Learning in bees Apis mellifera L. and wasps Vespula spp. when visiting several artificial flowers of different quality

Обучение у пчел Apis mellifera L. и ос Vespula spp. при посещении нескольких разнокачественных искусственных цветков

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ABSTRACT. In field experiments, individually marked bee or wasp regularly flew to artificial flowers for sweet lure. The flowers, identical in appearance and smell, differed in the presence of food in them. In a row of four flowers, to get satiated, it was necessary to collect "nectar" (sugar water) from the 1st and 3rd flowers, and the 2nd and 4th ones contained an aversive stimulus (a strong NaCl solution). As a result, the studied insects were divided into three groups: 1) some individuals statistically significantly learned to choose flowers with sugar water and did not check flowers without it, remembering their location — "solved the task"; 2) some individuals chose flowers randomly; 3) the remaining individuals (only some bees) regularly chose all the flowers in a row, while trying an unpleasant aversive stimulus. The wasps coped with the task better than the bees. For wasps, unlike bees, the task was made easier by some increasing the distance between experimental flowers. Differences were found between groups of bees of different breeds/subspecies as well. Problems associated with assessing the cognitive abilities of animals are discussed.

РЕЗЮМЕ. В полевых экспериментах индивидуально помеченная пчела или оса регулярно возвращалась на искусственные цветки за сладкой приманкой. Цветки, одинаковые по внешнему виду и запаху, различались наличием в них корма. В ряду из четырех цветков, чтобы насытиться необходимо было собрать «нектар» (раствор сахарозы) из 1-го и 3-го цветков, а 2-й и 4-й содержали отрицательный раздражитель (крепкий раствор NaCl). В результате исследуемые насекомые разделились на три группы: 1) часть осо-

бей статистически достоверно научились выбирать цветки с сахаром и не проверяли цветки без приманки, запоминая их расположение — «решили задачу»; 2) часть особей выбирали цветки случайно; 3) оставшиеся особи (только несколько пчел) закономерно выбирали все цветки подряд, пробуя при этом неприятный отрицательный раздражитель. Осы справлялись с задачей лучше пчел. Для ос, в отличие от пчел, задача облегчалась, когда увеличивали расстояние между экспериментальными цветками. Обнаружены также различия между группами пчел разных пород/подвидов. Обсуждаются проблемы, связанные с оценкой когнитивных способностей животных.

Introduction

Searching for food in natural conditions is one of the most difficult behavioral tasks for animals. It was during the search for sweet lure, sugar water, that the ability for individual learning in insects was clearly proven. Karl von Frisch studied the color vision of honey bees, but along the way he proved the ability to develop conditioned reflexes, although he himself did not describe insect behavior in such terms [Frisch, 1914]. The next step was taken by Professor G.A. Masokhin-Porshnyakov about half a century later. In his original experiments, the ability of bees, paper wasps and ants to generalize visual stimuli was proved [Masokhin-Porshnyakov, 1969; review in Kartsev, 1996]. It is clear that "generalization of visual stimuli" is nothing more than an example of intellectual activity, solving logical problems.

Following the generalization of visual stimuli, numerous other intellectual (cognitive sensu stricto) abili-

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ties of bees were discovered [for reviews see Srinivasan, 2010; Menzel, 2012], such as choice by example (the concepts of `sameness' and `difference' in an insect [Giurfa *et al.*, 2001]), the ability to situational learning [Kartsev *et al.*, 2015].

The capacity of bees to estimate the number of objects was also noted, and later the amazing ant talent for counting were proved by Zh. Reznikova and B. Ryabko; in the generalizing work of these authors, the counting abilities of various animals are considered [Reznikova, Ryabko, 2011]. A sign of intelligent animal behavior is the ability to recognize oneself in a mirror as well, a mirror test that various vertebrates, ants and partly crustaceans pass [Cammaerts M., Cammaerts R., 2015; Robinson, 2023]. This issue is currently being actively investigated. And, of course, one of the most outstanding examples of intellectual behavior is the use of tools and social training of bumblebees (for recent works, see Bridges *et al.* [2024]).

