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EXPERIMENTAL STUDIES IN THE HOMING OF CARPENTER AND MINING BEES

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It is surprising that experimental work in the homing of insects has been almost wholly neglected. It is true that some important details on the homing of ants, wasps and bees have been published by careful investigators, as the Peckhams, Wheeler, Turner and Bordage, but most of this work is either on close-to-ground creatures—the non-flying forms—or, in cases where flying forms were observed, the work has been on that portion of nest-finding after the creatures were already in close proximity to the nest, revealing only the fact that landmarks about the nest are minutely impressed upon the memory of the subject. A good sample of this type of work is that of Turner, who by moving up and down the window shades in a room where Sceliphron caementarium were at work, changed the landmarks so that the returning mothers could not find their own nests. There are records of many other instances in isolated cases wherein some object in close proximity to the nest was removed and the returning insect could not find the burrow until it was replaced. There is a wide difference in these activities between the aerial insects and the terrestrial ones, which, in moving about, can always depend upon landmarks on the ground. A study of the homing of the high-flying creatures means that insects properly marked must be carried to certain points and liberated, and the nests watched for their return. Of this type of work we have the publications of Lubbock, Buttel-Reepen, and Forel on the honey-bee, Fabre on Cerceris tubercula, Chalicodoma, Anthophora and Osmia, and myself on Polistes pallipes.

In my homing work on P. pallipes,[1] I considered the age, ex-

[1] Wasp Studies Afield, pp. 244–280, 1918.

perience and sex of every creature that was taken out to be liberated away from the nest. Because of this I felt that my conclusions were more significant than those of the other investigators, who took a certain number of bees or wasps on a long flight without knowing the age of each, or its experience in foraging about the neighborhood, without knowing whether it was actually a mother and how far to attribute the return or the indifference to the appeal of the young in the nest, and furthermore without considering the actual time consumed in making the return flight.

In Fabre's experiments, a certain number of creatures were liberated away from home; his interpretation is that all of them were especially endowed so that they returned automatically or by some special faculty to the nest, and that those which did not return were probably injured in handling.

In the details of the experiments which follow, the factors of age, sex, nest interest and experience were considered in each insect taken; hence we may attribute the failure of some to return to sheer stupidity or indifference, inexperience or youth, and those which did return have only themselves, their perseverance, their retention of memory pictures and their love of the nest to thank for their success.

There has been much controversy as to whether insects find their way home by the use of associated memory, or "some special faculty," or "a sixth sense," or as if "by magic," but I shall not go into these details here. In the work on the homing of Polistes pallipes, we conclude:

> In Polistes, the proportion that return to the nest is in inverse ratio to the distance they must travel to regain the home. There is, as the experiments seem to show, a limit to the distance from which they have the power to return. If a wasp is taken far enough away from home, it can be lost even though it be within the range of its physical endurance. Now if they were endowed with some mysterious power, or sixth sense, or magic, or unknown force, or what not, they would return to the nest regardless of the distance to be traversed, so long as it is easily within their physical power. Furthermore, since Polistes do not return at night . . . . then the suggested unknown power is of known impotence. Again if the mysterious sixth sense were adequate,

we should see all of the wasps drawn as if by magic at the same time to the nest.

The work on P. pallipes from which these conclusions were made brought into question the various systems of accounting, such as the sixth sense, magic, unknown power, etc.; and since the following work on two species of bees substantiates every detail of the conclusions for P. pallipes, it seems unnecessary to give further consideration here to the explanations based upon special senses.

If only I could compress my portly figure to fairy-like dimensions and ride on the back of one of these creatures as she flies home! Perhaps I should find, as she returned from Riverside, that she dropped down at each group of buildings—the villages—along the way, exploring here and there and resuming her journey, until she found her home; or that, following an erroneous clue in beginning or resuming her journey, she took the wrong course and eventually became hopelessly lost. Perhaps, if I could accompany one liberated at the trestle bridge, ½ mile from headquarters, I should find myself being carried directly home within a few minutes, or possibly I should be carried hither and thither, in trial-and-error method, until my hostess arrived home a day or more later than her more clever or experienced companion.

The present work was done on large numbers of two species of solitary bees which live in colonies, the carpenter-bee, Xylocopa virginica, and the mining-bee, Anthophora abrupta.

HOMING OF XYLOCOPA VIRGINICA

On April 25, 1922, I noticed these carpenter-bees in abundance about a certain wooden building at Wickes. Males and females were present, and while courtship flights were indulged in, the females were busy at their tunneling, and the golden sawdust was trickling to the ground in the sunlight; the advanced stage of their activity showed that this was not precisely the beginning of their year's work. On June 1, in addition to the tunneling activities, pollen gathering was the order of the day. The age of the creatures must then have been at least forty days. These

bees were, for most experiments, captured as they came home for the night, marked with dots of paint on the thorax, and carefully kept in wire cages for the trips. The task of marking was not always accomplished without stings to the fingers, but after one becomes accustomed to the sting one does not mind it so much. The pain is much less severe than that from the sting of Polistes annularis, but equals in severity that of Polistes pallipes, although its duration is shorter. The sting of Xylocopa is painful for from two to four minutes, and the pain in no case lasts for more than five minutes. They make their attack appear more formidable by using their jaws on one's flesh; their grip is astonishing. In addition, their method of defense when handled often resolves itself into shooting the contents of the anus into the air, and in one case the contents of the honey crop were emptied on my finger. The latter movement was not usually practised; hence I attributed this case to accident in excitement rather than to an attempt at defense. Every precaution was taken not to injure the bees, and the wings especially were handled with care. This especial caution was exercised in order that we might know that those which failed to return did so through causes other than injury inflicted in handling. In these experiments, the proportion of returns was sufficient to prove that my method was right; and I hope this series will prove that in later experiments with other species, wherein the insects do not return so readily to their homes, the fault was not due to the technique, but to something inherent in the organism. All of these had their tunnels in the board marked X in fig. 2. It was easily possible here for one to stand guard, net in hand, and capture these noisy creatures as they returned home. This colony was about 200 feet west of the railroad station of Wickes; which is the lower photograph in fig. 3 the "X" in the latter picture is the old club house, and gives the reader an idea of the distance. For five whole days, one or the other of us[2] was constantly at watch on the bank, catching with a net all of those that returned. Here those coming in from their first flight were taken, marked anew, caged

[2] I want here to express my thanks to Mr. M. M. Markovitz, a medical student, for the faithfulness with which he carried out his share of the work.

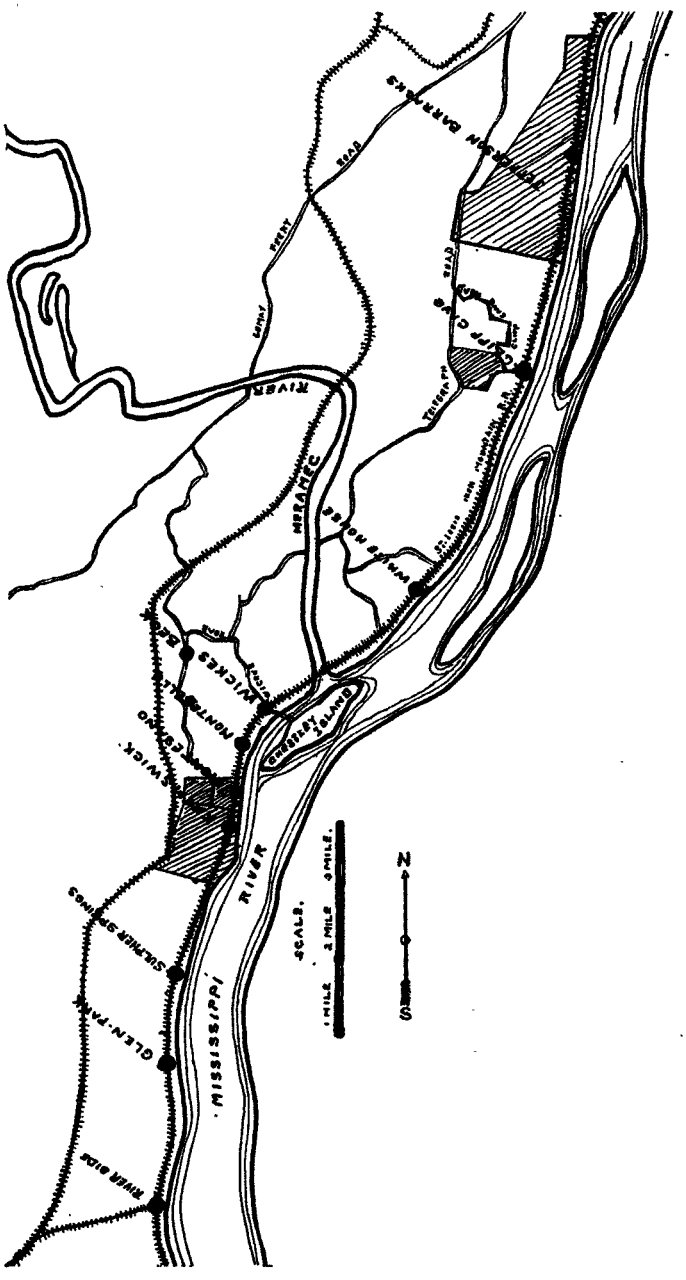

FIG. 1. WICKES, MO., AND VICINITY

in big wire fly-traps and again carried to distant stations. No Xylocopa was permitted to enter its burrow (in the five days the actual count showed the population to be seven males and eighty-seven females), and the reward for a mother that made a successful flight was to be recaptured and taken on another excursion—a cruel method, to be sure, but we knew that if once they were within their burrows, they would cautiously stay in hiding for several days. But the very interesting item is that, despite the fact that they could come only within sight of their

