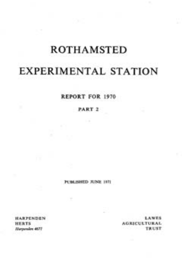
Rothamsted Experimental Station Report for 1970 Part 2



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J. B. Free (1971) *Management of Honeybee Colonies for Crop Pollination ;* Rothamsted Experimental Station Report For 1970 Part 2, pp 184 - 198 **- DOI: https://doi.org/10.23637/ERADOC-1-34808**

Management of Honeybee Colonies for Crop Pollination

J. B. FREE

Butler and Simpson (1953) reviewed fundamental work done at Rothamsted on the foraging behaviour of honeybees, especially in relation to nectar secretion. More recent studies of this type are discussed by Free (1970a). This review deals with the use of honeybee colonies to increase seed or fruit production.

Pollination requirements of crops

The extent to which insect pollination increases the yield of a crop differs greatly with different crops. A standard method of determining whether a crop benefits from insect visits is to compare the yields of plants that are : (a) covered by nylon screen cages containing honeybee colonies, (b) covered by cages to exclude insects and (c) not caged.

Insect pollination of some species produces either no increase in yield or such a small one as to be difficult to demonstrate. Thus, the average yield of *Brassica napus*, caged with bees, not caged, and caged without bees was respectively 806, 729 and 714 seeds per plant with a mean weight of 2·85, 2·98 and 3·05 g per 1000 seeds (Free & Nuttall, 1968a). Similarly, *Brassica juncea* produced a mean of 2727 seeds per plant when caged with bees, 2403 when not caged and 2302 when caged without bees (Free & Spencer-Booth, 1963a), and *Phaseolus vulgaris* plants produced a mean of 45 seeds of 0·64 g mean weight when caged with bees and 40 seeds of 0·61 g mean weight when caged without bees (Free, 1966a).

Other species yield substantially more with than without insect pollination. For example, *Brassica alba* produced a mean of 486 seeds per plant when caged with bees and 213 seeds per plant caged without bees (Free & Spencer-Booth, 1963a). *Vicia faba* also produced more seeds per plant when caged with bees than when caged without bees (broad beans, 23·9 : 15·1 respectively; field beans, 18·1 : 14·5 respectively; Free, 1966b). More *Fragaria x ananassa* flowers visited by bees than isolated from bees set fruit (65·5 : 55·7% respectively, Free, 1968a).

Some species cannot produce even a moderate crop without insect pollination; thus, *Phaseolus multiflorus* produced only 30 seeds per plant when isolated from bees but 206 seeds per plant when caged with bees (Free, 1966a; Free & Racey, 1968a) and *Helianthus annuus* heads isolated from insects set little or no seed (Free & Simpson, 1964).

Some species (e.g. *Ribes nigrum*, Free, 1968b) yield similarly whether cross-pollinated or self-pollinated, but others set fruit or seed only when they receive pollen from another clone or variety, and still others yield more when cross-pollinated. Thus, cross-pollination between heads of different plants of *Helianthus annuus* produced more seed than pollination between different heads of the same plant (45 and 24% set respectively) (Free & Simpson, 1964). Many varieties of *Prunus* and *Pyrus* are well known as needing cross-pollination. Despite suggestions to the contrary, it has been confirmed that insects are mainly responsible for transferring pollen from pollinizer to main variety trees and wind plays little or no part in doing so (Free, 1964a).

The pollinating efficiency per bee visit is usually less for species or varieties needing cross-pollination than for those that set well with self-pollination, because on many visits the insects do not carry compatible pollen. Thus, visits by single bees set fruit on only 11% of *Pyrus malus* flowers, var. 'Cox', which need cross-pollination, whereas they set 57% of 'James Grieve', which often sets well when self-pollinated (Free, 1966c). Many bee visits to *Trifolium pratense* flowers, which are almost completely self-sterile, also fail to cross-pollinate and set seed (Free, 1965a).

Insect pollination sometimes has advantages in addition to increased seed or fruit yield. Thus, bee visits not only increase the set of *Fragaria x ananassa* flowers but also produce larger berries and give fewer malformed berries (Free, 1968a). Pollination by bees can also produce an earlier and more uniform harvest. For example, although Riedel and Wort (1960) found no effect of bees on total yield of *Vicia faba* (field beans), the plants with bees produced more pods from flowers on low than on high nodes. Free (1966b) also found this effect with broad beans. Bees both increased the number of pods produced by *Phaseolus multiflorus* and the proportion of early maturing ones (Free, 1966a).

Although experiments with caged honeybees are useful in determining the pollination requirements of crops, the results sometimes underestimate probable yields when colonies are taken to a field of the crop, because caged plants often yield less than uncaged ones. This is partly because colonies confined in cages become increasingly inactive and forage less, so plants in the open plots are visited more freely by pollinating insects. This inertia can be avoided to some extent by confining the bees in the cages on alternate days only (Butler & Haigh, 1956), or by allowing most of the foragers of a colony continuous free range while diverting a few into the cages at intervals throughout the day (Free, 1966a). However, because bees do not cleanse their bodies thoroughly of pollen between foraging trips (Free & Durrant, 1966), the latter method is inadvisable when caged bees are being used for controlled plant breeding. Indeed, part of the reason for plants in the open plots yielding more may be that they are not restricted to pollen from one, or a few, sources.

Excluding bees from plants without otherwise altering the environment is impossible and the cages themselves can produce large differences in plant growth and yield. Diminished light in cages makes potential yield smaller and diminishes the benefit of insect pollination (e.g. *Vicia faba*, Free, 1966b). Prolonged flowering in cages without bees probably indicates that the plants concerned could bear more seed than that already set. Caging must also make wind pollination less likely.

However, cage experiments may also overestimate the yield response likely in the open. Sometimes this may be because caged honeybees can only visit the, possibly relatively unattractive, flowers in the cages, whereas those outside can choose any more attractive ones that are present. Also, honeybee visits may sometimes be more efficient in the cages than in the open field. Honeybees in the field often obtain nectar through holes bitten by 'robber' bumblebees (e.g. *Bombus lucorum* and *B. terrestris*) in the bases of flowers with long corolla tubes (e.g. *Trifolium pratense*, *Vicia faba*) and fail to pollinate the flowers. They cannot make such holes themselves, so in cages they must enter the flowers and thereby pollinate them. Although most honeybees fail to pollinate *Phaseolus multiflorus* flowers in the field (Free, 1968c), they are efficient pollinators in a glasshouse and produce an earlier and more profitable crop (Free & Racey, 1968a).

One method to avoid the difficulties associated with caging plants is to bag individual flowers or flower heads, except during periods of observation when any bee visits are recorded, and to determine later whether these visits have increased the set (Free, 1965a, 1966c). However, this can be done only with flowers that are easily bagged without damage and, although it shows the effect of insect pollination on the set of individual flowers or flower heads, it does not give information on the effect of increased pollination on the yield of the plant as a whole.