The above examples are related to solving logical problems, and therefore we consider them as examples of intellectual activity. What "logic" is as a philosophical science of "right thinking" is perhaps not entirely clear to a biologist. But what the author (VK) means by logic is the establishment of cause-and-effect relationships that are more complex than a simple conditioning. In a natural environment, any organism has to adapt to a specific situation by relating many parameters to each other. Complex learning also occurs here, although the logical structure of the task is not always clear and, moreover, different individuals can find different solutions. Sometimes such learning is called trial and error learning. Obviously, here too we can talk about intellectual activity.

The anthophilous insects used in the experiments described below select suitable plants in natural conditions, remember the location of a feeding site, and learn to search for pollen and nectar within a flower. In addition, they should fly in such a way as not to repeatedly check flowers that have just been emptied. Since the publication of our first work on the sequence of visits to several food objects by the honey bee and social wasps [Mazokhin-Porshnyakov, Kartsev, 1979], we have become convinced that model tasks with visiting flowerlike food objects can also be used to study the general principles of behavioral organization in insects [Kartsev, Mazokhin-Porshnyakov, 1989; Kartsev, 1996] and, possibly, in other animals. Such tasks allow to approach one of the most general problems of ethology, the problem of the relationship between the innate and the acquired in behavior [Thorpe, 1963], with quantitative statistical analysis.

Earlier in our experiments we found that when visiting several identical artificial flowers, bees and wasps chose the emptied flowers approximately twice as rarely as it could have happened by chance (approximately 40–50% of visits in which the insect did not examine the just emptied flowers with a random level of about 20% — Kartsev, 1996). And they preferred certain trajectories of movement among other possible ones. Obviously, this is

explained by the existence of initial (innate) rules of behavior. Thus, we noted that, having received a sufficient portion of food, the insect strives to fly to the nearest food object. This elementary rule was also confirmed in a number of works carried out within the framework of the theory of optimal foraging [Pyke, 1978; Heinrich, 1983] and in the work of Schmid-Hempbel [1984].

In a new series of experiments described in this paper, we created a situation where the innate search rules conflict with the real situation. We consider the ability to abandon these rules as the ability for intellectual (cognitive) activity. Four visually identical artificial flowers were arranged in a row, alternating every other flower with sugar water (reward) and with a strong solution of NaCl (aversive stimulus). At a distance, bees and wasps cannot distinguish between flowers with sugar and salt NaCl by sight or smell. To get satiated (fill the crop), it was necessary to take sugar water from the first and third flowers. It was possible to distinguish between these and other flowers only by their position relative to external landmarks including each other.

The following **goals** were set in the work.

- 1. To find out whether bees are capable of solving the experimental task, that is, remembering artificial flowers with aversive stimulus in the row of flowers and not check them. In preliminary experiments, not a single bee out of five solved the task (while wasps did). But are there any bees capable of this?
- 2. To compare bees and wasps with each other.
- 3. In addition, we aimed to compare bees from different colonies in different apiaries with each other, taking into consideration that our experimental bees had characters of different subspecies, or breeds (although we did not work with genetically pure lines of bees).
- 4. To study the effect of the distance between flowers on the solving the experimental task. We assume that with an increase in the distance between flowers, the task will become easier for insects, because it will be more convenient for them to remember each flower separately (which is required by the conditions of the experiment, but contradicts their innate search rules). Checking this assumption was the fourth goal of this work.

Material and Methods

Field experiments were conducted on the honey bee *Apis mellifera* Linnaeus, 1758 (Hymenoptera, Apidae) and the paper wasps *Vespula vulgaris* (Linnaeus, 1758) and *V. germanica* (Fabricius, 1793) (Hymenoptera, Vespidae). No differences were found between the wasp species in the experiment, and both species were further analyzed together (as *Vespula* sp.). As for bees, in different seasons, we worked with bees with characters of different subspecies/breeds (although genetic analysis of the studied bees was not carried out). Our experiments involved bees that can be attributed (with the above reservations) to the following groups (usually considered as subspecies): dark forest bee *Apis mellifera mellifera* Linnaeus, 1758; Carpathian bee *Apis mellifera carpatica* Foti *et al.*, 1965; Caucasian bee

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Apis mellifera caucasica Pollmann, 1889. Bees and wasps were trained in various ways to fly to the feeding place and then were involved in the experiment and individually marked with fast-drying paint. Each individual participated in the experiment only once.

