# THE BEHAVIOUR OF A POPULATION OF HONEYBEES ON AN ARTIFICIAL AND ON A NATURAL CROP

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(With Six Text-figures)

## INTRODUCTION

The behaviour of a population of honeybees on a crop is a problem of considerable theoretical interest and practical importance, and one which has so far received little attention. Experimental work has revealed much about the behaviour of the individual honeybee in respect of the method of communication between individuals, colour vision, olfactory and gustatory perception, etc. (Von Frisch, 1914, 1919, 1921, 1923, 1930), time sense (Kalmus, 1934), water perception sense (Hertz, 1934), etc., without, generally speaking, dealing with the problems of the population as a whole. However, Minderhoud (1931) published field observations on the area ranged over by a foraging bee working dandelion, clover and various cultivated plants, and reached the important conclusion that bees return time after time, even day after day, to an area of the crop a few yards square, probably not more than 10 yd. each way Similar observations made by Buzzard (1936) using marked bees went even further than those of Minderhoud, and showed that the same bees return continually to the individual plant upon which they were first observed. Each plant appeared to have its own population of bees which only trespassed on to a neighbouring bush of the same species when the branches of the two bushes actually interlaced.

Counts of bees on crops have, of course, been made, but their interpretation has usually proved difficult in the light of past knowledge and has seldom been correlated with experimental work upon the behaviour of the individuals of which the population was composed. These difficulties of interpretation have probably been largely due to the considerable differences existing between the conditions under which behaviour experiments are usually carried out and the complex conditions appertaining to the field. Experiments under conditions that are more nearly 'natural' than those under which observations have hitherto been made, but with conditions still under a considerable degree of control, may be expected to lead to a better understanding of the behaviour of the populations as a whole. This was achieved by using artificial nectar sources (Petri dishes) distributed over a large field. The obvious advantages of the use of these artificial nectar sources were that the behaviour of a small number of bees to an individual dish is already well known, that the concentration, quantity and time of presentation of nectar (sugar syrup) can be varied at will, and that the density of distribution of the nectar sources in the field, and their position relative to the colonies of bees, can be arranged according to the purpose of each experiment.

If the differences as appreciated by the bees between dishes and flowers were fully understood, certain conclusions concerning the behaviour of bees on natural crops could be drawn with confidence; however, as this is not so, experiments on the behaviour of a population on natural crops had also to be undertaken before any definite conclusions could be drawn.

## MATERIAL, METHODS, ETC.

Experiments were carried out during the summer of 1942 in a large field on the farm of the Rothamsted Experimental Station, next to the Home Apiary, which throughout contained about thirty-five colonies of bees of Caucasian, Italian and Caucasian-Italian strains.

The main observations were made in the field containing the artificial nectar sources and upon two natural crops. The artificial nectar sources (Fig. 1) were arranged so that they occupied part of a sector, of about 30°, of a circle the centre of which lay near the middle of the Home Apiary. The field containing the artificial nectar sources was fenced pasture, with few flowers, crossed by several footpaths and containing a few small clumps of trees. 112 Petri dishes were placed in the experimental field, arranged in thirteen curved rows on arcs of circles centred in the Home Apiary. The nearest of these curved rows was situated at a distance of 160 yd. from the centre of the apiary, and the most distant curved row was 400 yd. away. The radius of curvature of each row was increased by 20 yd. over that immediately preceding it. The dishes in each row were likewise placed 20 yd. from one another.

Each artificial nectar source consisted of the top or bottom section of a Petri dish in which a 1 lb.

honey jar full of sugar solution was inverted to act as a reservoir. A piece of blue pottery was placed upon the top of each jar and a similar piece of pottery was laid on the grass nearby. No scent was added to the syrup throughout the course of these experiments.

Most of the observations on natural crops were made on a piece of common land on which large patches of willow-herb (*Epilobium angustifolium*) were growing. For the observations made upon willow-herb a patch was selected about 50 yd. long × 40 yd. wide which had more or less well-

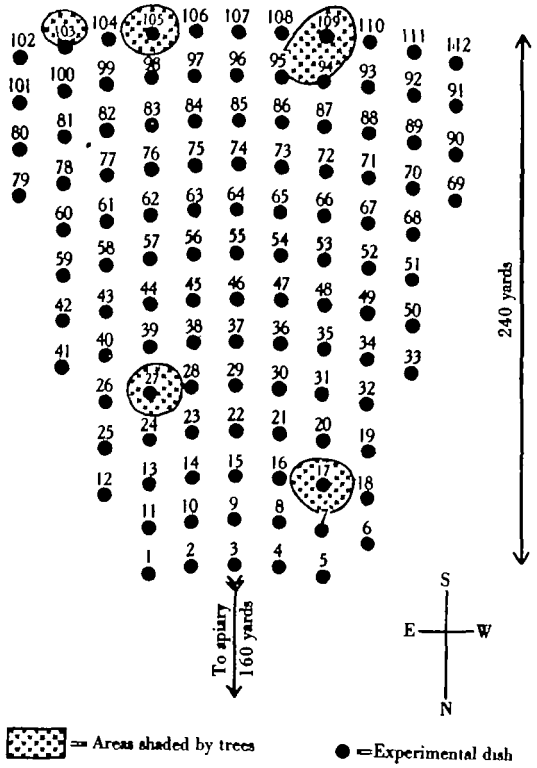


Fig. 1. Lay-out of Petri dishes on experimental field.

