A new method for evaluating the complexity of animal behavioral patterns based on the notion of Kolmogorov complexity, with ants' hunting behavior as an example

Zh. Reznikova *, S. Panteleeva, Zh. Danzanov

Institute of Systematics and Ecology of Animals, Siberian Branch RAS, Frunze 11, Novosibirsk, 630091 and Novosibirsk State University, Russia.

ARTICLE INFO

ABSTRACT

We suggest a method for evaluating the complexity of animal behavioral patterns based on the notion of Kolmogorov complexity, with ants' hunting behavior as an example. We compared complete and incomplete hunting stereotypes in members of a natural ant colony and in naive laboratory-reared ants. We represent behavioral sequences as "texts", and compress them using a data compressor. Behavioral units (10 in total), singled out from video records and denoted by letters, served as an alphabet. Successful hunting stereotypes appeared to be characterized by smaller complexity than incomplete ones. A few naive "born hunters" which enjoy "at once and entirely" complete hunting stereotypes are characterized by a lower level of complexity of hunting behavior. We conclude that innate complete stereotypes have less redundancy and are more predictable, and thus less complex. We suggest that this method for evaluating the complexity of behavioral "texts" can serve different purposes, from estimating behavioral variability within populations of animals to comparative analysis of neuronal assemblies within the brain. The method can also be applied to distinguishing between initial and transformed behavioral patterns in many fields of biology and medicine, including studying and diagnosis of neurological diseases reflected in the behavior.

1. Introduction

One of the main problems in studying animal behavior at different levels of organization, from individual and collective behavior of organisms to acting neurons in assemblies, is searching for a reliable criterion for evaluating the variability of patterns, and the notion of Kolmogorov complexity can be a useful tool here. The main idea is that comparison of complexity of certain behavioral patterns provides a quantitative criterion for identifying "pure" ("initial") patterns (behavioral stereotypes) among variable integrative phenotypes. In evolutionary biology variability is known as an important mechanism of speciation in animals, and differences in behavioral patterns have high diagnostic value for species identification. Within populations behavioral variability serves as a basis for behavioral, cognitive and social types of specialization which facilitate tuning of integrative reactions of an integral animal community to unpredictable influences in its changeable environment [16]. At the neurological level evaluation of variability and complexity of digitizing "behavior" of neurons within assemblies should provide a better understanding of the perceptive and cognitive processing in the brain [2,6,23].

The concept of complexity of animal behavior is still mainly intuitive. First of all, one has to distinguish between the complexity of flexible and stereotypic behavior. In the first case we mean levels of complexity of problems to solve and decisions to make, whereas in the second case we mean the inner coordination and regularity of species- specific repertoire. Surprisingly, despite many attempts to examine the organizational complexity of signal repertoires [3,4], there are no reliable tools for studying the complexity of animal behavioral patterns.

Since Down [5] associated particular patterns of behavior with a specific neurodevelopmental disorder (Down syndrome), recognition and description of behavioral patterns became one of key stones in human and animal behavioral studies. The prevalent method of comparative ethological studies is based on the analysis of the so-called ethograms, that is, recordings of behavioral sequences as alphabets consisting, in average, of 10–15 symbols or letters each corresponding to a certain behavioral unit (an act) [24]. For example, hunting attacks in many species, both vertebrates and invertebrates, are organized as more or less constant sequences of acts, and can be presented roughly as a recording like this: R (running)—A (approaching)—J (jumping)—F (fight)—C (capture)—H (handling)—K (killing).

* Corresponding author. Tel.: +7 383 2061303; fax: +7 3832 2170973.
E-mail address: zhanna@reznikova.net (Zh. Reznikova).

Attempts to apply the probabilistic approach for description and comparison of animal behaviors meet methodological difficulties. For example, if a behavioral pattern includes 10 acts, then, modeling this process with a Markov chain, we will find a connectivity (memory) of a chain not less than 10. Taking the number of letters in an alphabet to be 10, we then obtain the number of parameters describing this chain not less than 10^{10}. This means that a researcher has to estimate 10^{10} parameters. For example, in [8] the behavior of a selected worker honey bee was classified into 63 categories, based on the position of body parts, such as head, legs and wings, and then described using a discrete Markov model. However, there are no attempts to examine validity of the model by methods of mathematical statistics, so, there is no possibility to test whether this model is adequate for a real object.