The experimental insects were trained to visit feeders — models of flowers. The artificial flower consisted of a star cut out of blue paper, 6 cm in diameter, covered with glass. A miniature cup was placed above the star (Figure).

When the flowers were compactly arranged, they were placed on a white experimental table measuring approximately 50 cm by 50 cm, arranged in a line along its diagonal at equal distances from each other. A measured portion of a 50% sugar water (reward) was poured into the 1st and 3rd flowers. A solution of NaCl (aversive stimulus) was poured into the 2nd and 4th ones. In order to get satiated (fill the crop), the insect had to collect sugar water from two flowers. Having had enough, the insect flew to the nest and returned for a new portion of food. Sugar water was added each time while the bee or wasp carried current portion of food to the nest. Bees and wasps are unable to distinguish sugar and salt, as well as empty and filled artificial flowers, from a distance; this was verified in preliminary experiments. Measures were also taken to prevent the insects from orientation by their own odorous mark. Thus, it was possible to distinguish between the rewarded and non-rewarded feeders only by their location.

When the flowers were arranged at a distance, each of them was placed on a separate table measuring 10 cm by 10 cm. The tables were arranged in a line at a distance of 1 m from each other.

When describing the behavior of insects, we use the following **terms**.

VISIT — the cycle of actions of an insect that has flown from the nest, starting from the moment it appears above the experimental table or feeding place and ending with its saturation. CHOICE — testing a cup located in the center of a flower with its mouthparts or tarsi. CORRECT CHOICE — choosing a flower filled with sugar water. INCORRECT CHOICE — choosing a flower filled with a NaCl solution or emptied. CORRECT VISIT — a visit in which not a single incorrect choice is made. INCORRECT VIST — a visit in which at least one incorrect choice is made. THE TASK IS SOLVED if correct visits statistically significantly exceed the random level (about 16.7% — see below).

The incorrect choice did not prevent the insect from making correct choices later — choosing the rewarded flowers and getting satiated in each visit. Therefore, the individuals that, by our definition, did not solve the task, still collected a full portion of sugar water. Their behavioral strategy was also adaptive, although not optimal.

The random level of correct visits in our task (null hypothesis) is equal to the product of the probabilities of two



Fig. Marked bee on an artificial flower. Puc. Меченая пчела на искусственном цветке.

independent events: $1/2 \times 1/3 = 1/6$, or approximately 16.7%, where 1/2 is the probability of the first correct choice, 1/3 is the probability of the second correct choice. Sometimes, while consuming a portion of food, the insect, due to some reasons, flew up low and immediately landed on the flower again. Such actions were not recorded as separate choices and it was believed that the insect always flies from one flower to another.

Statistical assessment of the significance of the results was carried out using the chi-square test or Pearson's criterion. The program Statistics 8 was used or the criterion values were calculated manually. In some cases, we compared samples smaller than recommended for the chi-square test. However, using Yates's correction, we could only reduce the significance of the differences, not unreasonably increase it [Plokhinsky, 1970].

Results

1. Ability to solve the task

To what extent are insects able to optimize their behavior in an experimental situation? Are they able to remember the position of two flowers with a reward (sugar) among two similar flowers with an aversive stimulus (an unpleasant solution of NaCl)? The distribution of correct and incorrect visits is presented in Tables 1–3.

The task turned out to be quite difficult for the insects studied, especially for bees. However, both bees and wasps are capable of solving it, although not all individuals. On average, the proportion of correct visits for bees was only about 20% (with a random level of 16.7%); for wasps — approximately 30–40%, depending on the distance between flowers. The average figures are suitable only for the roughest assessment, because individual variability of behavior was very high. The maximum individual level was 65% (wasp No. 17 — Table 2), and the minimum — only 2% (bee No. 13, which checked a non-rewarded flower more often than randomly — Table 1).

The wasps as a whole solved the task better than the bees; we will confirm this fact below.

The proportion of correct visits in most of the individuals studied increased over time. This means that the bees and wasps learned during the experiment. Some individuals learned not to avoid the artificial flowers with aversive stimulus, but to taste the contents of the flower cups briefly, so as to receive as little unpleasant sensations as possible from falling into a strong NaCl solution.

2. The influence of the distance between artificial flowers

When the distance between the sought objects changed, the insects' behavior changed both quantitatively and qualitatively, and in different ways for bees and wasps. In general, when artificial flowers were located distantly, the proportion of correct visits more or less increased.

