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Rothamsted Report for 1966

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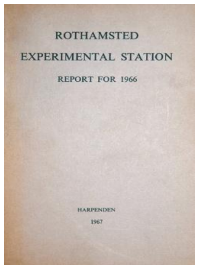

Bee Department

C. G. Butler

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P. A. Racey left and Doreen Watler was appointed to the staff. A new post for work on insect pathology was filled by N. Wilding. Dr. D. J. Fletcher (University of Natal) and A. Raw joined the department as temporary workers.

In September, L. Bailey attended a Colloquium on Insect Pathology at Wageningen.

Behaviour and physiology

Swarming. In recent years swarming has been observed from 10 out of 14 dequeened colonies (otherwise treated in various ways) in which much piping was heard when the young queens were ready to emerge from their cells, and from 0 out of 9 such colonies in which little or no piping was heard. There is thus little doubt that confining young queens in their cells by workers, which results in queen piping, is a necessary preliminary to swarming by uncrowded colonies with queens ready to emerge.

What makes colonies confine queens is still uncertain, though large colonies do it more readily than small ones. Crowding adult bees in their hive can make colonies swarm even when they are not rearing queens; in 1965 crowding bees on the brood remaining after most was removed from colonies was often followed by piping and swarming, but in an experiment during 1966 with very small colonies, crowding by diminishing hive space failed to promote piping, and one colony that was not crowded had much piping and swarmed. Although congestion promotes swarm emergence, it seemingly does not necessarily facilitate all the events that precede it.

Most young queens that pipe do so when about 2–5 days old and in response to other queens' piping, but individual queens differ greatly in their willingness to pipe. A few queens are so inclined to pipe that they do it when other queens are not piping. Others do not pipe even when surrounded by piping queens. The reasons for these individual differences are not known; if piping does promote swarming, the reason some colonies do not swarm even though they have young queens ready to emerge, may be that the queens fail to pipe rather than that they are not confined in their cells.

Examination of cells in which worker bees are confining queens suggests that the confined queens are slow to cut round their cell cappings preparatory to emerging and do not complete the cutting process till their integument is well hardened, i.e. at least 12 hours later than a queen without attendant workers emerges. Food adhering to the inside of the cuts shows that the workers feed the queens while they are still cutting. When a colony is not going to confine young queens when they mature, the workers remove the wax from the cell tips, leaving the cocoons exposed, but cells in which queens are being confined still have their tips covered with wax.

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Queens may be kept in their cells for as many as four days after they are ready to emerge. After queens finish cutting their cappings the workers must either inhibit their emergence, perhaps by feeding the queens, or forcibly prevent their emergence.

How colonies treat caged queens. The behaviour of colonies towards queens is being studied in observation hives with queens in cages open to the glass hive walls. A colony with a laying queen violently attacked virgin queens introduced to it in wire screen cages and soon killed them, probably by stinging, starving, suffocating or overheating. Even when the virgins emerged from their cells in the cages, they were attacked and killed as soon as their integument had hardened. The laying queen paid no attention to the virgins. A laying queen caged in a colony headed by a virgin queen was never seen to be ill-treated and survived until the virgin had mated and begun laying, when the older queen was found dead. Laying queens were unharmed in cages in a colony headed by a laying queen during summer, but during October they were quickly killed. When one or more virgin queens were attacked in cages in an otherwise queenless colony they were not killed, but the workers' hostility towards them did not diminish with time. These observations suggest that under some colony conditions, or at some times of the year, efficient queen supersedure (the production of a young laying queen by a colony while their old one is still alive) and the survival of more than one laying queen in a colony cannot occur. It also seems that, although caging a queen in a colony to which she is to be introduced does facilitate her introduction, those incompatibilities of queen and colony that are not resolved within a few hours are not overcome by caging for longer periods.

