ants and Forest Protection"* (Moscow, 1975), pp. 160–166.
17. Reznikova, Zh.I., "Forms of Territorial Organization in *Formica pratensis*," Zool. Zh. **58** (10), 1490–1499 (1979).
18. Reznikova, Zh.I., "Interspecific Communication among Ants," Behaviour **80**, 84–95 (1982).
19. Reznikova, Zh.I., *Interspecific Interactions in Ants* (Nauka, Novosibirsk, 1983) [in Russian].
20. Reznikova, Zh.I., "Ethological Mechanisms of Population Control in Coadaptive Ant Complexes," Ekol., No. 3, 210–215 (1999).
21. Reznikova, Zh.I. and Novgorodova, T.A., "Individual Roles and Information Exchange in Groups of Ant Workers," Uspekhi Sovrem. Biol. **118** (3), 345–356 (1998a).
22. Reznikova, Zh.I. and Novgorodova, T.A., "Individual and Social Experience of Ants in Their Interaction with Symbiotic Aphids," Doklady Ross. Akad. Nauk **359** (4), 572–574 (1998b).
23. Reznikova, Zh.I. and Ryabko, B.Ya., "Analysis of Ant Language Using the Information Theory Methods," Probl. Pered. Inform. **22** (3), 103–108 (1986).
24. Reznikova, Zh.I. and Ryabko, B.Ya., "Analysis of Ant 'Language' Using Information Theory," Zh. Obshch. Biol. **51** (5), 601–609 (1990).
25. Reznikova, Zh. and Ryabko, B., "Experimental Study of the Ants' Communication System, with the Application of the Information Theory Approach," Memorabilia Zoologica **48** (2), 219–236 (1994).
26. Reznikova, Zh.I. and Ryabko, B.Ya., "Transfer of Information about Quantitative Parameters of an Object in Ants," Zh. Vyssh. Nerv. Deyat. **45** (3), 500–509 (1995).
27. Reznikova, Zh.I. and Ryabko, B.Ya., "Experimental Study of the Ability of Ants to Add and Subtract Small Numbers," Zh. Vyssh. Nerv. Deyat. **49** (1), 12–21 (1999).
28. Reznikova, Zh. and Ryabko, B., "Sophisticated Communication in Group-Retrieving Ants: a New Tool to Find News," in *Revista de Etologia Suppl.* (*Contributions to the XXVIII International Ethological Conference), Brazil* (2003), Vol. 5, p. 69.
29. Ryabko, B. and Reznikova, Zh., "Using Shannon Entropy and Kolmogorov Complexity to Study the Communicative System and Cognitive Capacities in Ants," in *Complexity* (John Willey & Sons Inc., N.Y., 1996), Vol. 2, No. 2, pp. 37–42.
30. Schatz, B., Lachaud, J.P., and Beugnon, G., "Polyethism within Hunters of the Ponerine Ant, *Ectatomma ruidum* Roger (Formicidae, Ponerinae)," Insectes Soc. **43**, 111–118 (1196).
31. Wassmann, E., "Die psychischen Fähigkeiten der Ameisen," Zool. **26**, 1–133 (1899).
32. Wilson, E.O., *The Insect Societies* (Belknap Press, Cambridge, 1971).
33. Zabelin, S.I., "Tactile Transfer of Information about the Direction toward Food in the Ant *Tapinoma simrothi karavaevi*," Zool. Zh. **58** (8), 1168–1172 (1979).
34. Zakharov, A.A., *Intraspecific Relations in Ants* (Nauka, Moscow, 1972) [in Russian].