

# Estimate of Complexity of Behavioral Patterns in Ants: Analysis of Hunting Behavior in *Myrmica rubra* (Hymenoptera, Formicidae) as an Example

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**Abstract**—A method for estimating the complexity of behavioral patterns of ants based on the Kolmogorov complexity is considered. Behavioral sequences are presented as “texts” compressed with the KGB Archiver (v. 1.2). The elements of behavior (a total of 10) singled out from video records served as an alphabet. The comparison of “successful” and “incomplete” hunting behaviors in *Myrmica rubra* showed that successful hunting patterns were characterized by less complexity than “incomplete” ones. It was assumed that complete patterns had less redundancy and better predictability. The smallest complexity was revealed in complete hunting patterns of naive (laboratory reared) ants in comparison with members of a natural colony. In perspective, quantitative evaluation of complexity of behavioral patterns will help to evaluate the level of discrete variability within ant colonies.

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Ants are characterized by diverse behavior including both genetically determined responses and those based on individual experience and social learning. In some ant species with a high level of cognitive activity, the behavior of each individual may be “complex” enough. However, the concept of “behavioral complexity” is intuitive. The complexity of flexible and stereotyped behavior of animals can be differently evaluated at this intuitive level of understanding. In the first case the concept of complexity applies to the level of problems solved and decisions made by the animal, and in the second case, to the internal structure and “logic” of standard responses to repeated situations. Objective assessment of complexity of at least individual elements of animal behavior has not been attempted until now. Ants may serve as convenient models for such studies, since their behavior is diverse and largely similar to that of social vertebrates (Dlussky, 1984; Reznikova, 2007).

Within the framework of this research, we will consider stereotyped behavior typical of members of a species. Lorenz (1932) was the first to distinguish species-specific behavioral models in birds. The concept of species-specific behavioral pattern was introduced by Promptov (1940), also by the example of birds that have a rich and expressive repertoire of be-

havior. The available ethological literature includes hundreds of publications based on descriptions of ethograms of a broad range of species, both vertebrates and invertebrates. Since the terms and concepts used in ethogram analysis have become somewhat indistinct and ambiguous (Reznikova et al., 2009), they should be defined more clearly before we can proceed to assessing the complexity of stereotyped behavior.

Behavior can be described by subdividing it into basic or elementary movements and postures (Tinbergen, 1951), which will be referred to as *behavioral elements*. Any arbitrary set of consecutive behavioral elements is a *behavioral sequence*. An example of a highly variable behavioral sequence is the seeking behavior observed in many animal species. The stable, repeatable “chains” of behavioral elements can be described as *behavioral patterns*. The manifestation of different patterns in the general context of behavior has a probabilistic nature: some of their elements may be omitted or repeated, and also interspersed with elements not belonging to the given pattern (“noise”). The genetically determined sequences of behavioral elements with stable composition and order of execution (for review, see Zorina et al., 1999) will be referred to as *fixed action patterns* (FAPs), following the classical terminology. Examples of such sequences are

FAPs of prey capture, mating, or grooming. Triggered by the key stimulus, a FAP proceeds as a single series of actions until the final act. A FAP differs from a behavioral pattern in being indivisible: it will run to completion once it has started. Among other examples of FAPs, Lorenz (1950) considered the hunting behavior of a starling, which proceeded quite automatically in response to an adequate stimulus (or even an “innate releaser”) even in the absence of prey. In one of the variants, the starling caught the fly but it slipped out, after which the bird clicked its empty beak and even made swallowing movements. An example of this kind in our study is “tip-and-run” attack of the ant *Myrmica rubra* L. attacking a springtail: it jumps on the prey, grasps it with its mandibles, and kills it with its sting. The sequence runs to completion once it has started: if the prey manages to escape, the ant clicks the empty mandibles and then bends its abdomen with the characteristic “stinging” movement (Reznikova and Panteleeva, 2001). A prolonged behavioral pattern may include a FAP. For example, the complete pattern of hunting motile prey in *M. rubra* includes finding the potential victim and approaching it, the FAP of a “tip-and-run” attack, and grasping the prey in a way more convenient for killing and transporting. The hunting pattern is followed by prey transportation, which represents a separate, less complex behavioral pattern (Reznikova and Panteleeva, 2003).

