THE BEHAVIOUR OF BEES IN RELATION TO POLLINATION *)

K. M. DOULL
Member of the Nutrition Physiology Working Group
of the Bee Biology Standing Commission of APIMONDIA
AUSTRALIA

Efficient pollination of the flowers of any entomophilous crop requires that there should be close association between growers, beekeepers and bees.

The bees are indispensable and are the most important element of the association, and unfortunately beekeepers are often the most disruptive element — at least as far as the bees are concerned.

Pollination is simply an accidental side effect of the activities of bees foraging for food for their colonies and the activities of growers and beekeepers must be directed towards creating and maintaining in the fields and in the hives the environment that will provide the bees with the strongest stimulus to seek and gather nectar or pollen from the particular crop.

Provided growers and beekeepers carry out their activities effectively and provided of course that weather conditions are suitable the bees will fulfil their part in the association efficiently, for foraging is the result of their instinctive and therefore unavoidable responses to stimuli they perceive from their environment.

Some flowers may be pollinated equally well by bees that are seeking either nectar or pollen. The type of hive management required to provide efficient pollination of these crops is different from that required where the flowers of the crop can be pollinated efficiently only by bees that visit them for the specific purpose of gathering pollen.

The beekeeper's first task must be to gain an understanding of the nature of the flowers of the crop to be pollinated, and of the type of foraging activity that is required for most efficient pollination.

The number of foragers returning to the hive with pollen from any particular crop, or the amount of that pollen appearing in pollen traps is not a true guide to the type of foraging activity that will result in the pollination of the crop in question. Nor is it necessarily any guide to the efficiency of pollination of the crop.

Pollen that is brought into the hive may have been gathered by bees that were actively seeking pollen, or by bees that gathered pollen while visiting flowers in search of nectar. The two types of foraging activity may be readily distinguished by observation of the behaviour of the bees on the flowers.

A bee that is foraging for nectar may be distinguished by the fact that after alighting on a flower and locating the nectary, it extends its tongue and begins to imbibe the nectar. It remains still for a few seconds and after taking up all the nectar, flies without hesitation to another and repeats the process.

Nectar collecting bees must often crawl over or through the anthers of flowers to reach the nectaries and their bodies usually become dusted with pollen. Most of them disregard this pollen which falls from their bodies as they fly or is removed when they groom themselves. However, some bees that are obviously seeking nectar are apparently still able to respond to the pollen on their bodies for they pack it into their pollen baskets and thus return to the hive with both pollen and nectar. Clearly, the collection of pollen by these bees is incidental to the collection of nectar.

About 25% of foragers from any hive are actively seeking pollen in response to the stimulus presented by the brood. Their behaviour is quite characteristic. They do not show any interest in the nectaries of the flowers they visit, for normally they leave the hive with reserves of honey sufficient to provide the energy required for their flight to and from the flowers.

*) Paper delivered at the First Australian Apicultural Congress at Broadbeach, 1972

After alighting on the flower they scrabble actively over the anthers and stigma, biting the anthers and pulling them down towards their bodies. This activity releases pollen which accumulates on the bees' bodies. After they leave the flower they normally hover for a few minutes busily scraping the pollen off their bodies and packing it in their pollen baskets.

The type of foraging activity that is most likely to lead to efficient pollination of any crop is determined in the first instance by a number of factors that originate in the plant and in the crop.

Flower structure is particularly important, for in general, maximum yields of seed and fruit from entomophilous crops are obtained only when bees are available to transfer pollen from the anthers — the male parts of the flowers —, to the stigmas — the female parts of the flowers.

Where bees must make contact with both anthers and stigma of all flowers they visit, pollination may be effected by bees seeking either pollen or nectar. However, in some flowers bees may obtain nectar without making contact with anthers or stigma, and such flowers may be pollinated only by bees that are actively seeking pollen.

The quantity and quality of nectar and pollen produced by any crop and the ease with which bees may collect them determine the profitability of the crop as a source of food for bees. These are therefore important factors affecting the efficiency of pollination and the ability of any crop to compete with alternative sources of nectar and pollen.

Quality of nectar in terms of this discussion means basically the amount of sugars in the nectar. Honeybees exhibit a preference for nectar containing more than 20% of sugars, and the higher the sugar concentration the more profitable will be the flowers as a source of nectar. A few plants produce nectars with a very low concentration of sugars, and are poor competitors for visits by nectar-collecting bees.