defined boundaries. This patch was about 600 yd. east of the experimental apiary and contained gorse, brambles, wild raspberries, etc., in addition to many plants of *Epilobium*.

The second growing crop upon which observations were made was the cultivated ornamental thistle, *Echinops sphaerocephalus* L. This was growing in five isolated patches in a long border at one side of the experimental apiary, each patch being about 18 yd. from those on either side of it. Each patch was arranged to contain approximately forty flower heads at the time that the observations were made.

In order that they might readily be recognized, individual bees, whose behaviour it was desired to study, were marked with one or more brightly coloured paints, on the dorsal surface of the thorax or abdomen, or both. Since it was often desirable to mark bees in the field without catching the individuals concerned or disturbing them unduly, quick-drying paints were employed. These were prepared by mixing small quantities of dry, powdered pigments with a solution of rosin in acetone. The amount of pigment added was varied according to the intensity of colour desired, and sufficient rosin was added to produce a paint of good consistency. The bees were marked usually whilst actually on the flowers. Great care was taken to see that no paint was placed on the antennae, eyes, legs, or wings of the individuals concerned, since the presence of paint on these parts of the bee's body seriously interferes with its normal behaviour.

Marked and unmarked bees were observed, or counted, on the whole, or on a part, of one of the experimental sites as required, care being taken to interfere with their activity as little as possible. Most counts were made by one or more observers whilst walking over the field. It was seldom possible, nor indeed necessary, to station an observer at each dish.

The concentration and quantity of the sugar syrup at the artificial nectar sources was varied according to the requirements of particular experiments.

## EXPERIMENTS AND RESULTS

### (i) *Indications of constancy to a particular site in an artificial crop*

On 5 June 1942, a good flying day, two bees found visiting dish no. 85 on the experimental field (Fig. 1) 360 yd. from the apiary, were marked for purposes of recognition, their identification marks being *Y* and *YY*. A constant supply of sucrose solution (about 12% sugar) was maintained in this dish throughout the next few days. Between 11.26 a.m. and 12.30 p.m. (G.M.T.) continuous observation was kept on this dish and the number, duration and time of the visits of these two bees (*Y* and *YY*) to the dish were noted. The results obtained are shown in Table 1. Throughout the period of observation, bee *YY* chose a point on the west side of the experimental dish for feeding, and *Y* chose a point on the north side. Neither bee moved so much as an inch from its chosen position and each assumed a characteristic attitude while drinking, *Y* drinking from the side of the dish and *YY* settling head downwards on the reservoir.

At 4.25 p.m. (G.M.T.) *Y* and *YY* were still paying regular visits to the dish and must between them have already made at least 150 trips almost certainly without a break. At 9.20 a.m. (G.M.T.) on the following day these two bees were still visiting the dish with great regularity.

It should be pointed out that the two bees in order to reach their chosen dish 360 yd. from the apiary had to fly over or near a number of exactly similar dishes filled with syrup of the same concentration as that in the chosen dish, and were thus always in

position to choose to collect syrup from other dishes, in much the same way as in nature they would be free to collect nectar from any one or more of a number of flowers composing a crop.

At about 1.55 p.m. on the day on which observations given in Table 1 were made, the experimental dish was moved a farther 2 yd. away from the apiary

Table 1. *The number, duration and time of visits of two honeybees (Y and YY) to a dish of syrup, 5 June 1942*

