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THE "BUCKWHEAT PROBLEM" AND THE BEHAVIOR OF THE HONEY-BEE

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It has been abundantly demonstrated that the ordinary honey-bee can be quickly trained to associate given odors, or colors, or even color-patterns, with the presence of food so that, when foraging, it will hunt out the associated odor, color, or pattern among alternatives. Beling, in a most interesting and able paper[1] of which I was unfortunately not aware when reporting on the diurnal rhythm of certain Orthoptera,[2] has shown that this same bee can be trained to associate the presence of food with a certain time or times of the day even when in constant illumination, temperature, and humidity. This is quite different from what is ordinarily thought of as an "internal rhythm." He says that they appreciate points of time but not periods of time, since he could not train them to seek food every nineteen hours, in which case the feeding time came at a different point in successive twenty-four-hour days.

In discussing the biological aspects of his experiments, Beling speaks of what I have ventured to call the "buckwheat problem" as follows (translated):

> A sense of time so well developed has in all probability a biological significance. The observation of v. Buttel-Reepen (1915, 'Leben und Wesen der Bienen,' Braunschweig) gives the first clew: "For example, buckwheat produces nectar only in the forenoon up to about 10 o'clock. After that time one sees on the blossoming and fragrant fields scarcely any bees. On the morrow, however, at an early hour hundreds of thousands are again in evidence and disappear in turn toward 10–11 o'clock in spite of the fact that the fragrance and the wide blossoming meadow exercises the same attraction."
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> In this instance the biological significance of the time-sense ought to be sought. In view of the well-known activity of the bees in relation to flowers it is to be assumed that the buckwheat bees spend the remainder of the day in the hive. At artificial feeding places it may in fact be easily observed that during the feeding intermissions they remain quietly upon the combs. Here they are secure. Through frequent inspections of their dried-up springs they would merely expose themselves needlessly to the many dangers of their flight service and to no purpose would use up their energy.

[1] 1929, 'Über das Zeitgedächtnis der Bienen,' Zeit. f. Vergl. Physiol., IX, pp. 258–338.
[2] 1932, American Museum Novitates, No. 550.

Conceding that buckwheat has nectar only from 9–11 o'clock, it may well be that other plants as well produce nectar only at particular and limited hours of the day. The bees which visit in flight one and the same species as long as this species is productive are in this way "trained" to the daily periodic nectar production (perhaps also pollen production). In this way provision would be made for the punctual daily visit of all bee flowers; the time memory of the bees would accordingly be an adaptation to conditions of floral biology and concomitantly a weighty factor in the pollination of species of flowers through insects.

Beling then cites many instances of flowers which are open during only a limited and definite part of the day. Those used by Linnaeus in his "floral clock" are classic examples. If, however, the bees make use of their time-sense to guide them to one species of flower at one time of the day and to another at another hour, they must be able to do more than tell time and discriminate between colors and odors. They must be able to associate the combination of several colors or odors, times, and food.

The present experiments were designed to consider this problem alone. The subject itself and the apparatus used raised interesting questions concerning the psychology of individual bees but, possibly unwisely, attention is confined here to the behavior of the population as a whole.

Since it is said that the buckwheat does not change either color or (a bit doubtful) odor when it starts and stops secreting nectar, a simple experiment involves two kinds of "artificial flowers" differing only in color and times of offering food to the bees. We can have one of these kinds offering sugar-water between 9 and 11 A.M. and the other doing so between 2 and 4 P.M. However, to meet the requirements of the problem, the artificial flowers should be present and open at all times and, to prevent a change of odor, the odor, if any, of sugar-water should always be in each of them.

Two units were arranged. Each unit consisted of three boxes, each box being about 12 cms. on a side. The three boxes of each unit were placed in a row. The central box contained an inverted jar of sugar-water placed on strips of blotting paper in a shallow dish, constantly providing a supply of food without danger to the bees. This central food-chamber communicated by one-centimeter holes with the box on each side; but either or both holes could be shut off by wire screen. When a hole was screened the odor, if any, of the sugar-water could escape into the side-box but bees could not get from that box to the food.

Each side-box was provided with an entrance-hole about a centimeter in diameter in its front. Around each hole was a colored cardboard

about 6 cms. square with the hole at its center. Two colors were used: white strongly reflecting ultraviolet and white weakly reflecting ultraviolet. Any side-box might bear either color, but usually one side-box of a given unit bore one of the contrasted colors while the other side-box bore the other color. The combination of two units included two "flowers" of each color. The colored cards were not only changed frequently from box to box but fresh cards were put out every few days and in all tests so that bee-odors could not give a clew as to the right box.