Let us analyze the total proportions of correct and incorrect visits in different groups of insects. In this way, we will be able to identify only general trends. For precise calculations, a multiple increase in statistical material is necessary, because individual behavioral variability is very high.

Bees. A total of 24 bees of two breeds were studied in the experiment under similar conditions — 12 with compact and 12 with distant arrangement of artificial flowers. In total, with compact arrangement of flowers, the proportion of correct visits was 20%, and with distant arrangement — 24%. The differences are not significant — the bottom line "\subseteq both breeds" in Table 1. In the Carpathian bee, groups with different arrangement of flowers (five individuals each) differ statistically significantly, but at a low threshold of reliability (P<0.04). Thus, there is a tendency that with an increase in the distance between the flowers, the task for the bees becomes easier, but not very significantly.

It should also be noted that with the flowers located distantly, the behavior of the bees studied became more diverse (Table 1). With a compact arrangement, the percentage of correct visits did not differ from the random level for 9 bees, and exceeded it for 3 bees. With the flowers located distantly, the percentage of correct visits did not differ from the random level for 6 bees, and differed in one or another direction for the other 6 bees — for 3 it exceeded, and for 3, on the contrary, it was below the random level. The range of individual results also increased. With a compact arrangement of flowers, the percentage of correct visits varied from 8 to 40%, and with a distant arrangement — from 2 to 53% (according to the data in Table 1).

Wasps. With flowers arranged distantly, the task for wasps turned out to be easier, and no qualitative changes in behavior were revealed. With flowers arranged compactly, the total percentage of correct visits was 29%, and with flowers located far away, it was 41%, which is statistically significantly higher — the bottom line of Table 2.

The distribution of individuals into those who solved and those who did not solve the task with a compact arrangement of flowers is 5:7, and with a distant arrangement — 7:0. The sample is too small for statistical analysis, but the differences seem to be on the verge of reliability.

Obviously, the obtained results indicate that with a distant arrangement of flowers, wasps, unlike bees, cope with the task better than with a compact arrangement.

3. Flower choice sequences

In the flower row 1-2-3-4, two rewarded flowers (No. 1 and No. 3) can be chosen in two sequences — "1-3" and "3-1". Energetically, these sequences are identical. However, it turned out that all trained bees that successfully solved the task (see methods), significantly preferred the sequences "1-3" over "3-1". Here, all individuals were homogeneous. The results are presented in Table 3, which includes all bees regardless of the breed and the distance between the flowers in the experiment. In total, the sequence "1-3" makes up more than 90%. Thus, the bees learned to start from the edge of the flower row where the rewarded flower was located (No. 1), and then to skip the flower without a reward, but containing an aversive stimulus (No. 2). Among the dark forest bees (only one variant of the experiment

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with a compact arrangement of flowers was carried out), none solved the task, but in four out of five individuals studied, correct visit level was lower than random one (Table 4). However, they also demonstrated some ability to learn. When starting to fly around the flowers in each visit, they more often landed on the rewarded one. In

Table 1. Proportions of correct (+) and incorrect* (-) visits to visually identical artificial flowers depending on their arrangement. Bees Apismelliferaпри посещения правильных (+) и ошибочных* (-) прилетов при посещении внешне одинаковых искусственных цветковв зависимости от их расположения. Пчелы Apis melliferaразных пород/подвидов.

			Arrangement	of the flowers				
	compact			distant				
	Apis mellifera carpatica							
bee No.	+:-	% (+)	P	bee No.	+:-	% (+)	P	
1	3:34	8	ns	13	1:39	2	P<0.01!	
2	6:64	9	ns	14	10:60	14	ns	
3	17:52	25	ns	15	3:66	4	P<0.01!	
4	9:62	13	ns	16	32:29	53	P<0.01	
5	11:43	20	ns	17	13:47	22	ns	
Σ	46:255 ^A	15	ns	Σ	59:211 ^B	22	ns	
	Apis mellifera caucasica							
6	12:49	20	ns	18	4:66	6	P<0.05!	
7	7:63	10	ns	19	17:53	24	ns	
8	10:40	20	ns	20	16:54	23	ns	
9	28:42	40	P<0.01	21	15:55	21	ns	
10	19:51	27	P<0.05	22	23:49	32	P<0.01	
11	22:48	31	P<0.01	23	17:53	24	ns	
12	7:55	11	ns	24	27:34	44	P<0.01	
Σ	105:348	23	P<0.01	Σ	119:364	25	P<0.01	
∑ both breeds	151:603	20	P<0.02	∑ both breeds	178:575	24	P<0.01	

^{*} Correct/incorrect visit — a visit without/with choosing non-rewarded flower(s) with aversive stimulus (see material and methods)

Different superscript symbols in the line indicate statistically significantly different proportions (P<0.04).