Whatever method is used, some flowers should be hand-pollinated (e.g. Free, 1964a, 1966c) to know what is the maximum set possible in the prevailing conditions. Hand-pollination of experimental plots in a sample of fields can be used to find whether inadequate pollination is a factor limiting yield (Butler *et al.*, 1956).

Although blowflies and bumblebees can sometimes be used to pollinate plants in glasshouses or cages (Free & Racey, 1968a), economic methods of using wild bees to pollinate field crops have yet to be developed, although some preliminary tests have given interesting results (see Free & Butler, 1959; Butler, 1965; Free & Williams, 1970a). At present the honeybee is the only pollinating insect that is readily obtainable in large numbers when required. However, taking honeybee colonies to crops will rarely give such large increases in yield as exist between caged and uncaged plots because there are often many insects, including other honeybees, already visiting the flowers. The need for a grower to hire honeybee colonies depends on many factors including the attractiveness of the crop to honeybees and their ability to pollinate it, the number of other insects usually present, and the probable increase in yield from insect pollination. All these factors will differ with different species of crop. For example, Free (1968d) found that honeybees were usually more numerous than bumblebees on *Rubus idaeus*, although their numbers fluctuated more, whereas bumblebees were the more abundant on *Ribes nigrum*. Although many types of insects, especially Diptera, visited *Fragaria x ananassa* flowers, honeybees were scarce and tended to be limited to good weather. Hence, unless a *F. x ananassa* plantation is large, it might not be economically worthwhile for a grower to hire honeybee colonies. However, honeybee colonies can profitably be employed in glasshouses to obviate the need for laborious hand-pollination. If blowflies prove to be as efficient pollinators as honeybees in glasshouses, they would perhaps be even more convenient and economical.

Because of their structure and behaviour, bees are better pollinators than other flower-visiting insects, which often fail to transfer pollen. Correlations have been obtained between honeybee abundance on different parts of a crop and the yield obtained (e.g. Free, 1962a). Even when honeybees are much fewer than all other insects, they may be responsible for most of the pollination (Lewis & Smith, unpublished).

It is commonly supposed that the number of wild pollinating insects has been greatly diminished by changes in farming practice, including increased use of insecticides and herbicides. Partly because of this supposition the demand for honeybee colonies for pollination has increased and will probably continue to increase as the value of bees becomes more widely appreciated. However, the number of honeybee colonies in England and Wales has decreased greatly; by about 30% during the last decade alone. Hence, it is important that the remaining colonies should be used as efficiently as possible and protected from insecticides. It is perhaps significant that, despite frequent spraying of orchards, which growers recognise need insect pollination, bees are rarely poisoned in them, and most bee poisonings are attributable to spraying of *Vicia faba* (field beans) (Needham & Stevenson, 1966; Needham *et al.*, 1966), where the need for bee pollination is neither so obvious nor so well appreciated.

Number of bees needed

Although small colonies are more useful for pollination than was previously suggested (Free & Preece, 1969), large colonies have greater foraging populations at all times and are to be preferred. Hence, it is sometimes advantageous to feed colonies supplementary protein and carbohydrate (e.g. Butler *et al.*, 1952; Spencer-Booth, 1960; Free & Spencer-Booth, 1961) to encourage their growth in time for the flowering of crops needing pollination.

It is difficult to advise on the number of colonies needed for a given area of crop. Any estimate must take into account the size of the colonies, the attractiveness of the crop, the density of flowers, the amount of nectar and pollen, the number of pollinating insects including honeybees already present, the behaviour of bees on the crop and, of course, whether the flowers need cross-pollination.

In parts of the world where it is dry, warm and sunny during the flowering of a crop, the seed and fruit set can be correlated with the number of bees foraging per unit area, so that growers in these places know whether to increase the bee population by importing further colonies (Free, 1970a). The weather in Britain, which often prevents foraging, or makes the flowers unattractive, for long periods, precludes such assessments, and it is usually necessary to provide enough colonies to ensure adequate pollination when pollination is possible during only a part of the flowering period. Such estimates (Free, 1966c, 1970a) suggest that recommendations of 2½ colonies per hectare of well-planned orchard (e.g. Ministry of Agriculture, Fisheries and Food, 1962) are probably justified.

Wherever possible bees should be abundant soon after flowers open, because the viability of flowers of many species (e.g. *Trifolium pratense*, Free, 1965a) rapidly diminishes as they age.

Attempts to increase bee visitation to crops

Examining the pollen loads of successful foragers shows that very few honeybee colonies forage on anything like the maximum number of flower species visited by bees in their neighbourhood (Synge, 1947; Free, 1959). Colonies in the same location differ greatly in the number of flower species they visit, and some may visit twice as many as others. The differences between colonies usually show in species that provide only a small proportion of their total pollen requirements, but sometimes a colony will forage extensively on a species that neighbouring colonies rarely visit. However, the principal species on which bees forage tend to be visited to some extent by all colonies. Whereas these differences seem partly to depend on the preferences of bees for specific pollens, which exist even when the pollens are presented in glass dishes in the hive (Synge, 1947), they also depend on the previous foraging of the colony.

During a single foraging trip most bees (usually over 90%; see Free, 1963) visit only one species, but only about half the foragers remain constant to the original species for a week or more. The actual percentage that keeps constant differs in different conditions and with different colonies, but bees that collect the most common pollen tend to be the least likely to change, probably reflecting its greater attractiveness and abundance. Presumably changes from one species to another reflect changes in their qualities and the differences in specific constancy found in different experiments reflect differences in foraging conditions. However, when pollen is temporarily unobtainable from the species they are visiting, most bees stop foraging or collect nectar only, at least for a time, rather than collect pollen from another species. Hence, bees are reluctant, but not unable, to change species and this temporary fixation, together with adaptability over a longer period, seems to explain their rate of change (Free, 1963).

The behaviour of individual bees is reflected in the behaviour of the colony as a whole, and, although the amount of pollen of a given species that is collected by the colonies of a group often remains relatively constant over a short period, changes do occur. Thus, a colony that has collected only relatively small amounts of pollen from one species at an early stage of its flowering may eventually collect more of it than its neighbours, and, conversely, those that originally collected much of their pollen from one source may later collect only little from it (Free, 1959).

When colonies are taken to a crop before flowering has begun, most of the foragers become conditioned to visiting other flower species in the locality, and will not readily forsake them when the crop requiring pollination comes into flower. It has been found that the proportion of foragers visiting a crop can be greatly increased by not taking the colonies to it until it has begun to flower. Crops used in these experiments include *Vicia faba*, *Papaver somniferum*, *Prunus persica*, *Prunus avium*, *Pyrus malus*, *Lotus corniculatus*, *Medicago sativa*, *Trifolium pratense* and *Brassica nigra* (Free, 1959; Free *et al.*, 1960; Free, 1965b).