Both behavioral patterns and FAPs differ from simple behavioral sequences by “cohesiveness” of their elements, i.e., more (for FAPs) or less (for stereotyped behavioral patterns) distinct relations between them. An example of stereotyped behavior incorporating

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AAAAAAAAAAAAAAAAABAAAAAAAAABAAAAACAAAAAAAAAAAAAAAAAAAD  
 ADBCABBDDCABBCCDAABCCADAABCCDABABBCCDABAABABBBBA.

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The two sequences are of the same length and include the same number of elements (A, B, C, D); although both sequences are random, the second one appears to be “more complex.” The above reasoning is based on the informal understanding of “complexity.” The exact definition of Kolmogorov complexity was provided by Kolmogorov (1965); here it is sufficient to say that in Kolmogorov’s interpretation, the complexity of a sequence of letters is the length (in binary alphabet) of the minimal program that is able to “generate” the sequence in question. In our case, the alphabet includes the entire set of behavioral elements typi-

a FAP is the organized behavior of the larva of the caddis fly *Chaetopteryx villosa* building its “case” of sand grains and other particles. The building process takes place during pauses in locomotion and involves repeated sequences of probing and fastening the particles. During locomotion, these sequences are replaced by sequences of brief probing and rejecting the particles (Nepomnyashchikh, 2004).

Both behavioral patterns and FAPs may be species-specific. A classical example is the stable sequence of behavioral elements during courtship and pairing in various species of animals. It should be noted that behavioral patterns may include some elements based on experience, which become so strongly “embedded” in individual behavior that they may hardly be distinguished from genetically determined ones (Lorenz, 1950). The patterns can be “adjusted” in the process of interaction between the environment and individuals of the given species, resulting in a species-specific behavioral stereotype.

In our opinion, the complexity of behavioral patterns can be best assessed using the mathematical tools based on the concept of Kolmogorov complexity (Kolmogorov, 1965). For our purposes, the principles of this approach may be explained in the following way. If one pattern consists of a greater number of nonrecurrent elements than the other, it may be described as “more complex” but such a description will not reflect the exact situation. For example, let us compare the following sequences of behavioral elements:

cal of the given species, and the sequence describes the observed behavior. Since practical realization of this approach is quite complicated, one may use an approximate estimation of Kolmogorov complexity produced by data compression algorithms. A text compressed by an archiver is a certain “program” which can be interpreted (decoded) in such a way that the original text is restored. This “program” will be an attainable approximation of Kolmogorov’s minimal program (see, for example, Ryabko et al., 2006). It is known that the possible degree of compression of a sequence of symbols is closely related to such pa-

rameters as randomness and redundancy of the sequence. In the information theory these parameters are sometimes considered in terms of predictability. In particular, randomness is interpreted as uncertainty (unpredictability) of appearance of a certain symbol from the alphabet, and redundancy, as a measure of predictability of appearance of the next element in the sequence based on the preceding ones. Random (unpredictable) sequences of symbols with low redundancy can be compressed less efficiently than highly predictable sequences. This property allows the relative complexity of behavior to be estimated by the compression ratio of corresponding files.

In this study, representing the first step towards estimating the complexity of ant behavior, we have used an archiver program to compare the “successful” and “unsuccessful” hunting behaviors in *M. rubra*. By the example of this behavioral pattern we have shown that a successful, complete hunting process is less complex than unsuccessful behavior, which includes some separate fragments of the hunting pattern but is not completed by catching the prey. The lowest complexity can be observed in completed hunting patterns realized by the “naive” (laboratory reared) ants by the “all at once” principle.