Effect of prolonged restriction of oviposition in a colony. In a previous experiment lasting three weeks, restricting the number of cells in which the queens of colonies were allowed to lay eggs did not induce queen rearing or swarming. Two colonies have now been subjected to this treatment throughout the summer, one queen being confined by an excluder to five B.S. combs (19 × 34 cm), the other to 11 half depth combs; the severest restriction practised by beekeepers is usually to 10 B.S. combs. No occupied queen cells were seen in either colony at any time and the colonies did not become big enough to occupy more than 12 and 15 B.S. combs, respectively, with adult bees. Clearly there is no justification for the widespread belief that colonies are extremely sensitive to brood restriction and quickly react to it by rearing queens. (Simpson and Wilding)

Pheromones of queen honeybees. Drones were attracted upwind towards a hidden ball of cotton-wool with a surface area of about 50 cm^2 impregnated with the olfactory sex attractant of the queen, 9-oxodecenoic acid, when it was suspended 7 m above the ground. Within the range 0·025–50·0 mg 9-oxodecenoic acid there was no significant difference in the number of drones attracted in unit time, and it was doubtful whether they were attracted from farther afield by the larger than by the smaller amounts. Similarly, plaster-of-Paris blocks ranging in surface area from about 1·5–

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150·0 cm², but each impregnated with 0·025 mg 9-oxodecenoic acid, all attracted the same number of drones. Further, these blocks continued to attract drones, without any more sex attractant being added to them, after 14 months' exposure in the open air. These observations show the persistence of this sex attractant and strongly suggest that only a very small amount is necessary to attract drones, much less, in fact, than the average of 0·132 mg possessed by a nubile queen.

In insects, aphrodisiacs are usually quite distinct from sex attractants. After sex attractants have brought the sexes together an aphrodisiac, which is usually but not invariably produced by the male, is released as part of courtship behaviour and helps to prepare the opposite sex for mating. In some species, however, the same pheromone serves both as a sex attractant and as an aphrodisiac. That this is so with the honeybee has now been shown by the behaviour of drones induced to fly to models of queen honeybees suspended in air. When the olfactory sex attractant, 9-oxodecenoic acid, was exposed on or within a few centimetres of the models drones often seized and tried to copulate with models, but without the sex attractant they seldom attempted to do so. (Butler)

Pheromones of worker honeybees. The behaviour of foraging honeybees on returning to their hive after its entrance has been displaced in various ways (e.g. by closing the old entrance and opening a new one at the same level on an adjacent side of the hive) was further studied.

The degree of confusion among returning foragers when the new entrance is at 90° to the old one depends chiefly on the number of bees flying. When they are few, they usually approach the position of the old entrance and examine it while hovering in front of it, although some alight briefly. On failing to find the entrance in its old position, they extend their examination of the hive while in flight and soon find the new entrance. Such behaviour may continue for several days, but reorientation to the new entrance is fairly rapid. When many bees are flying those alighting at the site of the old entrance exert a strong, apparently visual, attraction for other returning foragers, with the result that agitated bees rapidly accumulate around the site of the old entrance. At the same time a few bees that find the new entrance, either when running or flying, stand near it and expose their Nassanoff scent glands, over which they fan currents of air with their wings directing the attractive scent towards the corner between the faces of the hive with the new and old entrances. Small groups of bees run in all directions around the site of the old entrance, and within a few minutes some of them reach the corner and run round and join the scenting bees. Some of these then expose their Nassanoff glands instead of entering the hive immediately, and in this way a line of scenting bees becomes established right round the corner of the hive, from the new entrance towards the old one, and is maintained until few bees remain. This line is reformed whenever the number of bees at the old entrance is again enough for a few to run as far as the corner. After about an hour it apparently becomes unnecessary for a more or less continuous line of bees to be maintained, and those alighting at the old entrance then run round to the new one. Most run round in small groups of up to seven bees, others individu-

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ally, without any exposing their Nassanoff glands. Such behaviour lasts for several weeks when conditions for flying remain favourable, particularly when they favour flying during the first few days after entrance change; but when conditions deteriorate within 24 hours of the change and remain poor an increasing number of individuals who initially displayed the running behaviour reorientate to the new entrance while flying, until, after 7–14 days, reorientation is complete. It is clear, therefore, that social facilitation, mainly in the form of attraction of returning foragers by bees that have already alighted, plays an important role in the perpetuation of running behaviour, although other factors also play a part.