In the early part of the work (up to July 26) bees entered and left a side-box by the same hole, the one in the center of the colored card. This is as it would be in a flower. However, it resulted in a bad traffic-jam at the hole of a right box during feeding time. Furthermore, incoming bees could readily determine from outgoing bees what the prospects were in a given box. Accordingly, starting July 27, a one-way traffic system was put into operation. After a bee had entered a side-box through the hole in the colored cardboard on the front of the box it went to the passageway from that box to the feeding chamber. If that passageway was not screened it obtained food and returned to the side-box. Whether it got food or not it could leave only by way of a rear exit.

Several devices were used to enforce this one-way traffic. A simple and quite satisfactory one was a trap-door made of light celluloid and hung so that it opened in only one direction, falling into place when a bee had passed. Bees trying to go the wrong way quickly learned to wait until a bee going in the right direction had opened a door. Then the waiting bee would slip in before the door completely closed. This was most frequent at the rear exits and was finally prevented by making the passageway barely the width of one bee.

This one-way traffic system involves several interesting points. There were no colored cards at the rear exits. A bee having obtained food in the central chamber and left by a rear uncolored door tended to come back to this door on its next visit, presumably because she made orienting observations as soon as she got into the open. Such observations would fix the location of the rear exit hole as the place where food might be obtained.[1] The bees, then, were required to learn not only that a given color meant food at a certain time but also that the surroundings in which they found themselves after getting food were not those to which they must come to get it.

[1]An apparatus similar to this might be useful in determining the relative value to the bee of such orientation observations (also as to the relative value of preceding and succeeding stimuli; and so on), but these problems were not attacked in the present work.

TABLE 1.—A summary of data

Mid-time	June 29 July 1		July 4, 6, 8		July 10, 12		Test July 14		July 18, 20, 24		July 30 Aug. 1		Test Aug. 2		Test Aug. 4		Test Sept. 12	
	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U	Aver. No. per Min.	Per cent U
7:50	17.5	44	10.6	45	5.7	47	0	..	9.0	52	7.0	21	6.0	63	...	..	7.2	67
8:10	16.0	42	8.5	41	8.3	45	6.0	42	9.0	67	6.3	36	8.4	55	10.0	70	12.8	89
8:30	9.7	31	10.8	42	14.3	47	17.0	44	10.7	66	8.3	61	10.0	50	17.0	88	12.4	95
8:50	10.0	32	11.8	34	19.3	55	31.0	31	7.6	61	9.0	43	11.2	50	14.0	79	21.6	96
9:10	61.7	62	62.7	60	52.3	66	27.5	56	62.8	71	28.3	58	19.6	52	31.0	93	24.8	97
9:30	93.3	76	105.3	71	94.5	78	20.5	46	99.2	75	33.5	71	30.4	47	30.0	93	29.6	89
9:50	95.3	71	88.5	78	101.5	79	19.5	41	101.0	81	55.3	66	23.2	47	47.0	98	36.4	78
10:10	109.5	75	101.2	81	114.8	79	17.5	43	87.7	79	56.3	81	16.0	42	42.0	95	27.2	69
10:30	103.5	82	94.5	81	108.5	83	10.0	25	87.7	87	68.0	87	16.8	43	31.0	93	5.6	74
10:50	95.7	87	102.3	81	101.3	87	8.0	31	84.5	82	73.0	80	12.8	47	36.0	97	3.6	71
11:10	....	..	....	..	....	..	7.0	21	....	..	116.7	71	9.2	47	46.0	91	0.4	50
11:30	34.3	75	37.0	71	64.8	67	3.5	43	15.3	74	24.7	65	6.8	39	42.0	93	0.8	100
11:50	21.0	62	21.0	53	34.5	63	4.0	38	14.0	75	7.7	52	2.0	40	49.0	92	1.2	60
12:10	17.5	71	21.3	48	10.0	80	15.0	33	14.3	63	7.0	85	2.0	40	37.0	95	...	..