#### MATERIALS AND METHODS

The study was carried out in 2009 under laboratory conditions, using three groups of *M. rubra* ants: members of a natural colony taken from a mixed forest in the Akademgorodok area (Novosibirsk), and two groups of naive ants reared from pupae in the laboratory, which had no experience of hunting in the nature. The natural colony comprised about 3 thousand workers and about 30 queens, whereas each of the “naive” groups included 30–50 individuals kept together with 1–2 queens. The groups lived in artificial nests installed in testing arenas ( $1 \times 2$  m for the natural colony and  $80 \times 50$  cm for the “naive” ones). Brood was constantly present in the colonies, and new larvae were regularly added to the nests to motivate the foragers to get proteinaceous food; carbohydrate food was supplied without limitation. Although the two groups of “naive” ants were kept in separate arenas, the data were later united into a single sample. It should be noted that all the three groups had a high genetic variability, since the ants represented progeny of many different queens, and the pupae added to the nests were taken from different colonies. The ants and brood

were sampled from biotopes with a high abundance of springtails representing the potential prey.

The “naive” ants were tested at the age of 3 to 12 days. Since our study was focused on the hunting behavior, the ants that were the most active in the arena were specially selected for testing. The age of ants from the natural colony was not determined; in this case, we also selected the active individuals that appeared in the arena. To observe the hunting process, single ants were placed in glass chambers with gypsum bottoms, 5 cm in diameter and 6 cm high, each containing 30 living springtails *Tomocerus sibiricus* Reuter and shreds of transparent plastic imitating the forest litter (for details, see Reznikova and Panteleeva, 2003). Each ant was tested only once, during 14–16 min. Some ants hunted several times during this period, each act of hunting being recorded separately. The behavior of ants was recorded using a Sony Digital Handycam TRV340E camcorder. The videos (a total duration of 6.5 h, with 26 ind. observed) were analyzed in  $1/5\times$  slow-motion with individual postures of the ants recorded using The Observer XT 7.0 software (ver. 7.0.214, Noldus Information Technology).

The behavioral elements were distinguished using the following protocol. The typical positions of the abdomen, legs, head, antennae, and mandibles combined with the current movement were designated with numerical indices (Table 1). These indices were then used to describe the observed behavioral elements as sets of movements and postures. In all, 10 behavioral elements were distinguished (Table 2). It should be noted that the behavior of *M. rubra* hunting springtails was previously described in a generalized way (Reznikova and Panteleeva, 2001, 2003), using behavioral elements at the same level that was used to characterize the differences between ethograms of individual ants (Reznikova and Bogatyreva, 1984). Here we used a more formal approach, allowing the entire behavior to be described in a standardized way.

Using the “alphabet” of 10 behavioral elements, we transformed the video records into alphabetic sequences and saved the individual behavioral patterns as separate text files (with .txt extension). The beginning of the hunting pattern was the moment when the ant approached the springtail to a distance comparable with the body length of the ant and started pursuing the prey. The end of the complete (successful) hunting pattern was the moment when the ant started running while carrying the killed prey, i.e., the transition from

**Table 1.** Indices used to describe the elements of ant behavior

Body parts, movement	State, position			
Abdomen ( <i>ab</i> )	Relaxed, straight (0)	Raised (1)	Bent (2)	Ready to strike with sting (3)
Legs ( <i>l</i> )	Relaxed (0)	Raised, tense (1)	Belligerent posture, standing on 4 legs (2)	
Head ( <i>h</i> )	Relaxed (0)	Protruded forward (1)	Raised (2)	Bent down (3)
Antennae ( <i>a</i> )	Relaxed (0)	Extended, straight, tense (1)	Feeling (2)	Tapping (3)
Mandibles ( <i>mnd</i> )	Relaxed, closed (0)	Slightly open (1)	Completely open (2)	Closed in grasp (3)
Movement ( <i>mv</i> )	Stop (0)	Slow walk (1)	Run (2)	Intermittent run (3)
	Attack (4)	Turn (5)	U-turn (6)	

