

Experimental paradigms for studying cognition and communication in ants (Hymenoptera: Formicidae)

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Abstract

In this review the results of long-term studies of ant cognition and communication by means of an information theory approach are summarised, and perspectives for further research are outlined. The main idea of the information theory approach is that experimenters "ask" ants to transfer to each other a specific amount of information in order to obtain food. In the experiments I describe, the information to be transferred by ants concerns a sequence of turns in the maze "binary tree" in one series of experiments, and the number of a branch in comb-like "counting mazes" in the other series. This method first of all reveals distant homing in ants, that is, their ability to transfer information about remote events. Firstly, it was experimentally demonstrated that in red wood ants and in *Formica sanguinea* LATREILLE, 1798 distant homing is based on a scout-foragers recruitment system: ants work in constant teams, and a scout shares the information on the discovered food only with members of its team. Then, important characteristics of the ants' communication and cognition were evaluated, such as the rate of information transmission, and the potential flexibility of communication systems. Group-retrieving *Formica* species were shown to be able to grasp regularities, to use them for coding and "compression" of information, and to add and subtract small numbers to optimise their messages. These intellectual skills can be considered specific cognitive adaptations to the particular architecture of the species' foraging environment. The proposed quantitative method can serve as a universal experimental paradigm for objective investigations of communication and cognition in ants and other highly social animals.

Key words: Recruitment, behaviour, intelligence, cognition, communication, information theory, counting, teams, task allocation, scouts, foragers, review.

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Introduction

The aim of this review is to present the overall results of long-term studies on cognition and communication in group-retrieving *Formica* species by means of the ideas and methods of information theory and to demonstrate what the information theory approach offers to myrmecologists and cognitive ethologists. The use of this approach has already allowed us to demonstrate the presence of potentially unlimited numbers of messages in ant "language" and to reveal such important properties of ants' cognition as their abilities to memorise and use simple rules, thus compressing the information available, and to add and subtract small numbers to optimise their communication (REZNIKOVA & RYABKO 1986, 1994, 2001). We believe that the experimental schemes described here open a new dimension in studying communicative and cognitive skills in social animals, with ants leading the way.

It has been possible to apply the concept of intelligence to hymenopterans when SCHNEIRLA (1929) and THORPE (1950) experimentally demonstrated that ants (two species of *Formica*) and solitary wasps perform almost as well as rats and dogs in maze learning and detour tasks. In our efforts to comprehend the multifaceted panorama of animal intelligence and cognition, social hymenopterans can serve

as a touchstone. These insects are known to combine highly integrative colony organisation with sophisticated cognitive skills implemented by individual tiny brains. Besides the primary division of labour between the reproductive caste and the worker caste, there exists a further division of labour among workers, whereby each member of the colony specialises in a subset of tasks required for successful group functioning. Different tasks have different levels of cognitive demand. For instance, scouting requires more cognitive resources than, say, defending a nest entrance. Even within the frame of the same task different ranges of complexity are required. In ants and bees scouts navigate rapidly and accurately to food sources and relevant sites for housing relying on their individual exploration, learning and memory. In order to attract nest mates to resource they have discovered, scouts of different species employ a range of communication methods, from a relatively simple one such as laying an odour trail for mass recruitment to the sophisticated system of distant homing. Distant homing here means that messages about remote events come from the scouting individual, without other cues such as scent trail or direct guiding (for reviews see: HÖLLDOBLER & WILSON 1990, REZNIKOVA 2007a).

"Language behaviour" is one of the most advanced manifestations of cognition not only in social insects but in the whole Animal Kingdom. One of the most striking examples of intelligent communication in non-human animals is the honey bee's Dance Language: scouting honeybees memorise the location and features of a new food source that is kilometres away and transfer this knowledge to their nest mates in the hive by generating a specific encoded message that describes the direction and the distance from the hive to the goal (FRISCH 1923, 1967). The use of some modern methods such as the robotic bee (MICHELSEN & al. 1993) and harmonic radar (RILLEY & al. 2005) has provided a quantitative description of how efficiently bees translate the code in the dance into flight to their destinations. The honey bee's Dance Language can be considered to be reliable evidence of distant homing. However, important cognitive aspects of distant homing in bees still remain unclear, such as the flexibility and productivity of this communicative system.

Ants possess complex forms of communications, and they are known to use a large variety of ways to attract their nest mates to a food source. These insects can also switch between different methods of communication according to the situation (for details see: DLUSSKY & al. 1978, MERCIER & LENOIR 1999, JACKSON & RATNIEKS 2006). It has remained unclear for a long time whether ants can use distant homing for communication. In this respect, the so-called tactile (or antennal) "code" has been discussed since WASMANN (1899) first hypothesised the existence of distant homing in ants. The hypothesis of tactile transfer of information about the direction to the food source was confirmed by ZABELIN (1979) on *Tapinoma* ants. However, attempts to decipher ants' "tactile language", that is, to extract definite signals from their tactile communication, did not give the desired results. It was concluded that antennal movements have no structural unity of signals and replies (LENOIR & JAISON 1982, BONAVIDA-COUGOURDAN & MOREL 1984).

The experimental results demonstrating ants' ability to transfer sophisticated information by means of distant homing (REZNIKOVA 1979a, 1983) were first obtained on *Camponotus herculeanus* (LINNAEUS, 1758). In laboratory experiments ants had to transmit to each other information about food placed on one of 12 branches of one out of 10 artificial "trees". The scouting ants were allowed to visit the "trees" and to find food there, then they went to a separate part of the arena and made contacts with foragers in the nest. The scouts were then isolated for a while, and the "trees" were replaced in order to eliminate odour trails laid by the scouts. Foragers successfully found a goal after their contacts with scouts, whereas control ("uninformed") ants failed to do this. These experiments enabled us to suggest that ants can transmit meaningful messages, but they did not reveal any characteristics of ant "language".

Recently, investigations of connections between the behaviour of scouting ants and the characteristics of the food they find (such as the type, quality and quantity of food) have enabled researchers to raise the question about the semantic value of ants' signals (for reviews, see: LE BRETON & FOURCASSIÉ 2004, DEVIGNE & DETRAIN 2006). However, in these investigations, methodological limitations have hampered the progress of studying the "linguistic potential" of ants' communication and related cognitive skills.

It is a natural idea to use the methods of information theory for studying ants' language behaviour, because this theory developed by SHANNON (1948) presents general principles and methods for investigating and developing effective and reliable communication systems. The fundamental role of this theory has been valued in the study of natural communication systems. In particular, in the 1950s and 1960s estimates of the entropy (the degree of uncertainty and diversity) for most of the European languages were obtained. It was shown that in all human languages the length of a message correlates with the quantity of information that is contained in this message (YAGLOM & YAGLOM 1976). It means that one can lodge on two pages twice as much information as on one page. Surprisingly, biological applications of information theory have been incorporated only in a few studies. HALDANE & SPURWAY (1954) made an attempt to estimate bees' message comprehension, and they counted 12 bits of information in bees' standard dances of mobilisation. WILSON (1971) applied the same method to the ant *Solenopsis saevissima* (F. SMITH, 1855). However, there were no experimental paradigms for direct examination of such properties of natural communication as the rate of information transmission, productivity and flexibility.