| Identity of bee | Time of visit (G.M.T.) | Duration of visit | Interval between visits |
|---|---|---|---|
| | hr. min. | sec. | min. |
| *YY* | 11 29·9 a.m. | 31 | — |
| *Y* | 11 33·5 | 40 | — |
| *YY* | 11 34·2 | 30 | 4·3 |
| *Y* | 11 38·1 | 41 | 4·6 |
| *YY* | 11 38·6 | 30 | 4·4 |
| *Y* | 11 42·0 | 30 | 3·9 |
| *YY* | 11 43·3 | 30 | 4·7 |
| *Y* | 11 46·0 | 38 | 4·0 |
| *YY* | 11 48·8 | 36 | 5·5 |
| *Y* | 11 51·0 | 43 | 5·0 |
| *YY* | 11 53·7 | 30 | 4·9 |
| *Y* | 11 55·3 | 37 | 4·3 |
| *Y* | 11 58·3 | 37 | 3·0 |
| *YY* | 11 58·3 | 32 | 4·6 |
| *Y* | 12 1·2 p.m. | 40 | 2·9 |
| *YY* | 12 2·0 | 30 | 3·7 |
| *Y* | 12 4·0 | 40 | 2·8 |
| *YY* | 12 5·2 | 28 | 3·2 |
| *Y* | 12 7·5 | 41 | 3·5 |
| *YY* | 12 9·3 | 35 | 4·1 |
| *Y* | 12 11·3 | 40 | 3·8 |
| *YY* | 12 13·0 | 32 | 3·7 |
| *Y* | 12 14·2 | 42 | 2·9 |
| *YY* | 12 17·5 | 35 | 4·5 |
| *Y* | 12 17·8 | 38 | 3·6 |
| *Y* | 12 22·0 | 44 | 4·2 |
| *YY* | 12 22·5 | 33 | 5·0 |
| *Y* | 12 26·0 | 46 | 4·0 |
| *YY* | 12 28·3 | 38 | 5·8 |
| *Y* | 12 30·0 | 40 | 4·0 |

Mean length of time between visits $Y = 3{\cdot}77 \pm 0{\cdot}17$ min., $YY = 4{\cdot}49 \pm 0{\cdot}20$ min.

Mean length of time spent drinking $Y = 39{\cdot}81 \pm 0{\cdot}89$ sec., $YY = 32{\cdot}28 \pm 0{\cdot}75$ sec.

The remarkable constancy of the behaviour of individual bees, such as is shown in Table 1, has been used by one of the authors (Kalmus, 1938) for investigating the internal urge which compels a nectar-collecting bee to fly either to or from the hive. However, the very definite differences between the individuals—*Y* being the quicker at flying but the slower at drinking would indicate some possibilities of further research. In addition, there are indications of similar trends in the time series of the two individual, which hint at a dependence of the visits on environmental factors.

at a time when both bees (*Y* and *YY*) were absent. Bee *Y* returned to the old site, flew diagonally across it and had found the dish within 12 sec. of crossing its original site, *YY* similarly crossed the original site and located the dish 7 sec. later.

A similar experiment using four other marked bees gave very similar results. Therefore it appears that so long as there is an abundance of nectar at a given source, bees will confine their visits to this one source for many hours and even over two consecutive days.

(ii) *The territorial constancy of a small population of bees marked near the centre of a group of dishes in the experimental field*

For several days prior to this experiment bees were fed at all the dishes in the experimental field, but care was taken to see that the syrup in dishes 84 and 85 did not become exhausted. On the evening of 25 June about one hundred bees feeding at these two dishes were marked. Fig. 2 shows the subsequent distribution of these marked bees on dishes 84 and 85 and the fifteen dishes nearest to them, as determined by eleven counts made at various times on the following day. Care was taken to see that all seventeen dishes upon which the counts were made were continuously supplied with syrup during this day.

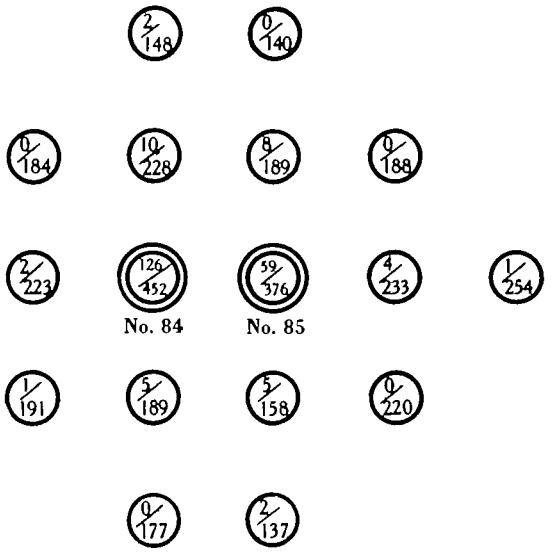


Fig. 2. Distribution of bees counted in eleven counts on seventeen dishes 26 June. The bees previously marked at dishes 84 and 85 are indicated in the numerators, total unmarked and marked in denominators.

As will be seen from Fig. 2 the marked bees exhibited a high degree of constancy in their visits to the dishes where they had been marked (nos. 84 and 85); however, some of the bees were recovered on the surrounding dishes, and of these most were found upon the dishes nearest to dishes 84 and 85 upon which they had been marked. This may be a demonstration of some degree of spreading subse-

quent to the marking, or alternatively these marked bees found on dishes other than 84 or 85 could be supposed to have been practically constant in their attention to the various other dishes upon which they were found, and merely to have wandered temporarily to dishes 84 and 85 at or about the time of marking. Either supposition entails the assumption of a certain small degree of inconstancy to a particular dish. This inconstancy may well have been induced by failure of the supply of syrup in certain dishes overnight (25–26 June) and neglect to refill them before the bees commenced to visit them next morning, so that bees at some dishes finding the supply at their customary site temporarily suspended had searched for and found other adjacent sources.

