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Time Factors in Relation to the Acquisition of Food by the Honeybee

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CONTENTS

SUMMARY

1. Of all the various methods for marking honeybees tried by the author, the one found best adapted for the present investigation was that of applying pigment combined with white shellac in alcohol.

2. A contrivance of simple construction was devised which, when placed in the entrance of a hive, caused practically every incoming and outgoing bee to pass thru the entrance dorsal side up, thereby enabling the observer to detect the marked bees.

3. A suitable method was discovered for distinguishing between nectar-carriers and water-carriers without injury to the bee.

4. The average speed determined for the flight of worker bees during a calm, was a little less than 15 miles per hour.

5. The time required for gathering a load of nectar varies greatly, but, under favorable conditions, one hour has been shown to be ample time for a nectar-carrier to make a round trip.

6. Ten trips per day, under favorable conditions, probably is as reliable an average as can be deducted from the data at hand for nectar-carriers.

7. The time required for a pollen-carrier to make a round trip varies greatly, but when gathering from corn under favorable conditions, trips are completed in a quarter of an hour or less, on the average.

8. The number of trips made by one pollen-carrier in a day was not great, as a rule, because corn pollen usually is not available after about noon; consequently an unqualified statement for the average number of trips made in a day would scarcely be justified.

9. A water carrier can make a round trip in about five minutes, on the average, when the supply is near at hand.

10. A water-carrier sometimes makes 100 or more trips in a day, but the average is probably less than half that number.

11. Field bees normally spend less than five minutes in the hive between field trips, regardless of whether they carry nectar, pollen or water.

Time Factors in Relation to the Acquisition of Food by the Honeybee

By O. W. Park*

The honeybee is largely a creature of instinct. It never has and, presumably, never can be domesticated or made to do man's bidding as have many other animals. By selective breeding, man has developed in the honeybee certain characters, such as gentleness and color; but, it remains essentially a wild creature. Since man cannot mold the nature of the bee to his will, his profit from her labors depends upon his ability to adjust his methods to her ways.

The remarkable progress made in the production of honey during the past three-quarters of a century has been possible only thru an accumulation of fundamental knowledge of honeybees and their habits. This had been secured, largely during the preceding 200 years, thru the persevering studies of such men as Swammerdam, Reaumur, Huber and Langstroth, besides scores of others who made lesser contributions. At present there are reasons to believe that honey production has probably advanced to its limit of perfection, under present knowledge of the life and activities of the honeybee.

A study of literature on beekeeping has led to the conclusion that, while the accomplishments of the honeybee colony as a unit are well known, there is a serious lack of definite information concerning the activities of the individuals which compose the colony. The accomplishments of the individual are fundamental, while those of the colony are but the end products of the combined activities of its members. The present studies have been made for the purpose of advancing knowledge concerning the fundamental activities of individual members of the colony.

METHODS AND APPARATUS

By far the most difficult and time consuming phase of many investigations is the development of methods which will yield satisfactory results. Studies of the activities of individual bees are not exceptions to the general rule in this respect. This fact is attested by the great dearth of reliable data on the subject.

*This paper is Part I of a thesis submitted to the graduate faculty of Iowa State College in partial fulfillment of the requirements for the degree, Doctor of Philosophy.

The first step was to find some way of marking individual bees so conspicuously that each one could be recognized instantly. This proved to be no easy matter, as will appear in the detailed description to follow. This phase of the work has not yet brought forth a completely satisfactory method, but means were found which were used with considerable success. An attempt to secure data upon marked bees showed at once that either the bees must be marked on the venter, as well as the dorsum, or it would be necessary to devise some means to force all the bees to enter and leave the hive "right side up" thru a passage way which could be watched easily by one person. As it did not appear practical to mark bees on the venter, the second step in the development of methods was the perfecting of a special entrance device. A third phase of the work called for some means for determining the nature of the contents of the honey-sac without injury to the bee. A simple test was discovered which has proven its value many times.

MARKING BEES

Lack of a dependable method of marking has held up investigations on the activities of individual bees more than any other phase of technique involved. Considerable work (3, 14, 15, 19, 20, 28, 30, 31, 33, 37) has been done on methods of marking bees and other insects for purposes of identification. The methods which appeared to be applicable to the present work were tried out both with and without variations. Up to the present, no wholly satisfactory method has been developed. Needs of the present investigation required a method which would permit instant recognition and positive identification of each of a number of individuals belonging to the same colony, and which would not interfere with the normal activities of the bees.

The only marking method found suitable was the use of various pigments combined with some adhesive which could be applied in small spots on the bee's thorax or abdomen, or both. Artists' oil colors in tubes were used with moderate success, but the most satisfactory combination tried was made by mixing equal parts by volume of white shellac (in alcohol), powdered pigment of the desired color and 95 percent alcohol. The amount of alcohol needed depends upon the consistency of the shellac used, but when ready for use, the preparation should be of such a consistency that it will just barely drop from the end of a toothpick which has been dipped into it and then held in a perpendicular position. In order to secure good results in marking, it is important that this preparation be neither too thick nor too thin. Experience alone will enable one to get it just right.

Systems of Color Combinations

Distinctive marking of individuals, in excess of the number of colors that can be instantly recognized, involved the use of some sort of a system of color combinations. The following seven colors were found to be most readily distinguished: white, pink, yellow, orange, red, light green and blue. Seven bees could then be marked on the thorax, each with a different color, and seven more could be marked on the abdomen. Then by using two spots of color, one on the thorax and the other on the abdomen, it was possible to mark 49 more individuals, or a total of 63 bees. It was never found desirable to have more than this number of marked bees in any one colony because it would have been impossible at times to record the desired data on a greater number, even tho a secretary was at hand who did nothing but record the data as reported by two observers.

Von Frisch (15) describes a system of combinations of color spots which permits the making of as many as 599 different combinations. The system which he describes probably is as good as has been devised for marking a great number of individuals.

The use of more than one color spot on the thorax was tested out. It was found that, altho such combinations were quite satisfactory for use on bees that could be observed at rest or moving slowly, they could not be identified on rapidly moving bees with sufficient certainty to permit their use in these investigations. The simpler plan of using only one color spot on either thorax, abdomen, or both, proved to be complicated enough when taking data rapidly from marked bees that were entering and leaving the entrance of a full colony having eight Langstroth frames of brood.

Technique of Marking

The colony to be used was first fitted out with a special entrance device, to be described later. This slowed down the ingress and egress of the bees very markedly when first put on, but after it had been in place for one day most of the bees seemed to have learned how to get thru with only a slight slackening of their usual gait. This slowing down was especially desirable on the first day because it made easier the capture of bees that were to be marked.

In catching a bee for marking, the only points considered were that it should not show signs of extreme old age and that it must carry the right kind of a load. The former point was judged on general appearances, including such well known indications as frayed wings and hairlessness. The determination of the latter point depended upon the nature of the load. A pollen-carrier, in order to be eligible to receive the distinguishing mark, must carry a pollen load gathered from a particular kind of plant such as ragweed, corn, or something else as the case might be. Usually it was easy enough to determine the source of a load of pollen from its color alone, but frequently the shape of the pollen load was an aid in distinguishing between pollens that were somewhat similar in color.

Selection of nectar-carriers and water-carriers was not so simple because these loads were carried inside the bee's body and, anyway they could not have been distinguished from each other had they been in plain sight. Experience soon enables one to recognize bees that have loads in their honey-sacs from the size and shape of the abdomen and the way it is carried in flight or when crawling, but to determine whether the load is of nectar or of water requires an actual test. A description.of the method which was discovered for making such a test will be given later.

It was found helpful to contract the entrance until a passage only large enough for one or two bees to pass at a time was left, for, then, one had a better opportunity to select and capture bees showing desired characteristics. Bees for marking were caught in glass vials measuring 15 millimeters inside diameter (fig. 1B,a). Vials both larger and smaller than this were tried out and it was found that, with the larger ones, it was not easy to get the bee to crawl up into the vial and, with the smaller ones, it was difficult to get the vial over a bee without pinching her, but with those of the proper diameter, the bee would begin to crawl up the side of the vial immediately.

The captured bee was then transferred to a smaller vial (fig. 1B, b) having a diameter of only 10 millimeters, from which removal was possible with less danger of her escape than with a larger vial. Several bees were then captured before proceeding to another step, each bee being placed in a separate 10 millimeter vial and confined there by means of a cork having notches cut in its sides to admit air. In dealing with pollen-carriers, the character of the load could now be examined more closely and, if found to be from the desired source, the bee was ready for marking. Nectar-carriers and water-carriers, however, were not ready for marking until the test was made to ascertain whether the honey-sac contained nectar or water.

Testing for water versus nectar was done as follows: A sheet of filter paper was laid on a table or hive cover. A 10-millimeter vial containing a bee was laid upon the filter paper. While holding the vial with the left hand, its cork was removed and the open mouth quickly guarded by means of a small piece of window screen held in the right hand. The piece of screen wire used measured about 40 by 60 millimeters and had a rectangular notch (fig. 1B,c) at one end just wide enough to per-

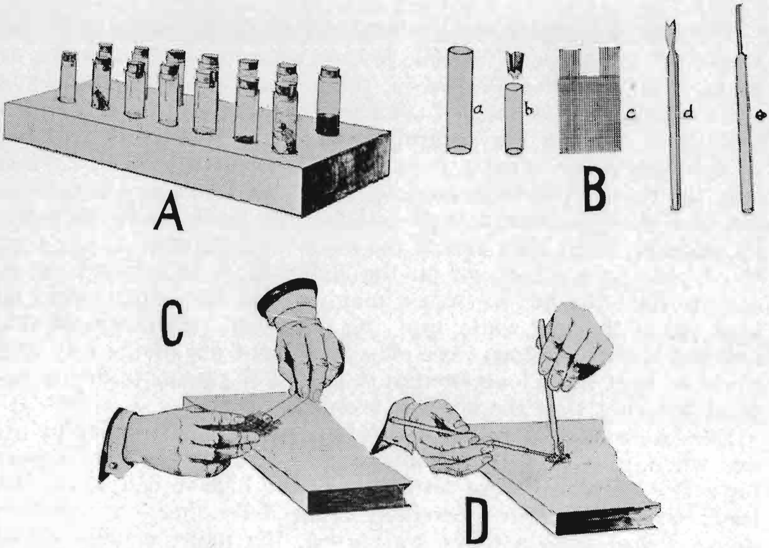

Fig. 1. Equipment used in marking bees.

mit the end of the vial to pass thru it, so that a portion of the screen extended on either side of the vial, thus helping to prevent the escape of the bee (fig. 1C). When the bee crawled out of the vial, the screen was brought down on top of her, with just enough pressure to prevent escape. A little gentle pressure on the abdomen usually caused the bee to disgorge a small quantity of her load which immediately soaked into the filter paper. The bee was replaced in her vial, which bore a number, to await the outcome of the test. A circle was drawn around the spot on the filter paper and marked with a number corresponding to the vial containing the bee. By the time each of half a dozen bees had been induced to give up a sample of her load, the result of the first test could be told and marking could be continued.