With B. Ryabko, I have elaborated an experimental approach for studying ants' communication based on the ideas of information theory (RYABKO 1993, REZNIKOVA & RYABKO 1994, 2003). The main point of this approach is not to decipher ants' signals but to concentrate just on the process of transmission of a measured amount of information and thus to evaluate the power of ants' language. The experimental paradigm is simple. All we need to do is to "ask" ants to transfer a specific amount of information to each other. The crucial idea is that we know exactly the quantity of information to be transferred. To organise the process of information transmission between ants, a special maze has been used, called a "binary tree" (REZNIKOVA & RYABKO 1986), where the number and sequence of turns towards the goal corresponds to the amount of the information to be transferred. In another series of experiments ants had to transfer the information about the number of a branch in comb-like "counting mazes". This experimental approach provides a new way for studying important characteristics of animal communication which have not been accessible to study before, such as the rate of information transmission, the complexity of transferred information and the potential flexibility of communication systems.

In this review I concentrate on such a fundamental problem of ants' cognition as flexibility of communication based on rule extraction. I first consider peculiarities of colony organisation in group-retrieving *Formica* species which underlie the sophisticated system of information transmission, and then summarise long-term experimental results which show that *Formica* ants are able to grasp the regularities and use them for coding and "compression" of information. These abilities may be considered the most complex properties not merely of ants, but of animal cognition and communication in general.

Distribution of cognitive responsibilities within an ant colony: information transmission within teams

Life-styles in ant species are highly varied. More than 12,000 species of ants have been described, and they display a great

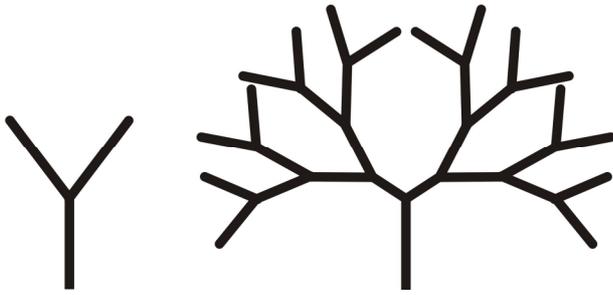


Fig. 1: The maze "binary tree" with one fork and four forks.

variety of specific adaptations at different levels of sociality (HÖLLDOBLER & WILSON 1990, CROZIER & PAMILO 1996). Among many taxonomic groups, ants of the genus *Formica*, in particular, red wood ants (the *Formica rufa* LINNAEUS, 1761 group) are possibly the most promising and surprisingly underestimated group for studying cognitive aspects of communication. In comparison with many sympatric species, red wood ants have hundreds of times more individuals in their colonies and spacious feeding territories. Every day they face complex vital problems: for example, in order to obtain honey-dew, the basic food for adults, red wood ants have to find and possibly memorise locations of thousands of aphid colonies within such a huge three-dimensional space as a tree is for an ant (WELLENSTEIN 1952); besides, each colony has to find, kill and transport thousands of invertebrates in order to feed larvae (GÖSSWALD 1952). DOBRZANSKA (1958) demonstrated that in red wood ants, groups of individuals return repeatedly to approximately the same parts of the colony's feeding territory and work together there. Studying site allegiance in red wood ants, ROSENGREN & FORTELIUS (1987) characterised red wood ants as "replete ants" storing not lipids in their fat-bodies but habitat information in their brains.

Although the *Formica rufa* group is one of those at the centre of myrmecological studies, for a long time amazingly little was known about the organisation of colonies and information transfer in them. Red wood ants are among the group-retrieving species, so we can suggest that their process of recruitment is based on intricate relations between scouting ants and their followers. Experimental evidence of task allocation between members of working teams within a colony first came from investigations of information transmission by distant homing in two species of *Formica* (REZNIKOVA & RYABKO 1986, 1994). In these experiments ants were confronted with a rather complex life-or-death task: they could obtain food only in a "binary tree" maze and only once every 2 - 3 days. Ants therefore were hungry and extremely motivated to obtain some food. They had to search for the food placed on one of several "leaves" of the "binary tree" maze (Figs. 1, 2). In various years three colonies of *Formica polyctena* FOERSTER, 1850 and two of *F. sanguinea* LATREILLE, 1798 were used. Ants lived in the 2 × 1.5 m laboratory arena, in a transparent nest that made it possible for their activity to be observed. The arena was divided into two sections: a smaller one containing the nest, and a bigger one with an experimental system (Fig. 2). The two sections were connected by a plastic bridge that was removed from time to time to modify the set-up or isolate the ants. To prevent access to the food in the maze by a straight path, the set-up was placed in a bath of wa-

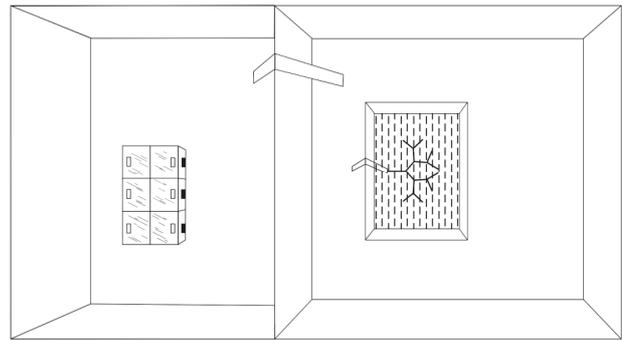


Fig. 2: The laboratory arena with the maze "binary tree".

ter, and the ants reached the initial point of the binary tree by going over a second small bridge.

The laboratory colonies consisted of about 2000 individuals each. All actively foraging ants were individually marked with coloured paint. In all series of experiments with the binary tree, the ants fed for 10 - 12 days on a one-fork set-up. In these cases the foragers left their nest as a result of a mass mobilisation. It was impossible to observe any structural units within the crowding ants. The ants' behaviour changed sharply when the trough with syrup was placed on one of the four leaves of the second turn of the binary tree, making their task more complicated.

The laboratory colonies were found to include teams of constant membership which consisted of one scout and three to eight recruits (foragers): the scout mobilised only members of its team to the food. The composition of the teams was revealed during special run-up experiments consisting of familiarisation trials lasting as long as two or three weeks. Ants freely visited the set-up and took syrup there. During this period a minority of scouts with poor records of competence were identified and discarded. "Qualified" scouts and foragers belonging to their teams received special "team marks" by colour paints. Then the main series of experiments started. In total, 335 scouts along with their teams were used in all experiments with the binary tree. In each trial one of the scouts that were actively moving on the experimental arena at that moment was placed on a leaf of the binary tree that contained a trough with the food, and then it returned to the nest by itself. All contacts between the scout and its team were observed each time.

All experiments were so devised as to eliminate all possible cues that could help the ants to find the food, except information contact with the scout. To avoid the use of an odour track, the experimental set-up was replaced by an identical one when the scout was in the nest or on the arena contacting its group. All troughs in the fresh maze contained only water to avoid the possible influence of the smell of syrup. If the group reached the correct leaf of the binary tree, they were immediately presented with the food.