However, although colonies moved to a new site exploit a crop that has recently come into flower more than do colonies that were there previously, sometimes they continue to visit species they visited at the old site (Free, 1959; Free, 1963). The species to which a bee changes at a new site is also sometimes influenced by the species previously visited; thus, moved bees that had previously collected Cruciferous pollen, but not *Brassica alba* collected more *B. alba* pollen than bees that had collected other pollen. The actual amount of a given pollen that a colony collects after being moved is sometimes related to the amount collected previously. The odour of the food stores in a colony also plays a part in determining the species the foragers will visit, although a less important one than the previous experience of the foragers (Free, 1969). The interaction of these factors determines the extent to which a moved colony concentrates on the crop needing pollination.

A crop may be less attractive than others further away, and the proportion of bees from colonies that visit it sometimes then decreases rapidly (Free & Smith, 1961). The adaptability of bees to better forage (Ribbands, 1949; 1955) and their short foraging lives (Free & Spencer-Booth, 1959), probably explain this decrease. Delaying taking colonies to such crops until they are in flower, is relatively even more advantageous because it ensures that pollination will be considerable before its bee population greatly decreases.

A flower presents most of its pollen at a time of day characteristic of its species (Synge, 1947). Thus, *Taraxacum officinale* presents most of its pollen during the forenoon and *Pyrus malus* during the afternoon. When both are flowering in the same area, *T. officinale* is a severe competitor to *P. malus* for bee visits (Free, 1968e). It has been found that more bees become conditioned to collecting *P. malus* pollen when colonies are prevented from foraging until the afternoon of the day they are taken to a *P. malus* orchard than when they are allowed to forage early in the morning (Free & Nuttall, 1968b).

The same principle probably applied to other crops (e.g. *Pyrus communis*, *Prunus persica*, *Trifolium repens* and *Vicia faba*) that present their pollen mostly or exclusively in the afternoon. Delaying release of the bees until the afternoon might be especially useful in inducing them to visit *Vicia faba*, a species they are often reluctant to work (Free, 1964b) although they sometimes do so enthusiastically, presumably when there is no competition from other flowers (e.g. Free *et al.*, 1967).

Attempts to induce bees to visit certain crops by feeding them with sugar syrup in which flowers of these crops have been immersed have failed at Rothamsted (Butler and Simpson, 1953; Free, 1958). Attempts to increase pollination of *Vicia faba* and *Pyrus malus* by spraying these crops with sugar syrup have also been unsuccessful (Free, 1965b) and, although spraying increased the number of bees collecting the syrup, fewer collected nectar and pollen, partly because many were diverted to collect syrup and partly because the anthers were wet. In the *P. malus* orchard spraying syrup actually decreased set.

Although the amount and concentration (Butler, 1945) and the composition (Wykes, 1952; 1953) of nectar present, and the amount of pollen (Synge, 1947) may be largely responsible for the greater attractiveness of some species or varieties of flowers than others (see Free, 1970a), other factors may also be important. Thus, Synge (1947) found that *Trifolium repens* pollen was preferred to *Trifolium pratense* pollen when taken from the flowers and presented to the bees in equal quantities, presumably because it had a more attractive odour. Perhaps differences in the attractiveness of odours in the nectar or floral parts of different species may also be important in determining the extent to which they are visited. The Nasonov scent gland of the worker honeybee is in a fold between its 5th and 6th dorsal abdominal tergites. Bees collecting water (Free & Williams, 1970b) or a plentiful supply of nectar and syrup (Free & Racey, 1966) often open these glands, especially at sites without any visual or scent orientation marks (Free, 1968f). The odour produced attracts other bees (Free & Butler, 1955), including scout bees and searching bees, to the source and stimulates them to alight (Free, 1968f) thus resulting in increased exploitation of the crop. Indeed, an experiment by C. R. Ribbands and J. B. S. Haldane (Butler, 1955), designed to assess the accuracy of crop communication, showed that body odour played an unexpectedly large part in attracting recruits to the immediate vicinity of foragers. Nasonov gland odour consists of geraniol (about 97%) and both isomers of citral (about 3%), and a mixture of these is about as attractive to foraging bees as the Nasonov gland odour itself (Butler & Calam, 1969). Therefore, Nasonov gland odour on flowers would probably attract 'scout' bees to them, in addition to the recruits directed to the flowers by the dances of successful foragers. Hence, if the Nasonov gland odour or attractive floral odours could be synthesised and applied economically, they might be used to increase the number of bees visiting agricultural crops that need pollination.

Foraging areas of colonies and their distribution in a crop

The distance bees have to fly to reach a crop is another factor that determines its attractiveness. When Ribbands (1951) sited groups of colonies at the edges of crops in flower and 0·6 km and 1·2 km away from them at places where there was little or no other forage, the amount of honey stored in the colonies decreased with increasing distance from the crop. This effect was greater during poor foraging weather (when bees tend to confine their foraging near their hives (Butler *et al.*, 1943), and sometimes, under such conditions, colonies at the crop gained weight while those in the other groups lost it. Hence, taking colonies to a crop is important in determining the number of bees that forage. It is also important in shortening the time spent flying between crop and hive, and so increasing the proportion of time bees spend in actual foraging. Because pollen loads are usually collected quicker than nectar loads (Ribbands, 1953), a pollen-gatherer spends more of its foraging trip in travelling to and fro; hence shortening the distance between the hive and crop benefits pollen-gatherers more than nectar-gatherers.

The optimum foraging range of colonies should be considered when determining their distribution on a crop. Individual bees tend to select the most favourable forage they find near their hives, this is reflected in the foraging areas of their colonies, and needs considering in trying to ensure an even distribution of foraging bees on a crop. It is convenient for both grower and beekeeper to put colonies in as large groups as possible, but when groups are too far apart foraging bees are concentrated near their hives,

https://doi.org/10.23637/ERADOC-1-5

especially during bad foraging weather, and there are few remote from them. An uneven distribution of foragers can be reflected in crop yield. When colonies in fruit orchards are put in small equidistant groups of four or five colonies, at the rate of 2½ colonies per hectare, the foraging area of adjacent groups overlaps enough to ensure a uniform distribution of foragers (Free & Spencer-Booth, 1963b). Foraging populations also decreased with distance from their hives on a field of *Brassica alba* (Free, 1970a) but the more advanced stage of flowering of one part of the crop also had a pronounced effect. The optimum size, for both grower and beekeeper, of the groups to be used will probably depend on the species of crop, and the many factors that may influence size and location of the foraging areas of colonies need further study. For example, Lewis and Smith (1969, and unpublished) found that more bees and other insects visited *Pyrus malus* in the shelter of large windbreaks than elsewhere in an orchard; whether this distribution reflected the greater amount of nectar and pollen in the shelter, or the effect of the shelter itself, remains uncertain.