Color mixtures used were kept in small glass vials, tightly corked and held in an upright position by being placed in auger holes bored into a block of wood (fig. 1A). Eight soft pine sticks, 6 inches long and $\frac{1}{4}$ inch in diameter completed the outfit. One stick was whittled so as to form a spatula-like portion at one end with a notch cut in the end of the spatula. (fig. 1B, d). This notched stick was to be used to hold the bee while applying the paint. A small nail-hole made in one end of each of the other seven little sticks admitted the end of a toothpick which was used instead of a brush for applying the spot of color. One such stick (fig. 1B, e) was for use with each different color of paint and when one toothpick became too thickly covered with paint it was thrown away and replaced with a new one.

The bee to be marked as released from the 10-millimeter vial under the rectangle of screen, just as when testing for water or nectar. Once under the screen, the bee was permitted to crawl out to the edge, the notched stick was thrust down over her narrow waist holding her securely, but permitting great freedom in applying color to both thorax and abdomen (fig. 1D). When only the thorax was to be marked, it was not necessary to use the notched stick because a very satisfactory mark could be made by painting right thru one of the meshes of the wire screen, but, when putting a color spot on the abdomen, it was found necessary to hold the bee in such a manner that the wings could be kept out of the way while applying the paint. By means of this notched stick the wings were effectively kept out of the way and could be kept there long enough to permit the paint to dry somewhat before giving the bee her freedom.

Bees were usually released within a minute or so after painting, when, generally, they would sail off into the air and be gone for a few minutes before returning to the hive to dispose of the loads they had been prevented from delivering on schedule time. When such a flight was taken, the paint usually dried nicely and, frequently, a bee would go right along with her work without paying any attention to the paint on her back.

Reactions of Bees to Marking

Different individuals reacted differently upon being painted. Some paid little, if any, attention to the presence of the paint, while others tried to scratch it off with their claws or with their pollen combs, depending on the location of the spot of paint and, unfortunately, they sometimes succeeded. Usually, however, a bee soon ceased to notice the paint and would go about her business as usual. The consistency of the paint and the nicety with which it was gotten onto the bee were also found to be important. A small spot well located and made with paint of the proper consistency seldom received much attention from the bee and was more likely to remain than a thick daub of color smeared promiscuously over her. Care had to be used to avoid getting paint on the eyes, as a bee seldom worked normally when her eyes were smeared, but would spend all her time trying to rub off the paint.

Conclusions

The use of pigments in one combination or another was the only method of marking bees found satisfactory to the needs of the present problem. Shellac, colored with various powdered pigments, gave better results than any other combination used, but no material tried, so far, has been found entirely satisfactory. Lack of a satisfactory method for marking bees has always been and still is one of the greatest obstacles to studying the life of the individual honeybee.

ENTRANCE DEVICES

Normal colonies of medium strength, in ordinary 10-frame Langstroth hives, were used exclusively in securing data on the number of trips per day and the time spent in the field and in the hive by field bees. Colonies in observation hives were not used for this purpose because of the possible objection that data secured from them might not be typical of average colonies.

It should be remembered that, in order to know when each marked bee passed into or out of the hive, it was necessary for the observer to see the back of every bee that went thru the entrance. And, while it often is difficult enough to see every bee that enters or leaves an observation hive, it requires strenuous watching to see every one that enters or leaves a full sized colony. There are three reasons for this: A much larger number of bees must be scanned constantly, ingress and egress are often rapid and bees leaving the hive frequently appear at the entrance upside down, clinging to the lower edge of the hive body. Bees very commonly take wing from an inverted position so that marks on their backs cannot be seen. Altho the two last named difficulties are encountered to some extent in the observation hive, they are vastly greater when one watches at the entrance of an ordinary hive. A special entrance device was constructed, the object of which was to reduce these difficulties as much as possible without materially interfering with the activities of the bees. In fact, several different devices were constructed.

The first device (fig. 2A) constructed was nothing more than a screen-covered tunnel 6 inches wide and 5/16 of an inch deep which extended 8 inches in front of the hive. This arrangement reduced the width of entrance by half and it was hoped that the bees would soon become accustomed to their new entrance and would pass back and forth in plain view under the wire screen. They had no trouble finding their way out, but they certainly had no notion of how to get in thru it. Incoming bees alighted and clustered on top of the tunnel and on the front of the hive where they would remain indefinitely. To remedy this defect, a board having the same dimensions as the front of the hive, was erected at the outer end of the tunnel as a false hive-front.

This board was a great improvement, but lacked much of perfection. An occasional bee would find its way behind the false front, alight on the screen over the tunnel and remain, trying to find a place to get thru the screen. The number of bees there increased constantly. Brushing them away did no good. Kill-

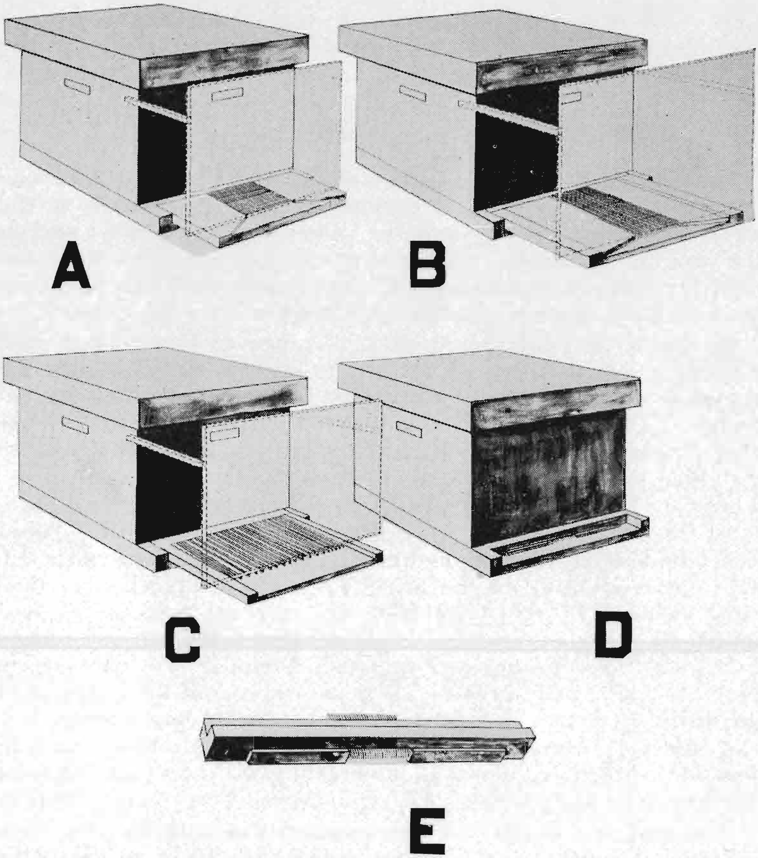

Fig. 2. Various entrance devices used when securing time records on marked bees.

ing them was little better. A pane of glass laid over the screen improved matters slightly, but it was more difficult to see the bees passing underneath than thru the screen alone. After the false front was erected, one observer watched them from above as they passed thru the tunnel while the other watched the entrance, but neither observer could watch both places at one time, nor did either position enable the observer to be entirely certain of all his observations. One of the worst features of this device was the fact that many bees crawled thru the tunnel upside down and took wing without giving either observer a chance to see whether they were marked.

The second entrance device (fig. 2B) was made along lines quite similar to the first but with several improvements. The tunnel was made narrower and longer, being only $3\frac{1}{2}$ inches wide and 12 inches long, thus providing a passage way still more easily watched. The greatest improvement, however, was made by allowing the screen cover of the tunnel to protrude nearly half an inch in front. The cross strands of wire were removed from the protruding portion so that a row of little prongs projected just above the entrance to the tunnel. The prongs were then bent downward, leaving barely room for a bee to pass beneath their points. This method caused bees crawling out thru the tunnel ventral side up to turn dorsal side up before taking wing and also prevented incoming bees from alighting and entering in an inverted position. A more marked slowing up of traffic than with the first device was a further result of this plan. But it was not wholly satisfactory because the false front had to be used with it and, as was pointed out before, this did not allow a view of the entrance and the tunnel at the same time; moreover, the observer was compelled to maintain an uncomfortable position in order to view the tunnel properly.

The third attempt was a radical departure from the two previous ones. A combination device was planned which would provide adequate opportunity to observe the passing bees and, coincidently, provide a means for catching and painting the bees expeditiously. It did neither. But, a knowledge of things that will not work is often useful, so a brief description of the apparatus follows. Numerous, narrow, glass-covered tunnels (fig. 2C) were arranged side by side so as to occupy the full width of the hive. Half of these tunnels were wide enough for a bee to crawl thru, but not wide enough for bees to pass each other. The remainder of the tunnels were just wide enough to permit two bees to travel side by side or to pass each other. Instead of a pane of glass over the whole set of tunnels, narrow strips of glass were used in such a way that each strip of glass covered nearly one-half of each of two adjacent tunnels. The glass strips did not fit close to each other, but were spaced apart, leaving a crack about 1/16 inch wide over the middle of each tunnel, running the full length of it. Provision was made for closing both ends of any or all tunnels in order that bees might be confined while being touched with a spot of color thru the crack between the glass strips.

As might be expected, the narrower tunnels were continually blocked because an outgoing and an incoming bee would meet and, in the absence of room to pass each other, a deadlock would ensue unless one bee could succeed in forcing the other to back up. The device was a flat failure because a large proportion of the bees walked on the side-walls of the tunnels where their backs could neither be painted nor be seen if they were marked.

The success of the second device, provided with a row of down-turned prongs at its entrance, pointed the way to a still more simple and more satisfactory apparatus. If all bees could be compelled to enter and leave the entrance dorsal side up, there was little need for a tunnel. Experience in using the device with the row of prongs suggested that a similar set of down-turned prongs, installed on the inside of the hive at the entrance, should cause the outgoing bees to right themselves before going thru the entrance. A very simple piece of apparatus embodying these ideas was constructed by tacking a strip of wire screen 2 inches wide to the under side of a regular entrance-reducer block. The wire projected about half an inch on each side of the reducer block and all the cross wires were removed from the projecting portions, leaving only a row of prongs on either side (fig. 2E). The prongs were then curved down slightly on both sides of the block and the device shoved into the regular hive entrance (fig. 2D). The entrance was only 3 inches wide, was easily watched and the down-turned prongs prevented the bees from getting thru too rapidly. Scarcely one bee per day succeeded in getting thru this arrangement without its back being seen. It was also less tiresome to make observations with this type of apparatus than with any other tried.

The only other device known to the writer corresponding in any way to the apparatus just described is one used by Von Frisch (15). It is constructed along very different lines, being a large tunnel made of boards which extends about 6 feet in front of the hive. The tunnel is about 18 inches square in cross-section at its outer end and for about half its entire length. From this point, the tunnel tapers to an opening only 2½ inches square at the front of the hive. Three glass covered openings in each of the two side-walls, afford opportunity to observe the bees as they pass thru the long tunnel.

