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TRANSMISSION OF INFORMATION REGARDING THE QUANTITATIVE CHARACTERISTICS OF AN OBJECT IN ANTS*

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Results of laboratory experiments demonstrating that ants are capable of assessing the number of objects within the limits of several tens and transmit this information to other individuals are described. It has been demonstrated that ants may use these capacities for transmitting information regarding the coordinates of an object.

It is now been established that the most highly organized mammals (primates, dolphins, fur seals, and some canids), as well as the corvid birds are capable of elements of abstraction and extrapolation, and may formulate for themselves some empirical rules on the basis of the regularities they have observed [5, 8, 19, 22]. The use of intermediary languages, which animals have been taught by experimenters, has been a new stage in the development of ethology. The capacity of higher monkeys to use symbols semantically, to group similar concepts, and to combine them for the expression of a wish in a goal-directed manner has been demonstrated [18]. However, the problem of the existence in them of a developed natural language remains an open one.

One of the highest manifestations of the cognitive activity of animals is their capacity to form concepts regarding quantitative attributes of objects. It has been demonstrated in numerous experiments that some species of mammals and birds are capable of distinguishing sets consisting of various numbers of elements, and to make a choice on the basis of the "greater than-less than" attribute [1, 6, 15, 17]. Experiments in primates and parrots which have been taught intermediary languages offer grounds for assuming that there are the rudiments of capacities for counting in them, by means of numerical symbols [18, 21]. However, the limits of their capacities for the formation of concepts regarding quantity still had not been established.

The cognitive capacities of insects have been studied no less intensively. Here, the classical works of K. von Frisch and his followers, who demonstrated the presence in a honey bee of the "dance language" which has the character of symbolic signaling, must be mentioned, first and foremost [3, 9, 16, 20].

It is now been established that the social Hymenoptera are capable of elements of abstraction, the formation of empirical rules, and possess a labile system of communication, as well as an individual hierarchy [4, 7, 10, 11]. It is known that the ants of highly social species are capable of joint, fairly complex activity, which includes the maintenance of colonies of aphids and cicadas in the dense crowns of trees, group foraging in high grasses, and the protection of the boundaries of extensive fodder territories [2, 4, 25].

Despite the numerous studies devoted to the investigation of the communicational capacities of animals, the problem of the presence of a developed language behavior for the majority of highly-social species has remained an open one (the "dance language" of the honey bee is the only exception). This seems paradoxical, if one considers that such animals very readily master complex intermediary languages proposed by experimenters. Apparently, the identification of natural language

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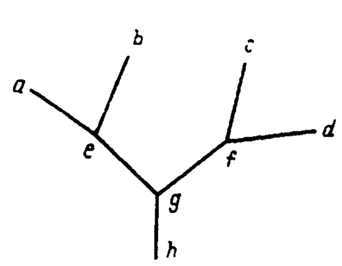

Fig. 1. Diagram of a "binary tree" maze.

behavior in such highly-social species as higher primates, dolphins, termites, and ants requires the development of an appropriate methodological approach. Majority of ethologists who have studied the communication systems of social animals openly or implicitly have attempted to discover "words," "phrases/sentences," and similar linguistic units in the system of their communication, i.e., to compile something like a dictionary.

We have previously proposed the fundamentally different approach to the study of communication systems and elementary intellective activity in ants [12, 13, 23, 24]. The essence of this approach, called the information theory approach, consists in the following: a situation was created in the experiment in which ants had to transmit information to one another regarding some quantitatively measurable magnitude, known to the experimenter, in order to obtain food. In the process, the time spent by the ants on the transmission of the information was measured.

Thus, in [12, 13, 23, 24], the results obtained by means of a "binary tree" maze were presented. A diagram of such a "tree" with two forks on each branch is depicted in Fig. 1. There are four "leaves" (a, b, c, d) on such "tree," three of which terminate in an empty food dispenser, and only one of which terminates in a food dispenser containing syrup. An ant, starting movement from point h, must choose whether to turn to the right or the left at point g and then at points e and f. The number of forks was varied in different experiments from one to six.