The scout had to make up to four trips before it was able to mobilise its group of foragers. Usually members of the team had already left the nest after the scout's first trip and were waiting on the arena for its return. Returning to the group, the scout contacted one to four foragers in turn, sometimes two of them simultaneously. Contacts were followed by numerous antennal movements (video records of the experiments are available at <http://www.reznikova.net/infotransf.html>). The experiments were designed to investi-

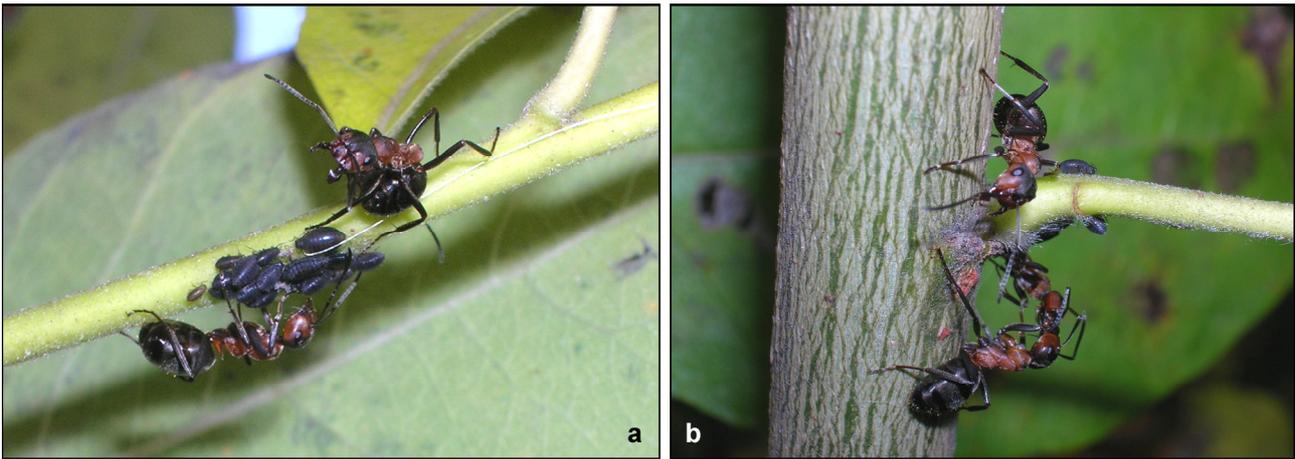


Fig. 3: "Professional specialization" in ants' working teams: (a) a "shepherd" milking aphids and a "guard" (with open mandibles) protecting an aphid colony; (b) a "transporting" ant receiving the food from a "shepherd" in order to transport it to the nest; a "guard" is also present here (Photographs by T. Novgorodova).

gate the characteristics of distant homing, so after the scout had contacted its team, it was isolated for a while, and the foragers had to search for the food by themselves. This process will be described in more details in the next section. Here it is important to note that the composition of the working teams remained constant in each colony from several days to several weeks, that is, during periods when a given scout was actively working (see detailed tables in: REZNIKOVA & RYABKO 1994). It is notable that in both *F. polycтена* and *F. sanguinea*, not all of the scouts managed to memorise the way to the correct leaf of the maze even after they had passed their "final exams" during the run-up trials. The number of scouts that succeeded in memorising the way decreased with increasing complexity of the task. In the case of two forks all active scouts and their groups (up to 15 per colony) were successful whereas in the case of six forks, only one or two coped with the task.

A field model of the situation in which ants act collectively to perform a specific task could be the organisation of honey dew collection by foragers in the tree crown. In this case, the task is to find an aphid colony, inform other ants about the new food source, and organise honey dew collection and transportation. REZNIKOVA & NOVGORODOVA (1998a) were the first to describe a system of intricate division of labour (professional specialisation) in aphid tenders. It turned out that in species that exhibited the recruitment system based on distant homing (*F. polycтена* and *F. sanguinea*), each aphid colony is attended by a constant group (a "team") of individuals which perform different tasks: "shepherds" only look after aphids and milk them, "guards" only guard the aphid colony and protect it from external threats, "transporting" ants transfer the food to the nest, and "scouts" search for the new colonies (see Fig. 3a, b). A given aphid tending "team" includes at least two to four shepherds, the same number of guards, and one scout. It is difficult to observe how a scout attracts its team to a new aphid colony, and we succeeded in doing this only twice. In both cases the scouts found a female aphid that had established a new colony and then by means of distant homing recruited members of their teams who were waiting for them at another branch of the same tree.

The intricate process of team formation in *Formica* has been monitored during an ontogenetic study. The results obtained were described by REZNIKOVA & NOVGORODOVA (1998a). We observed the ontogenetic trajectories of 80 newly hatched *F. sanguinea* ants in one of the laboratory colonies and watched the shaping of teams. There were 16 working teams in that colony which mastered binary tree mazes. From 80 individually marked naïve ants, 17 entered seven different working teams, with one to four individuals joining each. Three became scouts, two of them starting as foragers on joining two different teams and one starting as a scout at once. The three new groups were composed of "reserved" workers dissociated within the nest, and without roles in any teams. The age at which the ants were capable of taking part in the working groups as foragers ranged from 18 to 30 days, and those three ants which became scouts were aged 28 to 30 days.

Team fidelity was examined in two colonies of *F. sanguinea* and *F. polycтена*. In a separate experiment we removed foragers of nine teams (we moved them to another laboratory nest) thus leaving nine scouts alone in a common experimental colony (REZNIKOVA & NOVGORODOVA 1998a, b). Of those nine scouts three managed to attract new foragers, four scouts were working alone, and two ceased to appear in the arenas. In another experiment scouts from five *F. polycтена* teams were removed, and team members were left alone in a common experimental colony. Foragers from these groups sometimes appeared in the arena. We placed 15 of these foragers one by one on the leaves of the binary tree maze containing a trough with food. After they returned to the nest they made only a few occasional contacts with other ants, and did not try to form teams.

All these results in sum show that in group-retrieving *Formica* species colonies contain scout-foragers teams of constant membership in which distant homing is based on direct exchange of information between a scout and its foragers. Each scout shares information on the discovered food only with its own group of foragers (3 - 8 individuals). Formation of teams is apparently a complex process which is based on intricate long-term relations between scouts and foragers.

Distant homing based on rule extraction in ants: the binary tree study

The "binary tree" experimental paradigm based on the ideas of information theory first of all permits demonstration of the fact of distant homing in ants. Furthermore, this approach enables ant students to reveal important properties of ant cognition closely related to their communication. The experiments present a situation in which, in order to obtain food, ants have to transmit certain information which is quantitatively known to the researcher. This information concerns the sequence of turns towards a trough with syrup. The laboratory maze "binary tree" is used where each "leaf" of the tree ends with an empty trough with the exception of one filled with syrup. The leaf on which to place the filled trough was chosen randomly by tossing a coin for each fork in the path. The simplest design is a tree with two leaves, that is, a Y-shaped maze. It represents one binary choice which corresponds to one bit of information. In this situation a scouting animal should transmit one bit of information to other individuals: to go to the right (R) or to the left (L) – see Fig. 1. In other experiments the number of forks of the binary tree increased to six. Hence, the number of bits necessary to choose the correct way is equal to the number of forks, that is, turns to be taken (one and four in Fig. 1, and three in Fig. 2).