TESTS FOR NECTAR VERSUS WATER

Water-carriers cannot be distinguished from nectar-carriers by their appearance because water and nectar are both carried in the honey-sac which is located inside the abdomen of the bee. Yet, in order to study the activities of individuals engaged in these respective occupations, it became necessary to be able to determine whether a given bee was engaged in carrying water or nectar. One way was to kill the bee, dissect out her honey-sac and taste the contents. This manner of determining the honey-sac contents was frequently used to find out what proportion of incoming bees was carrying nectar and what proportion was carrying water. But a bee subjected to such a test was not a promising subject from which to determine such things as, for instance, the number of trips a water-carrier would make in a day. Hence, a means for finding the nature of the honey-sac contents without injury to the bee was greatly to be desired.

Chemical Tests

The question naturally arises as to whether or not a chemical test might be applied which would show positively the presence or absence of sugar even in a fraction of a drop of solution. Such tests exist, but, unfortunately, all those of which the writer has any knowledge are wholly unsuited to the needs of the case. Dilutions to 0.0001 of 1 percent of sugar can be detected by Molisch's reagent, but the presence of a fiber of filter paper or even a hair from the body of a bee is sufficient to vitiate this test. The phenylhydrazine method requires the use of laboratory facilities and results can be known only after the lapse of an hour or more. Furthermore, some of the sugars commonly present in nectar cannot be detected by this method. Other chemical methods seem even less promising; and, so far, skilled micro-chemists have been unable to suggest a practical solution to this problem.

The Filter Paper Test

A simple, but useful, test was discovered when it was found that a drop of sugar solution placed upon filter paper produced a translucent spot somewhat similar to the spot produced by a drop of oil on paper; while water, upon drying, left no such spot. It was found also that a bee could be induced to disgorge a portion of its honey-sac contents. The bee to be tested was caught as it returned from the field and was held fast on a sheet of filter paper while gentle pressure was applied to its abdomen. That part of its load which it disgorged, fell upon the paper, and less than half of a good load was sufficient for the test. That no appreciable injury was done the bee was attested by the fact that the bees subjected to this test continued to yield data as satisfactorily as pollen-carriers which, of course, did not have to undergo such a test.

Investigation of the limits of this test showed that it was useless for detecting the presence of sugar in aqueous solutions of honey containing less than 25 percent sugar. The test was, therefore, less delicate than the average human taste when dealing with quantities of solution sufficient to admit tasting; but, when dealing with a fraction of a drop of a solution which contains 30 percent or less of sugar, the human taste is seldom reliable. The filter paper test was convenient, it gave a semi-permanent record and in many other respects was better adapted to the needs of the case.

The fact that the sugar content of nectar is commonly said to be about 20 percent may lead some to doubt the truthworthiness of this test, but nectars having less than 25 percent sugar are not as common as has been supposed. Von Planta's (32) findings for sugar in the nectar of *Protea mellifera, Begnonia radicans, Fritillaria imperalis,* and *Hoya carnosa* form the basis for the above assumption. He found respectively 17, 15, 7 and 41 percent of sugar, and the mean of these is 20 percent. Owing to the very small number of nectars represented this figure is not significant. The plants just listed yield nectar in comparatively large quantities. Recent unpublished studies by the author, on the availability of nectar for bees, indicate that nectars normally secreted in small amounts are usually richer in sugar than those normally secreted abundantly. Since the great majority of the honey plants of Iowa yield nectar in comparatively small amounts, it is not remarkable that the filter paper test, as described above, should have given wholly reliable results. It is significant that the data obtained from marked bees selected by means of this test did not indicate, even in a single case, that an error had been introduced thru its use.

Limitations of the test as used thruout the present investigations were realized, however, and recently the usefulness of the filter paper test has been greatly increased thru certain modifications. The test now provides for the detection of as little as 2 percent of sugar in aqueous solutions; it gives an approximation to the concentration, and leaves a permanent record. In its original form this test made it possible to carry out careful studies on the habits and behavior of nectar-carriers and water-carriers which scarcely would have been possible in the absence of some such means for distinguishing them. In its improved form, the filter paper test bids fair to enter upon new fields of usefulness.

TIME FACTORS

"Aristotle," more than 2,000 years ago, "observed that a bee in gathering pollen, confines herself to the kind of blossom on which she begins, even if it is not so abundant as some others," according to Langstroth (21). During the 20 odd centuries that have intervened since Aristotle, many observers have studied one phase or another of the food getting habits of the honeybee. The names of Butler (4), Swammerdam (38), Reaumur (34), Thorley (39), Wildman (41), Huber (19), Cotton (10), Langstroth

(21) and others, from among the earlier writers, are intimately associated with the slow and tedious development of our still too scant knowledge of this subject. Among the more recent authors whose names are prominent because of their outstanding researches and observations on the food getting habits of the honeybee, Bonnier (2) and Casteel (6) should be mentioned.

Various early writers recognized a division of labor in the honeybee colony. According to Cotton (10), Aldamiri, who died in 1405, wrote, "The bees assemble together and divide the work; some make the wax, and some the honey; others bring water, and others again build their cells." Numerous investigators have reported on various phases of the division of labor within the hive, altho very few have made contributions on the division of labor outside the hive. In a general way, it has been recognized since early times that some bees carry nectar, some pollen and some water; but beyond this not much is known. A ray of light was shed upon this field in 1906 when Bonnier (2) published the results of his researches on "The Division of Labor Among Bees," and recent contributions have been made by Rosch (35).

SPEED IN FLIGHT

Bees have been considered speedy fliers, as is indicated by various estimates, some of which run as high as 120 miles per hour. Conservative writers have put their estimates at 30 miles and less. Those of Cheshire (7), Cowan (11), Cook (9), Buttel-Reepen (5) and Sabine (36) are based on more or less careful observations, but apparently none of the previous observers has taken particular account of that important factor, the wind.

Experiments have been carried on at the Iowa Agricultural Experiment Station to secure more definite information about the speed of the bee in flight and also for the purpose of studying the reactions of the bee to the influence of the wind. It was desired to know how much of the time spent away from the hive by a field bee was consumed in going to and from the field. The determination of the average speed of the bee in flight, together with a knowledge of the approximate limits of the range of its flight, gives a figure which, altho lacking exactness, enables us to arrive at a useful approximation. The time spent in the gathering of the load can then be found by deducting this figure from the total time the bee is gone from the hive.

Procedure

On a day after the close of the honeyflow, a marked bee was taken across an open field to a point about a fifth of a mile from her hive where she was allowed to fill up on syrup. The bee made repeated trips to this spot. One observer stood by the hive with a stop-watch in hand, while another was stationed near the dish of syrup. As the marked bee left the hive, the watch was set going and a signal given to notify the second observer that the bee was on her way. The instant the bee alighted, a signal was given to stop the watch. The return trip was timed in a similar manner. Records were obtained of about 25 consecutive round trips on each of four different days.

The velocity of the wind was determined at the beginning and at the end of each period by means of a portable anemometer, placed at about the height of the bee's flight. The average of the two readings was used in the calculations. The exact distance was determined by running a line with a surveyor's chain.

The experiments were carried out in such a way that one set of data (A) (see table I) was secured when the wind was directly *against* the bee as she left for the field and *with* her flight on the return. When the second set (B_1) was obtained, the wind was at right angles to the line of flight. In the case of the third (B_2) and the fourth (C) sets, the bee left the hive *with* the wind and returned *against* it. The designations B_1 and B_2 were employed to indicate that the same bee was used in securing these two sets of data.

Results

In accordance with one of nature's laws, a bee traveling with the wind is assisted in its flight to the extent of the velocity of the wind, or if traveling against the wind the bee's progress is hindered to the extent of the wind's velocity. If the bee flies at an angle to the wind, its rate of progress will be the resultant determined by triangulation.

Let us assume for instance, that a bee has flown due south at an observed velocity of 12 miles per hour, while a wind having a velocity of 9 miles per hour was blowing from the west. Here the two forces were acting at right angles to each other so their resultant is the hypotenuse of a right angled triangle, the other two sides of which represent the two forces as shown in fig. 3. In this case the sum of the squares of the two sides is 225, so the hypotenuse is 15. Therefore, had there been no wind, this bee would have gone 15 miles instead of 12 in the same length of time.

When flying at right angles to the wind, the bee must hold itself at an angle to the line of flight as shown by the line A D, thus flying against the wind just enough to offset the force of the wind which would otherwise carry the bee away from its line of flight. In the case above, the rate of flight was reduced 3 miles per hour by the 9 mile wind. Thus it will be seen that a wind blowing at right angles to the line of flight has the same effect as a somewhat lesser wind blowing directly against the bee.

Then the fair way to compute the normal speed of the bee is to reduce all results to terms of calm. This was done and the average of results obtained from each bee appears in the last column of table I. Thruout the remainder of this paper, all speeds mentioned are those which have been reduced to terms of calm, unless otherwise stated.

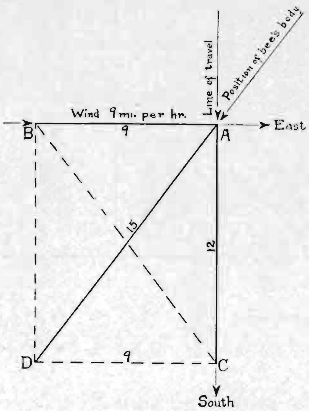

Fig. 3. The effect of a wind blowing at right angles to the line of flight may be determined by triangulation.

It will be noticed that the average speed found for loaded bees varied only a little, the lowest being 13 and the highest 16 miles per hour, while the grand average was approximately 15 miles. But the average speed of empty bees varied from 6.8 to 18 miles per hour. The grand average for empty bees was 12.5 miles, or 2.4 miles per hour less than that for homeward-bound bees.

The fact that the speed shown for outward-bound bees varied much more than that for homeward-bound bees, suggests the probability that a bee on its outward journey often does not make a so-called "bee-line" for the source of supply, but may do more or less scouting on the way. If this is the case, the distance actually traveled was greater than the measured distance. Then the speed for outgoing bees would be somewhat greater than indicated by the data. But the amount of time recorded was actually consumed during the outward trip, so calculations must be based on the recorded time.

It is significant that when flying at right angles to the wind, the outgoing bee flew at the rate of 13.3 and the incoming bee, 14.6 miles per hour, since each approaches rather closely the general average for its respective class. Furthermore, this case emphasizes the fact that, in spite of the heavier load, the homeward journey was usually accomplished in less time than the outward journey. As may be seen from the table, the only case in which the outgoing bee made better time than the incoming bee was when flying directly against the wind.