A situation was created in the experiments in which the ant, informed of the location of the bait, transmitted reports about this to other ants which using only this information found the food dispenser independently, practically without making erroneous turns (for greater detail see [13]). The number of turns from "root of the tree" (point h in Fig. 1) to the "leaf" with the food dispenser was the measurable magnitude in these experiments. This magnitude varied from one to six in different experiments, and it turned out that the time of transmission of the information by the ants was proportional to the number of forks.

In the study presented, the investigation of the capacity of ants to assess quantitative magnitudes (within the limits of several tens) and to transmit to relatives information regarding the number of objects and the coordinates of objects in a plane was continued by means of a modification of the experimental mazes.

METHODS

The experiments were carried out in 1984-1987 and in 1992 with *Formica polyctena* Foerst. ants. The ants were maintained in groups (800-1500 individuals) with the brood and a female in transparent nests in laboratory arenas measuring 2 m^2 in area. The living territory was divided into two parts: a smaller living space in which the nest was found, and a larger working space in which the experimental setup was located. The ants received food once in every two to three days and only in the experimental setup. All of the extra-net workers were marked individually.

It is known that in solving complex tasks, the search activity of ants of the species under investigation is organized in the following manner: the foragers are broken up into groups (three to eight individuals); one of the group, the prospector, finding food, attracts only its own foragers to it [13].

An experimental "ladder" setup was used to study the capacity of ants for the assessment of quantitative magnitudes and for transmitting information regarding the number of objects (Fig. 2a, b, c). Matches or small plastic rods served as the branches. Each branch ended in a food dispenser. One of the food dispensers contained syrup; the remaining were empty. The ants were required to transmit information to one another regarding the number of the "branch" with the food dispenser.

The prospector was set down on the "branch" with the filled food dispenser to familiarize it. Returning independently to the nest, the prospector sometimes immediately began to make contacts with the members of its group. After contact, the

TABLE 1. Results of Experiments on a "Vertical Trunk" Setup No. 1

No. of experiment	Date (1984)	Number of branch containing food dispenser	Time of contact of prospector with foragers, sec	Number of prospector-forager group
1	07/10	10	42	I
2	07/10	10	40	II
3	07/10	10	45	III
4	07/14	40	300	II
5	07/14	40	280	IV
6	07/17	[illegible]	90	II
7	07/17	13	98	I
8	07/17	28	110	III
9	07/17	28	120	V
10	07/19	20	120	V
11	07/19	20	110	III
12	07/19	35	260	III
13	07/19	35	250	V
14	07/23	30	160	I
15	07/23	30	170	III

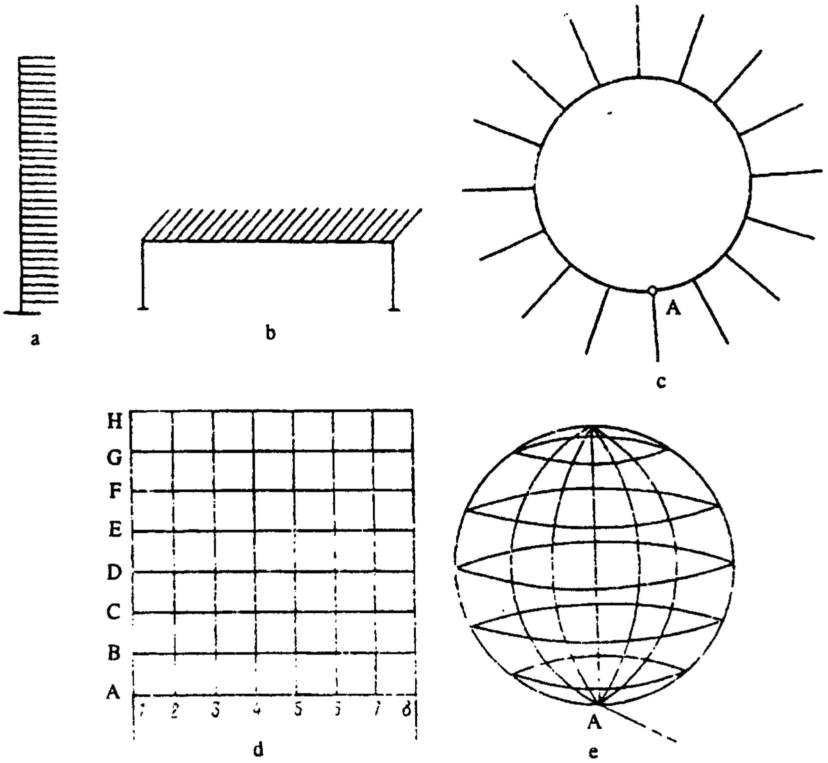

Fig. 2. Experimental setups for investigation of the capacity of ants for counting and transmission of information regarding the coordinates of a food dispenser: a) "Vertical trunk"; b) "horizontal trunk"; c) "circle"; d) "Cartesian coordinate" ("lattice"); e) "globe."