In a glasshouse, bees also prefer to forage near their colonies, and with one colony the bees are more evenly distributed when it is near the centre of a glasshouse than at one end. With two colonies, it is best to place them near diagonally opposite corners of the house to counteract the tendency of bees to work along rather than across the rows (Free & Racey, 1966).

Foraging areas of individual bees and orchard planning

A bee does not travel far over a crop while foraging, and all its flower visits during a single foraging trip may be within an area of a few squares metres (e.g. *Vicia faba*, Free, 1962b; *Helianthus annuus*, Free, 1964c; *Rubus idaeus*, Free, 1968d). The size of the area over which a bee forages during a single trip depends on many factors including the distance the plants are apart, the number of flowers per plant, the stage of flowering, their nectar and pollen production, weather; also on the number of pollinating insects, because this affects the food supply and the likelihood of them disturbing each other. However, a foraging trip usually comprises visits to several individual plants, so ensuring that pollen is transferred between plants needing cross-pollination. The tendency of bees to visit only a few of the flowers that are open on a plant helps achieve this. Thus, on average, a bee visits about 22 florets per *Helianthus annuus* head (Free, 1964c), about 20% of the florets on a *Trifolium pratense* head (Free, 1965a) and about 13% of the open flowers on a *Fragaria x ananassa* plant (Free, 1968d).

However, when the plants are large (e.g. fruit trees and bushes) the spread of an individual bee's foraging may be a factor limiting cross-pollination. In fruit orchards of standard trees a bee visits an average of only about two trees per foraging trip and moves between trees are usually between adjacent ones. When the distance separating rows is greater than that separating trees within a row, the bees tend to move along rather than across the rows (Free, 1960). This suggested that main variety trees needing cross-pollination that were next to a pollinizer variety would be better pollinated than trees further away. Observations in orchards of *Pyrus malus*, *Pyrus communis*, *Prunus avium* and *Prunus domestica* confirmed this and showed that fruit set often decreased greatly as the distance between pollinizer and main variety trees increased (Free, 1962a; Free & Spencer-Booth, 1964a). Further, the sides of main variety trees facing pollinizer trees often had a greater fruit set, more seeds per fruit, and more carpels with seeds per fruit than the far sides. Parts of trees containing cut branches of a pollinizer variety set better than parts without such 'bouquets'. These differences not only reflect the short movements of the individual foragers but also indicate that, when a bee moves from a pollinizer to a main variety tree, it probably pollinates only the first few flowers it visits; presumably the compatible pollen on its body is soon either packed into its corbiculae or greatly diluted with main variety pollen. In some orchards bees were more abundant on the south than on the north sides of the trees; partly because of this, perhaps, the set was also sometimes greater on the south side. In an orchard of dwarf pyramid *Pyrus malus*, most bees visited flowers in only about 9 m of a continuous row during one foraging trip and few changed from one row to another (Free & Spencer-Booth, 1964b). Because of this, set was greater on rows adjacent to a pollinizer row than on rows further away (Free & Spencer-Booth, 1964a; Free, 1966c).

In many of the orchards studied the average set was less than that necessary to obtain a good commercial crop. Pollination could be increased either by increasing the foraging areas of the individual bees, or by arranging the planting of the orchards to take the sizes of the foraging areas of the bees into account. Increasing the number of colonies in an orchard, and hence competition between the bees, might seem likely to increase the distances bees travel, but there is no evidence that it does (Free, 1966d). Because it might lead to a greater proportion of the bees foraging elsewhere, it could be wasteful, and it seems preferable to allow for the limited foraging areas of bees when planting orchards. Grafting scions of pollinizer varieties on the main varieties, is one way of getting a maximum and even set on each main variety tree but it creates picking problems. Another is to surround main varieties by pollinizers (see Free, 1970a, for planting arrangements); the ratio of pollinizer to main variety trees must strike a balance between the amount of set required and the relative value of the fruit of the two types. To increase pollination in dwarf pyramid orchards, pollinizer trees should be at intervals of not more than 3 m and in the same rows as the trees of the main variety.

Although set is usually greatest nearest to pollinizer trees, usually a few flowers set fruit on trees that are distant from pollinizers, and many more do so than would be expected from the behaviour of bees during a single trip. However, a bee usually covers a larger area during consecutive trips than during a single trip. In an orchard of dwarf *Pyrus malus* trees the mean size of areas visited was 338 sq m after two days foraging and 1016 sq m after eight days foraging (Free and Spencer-Booth, 1964b), by when the bees had made many moves between the two varieties, 'Cox's Orange Pippin' and 'James Grieve', in the orchard. Observations in an orchard of standard *Pyrus malus* trees of five varieties (Cox's Orange Pippin, Sunset, Laxton's Fortune, Merton Worcester, Tydeman's Late Orange) arranged in discrete rows showed that, provided a variety retained or increased its attractiveness, most bees kept to it and even preferred it to a more attractive variety (Free, 1966d). Over five consecutive days bees visiting the varieties that were persistently or increasingly attractive (i.e. Laxton's Fortune and Sunset) had smaller foraging areas than those originally visiting varieties that became less attractive (i.e. Merton Worcester, Tydeman's Late Orange). The attractiveness of a variety was correlated with the abundance of its flowers and its stage of flowering, and, as a variety became less attractive, the bees visiting it moved to another and so increased their total foraging areas, although they did not necessarily have larger foraging areas during a single trip. The attractiveness of a late flowering variety was enhanced by its proximity to a variety the bees had been visiting.

While bees are in their hives between foraging trips they fail to clean their bodies completely of pollen, and enough remains viable to pollinate flowers during the next trip (Free & Durrant, 1966). Hence, because consecutive trips are not to exactly the same area, and sometimes embrace more than one variety, compatible pollen is distributed more widely than during a single trip. Bees probably move between different varieties most often when the varieties are equally attractive, have concurrent flowering periods, and the bees do not differentiate between them. To encourage cross-pollination during consecutive trips the varieties concerned should not be separated in discrete rows.

However, cross-pollination is possible even when individual bees remain constant to one variety from trip to trip because, although most of the pollen on the body of a bee leaving a hive belongs to one species there are usually some grains of a few other species (Free, 1966e). Probably this 'foreign' pollen is transferred from bee to bee as they brush against each other in the hive between trips (Free & Williams, 1971a). At least some of this transferred pollen will probably be viable, and such transfers may explain the few fruits that set on trees remote from compatible varieties or where solid blocks of only one self-compatible variety are planted. Transfer of pollen within the hive could also be important when different varieties of a crop are grown for seed in the same locality, and could explain hybridisations over long distances although the bees remain constant to one variety. In fact, the only completely safe way of isolating plants for seed is to grow them in insect-proof glasshouses or cages.