The design of the binary tree experiments was briefly described in the previous section in which the ants' recruitment system was considered. Here we concentrate on the details that are important if the organisation of the ants' distant homing is to be understood. As already mentioned, the use of an odour trail was excluded by replacing the whole set-up with a fresh one in the course of each trial. During the experiments each scout was placed on the trough containing food, and after the scout had eaten it returned to the nest on its own. Sometimes the scout contacted its team at once, and the group began to move towards the set-up. In this case, after the scout contacted the foragers it was removed for a while, and the foragers had to search for the food by themselves. But more often the scout turned to go back to the trough alone. Sometimes it made errors and found the trough containing food only after visiting some empty ones. Then it returned to the nest again and contacted its team. Sometimes the scout had to make up to four trips before it could mobilise the foragers. In all cases of mobilisation the duration of the contact between the scout and the foragers was measured in seconds. The contact was considered to begin when the scout touched the first forager ant, and to end when the first two foragers left the nest for the maze. When the scout repeatedly returned to the trough alone, each of its contacts with foragers was measured. Only the duration of the contact that was followed by the foragers' leaving the nest was taken into account. These contacts were hypothesised to be "informative", and they differed sharply in duration from other contacts: all were more than 30 seconds. As a rule, all of the previous contacts between scouts and foragers were brief (about 5 seconds) and were made for the exchange of food.

During each series of experiments with the trough placed on the i -th leaf of the binary tree, all teams that were active on that day worked successively. While the trial was going on, the bridge leading to the working part of the arena was taken away, so as not to let members of other teams go there. While the scout was inside the nest,

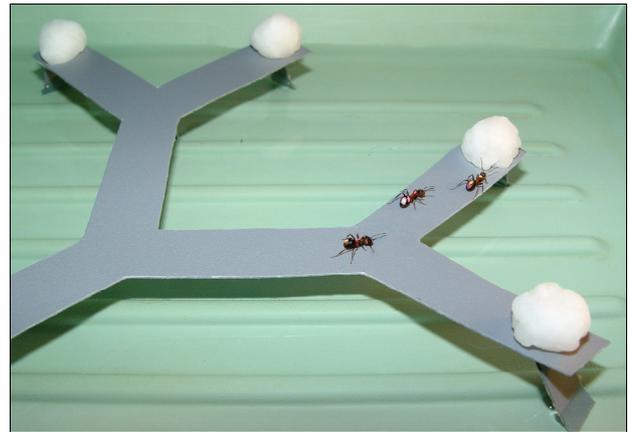


Fig. 4: Ants on the binary tree maze. Now all troughs are full with water (Photograph by I. Iakovlev).

Tab. 1: Comparison of duration of searching the trough by "uninformed" (U) *F. pratensis* ants and individuals that previously contacted with the successful scout ("Informed", I).

Sequence of the turns	Ants (U / I)	Mean	Numbers of experiments	P
RRRR	U	345.7	9	< 0.01
	I	36.3	9	
LLLL	U	508.0	9	< 0.01
	I	37.3	9	
LRRL	U	118.7	7	< 0.01
	I	16.6	7	
RLLR	U	565.9	7	< 0.01
	I	16.3	7	

the whole maze was replaced by a fresh one with all troughs empty. Foragers were presented with the syrup if they reached the correct leaf of the binary tree (Fig. 4).

Before analysing ants' "linguistic potential" and their ability to use rules for compression of information we consider the evidence of information transmission from the scouts to the foragers, which came from two sets of data: first, from statistical analysis of the number of faultless findings of the goal by a group, and second, from a special series of control experiments with "uninformed" ("naïve") and "informed" foragers.

The statistical analysis of the number of faultless findings of the goal was carried out by comparing the hypothesis H_0 (ants find the leaf containing the food by chance) with the hypothesis H_1 (they find the goal thanks to the information obtained), proceeding from the fact that the probability of finding the correct way by chance when the number of forks is i is $(1/2)^i$. We analyzed different series of experiments (338 trials in sum), separately for 2, 3, 4, 5, and 6 forks. In all cases H_0 was rejected in favour of H_1 , $P < 0.001$ (see: RYABKO & REZNIKOVA 1996), thus unambiguously demonstrating information transmission from scouts to foragers.

The control experiments were organised so as to compare searching results of the ants that had and had not pre-

vious possibility to contact the scout (the "informed" and "naïve" ants, respectively). The "naïve" and "informed" ants were tested one by one. Each ant was allowed to search for the food for 30 min. In Table 1 the time spent on searching the trough by "informed" and "uninformed" *Formica pratensis* RETZIUS, 1783 are compared (REZNIKOVA & RYABKO 2003, NOVGORODOVA 2006). For every trial, Wilcoxon's non-parametric test was used (see HOLLANDER & WOLF 1973) to test the hypothesis H_0 (data from both samples follow the same distribution) against H_1 (they follow different distributions) at significance level 0.01. We concluded that the duration of searching time is essentially smaller in those ants that had previously contacted the scout.

These data demonstrate that scouts transfer information about the discovered food to foragers by means of distant homing. We now can evaluate the rate of information transmission in ants. To do this, observe that the quantity of information (in bits) necessary to choose the correct route in the maze equals i , the depth of the tree (the number of turns to be taken), that is, $\log_2 n$ where n is the number of leaves. One can assume that the duration of the contacts between the scouts and foragers (t) is $a * i + b$, where i is the number of turns (the depth of the tree), a is the rate of information transmission (bits per minute), and b is an introduced constant, since ants can transmit information not related directly to the task, for example, the simple signal "food". Besides, it is not ruled out that a scout ant transmits, in some way, the information on its route to the nest, using acoustic (HICKLING & BROWN 2000) or some other means of communication. In this context, it is important that the route from the maze to the nest on the arena was in all experiments approximately the same. Being highly motivated, scouts hurried on to the nest in a beeline, and, therefore, the time before they made antennal contact with the foragers in the nest, which the scout could hypothetically use for message transmission, was approximately the same and did not depend on the number of turns to be taken in the maze (RYABKO & REZNIKOVA 1996).

From the data obtained, the parameters of linear regression and the sample correlation coefficient (r) can be evaluated. The rate of information transmission (a) derived from the equation $t = a * i + b$ was 0.738 bits per minute for *F. sanguinea* and 1.094 bits per minute for *F. polyctena*. It is worth to note that REZNIKOVA & RYABKO (1986, 1994) obtained a highly similar value (1.189 bits per minute) for *Camponotus herculeanus*, the same species as in the very first experiments on studying distant homing in ants (REZNIKOVA 1979a). The rate of information transmission is relatively small in ants.

To estimate the potential productivity of ants' "language", let us count the total number of different possible routes to the trough. In the simplest binary tree with one fork there are two leaves and therefore two different routes. In a tree with two forks there are 2^2 routes, with three forks 2^3 routes, and with six forks, 2^6 routes; hence, the total number of different routes is equal to $2 + 2^2 + 2^3 + \dots + 2^6 = 126$. This is the number of messages the ants must retain in order to pass the information about the food placed on any leaf of the binary tree with 6 forks.

Another series of experiments with the binary tree was inspired by the concept of Kolmogorov complexity and was designed to check whether highly social ant species possess such an important property of intelligent communications as the ability to grasp regularities and to use them for en-

Tab. 2: Duration of transmitting information on the way to the trough by *F. sanguinea* scouts to foragers (no. 1 - 8 regular turn pattern; no. 9 - 15 random turn pattern).