During the next 3 days no syrup was supplied in any of the dishes. On the following 3 days syrup was again supplied continuously in all dishes and a further eighty counts were made during this subsequent period. The results of these counts are given in Fig. 3, from which it will be seen that even after a 3-day interruption in the supply of syrup, the marked bees which were recovered were found close to the original site of markings.

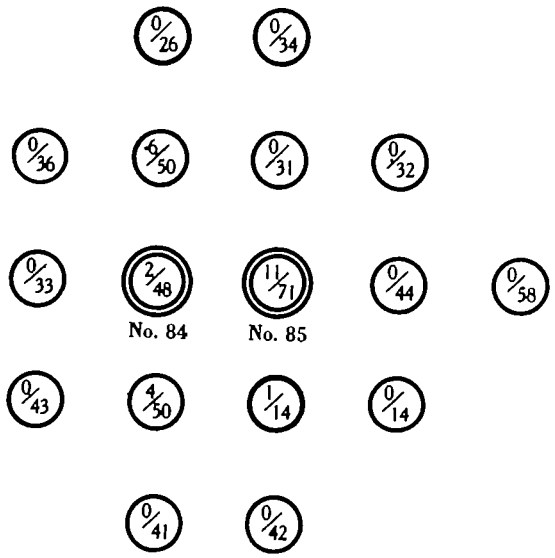


Fig. 3. Eighty counts made on the same dishes as in Fig. 2, 30 June–2 July inclusive, after three complete days without feeding.

(iii) *Visits of bees to a new source of syrup placed between previously established sources, and the effect when the established sources dry up*

Fig. 4 shows the distribution of bees on filled dishes spaced along a line at approximately 1 yd. intervals, running due south from the hives. On the previous days the dishes had been in groups over areas about 1½ yd. square at places *A*, *B* and *C*, with no dishes in between. (*Note.* The arrangement of the dishes for this particular experiment was different from that of the experimental field previously described and used for subsequent experiments.) The graph (Fig. 4—dots) which shows the results of a count made 1¼ hr. after the dishes had been spaced at the 1 yd. intervals, and filled, shows clearly that practically all the bees came back at or near to the three old sites, their numbers decreasing rapidly with distance from these sites. These dishes were all on a substantially uniform stretch of meadow, and there were no local landmarks by which, to human eyes at least, the old sites were noticeably different from the intervening spaces. During the 1¾ hr. following this count, the bees were allowed to finish up all the syrup in most of the dishes along this line, and the points marked with crosses on the graph show the numbers of bees on the various dishes half an hour after refilling all the dishes (about 2¼ hr. after the first count). These latter counts show great local variation, but the peaks at the old sites have now entirely disappeared. This can be explained by (1) the observed fact that the bees, when they had finished all the syrup at any one dish, after a time began to seek out other dishes, which necessarily proved to be some of the intermediate ones; and (2) the assumption that thereafter some of the bees retained a memory for the intermediate dishes they had found, and revisited them even after the dishes at the original sites had been refilled.

The work of Wolf (1926–31) may possibly throw some light on the fact that a bee is able to locate a dish at a given distance from its hive even when that dish is placed on a uniform piece of land which bears no distinctive marks by means of which the bee could memorize the site. Wolf, in his work on the home-finding sense of the honeybee, demonstrated that a bee possesses a definite sense of distance as well as of direction. On leaving the hive to visit a particular source of nectar she will fly in a more or less straight line for a definite distance in a given direction, and not until she is within a few feet of a position the correct distance from the hive will she deviate from a straight line and commence to make searching flights.

In order to explain more fully the behaviour of a bee when the food supply in a dish which it had grown accustomed to visit failed, let us assume that counts made at a given dish showed an average of twenty bees feeding there at any time during flying hours. The total number of bees visiting this dish would then be several times as great, on account of the fact that of the total time spent by a bee on any one foraging trip only a small proportion of this (according to conditions usually ½–1½ min.) was spent in drinking and the greater part of the time in flying to and from the hive and regurgitating the syrup collected.

As soon as the syrup in a dish begins to dry up, the bees can no longer fill their honey-stomachs

[illegible] the same rapidity as before and, as a consequence, have to spend a considerably longer time upon the dish in order to acquire a load. As a result of this the number of bees on the dish at any one time gradually increases as the ratio of the time required to collect a load of syrup and the time spent in flying to and from the hive is increased. Even when no syrup remains in the dish at all, the bees accustomed to feed at this dish eagerly search the site for syrup. However, after a few minutes most of them begin searching round the empty dish in concentric circles of ever-increasing size, but at intervals still returning to the dish, until they find a new dish or other source of food. Gradually the number of visitors to the dry dish decreases from this cause, and only occasional visitors persist in visiting it at longer and longer intervals, the frequency of such revisits depending upon the extent of the previous conditioning to this site, competition and other factors.

