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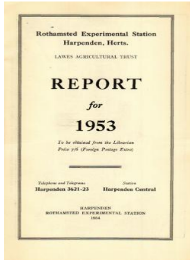
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Bees As Pollinators of Fruit and Seed Crops

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BEES AS POLLINATORS OF FRUIT AND AND SEED CROPS

By

C. G. Butler and J. Simpson

I. Introduction

It has been shown that a number of important agricultural crops require the services of insects as pollinators. Whilst this does not apply to the major crops required for human consumption, such as cereals and potatoes, it is particularly important in the case of the legumes, which play such an essential part in agricultural economy. Many other crops require insect pollination in order to produce fruit or seed, of which such horticultural crops as brassicae and orchard fruits are good examples.

It should also be mentioned that many grasses and forest trees, which rely on wind pollination, are frequently visited by large numbers of pollen-gathering bees (Synge, 1947).

Although adequate data are not yet available, it is probable that in many parts of Britain today, as a result of intensive cultivation, the number of wild pollinating insects is insufficient to ensure full production. However, the distribution of honeybee colonies is by no means ideal for this purpose, since the great majority are kept in the immediate neighbourhood of large cities and not in those areas where insect-pollinated crops are extensively grown. This state of affairs is harmful both to the farmer and to the beekeeper, whose honey yield suffers as a result of excessive competition for limited supplies of bee forage. Its rectification is, however, clearly a matter of organization rather than of research, and the research worker is more concerned with those cases where, despite the presence of bees, pollination still remains inadequate.

II. Insufficient Pollination

Many insects, including bees, visit the nectaries of flowering plants in search of food. It has been shown by Wykes (1952*c*) that honeybees prefer solutions containing sucrose, glucose and fructose to solutions of the same total concentration of any single one of these sugars. The fact that most nectars contain these three sugars in major proportions (Wykes, 1952*a*; 1953*a*) may, therefore, indicate an aspect of the mutual adaptation between plant and bee. Wykes (1953*b*) has also found that the removal of nectar from the nectaries of some plants stimulates further secretion—an interesting example of economy on the part of the plant.

In most cases the nectaries are situated within the flowers themselves and, when approaching them, the insects usually effect the pollination of the flowers concerned. Floral nectaries are probably more attractive than extra-floral ones, and also the more readily found on account of the colours and scents of the flowers. It has been shown by Oettingen-Spielberg (1949) that worker honeybees searching for new sources of food are particularly attracted to small, coloured objects. This has been confirmed by Butler (1951), who has also shown that bees will alight on such objects much more readily if suitable scents are also present. Furthermore, he has shown that bees that have been visiting a crop of scented flowers for some time will hesitate to enter them if the perfumes of the individual flowers are experimentally masked with another perfume, even with one which is normally attractive to bees. This probably explains the observation of Butler, Finney and Schiele (1943) that many bees are deterred, at least temporarily, from continuing to visit flowers when they are sprayed with insecticidal and fungicidal mixtures containing scented materials which are not, in themselves, strongly repellent to bees.

Bees are especially important as pollinating insects because, both as larvae and as adults, they are entirely dependent upon nectar and pollen for their food, and numerous visits have to be made to flowers to collect them. The branched hairs on their bodies, which enable them to collect pollen, also increase their pollinating efficiency. The honeybee is especially valuable because its colonies contain thousands of individuals which can readily be moved to those places where they are required.

Failure of bees to work on crops is often explicable by lack of nectar or by the presence of nectar which is too dilute to attract them. Some plants consistently produce nectar which, both in quantity and quality, is attractive to bees, whilst others cannot be relied upon to do so. Such variations in nectar secretion can usually be attributed to weather conditions, even to those of the previous year, through their effect on carbohydrate accumulation (Wykes, 1952*b*), but may also be affected by the availability of soil nutrients (Beutler, 1953). Ryle (1954*a*, 1954*b*) has investigated the effect of fertilizer treatment on nectar secretion in mustard, buckwheat, apple and red clover. She showed that with apple-trees the mean quantity of sugar produced per flower was significantly increased by extra potash. In sand-culture experiments with red clover, mustard and buckwheat, in which the levels of nitrate, phosphate and potash were varied, any treatment which checked growth at flowering, apart from a shortage of potash, increased the yield of nectar. However, with the clonal material used in the red-clover experiments, it was found that the differences caused by the fertilizers were small in comparison with those between clones. This suggests that it may be possible to select strains of red clover which, whilst retaining their present good vegetative qualities, will also have improved nectar-secreting properties.