Mid-time	June 29 July 1		July 4, 6, 8		July 10, 12		Test July 14		July 18, 20, 24		July 30 Aug. 1		Test Aug. 3		Test Aug. 4[1]		Test Sept. 12	
	Aver. No. per Min.	Per cent N	Aver. No. per Min.	Per cent N	Aver. No. per Min.	Per cent N	Aver. No. per. Min.	Per cent N	Aver. No. per Min.	Per cent N	Aver. No. per Min.	Per cent N	Aver. No. per Min.	Per cent N	Aver. No. per Min.	Per cent N	Aver. No. per Min.	Per cent U[2]
12:50	19.0	**44**	14.3	**49**	5.8	**40**	23.0	**72**	13.5	**19**	8.5	**59**	2.8	**44**	48.0	**2**	See text	
1:10	22.0	**36**	24.2	**50**	5.1	**41**	21.5	**58**	10.0	**60**	9.0	**44**	10.4	**44**	46.0	**4**		
1:30	16.3	**52**	20.0	**53**	6.6	**50**	24.5	**61**	....	..	16.3	**40**	9.6	**42**	43.0	**7**		
1:50	14.0	**54**	23.5	**54**	7.1	**46**	25.5	**70**	11.7	**43**	15.0	**48**	5.6	**33**	47.0	**4**		
2:10	35.5	**57**	46.7	**80**	19.7	**69**	19.0	**66**	41.5	**78**	22.0	**70**	2.8	**64**	53.0	**4**	1.2	**50**
2:30	82.3	**80**	75.3	**80**	25.3	**76**	20.5	**61**	95.8	**70**	44.0	**85**	7.2	**48**	53.0	**0**	2.4	**67**
2:50	89.3	**78**	76.4	**87**	28.3	**81**	13.5	**65**	111.8	**80**	64.5	**89**	19.2	**56**	45.0	**2**	9.2	**54**
3:10	101.7	**85**	94.2	**83**	26.8	**89**	15.5	**52**	85.0	**79**	62.3	**72**	16.4	**51**	41.0	**10**	23.6	**63**
3:30	91.5	**85**	80.2	**89**	26.8	**88**	14.0	**57**	88.7	**84**	67.3	**80**	13.6	**53**	46.0	**7**	45.6	**60**
3:50	78.5	**82**	79.0	**90**	27.3	**91**	4.0	**88**	100.0	**90**	66.0	**83**	9.6	**60**	34.0	**6**	57.6	**84**
4:10	....	..	....	..	....	..	4.5	**67**	....	..	84.7	**62**	8.4	**57**	37.0	**19**		
4:30	49.5	**71**	36.4	**74**	11.3	**77**	3.0	**67**	40.7	**74**	17.0	**53**	1.2	**50**	32.0	**34**		
4:50	22.5	**60**	13.0	**74**	4.5	**83**	1.5	**67**	16.5	**76**	4.0	**50**	0.4	**100**	38.0	**26**		
5:10	5.0	**60**	6.0	**44**	....	..	See text		....	..	....	..	....	...	See text			

[1]Bees swarmed the next day, possibly accounting for the small numbers.
[2]Note that in this case U, not N, is the "right" color, although N was also open in this test, but that feeding at either color in the afternoon is "wrong."

Starting with the type of apparatus in which the bees both entered and left by way of holes in colored cards, the two units, giving a total of two white-ultraviolet cards and two white-not-ultraviolet cards, were placed on a bench about fifteen meters from a hive but around a corner so that the apparatus was not visible from the hive. Owing to the shortness of the flight between the hive and the apparatus, frequent trips, hence frequent training, was possible. Individually marked bees were found to be making ten or twelve round-trips per hour during feeding times. During these times there were frequently, as may be seen in Table I, more than a hundred bees per minute entering the apparatus, or about 6000 per hour. If each bee made ten trips per hour, the experiment involved something like five or six hundred individual bees at a time. Of course, as the experiment progressed some bees died or were attracted elsewhere and, also, new ones joined the throng at the apparatus.

By means of marking bees which came to the apparatus in the afternoon and noting that they were also there in equal numbers in the morning, it was evident that we were not dealing with two populations, a morning one and afternoon one.