It should be pointed out that, although this behaviour is in principle probably the same as that which occurs on a natural crop of flowers when the nectar supply fails, the time relationships are not the same on a flowering crop as in the case of the dishes of syrup, since on flowers the time spent by the bees in collecting a load of nectar is usually greater than the time spent in flying to and from the hive. This ratio between time spent upon the crop and time spent flying, etc., will, of course, vary not only with the crop but also under different climatic conditions which will in their turn greatly influence the abundance and concentration of the nectar supply.

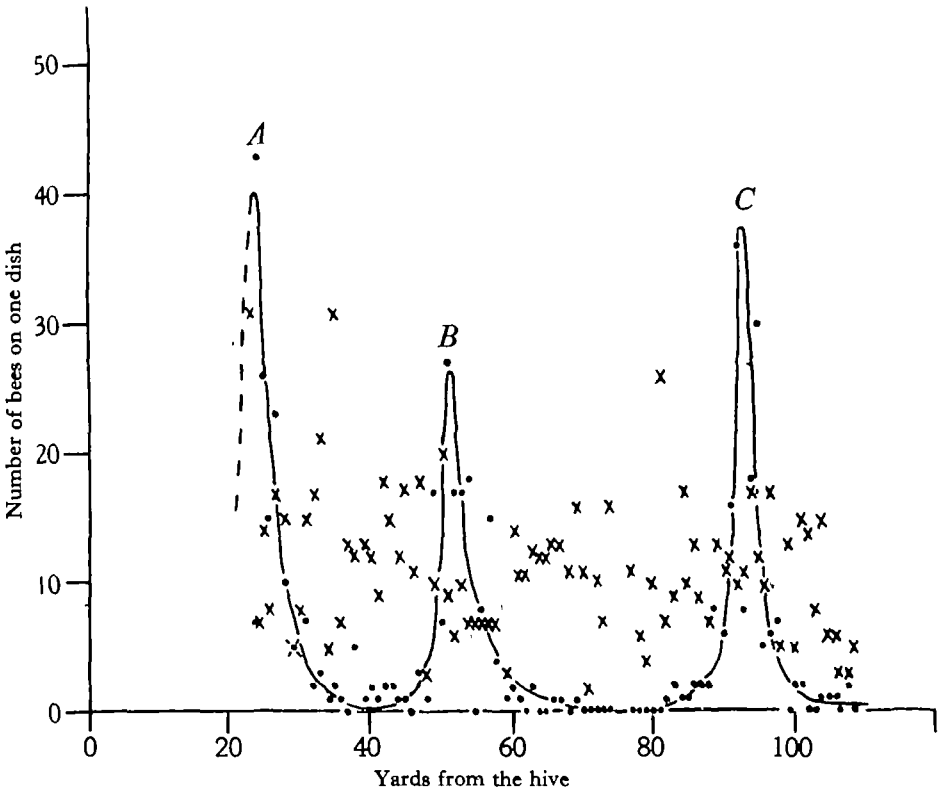


Fig. 4. Distribution of bees on a single line of Petri dishes, at the sites of some of which they had been previously fed. ● = 1½ hr. after the dishes had been spaced out along the line. × = 2½ hr. after that, when most dishes had dried up and had been refilled again.

(iv) *Some of the influences of the situation of a dish, distance of a dish from the hive, and weather conditions, upon the distribution of a population of bees in the experimental field*

(*a*) *Number of bees visiting dishes placed in shady surroundings*

The number of bees visiting dishes placed in the shadow of trees and other foliage was found to be very much smaller than was the case with dishes in more open surroundings. Three dishes (nos. 17, 27 and 109) situated among small groups of trees in the experimental field were very rarely visited by any bees. The number of bees visiting dishes situated in partial shade (nos. 7, 94 and 105) was also small. Table 2 shows the results of forty-one counts made

on all the dishes in the experimental field, which illustrate these points.

Table 2. *The effect of total and partial shade on the number of honeybees visiting dishes*

| | No. of dish | No. of bees | Average no. of bees per dish for all counts |
|---|---|---|---|
| Dishes in complete shade | 17 | 6 | 2·7 |
| | 27 | 2 | |
| | 109 | 0 | |
| Dishes in partial shade | 7 | 40 | 32·7 |
| | 94 | 37 | |
| | 105 | 21 | |
| Dishes in open positions | Remaining 106 dishes in experimental field | 17,157 | 161·9 |

Some observations were made which appeared to indicate that fewer bees visited the dishes placed on a line drawn from the apiary to one of the groups of trees in the experimental field, over distances within about 50 yd. of the group. Unfortunately, the data were insufficient to enable a definite conclusion to be reached. If in fact such a conclusion were reached it would indicate the reluctance of bees to fly in the direction of groups of tall trees, and their preference to direct their flight towards an open area.