entire group left the nest and moved in the direction of the setup. In this case we removed the prospector with tweezers and isolated it, thus compelling the group of foragers to search for the food independently. But, more often, following familiarization with the localization of the food, the prospector returned to the food dispenser alone: sometimes it was in error and found food after visiting several empty food dispensers. The number of solitary trips of the prospector could go as high as four before it led out its group. In all of the cases, we recorded the time of contact of the prospector with the foragers in the nest. Touching the first ant was considered the beginning of contact; the exiting from the nest of the first two foragers was considered the end. For calculations, the time of the last contact of the prospector with foragers, after which the group left the nest for food, was used.

In order to exclude the possibility of the use of an odor trace, in all variants of the experiment setup was replaced by an identical (new) one during the time that the prospector contacted the foragers in the nest. In the course of the experiment, the food dispenser was placed on various "branches," from the 1st to the 60th. The numbers of the "branches" in successive experiments were selected randomly. In the course of each experiment involving a food dispenser located on the ith branch, all groups of foragers which were active on that day (from I to IV) worked successively. In all, in 1984-1985, 26 groups of foragers from two laboratory families of *F. polyctena* participated in the experiments, and in 1992, six groups from one family. Fifteen experiments were carried out on a setup involving the vertical disposition of the "branches" (the "vertical trunk," Fig. 2a), during which five prospectors and their groups of foragers worked (groups I-V in Table 1). In order to test whether the time of transmission of information regarding the number of the "branch" depends on its length, as well as on the distance between the "branches," an analogous series of experiments (16 in all) was carried out on a similar "vertical trunk," in which the distance between the "branches" was twice as great, and the "branches" themselves were three times and five times longer (for various experiments). In order to investigate whether the time of transmission of information depends on the form of the setup, we used a "horizontal trunk" (Fig. 2b; 30 experiments were carried out in 1984-1985, and 10 experiments in 1992; 38 experiments were carried out in 1985 on a "circle" setup, Fig. 2c).

The investigation of the capacity of the ants for the transmission of information regarding the coordinates of an object was carried out in 1986 by means of a "Cartesian coordinate" setup, a flat grid of thin metal rods (8×8, 6×6, 5×5 lines, Fig. 2d), painted white with nitrocellulose enamel and fixed so that the ants could only reach the starting point of the maze across a small bridge (point A in Fig. 2d). The further movement was possible only along the lattice rods. In one of the variants the lattice had a form of a "globe" with five "meridians" and five parallels; in this case the bridge led to the lower "pole" (Fig. 2e). In the course of the experiments the food dispenser was placed at various nodes of the lattice, while on the other nodes the empty food dispensers were placed. Five groups of foragers from two laboratory families of *F. polyctena* worked on the four setups.

INVESTIGATION RESULTS

I. Capacity of Ants for Assessment of the Number of Objects and for the Transmission of This Information to Foragers. In the aggregate, 32 groups of foragers (5 in 1984, 21 in 1985, and 6 in 1992) worked on all five setups. Groups of foragers left the nest in all 152 times following contact with the prospector, and moved toward the food dispensers. In the process, a group of foragers went to the "branch" with the food dispenser immediately in 117 cases, without making erroneous visits to empty food dispensers. In the remaining instances, ants reached empty food dispensers and began to look for food by iterative examination of neighboring "branches." In all experiments (a total of 35), when the foragers did not find the food dispenser, the same "incapable" prospectors had been working. They were identified in the course of the experiments and were subsequently not permitted into the working part of the arena. In Table 1, the results of experiments on one of the setups are shown as an example.