The formation of a trail is facilitated by visual landmarks such as a coloured strip of hessian between the two entrances. This is especially so when the bees have previously learned to associate such a coloured strip with the entrance, as they tend to run along it after the old entrance has been closed. When all visual landmarks on the hive itself, such as the crack between the floor-board and the hive body, are eliminated by covering the whole hive (except the new entrance) with black polythene or unmarked hessian the trail is at first much broader, and is also less well defined later.

The most important factor in the maintenance of a trail once it has been formed (except for the number of bees flying) is an odour deposited by the running bees. A simple method of bioassay on this apparently persistent trail pheromone, which is probably perceived by chemotactic rather than olfactory receptors, was developed, and the active principle was obtained in solution and recovered from it. Also, active extracts were prepared from worker honeybees and from brood comb, although it has not yet been established whether the materials obtained from these two sources are identical. Attempts are being made (with Calam and Callow, Insecticides Department) to identify this pheromone, which seems to resemble the one deposited on a surface where a honeybee has alighted in search of food. It is quite distinct from colony odour, which plays a part in helping bees to recognise the entrance to their own hive once they have found it, because it is not colony-specific. It is also distinct from the Nassanoff pheromone, which is also not colony-specific. (Butler, Fletcher and Watler)

Production of drone comb. At various times during spring and summer the adult bees of colonies were shaken into empty hives and left to build comb. The proportion of drone to worker cells built was greatest during May; the first and more central combs that were built had fewer drone cells than the later outside ones, suggesting that drone cells were not built until there were sufficient worker cells for the colony's needs. Other experiments showed that the proportion of drone to worker cells built depended on the number of drone and worker cells already present, and when colonies had combs of worker cells added to them they produced a greater percentage of drone cells than when they had combs of drone cells added.

When combs were removed from colonies late in the summer the bees built worker cells only. The queens were removed from these colonies before they had laid eggs in the new comb, and comb built after this consisted entirely of worker cells. However, when a comb containing eggs and larvae was given to such a colony the bees built both drone cells and queen cells

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on it. It seems therefore that the presence of a queen, or of a queen larva, stimulated comb building in general. The lack of a queen by itself did not stimulate the building of drone cells; this stimulation happened with a queen larva but no queen. The relationship between the building of drone cells and the production of drones, and between queen rearing and drone production, remain to be determined. (Free)

Pollination and field behaviour

Factors stimulating pollen gathering. A population of bees foraging on a crop at any given time can usually be divided into at least three groups according to their behaviour. The bees of one group collect nectar only, those of another pollen only and those of a third collect both nectar and pollen. The behaviour of individual foragers seems to depend largely on the current requirements of their colony.

Because pollen-gatherers are often better pollinators than nectar-gatherers, attempts have been made to find out what makes bees collect pollen in preference to nectar. Brood in any stage of development, but particularly the larval stage, stimulates foraging in general and pollen gathering in particular. Experimental changes in the amount of brood present in a colony soon caused its foragers to alter their behaviour in such a way as to increase or decrease the amount of pollen collected. Although foragers are probably stimulated to collect pollen during direct contact with brood or, perhaps, with cells prepared to receive pollen, the smell of brood, or contact with bees that have recently been tending brood, is enough to stimulate pollen collection to some extent. Removing the queen from a colony did not affect foraging, but soon increased nectar collecting at the expense of pollen collecting. The presence of a queen, in addition to her brood, is necessary to maintain pollen collection. Feeding a colony with pollen increased the ratio of nectar-gatherers to pollen-gatherers, whereas feeding with honey had no influence on foraging. (Free)

Pollination of runner beans. It has been doubted whether honeybees can pollinate runner beans, although it has been assumed that the larger bumblebees can. The effect of honeybee visits to runner-bean flowers has now been investigated by growing runner-bean plants in large screen-cages with and without honeybees. Ripe pods on six plants in each cage were harvested every few days, and the pods on the remaining three plants in each cage left to produce mature seeds. Plants caged with honeybees produced nearly nine times as many pods and nearly seven times as many seeds as plants without bees, although the weight per pod and per seed was similar for both treatments. However, plants growing in the open produced more pods and mature seeds than those caged with honeybees, perhaps because caging affected plant growth adversely or because bumblebees visited the plants growing in the open throughout their flowering period, whereas honeybees did not begin visiting caged or uncaged plants until three weeks after flowering began.