Pollinating efficiency of flower visits

While foraging, nectar-gatherers have a greater proportion of pollen of 'foreign' species on their bodies than pollen-gatherers, but less total pollen (Free, 1966e; Free & Williams, 1971a). Hence, although they may be more important in speciation than pollen-gatherers, they are less likely to deposit pollen on the stigmas of the flowers they visit. The behaviour of many nectar-gatherers also makes them less effective as pollinators. This especially applies to bees visiting extra-floral nectaries, such as on *Helianthus annuus* (Free, 1964c) or *Vicia faba* (Free, 1962b). Visits were most numerous to the extrafloral nectaries of *H. annuus* during the afternoon and of *V. faba* during the forenoon. Few of the bees that visited the extrafloral nectaries of these crops ever made floral visits, although the visits to *H. annuus* extrafloral nectaries became fewer during flowering of the crop. Bees visited the *V. faba* extrafloral nectaries before the flowers opened, were numerous throughout the flowering period of the crop, and increased toward the end of flowering, presumably because the extrafloral nectaries continued to secrete nectar after the floral ones had finished doing so and because there was little pollen left. Therefore, it is especially important that colonies should not be moved to such a crop until the flowers open, otherwise a large proportion of the bees may become conditioned to work the extrafloral nectaries and not pollinate the flowers.

Bumblebees that obtain nectar through holes bitten in the bases of flowers with long corolla tubes do not pollinate the flowers directly, although they may do so by shaking pollen from the anthers onto the stigmas, provided that the flowers are not self-sterile. Although honeybees cannot bite holes, they use the holes bitten by bumblebees, and the numbers of 'robber' honeybees depend on the size of the 'robber' bumblebee population. Most of the honeybees on crops of *Trifolium pratense* (Free, 1958) and *Vicia faba* (Free, 1962b) are often robbing the flowers. Only bees that enter such flowers touch the stamens and stigmas and pollinate them. Often the nectar in the corolla tube is too low for the tongue of a bee to reach it and bees entering the flower collect only pollen. Indeed, they sometimes rob a few flowers of nectar during their foraging trips for pollen.

Individual bees foraging on *T. pratense* or *V. faba* are very constant in behaviour and they either enter flowers to collect pollen only or rob them of nectar. Thus, bees robbing *V. faba* flowers of nectar began working the crop about 4 hours earlier in the day than those that only collected pollen. Bees deserted the crop rather than change to a different type of visit, and differences in the relative proportions of the foraging populations on different days, and different times of the day, reflected changes in the bees present and not changes in the behaviour of individuals (Free, 1962b). However, bees foraging on *Phaseolus multiflorus* were more ready to change from robbing the flowers to entering them. Although the increase in honeybee population on the *Phaseolus multiflorus* crop was initiated by the appearance of robber bumblebees, its maintenance was independent of the population of robber bumblebees, and, after the robber bumblebees had disappeared for the season and no more holes were being bitten, many robber honeybees changed to collecting nectar through the mouths of the flowers (Free, 1968c). Presumably honeybees changed their type of behaviour more readily on *P. multiflorus* because they could more easily obtain nectar from the front of flowers than from the other leguminous flowers. Whatever the reason, hole-biting by bumblebees may be advantageous in attracting honeybees to the *P. multiflorus* crop that later enter the flowers and pollinate them. Similarly, the bumblebee's habit of biting holes in *Trifolium pratense* corolla tubes may also be advantageous, because honeybees are often otherwise unable to obtain nectar from the crop and the nectar-gatherers may recruit some pollen-gatherers that pollinate the flowers (Free & Butler, 1959).

Another example of bee and flower being ill adapted to each other is when the corolla tube is too wide and too long. Nearly all honeybees collecting nectar from *Freesia refracta* enter a flower on the side opposite to the stamens and stigma (Free & Racey, 1966), apparently following the prominent nectar-guides (Free, 1970b). Because of the flowers' width such a bee does not touch the stigmas or stamens while approaching the nectaries, though a few touch the stamens as they leave, usually with the ends of their abdomens or the tips of the wings; hence, few if any nectar-gatherers pollinate the flowers.

When visiting other flowers with short corolla tubes, and whose nectar is easily accessible, the behaviour of nectar-gatherers is mostly such as will probably pollinate. For example, nectar-gatherers visiting *Brassica napus* touched the stigmas of a mean of 76% of the 5984 flowers they were watched visiting (Free & Nuttall, 1968a). When visiting a *Ribes nigrum* flower a bee grasps the corolla, or more rarely a nearby leaf, and pushes its tongue and the front of its head between the stigmas and stamens down to the nectaries, so that on each flower visit one side of its head touches the anthers and the other the stigmas. When foraging on *Rubus idaeus*, a bee stands on the petals and stamens and pushes its head and extended tongue between the outer circle of stamens and central stigmas down to the ring of nectary tissue lining the receptacular cup, and, as it follows the ring, one side of its head and body touches the stigmas. Although nectar-gathering bees sometimes land on the petals of a *Fragaria x ananassa* flower and approach the nectary from the side, they nearly always proceed to walk over the stigmas and so may pollinate the flowers (Free, 1968d). However, a nectar-gatherer is not always such an efficient pollinator of tree fruit flowers. It stands either on the anthers or the petals of a flower and pushes its tongue and the front part of its body towards the nectar. When it stands on the anthers, it often touches the stigmas as well as the anthers, and so could pollinate the flower. But when it stands on the petals, it does not touch the stigmas when approaching the nectaries and so could not pollinate the flower; a nectar-gatherer standing on the petals of a flower with spreading stamens (e.g. *Prunus domestica*, *Prunus avium*, *Prunus armeniaca*) has to push past some of the anthers to reach the nectaries, and so may get pollen on its body, but a nectar-gatherer approaching *Pyrus malus* flowers, which have relatively stiff upright stamens, from the side, often does not even touch the anthers and so does not get pollen on its body. Nectar-gatherers tend to be constant to one or other type of behaviour (Free & Spencer-Booth, 1964b) and the proportion of nectar-gatherers that approach the nectaries of apple flowers from the top or sides depends on the thickness and length of the filaments. On varieties with relatively short, thin, filaments most nectar-gatherers pushed down to the nectaries from the top of the flower and so could pollinate, but on varieties with thicker and longer filaments the bees apparently had difficulty in reaching the nectaries in this way and approached them from the side and failed to pollinate (Free, 1960).