Since there were no more than 25 "branches" on all of the setups, the probability of random approach to the "branch" with the food dispenser on the first try was not more than 1/25. Thus, the high probability of an approach to the food dispenser on the first try can only be explained by the fact that the group of foragers was guided by information obtained from the prospector (the probability of reaching the food dispenser randomly no fewer than in 117 instances out of 152 is less than 10^{-100}). In control tests, the ants, including the prospectors, which were allowed onto the setup between sessions and which were not familiar with the coordinates of the food dispenser, as a rule, did not find food, although they actively searched for it, investigating empty "branches."

The results of experiments carried out on different setups are shown in the graph (Fig. 3). It can be seen that the association between the number of "branch," i and the time of contact of the prospector with foragers, t, is close to linear; the high significance of the coefficients of correlation also suggests this (see Table 2). On the "circle" setup, the number of the "branch" with food dispenser i was counted from point A counterclockwise, since in all cases the ants moved only in this direction following contact with the prospector, even when the clockwise pathway was substantially shorter (we do not know the reasons for this). It is also interesting to note that on a "vertical trunk" setup, foragers after contact with the prospector

TABLE 2. Coefficients of Correlation and Confidence Intervals for Coefficients of the Linear Regression Equation

Type of setup	Size of sample (number of experiments)	Maximal number of branches	Values		
				$a \pm \Delta a$	$b \pm \Delta b$
"Vertical trunk" No. 1	[illegible]	40	0.93	7.3 ± 4.1	-28.8 ± 0.53
"Vertical trunk" No. 2	[illegible]	60	0.99	5.88 ± 0.44	-17.11 ± 0.65
"Horizontal trunk" No. 1	30	25	0.91	8.54 ± 1.1	-22.2 ± 0.62
"Horizontal trunk" No. 2	[illegible]	17	0.88	4.92 ± 1.27	-18.94 ± 47.5
Circle	38	25	0.98	8.62 ± 0.52	-24.4 ± 0.01

Note: r, coefficient of correlation; ± Δ, 95% confidence interval.

TABLE 3. Trajectories of Ants when Moving to the Food Dispenser on an 8 × 8 Line "Lattice" (Fig. 1d)

Date, food dispenser coordinates	Prospector trajectories	Forager trajectories	Trajectories of foragers not reaching the goal
07/31/86 B_6	$A_1I_1I_3I_1I_3$ B_3B_6; $*A_1I_1I_3I_4D_4$ $D_3B_3B_6$; $*A_1A_6B_6$	$'A_1I_1I_8B_8B_6$; $A_1B_1B_6$; $A_1A_8B_8B_7C_7C_8$ $C_7B_7A_7A_8B_8B_6$; $A_1A_8B_8B_6$; $A_1C_1C_8C_6B_6$; $A_1B_1B_6A_5A_6B_6$	$A_1E_1E_3I_3I_6I_1A_1$ $A_6B_6I_6I_8F_8F_4I_4$ $I_7I_1A_1I_1A_1$; $A_1D_1D_2F_2F_4F_3I_3I_1$ $B_1A_1B_1B_2C_2C_1C_5G_6$ $G_9B_9B_1A_1$
08/09 D_4	$A_1A_8D_8D_4$	$A_1A_3B_3B_2G_1B_1I_1$ $G_1A_1I_1I_8C_8C_6D_4$ $A_1A_5D_5D_4$; $A_1A_5D_5D_4$; $*A_1I_1A_1I_1I_8H_9$ $B_9C_6C_4C_6D_6D_4$; $A_1A_2B_2B_6D_6D_4$	$A_1I_1I_8I_1A_1A_8A_6B_6$ $G_6G_4I_4I_8I_1A_1$; $A_1A_8A_5D_5G_5I_5I_1I_5$ $I_1A_1B_1B_2I_2I_4F_4G_4$ $I_4I_1C_1A_1A_2I_2I_1$ B_1A_1
08/11 D_4	$A_1B_1B_2B_6D_6D_4$	$A_1A_9D_9D_4$; $A_1A_8D_8D_4$; $A_1D_5D_5D_4$; $*A_1A_2I_2I_4D_4$; $A_1A_3D_3D_4$	$A_1A_8A_4I_4I_8H_8I_8$ A_8A_1; $'A_1C_1C_8A_8A_1$

Note: Repeated forager or prospector trajectories are designated by an asterisk; the symbol ";" divides trajectories of particular individuals.