It is also possible for flowers to contain nectar which is not available to all pollinating insects. Thus inadequate pollination of red clover by honeybees can be due to the long corolla-tubes of the flowers of this plant, which make it difficult, if not impossible, for the bees to reach the nectar unless it is very plentiful. The longer-tongued species of bumblebees, such as *Bombus agrorum* and *B. ruderatus*, are better able to pollinate this plant, but the short-tongued species, such as *B. terrestris* and *B. lucorum*, are often actually harmful, since, by biting holes at the bases of the corolla-tubes, they obtain the nectar without making contact with the stamens and stigma, and enable honeybees to do likewise. These facts have recently been verified by Free (1952). Ribbands (1951) has shown that in order to obtain maximum pollinating efficiency colonies of honeybees should be placed as close as possible to the crop, since the amount of foraging in bad weather is considerably reduced when the bees have to fly even short distances.

Numerous cases have been recorded of crops which would otherwise be reasonably attractive to bees being neglected in favour of still more attractive crops, which have sometimes actually been weeds. For example, Vansell (1942) has described a case of competition, a multiple case, between the flowers of apple, peach, nectarine, plum, sour cherry, winter Nelis pear and Bartlett pear, in which the two varieties of pear were almost completely neglected by the bees present in favour of the apple and other flowers. Butler (1945*a*) has described similar cases of competition between pear and hawthorn, in which the pear blossom was neglected in favour of the hawthorn, and also between greengage and dandelion, in which the dandelions received the bulk of the bee visits. Hammer (1949) showed that red clover, even when it was yielding nectar well, was liable to be deserted in favour of mustard, lucerne or carrot. He found that this difficulty could be overcome by providing more bees than the competing crops could carry.

Bees foraging for nectar may in some instances be ineffective as pollinators if the floral structure permits them to reach the nectaries without touching the stamens and stigma. Thus some varieties of apples have long, erect stamens beneath which bees can crawl to reach the nectaries. In the case of flax many bees learn to approach the nectaries by thrusting their tongues between the petals from the back of the flower (Gubin, 1945), in which behaviour they are possibly encouraged by the fact that flax petals are extremely loosely attached and perhaps do not provide an adequate support for a bee (Simpson, 1949). In the same sort of way nectar-gathering honeybees rarely accomplish the tripping of lucerne flowers, which is necessary for their pollination, having learned to obtain the nectar without thrusting their heads into the corolla-tubes (Tysdal, 1940). Honeybees often take a little time to learn such irregular methods of obtaining nectar (Butler, 1949), and Dadant (1951) has suggested changing the colonies on the crop regularly to reduce the effects of such learning.

Extra-floral nectaries on plants also allow insects to obtain nectar without effecting pollination. It is surprising, therefore, that in some plants, such as the field bean and cotton, such nectaries are active at the time of flowering.

Where it is sufficiently abundant, pollen of itself may attract pollinating insects. This occurs with a few nectarless plants such as poppies. Since pollen-collecting bees almost invariably pollinate the flowers which they visit, most pollinating difficulties could be overcome by increasing the number of bees gathering pollen from the crop. This can be done by increasing the total bee population in the district. About one colony of bees per acre is usually sufficient to ensure the pollination of crops where nectar-gatherers are the effective agents (Hutson, 1926), but advantages have been shown in increasing this number to three to four per acre in the case of red clover, from which the bees often obtain insufficient nectar (Hammer, 1950), and to five per acre with lucerne, where nectar-gatherers do not pollinate the flowers (Dadant, 1951).

Many more individuals are usually necessary to gather the nectar required by a colony of honeybees than are required to collect its pollen. It follows, therefore, that if the population of honeybees in any given area is increased, until the number of pollen-gathering bees is sufficient to pollinate a given crop, the colonies used are unlikely to give a satisfactory return of honey and may even require to be fed. The economics of this system of ensuring pollination in any particular instance should, therefore, be carefully examined. The females of many solitary bees, for example *Megachile* sp., are mainly concerned with pollen collection when foraging, and are, therefore, probably more useful as pollinators of crops such as lucerne (Franklin, 1951), from which honeybees can obtain nectar without effecting pollination. Attempts have already been made in America to propagate *Nomia melanderi* for this purpose (Menke, 1952); otherwise this possible method of solving the problem appears to have received little attention.