**Table 2.** Behavioral elements in the hunting patterns of *Myrmica rubra*

Symbol	Behavioral element	Combination of indices
W	Wait / stop	<i>ab</i> -0,1 <i>l</i> -0 <i>h</i> -0,1 <i>a</i> -0 <i>mnd</i> -0,1,2 <i>mv</i> -0
S	Slow walk	<i>ab</i> -0 <i>l</i> -0 <i>h</i> -0 <i>a</i> -1 <i>mnd</i> -2 <i>mv</i> -1
R	Interrupted running / pursuit	<i>ab</i> -0 <i>l</i> -1 <i>h</i> -3 <i>a</i> -2 <i>mnd</i> -0,1 <i>mv</i> -3
T	Turn	<i>ab</i> -0,2 <i>l</i> -0,1 <i>h</i> -0,2 <i>a</i> -0,1,2 <i>mnd</i> -0,1 <i>mv</i> -5
U	U-turn	<i>ab</i> -0,2 <i>l</i> -0,1 <i>h</i> -0,2 <i>a</i> -0,2 <i>mnd</i> -0 <i>mv</i> -6
B	Belligerent posture (before attack)	<i>ab</i> -3 <i>l</i> -2 <i>h</i> -2 <i>a</i> -1 <i>mnd</i> -2 <i>mv</i> -0
A	“Tip-and-run” attack	<i>ab</i> -3 <i>l</i> -3 <i>h</i> -2 <i>a</i> -1 <i>mnd</i> -3 <i>mv</i> -4
C	Capturing and handling of a prey	<i>ab</i> -3 <i>l</i> -2 <i>h</i> -2 <i>a</i> -1 <i>mnd</i> -0 <i>mv</i> -0,1,2
K	Kicking a fixed victim by a sting	<i>ab</i> -3 <i>l</i> -2 <i>h</i> -2 <i>a</i> -1 <i>mnd</i> -0,2 <i>mv</i> -0
P	Interrupted running transporting a prey	<i>ab</i> -2 <i>l</i> -1 <i>h</i> -3 <i>a</i> -2 <i>mnd</i> -4 <i>mv</i> -3

Notes: The indices are designated as in Table 1. In the “belligerent posture” before attack (B), the ant stands on 4 legs with the 2 fore legs raised high above its head.

the pattern of hunting to that of transportation. If the ant failed to grasp the springtail or the prey broke loose and escaped so that the ant had to start seeking prey anew, an incomplete hunting pattern was recorded.

In cases when the ant demonstrated the same behavioral element (for example, holding the prey) for a long time, this period was subdivided into 3-s intervals and each interval was interpreted as a behavioral element. Thus, repetition of identical symbols reflects the duration of the corresponding behavioral element.

The text files were compressed by archiver programs, and the compression ratios of files containing complete and incomplete behavioral patterns were compared. The compression ratio is determined here as the size of the compressed file related to that of the initial file. The smaller size of the archive file means the lower compression ratio, or the greater efficiency of compression. The archiver program was chosen

based on the following requirements: the absence of data loss during compression and the maximum efficiency of compression of the particular type of files. Considering all the parameters, we chose the KGB Archiver (v. 1.2). Since the text files describing individual behavioral stereotypes were small (less than 1 kb), the archive files proved to be larger than the initial ones, i.e., the resulting “compression” ratio was greater than 100%. Therefore, all the complete patterns for each group were merged in a single file (with the sequences of elements separated by spaces), and the incomplete ones, in another file. As a result, we obtained 4 files: the complete and incomplete patterns for naive ants and the corresponding pair for ants from the natural colony. The different compression ratios of these “combined” files were supposed to reflect the differences in complexity of the behavioral sequences encoded in them. It should be noted that other conditions being equal, longer files tend to be compressed more efficiently; therefore the combined files with