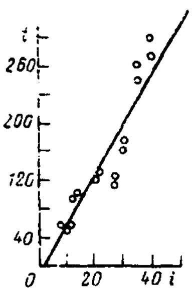

Fig. 3. Relationship of time of contact of prospector with foragers t to the number of "branch" with food dispenser i. "Vertical trunk" setup No. 1.

TABLE 4. Results of Experiments on "Cartesian Coordinate" Setups

Experimental setup	Experiment number	Food dispenser coordinates	Number of foragers reaching (+) and not reaching (−) the food dispenser		Time spent by prospector for contact with foragers, sec
			«+»	«−»	
8 × 8 "lattice"	1	G_7	4	2	60
	2	B_6	5	2	70
	3	B_6	3	1	80
	4	B_6	5	0	65
	5	D_4	4	2	90
	6	D_4	4	2	100
	7	D_4	7	1	95
	8	H_4	6	2	90
	9	H_4	5	0	105
	10	G_2	5	1	110
	11	G_2	5	0	105
6 × 6	12	C_2	6	0	60
	13	C_2	[illegible]	0	55
	14	C_4	5	0	70
	15	E_2	6	0	44
	16	E_2	5	1	52
	17	E_2	6	1	48
5 × 5	18	C_6	4	0	40
	19	C_6	4	0	45
	20	C_6	5	1	40
	21	C_2	6	2	50
	22	B_1	4	0	56
"Globe"	23	$\underline{B_4}$	3	0	80
	24	$\overline{\underline{B_4}}$	4	1	72
	25	$\overline{B_4}$	4	0	65
	26	$\bar{D}_4$	4	0	50
	27	$\bar{D}_4$	4	0	58
	28	D_2	6	1	45
	29	D_2	5	2	52
	30	D_2	3	0	50
	31	D_2	3	0	60

rose initially rapidly to the upper end of the "trunk," and then slowly returned backwards, to the "branch" with the food. Therefore we count the number of the "branch" i from the upper point of the "trunk."

For all of our setups which have a different form and orientation, as well as a varied length of the branches and a different distance between them, the relationship of the time of transmission of information t to the number of "branch" i is identically well described by an empirical equation of the type $t = ai + b$.

II. Transmission of Information Regarding the Coordinates of an Object. In aggregate, five prospector-forager groups worked on the four experimental setups. In all, a group left the nest 40 times and moved toward the food dispenser. Let us recall that the prospector was purposely removed. In this case, foragers reached the food dispenser in 31 cases in less than 5 min. In the remaining instances, the ants reached empty food dispensers and began to search for food by iterative examination of the "nodes."

It is interesting to note that in those cases in which the group moved toward the food dispensers following contact with the prospector, the foragers moved from the initial point fairly quickly, but not in a compact group, and reached the "node" with the food dispenser each by its own pathway, and the path chosen by a forager the first time was far from always used by it on repeat raids. The specific trajectories are presented in Table 3. Data on the time spent by the prospectors on contact with their groups are presented in Table 4.

In order to test whether the forager ants actually are guided by information obtained from the prospector when visiting the food dispensers, a series of control experiments was carried out in which all of the ants were given the opportun-

TABLE 5. Results of Control Experiments on "Cartesian Coordinate" Setups

Experimental setup	Number	Food dispenser coordinates	Number of ants visiting the maze	Results of 15-minute searches
8 × 8 "lattice"	1	G_7	12	–
	2	B_6	7	-
	3	B_6	10	
	4	B_6	6	-
	5	D_4	12	-
	6	D_4	4	–
	7	D_4	1	–
	8	H_4	9	–
	9	H_4	5	-
	10	G^2_2	8	–
	11	C_4	8	–
6 × 6	12	C_4	8	-
	13	C_4	6	-
	14	G_2	4	–
	15	G_2	9	–
	16	G_2	2	–
5 × 5	17	C_6	4	–
	18	C_6	5	+
	19	C_6	6	–
	20	B_2	6	–
	21	B_2	3	–
	22	B_4	3	–
	23	B_4	9	+
	24	B_4	10	–
"Globe"	25	D_4	11	–
	26	D_4	10	–
	27	D_2	6	+
	28	D_2	7	–
	29	D_2	12	–
	30	D_2	3	–

ity of access to an 8 × 8 "lattice," on one of the "nodes" of which the food dispenser was found, and were able to walk about it for 15 min. (Let us recall that in the experiments the prospector was purposely set down on the food dispenser.) The results are presented in Table 5. A result in which during the allotted time (15 min) at least one ant found the food dispenser, was considered positive. Not one forager found food in 22 cases out of 30.