When visiting many of the species with shallow flowers (e.g. *Prunus* spp. and *Pyrus* spp., *Fragaria x ananassa*, *Rubus idaeus*) some bees deliberately scrabble over the anthers, pulling at them with their legs and biting them with their mandibles, so that their hairy surfaces get covered with pollen which is transferred to their corbiculae. Such bees are valuable pollinators because they always touch the anthers and stigmas.

On many crops, nectar-gatherers also collect some pollen incidentally as they brush against the anthers, although they do not deliberately scrabble for it. Whereas some nectar-gatherers push it into their corbiculae, others scrape it from their bodies and discard it. Some nectar-gatherers foraging on *Helianthus annuus* (Synge, 1947; Free, 1964), *Brassica napus* (Free & Nuttall, 1968a), and *Rubus idaeus* (Free, 1968d) discard pollen. All these crops provide abundant pollen; perhaps this happens with other species but because less pollen is collected incidentally it is less obvious.

The proportions of nectar-gatherers that collect pollen loads differ greatly on different days and different times of the day, and seem to depend on the amount of pollen available (e.g. tree fruits, Free, 1960; Free & Spencer-Booth, 1964b). Although individual nectar-gatherers foraging on shallow flowers such as *Pyrus malus* or *Rubus idaeus* tend to be constant either to discarding or retaining pollen that collects on their bodies, or to scrabbling for pollen (e.g. Free & Spencer-Booth, 1964b; Free, 1968d), the transition between scrabbling and collecting nectar is much easier than on leguminous crops.

The pollinating efficiency of visits by nectar and pollen-gatherers to *Pyrus malus* and *Trifolium pratense* flowers differs. The percentage of flowers of 'James Grieve' and 'Cox's Orange Pippin' that set fruit following a single visit by bees that (a) scrabbled for pollen was 63 and 18 respectively and (b) that did not scrabble for pollen was 45 and 5 respectively (Free, 1966c). The greater success of bee visits to 'James Grieve' than 'Cox's Orange Pippin' can be explained by the ability of 'James Grieve' to set well when self-pollinated. The small set of the 'Cox's Orange Pippin' flowers shows the ineffectiveness of many visits to varieties that need cross-pollination.

The percentage of *Trifolium pratense* florets that set seed after each had received a single frontal visit by bees that collected nectar only, was 20 and by bees that collected pollen, was 46 (Free, 1965a). This large difference was surprising because nectar- and pollen-gatherers enter a flower in the same way and both release the floral mechanism. Perhaps *T. pratense* nectar-gatherers also discard any pollen they collect inadvertently and keep their heads and fossae freer from pollen than pollen-gatherers. This could explain the greater pollinating efficiency of bees with pollen loads.

Although pollen-gatherers are usually more efficient pollinators, they are not invariably so. Honeybees scrabbling for *Helianthus annuus* pollen go to male stage florets and do not pollinate. Honeybees collecting nectar also mostly go to male stage florets, but they stand on the female florets while doing so and so may pollinate (Free, 1964c). In fact, in contrast to most other crops, bees that scrabble for pollen may be disadvantageous because they remove pollen with which nectar-gatherers might become dusted.

Factors controlling pollen collection and attempts to increase it

Pollen-gatherers are better pollinators than nectar-gatherers of most crops, so increasing the proportion of pollen-gatherers would increase pollination.

One way to do this is to feed colonies sugar syrup. In a series of ten experiments, colonies fed sugar syrup collected two to five times as much pollen as other colonies (Free & Spencer-Booth, 1961; Free, 1964b; Free & Racey, 1966). Further, because pollen-gatherers are more inclined than nectar-gatherers to forage near their colonies, feeding syrup also increased the proportion of pollen-gatherers working the nearby crop. Colonies fed sugar syrup collected more pollen mostly because the behaviour of individual foragers changed, although a greater tendency to collect pollen by bees starting to forage might well contribute to the result (Free, 1965c). When sugar syrup is provided inside the hive, most of the bees that collect it have not foraged previously, and are at the stage of their lives when they would usually receive nectar loads from foragers (Free, 1965d). Therefore, feeding sugar syrup probably creates a shortage of bees ready to receive nectar loads, with the result that nectar-gatherers have difficulty in getting their nectar loads accepted by others; many would, therefore, be discouraged from collecting more nectar and change to collecting pollen. This would explain the rapid change in the behaviour of individual foragers.

Any increased pollination that has resulted from attempts to ‘direct’ bees to crops by feeding them with sugar syrup containing the scent of the flowers of the target crop, might well come from feeding syrup alone, rather than from the added scent actually ‘directing’ the bees.

It has been suggested that removing a proportion of the pollen loads of returning foragers by ‘pollen traps’ at the entrance to hives, might increase the amount of pollen collected. However, the obstruction to foraging the traps create at the hive entrance seems to balance any increase in the proportion of foragers that collect pollen (Free, unpublished).

Adding pollen to colonies decreases pollen collection (Free, 1967a; 1970a), so although feeding a colony supplementary pollen during spring may be valuable in stimulating colony growth, it should not be done when the crop needing pollination is in flower.

Pollen collected by a colony is the source of nitrogen fed to its developing brood (Ribbands, 1953; Simpson, 1955). It is not surprising, therefore, that the presence of brood stimulates foraging in general, but pollen-gathering in particular (Free, 1967a) and that the proportion of foragers of a colony that collect pollen and the amount of pollen collected depends on the amount of brood. Individual bees quickly change from collecting nectar to collecting pollen and *vice versa* in accordance with an increase or decrease in the amount of brood. Hence, colonies to be used for pollination should contain plenty of brood.

Brood of all stages stimulates pollen collection, but sometimes larvae are more effective than pupae. Although access to the brood area is the most important factor stimulating pollen collection, the smell of the brood and contact with bees tending the brood are partly responsible. Perhaps, therefore, adding pheromones produced by brood might increase pollen collection.

As a colony grows the ratio of brood to bees decreases (Free & Racey, 1968b); the relatively larger amount of brood per bee in small than large colonies probably helps to explain why a larger proportion of bees in small colonies usually forage, and why small colonies have less scope than big ones for increasing their foraging when conditions improve (Free & Preece, 1969).

The presence of a queen stimulates foraging (Free, 1967a), comb production (Free, 1967b) and deposition of nectar and pollen loads (Free & Williams, 1971b), probably because of the pheromones she produces (Butler, 1954, 1967; Butler *et al.*, 1961). Removing the queen decreases the number of loads of pollen collected and many bees collecting pollen subsequently collect nectar only. Because most bees collecting pollen loads also collect nectar, loss of a queen probably diminishes foraging in general. The queen's pheromones are probably less diluted among the bees of small than large colonies, so bees of small colonies receive more stimulus to forage (Free & Preece, 1969) from the relatively greater amount of queen and brood pheromone each receives. Giving additional queen pheromones to colonies might also increase foraging and pollen collection. Queenless packages of bees, in cheap containers, both of which can be destroyed when the pollinating task is complete, could be usefully employed in some circumstances. Synthesised queen pheromones might be used to substitute for a queen in stimulating foraging and comb building in such colonies, but unless a stimulus as powerful as brood is also discovered and used, such colonies are unlikely to forage as efficiently as natural ones (Free, 1967a).