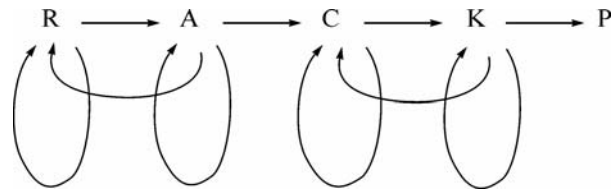
complete and incomplete patterns had to be of approximately the same initial size. In order to produce files of the same size, three of the original files were reduced to the size of the fourth, smallest file. Reduction was accomplished by excluding entire patterns rather than their parts, so that the final variants of the files consisted only of entire patterns (both complete and incomplete), and represented as many the individuals from the original samples as it was possible.

## RESULTS

Among the 14 tested ants from the natural colony, both complete and incomplete hunting patterns were observed in 7 ind., only incomplete patterns in 3 ind., only complete patterns in 1 ind., and 3 ants did not demonstrate hunting behavior. In all, 19 complete and 20 incomplete hunting patterns were recorded for this group (Table 3). Among the 12 "naive" ants, both complete and incomplete hunting patterns were observed in 5 ind., only incomplete patterns in 2 ind., only complete patterns in 1 ind., and 4 ants did not demonstrate hunting behavior. In all, 20 complete and 31 incomplete hunting patterns were recorded for this group (Table 4).

Both complete and incomplete patterns showed different frequencies of particular behavioral elements (Table 5). Some elements were rare: for example, the "belligerent posture" (B) was observed only in 0.4 and 1.6% of complete and incomplete patterns in ants from the natural colony, respectively, and was never observed in the naive ants.

The length of complete patterns varied from 6 to 22 elements (the mean value  $13.42 \pm 1.08$ ) in ants from the natural colony and from 5 to 18 in naive ones ( $8.75 \pm 0.71$ ). The length of incomplete patterns varied from 4 to 14 elements ( $6.55 \pm 0.51$ ) in ants from the natural colony and from 3 to 17 ( $6.03 \pm 0.57$ ) in naive ones. The complete patterns demonstrated by members of the natural colony included the following core elements: the pattern started by pursuit (R), which was followed by attack (A), capture and hold of the prey (C), kick with the sting (K), and interrupted run with prey (P). These elements formed the sequence R-A-C-K-P. The beginning of the complete patterns was found to vary to some extent in the naive ants. In 16 out of 20 cases the complete pattern started with a chase (R), in 1 case, with waiting (W), and in 3 cases, with a slow walk (S). It should be noted that the last 3 cases were observed as repeated patterns in



Schematic representation of a complete behavioral pattern. For designations, see text.

the same ant. In other aspects the key elements of complete patterns shown by the naive ants were the same as in the members of the natural colony. Some elements and sets of elements included in the complete pattern, such as attacks, kicks with the sting, and pairs "chase-attack" and "hold-kick" may be repeated. Some optional elements constituting the "noise," such as turns and stops, may be present between the key elements. All these variants do not change the principal scheme of the pattern (figure).

It should be noted that in 5 out of 19 cases in ants from the natural colony and in 2 out of 20 cases in naive ones the complete hunting pattern ended without stinging the prey: the ants killed the prey by crushing it with the mandibles and switched to the transportation pattern. In all these cases the springtails were considerably smaller than the average size. It may be assumed that ants are able to evaluate the size of the prey and use a different hunting pattern that does not include the final kick with the sting.