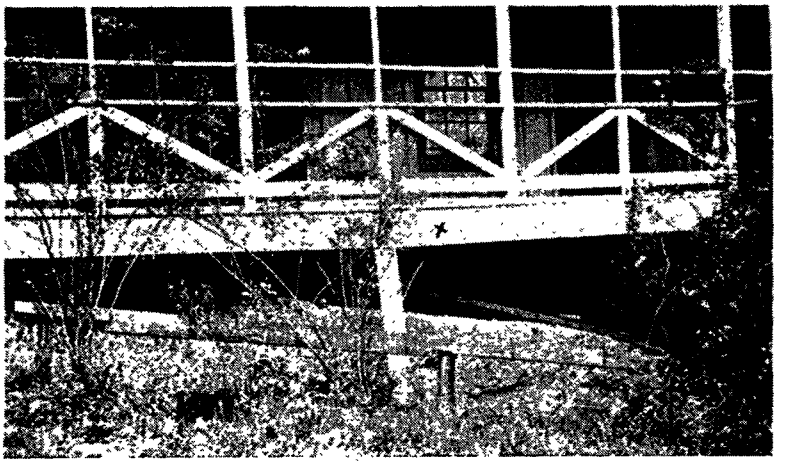

FIG. 2. THE CLAY BANK UNDER THE PORCH INHABITED BY THE MINING BEE, AND (×) THE HOME OF THE CARPENTER BEES IN THE WOODEN BOARDS

homes, and even though they never really entered them, some mothers made the flight successfully for three or four times. While in the cages they were fed honey or jelly, which some of them ate with relish. In the experiments with the carpenter bee, as well as with the mining bee, due care was exercised to keep from counting a marked bee more than once. To be sure of this, no returning bees were permitted to enter the nests, but all were caught and caged, and often remarked and used for subsequent experiments; when they were not used again they were kept in the wire cages and fed on honey until the termination of

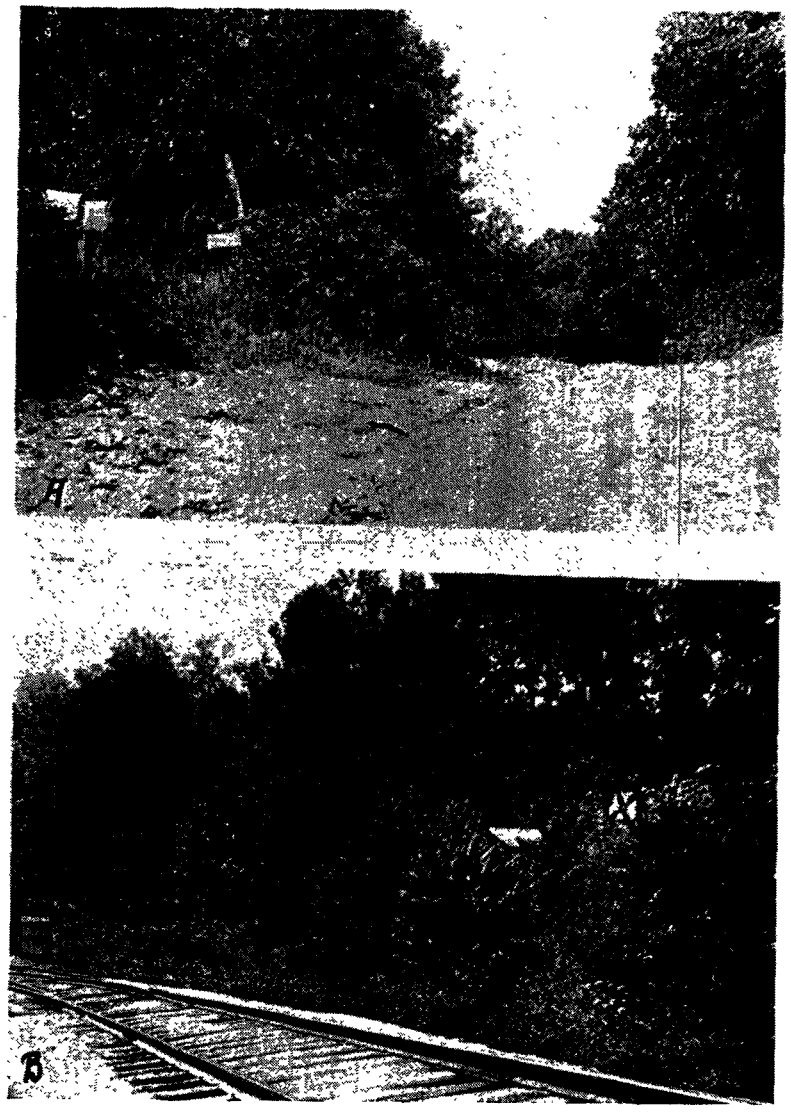

FIG. 3. WICKES, MO. STATION 9 (FIGURE A) AND STATION 1 (FIGURE B)

the experiments, when they were liberated and allowed to resume their nesting work. This method gave me absolutely clear records.

The length of time that each bee took to return to the nest must be regarded as practically the time actually consumed in finding the way home, since out of this aggregate of 106 flights made by Xylocopa, it was apparent that only three had stopped on the way to gather pollen.

The males were few; during the five days only seven were seen. These were all taken on short flights, but we can dispose of them immediately by saying that not one of them returned.

In all of these experiments, whether the insects were taken on the train or carried by the footpath to the stations, the cages were always wrapped in several layers of newspaper to exclude the light or any other possibility of the insects' seeing whither they were going. The stations where they were liberated were as follows (see map, fig. 1):[3]

Station 1. Home; Wickes. (Fig. 2).
Station 2. A railroad bridge over the Meramec River, $\frac{1}{2}$ mile north.
Staton 3. Railroad station at Montebello, exactly 1 mile due south.
Station 4. Town of Kimmswick, just 2 miles south.
Station 5. Village of Becks, $2\frac{1}{8}$ miles west by the winding road, but over the hills as a bird flies, $1\frac{3}{4}$ miles.
Station 6. The station of White House, $2\frac{3}{4}$ miles due north. To return from this point, the bees must fly over the Meramec River.
Station 7. The station of Cliff Cave, north of Wickes on the railroad track $5\frac{3}{4}$ miles.
Station 8. Town of Riverside, $7\frac{3}{4}$ miles south.
Station 9. Hilltop $\frac{1}{8}$ mile west (see fig. 3A).

An idea of the general topography may be gained from figure 3. The country was for the most part wooded hills, with here

[3] In figure 1 there may be slight errors in the scaling of the stations, but the measurements given above, taken from the United States Topographical Map, are correct.

and there open fields. The two conspicuous landmarks were the railroad track, (fig. 3B) from north to south, and the Mississippi River, which flowed parallel to it and about ¼ mile to the east of it. These could serve excellently as guides for any creature capable of using them.

Experiment 1. Station 2, ½ mile north. To get home from this point was only a small task for the insects, since the distance was short. They were liberated on the railroad track, and their home was only a few feet west of the track further down.

This group consisted of 10 bees, each bearing a green paint mark on the thorax. They were liberated at 8:45 a.m., on June 2. Out of the 10 bees taken on the trip, all made the return flight successfully, 9 of them arriving the same day and 1 the next day. On June 2 the returns were made one each at 9:00, 9:15, 10:25, 10:45, 11:45 a.m., 4:12, 4:27, 4:48 and 5:35 p.m.; on June 3, the last one came in at 10:45 a.m. It is cause for reflection that the largest bees in existence, in making the home flight of only ½ mile, varied from 15 minutes to 26 hours.