The possibility of varying the proportion of pollen to nectar loads collected by honeybee colonies has been considered. There is some evidence that this can be done by creating a pollen shortage in the hive by using a pollen trap to remove pollen from the legs of returning foragers (Hirschfelder, 1951; Lindauer, 1952). Most traps, however, remove only about 20 per cent of the loads of pollen brought in by bees, and although a trap which removes as much as 75 per cent has been produced at Rothamsted, the obstruction which it causes reduces the foraging level of the colony excessively. Unless this difficulty can be overcome, it seems improbable that pollen trapping will prove to be useful in this respect. Pollen collection may also be increased by adding to the amount of brood in the colony, but this, too, involves considerable beekeeping difficulties.

III. Cross-Pollination

Many plants of considerable economic importance are wholly or partially self-sterile, or possess mechanisms which hinder self-pollination. It is important, therefore, that pollinating insects should carry pollen from plant to plant.

Individual honeybees do not forage over the whole of the area within flight range of their hive, but tend to return continually to a small part of this area (Müller, 1882). This type of behaviour is also shown by other insects (Minderhoud, 1951), and may well be a characteristic of foraging animals in general. Individual bees also frequently restrict their activities, at least for a time, to the flowers of one of several available species of plants (Aristotle).

It is obviously desirable that the foraging areas of individual honeybees should be large where the transference of pollen between trees, often between widely separated trees (as in orchards interplanted with compatible varieties), is necessary; and that they should be small where transfer of pollen between adjacent plots, as when growing seed of compatible varieties of brassicae, must be avoided.

Butler (1943) described honeybees restricting their foraging on a crop to areas of 5 yards or less in diameter, and the existence of foraging areas of similar size was deduced by Crane and Mather (1943) from a study of the distances necessary for isolation between crops of different varieties of radish. It was pointed out by Butler (1943) that bees foraging in such small areas cannot be responsible for cross-pollination in orchards, and, since the necessary transfer of pollen between trees does occur, he postulated (1954*b*) the existence of an additional " wandering " population of bees. He considered that these were probably mainly young bees which had not yet found satisfactory foraging areas. It was known, however, that bees tend to extend their foraging areas and to wander when the crop on which they have been foraging begins to fail. Thus in an experimental field, which extended over a considerable area, in which artificial flowers (dishes of syrup) were spaced 20 yards apart from one another, Butler, Jeffree and Kalmus (1943) found that honeybees which were accustomed to collect food from particular dishes moved elsewhere when the supply of syrup in these dishes failed, but, nevertheless, returned from time to time to these dishes and examined them. If the supply of syrup was subsequently replenished and maintained, the bees would often be found to have enlarged their original foraging areas to include several dishes, some of which they visited only occasionally. Similarly, Ribbands (1949) found that honeybees that were gathering pollen from Shirley Poppies spread their activities over a greater number of flower-heads as the supply of pollen became exhausted. From this and other observations with different crops he came to the conclusion that the size of a honeybee's foraging area is liable to continuous change, and is dependent at any given moment on the extent to which she is satisfied with the return for her foraging activity. Since von Frisch (1934) has shown that such satisfaction is related to the previous foraging experience of a bee, it is probable that as different bees have had different experiences they are liable to be variously satisfied, and Ribbands (1949) has concluded that one is likely to find a wide range of sizes of foraging areas amongst any population of honeybees working on any crop at any given time. Thus both Butler and Ribbands agree that the sizes of the foraging areas of individual bees vary from time to time, but explain this phenomenon in different ways.

Butler (1945) supposed that the proportion of " wandering " bees could be raised by increasing the density of bees on the crop, but Ribbands (1953) has concluded that the effect of competition on the sizes of foraging areas is unpredictable from the available evidence. This problem, which clearly has an important bearing on orchard pollination, still remains to be solved experimentally.

IV. The Directing of Honeybees to Crops

Von Frisch's (1925) discovery that successful foragers are able to communicate the scent of the flowers from which they have been gathering food to other bees has led to attempts to direct honeybees to crops which need to be pollinated. The method used has been to feed syrup, containing the scents of the flowers of the crops requiring to be pollinated, to colonies of bees.

Foragers that are seeking food are attracted to flowers by their movement (Wolf, 1937) and by their colour and scent (Butler, 1951). Ribbands (1949) has demonstrated that when a honeybee knows of more than one source of food she appears to select the best

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of these at any given time, and von Frisch (1946) has shown that she is able to communicate to other members of her colony the positions of any of these sources.