(*b*) *Range of feeding and weather conditions*

It is well known that wet or stormy weather usually reduces the total number of foraging bees present in the field at any given time. A heavy cloud passing over the sun is sufficient to cause large numbers of bees to return to their hives. It has also sometimes been suggested that such unfavourable conditions also reduce the distance from the hive which foraging bees will fly, causing the whole foraging population to work that part of the crop nearest to the hive. Unfortunately, it was not possible to establish definite conclusions on this point, but some data were collected which indicate that sudden changes in the weather do not cause individual bees which have become established at the more distant feeding places to leave them in favour of others nearer home. All the evidence points to the conclusion that if a sudden deterioration in the weather causes a proportion of the foraging population to return to the hive, this returning population is mainly composed of the bees which were working farthest afield, and that having returned to the hive they do not leave it again until weather conditions improve sufficiently for them to go back to their original sites. The foraging distance of the individual bee is not apparently reduced, but the more distant foragers are the more likely to return to the hive until conditions improve.

(*c*) *Effect of tall herbage surrounding feeding place*

Some of the dishes in the experimental field were situated in the middle of nettle-beds and other rather tall herbage. Dish 95, for example, was rather hidden amongst plants growing about 2 ft. high. It was found that very few bees visited this dish and it often remained neglected, although full of syrup, even when the food supply in the other neighbouring dishes had failed. However, on 3 June several bees found this dish and thereafter it was visited quite frequently. It would appear that the earlier neglect of this and similarly situated dishes was caused not so much by the slight shade thrown by the surrounding herbage, as by the fact that this dish was somewhat hidden.

There were other local factors, such as sheep troughs, paths and fences, in the experimental field, which sometimes apparently exerted some influence on the number of bees which visited the dishes nearest to them, but little more than indications on these factors could be obtained.

(v) *Effect of nectar concentration upon number of visiting bees*

On account of frequent failures in the supply of syrup in the dishes in the experimental field during the latter part of the season, a state of affairs developed such that many bees had an interest in more than one dish. This appeared to be an excellent opportunity to test the effect of using two or more concentrations of syrup in the field simultaneously.

After several consecutive days upon which syrup of a moderately high concentration was supplied in all the dishes, the dishes were all emptied on the evening of 18 June and were not refilled until 1 p.m. (G.M.T.) on 19 June by which time the total number of bees visiting the field was small. Alternate dishes in the rows nearest to the hives and alternate groups of two and three dishes at greater distances from the hives, were then filled as quickly as possible with sugar solutions of two different concentrations (7·4 and 19·4% sugar by weight). Continuous counts were then made by three observers patrolling the field from 3.30 p.m. until 6.30 p.m., when all the dishes were emptied once again. Fig. 5 shows the results of these counts.

There is no doubt that many more bees were attracted to the dishes containing the higher concentration syrup than were attracted to the dishes containing the syrup of lower concentration. The following day all the dishes were refilled with syrup of a medium concentration (13·8% sugar by weight) and counts were made. An uneven distribution of the bees on the dishes was still observed for some hours, and in the three counts made before noon a total of 960 bees were found on the fifty-four dishes which had contained the syrup of higher concentration (19·4%) on the previous day, and 534 bees on the dishes which had contained the syrup of lower concentration (7·4%).

*The area of a crop of willow-herb visited by individual bees*

The 'fixation' of honeybees to localized artificial feeding sources as shown above supports Minderhoud's (1931) observations that individual bees restrict their feeding activities to a small area when working clover, dandelion and other crops. Buzzard (1936) also reported cases of individual bees returning at frequent intervals to one particular flower or small group of flowers. We were able to obtain data supporting these observations by studying the distribution of a population of bees visiting the flowers of willow-herb and the heads of the ornamental thistle, *Echinops*.

(*a*) *Observations on willow-herb*

The following observations provide information on the local constancy of bees working on a small area of willow-herb situated in the middle of a much greater area of this plant. On this small patch of *Epilobium* (see p. 66 for description of area) which was approximately 5 × 8 yd. in extent, being somewhat separated from the remainder of this crop, most of the bees (about 100) visiting the flowers during a period of 2 hr. were marked red. Round the central point of the area counts of marked and unmarked bees were made in annular concentric zones, each zone being 1 yd. in radial width. Fig. 6 shows that percentage of marked bees counted in each of these zones at various periods after marking.