One more problem is that the majority of mathematical models deal with stationary and ergodic processes. However, animals can gain experience, and, for instance, one successful hunting can influence the result of the next one (see details in [16]). We suggest that methods of evaluation of complexity of behaviors based on the concept of Kolmogorov complexity are more adequate to compare sequential data (ethological "texts") and to distinguish between "regular" and "chaotic" behavioral patterns. This is important for understanding the role of behavioral mechanisms in speciation, population dynamic, and individual development.

Since Kolmogorov complexity is not computable [10], it can only serve as a clue. We suggest to use the length of compressed sequences as an estimate of their Kolmogorov complexity. It is worth to note that data compression has been used as a tool for obtaining estimates of Kolmogorov complexity in different fields of science including linguistic, bioinformatics, robotics, medicine and different branches of mathematics (see, for example, [7,12,13,20]. However, the experimental study [16,19,21] of "ant language", that is, ants' ability to "compress" messages based on the alphabet consisting of two letters R (right) and L (left), still remains the sole application of Kolmogorov complexity to the analysis of animal behavior. The cited study concerns experimental situations in which animals should transfer to each other the exact information of definite length and complexity specified by experimenters. Natural behavioral patterns of animals, being presented as sequential data, as far as we know, had never been analyzed by means of Kolmogorov complexity.

In this paper we suggest a method for evaluating the complexity of animal behavioral patterns based on the notion of Kolmogorov complexity, with ants' hunting behavior as an example. A distinctive advantage of the proposed method as compared to other approaches to the analysis of animal behavior is that it furnishes ethologists a new tool for quantitative comparative analysis of sequential data (ethological "texts"). This tool is based on data compression. Ants can serve a good example here because these insects exhibit diverse behavioral patterns, both flexible and inherited.

We examined the hunting behavior of common litter-dwelling Myrmica rubra L. as an example of comparative analysis of ethological sequential data. This species can serve as a good candidate for studying variability and complexity of ethograms, because species of the genus Myrmica do not display strong division of labor within their colonies that consist of several hundreds to several thousands of individuals [1]. Each worker could be employed in many different jobs, and it is possible for experimenters to observe long behavioral sequences. It is important to note that members of Myrmica colonies are highly genetically variable [22]. Reznikova and Panteleeva [17] were the first to describe an expressive behavioral pattern for catching jumping springtails in these ants. A great deal of variability has been revealed: only a few ants possessed the whole hunting

pattern and displayed it from the very first encounter with a potential victim, whereas others displayed hunting patterns of different levels of completeness [18].

The use of ideas of Kolmogorov complexity enabled us to reveal relations between innate and learned behavior in ants and to evaluate the level of variability of hunting behavior within ant populations. The results were discussed at the 7th "Measuring Behavior" Conference [15] in 2010 and at the 8th International Conference on Computability and Complexity in Analysis in 2011. We think this method is applicable when we wish to analyze and compare any patterns consisting of sequences of units, from animal and human behavioral patterns accomplished at the individual and social level to digitizing actions of neurons within neuronal assemblages in the brain.

2. Notation and problem statement

Let us define the notions that we use to describe behavior. We selected elementary movements and postures as minimal units of behavior ("behavioral elements", for brevity). We call a "behavioral sequence" an arbitrary sequence of successive behavioral elements, and a "behavioral stereotype" – a relatively stable chain of behavioral elements. The display of behavioral stereotypes in the context of species-specific behavior is somewhat stochastic: some elements can be duplicated or dropped out; they also can be "diluted" with accessory behavioral elements ("noise"). Fixed action pattern (FAP) is defined as an instinctive behavioral sequence that is invariant and indivisible [24]. It is possible that a behavioral sequence includes a behavioral stereotype, and the latter includes a FAP.

We analyzed a rather complex behavioral stereotype as an example, that is, the hunting stereotype of M. rubra towards jumping springtails Tomocerus sibiricus (Reuter) As it was shown earlier [17], this stereotype includes determining the victim, approaching it, and then performing the FAP that we call "tip-and-run attack": the ant attacks the prey, bend the abdomen and head to the thorax, jumps to the springtail, falls on it abruptly, and stings. Then the ant intercepts the victim and transports it to the nest.