In another experiment runner beans were grown in a large glasshouse and four plots, each containing 24 plants, were caged. A honeybee colony was

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put in one cage, bumblebee colonies in another and blowflies in a third; the fourth was kept free from insects. Three honeybee colonies were kept in the house to pollinate uncaged plants. During the first three harvests the plot without insects produced three pods, that with blowflies 37 pods, with bumblebees 222 pods, with honeybees 259 pods, and six uncaged plots produced an average of 257 pods each. These results indicate that in glasshouses honeybees are as successful as bumblebees in pollinating runner beans and can be used to produce earlier, and hence more profitable, crops. (Free)

Pollination in glasshouses. The behaviour of honeybees visiting the flowers of *Freesia refracta* in glasshouses was studied to find better ways of using bees as pollinators of glasshouse crops. As with other crops, pollen-gatherers proved to be much better pollinators than nectar-gatherers, and the proportion of the foragers of a colony that collected pollen was trebled by feeding the colony with sugar syrup. Even in the small enclosed area of a glasshouse (about 10,000 ft^2) the bees were most numerous on plants nearest to their hives and tended to work along rather than across the rows. Therefore, to distribute bees to the best advantage on a crop in a glasshouse, a single colony should be placed near the centre of the house; when two colonies are used they are best sited in diagonally opposite corners.

One nectar-gatherer was seen to expose her Nassanoff scent gland while in a *Freesia* flower, presumably in response to the large amount of nectar present. This is a very rare occurrence with the European honeybee, *Apis mellifera*, and seems only to have been reported once before (Frisch & Rösch, *Z. vergl. Physiol.* (1926) **4**, 1). (Free and Racey)

Tree fruit pollination. Attempts were made to wind-pollinate pear flowers. Air from a spraying machine was blown twice a day during the flowering period through a row of Conference trees into an adjoining block of Comice trees. The Comice trees adjacent to the Conference trees had 1·7% of their flowers set fruit compared with 1·3% in each of the next two rows, but in untreated blocks the set was 2·0% on the Comice row adjacent to the Conference and 1·6% on each of the next two rows. These results support those of previous experiments and indicate that wind pollination of fruit trees is negligible. (Free)

Bee diseases and pests

Paralysis. Thirty per cent of the comparatively few dead and moribund worker bees, but no more than 4% of drones, collected in traps beneath apparently normal colonies in summer contained as much chronic bee-paralysis virus (CBPV) as the 90% or more of the many similar bees trapped from colonies obviously affected by paralysis. CBPV was detected in bees from at least 15 of 18 apparently normal colonies out of flight range of those with paralysis.

Some paralysed bees from paralysis colonies are black and hairless, but the greater number of paralysed bees with normal body surfaces from the

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same colonies contained as much CBPV. Black hairless bees occur very occasionally in apparently normal colonies and contain as much CBPV as those from paralysed colonies.

Two colonies with paralysis were maintained throughout the year and yielded between 200 and 1,000 paralysed bees daily during summer. One of these colonies, which has now been headed by the same queen for three years, seemed normal in 1965 but yielded many paralytic bees in 1964.

Queens reared from paralytic colonies were used to replace those in ten normal colonies. One of these began yielding many paralytic bees about two months later.