Table I shows the average number of bees per minute actually entering the apparatus. The countings on which these averages are based were timed by a device that gave an audible signal at one-minute intervals. When the bees were entering in large numbers it was possible to count those at only one hole at a time. Some time was consumed in recording the scores and, consequently, there were usually not more than two one-minute counts for each box in any one ten-minute interval. Particularly before the one-way system was installed, it was difficult for more than forty bees per minute to enter through one hole. This results in the table understating the maxima. For example, for 10:30 A.M., June 29 and July 1, the Table shows that on the average 82 per cent of 103 bees entered the two white-ultraviolet boxes. This is 42 bees per minute per box. When that rate was reached or even approached many bees were crowded around the holes in the white-ultraviolet cards trying to get in. On the other hand, the table somewhat overstates the number of bees at the apparatus when the food was screened off. This is due to the fact that a bee, not being able to get food at one box, would enter one or two others and might even re-enter them before leaving, whereas if it had found food it would have remained to feed. Thus, when the table states that an average of five bees per minute entered the apparatus there may actually have been an average of only, say, three individuals involved.

In the first part of the experiment food was to be had during the morning hours from nine to eleven by going to the white-ultraviolet boxes and during the afternoon hours from two to four by going to the white-not-ultraviolet boxes. The first three and the fifth double columns of Table I show the behavior of the bees during the first eight weeks of such training. A few bees were exploring the apparatus at all times but within a few minutes after the screens were removed at 9:00 A.M. from the holes leading from the white-ultraviolet boxes to food many more bees came and most of them entered the white-ultraviolet boxes. Shortly after these holes were screened at eleven the number of visiting bees dropped off but increased again when the holes leading from the white-not-ultraviolet boxes to food were unscreened at 2:00 P.M. From 2:00 P.M. to 4:00 P.M., while these latter holes were open, most of many visiting bees entered the white-not-ultraviolet boxes. When these gates were closed with wire screen at 4:00 P.M. the number of visiting bees again dropped off to a small number which kept coming as long as daylight lasted. No records are given for the 11:10 and the 4:10 periods because immediately after the passageways to the feeding chamber were screened the entrance-holes in the side-boxes became clogged with bees, some trying to get out because they had found access to food cut off and others trying to get in.

It is to be noted (1) that bees were very abundant during feeding times and not very abundant at other times; (2) that at feeding times most of them went to the right boxes (U in the morning and N in the afternoon); but (3) before the screens were removed there was not a very marked preponderance of bees going to what would shortly be the right color.

The fourth double column of Table I gives the result of a test made July 14, after about two weeks of training. During this test the screens were not removed but everything else was kept as it was during training. There appeared to be a slightly increased number of visiting bees just before and in the early part of normal feeding times but, as to choice of colors, there was a slight preponderance of bees going to the white-not-ultraviolet color in the morning as well as in the afternoon. This was the color at which the bees had last found food (during the afternoon of the day before). At 5:10 P.M. on the day of this test the screens between white-not-ultraviolet boxes and food were removed. During the succeeding ten minutes bees came at the rate of about one per minute. Those that entered the white-not-ultraviolet boxes fed and returned to the hive. Almost immediately a horde of bees came to the apparatus.

Thus, in the next ten minutes (5:20 to 5:30) they came at the rate of 80 per minute, of which about 91 per cent went to the two white-not-ultraviolet boxes. This kept up as long as good daylight lasted—long after normal feeding time.

As previously stated, the one-way system was installed July 26. The sixth double column of Table I gives a sample (July 30, August 1) of the behavior of the bees under this system. The smaller number of bees in the record is to be accounted for by the fact that many, perhaps most, of the visitors spent considerable time trying to get in by way of the rear exits. Otherwise there seemed no marked difference. To be sure, the July 18, 20, 24 bees were about 80 per cent "right" during feeding times and the July 30, August 1 bees were only about 77 per cent right during these times but, even if this difference were significant, it might be accounted for by the fact that after the one-way system was put into effect incoming bees could get no information from outgoing ones as to which was the right box.

The next test was divided between the morning of August 2 and the afternoon of August 3. In the afternoon of August 2 the white-not-ultraviolet boxes and in the morning of August 3 the white-ultraviolet boxes gave access to food as usual, but during the morning of August 2 and the afternoon of August 3 the screens were not removed. These tests confirmed that of July 14. The bees had learned a certain amount of periodicity but they had not developed a fixed habit of going to white-ultraviolet during the morning and white-not-ultraviolet during the afternoon.

In the test of August 4 the screens between the white-ultraviolet boxes and food were removed at the start and not replaced during the rest of the day. The screens between the white-not-ultraviolet boxes and food were not removed. It will be noted in the August 4 columns of Table I that the bees came in considerable numbers throughout the day and visited almost exclusively the white-ultraviolet boxes. In fact, as late as 7:00 P.M. they were still coming at the rate of eight per minute, of which 90 per cent went to the white-ultraviolet boxes.