REFERENCES

BUTLER, C. G. (1945) The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance. *J. exp. Biol.* **21**, 5–12.

BUTLER, C. G. (1954) The method and importance of the recognition by a colony of honeybees (*A. mellifera*) of the presence of its queen. *Trans. R. ent. Soc. Lond.* **105**, 11–29.

BUTLER, C. G. (1956) Bee Department Annual Report. *Rep. Rothamsted exp. Stn for 1955*, 139–243.

BUTLER, C. G. (1965) Sex attraction in *Andrena flavipes* Panzer (Hymenoptera: Apidae) with some observations on nest-site restriction. *Proc. R. ent. Soc. Lond.* (A) **40**, 77–80.

BUTLER, C. G. (1967) Insect pheromones. *Biol. Rev.* **42**, 42–87.

BUTLER, C. G. & CALAM, D. H. (1969) Pheromones of the honey bee—the secretion of the Nassanoff gland of the worker. *J. Insect Physiol.* **15**, 237–244.

BUTLER, C. G. & HAIGH, J. C. (1956) A note on the use of honey-bees as pollinating agents in cages. *J. hort. Sci.* **31**, 295–297.

BUTLER, C. G. & SIMPSON, J. (1954) Bees as pollinators of fruit and seed crops. *Rep. Rothamsted exp. Stn for 1953*, 167–175.

BUTLER, C. G., CALLOW, R. K. & JOHNSTON, N. C. (1961) The isolation and synthesis of queen substance, 9-oxodec-trans-2-enoic acid, a honeybee pheromone. *Proc. R. Soc. B* **155**, 417–432.

BUTLER, C. G., CARLISLE, E. & SIMPSON, J. (1953) Pollen supplement trials. *Rep. Rothamsted exp. Stn for 1952*, 124–125.

BUTLER, C. G., FREE, J. B. & SIMPSON, J. (1956) Some problems of red clover pollination. *Ann. appl. Biol.* **44**, 664–669.

BUTLER, C. G., JEFFREE, E. P. & KALMUS, H. (1943) The behaviour of a population of honeybees on an artificial and on a natural crop. *J. exp. Biol.* **20**, 65–73.

FREE, J. B. (1958) Attempts to condition bees to visit selected crops. *Bee World* **39**, 221–230.

FREE, J. B. (1959) The effect of moving colonies of honeybees to new sites on their subsequent foraging behaviour. *J. agric. Sci.* **53**, 1–9.

FREE, J. B. (1960) The behaviour of honeybees visiting flowers of fruit trees. *J. Anim. Ecol.* **29**, 385–395.

FREE, J. B. (1962a) The effect of distance from pollinizer varieties on the fruit set on trees in plum and apple orchards. *J. hort. Sci.* **37**, 262–271.

FREE, J. B. (1962b) The behaviour of honeybees visiting field beans (*Vicia faba*). *J. Anim. Ecol.* **31**, 497–502.

FREE, J. B. (1963) The flower constancy of honeybees. *J. Anim. Ecol.* **32**, 119–131.

FREE, J. B. (1964a) Comparison of the importance of insect and wind pollination of apple trees. *Nature, Lond.* **201**, 726–727.

FREE, J. B. (1964b) The effect on pollen collection of feeding honey-bee colonies with sugar syrup. *J. agric. Sci.* **64**, 167–168.

FREE, J. B. (1964c) The behaviour of honeybees on sunflowers (*Helianthus annuus* L.) *J. appl. Ecol.* **1**, 19–27.

FREE, J. B. (1965a) The ability of bumblebees and honeybees to pollinate red clover. *J. appl. Ecol.* **2**, 289–294.

FREE, J. B. (1965b) Attempts to increase pollination by spraying crops with sugar syrup. *J. apic. Res.* **4**, 61–64.

FREE, J. B. (1965c) The behaviour of honeybee foragers when their colonies are fed sugar syrup. *J. apic. Res.* **4**, 85–88.

FREE, J. B. (1965d) The allocation of duties among worker honeybees. *Zoo. Soc. Lond. Symposium No. 14.* 39–59.

FREE, J. B. (1966a) Pollination of the beans, *Phaseolus multiflorus* and *Phaseolus vulgaris*, by honeybees. *J. apic. Res.* **5**, 87–91.

FREE, J. B. (1966b) The pollination of broad beans and field beans (*Vicia faba*) by honeybees. *J. agric. Sci.* **66**, 395–397.

FREE, J. B. (1966c) The pollinating efficiency of honeybee visits to apple flowers. *J. hort. Sci.* **41**, 91–94.

FREE, J. B. (1966d) The foraging areas of honeybees in orchards of standard apple trees. *J. appl. Ecol.* **3**, 261–268.

FREE, J. B. (1966e) The foraging behaviour of bees and its effect on the isolation and speciation of plants. *Reproductive biology and taxonomy of vascular plants.* Ed. J. G. Hawkes. London: Pergamon. pp. 76–92.

FREE, J. B. (1967a) Factors determining the collection of pollen by honeybee foragers. *Anim. Behav.* **15**, 134–144.

FREE, J. B. (1967b) The production of drone comb by honeybee colonies. *J. apic. Res.* **5**, 177–182.

FREE, J. B. (1968a) The pollination of strawberries by honeybees. *J. hort. Sci.* **43**, 107–111.

FREE, J. B. (1968b) The pollination of blackcurrants. *J. hort. Sci.* **43**, 69–73.

FREE, J. B. (1968c) The behaviour of bees visiting runner beans (*Phaseolus multiflorus*). *J. appl. Ecol.* **5**, 631–638.

FREE, J. B. (1968d) The foraging behaviour of honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.) on blackcurrants (*Ribes nigrum*), raspberry (*Rubus idaeus*) and strawberry (*Fragaria x ananassa*) flowers. *J. appl. Ecol.* **5**, 157–168.

FREE, J. B. (1968e) Dandelion as a competitor to fruit trees for bee visits. *J. appl. Ecol.* **5**, 169–178.

FREE, J. B. (1968f) The conditions under which foraging honeybees expose their Nasonov glands. *J. apic. Res.* **7**, 139–145.

FREE, J. B. (1969) Influence of the odour of a honeybee colony's food stores on the behaviour of its foragers. *Nature, Lond.* **222**, 778 only.

FREE, J. B. (1970a) *Insect pollination of crops.* London: Academic Press.