No.	Sequences	Mean duration (s)	SD	Numbers of experiments
1	LL	72	8	18
2	RRR	75	5	15
3	LLLL	84	6	9
4	RRRRR	78	8	10
5	LLLLLL	90	9	8
6	RRRRRR	88	9	5
7	LRLRLR	130	11	4
8	RLRLRL	135	9	8
9	LLR	69	4	12
10	LRL	100	11	10
11	RLLR	120	9	6
12	RRLRL	150	16	8
13	RLRRRL	180	22	6
14	RRLRRR	220	15	7
15	LRLRL	200	18	5

coding and "compressing" information. This concept is applied to words (or text) composed of the letters of any alphabet, for example, of an alphabet consisting of two letters: L and R. We interpret a word as a sequence of left (L) and right (R) turns in a maze. Informally the complexity of a word (and its uncertainty) equates to its most concise description, according to KOLMOGOROV (1965). For example, the word "LLLLLLLL" can be represented as "8 L", the word "LRLRLRLR" as "4LR", while the "random" word of shorter length "LRRLRL" probably cannot be expressed more concisely, and this is the most complex of the three.

We analysed the question of whether ants can use simple regularities of a "word" to compress it. It is known that Kolmogorov complexity is not algorithmically computable. Therefore, strictly speaking, we can only check whether ants have a "notion" of simple and complex sequences. In our binary tree maze, in human perception, different routes have different complexities. In one particular series of experiments, *F. sanguinea* ants were presented with different sequences of turns. Testing the hypothesis H_0 (the time for transmission of information does not depend on the text complexity) against the hypothesis H_1 (that time actually depends on it) allowed us (RYABKO & REZNIKOVA 1996) to reject H_0 , thus showing that the more time ants spent on the information transmission, the more information – in Kolmogorov's terms – was contained in the message. It is interesting that the ants began to use regularities to compress only quite large "words". Thus, they spent from 120 to 220 seconds to transmit information about random turn patterns on the maze with five and six forks and from 78 to 135 seconds when turn patterns were regular. On the other hand, there was no essential difference when the length of sequences was less than 4 (Tab. 2).

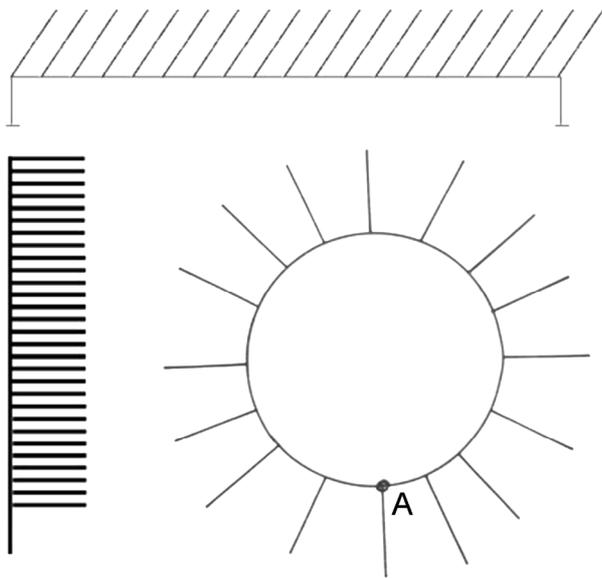


Fig. 5: The comb-like set-ups for studying numerical competence in ants: a horizontal trunk, a vertical trunk and a circle.

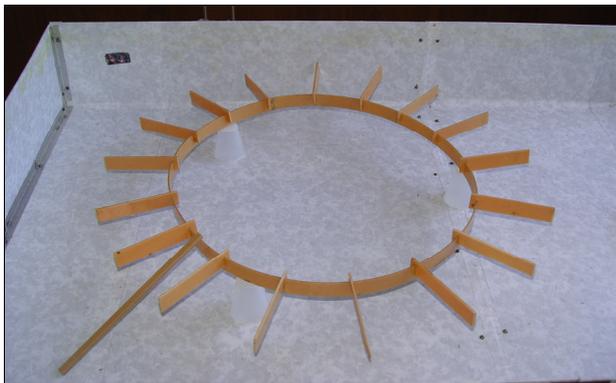


Fig. 6: A circle maze on the laboratory arena (Photograph by P. Panteleeva, 2005).

These results enable us to suggest that ants not only produce a large number of messages but can use rule extraction in order to optimise their messages. The ability to grasp regularities and to use them for coding and "compression" of information should be considered as one of the most important properties of language and its carriers' intellect. Thus we can consider the ants' communication system as rational and flexible.

Ants' numerical competence and flexibility of their communication

Basic number-related skills, that is, the ability to reason about quantities and their relations, is one of the higher manifestations of cognition in animals. There is some evidence that social hymenopterans are able to estimate quite precisely numbers of encounters with different objects. Red wood ants (REZNIKOVA 1980, 1994, 1999, 2007b) and seed-harvesting ants (GORDON 1996) estimate numbers of encounters with members of other colonies on their feeding territories. The experiments of CHITTKA & GEIGER (1995) demonstrated that honey bees are able to use the number of landmarks as one of the criteria in searching for food sources.

An experimental paradigm was elaborated that permitted investigation of ants' numerical competence to be studied using their own communicative skills (REZNIKOVA & RYABKO 1993, 1994, 1996, 2001). A scouting ant had to transfer the information about the number of an object (in our case, a branch of a maze) to its nest mates. Quantitative characteristics of the ants' communications were used for investigating their ability to count. The main idea of this experimental paradigm is that experimenters can judge how ants represent numbers by estimating how much time individual ants spend on "pronouncing" numbers, that is, on transferring information about numbers of objects.

The experiments were based on a procedure similar to the binary tree study. Ant scouts were required to transfer to foragers in a laboratory nest the information about which branch of a special "counting maze" they had to go to in order to obtain syrup. "Counting maze" is a collective name for several variants of set-ups. All of them serve to examine how ants transfer information about numbers by means of distant homing. The first variant of the counting maze is a comb-like set-up consisting of a long horizontal plastic trunk with 25 to 60 equally spaced plain plastic branches, each of them 6 cm in length (Fig. 5). Each branch ended with an empty trough, except for one filled with syrup. Ants came to the initial point of the trunk over a small bridge. The second variant is a set-up with vertically aligned branches. In order to test whether the time of transmission of information about the number of the branch depends on its length as well as on the distance between the branches, one set of experiments was carried out on a similar vertical trunk in which the distance between the branches was twice as large, and the branches themselves were three times and five times longer (for different series of trials). The third variant was a circular trunk with 25 cm long branches (see Fig. 6).

Similarly to the binary tree study, ants were housed in a laboratory arena divided into two parts, one containing a plastic nest with a laboratory ant colony and another containing one of the variants of the counting maze. In various years two laboratory colonies of *F. polyctena* were used in this set of experiments. Each series of experiments was preceded by the run-up stage consisting of familiarisation trials. In order to force a scout to transfer the information about food to its nest mates we showed it the trough containing syrup (placing the scout directly on the trough) and then let it return to the nest. After allowing it to contact the foragers within the nest, the scout was removed and isolated for a while, so that the foragers had to search for the food by themselves, without their guide.