Experiment II. Station 4. This cage was wrapped and taken on the train, and the bees liberated at 8:45 a.m. at Kimmswick, 2 miles south, near the railroad track and the Mississippi River. This lot comprised 11 bees, each marked with a drop of red paint on the thorax. In this case we had 100 per cent returns, 9 bees again coming back the same day and 2 the following day. The exact time that each made its return was as follows: June 2, 9:30, 10:25, 10:40, 10:45, 11:05, 11:30 a.m.; 2:45, 4:36 and 5:45 p.m.; June 3, 2:45 and 4:20 p.m. The first bee to return made the 2-mile flight in 45 minutes, and the last one in 32½ hours.

Experiment III. Station 6. These bees were taken on the train to White House and liberated at 7:30 a.m. The 17 bees each bore a white mark on the thorax. The guiding landmarks in this case were the same as before, but the distance was slightly greater, 2¾ miles. As in all other cases, the bees in starting off from the cage did not all fly in the same direction, but they displayed a great variety of flights of orientation and chose a variety

of directions of flight.[4] Of the 17 in this group, 15 returned, 9 the same day and 6 the next. The exact time of their returns was: June 2, 9:35, 10:00, 11:05, 11:25 a.m.; 12:10, 2:48, 3:48, 4:00 and 5:37 p.m.; June 3, 12:20, 12:35, 12:55, 1:30, 2:15 and 4:50 p.m.

In this experiment we see that only 2 out of 17 became hopelessly lost on a $2\frac{3}{4}$-mile trip, and that while the first made the trip in $2\frac{1}{12}$ hours, it took the last one $33\frac{1}{3}$ hours to make the same distance.

Experiment IV. The three preceding experiments were north or south flights for comparatively short distances, and all were performed by bees out for their first enforced flight. In this trial, the bees were taken west over the hills to Becks, a distance of $1\frac{3}{4}$ miles. At intervals during the afternoon heavy clouds darkened the sky, but the sun was shining when the bees were liberated at 3:40 p.m. At times a wind was blowing from the

[4] When the bees were liberated, they all made flights of orientation of various types, a sample of which is given below from the records of the experiments.

One zig-zagged upward for ten feet, made a wide semicircle and landed on the vegetation.

One made three circles in flight, the last the largest, and alighted on the vegetation.

One made two complete circles and landed on the vegetation.

One soared in one large, complete circle above my head and alighted on the vegetation.

One quickly made two small circles, then soared high and was lost in the sunlight.

One made one complete circle and continued a zig-zag course until lost in the trees.

One made two complete and very symmetrical circles over my head and dashed away in the dazzling sun.

One made four small, complete circles in front of me and rested on the shrubs.

One made many circles and a series of S's, then alighted on the ground and entered the cage from which it had just been liberated, remained in it for a few minutes, flew out, made a few circles and landed on the top of the cage. Here it remained until I carried it and placed it on a bush.

One made several small circles in front of me, then continued in a long zig-zag flight, then flew in a dozen or more circles of ever increasing width and eventually alighted on a shrub.

One described a series of S's before alighting on a shrub.

One made three circles of increasing size and soared away to a tree.

One flew away toward the south, came back by way of the north, then described a small, perfect circle and then dropped to the ground.

southwest, in the proper direction to assist them on their homeward flight. This time the bees had no buiding landmarks (such as the railroad tracks) that we could perceive; their route home was over wooded hills and irregular farms (Station 5).

This experiment was made with 32 females, 16 of which were taken out for the first time, each marked with a yellow dot on the thorax, and 16 which had made previous flights, as follows: 5 bees that had made the successful flight from Station 6, and still bore the white dot, in addition to which they were given a dot of yellow; 5 bees that had returned from Station 2, and still wore their green dots and were given the yellow also; 6 bees from Station 4, still wearing their red dot, to which was added a dot of yellow. So all in this experiment bore yellow, with or without additional color as they had or had not made a previous trip. Of these 32 insects, 26 successfully returned home; 13 or just half of them arriving the same day and within 2 hours after they had been liberated, 10 of them the next day, and 3 on the third day. The exact time of their return was as follows:[5]

June 2, 1922			*June 3, 1922*		
Station 5.....	4:30 p.m.	:50	Station 5, 6....	8:00 a.m.	16:20
Station 5.....	4:32 p.m.	:52	Station 5.....	10:45 a.m.	19:05
Station 5.....	4:35 p.m.	:55	Station 5, 6....	10:50 a.m.	19:10
Station 5.....	4:40 p.m.	1:00	Station 5.....	11:10 a.m.	19:30
Station 5.....	4:43 p.m.	1:03	Station 5, 4....	11:30 a.m.	19:50
Station 5, 4.....	4:45 p.m.	1:05	Station 5.....	11:45 a.m.	20:05
Station 5, 6.....	4:47 p.m.	1:07	Station 5.....	2:20 p.m.	22:40
Station 5.....	4:47 p.m.	1:07	Station 5, 6....	2:30 p.m.	22:50
Station 5.....	4:55 p.m.	1:15	Station 5.....	3:40 p.m.	24:00
Station 5.....	5:06 p.m.	1:26	Station 5, 2....	5:00 p.m.	25:20
Station 5, 2.....	5:07 p.m.	1:27	*June 4, 1922*		
Station 5.....	5:30 p.m.	1:50	Station 5.....	10:35 a.m.	42:55
Station 5, 4.....	5:30 p.m.	1:50	Station 5.....	11:00 a.m.	43:20
			Station 5, 6....	4:50 p.m.	49:10

Thus 26 out of 32 returned to their nests. The 6 absentees were 3 which had previously made the return from Station 2,

[5] The first column indicates the station from which the bee is returning and the stations, if any, from which it has previously returned. The second column shows the hour of its return, and the third gives the number of hours and minutes it was out; 16:20 is read sixteen hours and twenty minutes.

a short flight, and 3 which had returned from Station 4, a point 2 miles south. It is interesting to note that all those out for their first flight came back; in fact, as a group they seem to win the laurels; it is noticeable that they lead in the returning procession, and none of their numbers were lost. At the same time we must not lose sight of the fact that, although some of the first-flighters came in early, others came straggling in among the latest. The same irregularity governs the experienced travelers as well; some came in early and others late, and a few came not at all. This to my mind indicates that the homing of these bees is not controlled by an impelling special sense, else it would function more uniformly in so simple a test. Thus their action or failure can be explained only in terms of individual temperament, age or experience, and perseverance, or combinations of these factors. One may add fatigue also to the list of controlling factors, although this is probably not so important as one would at first think.

Experiment V. Station 7. The 27 bees in this experiment were in part first-flighters, and in part those which had successfully made a trip of greater distance before. Of these, 7 were out for the first time; 5 had already made their first flight from Station 2, a distance of $\frac{1}{2}$ mile; 6 had made the flight from Station 5, $1\frac{3}{4}$ miles distant over the hills from the west; 3 were bees marked in red, indicating a successful two-mile flight from Station 4; 3 had made the trip of $2\frac{3}{4}$ miles from Station 6; and, finally, 3 were bees that had made more than one successful flight, as follows: 1 wearing white and yellow, showing successful returns from both Stations 6 and 5, 1 in green and yellow, indicating trips from Stations 2 and 5, and 1 wearing red and yellow insignia, showing honorable records from Stations 4 and 5. These were all given additional markings in black, duly recorded, and carried in darkness on the train to Station 7, Cliff Cave, $5\frac{3}{4}$ miles north of their homes. They were liberated on June 3, at 7:30 a.m., with a gentle wind blowing from SSW., which was against them in their flight toward home.

Out of these 27 liberated, only 8 came back. Their records were:

June 3, 1922			*June 4, 1922*		
Station 7, 5, 2....	12:15 p.m.	4:45	Station 7, 5, 2..	10:35 a.m.	27:05
Station 7, 6, 5....	3:43 p.m.	8:13	Station 7, 5....	12:16 p.m.	28:46
Station 7.....	3:50 p.m.	8:20	Station 7, 6....	4:00 p.m.	8:30
Station 7, 4.....	3:55 p.m.	8:25	Station 7, 2....	4:15 p.m.	8:45

These cold and stiff tables are pitifully inadequate to convey to the reader the thrill of excitement which the homecoming of these bees aroused. To see one of these earnest contestants coming wearily in to the goal, wearing the colors showing that it had qualified in two or perhaps three successive marathons, making long distances over unfamiliar courses, was to me quite as thrilling as to see the select of its intellectually-endowed fellow-creatures do the same thing on the measured track of a new million-dollar stadium amid the wild cheers of his fellow-intellectuals!