One of the marked bees was observed near the centre of the plot in company with fourteen unmarked individuals 17 days after marking. The results, although not allowing an accurate assay of the dimensions of the 'fixation' areas of individual workers, do indicate that the majority of the bees observed restricted their activities to areas of a diameter of less than 5 yd. This can be estimated from the shape of the curves in Fig. 6 where the vertical line *A* represents the minimum distance (2½ yd.) from the centre to the boundary of the marking area. Had each bee restricted its activity to one fixed point only, the curves would show fairly horizontal portions up to the limit *A* (2½ yd.) followed by a steep and rather uniform decline to zero at *B* (4¾ yd.), the maximum distance from the centre to the boundary. From the departure of the curves, drawn from observed points, from this theoretical shape it appears that the bees did move, in fact, but only rarely more than 2–3 yd., seldom more than 5 yd. Fig. 4 also indicates that 24 hr. after marking, the bees had moved farther than they had 3–5 hr. after marking.

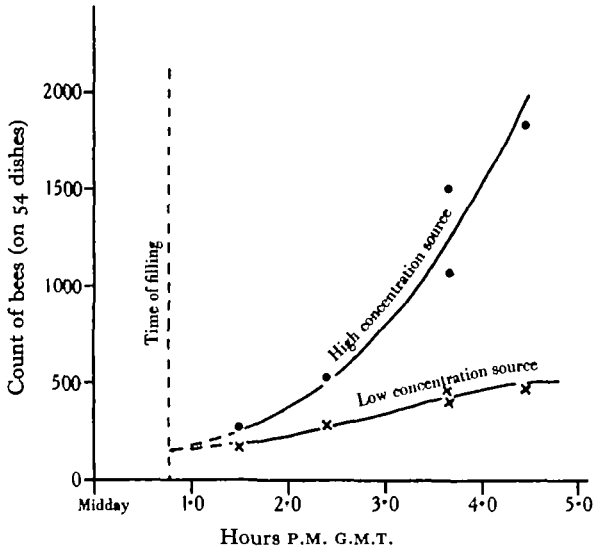


Fig. 5. Numbers of bees for a series of counts on fifty-four Petri dishes filled with 19·4 % sugar (●), and on fifty-four dishes filled with 7·4 % sugar (×), at various intervals after filling.

(*b*) *Observations on* Echinops

Observations on the local attachment of bees working isolated patches of the decorative thistle, *Echinops*, were also made. The site of these observations has been described on p. 66. The length of time spent by an individual bee on any one foraging trip on the heads of the *Echinops* plants varied between 20 and 60 min. This is very much longer than the time spent on a dish of syrup (½–1½ min.); however, the time spent in the hive depositing the *Echinops* nectar was about 3–4 min., which is of the same order as that spent in delivering a load of syrup.

By marking newcomers to three alternate plots of *Echinops* (nos. 1, 3 and 5) out of the five in the row, using different colours each day for 4 weeks, popu-

lations of marked bees built up on each plot and were remarkably constant in their attachment to their own particular plots, the individuals from which they were composed seldom visiting neighbouring plots. Bees of one marking colour were observed over periods up to 16 days, though the number of individuals of each colour present gradually decreased from day to day. After the first few days there were always more bees present which were marked with colours other than that in use of the day in question, i.e. the majority of bees present had been visiting the plot for more than 1 day.

On the two intervening plots (nos. 2 and 4) all visiting bees were caught and were not subsequently released. As a result there was always more nectar available per flower in these two plots than in the other three plots, so that bees straying to the former with natural conditions, where the time spent, per trip, in collecting from flowers is very much greater even under the most favourable conditions.

Lundie (1925), using an automatic bee counter, found that under the conditions prevailing at the time that his observations were made, the bees spent between 8 and 104 min. on any one foraging trip, according to conditions. This is in approximate agreement with the 20–60 min. periods which were our usual findings on *Echinops*, and is many times longer than the time spent on the syrup dishes.

As a consequence of the difference in the time spent by the bees on an artificial as compared with a natural source of nectar, it could be shown that only a small proportion, differing with conditions, but approximately a seventh, of the bees collecting syrup from a particular dish were present at any one time. The proportion of the fixed population present upon

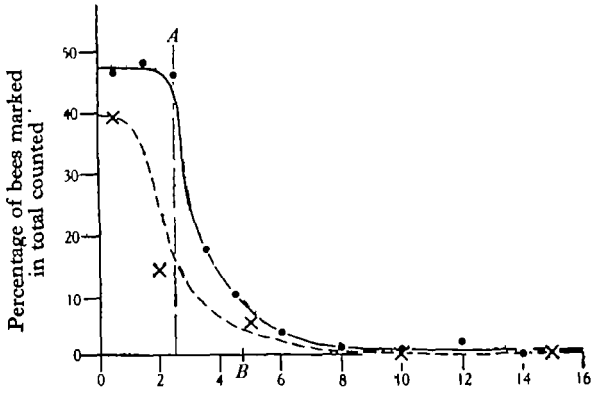


Fig. 6. Percentage of marked bees against distance from the centre of an oblong area studded with *Epilobium*, on which they had been marked previously. Each point is based on a count of at least fifty bees, usually between 100 and 200. ● = bees counted 3–5 hr. after marking; × = bees 24 hr. after marking.

tended to remain there. In view of the short distance between the plots of *Echinops* and the hives, many new unmarked bees were captured there, but the proportion of bees marked at plots 1, 3 or 5 to stray over the 18 yd. distance between plots was only of the order of 10% per day. Thus the observations made upon isolated plots of *Echinops* also revealed a considerable, but not absolute, degree of constancy of visit of the individual bee to a small area, as did the experiments with dishes and the observations on the small area of willow-herb situated in the middle of a much larger area of this plant.