In general, when able to choose between sources of nectar, bees will prefer the one from which they can gather a full load of nectar in the shortest time. Thus they prefer crops in which individual flowers produce comparatively large amounts of nectar, or that have an abundance of flowers. For example, clovers, which normally produce nectar containing 30 to 40% sugars, and which may have several million flowers per acre, are very strong competition for visits by nectar-collecting bees, even though the amount of nectar produced per flower is comparatively small.

The quality and quantity of pollen are also important. Quality is determined by the strength of the stimulus that the pollen presents to the bees, for bees seeking pollen are induced to alight on flowers and to scrabble for pollen by stimuli presented by certain chemicals in the pollen. Pollens of different plants vary in the amounts of these chemicals they contain, and thus in the strength of the stimulus they present to pollen collectors.

Both the abundance and concentration of nectar are subject to considerable fluctuation during any one day, and from day to day. The threshold temperature for nectar secretion — that is, the lowest temperature at which the flowers will begin to secrete nectar — and the temperature above which nectar secretion stops, are usually specific for individual species or varieties of plants, and in changeable weather nectar secretion of some flowers fluctuates with temperature. Irrespective of temperature, however, nectar secretion is always reduced in dull cloudy weather. The amount and concentration of nectar secreted is also influenced by the moisture level and nutrient status of the soil, by atmospheric pressure and humidity, and by wind and rain.

The quality and quantity of pollen produced by the flowers of any plant may also vary, so that the attractiveness of the flowers to pollen-collecting bees also varies. Little is known of the causes of these variations, but there is evidence to suggest that it is associated with the state of growth of the plant. For instance, it appears that lucerne plants that are producing fresh vegetative growth following rain or excessive irrigation may produce a high proportion of infertile pollen grains.

Thus the attractiveness of any crop will vary at different times during the day, from day to day, and at different stages of flowering, and it is not uncommon to find adjacent crops of the same plant exhibiting different levels of attractiveness to honeybees.

Growers' efforts may affect the amounts of nectar and pollen produced by the flowers and thus will affect the attractiveness of the crop to bees. For example, most irrigated seed crops appear to be more attractive to bees and to produce better yields of seed when they are subjected to some degree of moisture stress before and during early flowering.

In some cases soil nutrient stratus affects nectar secretion as for example in clovers which often benefit from application of potassium fertiliser.

The distribution of pollenizer varieties is important with many orchard fruits. Individual foragers usually confine their activities to relatively small foraging areas, and pollenizer varieties must be so placed that bees will regularly move between these trees and the main variety.

Co-operation between growers and beekeepers to identify the main competing flora may also lead to improved pollination. In some instances, flowering may be delayed to avoid the worst effects of competition while in orchards it may be helpful to mow the ground cover and so remove weed flowers that are often important competitor sources of pollen.

Flowers of all plants are receptive to pollen for restricted periods, and even though many flowers may remain open for 7 days or more, most flowers must be pollinated within a day or two of opening. Thus for example delays of one or two days with Delicious apple produce fruit set of only 27% and 11% respectively while with almonds virtually no nuts are set if pollination is delayed for four days after the flowers have opened.

This has several implications for the beekeeper. It means that there should not be any delay in placing hives in the crop once flowering has started, and it means that there must always be enough foragers working in the crop to ensure rapid pollination of all flowers once they have opened. It also has particular implications in the pollination of crops that flower in spring when the weather may be cool and changeable. In such weather conditions bees tend to forage close to their hives, and so the hives should be dispersed in small groups throughout the orchard.

The management of colonies for pollination has important effects on their efficiency as pollination units .

The behaviour of honeybees is influenced by their reactions to what may be called "reward — no reward" situations. If any activity fails to produce a "reward", they eventually stop responding to the stimulus that elicits the activity. For example, when storage space in the hive is filled with pollen and honey, incoming bees are unable to dispose of the food they carry, and eventually cease foraging.

Management of colonies used for pollination must be such as to ensure that this situation does not arise and that there is always sufficient comb space for storage of all the pollen and nectar the bees can gather. It is never possible to forecast yields of nectar and it is always advisable to start off with one more super than is thought necessary. Routine management must include examinations of storage space and if necessary the removal of surplus honey or the provision of additional supers.

Colonies used for pollination of crops that require the activities of nectar collecting bees should be as strong as is possible. If the crop has a short flowering period, little harm will be done if brood rearing is restricted. In fact this will improve pollination for with less brood there is a weaker stimulus for pollen collection and a higher proportion of bees will gather nectar.