The only obligatory element present in the incomplete patterns was the attack. The beginning of the incomplete pattern varied: in ants from the natural colony, it started with a chase in 15 cases, with waiting in 4 cases, and with a slow run in 1 case; in naive ants, the incomplete pattern started with a chase in 16 cases, with waiting in 7 cases, and with a slow run in 4 cases. Capture of prey after attack was recorded in 20% of incomplete patterns for ants from the natural colony and in 25% of cases for naive ones; stinging the prey was recorded in 25 and 32% of cases, respectively. These figures indicate different degrees of completeness of the pattern. It should be noted that stinging the prey in an incomplete pattern reveals some features of a FAP: having failed to grasp the springtail with the mandibles, some ants performed aimless kicks with their stings, finishing the sequence of actions. Intermittent run with prey is the final element of a complete pattern, therefore it can never be found in an incomplete one.

**Table 3.** The number of recorded patterns (*N*) and their sequences for ants from a natural colony

No. of ant	Complete patterns		Incomplete patterns	
	<i>N</i>	sequences	<i>N</i>	sequences
1	2	RACACKCRUACKCKCCCCP	3	WARURW
		RARURACKCKCKCP		RTARW
				RARTRRW
2	3	RUACCKKCWTTWCUCP	1	RTRACTTRAUTRAC
		RUACRUTURACRURCP		
		RURBRARRACKCKCCP		
3	0		1	WBBAT
4	3	RARWTTRACCKCKCCKKCKCTP	3	RARRURAARW
		RURAAACTCKCKCCKCKCCCP		WRSA
		RACKCKCCCCP		RTRUA
5	0		1	RART
6	1	RAUURRTRACP	3	RARAK
				RUWRAW
				RARRUAR
7	4	RACKSSWSSSCCCCCP	2	RARAK
		RACKCKCP		WCKCKR
		RACCCP		
		RURARCKCKCCKCCCCP		
8	0		0	
9	2	RTRACCKCP	1	RWTAAU
		RARACP		
10	0		0	
11	2	RARARRACKKCCP	3	RTARATW
		RTACKCKCP		SWATAW
				RARUARAK
12	0		0	
13	0		2	RTAAUUAU
				RUARAW
14	2	RACWKSSKCCP	0	
		RAACCKKKCCP		
Total	19		20	

Note: The behavioral elements are designated as in Table 2.

The manifestations of incomplete and complete hunting patterns in individual naive ants should be considered in greater detail. In our previous publications (Reznikova et al., 2008; Reznikova and Pan-teleeva, 2008) it was shown that some ants in *M. rubra* colonies already in the early imaginal age possessed complete innate patterns of hunting motile prey, which manifested themselves by the “all at once” principle. It

was then assumed that the remaining members of the colony possessed incomplete patterns that could be subsequently “finished” by individual and social ex-perience. This issue will be considered in greater de-tail in the *Discussion*. Here, it should be noted that some individuals in our experiments killed one spring-tail after another without switching to prey transporta-tion, which was regarded as an incomplete pattern. For

**Table 4.** The number of recorded patterns (*N*) and their sequences for naive ants

No. of ant	Complete patterns		Incomplete patterns	
	<i>N</i>	sequences	<i>N</i>	sequences
1	0		4	STAW STAR RWARU WARW
2	0		1	WCCCCW
3	0		0	
4	3	RTRACKUCCP WTACKCCCCP RACKCP	4	RURAU RARRTAR RAUR RAUW
5	4	RTACKUP RACTTTP RTACKRTRRCCP RTRACKCP	4	RATWRAT RTRAT RTRAT WTAK
6	5	RACKCCKCP RACKCKCP RACKCCKCCCP RACKCP RACKCCP	3	WTARTUR WAKW RTACKCKCR
7	4	RUACKCP RACKCCCCCCCCCCCCP RTATACCUKCCCCCP RACKP	7	RTACKRU RAUR RACRU RUACKCKCR RACKKTCCCCCCCCCCR RACKCKCCR RACKRARACKUR
8	0		0	
9	1	RACKCP	0	
10	0		0	
11	0		0	
12	3	SACCCCP STACCKCP STAACKCP	8	WAW STAR STATS WUAUTS SARURW SAKS SATUTS SASU
Total	20		31	

Note: The behavioral elements are designated as in Table 2.