Again, similar to the binary tree study, the experiments with counting mazes were devised so as to eliminate all possible ways for the members of each foraging team to find a goal, except by distant homing, i.e., an information contact with their scout (as always, the set-up was replaced with a fresh one, with all troughs filled with water, while the scout was in the nest; if the foraging team reached the correct branch in a body, then the water-filled trough was replaced with one with syrup; thus foragers had to rely solely on the information from the scout).

The findings concerning number-related skills in ants are based on comparisons of duration of scout - foragers information contacts which preceded successful trips by the

Tab. 3: The results of experiments in the "vertical trunk 1" with *F. polyctena*.

Experiment number	Number of food-containing branch	Duration of scout-forager contact (s)	Working team number (= the scout's "name")
1	10	42	I
2	10	40	II
3	10	45	III
4	40	300	II
5	40	280	IX
6	13	90	II
7	13	98	I
8	28	110	III
9	28	120	X
10	20	120	X
11	20	110	III
12	35	260	III
13	35	250	X
14	30	160	I
15	30	170	III

Tab. 4: Values of correlation coefficient (r) and regression coefficients (a, b) for vertical trunk (vert.), horizontal trunk (horiz.), and circle in the experiments with *F. polyctena*.

Type of setup	Sample size	Nr. of branches	r	a ± Δ a	b ± Δ b
Vert. 1	15	40	0.93	7.3 ± 4.1	-28.9 ± 0.51
Vert. 2	16	60	0.99	5.88 ± 0.44	-17.11 ± 0.65
Horiz. 1	30	25	0.91	8.54 ± 1.1	-22.2 ± 0.62
Horiz. 2	21	25	0.88	4.92 ± 1.27	-18.94 ± 4.75
Circle	38	25	0.98	8.62 ± 0.52	-24.4 ± 0.61

foraging teams. Duration of contacts of the scout with its team was measured when the scout returned from the experimental set-up, loaded with both syrup and information.

In total, 32 scout - foragers teams worked in three kinds of set-ups. The teams left the nests after they were contacted by scouts and moved towards the trough by themselves 152 times (recall that the scouts were removed). In 117 cases the team immediately found the correct path to the trough, without making any wrong trips to empty troughs. In the remaining cases, ants came to the empty troughs, and began looking for food by checking neighbouring

branches. Some scouts were experimentally found to be incapable of this task: in all experiments (31 in total) involving them the foragers failed to find the food. Such scouts were removed from the working part of the arena.

Since all set-ups had no fewer than 25 branches, the probability of finding the correct trough by chance is not more than 1 / 25. Thus, the success ratio which was obtained experimentally can only be explained by information transmission from the scouts. The probability of finding the food-containing trough by chance in 117 cases out of 152 is less than 10⁻¹⁰. In addition, in control experiments ants, including scouts placed in the set-up, without information on which trough contained food usually failed to find the food, even though they actively searched for it.

Data obtained on the vertical trunk are shown in Table 3 as an example. It turned out that the relation between the number of the branch and the duration of the contact between the scout and the foragers is well described by the equation $t = a * i + b$ for different set-ups which are characterised by different shapes, distances between the branches and lengths of the branches. The values of parameters a and b are close and do not depend either on the lengths of the branches or on other parameters. The correlation coefficient between t and i was high for different kinds of counting mazes (Tab. 4). All this enables us to suggest that the ants transmit information solely concerning the number of the branch.

The likely explanation of the results concerning ants' ability to search the "right" branch is that they can evaluate the number of a branch in the sequence of branches in the maze and transmit this information to each other. As noted before, foragers in the nest were absolutely uninformed about the location of the reward in the maze, and, taking into account that the set-up was replaced with a new one lacking both possible odour trails and any smell of syrup, they could only obtain this information from an experienced scout. Presumably a scout could pass messages not about the number of the branch but about a distance to it or about the number of steps and so on. This would be a quite natural explanation taking into account recent data concerning navigation in desert ants, *Cataglyphis*: ants measure distances while travelling by using some kind of "step counter" (WITTLINGER & al. 2007). What is important is that even if ants operate with distance or with the number of steps, this shows that they are able to use quantitative values and pass on information about them.

It is interesting that quantitative characteristics of the ants' "number system" seem to be close, at least outwardly, to some archaic human languages: the length of the code of a given number is proportional to its value. For example, the word "finger" corresponds to 1, "finger, finger" to the number 2, "finger, finger, finger" to the number 3 and so on. In modern human languages the length of the code word of a number i is approximately proportional to $\log i$ (for large i 's), and the modern numeration system is the result of a long and complicated development. Note that when using our numerical system, people have to make simple arithmetical operations: for example, 23 = 20 + 3. It is particularly obvious in Roman numerals: for example, VII = V + II.

The second series of experiments enabled us to suggest that ants are also capable of simple arithmetical operations. A new experimental scheme was elaborated for studying

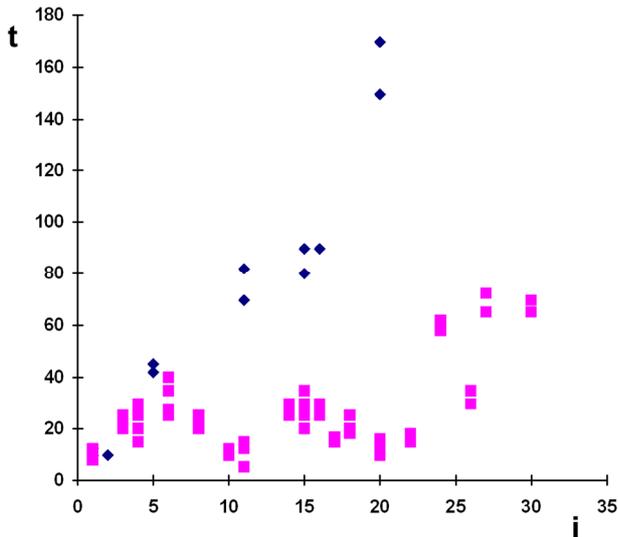


Fig. 7: Dependence of the time (t ; measured in seconds) of transmission of information about the number of the branch having food on its ordinal number (i) in the first and the third series of experiments in the ant *Formica polyctena*. Diamonds, the time taken for transmission of information at the first stage; squares, the same at the third stage.

ants' "arithmetic" skills based on a fundamental idea of information theory, which is that in a "reasonable" communication system the frequency of usage of a message and its length must correlate. The informal pattern is quite simple: the more frequently a message is used in a language, the shorter is the word or the phrase coding it. Professional jargon, abbreviations, etc. serve the same purpose. This phenomenon is manifested in all known human languages.