Bees with paralysis symptoms sent from Mexico and Australia contained as much CBPV as paralysed bees from Britain and many other parts of the world (*Rep. Rothamsted exp. Stn* for 1965 p. 201) and of the same serological type. (Bailey)

Extracting paralysed bees with ether + carbon tetrachloride + water yielded more particles of CBPV that were better purified by differential centrifugation than were obtained by the previously employed carbon tetrachloride + water. Purified preparations divided into three components when centrifuged at high speeds (see Report of the Plant Pathology Department) and fractions composed mostly of particles that sedimented slowest were the least infective when injected into bees. The same schlieren diagram with three components was obtained in the analytical centrifuge with all preparations of CBPV whether obtained from naturally infected bees in the two colonies with paralysis or from bees injected in the laboratory with CBPV, even when the inoculum was composed mainly of the slowest sedimenting fraction.

Electron microscopy showed no particles of acute bee-paralysis virus (ABPV) in preparations of CBPV from bees found paralysed in colonies. Antiserum prepared against this CBPV cultured in bees in the laboratory was only little better than normal serum in neutralising the infectivity of ABPV, and antiserum prepared against ABPV maintained almost all its homologous titre when absorbed with CBPV from bees found paralysed in the field. This suggests the two viruses are scarcely, if at all, related serologically and that ABPV plays no part in paralysis in colonies, even though it seems to be common in most apparently normal bees. (Bailey with Gibbs and Woods, Plant Pathology Department)

Workers elsewhere have seen ABPV in sections of fat-body but not in other tissues of bees acutely paralysed with a Rothamsted strain of ABPV. The infectivity per unit weight of brains of bees paralysed with ABPV or CBPV is, however, at least equal to that of whole bees.

Specimens received of *Apis cerana* ssp. *indica* suffering from unknown diseases in India and Pakistan seemed to contain more ABPV than normal bees in Britain, but not enough to be certainly causing disease. (Bailey)

Nosema. Following reports from elsewhere that *Nosema apis* develops in tissues of adult bees additional to the ventriculus, especially in the hypopharyngeal glands, these glands were examined from the heads of bees found with mid-guts severely infected with *N. apis* in spring. Of the first 20 heads examined spores resembling those of *N. apis* were seen in a prepara-

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tion of glands from one. Of a further 80 heads of similar bees that were first washed no spores were seen in the gland preparations, but many in the washings. The surfaces of the bees' bodies seemed contaminated with spore-laden faeces, which are probably transferred sometimes to glands when these are dissected out of unwashed heads. (Bailey)

European foulbrood. Cultures of bacteria isolated in Brazil from diseased honeybee larvae were identified as *Streptococcus pluton* closely related serologically to that isolated from bees with European foulbrood in Britain. (Bailey)

Poisoning of bees by insecticides

Granular insecticides harmless to bees on beans. Spraying field beans with systemic organophosphates is the major cause of honeybees being poisoned by insecticides in England and Wales (Needham & Stevenson, *J. Sci. Fd Agric.* (1966), **17**, 133). The acreage of beans grown is now increasing and pollination by honeybees increases yields, so it is important to find a way to control bean aphis without killing bees. Experiments near Toddington, Beds., and Winchester, Hants., compared effects of organophosphate insecticides applied as spray and as granules during good weather when many bees were flying. Some honeybee colonies were beside each field, and others were enclosed in cages in the crop. The effects were assessed in five ways: the dead bees in front of the hives were counted; the population of each colony was estimated before and after the insecticide was applied; foragers in the crops were counted before and after the insecticide was applied; the cholinesterase activity was estimated in dead bees; the pollen collected in pollen traps was weighed and analysed.

Spraying with demeton-S-methyl or oxydemeton-methyl killed many bees, whereas applying granules of either disulfoton or phorate did not; indeed, no more bees than is customary died in colonies adjacent to fields that received granules, either when they were applied or subsequently, indicating that even after becoming systemic the insecticide did not harm bees collecting bean nectar and pollen. The granules effectively controlled bean aphis, so it is preferable to apply insecticide as granules rather than as spray, although further work will be necessary to know whether there are conditions in which granules may adversely affect bees. (Free and Racey; Needham and Stevenson, Insecticides Department)

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