**Table 5.** Incidence of different behavioral elements in the complete and incomplete patterns

Behavioral elements	Fraction of total sequence,%			
	complete patterns		incomplete patterns	
	natural colony	naive ants	natural colony	naive ants
Wait / stop (W)	2.1	0.6	10.5	8.6
Slow walk (S)	2.9	1.7	1.6	7.0
Interrupted running / pursuit (R)	17.2	12.0	32.5	22.6
Turn (T)	4.1	7.4	11.4	11.3
U-turn (U)	5.3	2.3	8.1	8.6
Belligerent posture (B)	0.4	0.0	1.6	0.0
“Tip-and-run” attack (A)	12.7	12.6	26.7	18.3
Capturing and handling of a prey (C)	33.6	40.0	3.5	16.1
Kicking a fixed victim by a sting (K)	14.3	12.0	4.1	7.5
Interrupted running transporting a prey (P)	7.4	11.4	0	0

Note: The values are calculated for the sequences of behavioral elements in the combined files for the complete and incomplete patterns.

**Table 6.** Compression ratios of the combined files with complete and incomplete patterns

Parameter	Natural colony		Naive ants	
	complete patterns	incomplete patterns	complete patterns	incomplete patterns
Size of file before compression, bytes	147	147	147	147
Size of file after compression, bytes	93	103	83	100
Compression ratio, %	63.27	70.07	56.46	68.03

example, ant no. 7 (Table 4) already at the age of 3 days killed 4 springtails in succession and left them on the spot. In an earlier field study, we observed an ant that killed 9 springtails in succession and abandoned its prey in the experimental chamber. Since foragers of *M. rubra* hunt singly, the possibility of division of labor (some ants kill, others transport the prey) cannot be considered in this case. Such cases are more likely to result from “incompleteness” of the pattern (probably temporary) with enhancement of one of its elements, in particular killing the prey. Some naive ants showed “errors” in complete patterns. For example, the sequences RACKCCCCCCCCCCCCP and RTATACCUKCCCCCP in ant no. 7 (Table 4) describe the following activity: the ant stays in the same place for up to 40 s, twisting the prey (element “C”) in different positions. However, if these two sequences with clearly redundant actions are excluded, the early emerging complete patterns observed in naive ants appear to be more compact and streamlined than in ants from the natural colony. One may say that such ants, with an early manifestation of the hunting pattern, act in a more purposeful way, without being “distracted” by the “noise” activity. This is indicated

both by comparison of the lengths of complete patterns realized by the members of the natural and naive groups, and by analysis of the patterns themselves. The difference between these two samples (not counting the two redundant sequences mentioned above) was shown to be significant by Mann-Whitney test:  $U_{\text{emp}} = 51.5$ ,  $U_{\text{cr}} = 116.0$ ,  $p = 0.05$ . The complete patterns were significantly shorter in naive hunters than in members of natural colonies; they had a higher incidence of key elements (90.3% for naive ants and 85.2% for those from natural colonies) and a lower incidence of optional, “noise” elements (9.7 and 14.4%, respectively). It should be noted that the “noise” in the behavior of members of natural colonies consisted of such elements as “wait / stop” (W), “slow walk” (S), “turns” (T), and “U-turns” (U). In the complete patterns realized by naive ants, elements W and S represented the beginning of the pattern (in 20% of cases), whereas “noise” consisted only of turns and U-turns.

In order to obtain an objective assessment of the differences between complete and incomplete hunting patterns in ants of the natural and naive groups, the



complexity of these samples was estimated. Since the original combined files with complete and incomplete patterns varied essentially in length, their “complexity” could not be adequately compared using the compression algorithm. Therefore, we reduced the files to the same final size (see *Materials and Methods*). The results of compression of these files are shown in Table 6. First, the complete patterns could be compressed more efficiently than incomplete ones, both for ants from the natural colony and for the naive group. Second, both complete and incomplete patterns showed a higher compression ratio for members of the natural colony, as compared to the naive ants. The lowest compression ratio, i.e., the lowest complexity was observed in complete hunting patterns of naive ants.