The main experimental procedure was similar to other experiments with counting mazes. In various years four colonies of *F. polyctena* were used in this set of experiments. The scheme of the experiments was as follows. Ants were offered a horizontal trunk with 30 branches. The experiments were divided into three stages, and at each of them the regularity of placing the trough with syrup on branches with different numbers was changed. At the first stage, the branch containing the trough with syrup was selected randomly, with equal probabilities for all branches. So the probability of the trough with syrup being placed on a particular branch was $1/30$. At the second stage we chose two "special" branches A and B (N 7 and N 14; N 10 and N 20; and N 10 and N 19 in different years) on which the trough with syrup occurred during the experiments much more frequently than on the rest – with a probability of $1/3$ for "A" and "B", and $1/84$ for each of the other 28 branches. In this way, two "messages" – "The trough is on branch A" and "The trough is on branch B" – had a much higher probability than the remaining 28 messages. In one series of trials we used only one "special" point A (the branch N 15). On this branch the food appeared with the probability of $1/2$, and $1/58$ for each of the other 29 branches. At the third stage of the experiment, the number of the branch with the trough was chosen at random again.

Now let us consider the relationship between the time which the ants spent to transmit the information about the branch containing food, and its number. The information

Tab. 5: Dependence of the time of information transmission (t) on the distance from the branch with a trough to the nearest "special" branch (special branches are 10 and 20).

The number of the branch having food (experiments on different days, consequently)	Distance to the nearest special branch	Times of transmission of information about the branch number for different scouts (s)
26	6	35, 30
30	10	70, 65
27	7	65, 72
24	4	58, 60, 62
8	2	22, 20, 25
16	4	25, 8, 25
16	4	25
22	2	15, 18
18	2	20, 25, 18, 20
15	5	30, 28, 35, 30
20	0	10, 12, 10
6	4	25, 28
16	4	30, 25
15	5	20, 25, 20
14	4	25, 28, 30, 26
17	3	17, 15
11	1	10, 12

obtained at the first and third stages of the experiments are shown on the graph (Fig. 7) in which the time of the scout's contact with foragers (t) is plotted against the number (i) of the branch with the trough. At the first stage the dependence is close to linear. At the third stage, the picture was different: first, the information transmission time was very much reduced, and, second, the dependence of the information transmission time on the branch number is obviously non-linear: depression can be seen in the vicinities of the "special" points (10 and 20). So the data demonstrate that the patterns of dependence of the information transmission time on the number of the food-containing branch at the first and third stages of experiments are considerably different. Moreover, in the vicinities of the "special" branches, the time taken for transmission of the information about the number of the branch with the trough is, on the average, shorter. For example, in the first series, at the first stage of the experiments the ants took 70 - 82 seconds to transmit the information about the fact that the trough with syrup was on branch N 11, and 8 - 12 seconds to transmit the information about branch N 1. At the third stage it took 5 - 15 seconds to transmit the information about branch N 11. These data enable us to suggest that the ants have changed the mode of presenting the data about the number of the branch containing food.

Tab. 6: Values of correlation coefficient (r) in the experiments with different "special" branches.

Sample size	Numbers of "special" branches	r for the first stage of the experiments	r for the third stage of the experiments
150	10, 20	0.95	0.80
92	10, 19	0.96	0.91
99	15	0.99	0.82

What about ants' ability to add and subtract small numbers? Analysis of the time duration of information transmission by the ants raises the possibility that at the third stage of the experiment the scouts' messages consisted of two parts: the information about which of the "special" branches was the nearest to the branch with the trough, and the information about the distance from the branch with the trough to this definite "special" branch. In other words, the ants, presumably, passed a "name" of the "special" branch nearest to the branch with the trough, and then the number which had to be added or subtracted in order to find the branch with the trough.

In order to verify this statistically, the coefficient of correlation was calculated between the time required for transmission of information about the trough being on the branch i and the distance from i to the nearest "special" branch. The results confirmed the hypothesis that the time for transmission of a message about the number of the branch is shorter when this branch is closer to any of the "special" ones. For this purpose, the data obtained at the third stage of the experiment were transformed to present them in the form shown in Table 5 where data of one year are given as an example. In this table we do not include branches that are close to the starting point of the set-up (N 1 - 4) because there is no need to use "arithmetic" for ants where rewarded branches are very close to the first one (in fact ants spent roughly the same time transmitting information about these branches: from 10 to 20 seconds).

It can be seen from Table 6 that the coefficients of correlation between the transmission time and the distance to the nearest special point have quite high values and they differ significantly from zero (at the confidence level of 0.99). So the results support the hypothesis that the time for transmission of a message about the number of the branch is shorter when this branch is close to either of the special ones. This, in turn, shows that at the third stage of the experiment the ants used simple additions and subtractions, achieving economy in a manner reminiscent of the Roman numeral system when the numbers 10 and 20, 10 and 19 in different series of the experiments, played a role similar to that of the Roman numbers V and X.

Our interpretation is that ants of the species under consideration can add and subtract small numbers (REZNIKOVA & RYABKO 1996, 2000). This also indicates that these insects have a communication system with a great degree of flexibility. Until the frequencies with which the food was placed on different branches started exhibiting regularities, the ants were "encoding" each number of a branch with a message of length proportional to N, which suggests un-

itary coding. Subsequent changes of code in response to special regularities in the frequencies are in line with a basic information-theoretic principle that in an efficient communication system the frequency of use of a message and the length of that message are related.

Evaluation of ants' intelligent communication: the outlook for cognitive and myrmecological research

Long-term experiments based on ideas of information theory demonstrated that several group-retrieving *Formica* species are able to grasp regularities, use them for coding and "compression" of information, and add and subtract small numbers to optimise their messages. These data are based on two main experimental schemes: investigation of ants' ability to memorise and transfer sequences of turns in the binary tree maze, and examining their ability to use the numbers of branches in the counting mazes.

Here we are trying not to overburden the empirical data with interpretations and do not hasten to apply far-fetched concepts (such as teaching, mentality, consciousness) to explain the ants' behaviour. We prefer to operate with terms that can be precisely defined (such as information transmission), and only attribute to our subjects (the ants) those skills (such as the ability to compress information) that can be accurately measured. Perhaps primatologists are driven by similar precautions when they speak about cognitive abilities of this kind in chimpanzees: during 10 years of investigations BOESCH (1995) characterised only three cases of interactions between chimpanzees as teaching, whereas hundreds of other cases were referred to more simple forms of social learning. In many animals, including ants, cognitive abilities represent the "tip of an iceberg" of species-specific behaviour which is based, in many respects, on inherited behavioural stereotypes. Of course, in non-humans the majority of "icebergs" lack their tips, that is, species-specific behavioural stereotypes do not include elements of cognition.

Instead of eroding the concept of cognition, it is apparently more productive to apply quantitative experimental methods for studying specific domains where ants' behaviour appears intelligent. Ants' "species genius" revealed with the use of the information theory approach could be considered a specific cognitive adaptation, together with extraordinary classificatory abilities in pigeons (HERRSTAIN & LOVELAND 1964, HUBER 1995), honey bees (MAZOKHIN-PORSHNYAKOV 1969a, b, GIURFA & al. 2001) and social wasps (MAZOKHIN-PORSHNYAKOV & KARTSEV 1979, 2001), an ability to memorise and recognise many mates by facial features in chimpanzees (PARR & DEWAAL 1999) and paper wasps (TIBBETS & DALE 2007), social learning in ants (REZNIKOVA 1982), huge data storage in food caching birds and mammals (SHETTLEWORTH 1998), and so on. It is known that some species, both vertebrates and invertebrates are predisposed to intellectual feats within narrow limits of solving life-or-death problems (for details see: REZNIKOVA 2007c). For ants such problems could be searching for food in complex situations and transferring information about new food sources to each others.