 Table 2. Proportions of correct (+) and incorrect (-) visits to visually identical artificial flowers depending on their arrangement. Wasps

 Vespula sp.

 Таблица 2. Распределения правильных (+) и ошибочных (-) прилетов при посещении внешне одинаковых искусственных цветков

Таблица 2. Распределения правильных (+) и ошибочных (–) прилетов при посещении внешне одинаковых искусственных цветков в зависимости от их расположения. Осы *Vespula* sp.

Arrangement of the flowers							
compact			distant				
wasp No.	+:-	% (+)	P	wasp No.	+:-	% (+)	P
1	13:43	23	ns	13	32:38	46	P<0.01
2	13:44	23	ns	14	27:43	39	P<0.01
3	28:31	47	P<0.01	15	23:47	33	P<0.01
4	30:28	52	P<0.01	16	22:48	31	P<0.01
5	18:36	33	P<0.01	17	20:11	65	P<0.01
6	12:58	17	ns	18	21:34	38	P<0.01
7	7:33	17	ns	19	17:13	57	P<0.01
8	6:35	15	ns	_			
9	14:41	25	ns	_			
10	17:53	24	ns	-			
11	13:29	31	P<0.05	-			
12	22:48	31	P<0.01	-			
Σ	193:479 ^A	29	P<0.001	Σ	162:234 ^B	41	P<0.001

Legend and comments as in Table 1.

Different superscript symbols in the line indicate statistically significantly different proportions (P<0.0001).

P—statistical significance of differences between random (null hypothesis) and empirically obtained proportions (+): (–). Random percentage of (+) according to the null hypothesis is about 16.7%. Explanations in the text.

ns — not significant

The "!" sign means that incorrect visits prevailed statistically significantly.

total, in the first choice, the proportion of the rewarded and non-rewarded flowers was 225:152 (1.5:1), which significantly (P<0.001) differs from the random distribution in the ratio 1:1. Thus, the bees still remembered the first rewarded flower, but then regularly flew to the neighboring, closest one, which, according to the conditions of the experiment, did not contain the reward.

Totally, wasps also preferred the flower choice sequence "1-3". The proportion of sequences "1-3":"3-1" is 165:87, the sequence "1-3" is 65% and statistically significantly prevails ($165:87 \neq 1:1$, P<0.001). Among the wasps there was also one individual (No. 15 by Table 2), in which the sequence "3-1" prevailed ($6:17 \neq 1:1$, P<0.05).

In general, all the insects studied preferred the sequence "1-3", and this preference was stronger in bees than in wasps — see below.

4. Differences between bees and wasps

The wasps as a whole solved the task better than the bees. Among 29 bees studied at different flower arrangements (Tables 1 and 3) only six individuals solved the task. The distribution of wasps into those that solved and those that did not solve the task was 7:12 (Table 2). Despite the small sample size, the differences are significant. Proportion $23:6 \neq 7:12$, P<0.01 (the program Statistica gives the chi-square value with Yates' correction 7.1).

This is also confirmed by comparing the total distributions of correct and incorrect visits of bees and wasps.

In total, in all variants of the experiment, the proportion of correct and incorrect visits for all bees is 348:1515 (19% correct visits) — data from Tables 1 and 3, and for wasps — 355:713 (33% correct visits) — Table 2. The difference between these proportions is highly reliable (P<0.00001, chi-square 78.1). This additionally indicates that wasps solved the task better than bees, at least the wasps and bees that participated in our experiment.

Bees turned out to be more heterogeneous than wasps. Among the 29 bee individuals studied, there were 7 that reliably had a predominance of incorrect visits (marked in Tables 1 and 4 with the sign "!"). No such individuals were found among the wasps. Perhaps, with an increase in the sample, a wasp would still be found that regularly inspected flowers without reward, but judging by the fact that almost all the wasps studied showed some predominance of correct visits, this possibility is not very likely.