The least speed was shown when flying with the wind, on both outward and homeward trips; the greatest speed in each case was attained when flying directly against the wind. It appeared that, when going with the wind, the bee showed a tendency to

TABLE I. INFLUENCE OF WIND ON SPEED OF HONEYBEE*

Relation to Wind	Velocity of Wind	Bee	Observed Speed	Correction for Wind	Speed in a Calm
		(Empty (out)			
With	7.7	B_2	19.7	—7.7	12.0
With	4.5	C	11.3	—4.5	6.8
Against	5.6	A	12.4	+5.6	18.0
At right angles	10.0	B_1	8.8	+4.5	13.3
Grand average					12.5
		Loaded (in)			
With	5.6	A	18.6	—5.6	13.0
Against	7.7	B_2	8.3	+7.7	16.0
Against	4.5	C	11.5	+4.5	16.0
At right angles	10.0	B_1	10.7	+3.9	14.6
Grand average					14.9

*Speed is given in miles per hour.

slacken her own efforts whereas, when traveling against the wind, she increased them in an attempt to overcome the wind's retarding influence.

The maximum speed recorded for any one trip, under each of the various combinations of conditions of wind and load, is shown in table II. Here, again, the greatest speeds were obtained when the bee was exerting herself against the wind, either directly or as when flying at right angles to it. The two lowest records that appear in this table were produced by outgoing bees. A maximum of approximately 25.5 miles was recorded for both outgoing and incoming bees, but it was found that bees would not long continue to work in a wind blowing much over 15 miles per hour.

Temperatures were relatively high during these experiments, being between 70 and 80 degrees F. at all times. No relationship between temperature and rate of flight was apparent within this range, but a wider range in temperature might yield a correlation.

TABLE II. GREATEST SPEEDS RECORDED*

Relation to Wind	Velocity of Wind	Bee	Observed Speed	Correction for Wind	Speed in a Calm
		(Empty (out)			
With	7.7	B_2	23.4	—7.7	15.7
Against	5.6	A	20.0	+5.6	25.6
At right angles	10.0	B_1	11.5	+3.7	15.2
		Loaded (in)			
With	5.6	A	24.8	—5.6	19.2
Against	4.5	C	15.1	+4.5	20.4
At right angles	10.0	B_1	23.4	+2.0	25.4

*Speed is given in miles per hour.

A Check on the Results—A fortunate combination of circumstances was responsible for a very satisfactory check on the experiments just related. On August 20, 1921, one of the marked water-carriers was discovered by the author's assistant while getting her load from a watering place for bees in his yard. He at once got in touch with the writer by telephone and, after setting our watches together, we proceeded to record the time of arrival and departure of this bee at both ends of the line.

The bee flew at right angles to a light breeze having an estimated velocity of 3 miles per hour. Later, the distance traveled by the bee was found to be just two-thirds of a mile in a direct line. The records, when brought together, showed that the average rate of flight, whether loaded or empty was 14 miles per hour which, in terms of calm, would be 14.3 miles. This result checks very closely with the averages obtained in the experiments related above.

Conclusions

1. Time records for homeward-bound bees showed considerably less variation than did those for outward-bound bees.
2. On the average, less time was consumed on the homeward trip than on the outward trip, but when flying directly against the wind, the empty bee flew slightly faster than did the loaded bee.
3. The effort put forth by empty and by loaded bees was least when flying with the wind and greatest when flying against it.
4. A maximum speed of 25 miles per hour was found for both outgoing and incoming bees.
5. Bees made but little progress against a wind having a velocity of 15 miles per hour.
6. The average speed found for the flight of bees in a calm was a little less than 15 miles per hour.

NECTAR CARRIERS

Review of Literature.

According to Hommell (18), Reaumur, Girard and Sylviac, after studying the habits of field bees, all came to the conclusion that "the better average for the number of trips of a worker is 6 per day." Hommell is inclined to take issue on this point and cites experiments made by Astor who found that a bee made 110 trips in a day when feeding on diluted honey. Hommell considers Astor's results to be typical for bees that are getting their supplies from another hive or from a dish and admits that their work is less rapid when gathering from flowers. He then says: "M. Demeure has observed that a marked bee made 60 trips in 12 hours, or 5 per hour, including the two minutes which she employed each time to dispose of her load." He states also that Maujean found that marked bees returned to the same cluster of flowers after an absence of 32 minutes, which gives 19 trips per day.

About 1815, Huish (20) sprinkled flour on some field-going bees. All but one of these proved to be pollen-carriers, but this one returned with a load of nectar after an absence of 35 minutes.

In 1914, Luden, whose experiments were reported by Heberle (17), caught and marked six bees—each a different color—on the forenoon of July 14. He found that marked bees behaved no differently from others and at 6 o'clock the next morning he took up his station near the hive to keep time records on the marked bees. The weather was fine, except for a thunderstorm between 4 and 5 o'clock in the afternoon, and he continued his observations until 7 in the evening, even taking his meals near the hive. The honeyflow was from clover and the net gain for that day was about 4 pounds. His results showed that a field-bee makes about 10 trips per day, each trip consuming from about 30 minutes to 2 hours, with an average of about 1 hour. The marked bees remained from 5 to 10 minutes in the hive between trips. Observations were continued the next day with similar results.

Lovell (23), attempted to check Luden's results by noting the number of visits made by an individual bee to a dish of honey in an hour under ideal conditions. Like Demeure, he found approximately 5 trips per hour and concluded that if the apiary were near a large buckwheat field or a basswood forest, a bee would probably make between 40 and 50 trips in a day of 10 hours.

The most recent work along this line is that of Lundie (24), who made use of a mechanical device for counting all outgoing and incoming bees. He obtained no records on the time spent in the hive between trips, however, and was unable therefore to derive a satisfactory average for round trips. But, by making use of hive-stay records secured during the present investigation, the writer has derived from Lundie's data 15 trips per day as a close approximation to the average number of round trips made during the period of the honeyflow.

Observations.

In the present investigation, individual bees were marked and records kept of the time of departure and return of each marked bee. Observations were begun as soon as possible after marking the bees and were continued without interruption until bees ceased flying at night. They were begun again early each morning and continued all day long for a number of days in succession. Two observers were watching the entrance practically all of the time, so that the chances for a marked bee to pass unnoticed were reduced to a minimum. Only full strength colonies were used in securing data. So long as the number of bees to be watched was small, one of the two observers recorded the necessary data on a sheet so ruled that only the hour and minute needed to be written in the proper square each time a marked bee passed the entrance. But, when data were being secured from a larger number of individuals, a third person acted as recorder, while both observers gave their full attention to the entrance. At such times, the marked bees often kept all three persons working full speed to keep up.

The system used in recording the data for a few bees was not so well suited for a larger number because too much time was consumed in locating the right square on the larger sheet. The record sheet was then reduced to two double columns, one for outgoing, the other for incoming bees. The left hand side of each double column was for time, while the right was for designation of the individual. Frequently, several marked bees would enter or leave the hive almost together and, in such cases, it was necessary to make only one entry in the time column. In reading the mark on any bee, the color combination was spoken by the observer who always gave the thorax color first, thus, "green-yellow" which indicated green on the thorax and yellow on the abdomen, and was recorded by the abbreviation "g y". A bee having no mark on the thorax, but having yellow on the abdomen was called "blank-yellow" and recorded "—y". If there was a red spot on the thorax and no color on the abdomen, the bee was registered "r—". A designating number was assigned to each marked bee and at a later date all the records for that bee were brought together in their proper order, thus giving practically a complete record of the number and duration of her field trips and hive-stays for the entire period.

Since honeyflow and weather conditions have such a direct influence upon the gathering of nectar, the time records secured under any given set of conditions are not likely to be duplicated, except under similar conditions. During the period of observation in 1920, average colonies stored about five pounds per day from white sweet clover, (*Melilotus alba*), while in 1921, average colonies gained only a little over one pound per day from the same source. Weather conditions were highly favorable for honey production in the former instance but were only fair in the latter. Summarizing, it may be said that one set of data was secured under very favorable conditions, whereas, the other was obtained under conditions which were from mediocre to poor. The data for field trips, hive-stays and round trips have been plotted as frequency curves in which the records obtained under *favorable* and *unfavorable* conditions are compared.

Of the records obtained for field trips made by nectar-carriers in 1920, 31 percent fell within the 21-30 minute class, as shown in fig. 4. About 68 percent fell between 10 and 40 minutes, and 95 percent occupied less than 1 hour. The mean time was about 34 minutes but the modal or most frequent interval spent in the field was 26.8 minutes. Modal values have been determined by use of W. I. King's formula given in his "Elements of Statistical Method," p. 124.

In 1921, only 19 percent of the field trip records fell within the 41-50 minute class in which the peak of the curve appeared. About 48 percent fell between 30 and 60 minutes, and 76 percent were completed within 1 hour. The mean time for field trips was 49 minutes, but the modal interval was 45 minutes.

The average speed of the bee, as previously shown under the heading, "Speed in Flight," was found to be approximately 15 miles per hour, or it takes a bee about 4 minutes to go a mile. Estimating the average distance to the field as three-fourths of a mile during the favorable season and as one mile during the less favorable season, 6 minutes is the probable time spent in going to and from the field in 1920, and 8 minutes in 1921. By subtracting the time thus spent from the total time the bee was absent from the hive, the net time spent in gathering the load may be

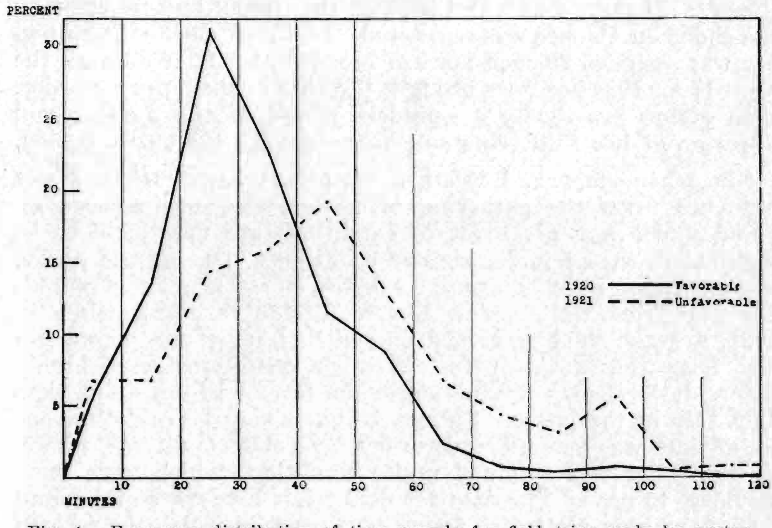

Fig. 4. Frequency distribution of time records for field trips made by nectar-carriers under *favorable* and *unfavorable* honeyflow conditions.