These numbers are of course so small that we must not lay too much stress upon percentages, yet we cannot ignore the fact that when these bees were put to the extreme test of finding their way home when lost almost six miles away, only one of the seven inexperienced travelers succeeded; four out of seventeen that had had one previous flight came back, but all three that had made two previous flights came in, two of them being the first to arrive. There is added interest in the fact that the first two of these made the three long flights in two days, while the other one returned from its third trip on the morning of the third day. This indicates, if it shows anything, that experience and perseverance in the school of trial and error are chief factors controlling their action. At the same time we must not lose sight of the fact that bees out for their first enforced flight can make a six-mile trip, even though our proof depends upon only one out of seven individuals.

Experiment VI. Station 8. The material for this experiment included 27 bees; 9 were first-flighters, 14 had made one successful flight previously, 2 had made two flights before this and 2 had already made good in three tests. The 14 bees that had made one previous flight were as follows: 4 from Station 6, 7 from Station 2, 1 from Station 5, 1 from Station 4 and 1 from

Station 7. Of the two bees that had taken two flights each, one was from Stations 4 and 5, and the other from Stations 5 and 2, while the two that had made three flights each bore marks indicating trips from Stations 6, 5, 7, and 4, 5, 7. We were now almost under the necessity of contriving an extension to the bee's anatomy to carry the additional colors, but at length we gave them all their additional decoration of yellow. These 27 were taken in darkness to Riverside, $7\frac{3}{4}$ miles south, on the 4:15 train and liberated near the railroad track at 4:30 p.m. on June 3. This hour would give them ample opportunity to make their way home in the dark if they chose to utilize the night hours. The oncoming night may have been a factor in confusing them; at any event, only 7 out of the 27 made the long distance, 4 coming back the next day and 3 returning a day later. The order in which they returned was as follows:

June 4			*June 5*		
Station 8, 4.....	11:20 a.m.	19:50	Station 8, 5....	9:34 a.m.	41:04
Station 8, 6.....	1:05 p.m.	20:35	Station 8,4,5,7.	10:18 a.m.	41:48
Station 8.....	1:55 p.m.	21:25	Station 8, 6....	10:42 a.m.	42:12
Station 8, 5.....	3:45 p.m.	23:15			

In these 7 that returned, we see 1 first-flighter, 5 that had made one trip before and 1 that had previously made three trips (2, $1\frac{3}{4}$, and $5\frac{3}{4}$ miles respectively. Further deductions from these limited data would be unwise, but we may pause to wonder if the increasing proportion of failures to return is due to the exhaustion of the bees, their old age, the increased distance, the fall of night soon after their liberation, or other causes.

Experiment VII. Station 3. This experiment with 12 insects of various previous experience was to determine the nature and extent of the function of the antennae in successfully making the home flight. This group of 12 bees included: 6 first-flighters, 2 that had made one previous flight (from Stations 4 and 5), 3 that had made two flights each (from Stations 2 and 5, 6 and 5, and 6 and 7 respectively), and finally 1 that had made three flights, from Stations 4, 5 and 7. All these, with their antennae cut off close to the base, were liberated at 11:25 a.m., June 4, near the railroad track at Montebello, one mile from their home.

Of this number, 8 returned, 6 the same day and 2 the next day. The actual succession of their returns was:

June 4			Station 3, 6, 5..	5:15 p.m.	5:50
Station 3, 2, 5.....	1:20 p.m.	1:55	Station 3, 6, 7..	5:45 p.m.	6:20
Station 3, 5.....	1:55 p.m.	2:30	*June 5*		
Station 3.....	3:25 p.m.	4:00	Station 3.....	11:58 a.m.	24:33
Station 3, 4.....	3:35 p.m.	4:10	Station 3.....	2:07 p.m.	26:42

While this little test does not prove that the antennae are of no value in guiding the bees homeward, it does prove that they are not necessary to a successful and prompt return. Here again there is evidence that previous experience increases efficiency, for just half of the inexperienced ones came back, while all of those out for the third or even the second time were successful.

Experiment VIII. Station 4. This experiment was to all intents and purposes the same as the last, excepting that the distance was doubled and the bees had either the right, the left or both antennae amputated. They were taken out at twilight on June 4. The cage was opened and placed in the bushes, but they did not venture forth, so the time consumed in their return was calculated from 7 o'clock the next morning. Their records were:

June 5

Station 4, 6, 5.....	all left antenna off.....	9:22 a.m.	2:22
Station 4, 6, 5.....	all left antenna off.....	9:42 a.m.	2:42
Station 4, 5, 7.....	all right antenna off.....	9:56 a.m.	2:56
Station 4, 6, 5.....	all left antenna off.....	10:05 a.m.	3:05
Station 4, 5, 4.....	all both antennae off.....	11:00 a.m.	4:00
Station 4, 4.....	all right antenna off.....	11:16 a.m.	4:16
Station 4.....	all left antenna off.....	11:35 a.m.	4:35
Station 4, 5.....	all both antennae off.....	11:35 a.m.	4:35
Station 4, 5.....	half of each antenna off.....	12:07 p.m.	5:07
Station 4.....	all right antenna off.....	12:20 p.m.	5:20
Station 4, 5.....	all left antenna off.....	1:03 p.m.	6:03
Station 4, 3, 5.....	all both antennae off.....	2:48 p.m.	7:48
Station 4, 6, 7.....	all both antennae off.....	4:30 p.m.	9:30
Station 4, 6, 5.....	all both antennae off.....	4:34 p.m.	9:34
Station 4, 3.....	all both antennae off.....	no return.	
Station 4, 4.....	all both antennae off.....	no return.	
Station 4, 5.....	all right antenna off.....	no return.	

So here we see 14 out of 17, with various mutilations of the antennae, and with or without previous experience in long flights, returning from a distance of two miles. Again there is no evidence that they try to travel at night, for, even though they were out all night, none of them came in before 9:22 the next morning. Hence the antennae do not seem to be functioning factors in directing their return, at least from a distance of 2 miles.

Experiment IX. This was practically the same as Experiment III, only made two weeks later. Nine new individuals were found, marked and taken to Station 6 on June 16 and liberated at 7:15 a.m. Of these, 7 returned the same day, at the following hours: 9:15, 10:15, 11:05, 12:05, 12:40, 4:50, and 6:05. This proportion of returns is practically the same as in the previous test from that station.

Summary

Table 1 brings together the results of these nine experiments. This summary shows that when female Xylocopa were liberated at various distances from their home, 106 out of 162, or 65 per cent returned successfully. It is not surprising that as the distance increased the proportion of returns decreased. In all the experiments involving short flights (less than 3 miles) there were 91 successful returns out of 108 flights, or 84 per cent, while in the longer flights, $5\frac{3}{4}$ and $7\frac{3}{4}$ miles, only 15 out of 54 came back, or 28 per cent. Of these 15, 13 were experienced fliers. Previous experience is not a necessary factor in accomplishing short flights; a moment's calculation reveals that, when the two tests involving long flights are excluded, the proportion of experienced bees and inexperienced bees successful in their flights were practically the same. On the other hand, in the two long tests, $5\frac{3}{4}$ and $7\frac{3}{4}$ miles, only 12 per cent of the novices came back, against 34 per cent of the experienced bees. We must not be hasty in concluding, after a glance at the table, because 76 per cent (66 out of 87) of the first-flighters returned, against 54 per cent (40 out of 75) of the old-timers, that the new ones are more capable than the old ones in making flights. We must give due consideration to the fact that the new ones are fresh and full of vigor, while the

chances of success of the old ones are greatly reduced by fatigue, senility and various chances of death and disaster which cannot be reckoned on this handful of data. When a returning bee is captured, before it can enter its home, marked, and again carried to a distant station and sometimes even required again to pass through the whole ordeal, some allowance must be made for the

TABLE 1

Homing of Xylocopa virginica. Females

DATE (1922)	EXPERIMENT NUMBER	NUMBER OF BEES USED	NUMBER OF BEES RETURNED	DISTANCE TO HOME	DIRECTION OF HOME	NUMBER OF BEES OUT FOR FIRST TIME	NUMBER OF BEES USED IN PREVIOUS FLIGHTS	NUMBER OF FIRST FLIGHTERS THAT RETURNED	NUMBER OF PREVIOUS FLIGHTERS THAT RETURNED	REMARKS
				miles						
June 2.....	I	10	10	½	S	10	None	10	—	
June 2.....	II	11	11	2	N	11	None	11	—	
June 2.....	III	17	15	2¾	S	17	None	15	—	
June 2.....	IV	32	26	1¼	E	16	16	16	10	
June 3.....	V	27	8	5¾	S	7	20	1	7	
June 3.....	VI	27	7	7¾	N	9	18	1	6	
June 4.....	VII	12	8	1	N	6	6	3	5	
June 4.....	VIII	17	14	2	N	2	15	2	12	Antennae of all mutilated
June 16.....	IX	9	7	2¾	S	9	None	7	—	Antennae of all mutilated
Total.....		162	106			87	75	66	40	
Per cent returned....			65%					76%	54%	

physical exhaustion and especially the nervous shock which it must necessarily suffer. If experiments could be made, eliminating fatigue and senility, I believe the results would show (and the figures bear out this deduction) that experienced fliers return in much greater proportion.