Another important difference between bees and wasps was already mentioned above. For wasps, unlike bees, the task with distant flower arrangement was easier than with compactly arranged ones.

Bees and wasps also differed in the way they solved the problem, namely, in the sequences of choosing the rewarded flowers in correct visits. Bees that successfully solved the task preferred the "1-3" sequence in 90% of cases. Wasps had a weaker preference, the "1-3" sequence accounted 65%. The "1-3": "3-1" proportions in bees and wasps are statistically significantly differ-

Table 3. Rewarded flower choice sequences in correct visits in bees *Apis mellifera*. **Таблица 3.** Последовательности выбора подкрепляемых цветков в правильных прилетах у пчел *Apis mellifera*.

Bee No.*	Sequences «1-3»:«3-1»	P	
9	26:2	P<0.001	
10	16:3	P<0.01	
11	18:4	P<0.01	
16	31:1	P<0.001	
22	23:0	P<0.001	
24	25:2	P<0.001	
Σ.	139:12	P<0.001	

Legend and comments as in Table 1

Табл. 4. Распределение правильных (+) и ошибочных (–) прилетов при посещении внешне одинаковых искусственных цветков, расположенных компактно. Пчелы *Apis mellifera mellifera*.

Bee No.	+:-	%(+)	P
25	4:95	4	P<0.01!
26	8:47	15	ns
27	2:60	3	P<0.01!
28	3:77	4	P<0.01!
29	2:58	3	P<0.01!
Σ	19:337	5	P<0.001!

Legend and comments as in Table 1.

P—statistical significance of differences between theoretically calculated and empirically obtained proportions "1-3":"3-1". Random ratio is 1:1. * The bee numbers correspond to the numbers in Table 1.

Table 4. Proportion of correct (+) and incorrect (-) visits to visually identical artificial flowers arranged compactly. Bees *Apis mellifera mellifera*.

^{*}The bee numbers continue the continuous numbering started in Table 1.

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ent — 139:12 \neq 165:87, P<0.0001. Thus, bees are generally more heterogeneous, but their behavior in the case of a successful solution of the task is more uniform.

Obviously, all differences between bees and wasps are due to innate species differences in the organization of search behavior and learning, which in turn can be explained by differences in lifestyle and feeding habits.

5. Differences between bee breeds

When solving the experimental task, bees show very high individual variability. However, in general, the groups of bees of different breeds studied in the experiment differ significantly from each other. With a compact arrangement of flowers, the distribution of correct and incorrect visits for dark forest bees is 19:337 (5% correct visits — Table 4), for the Carpathian bee 46:255 (15% correct visits — Table 1), and for the gray Caucasian bee 105:348 (23% correct visits — Table 1). These proportions differ statistically significantly in pairs (P < 0.01) or at a higher threshold). Thus, with a compact arrangement of flowers, the Caucasian bee coped with the task best of all. It has the highest level of correct visits in total as well, which exceeds the random level. Next comes the Carpathian bee, it approximately corresponds to the random level according to the adopted null hypothesis. And the dark forest bee differs from all, demonstrating, on the contrary, a significantly lower level of correct visits than random one. We assume that it is the breed characteristics that determine the differences in the experimental groups. This issue requires special study and special experiments with genetically pure lines of bees and with colonies of equal number of individuals.

Discussion

Our results confirm that the solution of a particular cognitive task depends not only on its logical structure, but also on how it is organized in details. It was proven on wasps that they distinguish different-quality artificial flowers better if they are spaced a meter apart, but not arranged compactly. Formally, the task remained the same, but was organized differently.

Increasing the distance between flowers did not significantly help the bees to solve the task. It would probably be possible to select a distance between flowers at which they would solve the task better (which requires experimental verification). In consequential visits, bees are able to learn the order of alternating three feeding places [Lopatina, 1971].