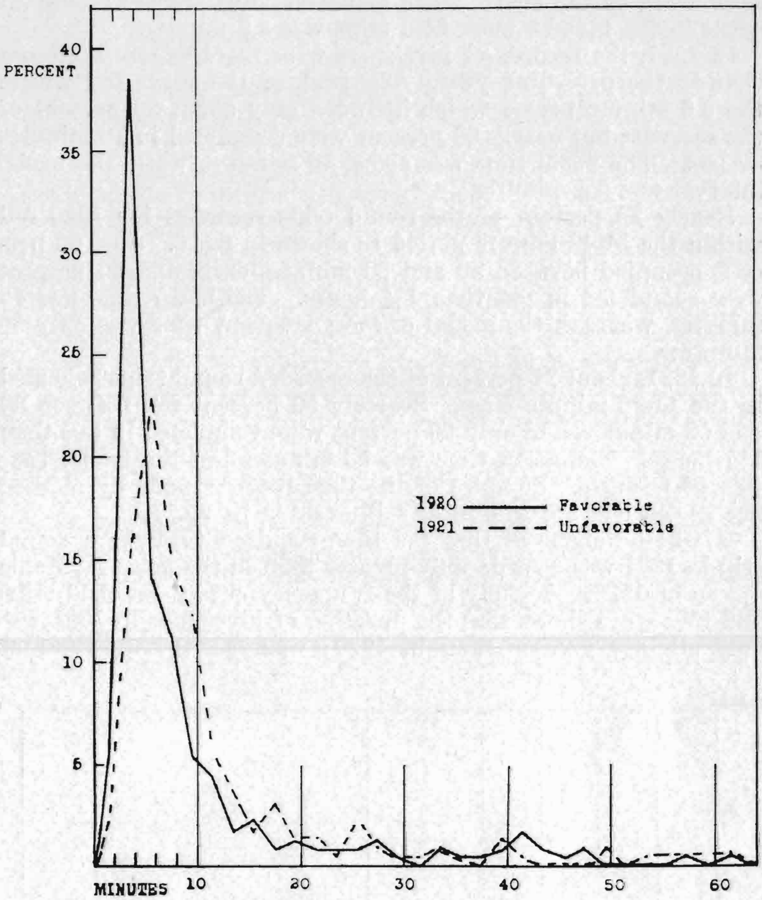

Fig. 5. Frequency distribution of time records for hive-stays made by nectar-carriers under *favorable* and *unfavorable* honeyflow conditions.

found. The most frequent interval spent away from the hive was 27 minutes in 1920 and 45 minutes in 1921, and by subtracting 6 and 8 minutes, respectively, we find the probable time spent in gathering the load to have been 21 minutes for 1920 and 37 minutes for 1921.

As shown in fig. 5, the 3 and 4 minute records of hive-stays by nectar-carriers comprised nearly 40 percent of the total number recorded in 1920. Over 75 percent were completed within 10 minutes. The average time for all hive-stays was 11.6 minutes, but the figure is not very significant owing to the markedly skew form of the curve. The modal or most frequent interval spent in the hive between field trips was 3.9 minutes.

In 1921, the records of hive-stays were more widely scattered than in the preceding year. The peak of the curve fell within the 5-6 minute period which included only about 23 percent of the records; but nearly 68 percent were completed in 10 minutes or less. The mean time was about 16 minutes, while the modal interval was 5.5 minutes.

Nearly 25 percent of the round trips recorded for 1920 fell within the 31-40 minute period as shown in fig. 6. Just 66 percent occupied between 20 and 50 minutes each, and 90 percent were completed in less than 1¼ hours. The mean time was 45 minutes, whereas, the modal or most frequent time was only 35 minutes.

In 1921, about 21 percent of the recorded round trips belonged in the 41-50 minute class. Scarcely 50 percent fell between 20 and 50 minutes, and only 80 percent were completed in less than 1¼ hours. The mean time was 63 minutes but the modal time was 46 minutes. Samples of the time records made by marked nectar-carriers are graphically illustrated in fig. 7.

It will be observed that the time required to make a round trip in 1921 was considerably greater than in the more favorable season of 1920. A study of the frequency curves for field trips and hive-stays shows that the duration of hive-stays in 1921 was only slightly greater than in 1920; whereas, the duration of

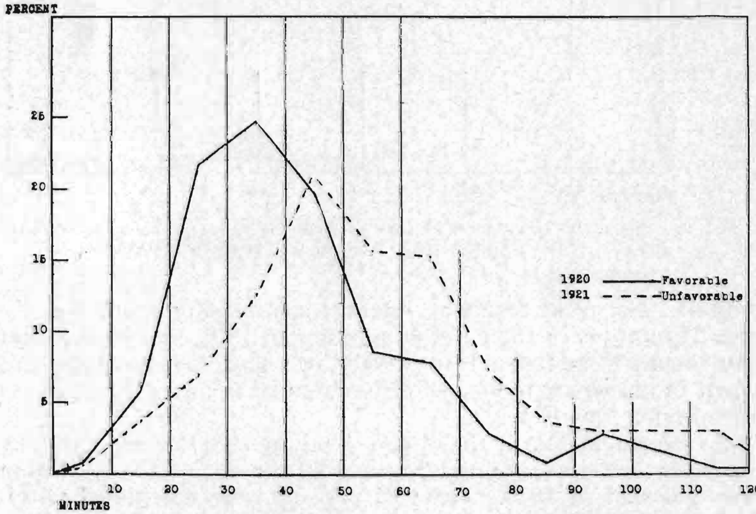

Fig. 6. Frequency distribution of time records for round trips made by nectar-carriers under *favorable* and *unfavorable* honeyflow conditions.

field trips was increased to a marked extent. Since the nectar source was the same in both cases, this increase is to be attributed largely to the greater difficulty experienced by the bees in obtaining nectar during the poor honey-flow.

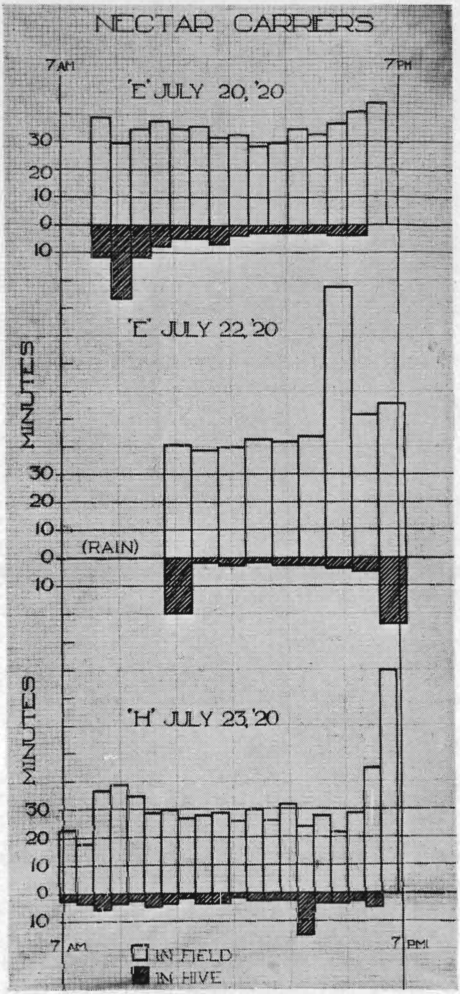

Fig. 7. Illustrating the trips made in a day by nectar-carriers.

By tabulating the number of trips made by each nectar-carrier on each day of observation and arranging these data in frequency curves, it was found that the modal class for 1920 was the 11-15 trip class which comprised 41 percent of all records (fig. 8). A total of 37 percent fell in lower classes, while a total of 22 percent fell in classes higher than the modal class. As has been shown already, the time required for a round trip was approximately 50 percent greater during the unfavorable season of 1921 than during the favorable season of 1920. The difference in the two seasons is reflected also in the number of trips made in a day. The 6-10 trip class received the largest number of records in 1921, but this was only 6 percent more than the 1-5 trip class received. Six percent fell within the 11-15 trip class, only 2 percent within the 16-20 trip class and none in the 21-25 trip class. Only 8 percent of the 1921 records showed more than

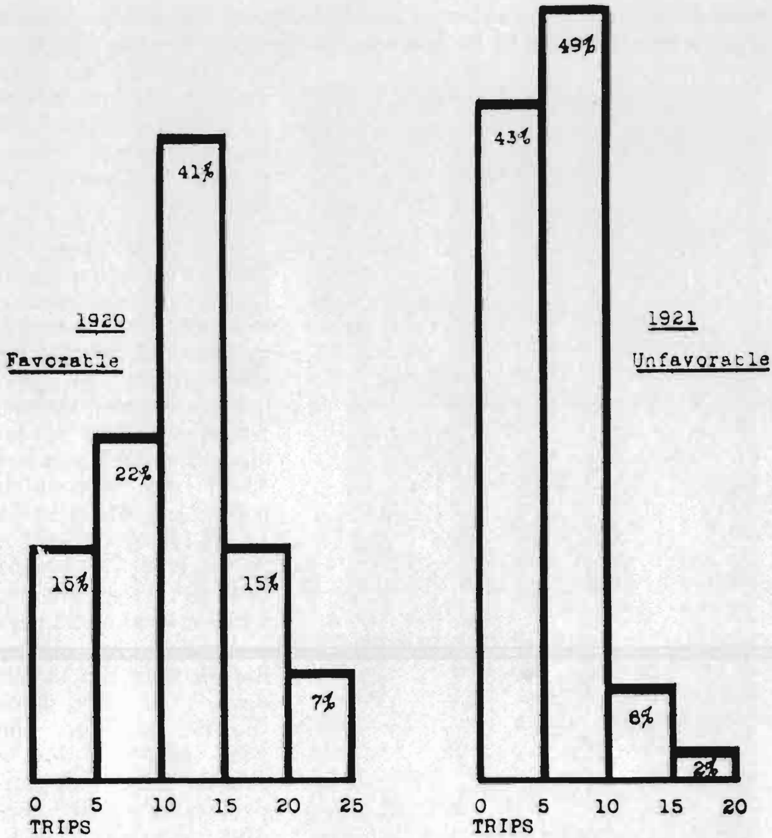

Fig. 8. Frequency distribution of records showing trips per day for nectar-carriers under *favorable* and *unfavorable* honeyflow conditions.

10 trips in a day, whereas, 63 percent of the 1920 records showed more than that number.

The maximum number of trips recorded in one day for a nectar-carrier was 24 in 1920 and 17 in 1921. The average number of trips per day was found to be 13½ in 1920 while in 1921 the average was only 7. If the mean time for round trips for each year be multiplied by the average number of trips per day for the same year, we arrive at an approximation to the average time per day spent in nectar gathering. This gives about 10 hours for field work in 1920 and about 7½ in 1921.

Discussion

In order to compare the results obtained by the different workers on some common basis, they have been transcribed into figures which indicate the average number of trips per day, as follows:

Astor	85 trips	*Huish	17 trips
*Demeure	50 "	Lundie	15 "
*Lovell	45 "	Luden	10 "
†Zander	40 "	Reaumur	6 "
†Klaus	25 "	Girard	6 "
*Maujean	19 "	Sylviac	6 "
		Demuth	4 "

In the cases in which sufficient data were given, figures in the foregoing list were calculated on the basis of a 10 hour day. Those marked with the asterisk (*) are based on the record of a single bee in each instance, while, in the case of those marked with a dagger (†), there was nothing to indicate whether the results were obtained from one bee or many.