However, where the crop has a long flowering period, the need to maintain the optimum force of nectar-collecting bees must be balanced against the need to maintain colony strength. In general, with these crops it is necessary to inspect the brood-nest regularly and to ensure that the queen has plenty of room in which to lay eggs.

Colonies that are to pollinate crops needing the activities of pollen-collecting bees require careful and regular attention to maintain the optimum rate of brood rearing and to ensure that, if possible, they suffer a continuing mild shortage of pollen. The proportion of bees that seek pollen is directly related to the amount of brood to be fed and in broad terms, the management required for these colonies must include the regular removal from the brood-nest of combs containing honey and excessive amounts of pollen, so that the queen may maintain a high rate of oviposition.

In some cases — particularly in spring — brood rearing is inhibited by a lack of nectar, and it is often beneficial to feed the colonies with thin syrup or even to give them sticky combs.

Finally, some brief comments on the type of pollination activity that is likely to provide most efficient pollination of some crops grown in Australia.

The flowers of all *clovers* may be pollinated equally well by bees that visit them to collect either nectar or pollen. The anthers and stigma are enclosed in the keel petals, and are exposed when a bee alights on the flower. As the bee pushes her tongue or head into the throat of the flower, the anthers and stigma are pressed against the underside of the bee's head, and pollination occurs. The anthers and stigma return to their position in the keel petals when the bee leaves.

Clover flowers are not ideally suited for bees that are actively seeking pollen, for they cannot complete the full scrabbling behaviour pattern. However, some bees exhibit modified pollen gathering behaviour in which they scrape their forelegs over the anthers to release the pollen.

The most efficient pollination of clovers will be achieved with strong colonies managed for maximum honey production.

Many of the varieties of *fruit trees* grown in Australia difer from those grown in other countries. Varietal differences in flower structure influence the type of foraging activity most likely to lead to effective pollination, and since information on flower structure is not readly available, it is possible to speak only in broad generalisations.

Pollination of orchard fruits is unusual in that the grower does not always require pollination of the maximum number of flowers. In the case of apples, pears, peaches and apricots, for example, a commercial crop may be obtained if 10 to 15% of flowers set fruit, while for cherries and almonds pollination of all flowers is required.

Pears provide the main problem in orchard pollination, for with nectar usually containing less than 20% sugars, they compete very poorly for nectar collectors. Pollination of pears is best achieved by bees actively seeking pollen. Unfortunately, it appears that pears may also be poor competitors with alternative sources of pollen. In fact the evidence suggests that fruit trees often compete relatively poorly with alternative sources of pollen, especially with ground flora, which normally flowers profusely at the same time as fruit trees.

The evidence available suggests that most effective pollination of orchard fruits may be achieved with colonies managed to produce a maximum stimulus for pollen collection, but there is room for research on this aspect of pollination.

Lucerne pollination is a continuing problem in Australia. Bees may obtain nectar without pollinating the flowers and nectar collectors in general pollinate only 1 to 2% of the flowers they visit, whereas bees seeking pollen will trip and pollinate up to 98% of the flowers they visit. Unfortunately lucerne is a poor competitor for pollen collecting bees. The pollen presents a relatively weak stimulus, the flowers are difficult for bees to work and produce relatively small amounts of pollen. Best yields of lucerne seed are produced in conditions in which there is minimal competition for pollen, where the weather is fine, dry and hot, and where honeybee colonies are carefully managed to maintain a high rate of oviposition and a continual shortage of pollen. There are few areas in which this combination of conditions occurs with any regularity.

The flowerheads of *sunflowers* consist of a large number of small florets with both anthers and stigma rising above the corolla tube so that any bee alighting on the flowerhead in search of nectar will pollinate the florets. Bees appear to visit sunflowers mainly to obtain nectar and hives prepared for maximum honey production are likely to be most efficient pollinators of sunflowers.

The flowers of *oilseed rape* compete strongly as sources of nectar, for they produce relatively large quantities of nectar with a high concentration of sugars. The available evidence suggests that bees do not normally visit oilseed rape specifically to gather pollen and hives managed for maximum honey production are probably best suited for pollination of this crop.

In overseas countries — particularly in USA — new methods of culturing crops and particularly the use of male sterile hybrids are creating increased pressure for efficient pollination services. Up to the present, Australian growers have not used these new techniques, and do not usually face major problems of pollination, since wild swarms of honeybees often account for a high proportion of foraging bees in their orchards and crops.

However, the need for higher yields and lower costs of production per pound of seed or fruit will change this in time, and the Australian beekeeping industry will need to improve its services to growers to meet these needs.