Close observations suggest that colonies of honeybees possess very effective methods of finding and exploiting the best of the crops within their foraging range, so that although it might be possible to mislead them into pollinating one of the poorer crops, no increase in honey yield could result from this procedure. However a colony's methods of finding the best crops available do not, in fact, appear to be as effective as one might expect them to be, as it has been noted that colonies in the same apiary will frequently collect the bulk of their food from very different sources (Synge, 1947). It has also been shown that colonies of bees that have been moved to a heather area before the heather flowers have opened, and have commenced to forage on other kinds of flowers, have failed to transfer their activities to the much more abundant heather flowers when these became available (Moore-Ede, 1947). It seems possible, therefore, that when colonies of bees are directed to crops to pollinate them their honey yields may occasionally be increased.

In early practical experiments to direct bees to crops Russian workers, such as Veprikov (1936), claim to have obtained considerable increases in the number of bees visiting the experimental crops and in the amount of seed produced. However, later investigations by von Frisch (1947) produced less definite results; in his experiments the number of honeybees foraging on the experimental crops appear almost invariably to have been increased, but the figures obtained for set of seed, and for seed yield at harvest, are less satisfactory. On crops other than red clover increased honey yields (allowance being made for the sugar fed) were obtained. In the case of red clover, however, the effects on honey yield were not significant. This suggests that although von Frisch was successful in directing the bees to red clover, they were unable to obtain any more nectar from these flowers than they would have done from others.

Von Frisch (1947) pointed out that directing bees to crops from which they cannot obtain nectar is not likely to result in much additional pollination of the crop. He, therefore, suggested that in such cases it might be possible, and more profitable, to attempt to direct pollen-gathering bees to the crop rather than nectar-gatherers, by feeding syrup scented with the pollen of its flowers. Unfortunately, experiments at Rothamsted to direct bees to red-clover crops, by feeding red-clover pollen in syrup, have produced no evidence that the proportion of pollen gathered from red-clover flowers can be increased by such treatment.

Von Frisch (1947) also showed that it is more effective to feed scented syrup to bees outside the hive than inside. Some unpublished observations by Butler suggest that this may be due to the very much greater tendency of bees that have collected food in the light to perform recruiting dances, and also that intermittent feeding is likely to be more effective than continuous feeding, as most of the dances are performed by the first few bees which visit the feeder.

V. Use of Honeybees as Pollinators in Particular Instances

(a) *Orchard pollination*

Brittain *et al.* (1933) have pointed out that the number of colonies of honeybees required to yield the necessary proportion of bees to flowers in an orchard depends on many factors, including, of course, the area of the orchard and also the amount of bee forage, other than that provided by the fruit-trees, available in and around the orchard. Butler (1948) recommended that a group of colonies should be placed in the centre of each 15–20 acres or orchard. Although the validity of the suggestion that this method of placing the colonies increases the degree of competition between the bees and also increases their tendency to wander from tree to tree, and thus to effect cross-pollination, has not yet been adequately demonstrated, there is no doubt that it possesses certain advantages. By keeping the colonies away from the edges of the orchards it probably reduces the tendency of the bees to forage outside them, and further it enables the grower to determine, over a period of time, the number of colonies of a given strength necessary to produce an adequate set of fruit, since if an insufficient force of bees is present the set of fruit falls off at some distance from the hives, and when an even set of fruit has been obtained throughout an orchard the force of bees is probably correct (Butler, 1942). Grouping of the colonies together is also advantageous to management both by the beekeeper and the grower. In spite of Ribbands' (1951) observations of the large diminution of foraging in bad weather with increased flying distance, it is unlikely that the method of locating colonies suggested by Butler (1948) will result in any serious diminution of foraging activity, since the radius of a circle of an area of 20 acres, in the centre of which it has been suggested that the colonies should be placed, is only 176 yards. Larger groupings, however, are undesirable.

(b) *Pollination in confined spaces*

Colonies of honeybees are sometimes used to cross-pollinate such crops as peaches in glass-houses (Thompson, 1940). Unfortunately, however, although honeybees have been found to be very satisfactory for such purposes, and to save much manual labour, the condition of the colonies used tends to deteriorate very rapidly and the foraging force to diminish during the first few days of confinement to the house, on account of many of the bees dying in attempts to escape. However, the young bees which replace the original foragers show a much reduced tendency to behave in this way.

Recently colourless nylon screen-cages have been found useful in work on the pollination of red clover and other crops, as well as for work on the breeding of brassica varieties. It has been found at Rothamsted that bees behave well in these cages and that normal plant growth is maintained within them. Indeed it seems probable that this type of cage may prove extremely valuable in plant breeding.

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