As it was briefly mentioned before, M. rubra ants possess hunting behavioral patterns of different levels of completeness: from the complete successful hunting stereotype to imperfect ones, that is, useless fragments of hunting behavior. Such variability may have different reasons: differences in genetic programs, social and individual experience, which, in turn, is age-related, etc. In a developmental study on laboratory-reared naive ants we ascertained that a few members of naive Myrmica colonies (about 6% of a colony) demonstrated "at once and entirely" complete hunting stereotype at a very early age. This means that these individuals display a hunting behavioral pattern fully completed and effectively working from their very first encounter with a potential victim, and there is no need to improve the stereotype by means of individual and social experience. Among other members of ant colonies, some ants possessed imperfect fragments of hunting behavior that needed to be completed, and others did not react to potential victims at all [18].

In this study we assumed that complete successful hunting stereotypes demonstrated by naive ants reflect inherited ("initial", "pure") behavioral patterns which are more regular and less complex than imperfect stereotypes. We applied the method based on ideas of Kolmogorov complexity to distinguish between "pure" and "noisy" behavioral patterns in ants.

3. Materials and methods

We compared two groups of highly genetically variable ants: members of a natural colony ("wild" for brevity) and naive

(laboratory reared) ants of age from 3 to 12 days. Ants were housed in transparent laboratory nests on arenas (1×2 m for the "wild" colony, and 80×50 for each of the naive colonies) and received sugar sirup and water ad libitum. The wild colony included about 3000 completely matured workers of unknown age housed with about 30 queens, and three naive colonies included 300 workers each with 1–3 queens. All naive ants were raised from pupae in separate laboratory nests. The control colony as well as pupae for raising naive groups were taken from sites with high density of springtails (potential victims of ants). All pupae were at their late stage, and they did not need help of adult nest mates to emerge. When young imagoes emerged, we added packets of eggs and small larvae in order to motivate young ants to hunt. As a result, both "wild" and naive colonies contained brood in numbers sufficient to force hunting activity in ants. As it is known, ants consume carbohydrates for themselves, and they hunt for protein food in order to provide larvae with nutrient [Brian].

We isolated naive ants from contacts with potential prey, as well as from contacts with adults (except for queens but the queens in *Myrmica* do not demonstrate any elements of hunting behavior), in order to deprive them of any outgoing signals concerning specific behaviors. This allows us to judge which behaviors awake developmentally, and which need signals from experienced workers.

It is worth to note that not all naive ants were tested. It was shown in [18] that within ant colonies about 5% of all members are "born hunters", and they display the hunting stereotype "once and entirely". In this study we intentionally chose the most active ants, and from 12 individuals there were 6 that demonstrated the completed hunting stereotype ended with killing the prey. All ants were placed one by one into glass containers with 30 live springtails, and each individual was tested once, during, on average, 15 min. This is a long period for hunting, so, some ants caught springtails several times. In these cases we counted the corresponding numbers of hunting patterns for them. To analyze ethograms from video records, we used the Observer XT 7.0 (version: 7.0.214, Noldus Information Technology). In total, we analyzed 6.5 h by the second, for 26 ants.

In order to select behavioral units, we used the following protocol. For the abdomen, legs, head, antennae and mandibles, in combination with current movements, typical states were designated by symbols (Table 1). With the use of these symbols, we described behavioral units that included "blocks" of locomotions and postures. In total, we selected 10 behavioral units (Table 2).

Using the "alphabet" of 10 behavioral units, we expressed the hunting stereotypes as text files. Every sequence (file) was constructed manually (by the researchers) from the corresponding video fragment. As the starting point of a hunting stereotype we considered the ant's approach to the victim and the display of purposive movements; transportation of a killed victim was considered the end of the complete stereotype. All cases of loss of a victim and switching to another one were considered ends of incomplete stereotypes. We represented behavioral sequences as "texts" in which behavioral units (10 in total), singled out from video records and denoted by symbols (letters), served as an alphabet: W (waiting), S (slow walking), R (running), T (turning), U (turning around), B (belligerent posture), A (attack), C (capturing a prey), K (kicking a victim by a sting), T (transporting a prey). Pooling individual ethograms of members of four groups, we obtained 4 files which included: 19 complete and 20 incomplete hunting stereotypes in "wild" ants and, correspondingly, 20 and 31 stereotypes in "naive" ants. We reduced these files to equal initial length of 147 units, compressed them with the use of a compressor called KGB archiver (v.1.2) [25] and compared ratios of compression in different stereotypes.