The removal of the antennae or parts thereof did not exert any observable influence against their ability to return, since 22 out of 29 bees so mutilated made the return.

The last column in the small individual tables, which gives the length of time consumed by each bee in making the return trip, brings to light the fact that the individual bees varied from a few minutes to 49 hours in effecting their returns. This should show clearly that they were not led back by magic or by a blind sixth sense, else they surely would have returned from the same station at more nearly the same time. This throws us back on the conclusion that experience, perseverance and memory are factors in bringing them home when they do successfully return, but that they sometimes fail, through the lack of these qualities, or, in other words, they are lost because of stupidity, lack of memory, wrong trials, etc.

The map (fig. 1) shows how conspicuous are the railroad track and the Mississippi River in the landscape. It has already been pointed out that the nesting site was near the railroad tracks and a short distance from the river. This streak of glistening steel and light-gray ballast, and the shining river, both near to their home, certainly could serve as landmarks and guides. Now Xylocopa is a genus of large-sized bees, and X. virginica is one of the largest species extant. Correlated with this great size are very large compound eyes, which, in all probability, can encompass the two landmarks mentioned without flying unreasonably high. But besides these large and conspicuous landmarks, there were others of a confusing nature to be reckoned with. For instance, the bees making the return flight from White House would see no group of buildings to confuse them until they arrived at Wickes, near the railroad; hence we should expect a large proportion of returns. This I found actually to be the case, for in the two tests from that point, 22 out of 26 arrived home. In the opposite direction the same conditions are present from Stations 3 and 4, and from these points we got approximately the same proportion of returns. On the homeward route from the more distant stations, there were various villages and groups of buildings to be passed which could easily serve as false landmarks and thus seriously confuse the travelers. Just the extent of such confusion as this we can never know, but we feel safe in assuming that it was very variable, and that it varied with the

native ability and experience of the performer. In this very connection it is worthy of note that in the case wherein 26 bees returned from Becks (Station 5) over wooded hills, fields and farmyards, one-half of that number made the trip in less than 2 hours, and the other half consumed in the same trip from 16 to 49 hours.

HOMING OF THE MINING BEE, ANTHOPHORA ABRUPTA

In working with Polistes in homing experiments, we knew their ages, and the results could be interpreted in terms of age. In the experiments with Xylocopa also, this was approximately true, for on April 25 we found the population of these bees out and just beginning their carpentry, and by June 1, they were busily bringing in pollen. These were all of the first generation, since on June 1 it was too early for the second generation to have appeared. Thus age may, in a general way only, enter into the considerations here. In Anthophora abrupta we have a species whose life-habits differ to a great degree from those of both P. pallipes and X. virginica, for its life-cycle is short. For five successive years I have seen at the clay bank their simultaneous emergence, i.e., within three or four days all of the insects of this species in that locality emerge, the males die off soon after emerging and the females carry on the nidification. The life cycle lasts only for thirty or thirty-five days, and then all their work is over; usually early in July none are to be seen.

It occurred to me that this species would be ideal for homing experiments. Here we have an insect species, the simultaneous emergence and the simultaneous demise of whose members make their ages ascertainable with practical certainty when flights are to be made, so that if they return to their nests simultaneously after having been liberated together at a certain distance, then we may almost assuredly conclude that they are brought back by a special homing instinct or sixth sense *per se*. If, however, they return by observation and perseverance, or trial and error, then such tests ought to give positive evidence of the fact in the following way:

a. Testing very young bees, 1 to 4 days old, in enforced flights

for short distances should give negative results (none should find their way home).

b. Taking middle-aged bees out for short distances should give "fair to middling" positive returns.

c. Old and experienced bees which have had time to become acquainted with the topography, when taken out to repeat the tests imposed upon classes "a" and "b," should give 100 per cent positive results (excepting, of course, that due allowance must be made for senescence). With these theoretical considerations in mind, the following experiments were undertaken. The records following will show how nearly the results bear out the theory.

Experiment I. June 2, 1922. These 14 bees, 7 males and 7 females, were taken to Station 2, the railroad bridge only a half-mile distant, and liberated at 7:30 a.m. The cage in which they were carried was not wrapped, and the bees were given every opportunity to use their eyes. During the four days of our careful watching, not one of these returned.[6]

Experiment II. June 2, 1922. This time 17 insects, 6 males and 11 females, were taken, in open cages, to the top of the hill (fig. 3, A) only $\frac{1}{8}$ mile away and liberated at 3 o'clock. Their homeward course was straight down the road, and a strong wind was blowing in the direction to assist them on their homeward flight. The next day three returned at almost the same time, after having been out about 21 hours. They arrived at 11:55, 11:58 and 12:00 noon (Station 9).

Experiment III. June 2, 1922. Since the first test showed that these youngsters were hopelessly lost a half-mile from their nests, we next tried 12 bees (4 males and 8 females) at a point down the railroad track at just half that distance, or $\frac{1}{4}$ mile. They were liberated at 8:50 a.m., when their zest should have been at its height, but none came back.

Experiment IV. June 2, 1922. Since 3 bees had returned from the hilltop $\frac{1}{8}$ mile west of the nests, these 3 in addition to

[6] I wish here to thank Mr. Ernst Schwarz and Mr. Anton Klein, who at various times relieved me in watching for the returning bees—a monotonous task which they faithfully performed.

18 other females were taken to a point in an open field ⅛ mile east of their homes. Again none returned.

These simple tests give ample proof that these young bees have no aptitude for finding their way home. It is not surprising that the 17 males were all lost, but it does seem surprising at first that out of 47 healthy, young females, only 3 eventually found their way down the road for ⅛ mile, and even these were lost when taken out into an open field the same distance in the opposite direction. Of course all the bees were at this time very young—only a few days old—burrowing had not begun but they still used the old tunnels for sleeping quarters.

On June 15, I found all males at the bank had died. The females were much larger than they had been two weeks previously; this condition was probably due to the maturation of the ova and to their having the honey crops filled with water or varnish. The bees were busy burrowing in the bank, cleaning the debris out of old burrows and building turrets. The building was rendered unusually difficult by the condition of drought that prevailed, and those that had water to build with must have brought it from long distances. Out of about 300 mothers seen at work, only 3 were carrying in pollen; this indicated that their first stage of mining was about over and provisioning was about to begin. Their industry was really surprising; now they were earnestly working until 6:30 or even 7 o'clock in the evening, whereas two weeks before they had all been seen going to bed long before that time. All this indicates that I had come just in time to get the individuals at middle age for my experiments.

These bees, in the prime of their vigor, were taken at twilight as they were returning to their burrows, and all from one small area, so that attention could be concentrated upon it in watching for the returning bees, and thus none could escape my notice. The bees were given markings while they were asleep to distinguish them sharply from any marked individuals of previous tests which might have wandered back, though none were ever seen. To do this the bees were taken in the fingers; they have stings, but none were able to penetrate the skin. Occasionally when they were taken in the fingers, they emptied

the gullet of water on my finger, and often they spat out in like manner a brownish sticky substance that looked much like thick grasshopper spittle. The bees when disturbed give off a sharp, acid odor, and when this brown substance was emptied on my finger, it was found to have the same odor as that emitted by the bees. This was undoubtedly the varnish that is plastered on the inside of the brood-cup, which seems to make it waterproof, but from what source it comes I do not know. These bees seemed in healthy condition and good vigor; most of them flew out of the cage briskly, and the few that were not perfectly alert and were not included in the tests, but were consigned to the cyanide jar; hence any failures to return cannot be attributed to any physical weakness, but only to psychic causes.

Experiment V.[7] June 15, 1922. On this date 18 marked females were liberated at the railroad bridge ½ mile north of their homes at 9:10, as in Experiment I. A very strong wind was blowing toward the north, against which they must fly to reach home. In spite of this unusual difficulty, exactly one-half of the bees returned safely. It is of interest to know that it took them various periods, from 1½ to 6 hours, to make the trip that, according to their physical strength, should not consume more than five minutes. The hours of their returns were: 10:40, 11:05, 11:10, 11:12, 12:15, 12:40, 1:35, 2:40, and 3:05. However, it is gratifying to see 50 per cent of these middle-aged individuals successfully making the return flight, after others had scored almost 100 per cent failures in their early youth.