FREE, J. B. (1970b) Effect of flower shapes and nectar guides on the behaviour of foraging honeybees. *Behaviour* (in press).

FREE, J. B. & BUTLER, C. G. (1955) An analysis of the factors involved in the formation of a cluster of honeybees (*Apis mellifera*). *Behaviour* **7**, 304–316.

FREE, J. B. & BUTLER, C. G. (1959) *Bumblebees.* London: Collins.

FREE, J. B. & DURRANT, A. J. (1966) The transport of pollen by honeybees from one foraging trip to the next. *J. hort. Sci.* **41**, 87–89.

FREE, J. B. & NUTTALL, P. M. (1968a) The pollination of oilseed rape (*Brassica napus*) and the behaviour of bees on the crop. *J. agric. Sci., Camb.* **71**, 91–94.

FREE, J. B. & NUTTALL, P. M. (1968b) Effect of the time of day at which honey-bee colonies are first allowed flight in a new location on their choice of flower species. *Nature, Lond.* **218**, 982.

FREE, J. B. & PREECE, D. A. (1969) The effect of the size of a honeybee colony on its foraging activity. *Insect Soc.* **16**, 73–78.

FREE, J. B. & RACEY, P. A. (1966) The pollination of *Freesia refracta* in glasshouses. *J. apic. Res.* **5**, 177–182.

FREE, J. B. & RACEY, P. A. (1968a) The pollination of runner beans (*Phaseolus multiflorus*) in a glasshouse. *J. apic. Res.* **7**, 67–69.

FREE, J. B. & RACEY, P. A. (1968b) The effect of the size of honeybee colonies on food consumption, brood rearing and the longevity of bees during winter. *Ent. exp. and appl.* **11**, 241–249.

FREE, J. B. & SIMPSON, J. (1964) The pollination requirements of sunflowers (*Helianthus annuus* L.). *Emp. J. exp. Agric.* **32**, 340–342.

FREE, J. B. & SMITH, M. V. (1961) The foraging behaviour of honeybees from colonies moved into a pear orchard in full flower. *Bee World* **42**, 11–12.

FREE, J. B. & SPENCER-BOOTH, YVETTE (1959) The longevity of worker honey bees (*Apis mellifera*). *Proc. R. ent. Soc. Lond.* (A) **34**, 141–150.

FREE, J. B. & SPENCER-BOOTH, YVETTE (1961) The effect of feeding sugar syrup to honey-bee colonies. *J. agric. Sci.* **57**, 147–151.

FREE, J. B. & SPENCER-BOOTH, YVETTE (1963a) The pollination of mustard by honeybees. *J. apic. Res.* **2**, 69–70.

FREE, J. B. & SPENCER-BOOTH, YVETTE (1963b) The foraging areas of honey-bee colonies in fruit orchards. *J. hort. Sci.* **38**, 129–137.

FREE, J. B. & SPENCER-BOOTH, YVETTE (1964a) The effect of distance from pollinizer varieties on the fruit set of apple, pear and sweet-cherry trees. *J. hort. Sci.* **39**, 54–60.

FREE, J. B. & SPENCER-BOOTH, YVETTE (1964b) The foraging behaviour of honeybees in an orchard of dwarf apple trees. *J. hort. Sci.* **39**, 78–83.

FREE, J. B. & WILLIAMS, INGRID H. (1970a) Preliminary investigations on the occupations of artificial nests by *Osmia rufa* L. (Hymenoptera, Megachilidae). *J. appl. Ecol.* **7**, 559–566.

FREE, J. B. & WILLIAMS, INGRID H. (1970b) Exposure of the Nasonov gland by honeybees (*Apis mellifera*) collecting water. *Behaviour* (In the press.)

FREE, J. B. & WILLIAMS, INGRID H. (1971a) The transfer of pollen between the bodies of honeybees and its implication on the cross-pollination of crops. (Not yet published.)

FREE, J. B. & WILLIAMS, INGRID H. (1971b) Hoarding by honeybees (*Apis mellifera*). (Not yet published.)

FREE, J. B., FREE, NANCY W. & JAY, S. C. (1960) The effect on foraging behaviour of moving honey bee colonies to crops before or after flowering has begun. *J. econ. Ent.* **53**, 564–566.

FREE, J. B., NEEDHAM, P. H., RACEY, P. A. & STEVENSON, J. H. (1967) The effect on the mortality of foraging bees of applying insecticides as spray or granules to field beans. *J. Sci. Fd Agric.* **18**, 133–138.

LEWIS, T. & SMITH, B. (1969) The insect faunas of pear and apple orchards and the effect of windbreaks on their distribution. *Ann. appl. Biol.* **64**, 11–20.

MINISTRY OF AGRICULTURE, FISHERIES & FOOD (1962) The use of honeybees in orchards. *Adv. Leafl. Minist. Agric. London*, 328.

NEEDHAM, P. H. & STEVENSON, J. H. (1966) Insecticides and beekeeping in England and Wales. *Bee World*, **47**, 65–70.

NEEDHAM, P. H., SOLLY, S. R. B. & STEVENSON, J. H. (1966) Damage to honey bee colonies (*Apis mellifera*) by insecticides in Great Britain, 1956–65. *J. Sci. Fd Agric.* **17**, 133–137.

RIBBANDS, C. R. (1949) The foraging method of individual honey-bees. *J. anim. Ecol.* **18**, 47–66.

RIBBANDS, C. R. (1951) The flight range of the honey-bee. *J. anim. Ecol.* **20**, 220–226.

RIBBANDS, C. R. (1953) *The behaviour and social life of honeybees.* London: Bee Research Association.

RIBBANDS, C. R. (1955) Communication between honeybees. II. The recruitment of trained bees, and their response to improvement of the crop. *Proc. R. ent. Soc. Lond.* (A) **30**, 26–32.

RIEDEL, I. B. M. & WORT, D. A. (1960) The pollination requirements of the field bean (*Vicia faba*). *Ann. appl. Biol.* **48**, 121–124.

SIMPSON, J. (1955) The significance of the presence of pollen in the food of worker larvae of the honeybee. *Quart. J. Micro. Sci.* **96**, 117–120.

SPENCER-BOOTH, YVETTE (1960) Feeding pollen, pollen substitutes and pollen supplements to honeybees. *Bee World* **41**, 253–263.

SYNGE, A. D. (1947) Pollen collection by honeybees (*Apis mellifera*). *J. anim. Ecol.* **16**, 122–138.

WYKES, G. R. (1952) The preference of honeybees for solutions of various sugars which occur in nectar. *J. exp. Biol.* **29**, 511–518.

WYKES, G. R. (1953) The sugar content of nectars. *Biochem. J.* **53**, 294–296.

https://doi.org/10.23637/ERADOC-1-5