4. Results

From 14 members of the wild ant colony, 7 ants displayed both complete and incomplete hunting stereotypes, 3—incomplete ones only, 1—only the complete one, and 3 ants did not hunt at all. In total, we obtained 19 complete and 20 complete hunting stereotypes in wild ants (Table 3). From 12 naive ants, 5 individuals displayed both complete and incomplete hunting stereotypes, 2—incomplete ones only, 1—only the complete one, and

Table 1
Notation used for description of behavioral units in ants.

Body parts and movements	State, stand and movement			
Abdomen (ab)	Quiet, strait (0)	Elevated (1)	Tucked up (2)	Ready to kick (3)
Legs (l)	Quiet (0)	Raised and straited (1)	Belligerent posture on four legs (2)	
Head (h)	Quiet (0)	Stretched out (1)	Raised (2)	Bended (3)
Antennae (a)	Quiet (0)	Stretched out (1)	Feeling (2)	Tapping (3)
Mandibles (mnd)	Close quietly (0)	Half -open (1)	Open (2)	Snapped (3)
Movement (mv)	Stop (0)	Slow walking (1)	Running quietly (2)	Interrupted running (3)
	Attack (4)	Turning (5)	Turning around (6)	

Table 2
Behavioral units in hunting stereotypes of *Myrmica rubra*.

Unit symbol	Behavioral unit	Description in symbols
W (wait)	Waiting/stop	ab-0,1 l-0 h-0,1 a-0 mnd-0,1,2 mv-0
S (slow walk)	Slow walking	ab-0 l-0 h-0 a-1 mnd-2 mv-1
R (run)	Interrupted running/pursuit	ab-0 l-1 h-3 a-2 mnd-0,1 mv-3
T (turn)	Turning around	ab-0,2 l-0,1 h-0,2 a-0,1,2 mnd-0,1 mv-5
U (U-turn)	180 degree turn	ab-0,2 l-0,1 h-0,2 a-0,2 mnd-0 mv-6
B (belligerent posture on four legs)	Belligerent posture starting to attack	ab-3 l-2 h-2 a-1 mnd-2 mv-0
A (attack)	"Tip-and-run" attack	ab-3 l-3 h-2 a-1 mnd-3 mv-4
C (capture)	Capturing and handling of a prey	ab-3 l-2 h-2 a-1 mnd-0 mv-0,1,2
K (kick)	Kicking a fixed victim by a sting	ab-3 l-2 h-2 a-1 mnd-0,2 mv-0
P (prey)	Interrupted running transporting a prey	ab-2 l-1 h-3 a-2 mnd-4 mv-3

Table 3
Number of behavioral stereotypes (N) and corresponding behavioral sequences for "wild" ants.

Ant index number	Complete stereotypes		Incomplete stereotypes	
	N	Sequences of units (symbols as defined in Table 2)	N	Sequences of units (symbols as defined in Table 2)
1	2	RACACKCRUACKCKCCCCCP RARURACKCKCKCP	3	WARURW RTARW RARTRRW
2	3	RUACCKKCWTTWCUCP RUACRUTURACRURCP RURBRARRACKCKCCP	1	RTRACTTRAUTRAC
3	0		1	WBBAT
4	3	RARWTTRACCKCKCCKKCKCTP RURAAACTCKCKCCCKCKCCCP RACKCKCCCCP	3	RARRURAARW WRSA RTRUA
5	0		1	RART
6	1	RAUURRTRACP	3	RARAK RUWRAW RARRUAR
7	4	RACKSSWSSSCCCCCCP RACKCKCP RACCCP RURARCKCKCCKCCCCP	2	RARAK WCKCKR
8	0		0	
9	2	RTRACCKCP RARACP	1	RWTAAU
10	0		0	
11	2	RARARRACKKCC. RTACKCCKCP	3	RTARATW SWATAW RARUARAK
12	0		0	
13	0		2	RTAAUAU RUARAW
14	2	RACWKSSKCCP RAACCKKKCCP	0	
Total	19		20	

4 ants did not hunt at all. In total, we obtained 20 complete and 31 incompete hunting stereotypes in naive ants (Table 4).