Experiment VI. June 15. This is a repetition of Experiment III, wherein 11 females were liberated at 9:20 at a point ¼ mile up the track. Again the wind was blowing against them, yet of these 11, 5 returned at 10:20, 10:55, 11:25, 1:30, and 1:40.

Experiment VII. June 15. In this test 14 bees were liberated on the hilltop ⅛ mile west at 9 o'clock, before the wind became so strong. During the day 7 of these returned in from 2 to 5 hours, as follows: 11:05, 11:20, 12:40, 12:42, 1:15, 1:35, and 2:00 (Station 9).

[7] This and subsequent work was done with darkened cages.

Experiment VIII. June 15. This time 35 bees were taken out for a longer flight, $2\frac{3}{4}$ miles, and liberated at Station 6. On account of the distance, we were not surprised that none of them ever found their way back. Even on my visits to the clay bank several times later in the season, there was no evidence that these individuals had ever wandered back.

The third set of experiments was undertaken during the old age of these bees, or from June 29 to July 3. The most of them were at that time carrying in pollen, which indicates that they were finishing the task of provisioning their nests. Subsequent observations showed that they were all dead within ten days after this date; hence I was fortunate in catching them when their store of life's experiences was almost complete, and yet before their vitality was seriously waning.

Experiment IX. June 30. In this experiment, 41 A. abrupta and 15 A. raui, were taken to Station 6, $2\frac{3}{4}$ miles north, and liberated at 7:10 a.m. There was no perceptible wind; the morning was cloudy, but a few minutes after they were liberated the sun shone out brightly. Vigilance for the three days following, from sunrise to sunset, and occasional subsequent visits, proved that not one of these 56 ever returned. Considering the large number tested, we may safely conclude that this distance is too great for these insects to traverse, even at their best.

Experiment X. June 30. At 8:40 a.m., 22 A. abrupta were liberated at the edge of the town of Kimmswick, 2 miles south of their home. The sun was shining and a mild wind was blowing in their favor. The storm and rain on that afternoon and night probably did much to reduce the number that returned; at any event, the four bees that did return came in before the storm broke. They arrived at 9:00, 10:05, 10:30, and 12:15.

Experiment XI. June 30. On the same morning at 8:45, 7 bees were liberated at Station 3, just half way between Kimmswick and home. Strange to say, all of these seven arrived home, but only one came in the same day, one hour and ten minutes after it was set free; the others came straggling in the next morning at 9:00, 9:05, 9:48, 10:10, 10:57, and 11:00 o'clock. The remarkable point in the episode is that, since they did not arrive

during the fair weather, as they had plenty of time to do, they weathered the storm and night somewhere and yet came home after that.

Experiment XII. This time 30 A. abrupta were liberated on the hilltop ⅛ mile west of the home site at 11:05 a.m. on June 30. Although they were almost within sight of their home, only one arrived the same day, over 4 hours later; 8 others came back the second day (9:30, 9:45, 9:50, 10:45, 10:47, 10:50, 12:20, 12:30), and the tenth and last one came in on the third day at 1:15 p.m. (Station 9).

Experiment XIII. June 30. Once more we tested them in a flight of ½ mile from the north, this time using 25 A. abrupta. The wind which they had to face on their return was very slight. One lone wanderer came back, and that one did so the next day at 11 o'clock; just one out of 25, and it consumed 25 hours in making a trip which I walked in ten minutes.

Experiment XIV. June 30. Another consignment of 26 A. abrupta were taken to a point ⅛ mile east of their homes and liberated in the field. The day was fair and quiet. Four of the 26 returned, but not until the next day at 10:00, 10:30, 12:20, and 12:30.

Experiment XV. July 1. Fourteen A. abrupta were set free at the railroad bridge ½ mile north at 8:15 a.m. One of these had previously made a successful flight from Station 3, one mile south. Seven of the 14 returned, the first to arrive being our experienced traveler, which came in at 9:50; the others followed at 9:55, 9:57, 10:00, 10:24, 10:43 and 12:22. Just why they should take so long for a short flight and then come in so nearly together, I cannot imagine.

Experiment XVI. July 1. The material for the next simple test was a mixed lot; 30 A. abrupta were first-flighters, 1 had returned from the field ⅛ mile east, 1 had come back from Kimmswick 2 miles south, and 1 had come back from Station 3, 1 mile south. These were taken up the road to the hilltop ⅛ mile west and liberated at 9:20. Of the 33 bees, 21 came back, and the three that had made previous flights were the first, third and eighth to reach home. The hours of their arrival were: July 1,

10:20, 10:40, 10:42, 10:43, 10:55, 11:05, 11:15, 11:45, 12:20, 12:45, 2:25, 2:30, 2:40, 3:00, 3:20, 3:50, and 4:30; July 2, 9:10, 9:30, 11:15 and 11:20 (Station 9).

Experiment XVII. July 1. This lot of bees consisted of 14 A. abrupta, all out for the first test, and 22 that had already made one successful flight each, as follows: 6 which had, in two different tests, come back from the railroad bridge ½ mile north, 3 which had returned from Station 3, one mile south, 1 from the field ⅛ mile east, 10 from the top of the hill ⅛ mile west, and 2 from Kimmswick, 2 miles south. All of these 36 were given additional markings and liberated at Station 3, a mile south, at 12:50 on July 1. Of these, 10 returned, 4 of them "first-flighters" and 6 "old-timers." Their hours were: July 1, 2:15, 2:45, 2:55, 3:10, 3:28, 4:10, 4:30, 5:10; July 2, 11:40 and 1:20.

SUMMARY OF THE HOMING OF ANTHOPHORA ABRUPTA

I started out with the theory that young bees, only 2 or 3 days old, would all be unable to find their way home; that middle-aged bees would give positive results to the extent of 50 per cent, and that old bees would give us (barring debility) 100 per cent positive results. A. abrupta emerged from the clay-bank May 30 to June 1, and by July 8, they had completed their life cycle and died. Thus the time selected for the flights coincided nicely with these dates—thanks to observations during previous years. The experiments were made on June 2 for young bees, June 15 for middle-aged bees, and on June 30–July 1 on old bees. The latter date was carefully selected because it was as late as I dared risk before their death, and probably (although this is hard to estimate) would be at a time when the mothers would still have an interest in the nest, and also when the factor of senescence and debility would not seriously affect their powers. After each experiment the bank was watched for three or four days to give every straggler due consideration. It is at once apparent that in the experiments with old bees the live material was much more liberally used than in the young or middle-aged ones. This was because I soon saw that the majority of those taken out were lost, and if I used large numbers early, I should run the risk of exterminating them.

TABLE 2

Homing of Anthophora abrupta. All females

DATE (1922)	EXPERIMENT NUMBER	NUMBER OF BEES USED	NUMBER OF BEES THAT RETURNED	DISTANCE TO HOME	DIRECTION OF HOME	NUMBER OF BEES OUT FOR FIRST TIME	NUMBER OF BEES USED IN PREVIOUS FLIGHTS	NUMBER OF FIRST FLIGHTERS THAT RETURNED	NUMBER OF BEES THAT RETURNED THAT WERE USED IN PREVIOUS FLIGHTS	REMARKS
				miles						
A. Young bees:										
June 2	I	7	0	¼	S	All 7	0	0	—	7 males also liberated and were lost
June 2	II	11	3	¼	E	All 11	0	3	—	6 males also liberated and were lost
June 2	III	8	0	¼	S	All 8	0	0	—	4 males also liberated and were lost
June 2	IV	21	0	⅛	W	All 18	3	0	0	
Total		47	3			44	3	3		
B. Middle aged bees:										
June 15	V	18	9	½	S	All 18	—	9	—	
June 15	VI	11	5	¼	S	All 11	—	5	—	
June 15	VII	14	7	¼	E	All 14	—	7	—	
June 15	VIII	35	0	2¼	S	All 35	—	0	—	
Total		78	21			78		21		
C. Old bees:										
June 30	IX	56	0	2¼	S	All 56	—	0	—	41 A. abrupta; 15 A. raui used
June 30	X	22	4	2	N	All 22	—	4	—	Rain part of the time
June 30	XI	7	7	1	N	All 7	—	7	—	Rain part of the time
June 30	XII	30	10	⅛	E	All 30	—	10	—	Rain part of the time
June 30	XIII	25	1	¼	S	All 25	—	1	—	Rain part of the time
June 30	XIV	26	4	¼	W	All 26	—	4	—	
July 1	XV	14	7	½	S	13	1	6	1	
July 1	XVI	33	21	½	E	30	3	18	3	
July 1	XVII	36	10	1	N	14	22	4	6	
Total		249	64			223	26	54	10	
Grand total		374	88			345	29	78	10	

Table 2A, the record of the young bees, shows that in four very short flight tests, all under ½ mile, practically all were lost; only 3 out of 47 returned, and these required over 20 hours to come ⅛ mile down the road. The most puzzling part of the story is that all three arrived at practically the same time. To be perfectly honest, how vexing it is that they should have come home at all! Let's pretend that it was only an accident,—that these three eventually landed here just as the other 44 eventually landed at some other point in the vicinity. At least we felt avenged when in the next test they were required to repeat their performance and failed.