### DISCUSSION

The behavioral sequences of the *M. rubra* hunting patterns were encoded as “texts” to be compressed by the KGB Archiver (v. 1.2). The “alphabet” of these texts included 10 behavioral elements distinguished by analysis of video records.

The efficiency of archiver programs has been demonstrated in different applications, in particular, for authorship identification (Kukushkina et al., 2001) and prediction (Ryabko and Monarev, 2005). In biology this method is widely used for estimating similarity and complexity of genetic sequences (for reviews, see Gusev et al., 1999; Li and Vitányi, 2008). However, the only case of Kolmogorov complexity concept being applied to animal behavior was the experimental study of communication in ants, which showed that the time required for information to be passed from the scout to the foragers depended on the complexity of the “text” using the alphabet {L, R}, which encoded left and right turns (Ryabko and Reznikova, 1996). This approach has never been applied to studies of natural behavior of animals.

Comparison of “successful” and “unsuccessful” hunting behavior in *M. rubra* showed that the successful, completed process of hunting was less complex than behavior that included separate fragments of the hunting pattern but did not end in capturing the prey. This may be explained by the fact that incomplete patterns are “more random” or “less regular.” In our case, this means that the sequences of complete patterns, which can be compressed more efficiently, are characterized by greater “cohesiveness,” or predictability of the next element in the chain of behavior.

It is interesting that according to our data (preliminary as they are due to a small number of samples), the file compression ratio was smaller for naive ants than for hunters from natural colonies. It follows that the hunting behavior of naive ants should be less random and more predictable, i.e., less complex. An additional argument in support of this assumption is the higher frequency of some key elements in the behavioral sequences of naive ants. Moreover, the complete patterns of naive ants are on average significantly shorter owing to a smaller fraction of “noise.”

In order to explain the observed differences in the behavior of ants reared in the laboratory and taken from natural habitats, one may consider our previous data on the scenarios of development of hunting patterns in this species (Reznikova and Panteleeva, 2008). It has been experimentally shown that the pattern of hunting motile springtails is innate in a small fraction of a *M. rubra* colony. This pattern appears “all at once” quite early in the imaginal life, at the age of 7 and even 3 days in some individuals. The number of such “natural born hunters,” i.e., individuals with a complete innate hunting pattern, may be variable; in the cited work such ants comprised only about 5% of the colony. It is essential that the hunting pattern manifests itself in full only in a few members of the colony, whereas in others it requires several stages of completion (Reznikova and Panteleeva, 2005; Reznikova et al., 2008). Since we selected the most active individuals for testing, the fraction of “natural hunters” in our groups may not reflect their actual relative abundance in the colonies. It may be assumed that our sample of 12 naive ants included 8 “natural hunters” (4 individuals did not hunt at all), whereas the group of ants sampled from the natural habitat consisted of individuals with different scenarios of development of the hunting behavior; it might include both “natural hunters” and individuals with innate fragments of the hunting pattern, subsequently supplemented by individual and social experience. Based on our data it may be hypothesized that the innate complete hunting pattern, appearing in some ants by the “all at once” principle, is characterized by a lower complexity than the same pattern “completed” by learning. This hypothesis needs to be tested during the future studies.

In general there are grounds to believe that adequate estimation of complexity of behavioral patterns may provide means of objective assessment of intra- and interpopulation variability with respect to the presence and completeness of a particular pattern. Assessment

of differences in the complexity of behavior between “natural hunters” and individuals showing only fragments of hunting behavior will allow us to understand the mechanisms of discrete variability of behavioral patterns in the ant colony.

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