Both in complete and in incomplete stereotypes, some behavioral units differ by their frequencies of occurrence (Table 5). Several behavioral units are rare. For example, "B" ("Belligerent posture") was recorded only in 0.4% from complete stereotypes and in 1.6% from incomplete ones within the wild colony, and it was never met in naïve ants. The length of the complete stereotypes varied from 6 to 22 units (13.42 ± 1.08 in average) in the wild ants and from 5 to 18 in naive ants (8.75 ± 0.71 in average). The length of the incomplete stereotypes varied from 4 to 14 units (6.55 ± 0.51 in average) in the wild ants and from 3 to 17 in naive ants (6.03 ± 0.57 in average).

The following units appeared to be key ones for the complete hunting stereotype in wild ants: the stereotype began from pursuit (running, R), then capturing (C), attack (A), kicking (K) and transporting of a prey (P) followed; so, the complete stereotype looked like " R–A–C–K–P" . In naïve ants initial parts of the complete hunting stereotype are variable. In 16 from 20 cases hunting started from R, in one case – from W, and in three cases from S. In general, key elements are the same in wild and in naive ants. It is worth to note that some units (and blocks of units) repeat themselves. This concerns, for example, attacks (A), kicking (K), as well as pairs of units "R–A" and "C–K". It is possible that key units alternate with optional ones that can be considered "noise" (such as turns and stops). In several cases (5 in wild ants and 2 in naive ones) the complete stereotype ended with killing a victim by clenching mandibles and not by kicking it with a sting. In all cases a springtail was smaller than average. We assume that ants can evaluate the size of the potential victim and use an alternative hunting stereotype which is simpler for a smaller prey. However, a basic scheme of the complete stereotype is stable (Fig. 1).

Incomplete stereotype includes only one obligatory unit: the attack (A). Initial parts of an incomplete stereotype are variable. In wild ants incomplete stereotypes started from R in 15 cases, from W in 4 cases, and from S in 1 case. In naive ants incomplete stereotypes started from R in 16 cases, from W in 7 cases, and from S in 4 cases. Attacks were followed by capturing in 20% of incomplete stereotypes in wild ants, and in 25% in naive ants, and capturing was following by kicking in 25% and 32% correspondingly. This indicates variable degrees of completeness of hunting stereotypes. It is worth of noting that, being included into the incomplete stereotype, kicking by a sting (K) indicates Fixed Action Pattern (FAP). Even not capturing a prey by their mandibles, some ants "stabbed air" by their stings thus finishing a behavioral sequence they have started.

Before comparing complete and incomplete stereotypes in naive and wild ants, it is important to consider some individual peculiarities of hunting behavior in naive ants. As it was shown earlier [18], some members of an ant family enjoy "at once and entirely" hunting stereotype. They are able to catch and kill jumping springtails from the very first encounter. It is possible that other members of the family possess incomplete hunting stereotypes and they can complete their hunting patterns by means of individual and social experience. Naive ants can demonstrate not only complete and effective hunting patterns but also incomplete but rather expressive ones. For example, in our experiments several naive ants killed one springtail after another; however, they did not carry their victims to the nest, so these stereotypes were considered incomplete. For example, the individual N 7 (Table 4), when it was only three days old, killed 4 springtails one by one leaving them on site and not transporting to the nest. Earlier we observed an ant that killed 9 springtails in

Table 4
Number of behavioral stereotypes (N) and corresponding behavioral sequences for naive ants.