There is nothing surprising in the fact that none of the males returned, for we know that they are interested in the nests only as sleeping quarters and the domiciles of their females. After the first series of tests, of course all the males were dead.

In the second series, (see Table 2B), 78 females figured in the tests, but since all of the 35 taken out to Station 6 were lost, I felt justified in concluding that the distance of 2¾ miles is an impossible task for them, and this test was not further considered in the calculations. The other three tests involving flights of ½ mile or less give us 21 successful returns out of 43 flights, or 49 per cent. Considering the interference of accident and various elements of chance outside the factor of psychic potentiality, this does not miss far the theoretical 50 per cent with which we started. Of course if these elements of accident were eliminated, the percentage of successful returns would run in excess of this 50. There is another outstanding feature of this series of tests worthy of attention: all of these middle-aged individuals made their return trips in less than 6 hours, while the 3 youngsters that came back in a ⅛-mile test took over 20 hours for the trip.

The summarized results of the third series of experiments, as shown in table 2C, are at first sight disappointing in that they fall short of the expected high percentages. Just how accurate an index of their physical ability this is we cannot be sure, since two prominent factors were exerting their influence against them at that time. The first is the factor of old age (a week after the conclusion of these tests, all bees in the colony were dead), which

was probably at this time cutting down their energy; the second was the inclement weather. It is only reasonable to believe that the heavy rain and storms which occurred while these bees were out on their flights must have been the cause of a considerable number of their failures to return. The effect of these factors cannot be calculated, and we can only bear them in mind in reading the results. Only 34 per cent of these came back (64 out of 193). The time consumed in their flights shows much confusion; they required from 20 minutes to 50 hours for these simple trips. Once more it is demonstrated here that the distance of $2\frac{3}{4}$ miles is too much for these medium sized bees; of 56 which were taken to that distance, none at all made their way back. Of the 22 that were taken 2 miles, only 4 found their way home; these, especially the first, came in so promptly that one is inclined to suspect that they merely "struck it lucky" in making their first choice of direction homeward. After giving due consideration to the circumstances, I think these results are not so bad for individuals with three feet in the grave, and I firmly believe that if the experiments could be repeated with bees yet in their full vigor, and in fair weather, the results would not fall far short of what I expected.

In comparing the records of all the bees taken out for their first test and those out for their second flight, there is not a significant difference between the two groups; the "first-flighters" (exclusive of those that were lost in too long flights in experiments VIII and IX) returned in 31 per cent of their flights (78 out of 254), and the bees out for their second flight came back in 35 per cent (10 out of 29) of the cases.

It has been suggested that the direction of the light is a principal factor guiding their flight. From Table 2 it is evident that of the 88 which returned to the home site, 44 flew east, 4 flew west, 21 flew north and 17 flew south. At first we thought that the morning rays of the sun had a strong lure for them and aided greatly those which by chance needed to travel eastward, and that since the bees' most active time of the day is in the morning hours, and the majority of returns were made then (71 per cent before 1 p.m.), this lure of the eastern light was more potent.

More careful calculation shows, however, that the present experiments lend no support to such a belief. When we consider, not the actual number of returns, but the percentage of the possible number, then we find that 21 out of a possible 65, or 32 per cent, returned toward the north, 27 per cent of the number taken in the opposite direction returned toward the south, 33 per cent of those traveling eastward succeeded, and only about 9 per cent of those westward bound came in. These three proportions, 27, 32 and 33 per cent, are strikingly similar, while the divergent one, 9 per cent, is easily explained: the three former directions offered, along the railroad track and the roadsides, many allurements in the way of flowers and vegetation to invite the bees to become acquainted with those regions, while the latter was merely a point in a large corn-field where the bees had no interest and hence probably were not in the least acquainted.

The question will naturally arise in the minds of many readers, if the carpenter-bees in the previous experiments could traverse far greater distances, why should we not expect as much of these also? It must be borne in mind that the former species is a much larger insect— at least three times as large as the Anthophora— with very large compound eyes. Now we have been acting upon the supposition that these large eyes can comprehend a wide field of vision, and that only by this means can the insects discern their landmarks and thus be able to do such remarkable feats of homing. Hence we rejoice in the assurance from the expert testimony of Exner and Forel[8] which justifies the assumption that the large compound eye of *Xylocopa* can, on account of its larger number of facets and greater convexity, comprehend a much wider field of vision than can the compound eye of the *Anthophora* type. This is really too beautiful an instance of the correlation of form and function to throw away by attributing the animal's accomplishments to tropisms or unknown senses. Whether we argue that the long and persistent exercise of the function led to the high morphological specialization, or whether we turn it about and say that the peculiar morphological varia-

[8] Their work is fully discussed in later pages.

tion gave rise to the remarkable habits, the fact remains that here in these two species of bees in the same locality, and subjected, as nearly as possible, to the same tests, we find that their habits and their ability to perform their essential duties have by these experiments been proven to be in direct proportion to their degree of morphological development. This simple point is too significant to be ignored until it has been overshadowed by some explanation more luminous and demonstrable than the theories extant involving tropisms and special senses.

I have often wondered if the sense of smell can in any way be a guide toward their home. This idea has been advanced by other investigators concerning other material. Bouvier[9] lends his voice to this opinion when he says:

> To the memory of visual sensations must be added the memory of olfactory sensations. Ferton gives some curious examples in his studies of the shell inhabiting Osmias. Displaced for some centimeters, the shell in which the bee nests is found on the sand, even when it is crushed; it is also found when it is hidden in a tuft of herbage; and when it is replaced by another shell of the same species, the insect notices the fact, disdains the substitute, and leaves in search of the shell which belongs to it.

One of the problems still open is for someone to devise, if possible, experiments which will put to test the olfactory sense in the homing of some of these flying creatures. That sense may well be an efficient guide for terrestrial forms—walking or creeping animals which may pick up or follow a trail—but it requires an elastic imagination to conceive of the sense of smell guiding these errant creatures through the pathless air for such distances. Yet we must not be skeptical when we know that many a male moth or butterfly does precisely that to meet his queen. These cases, however, would probably come under the heading of sex-odor or species-odor rather than the odor of a specific nest. The only point where these experiments approach near this phase of the question is the series of homing tests which were conducted in the rain. To our human olfactory senses, it seemed that the

[9] Psychic life of insects, p. 250, 1922.

intermittent showers and occasional downpours of rain and the accompanying cleansing winds during those three days surely transformed the odors of the Wickes region; the purification of earth and air seemed to us complete. This may, however, only emphasize the subtlety of the sense of the bees in contrast to our crude ones. At any event, in every experiment in that series, from 1 to 8 bees returned after the cleansing of the vegetation and atmosphere by the rain. Hence the nest-odors, if any exist for this purpose, must be of a nature to remain unaffected by mere rain and wind.

The most baffling point demanding our consideration is the wide variation in the time consumed by the different bees in making their returns. We find in this a minimum of 20 minutes and a maximum of over 50 hours, and, strange to say, the distance had nothing to do with this, because in 20 minutes the one bee accomplished a 2-mile journey, while the other in 50 hours groped its way back from only $\frac{1}{8}$ mile! The more credit, it seems to me, belongs to the slow one than to the one which found the way so easily, since despite the fact that the slow one was lost for a time, she retained for two days and nights a memory-picture of her home strong enough to serve her need. The table below gives a summary of the time consumed in making the flights. The night hours are included in this, for, although of course the bees were not then flying or searching for home, yet they were spending these hours under conditions which would tend to alienate them from the nest and to dim their memory-pictures of home.