Astor's 85 and Lovell's 45 trips were obtained from bees working under conditions equivalent to robbing and, under such conditions, bees work with feverish haste. Furthermore, a bee can secure from a dish in 2 minutes, a load which it would scarcely be able to obtain from flowers in 10 minutes, even under unusually favorable conditions. Data obtained under abnormal conditions may be interesting, but cannot be accepted as representative of the number of trips a bee will make under normal conditions when gathering from flowers.

Of Demeure's 50 trips, we are told only that the record is based on the work of one bee for one day and, since the figure corresponds more closely to the results obtained under conditions of robbing than it does to those obtained under normal conditions, it cannot be given much weight. No details, are given in connection with either Klaus's 25 or Zander's 40 trips.

Maujean's 19, Huish's 17 and Luden's 10 trips per day are based on direct observations, as probably are also the 6 trips of Reaumur, Girard and Sylviac. It will be noticed that these results are all below 20 trips per day and correspond very well with the results obtained during the present investigation. Huish's figure is for only one bee for one trip, hence it is not in itself very significant. Maujean's figure is for one bee working one day. The writer has no information as to how Reaumur, Girard and Sylviac arrived at their figure, but Reaumur's reputation goes far in giving weight to this result.

Luden's figure of 10 trips per day is based on records of six bees working for two days under absolutely normal conditions and, therefore, it cannot be refuted successfully. The bees were working on clover under honeyflow conditions slightly less favorable than those of 1920 when the writer found bees making an average of $13\frac{1}{2}$ trips per day, by actual observations covering a period of nearly a week at one time.

Demuth's result of 4 trips per day is, obviously, too low to be representative. Being based on computations, his results probably are in error due to the influence of some unknown factor or factors which are automatically excluded when direct observations are made.

Lundie (24), whose work has been referred to briefly, secured a large amount of valuable data on flight activities of the honeybee thru the use of a mechanical device which he developed for counting all outgoing and incoming bees from a given colony. The records secured enabled him to compute the average number of bees in the field during a given period so that it was found possible to derive the average duration of field trips or to be more exact, the average duration of all absences from the hive.

As will be shown later, the writer found that trips for pollen, as a rule, required much less time than did those for nectar and that trips for water were especially short. So far as known, no time records have been secured on the time required for any of the other activities outside the hive, but casual observation shows that the total duration of the so-called "play spell" of a group of young bees seldom lasts over 20 minutes and often is much less, indicating that individual flights on such occasions are quite short. These several distinct kinds of hive absences differ greatly from each other, as well as from those of nectar-carriers, in the amount of time normally required per trip. During a dearth, these miscellaneous activities constitute practically all of the hive-absences, but, during a good honeyflow, the work of gathering nectar so far over-shadows all other activities outside the hive that the influence of trips made by others than nectar-carriers becomes almost negligible. Hence, the averages secured during a period of honeyflow and no others can be considered as typical of nectar-carriers.

Of the 29 averages for duration of hive absences given in table 2 of Lundie's paper, the 7 which were secured during the honeyflow are listed here in table III. The first two of these averages were secured when the bees were gathering from the black locust (*Robinia pseudacacia*) entirely, and the next three when only the tuliptree (*Liriodendron tulipfera*) was secreting nectar. The sources available on May 20 and 22 were not mentioned, but it seems probable that tuliptree may have been the principal source; supplemented, perhaps, by miscellaneous minor sources. Anyone knowing the character of the blossom structure and the nectar yielding capacity of these two species can readily justify the difference in time required to get a load of nectar from them and, moreover, the distance to the black

TABLE III. DURATION OF FIELD TRIPS DURING HONEYFLOW
(From Lundie)

Date	Period of Day	Gain for Day (grams)	Average Field-trip (min.)	Source
May 8	11:30- 4:30	320	35	Black locust only
May 9	11:00- 6:00	500	43	Black locust only
May 15	9:45- 3:00	850	15	Tuliptree only
May 15	4:15- 5:15	850	12	Tuliptree only
May 17	12:30- 2:30	220	14	Tuliptree only
May 20	12:00- 2:00	1,170	31	
May 22	10:30-12:45	1,130	40	
Average			27	
Weighted average			29	

locusts was three times as great as to the tuliptrees. The weighted average for all seven periods gives approximately 30 minutes as the average time spent in the field during a good honeyflow. This figure compares rather favorably with the 34 minute average found by the writer during a good honeyflow from white sweet clover.

The number of trips per day depends in part upon the time spent in the hive between field trips. Lundie secured no data on hive-stays and his computations as to the number of trips per day were based in part upon the erroneous assumption that bees spend as much time in the hive between trips as they do in gathering their loads. So far as the writer is aware, no data have been published which would support such an assumption. Luden reported finding that hive-stays lasted from 5 to 10 minutes and his results have been substantiated by those of the writer who found that field bees did not often spend as much as 10 minutes in the hive between trips—in fact, the majority of hive-stays lasted only 5 minutes or less. If a liberal hive-stay of 10 minutes be added to the 30 minute average found above for time spent in the field, 40 minutes is obtained as a close approximation to the average time required to gather and deliver a load of nectar during the honeyflow mentioned above. This shows that, during a good honeyflow from such sources as black locust and tuliptree, an average of 15 trips per day is to be expected.

In the specific case cited on pages 32 and 33 of the paper (24) referred to before, the records were taken on May 15 between 9:45 a. m. and 3:00 p. m. during a strong honeyflow from the tuliptree. These records show that, on the average, 1,567 bees were in the field thruout the period; that a total of 32,492 trips were made; and that the mean time spent in the field was 15 minutes. Considering the strength of the honeyflow on this day, 5 minutes should be ample time to allow for hive-stays. On this basis, there must have been, on the average, one-third as many field bees in the hive as in the field, or a total of 2,089 bees engaged in field work. Then each bee must have made as many trips as 32,492 divided by 2,089 or 15.6 trips, instead of 10.27 trips as calculated in the report under consideration. Furthermore, the 5 hours and 15 minutes covered by these records is only half a day, so at this rate approximately 30 trips could be made in a day. This figure is somewhat higher than the single maximum record of 24 trips found during the present investigation, but it is to be expected that loads would be secured much more quickly from tuliptree than from sweet clover.

Lundie's records indicate that averages of 25 to 30 trips per day are sometimes made under highly favorable conditions and that an average of 15 trips is to be expected during a strong honeyflow.

Most of the figures on trips per day discussed so far fall into two classes or series, one series running from 40 up, and the other from 25 down. In the light of all the data at hand, it appears most likely that the figures showing 40 or more trips per day have been based upon observations on bees working under the robbing impulse and on that account cannot be accepted as the results of bees working naturally on flowers. It is possible that, in some instances, the bees under observation may have been carrying water instead of nectar. Klaus's figure of 25 trips seems high for an average, but compares favorably with the maximum average of 30 trips derived from Lundie's data and also with the maximum of 24 trips recorded by the writer in the case of a single bee in 1920. Maujean's 18 and Huish's 17 are not averages, but lend weight, nevertheless, in behalf of the latter series. Demuth's figure, 4 trips, is hardly comparable as has been pointed out already. Reaumur, Girard and Sylviac with 6 trips perhaps are not far wrong for poor honeyflow conditions. Results secured by the writer, during the unfavorable season of 1921, showed an average of only 7 trips.

The average of 15 trips, determined from Lundie's data, Luden's figure of 10 trips per day and the writer's two averages of 13½ and 7, respectively, are in fairly close agreement. Considering that honeyflow, weather conditions and other factors have a great influence on the number of trips bees will make in a day, a considerable variation is to be expected. Under favorable conditions 10 to 15 trips per day may be expected; under unfavorable conditions, anywhere from about 7 down; while under exceptionally favorable conditions, bees will make from 20 to 30 trips in a day.

Conclusions

Time required for gathering a load of nectar varies greatly, but, under favorable conditions, an hour is ample time for a nectar-carrier to make a round trip. Ten trips per day under favorable conditions probably is as reliable an average as can be derived from the data at hand.

POLLEN CARRIERS

Pollen is almost as essential as honey to the honeybee, because little, if any, brood can be reared without it. It is not used in such great quantities as honey, but a colony permanently deprived of pollen is doomed as certainly, altho less speedily, than one which has no honey. In fact, its doom is even more certain because bees can thrive on a substitute for honey, such as cane sugar, while, up to the present time, no substitute has been found for pollen. Rye meal and various other pulverized cereals have been advocated and success is often claimed from their use. In times of scarcity, bees do carry such materials to the hive and store them in the comb. Recent studies by Parker (29) indicate that pollen substitutes may stimulate egg laying, but that the resulting larvae die within about two days after hatching, none ever reaching maturity.

It has been claimed that pollen is needed by adult bees when secreting wax, but Huber (19) found by a series of experiments that bees fed on nothing but honey and water produced wax, while if fed on pollen only, none was produced. Altho some evidence supports the general assumption that adult bees can and at times do use pollen for their own nourishment, present knowledge on this point is very limited. It is known, however, that adult bees winter best on stores that contain no pollen.

According to Langstroth and Dadant (22), a young bee's first visit to the flowers occurs at the age of about 15 days when she brings in a load of pollen. Recent investigations by Rosch (35) indicate that field duties usually are begun at the age of about three weeks; while it has just been shown by Nelson (26) that in a colony composed entirely of newly hatched bees, and hence abnormal, the first pollen was carried in by marked bees known to be only eight days old.

According to Langstroth (21), the fidelity of the honeybee to her flower was noticed by Aristotle. It may be observed that the pollen carried at one load usually is uniform in color and texture, indicating that the bee gathered from one kind of flower exclusively. Investigations by Betts (1), and by Clements and Long (8), show that even the occasional loads which are mixed usually are composed largely of some one kind of pollen, and that the presence of three or more kinds in one load is rare. The great importance of the honeybee as a pollenizer depends largely upon this trait of fidelity and upon the fact that the honeybee is the only one of all insect pollinators that man has under his control and can provide in large numbers at will. The value of the honeybee in this capacity cannot be computed, but it has been remarked repeatedly that the honeybee is of more value to agriculture in general than to apiculture in particular.

Review of Literature

Aside from a few general statements given by Cotton (10), and by Miller (25), no data have been found on the time required for a bee to gather a load of pollen, except a brief account of an observation by Huish (20) whose "Treatise on Bees" was published in 1815. With watch in hand, Huish sprinkled flour on some bees as they left for the field. The first to return carried a good sized load of pollen, secured during an absence of 15 minutes. The time is not given for the others, but it is recorded that the last returned in 35 minutes without any pollen, but with a load of nectar.

Observations

Time records for field trips, hive-stays, and round trips by bees gathering pollen from corn (*Zea mays*) were secured in 1920 and again in 1921. Weather conditions in both instances apparently were favorable enough for the production of pollen by the plant and for field work on the part of the bee. But in 1920, the data were taken at times when there was an abundance of corn in bloom, whereas, in 1921 the main period of bloom had passed before the records were obtained. We have, then, as for nectar-carriers, one set of data secured under favorable conditions, and the other under less favorable conditions. The records for the two seasons, plotted against each other in the form of frequency curves, appear in figs. 9, 10 and 11. In every case the curve is a decided skew, so for purposes of comparison, the *mode* is used in preference to the *mean*.