Ant index number	Complete stereotypes		Incomplete stereotypes	
	N	Sequences of units (symbols as defined in Table 2)	N	Sequences of units (symbols as defined in Table 2)
1			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 RACKCCCCCCCCCCCCCP RTATACCUKCCCCCP RACKP	7	RTACKRU RAUR RACRU RUACKCKCR RACKKTCCCCCCCCCCR RACKCCKCCR 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	

Table 5
Proportion of different behavioral units in complete and incomplete stereotypes.

| Behavioral unit (as in Table 2)	Percentage in the whole behavioral sequence (%)			
	Complete stereotypes		Incomplete stereotypes	
	Wild ants	Naive ants	Wild ants	Naive ants
W (wait)	2.1	0.6	10.5	8.6
S (slow walk)	2.9	1.7	1.6	7.0
R (interrupted running /pursuit)	17.2	12.0	32.5	22.6
T (Turning around)	4.1	7.4	11.4	11.3
U (180 degree turn)	5.3	2.3	8.1	8.6
B (belligerent posture starting to attack)	0.4	0	1.6	0
A ("tip-and-run" attack)	12.7	12.6	26.7	18.3
C (capturing and handling of a prey)	33.6	40.0	3.5	16.1
K (kicking a fixed victim by a sting)	14.3	12.0	4.1	7.5
P (interrupted running transporting a prey)	7.4	11.4	0	0
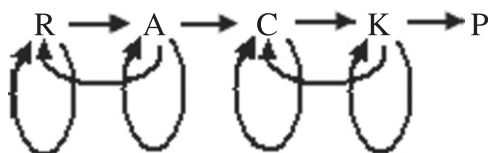
Fig. 1. A scheme of a complete stereotype (symbols as defined in Table 2).

succession. As it was mentioned before, there is no division of labor in *Myrmica* ants (when some ants kill a prey and others transport it), therefore, we should rather consider these stereotypes as incomplete (perhaps, provisionally). Sometimes complete stereotypes in naive ants malfunctioned as well. For example, the individual N 7 demonstrated sequences RACKCCCCCCCCCCCCCP and RTATACCUKCCCCCP. However, if we exclude these two specific

Table 6
The compression ratios of the resulting files containing complete and incomplete stereotypes.

Parameters	Wild ants		Naive ants	
	Stereotypes		Stereotypes	
	Complete	Incomplete	Complete	Incomplete
Size of the file before compression (in bytes)	147	147	147	147
Size of the file after compression (in bytes)	93	103	83	100
Compression ratio, %	63.27	70.07	56.46	68.03

redundant patterns, then, in general, early displays of complete hunting stereotypes in naïve ants seem to be more laconic and integral than complete stereotypes in wild ants. Naive "born hunters" demonstrate goal-seeking behavior, that is, they do not include "noise" units in their stereotypes and do not get distracted from hunting. This can be confirmed by comparing lengths of complete stereotypes in naïve and wild ants as well as the analysis of stereotypes themselves. We excluded two "redundant" behavioral patterns (demonstrated by the ant N 7) mentioned above and tested the difference between the lengths of complete stereotypes in naïve and wild ants by Mann–Whitney U test:

U empirical$=51.5$, U critical$=116.0$, $P < 0.05$. Complete hunting stereotypes in naïve ants appeared to be reliably shorter than in members of wild colonies. Key elements are more frequent in the first case: 90.3% versus 85.2% in wild ants.

The application of the archiver revealed that the successful (complete) hunting stereotypes in "wild" ants were characterized by smaller complexity than the incomplete ones: the compression ratio is 63.27% for the first file, and 70.07% for the second one. It is likely caused by a greater frequency of key elements and less "noise" in complete stereotypes. The complete stereotypes also appeared to have less redundancy and to be more predictable. The same was found in naïve ants: 56. 4% and 68.03%, correspondingly (Table 6).

We tested the Hypothesis H_0 (the sequences from two sets are generated by one source) against H_1 (the complexity of sequences from one set is, on average, larger than the complexity of sequences from the other) by the Mann–Whitney–Wilcoxon test. It turned out that files corresponding to the successful hunting stereotypes compress better than those corresponding to incomplete hunting stereotypes both in wild and in naïve ants. So, H_0 is rejected, and we can conclude that, on average, the complexity of sequences from the first set is larger than in the second. In sum, these data support our initial suggestion that successful hunting stereotypes in ants are less complex.

5. Discussion and conclusion

Applying the suggested method based on data compression to comparison of ethograms in different groups of ants we have revealed that both in "wild" and naive (laboratory-reared) ants complete hunting stereotypes are characterized by smaller complexity than imperfect stereotypes which need to be completed. It turned out that complete stereotypes contain more "key" behavioral elements and thus less "noisy" than incomplete ones.