The results to this date seem to point very clearly to the following conclusions so far as this experiment is concerned. The behavior of the bees when food is available at one color during certain morning hours and at another color during certain afternoon hours is distinctly practical. They come in large numbers to the right color at the right time but there are always a few individuals "prospecting" at other colors and during other times. However, when conditions change, as when on July 14 food

was suddenly offered long after "normal" time or on August 4 when one color offered food during the whole day, the bees almost immediately took advantage of the new situation. Likewise, it was found that the coming of bees in large numbers during a normal feeding time would stop within a few minutes if the screens were replaced, preventing them from getting food. In other words, the bees as a whole did not spend much time in unrewarded endeavor.

It is not clear whether the population was or was not trained to come at definite times of the day. The behavior when food was offered at these times may be and probably is largely explained by the known fact that "prospecting" bees returning to the hive with food stir the swarm into activity. The July 14 and August 2–3 tests, when food was present but not available, show slight increases in the number of visiting bees at or near normal feeding times. These increases certainly are not great. Nevertheless, the tendency may have been there but kept from being more evident by the failure of prospecting bees to return to the hive with food.

It seems quite evident that the population acquired no very definite association between color and time of feeding. Even if this be true, it is not proof that the bees could not acquire such an association. From a practical point of view such an association was not necessary; the bees could quickly determine which color, if either, offered food and govern themselves accordingly.

If these things be true, it would seem that the solution of the "buckwheat problem" is rather simple and does not necessarily involve any training to either feeding time or color. During daylight hours there are always "prospecting" bees hunting here and there in the buckwheat fields as well as elsewhere. If they find buckwheat offering nectar they feed and return to the hive. Their return starts an activity in the swarm[1] and soon the buckwheat field is full of bees. When the buckwheat stops offering nectar most of the bees stops visiting it and turn their attention elsewhere.

On August 5 the hive used in the experiment just discussed sent off a large swarm. In fact, the relatively small number of bees in the August 4 test, when food was offered all day, may have been due to preparations for this swarming. Furthermore, circumstances arose which prevented me from continuing detailed observations on bees. It was possible, however, to add the following as a sort of an appendix to the foregoing.

[1]See von Frisch.

Since the colors used, "white-ultraviolet" and "white-not-ultraviolet," appeared to human eyes to be practically alike,[1] it is natural that students who are not yet thoroughly convinced that bees in nature differentiate between these colors should question the validity of conclusions based on their use. Personally, I think that the foregoing experiments answer that question quite clearly. During the feeding times the positions of the cards and, of course, the corresponding positions of the wire screens were changed every fifteen or twenty minutes on the average. Nevertheless, once the bees found which color was offering food, they were rather faithful to that color until it failed them. Without doubt they were somewhat confused by the fact that sometimes it was one color and sometimes it was the other; but there was evidence that they remembered overnight which color was last the "right" one. It is quite possible, but far from certain, that the bees can not, as well as did not, acquire and act upon the complicated associations offered.

Starting August 7, the bees were fed at white-ultraviolet between 9:00 and 11:00 A.M. as before, but the screens were not removed at other times. Although the white-not-ultraviolet cards were out as before, the corresponding screens were not removed.

On the morning of September 12 (see Table I) all food was removed from the food-chambers and all of the openings to them were left unscreened. There was an evident peak in the number of visiting bees during what had been feeding time and at first there was a marked faithfulness to the feeding-color, white-ultraviolet. This faithfulness decreased, one is tempted to say, when it was found to be unrewarded. Starting at 2:15 P.M., food was put in the feeding chambers and all of the openings were still left unscreened. It will be seen (1) that, although it was not normal feeding time and only a few "prospecting bees" were about, the sudden supply of food quickly brought others in large numbers and (2) that, although food was just as available at white-not-ultraviolet as at the white-ultraviolet (to which food had for the preceding month been confined during two morning hours), the bees tended to secure the food by way of the accustomed white-ultraviolet.

This supplementary experiment, incomplete as it is, is in line with the preceding one and strengthens the belief that, even though the bees may be able to acquire the complicated associations involved in Beling's solution of the "buckwheat problem," they do not need and probably do not use this ability. They take their food where, and when, they find it, apparently being guided largely by the circumstances of the moment.

[1]See Lutz, 1933, American Museum Novitates, No. 641.