Field trips by pollen-bearers were found to be considerably shorter, as a rule, than those made by nectar-carriers. As shown in fig. 9, almost 40 percent of the field trip records for 1920 fell within the 6-10 minute class, and 97.5 percent were completed in 30 minutes or less. None of the 1921 records for field trips fell within the 2-6 minute class, and only 20 percent fell within the 6-10 minute class, yet 99 percent were accomplished in 30 minutes or less. The modal time, however, was 15.5 minutes as against only 8.6 minutes in 1920.

The curves for hive-stays appear in fig. 10, and are very sim-

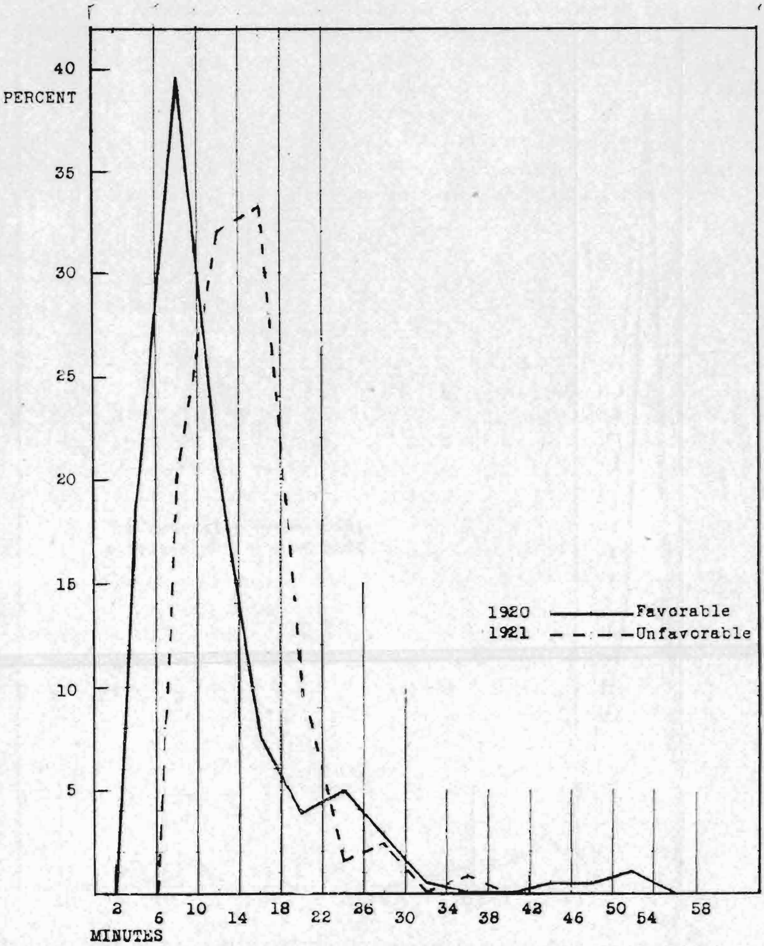

Fig. 9. Frequency distribution of time records for field trips made by pollen-carriers when gathering from corn under *favorable* and *unfavorable* conditions.

ilar for the two seasons. The peaks both fell within the 2-4 minute class. In 1920, this class received 38 percent of the records as against 36 percent in 1921, but the percentage of hive-stays that occupied 15 minutes or less was 98 in 1921 as against 88 in 1920. The most frequent interval spent in the hive between trips was 3.4 minutes in 1920 and 3.7 minutes in 1921.

In fig. 11, are the curves for round trips. The modal interval for the 1920 records was 12.6 minutes, but was 16.5 minutes in 1921. The percentages of records falling within the modal class

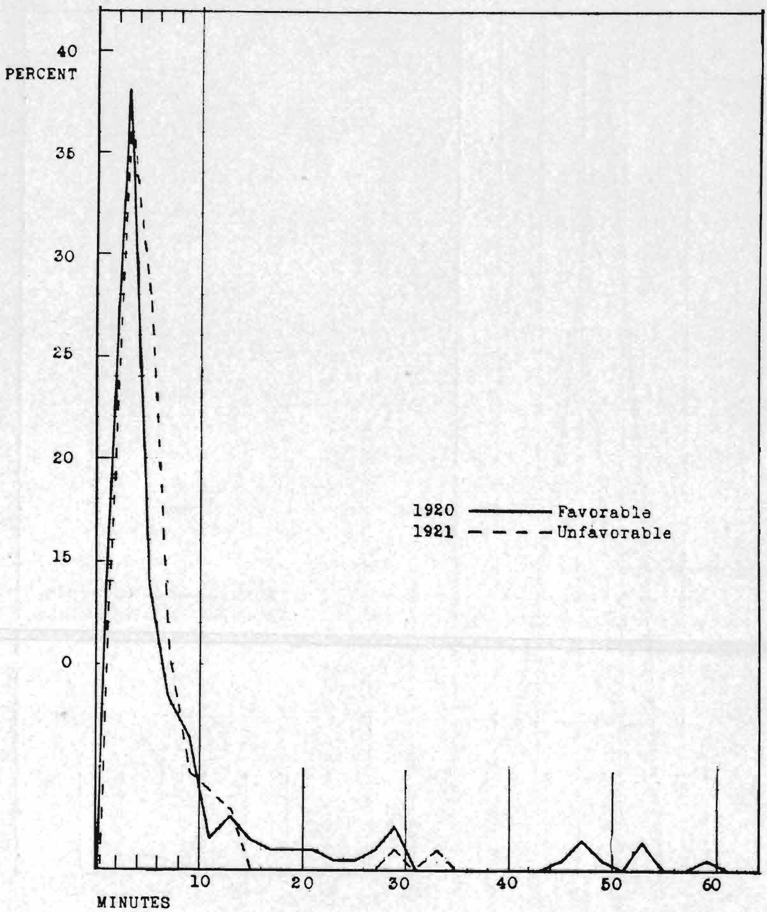

Fig. 10. Frequency distribution of time records for hive-stays made by pollen-carriers when gathering from corn under *favorable* and *unfavorable* conditions.

were nearly the same in both cases. In fact, the two curves are much alike as to area and shape, but the one for 1921 stands about 4 minutes farther to the right than does the other. This indicates in a general way that the bees that gathered corn pollen during the period of observation in 1921, consumed about 4 minutes per trip more than did those in 1920 when corn pollen was more plentiful.

The maximum number of trips recorded in one day for a bee gathering pollen from corn was 20 in 1920 but only 11 in 1921, while the averages were about 8 and 5½, respectively. As a rule, corn pollen was not available in the afternoon so these figures represent only about half a day in actual working time.

Discussion

As in the case of nectar gathering, it is clear that the time required to gather a load of pollen is influenced by the numerous factors which go to make up what we call favorable or unfavorable conditions. Most of these factors were pointed out in connection with nectar gathering and will be passed over here. Humid, cloudy days, if not too cool, seem to be more favorable for nectar gathering. The reason for this is that on a hot sunny day the anthers of the flowers shed their pollen quickly so that by noon or before, no more pollen is available, whereas, on humid, cloudy days the flowers continue to yield pollen most of the day. The kind of flower is another factor which has much to do with the length of time required for a bee to get its load of pollen. Other things being equal, a load of pollen can be gathered more quickly from corn or ragweed than from clover because of its greater abundance and ease of access.

With reference to the data given herewith, in both 1920 and 1921 practically all the field trips made by bees carrying corn pollen were completed in less than 30 minutes. Huish's observations correspond with this figure. The influence of the less

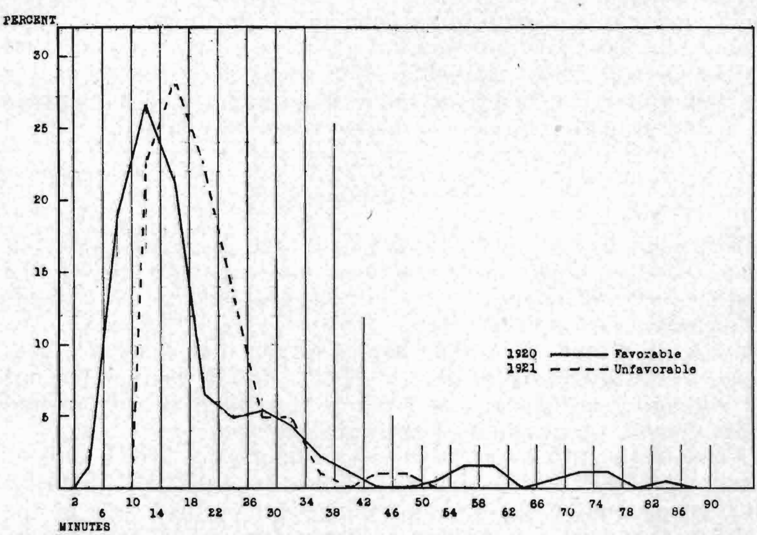

Fig. 11. Frequency distribution of time records for round trips made by pollen-carriers when gathering from corn under *favorable* and *unfavorable* conditions.

favorable conditions in 1921 showed up mostly in lengthening the field trips. The poor season made very little difference in the length of the hive-stays.

The number of trips per day by pollen-carriers was small considering the comparatively short time required for each trip. The reason for this becomes clear when it is understood that pollen-carriers working on corn (*Zea mays*) usually ceased going to the field about noon or shortly after. But why did these bees seldom go to the field in the afternoon? Two important factors are involved. One is that, on a sunshiny day, most of the pollen of corn (*Zea mays*) is shed by noon. The writer's observations on this point are in agreement with those of Gernert (16), Weatherwax (40) and Parker (29). The second factor is the long continued fidelity of the bee to her flower species. It has been commonly observed that a honeybee seldom gathers from more than one species of plant on any given trip; but it was first pointed out by the writer (27) that during any portion of the day when no nectar (or pollen) is available from her particular flower species, she seldom goes to the field at all, altho nectar (or pollen) could be obtained from other species by so doing.

Conclusions

The time required for a pollen carrier to make a round trip varies greatly, but under favorable conditions, trips are commonly made in a quarter of an hour and often in less time. The number of trips per day was not great as a rule, because corn pollen usually is not available after about noon; consequently an unqualified statement for the average number of trips made in a day by pollen-carriers would scarcely be justified.

WATER CARRIERS

Everyone is familiar with the fact that bees visit watering places, and no doubt there are those who have never given the matter a second thought but take it for granted that all animals drink water to slake their thirst. Indeed, Cotton (10) says, "In the Isle of Wight, the people have a notion that every bee goes down to the sea to drink once a day." But it was pointed out by Aldamiri, as long ago as 1405, in a passage already quoted from Cotton, that some bees are water-carriers.