It is of particular interest that in ant colonies naive "born hunters" which possess "at once and entirely" hunting stereotypes are characterized by a lower level of complexity of hunting behavior. Their hunting stereotypes are possibly most "laconic" and clear. We conclude that innate complete stereotypes have less redundancy and are more predictable, and thus less complex. This supports the hypothesis of distributed social learning by Reznikova and Panteleeva [18] that a few carriers of the whole hunting stereotype to be spread within an ant colony, can serve as catalysts of social learning for other

individuals which possess only fragments of relevant behavioral patterns. Indeed, it could be rather costly for animal brains to be equipped with composite stereotypes for all possible vital situations. Propagation of composite stereotypes, new for certain populations, is based on relatively simple forms of social learning such as social facilitation which underlies species' predisposition to learn certain behaviors and does not require feats of intelligence from animals. It is possible that similar mechanisms underly propagation of some sophisticated behaviors in populations of highly intelligent species, such as stone-handling in Japanese macaques [11], tool use in New Caledonian crows [9], and hand-clasp grooming in chimpanzees [14]. We speculate that such a mechanism of propagation of composite behavioral patterns could be more parsimonious than "culture" in some species and some situations. In order to address this question a relevant method is needed to extract "initial" behavioral patterns.

Basing on the cited studies and presented data on evaluation of complexity of behaviors, it seems that individual variability of behavioral patterns plays greater role than it was suggested so far. Our concept of successful phenotypes based on distribution of fragments of relevant behavioral patterns within populations and abilities of individuals to complete their imperfect patterns can be considered a compromise between learned behaviors and, alternatively, the products of longer-term selection for specific motor traits. This can be considered a display of the thin balance between highly behavioral flexibility in changeable environment and maintaining a standard of average responses across populations. The proposed method provides a tool for selecting and describing "initial" behavioral patterns basing on sequential data, that is, on ethological "texts", and evaluate deviations from species – specific standards.

In perspective, the use of ideas of Kolmogorov complexity for studying animal behavior is a promising tool to be used in different areas of behavioral and evolutionary research. In particular, this method can help to extract "basic" (completely innate) behavioral patterns by comparing behavioral sequences of different levels of complexity and flexibility. This is particularly important for evolutionary and ethological studies in the field. We suggest that this method for evaluating the complexity of behavioral patterns can serve different purposes, from estimation of behavioral variability within populations of animals to comparative analysis of neuronal assemblies that are active during learning, recall and forgetting. This method can also be applied to distinguishing between initial and transformed behavioral patterns in many fields of biology and medicine, including studying and diagnostic of neurological diseases.

References

[1] M.V. Brian, Feeding and growth in the ant *Myrmica*, J. Anim. Ecol. 42 (1973) 37–53.

[2] D. Berger, D. Warren, R. Normann, A. Arieli, S. Grün, Spatially organized spike correlation in cat vizual cortex, Neurocomputing 70 (10–12) (2007) 2112–2116.

[3] T.J. DeVoogd, Neural constraints on the complexity of Avian song, Brain Behav. Evol. 63 (2004) 221–232.

[4] L.R. Doyle, B. McCowan, S.F. Hanser, C. Chyba, T. Bucci, E. Blue, Applicability of information theory to the quantification of responses to anthropogenic noise by Southeast Alaskan Humpback Whales, Entropy 10 (2008) 33–46.

[5] J. L. H. Down, Mental Affections of Childhood and Youth, London: Churchill (1887), (1990) re-issued as Classics in Developmental Medicine, No. 5. London: MacKeith Press.

[6] R.F. Galán, G.B. Ermentrout, N.N. Urban, Predicting synchronized neural assemblies from experimentally estimated phase-resetting curves, Neurocomputing 69 (10–12) (2006) 1112–1115.

[7] K. Hecox, S. Nayak, K. Gin, A. McGee, W. van Drongelen, Linear and nonlinear measures of the human neonatal EEG, Neurocomputing 52–54 (2003) 779–786.

[8] H. Ikeno, T. Ohtani, Reconstruction of honeybee behavior within the observation hive, Neurocomputing (38–40) (2001) 1317–1323.