Hours or less	*Number of bees*	*Hours or less*	*Number of bees*
1	2	21	3
2	18	23	1
3	9	24	9
4	8	25	5
5	5	26	7
6	8	27	4
7	1	28	1
8	1	51	1
20	3	Total	86

Of course the promptness of return of any insect to its nest is dependent upon three factors; the insect's ability to find its way

back, its physical strength to make the journey, and the intensity of its desire to return at once. The utter failure of all males to return is at once attributable to their lack of interest in the nest. The experiments were so placed in the lives of the females, especially the middle-aged and old ones, that their interest in the nest should be very keen.

To be sure we have found, in some wasps and other species of bees, that they have astonishing propensities for loafing—that in the midst of a busy nesting season, or even with a cell half done, they will stop and preen themselves, or sip nectar, or just blissfully loaf about for some minutes or some hours. The extent to which this may have interfered with the prompt return of many of our unwilling performers, I have no way of knowing. These bees are by nature usually industrious, but the best of them are entitled to an occasional lapse from virtue, especially since they do not know that scientific data are at stake. The experiments proved that the bees' strength, either physical or psychic, limited their ability to return to a distance of 2 miles; if taken beyond that, they all either perished or were permanently lost.

GENERAL CONSIDERATIONS

In reviewing the results of the homing work on the two species of solitary wild bees, one the carpenter-bee belonging to a genus of the largest bees extant, and the other a mining bee of medium size, one cannot help being impressed with the fact that these bees find their way home by means other than a mysterious unknown or sixth sense, as a certain school of naturalists would have us believe. Indeed the various explanations of the homing of insects involving the mysterious theory of special sense, or sixth sense, or magnetism, have already been dealt with by Forel, Buttel-Reepen, Turner and others, whose adverse criticism is based upon the results of well planned experiments. Here the results of the experimental work on both Anthophora and Xylocopa also bear out and substantiate the criticisms advanced by these investigators; indeed the discussion of the subject by Forel in his "Senses of Insects" and by Buttel-Reepen in "The Natural History of the Honey-bee" would serve admirably for the conclusions of this paper.

The reader who has followed the busy mothers of Anthophora and Xylocopa hurrying home to the nest from a distant enforced flight, or who perhaps sympathizes with those which become hopelessly lost will agree with me that a blind homing instinct *per se* could not account for all the interesting data that the actions of these bees have given us. Neither is it necessary to call in the aid of a mystic sixth sense to explain circumstances in the activities of the bees which are so comparable with the circumstances in our own activities, as for instance, the fact that some consume only a few minutes to make a long flight, while others require a much longer time for a short one, or that some mothers with previous experience in flights are more successful in subsequent ones, or that as the distance from home is increased the number of successful returns decreases. The facts that there is an absolute maximum distance for each species from beyond which they cannot find their way back, and that night interferes with their returning also contribute to the evidence that they are not drawn home by a blind instinct alone. Much easier would it be to say that each act of the homing insect can be explained in the same way that human behavior under the same conditions would be explained. If now we wish to work back to an analysis of the causes of conduct, we may enjoy the added advantage of being able to make it a subjective study in terms of our own experience, comprehensible at least to our own species, instead of a purely objective study, in terms so coldly artificial that the explanation loses all warmth of life, and which, I doubt not, the bee herself would not recognize as her own mental processes.

It is evident from the foregoing investigations that age, nest-interest, experience, memory, and perseverance of the successful individuals are the chief factors in bringing them safely home, and those that are lost have only their youth, stupidity or ignorance to blame. One has only to read Forel to find explanations for the phenomena herein recorded, even though his explanation anticipated these experiments by many years.

The results show that in my work the return flights were successful only when I started at a point in the life of the bees after they had acquired visual impressions of the nest and its

relation to surroundings. This brings me to the point of memory pictures; and since memory pictures can function only through the agency of the eye, I should like to discuss the relation of sight to the problem of home finding.

The most interesting comparative evidence brought out in the foregoing experiments is the fact that the large Xylocopa can find its way home for a distance of almost eight miles, while for the medium-sized Anthophora, the maximum distance is two miles. The giant of the bee world naturally has large eyes. Eyes enormously larger than are the eyes of the Anthophora bees. "Insects that have large, convex eyes with many facets evidently see not only very clearly but much farther than those with small flat eyes." These combined facts again play into the explanation of Forel, who bases much of his discussion on the brilliant investigations of Exner.

Forel,[10] in summing up what is known of sight in insects, says that:

1. Insects guide themselves in flight almost entirely, and on the ground partly, by means of their faceted eyes. The antennae and the buccal sensory organs cannot help in aerial steering: Their extirpation does not in the least diminish their faculty of guiding themselves on the wing.

2. The theory of mosaic sight of J. Mueller is the only true explanation. The retinules of the compound eyes do not receive any image, but each a single luminous pencil more or less distinct in origin from that of its neighbours.

3. The larger the number of facets, and the longer the crystallines, the more distinct is the sight and the longer is the relatively distinct sight.

4. Insects perceive the motion of objects particularly well, i.e., the displacements of visual images relatively to the compound eye. They therefore see better when on the wing than at rest, for during flight the image of immobile objects is displaced relatively to the eye. This perception of the mobility of objects diminishes (as does the relative displacement to the eye) according as the distance increases.

[10] The Senses of Insects, p. 41, 129, 1907.

5. Insects only distinguish the contours and forms of objects in a more or less indistinct fashion, the more indistinct as the number of facets is less, as the crystallines are shorter, as the object is further off, or as it is smaller. Insects which have large eyes with several thousand facets see form fairly distinctly.

6. Insects appreciate the direction and distance of objects very clearly during flight, by the aid of their compound eyes. This is at least correct for near distances. They can also appreciate, even when at rest, the distance of immobile objects.

7. Certain insects (bees, bumble-bees) distinguish colour clearly and recognise colours better than forms. Among others (wasps) the perception of colour appears, on the contrary, to be very rudimentary. Ants perceive the ultra-violet rays.

8. The ocelli appear to give a very incomplete sight and to be only mere accessories in insects which possess compound eyes. They yet may serve, perhaps, for the sight of very close objects in an obscure medium; the fact that they are found especially developed in those aerial insects which inhabit complex and dark nests where they have to guide themselves tends to verify this.

9. The rapidity with which the increase of distance diminishes in regular proportion the distinctness of contours must necessarily help insects to appreciate distances.

Aerial insects and aerial beings in general, soaring above terrestrial objects, ought to have, and have, a knowledge of places very different to that of wingless beings, much more compendious and much more extended. Terrestrial beings see their horizon continually obstructed, which makes their direction by sight much more difficult. If we reflect on the geographical *coup d'oeil* "as the crow flies" that one obtains on the summit of a hillock, we shall have a feeble idea of what the vision of the aerial being can be, with this difference, that in the twinkling of an eye it moves and alters its horizons, which we cannot do.

With wonderful technique,

Exner has succeeded in discovering and fixing the single direct image formed by the faceted eye of Lampyris splendidula (glow-worm), and no doubt more or less clearly distinguished by the brain of the insect. . . . . a Lampyris will recognise the separate stripes of a barred

surface when they are 5 cm. apart, at a distance of 2.25 metres. At the distance of a centimetre it will still recognise stripes 0.22 mm. broad. The distinctness of this image corresponds to the number of nerve elements (in other words to the number of facets, since each facet has a rhabdome with a fixed number of seven cells in this particular case), and Exner adds rightly that other insects and crustaceans with eyes larger and richer in elements give no doubt much more distinct images.

In reply to a precise question put on this subject, Professor Exner has answered me in the following words: 'I can now affirm with certainty that the distinctness of the image increases with the number of facets falling under the same angle of the convexity of the eye.

. . . . we have always held that insects, even those that have the best eyes, see objects in repose much less distinctly than we do. The image of the Lampyris of Exner confirms it. Exner has further already shown, in 1875, that the faceted eye was specially and admirably adapted for seeing movements. Our observations have confirmed this, and Plateau is merely working to confirm it afresh. . . . . But Plateau forgets that "vision of motion" consists not in the movement of the object seen, but in the displacement of the image on the retina. . . . . if an insect moves on the wing or on the ground towards an immobile object, the image of this object will be displaced on its retina, and it will see "a movement of the immobile object," as the scenery moves to our eyes when we are travelling on a railway. I ask the reader's pardon for this obvious truth. But . . . . we ourselves pay much more attention to objects of which the image is displaced on our retina than to those which are immobile.

It is gratifying to find that these two lines of study, the profound researches of Forel and Exner, and the observations and experiments herein recorded, while they approach the subject from different angles, yet they converge sharply to the one conclusion—that the sense of sight is in all probability the chief factor in guiding these organisms on their homeward flight. While the above data and quotations give sufficiently convincing evidence that sight is the chief factor for distant orientation, in all probability for proximal orientation other senses, such as smell, etc., come into play.