Langstroth (21) says, "that bees cannot raise brood without water has been known since the times of Aristotle." Butler (4), whose quaint old book was published in 1623, was of the opinion that bees needed water chiefly for their brood, for he had observed that "when the drones are done away and breeding is ended, the bees are nothing so frequent at the watering places.'' Cotton (10) says that Buera of Athens, about the year 1797, wrote, ''Bees daily supply the worms with water; should the state of weather be such as to prevent the bees from fetching water for a few days, the worms will perish.'' Cotton also says that Sydserff, writing in 1792, mentioned the ''bladder or bag in which the bee fetcheth water to mix up the bee-bread for feeding the young; in this bag also they carry their honey.''

So far as the writer is aware, no data have been published previously on the time required for water-carriers to make their trips, nor on the number of trips they make in a day.

Observations

On the afternoon of August 17, 1921, which was after the close of the honeyflow, a number of bees suspected of being water-carriers were caught and submitted to the test described earlier in this paper. Seven of those which were shown by the test to be water-carriers, were marked and released. Of the seven, three made no more trips that day, but the other four made from three to eight trips each. The hive entrance was carefully watched by two observers from early morning until late evening on August 18 and 19. Observations were begun again on the twentieth but the day was so cool that very few bees left the hive and at 10:30 observations ceased. In the afternoon of that day, the entrance was watched from 1:30 to 3:05, when the bees practically ceased flying. No further observations were attempted until August 24, when the entrance was watched from 8:45 until noon, when, on account of the inactivity of field bees, the series of observations was ended.

Very little brood was being reared at that time and the weather was exceptionally cool for August, so the data secured can scarcely be considered representative of the average number of trips per day. The results found for average time spent in making field trips, hive-stays and round trips, however, probably are not very different from results which might be obtained under conditions which would induce the water-carriers to work longer hours. And the maximum number of trips found in this experiment for one bee in a day, perhaps might be found to be only slightly above the average under conditions of warmer weather and heavy brood-rearing.

Of the five days on which data were taken, only two can be recognized as in any way representing normal conditions. Table IV contains a summary of the records for those two days, August 18 and 19. On the eighteenth, all seven bees made trips for water, but on the nineteenth, No. 96 and No. 97 failed to show

TABLE IV. TRIPS BY WATER-CARRIERS

Bee Number	Field Work Began	Field Work Ended	Total Minutes	Total Trips	Mean Time (minutes)
August 18					
94	8:54	5:00	486	69	7.0
95	8:44	3:28	404	53	7.6
96	12:44	2:07	83	7	11.9
97	9:14	4:58	464	48	9.7
98	10:05	4:58	413	19	21.7
99	9:29	5:01	452	50	9.0
*100	8:13	4:58	525	38	13.8
Average			404	41	
August 19					
94	7:21	5:09	588	114	5.2
95	7:59	1:18	319	32	10.0
98	7:56	4:31	515	60	8.6
99	7:09	8:53	104	14	7.4
*100	7:00	4:49	589	40	14.7
Average			423	52	

*This bee was found to be going a distance of two-thirds of a mile.

up and were not seen again. Whether they lost their lives or only their marks was not learned.

Six of the seven marked water-carriers put in a fairly good day's work on August 18, with an average of 7.6 hours each; but No. 96 worked only 1.4 hours, so the average for all seven was 6.7 hours. On the nineteenth, three of them worked practically a full day, putting in respectively 8.6, 9.8 and 9.8 hours, but the short hours worked by Nos. 95 and 99 reduced the average for all five to 7.0 hours. It is very noticeable that these bees began to carry water more than an hour earlier on the nineteenth than on the eighteenth. It is believed that this difference was due largely to the fact that the temperature on the morning of the nineteenth averaged 12 degrees F. warmer than on the preceding morning when the thermometer registered only 64 degrees F. at 8 o'clock.

The average number of trips made on the eighteenth was 41; two bees made considerably less than this number but four exceeded it. No. 94 made 69 trips which was the maximum recorded for that day. Three of the five marked water-carriers which worked on the nineteenth, made less than 52 trips, the average for all; but of these only No. 99 fell far below this figure. No. 94 again provided the maximum number recorded for the day, being credited with 114 trips or more than twice the average for the day.

As shown by the figures in the last column of table IV, the mean time per trip varied considerably. In at least one case, the long trips were due to the distance to the source of supply visited by the individual. No. 100 which averaged nearly 15 minutes per round trip was found to be going two-thirds of a mile to get salt water instead of taking the brook water that was available at the edge of the apiary. Records obtained on the time spent by this bee in flying to and from the salt water supply showed that on the average she spent three minutes going and the same in returning; hence a total of six minutes or two-thirds of the time she spent in the field was used in flight. While it was not known

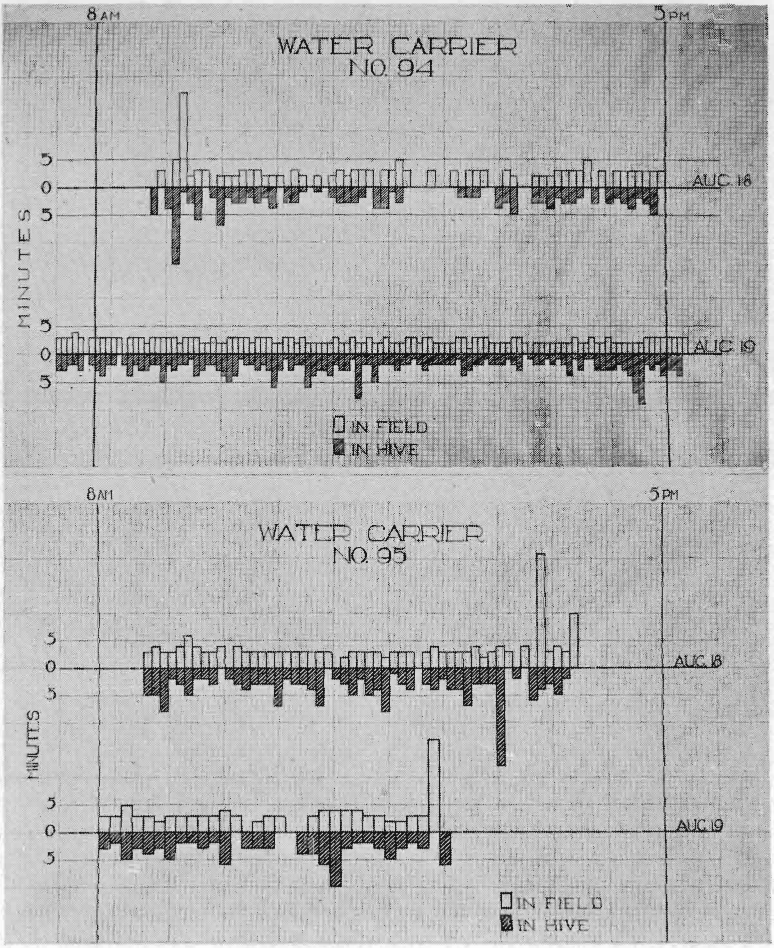

Fig. 12. A graphic representation of the trips made during two successive days by water-carriers number 94 and number 95.

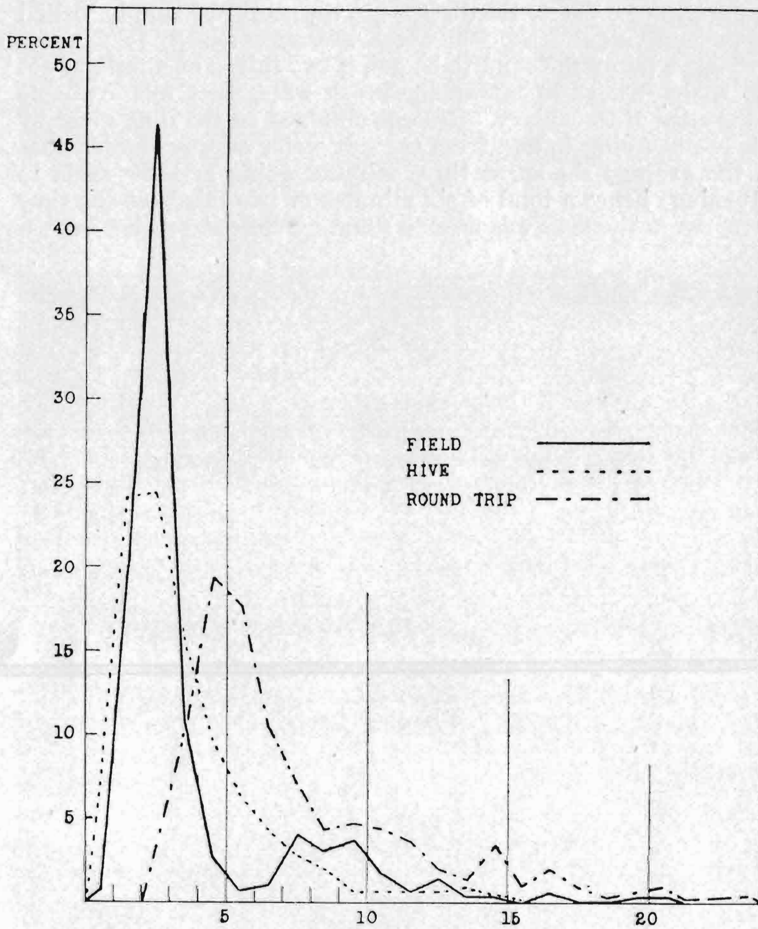

Fig. 13. Frequency distribution of time records for field trips, hive-stays, and round trips made by water-carriers.

positively where the others secured their loads, it was presumed that most of them availed themselves of the abundant supply near at hand. This seemed quite certain in such cases as No. 94 and No. 95 (see fig. 12), for which the records showed that they seldom were gone from the hive for more than three minutes at a time. Observations have shown that a bee commonly spends from one to two minutes in taking up a load of water, and it has been shown already that it takes one minute for a bee to fly a quarter of a mile; so it seems clear that those bees which returned regularly with loads of water in three minutes or less, could not have gone much if any farther than the brook.

Some of the means shown in the last column of table IV are not truly representative because of an occasional extra long trip which outweighs a number of short ones in the determination of the mean. On this account all of the time records obtained for field trips, hive-stays and round trips by water-carriers have been arranged according to their frequency distribution and appear in fig. 13. As may be computed from the freqquency curves, 67 percent of all recorded field trips for water were completed in 3 minutes or less, and 92 percent in 10 minutes or less.

The time spent in the hive by water-carriers was found to be from 2 to 3 minutes as a rule and very seldom did one remain as long as 5 minutes. The percentage of hive-stays which occupied 3 minutes or under, was 54; 5 minutes or under, 79; and 10 minutes or under, 95 percent.

The most frequent time interval consumed by water-carriers in making round trips was between 5 and 6 minutes, as may be seen from fig. 13. Fifty percent of all round trips were completed in 6 minutes or under, 77 percent in 10 minutes or under, and 91 percent in 15 minutes or less. Thus it is seen that less than 10 percent of all round trips recorded were of more than a quarter hour duration.

Conclusions

A water-carrier can make a round trip in 5 minutes when the supply is near at hand. Sometimes 100 or more trips are made in a day by a single water-carrier, but the average probably is nearer half this number.

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