[9] A Kacelnik, Tools for thought or thoughts for tools? Proc. Nat. Acad. Sci. 106 (2009) 10071–10072.

[10] A.N Kolmogorov, Three approaches to the quantitative definition of information, Prob. Inform. Transm. 1 (1965) 1–7.

[11] J.B Leca, N. Gunst, M.A. Huffman, Complexity in object manipulation by Japanese macaques (Macaca fuscata): a cross-sectional analysis of manual coordination in stone handling patterns, J. Comp. Psychol. 125 (2011) 61–71.

[12] M. Li, P. Vytanyi, An Introduction to Kolmogorov Complexity and its Applications, Springer Verlag, 2008.

[13] V.F. López, R. Aguilar, L. Alonso, M.N. Moreno, J.M. Corchado, Grammatical inference with bioinformatics criteria, Neurocomputing 75 (2012) 88–97.

[14] W.C. McGrew, The Cultured Chimpanzee: Reflections on Cultural Primatology, Cambridge University Press, 2004.

[15] S. Panteleeva, Zh. Danzanov, Zh. Reznikova, Using ideas of Kolmogorov complexity for studying animal behaviour patterns, Proceedings of Measuring Behavior – 2010: 7th International Conference on Methods and Techniques in Behavioral Research, (2010) 174–176. Eindhoven, The Netherlands, Noldus Information Technology.

[16] Zh. Reznikova, Animal Intelligence: From Individual to Social Cognition, Cambridge University Press, Cambridge, 2007.

[17] Zh. Reznikova, S. Panteleeva, Interaction of the ant *Myrmica rubra* L. as a predator with sprigtails (Collembola) as a mass prey, Dokl. Biol. Sci. 380 (2001) 475–477.

[18] Zh. Reznikova, S. Panteleeva, An ant's eye view of culture: propagation of new traditions through triggering dormant behavioural patterns, Acta Ethol. 11 (2) (2008) 73–80.

[19] Zh. Reznikova, B. Ryabko, Numerical competence in animals, with an insight from ants, Behaviour 149 (2011) 150–172.

[20] B. Ryabko, J. Astola, A. Gammerman, Application of Kolmogorov complexity and universal codes to identity testing and nonparametric testing of serial independence for time series, Theor. Comput. Sci. 359 (2006) 440–448.

[21] B. Ryabko, Zh. Reznikova, Using shannon entropy and Kolmogorov complexity to study the communicative system and cognitive capacities in ants, Complexity 2 (1996) 37–42.

[22] P. Seppä, P. Pamilo, Gene flow and population viscosity in *Myrmica* ants, Heredity 74 (1995) 200–209.

[23] F.T. Sommer, T. Wennekers, Synfire chains with conductance-based neurons: internal timing and coordination with timed input, Neurocomputing (2005) 449-454.

[24] N. Tinbergen, The Study of Instinct, Oxford University Press, London and New York, 1951.

[25] ⟨http://www.softpedia.com/get/Compression-tools/KGBArchiver.shtml⟩.

Zhanna Reznikova, Prof., Dr. Sci (Moscow State University, 1990). She is the head of Laboratory of Community Ethology at the Institute of Systematics and Ecology of Animals, Siberian Branch Russian Academy of Science and the head of Department of Comparative Psychology at the Novosibirsk State University. She is an expert in experimental ethology, behavioral ecology and measuring behavior. She has published more than 100 papers in international journals and conference proceeding, and the book "Animal Intelligence: From Individual to Social Cognition" (Cambridge University Press, 2007).

Sofia Panteleeva received a PhD degree in entomology at the Institute of Systematics and Ecology of Animals, Siberian Branch RAS in 2004. She is a researcher in Laboratory of Community Ethology at the Institute of Systematics and Ecology of Animals, and the assistant professor at the Novosibirsk State University. She is co-author of papers in several journals. Her research interest are in the areas of experimental ethology, behavioral ecology and measuring behavior.

Zhargal Danzanov received a M.Sc. In Mathematical Biology at the Novosibirsk State University in 2010, and currently he is a PhD student at the Institute of Systematics and Ecology of Animals. His research interest are in the areas of experimental ethology, behavioral ecology and measuring behavior.