The main results of the long-term ant study presented in this review that may be of importance for the development of cognitive ethology are the elaborated experimental paradigm for studying communication and related cognitive skills in animals based on the ideas and methods of in-



Fig. 8: A nest of *Formica pratensis* in the steppe landscape, South Siberia (in the vicinity of Karasuk town) (Photograph by T. Novgorodova).

formation theory, and the empirical data themselves that revealed concrete and advanced properties of ants' "language".

Our data and experimental procedures developed open a multitude of interesting questions for myrmecological studies, such as an opportunity to look for links between ecological traits, social systems and cognitive abilities in ants, and between ants' intelligence and their brains.

The binary tree paradigm first of all helps myrmecologists to reveal the informational foundation of the functional organisation of an ant colony, and, in particular, to reveal distant homing in some species. In ants distant homing is probably related to the particular architecture of their foraging environment. It is worth noting that in the course of the binary tree study no evidence of distant homing was revealed in *F. cunicularia* LATREILLE, 1798 or *Myrmica rubra* (LINNAEUS, 1758) (REZNIKOVA & RYABKO 1994). Some species with small colony size and a correspondingly small feeding territory can use tandem running for pair recruitment and odour trails for mass mobilisation to any point within their range, whereas some species with large colonies and spacious feeding territories (such as red wood ants) have to use intermediate stations for contacts between scouts and foragers: a scout can not attract effectively many inactive foragers to a food source from a distant ant-hill, nor can it lay a scent trail for such a long-distance transmission. Distant homing is perhaps the most efficient means of communication in this case. Foraging within a tree crown in red wood ants is a good example, but it is also possible for ants to use distant homing in the steppe plains. For example, the binary tree paradigm revealed distant homing in *F.*

pratensis based on the "relay" mode of information transmission, in contrast to red wood ants and *F. sanguinea*, with their strong team fidelity (NOVGORODOVA 2006). *Formica pratensis* dominates ant species communities in steppe landscape (Fig. 8), much as red wood ants dominate forests (REZNIKOVA 1974, 1980, GALLÉ 1978). This species uses a strong division of labour between two main groups of out-of-nest individuals: scouting ants who freely investigate wide territories, and idle foragers who travel back and forth along segments of foraging routes waiting for preparedness signals from scouts (REZNIKOVA 1979b). Binary tree experiments demonstrated that, based on such a recruitment system, the relay mode of distant homing in *F. pratensis* facilitates rapid dissemination of information and efficient recruitment of foragers to a priority task (NOVGORODOVA & ZHUKOVA 2007). Considerable differences observed in the coordination of work and information flow in the colonies of *F. polyctena* compared with *F. pratensis* indicate that communication systems based on distant homing could be variable and species specific, and possibly defined by ecological traits.

Social systems of ants vary between species but little is known about scales of diversity of social systems within species. It was experimentally demonstrated with *F. pratensis* that a colony can switch between several systems of social organisations, where the lower level is the use of a protected territory by a colony inhabiting a single domicile, and the highest level is unicoloniality (REZNIKOVA 1979b). It is important to note that ants readily switch their recruitment modes in accordance with the levels of social organisation, and that this takes only a few weeks. Similar patterns, although within narrow limits, have since been revealed experimentally in *F. cunicularia*, by NOVGORODOVA (2003). It is very likely that some ant species possess "toolkits" of social systems, and it would be very interesting to investigate how cognitive activity changes in accordance with social systems. It is possible that hidden cognitive abilities would become observable when an ant colony switches to a higher level of social organisation.

It is, however, possible that in some ant species brains limit cognitive activity. Looking at the great diversity of social hymenopterans, we can find widely differing ways in which these insects use their brains in their lives. Taking only the problem of nest mate recognition, the solutions range from the use of a specific sensory sensillum on carpenter ant antennae that functions directly in sorting individuals without involving the brain at all (OZAKI & al. 2005) to the existence of specific brain structures responsible for individual recognition of sisters in paper wasps (GRONENBERG & al. 2008). The binary tree scheme provides an experimental paradigm for investigating the relationship between the design of brains and cognitive achievements in ants. Different species may be compared for the purpose of examining whether modes of information transmission within a colony are connected with peculiarities of information processing in their brains. Another interesting problem is whether specialised members of a colony, such as scouts and foraging team members are equipped with brains of different sizes and powers, and correspondingly have different capacities of learning.

In sum, there are intriguing problems for future generations of myrmecologists: to understand how sophisticated cognitive abilities discovered at the individual and team

levels are integrated at the colony level in ants, how they are influenced by the particular traits of the ants' foraging environment, and whether the complex behaviour of a whole colony emerges from a diversity of specialised tiny brains of individuals with different cognitive limitations. The experimental paradigms presented in this review provide effective and relatively easy ways of solving these and many other problems. It is a challenge to apply these methods for studying communication and cognition not only in ants but in a wide variety of social animals.

Acknowledgements

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Zusammenfassung

In diesem Übersichtsartikel werden die Ergebnisse von Langzeitstudien zu Kognition und Kommunikation bei Ameisen mittels eines Informationstheorie-Ansatzes zusammengefasst sowie Perspektiven für zukünftige Forschung umrissen. Die grundlegende Idee des Informationstheorie-Ansatzes ist, dass die Forscher Ameisen die Aufgabe stellen, eine bestimmte Informationsmenge zu übertragen, um Futter zu erhalten. In den Experimenten, die ich beschreibe, bezieht sich die Information, die von Ameisen übertragen werden soll, auf eine Abfolge von Gabelungen in dem Labyrinthtyp "binärer Baum" in der einen Experimentserie, und auf die Nummer eines Asts in einem kammartigen "Zählabyrinth" in der anderen Serie. Diese Methode zeigt vor allem die Fähigkeit von Ameisen Information über entfernte Ereignisse zu übertragen ("Distant homing"). Zunächst wurde experimentell nachgewiesen, dass diese Fähigkeit bei Roten Waldameisen und bei *Formica sanguinea* LATREILLE, 1798 auf einem Kundschafterin-Sammlerinnen-Rekrutierungssystem basiert: Die Ameisen arbeiten in konstanten Teams, und eine Kundschafterin teilt die Information zu einer entdeckten Futterquelle nur den Sammlerinnen ihres Teams mit. Weiters wurden wichtige Charakteristika der Kommunikation und Kognition der Ameisen bewertet, wie beispielsweise die Rate der Informationsübertragung und die potentielle Flexibilität des Kommunikationssystems. Gruppen-rekrutierende *Formica*-Arten erfassen nachweislich Regelmäßigkeiten, um sie zur Kodierung und zur "Kompression" von Information zu verwenden, und um kleine Zahlen zur Optimierung der Botschaften zu addieren und zu subtrahieren. Diese intellektuellen Fähigkeiten stellen möglicherweise spezifische kognitive Anpassungen an die jeweilige Struktur der Umwelt der Ameisen dar, die sie zum Fouragieren nutzen. Die vorgestellte quantitative Methode kann als universelles experimentelles Paradigma für objektive Untersuchungen von Kommunikation und Kognition bei Ameisen und anderen hochsozialen Tieren herangezogen werden.

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