Obviously, the inability to solve a cognitive problem may mean either that animals of a given species are incapable of solving problems of this type in principle, or that we have organized the experiment incorrectly. Thus, a positive result is perceived unambiguously (if only the methodology was adequate), while a negative one is not so clear. In each behavioral task, in addition to its logical structure, it is necessary to consider how *natural* this task is for a given animal species, i.e., how consistent it is with their natural abilities. For example, the important

works proving the ability of bumblebees to use tools, to open a novel two-step puzzle box (for recent works see [Bridges *et al.*, 2024]) would hardly have been possible in the honey bee or, even more so, in various small bees.

Our experimental task is difficult for insects because it is unnatural. Having found a large portion of sugar water (nectar) in an artificial flower, a bee or a wasp tends to fly to a neighboring flower that looks the same. And in our situation, this leads to an error — trying a flower without reward, but with aversive stimulus. Only a small part of the studied bees (6 out of 29 in all variants of the experiment) coped with the task in the given time (checked non-rewarded flowers with aversive stimulus reliably less often than at a random level — see the methods).

Some bees (7 out of 29) not only failed to cope with the task, but also made mistakes regularly: they tested non-rewarded flowers reliably more often than could have happened by chance. These individuals found it easier to try a stimulus that was unpleasant to them (NaCl) than to mentally overcome themselves and refuse to fly to the nearest flower (some individuals trained not to avoid flowers with aversive stimulus, but to check them briefly, so as to receive as few unpleasant sensations as possible). In any case, individuals that regularly tried the aversive stimulus (in our terminology, made incorrect visits) received a full portion of sugar water on each visit and became satiated, so choosing all the flowers in a row is also an adaptive, although not optimal, behavioral strategy.

The bees were very heterogeneous, the percentage of correct visits (without choices non-rewarded flowers) varied from 2 to 53% (random level according to the null hypothesis is 16.7% — see the methods). Such a range of variability obviously indicates the unnaturalness of the experimental task for bees.

We believe that our unnatural experimental task is difficult for bees and is at the border of their cognitive (intellectual) abilities.

The wasps were significantly different from the bees. They coped with the task better. The proportion of individuals who solved the task was higher for them than for the bees. The total percentage of correct visits in the group was also higher for the wasps. The wasps, like the bees, differed significantly from each other, but were less heterogeneous. The proportion of correct visits in the studied wasps varied from 15 to 65%. No wasps with a predominance of incorrect visits were found.

For wasps, unlike bees, increasing the distance between flowers made the task easier. The level of correct visits increased in the experiment from 29 to 41%, the differences are reliable.

It can be concluded that the search behavior of bees and wasps is organized differently. Wasps remember food sources separately better, while bees are adapted to collect food in a honey plant array. This is primarily evidenced by the fact that wasps worked better on distant flowers. In addition, bees mainly (in 90% of cases) chose flowers in the sequence "1-3", while wasps often encountered an alternative sequence, "3-

1". In this aspect, their behavior turned out to be more diverse.

So, wasps coped with the experimental task better than bees. But does this mean that their cognitive (intellectual) abilities are higher? This question needs special discussion. The obtained facts can be explained by differences in the innate mechanisms of search behavior of different species. The experimental task simply turned out to be more natural for wasps than for bees.

Conclusions

- 1. Honeybees *Apis mellifera*, like paper wasps *Vespula* sp., are able to learn to choose two rewarded flowers with sugar water (1st and 3rd) in a row of four artificial flowers identical in appearance and smell, and to avoid two non-rewarded flowers with a strong NaCl solution (2nd and 4th).
- 2. The task turned out to be difficult for the insects studied and not all individuals coped with it during several dozen returned visits for food during the experiment (although even when checking non-rewarded flowers, they still got full on each visit, filling their crops with food).
- 3. Some individuals (6 bees out of 29 studied) regularly chose all flowers in a row (1-2-3) and checked the non-rewarded flower more often than by chance.
 - 4. The wasps coped with the task better than the bees.
- 5. Unlike bees, wasps coped better with the task when flowers were arranged distantly (at a distance of 1 m from each other) than when they were arranged compactly (on a flat surface on an experimental table measuring approximately 50 x 50 cm).
- 6. Most individuals chose the rewarded flowers, starting from the edge of the row (sequence "1-3") and significantly less often, starting from the flower in the middle ("3-1").
- 7. The behavior of different groups of bees in the experiment differed from each other, which is most likely due to breed/subspecies differences (A. m. mellifera, A. m. carpatica, A. m. caucasica).

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