## DISCUSSION

Most of the findings in this paper are self-explanatory, and practical deductions can be drawn from them. However, it should perhaps be stressed again that there is one important difference between experiments with artificial sources of nectar and experiments with natural sources of nectar; the short time spent by a bee on a dish does not correspond a given patch of flowers in good weather was always much larger, on account of the very much greater time the individual bee spends in collecting a load. This agrees with the observation that no corresponding increase in time is taken in discharging the load. However, it is difficult to estimate with any accuracy the relation between the time spent by the bees in the hive and on the crop on any given day, nor do Lundie's or other observations give any certain clue. So long as this is not known, no statements can be made as to the number of bees permanently attached to a given area, nor can any variation in local constancy of individual bees be determined.

The fact that foraging honeybees work only a limited area has an important bearing on the genetics of those flowering plants which they pollinate. If such a species is self-sterile and covers a large coherent area in great density it will still not form a homogeneous interbreeding population but rather an aggregate of small visiting systems in the sense of Wright (1921) which do not exceed a few yards

diameter. In short the local constancy of bees results in a considerable degree of inbreeding in the pollinated plants.

## SUMMARY

One hundred and twelve Petri dishes filled with sugar syrup were arranged at 20 yd. intervals from each other in a meadow. Individual bees were observed to visit one chosen dish with great regularity for one or more days, provided that the supply did not become exhausted.

Occasionally bees marked on one dish were observed to visit an adjacent dish. This occurred most frequently when the supply of syrup temporarily failed at the original site of feeding, but, even after a 3-day interruption in the syrup supply bees often returned to feed at the original site.

Bees feeding at a dish full of syrup spent only a fraction of their time (about 1 min.) per visit drinking, but several times as long flying to and from the hive and delivering their load.

When the supply of syrup in a dish became exhausted all the bees accustomed to visit that dish gradually accumulated there impatiently seeking for food; after some minutes they extended their radius of search, and many located another source near at hand. Thereafter they visited either the new source or the old, or both, when the syrup at the original site was replenished. The nearer such a new source was to the original one the more likely a bee was to find it; a dish 20 yd. away from the original site was quickly found despite the fact that such a second dish would seldom be visited if the syrup at the original site was constantly maintained.

Bees were deterred from collecting syrup from dishes placed even partially in shade; they very seldom worked beneath the shade of trees. There were even some indications that they prefered not to fly in the direction of shady trees.

Over the range of distances covered (160–400 yd.) there were always more visitors to the nearer than to the more distant dishes. The extent of this difference, however, varied from day to day. Bees accustomed to collect syrup from the dishes farthest from the hive did not move to sites nearer home when the weather became unfavourable. There was some evidence, however, that bees working a long way away from the hive were more easily deterred from foraging by unfavourable weather than those working close to the apiary.

When two different concentrations of syrup were offered in different groups of dishes simultaneously the number of visitors to the dishes containing the syrup of high concentration rose considerably higher than that of the visitors to the dishes containing low-concentration syrup; even after all the dishes had been refilled with syrup of uniform concentration on the following day, this difference remained noticeable.

Bees marked on a patch of willow-herb (*Epilobium angustifolium*) situated in the midst of a large crop of this plant, were usually recovered within 5 yd. of the point of marking. Such bees remained 'fixed' to this area for several days. Observations were made upon isolated patches of the cultivated thistle; *Echinops sphaerocephalus*, of bees which continued to visit the patches upon which they were marked for periods up to 16 days. The majority of the bees working the patches showed great constancy: and of such regular visitors the percentage per day observed to stray to other patches of *Echinops* 18 yd. away was comparatively small.

The time spent by foraging bees upon the flower-heads of *Echinops* on any one visit greatly exceeded the time spent in collecting syrup from a dish (20–60 min. as against 1 min.); but the time spent in flying between the hive and the flowers, or dish, and unloading was approximately equal in each case. Only a small proportion of the population of bees working on a particular dish could be found feeding there at any one time, whereas on a patch of flowering plants, under good weather conditions, most of the population visiting that patch would be found there at any one time. This great difference in behaviour on dishes as compared with plants must be borne in mind in any attempt to draw conclusions from dish experiments as to the behaviour of bees.

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