Let us introduce two statistical hypotheses: H_0, the probability of finding the food dispenser in experiments in which the ants were "directed" by the prospector is the same as in the experiments with free search for the food dispenser; the alternative hypothesis H_1, the probability of finding food by "directed" foragers is greater than in cases of free search for the food dispenser. In order to test H_0 against H_1, we use the χ^2 test [14]. Computations show that hypothesis H_0 is rejected in favor of H_1 at a significance level of 0.001. Thus, it follows from the data presented that ants are capable of transmitting the information regarding the coordinates of the food dispenser in a plane to one another.

DISCUSSION OF RESULTS

It follows from the experiments described in section I that ants can assess the number of objects within the limits of several tens and are capable of transmitting this information to one another. Hypothetically the ants could have transmitted information not regarding the number of "branch," but, let us say, the distance to it or some other quantitative characteristics, for example, the number of "steps" to the food dispenser, etc. Even if this hypothesis is correct, the conclusion follows that the ants operate using quantitative characteristics and transmit information regarding them to one another. However, for all of our setups, which have various forms of and orientations, as well as a varied length of "branches" and a varying distance between them, the relationship of the time of transmission of information t to the number of "branch" i is identically well described by empirical equations of the type $t = ai + b$. At the same time, the values of parameters a and b are close for all variants, and do not depend either on the length of the "branches" or on other characteristics of the setups. Consequently, the conclusion that ants transmit information precisely about the number of "branch" is highly probable.

The results of the experiments involving the "Cartesian coordinate" setup (section II) showed that ants are capable of memorizing and transmitting information regarding the location of a food dispenser in a plane. Various mechanisms of coding or representation of information regarding the location of the food dispenser can be hypothesized *a priori*: one hypothetical method is to number all the nodes of the lattice and to transmit the number of the node containing the food dispenser. Another method, which we have provisionally called the "coordinate" method is as follows: to memorize and transmit the number of the line and the number of the column at the intersection of which the food dispenser is found. For example, in Fig. 1a, the coordinates of the food dispenser are coded with numbers "2" and "6." Of course, other methods are possible as well.

Comparison of the results obtained with data regarding the time of transmission of information regarding the number of objects which was made above makes it possible to reject the first variant: in "numbering" all of the nodes of the lattice, the ants would have to transmit all the numbers from 1 to 64 (32 on average in the case of 8×8 labyrinth). In order to transmit the number 32, 170-250 sec would be spent in this species of ants, while in the experiments involving the 8×8 lattice, the time of contact of the prospector with the foragers was 60-150 sec (87.2 on average), i.e., approximately two times less. In the case involving 6×6 and 5×5 lattices, the average time of transmission of information regarding the coordinates of the food dispenser is also 2-2.5 times less than in the case of transmission of the numbers 18 and 12, respectively. Thus, the data obtained make it possible to reject the hypothesis of the "numbering" of the cells of the lattice by the ants, and do not contradict the hypothesis of the use of the "coordinate" method by them.

The results presented, just like the data of previous studies [12, 13, 23, 24], make it possible to draw a conclusion regarding a fairly high level of elementary intellective activity of particular individual ants of the species *Formica polyctena;* this includes the presence of a comparatively well-developed linguistic behavior. The capacity of ants of this species to orient themselves in the crowns of trees and in high grass within the limits of extensive protected territories [2, 4, 25] is a good confirmation of this.

CONCLUSIONS

1. *Formica polyctena* ants are capable of perceiving, memorizing and transmitting to one another information regarding the number of objects within the limits of several tens.

2. Particular individual ants can memorize and transmit information regarding the location of an object in a plane, apparently using a coordinate method of representation of information.

3. The presence of a relatively well-developed linguistic behavior gives a notion of a relatively high level of elementary intellective activity in ants.

4. The proposed information theory approach may be used for the study of communication systems and elementary intellective activity of other species of social animals.

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