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Report for 1969 - Part 1

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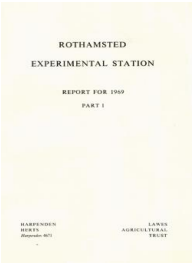
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PART 1

Bee Department

C. G. Butler

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BEE DEPARTMENT

C. G. BUTLER

The Department studies the development and social organisation of the honeybee colony, to find in what ways these depend on intrinsic and extrinsic factors, and how the factors can be manipulated or modified in ways advantageous both to beekeepers and to growers of fruit and seed. Work continued on the behaviour, physiology and pathology of the honeybee and on possible applications of some discoveries to practical beekeeping and seed production. Work also continued on the pathogens and pheromones of some insects other than the honeybee.

Behaviour and physiology

Queen piping. When 'grafts' (larvae taken from worker cells and put into artificial queen cells to be reared as queens) were placed in rearing frames in queenless colonies, more of those near the outsides of the frames than of those near the centres were rejected by the bees; a larger proportion near the outside also failed to hatch and those that did gave queens that piped less. When ten queens that piped much and ten that did not pipe at all were caged in mating nuclei, to facilitate their introduction to colonies, six of the ready pipers were alive the next day but all the non-pipers were dead. These observations support last year's evidence that the willingness of queens to pipe is influenced by the conditions under which they are reared. They also suggest that non-piping queens are defective in some respects and that queen rearing in our climate is most satisfactory in the warmest parts of colonies. (Simpson and Moxley)

Annual physiological cycle in colonies. During summer the hypopharyngeal glands of young bees are large and contain little invertase, whereas the glands of old bees are shrunken and contain much invertase. This age difference does not occur during autumn, when bees of all ages have large glands with much invertase. The glands also differ little with age during spring, but they are then large with little invertase. Thus, whereas the relationship of gland size to age undergoes a change during early summer that is reversed during late summer, the amount of invertase in the glands exhibits a one-way trend throughout the active season. It seems that the amount of invertase in the glands is least when the colonies have proportionately most brood to feed and that gland shrinkage with age is greatest when most nectar is collected. (Simpson)

Denatured sucrose for feeding bees. Results last year (*Rothamsted Report for 1968*, Part, 1, 224) showed that sucrose 'denatured' with 0·05% sucrose octo-acetate ('Octosan') and 0·002% of the dye 'Green S' was harmless when fed to caged bees in the laboratory. Field tests have now shown that it causes no harm to overwintering colonies. From 147 colonies that had

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very little honey in September 1968, 36, selected at random, were fed entirely with syrup made from such denatured sugar. The other 111 colonies were fed with pure sucrose syrup. By mid-April 1969, five of the test colonies and 12 control colonies had died, one test and seven control colonies were queenless; in the remainder, the average number of combs of brood per test and per control colony was 3·6 and 3·8 respectively, a difference not statistically significant. Thus the denatured sugar seems a satisfactory winter food for colonies. The unpalatibility of the sugar to people because of the 'Octosan', had disappeared by mid-April 1969, but the dye was permanent and visible even after the sugar syrup was diluted 1 : 100 with honey. The dye did not stain the combs. (Bailey)

Egg-eating by bumblebees. At about the time when a colony of the bumblebee, *Bombus lapidarius*, reaches its maximum size and produces males and queens, some of the workers try to open egg-cells and eat eggs. This behaviour was watched in a *B. lapidarius* colony whose bees were marked and later dissected to determine how much their ovaries were developed.

The workers initiated egg-cell building, but while a cell was being built, or after it had just been built, the queen attacked the builders, broke down the cell and ate any workers' eggs it contained. However, later the queen adopted some of these cells, laid in them and tried to defend them, not always successfully, against the workers.

Workers that built or demolished cells, laid or ate eggs, had ovaries that were more developed than average. Although workers sometimes attacked each other, they showed no evidence of any hierarchy of dominance correlated with ovary development, such as occurs in other species of bumblebees. The biological function of such egg-eating behaviour remains obscure. (Free, Weinberg, and Mr. A. Whiten)

Drone production. Observations were made of when large and small colonies of honeybees began to rear drones in each of several years, using about ten colonies each year. To provide the queen with a suitable and conveniently placed comb for rearing drones, a worker comb in the centre of which a piece of clean, drone comb (75 mm × 50 mm) had been fixed, was put in the middle of the brood nest during February. Each year, irrespective of size, all the colonies began to rear their first drones of the season within a few days of each other. Also, colonies that had been kept continuously for periods ranging from 5 to 16 weeks at mid-June temperatures and humidities, and in artificial light in a flight-room, began rearing drones at the same time as similar colonies outside in an apiary nearby. In a heated observation hive, the queen ignored the drone comb for several weeks while continuing to lay eggs in the surrounding worker comb. However, she then began to lay in the drone comb, but as soon as she laid an egg in a drone cell a worker entered the cell and ate the egg. After 11 days, the workers began to tolerate eggs laid in drone comb and to rear drones from them. The factors controlling this behaviour are being investigated. (Butler)

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Pheromones of queen honeybees. The technique for selecting young, mated honeybee queens for their power to inhibit queen rearing described in the *Rothamsted Report for 1967*, 213, has had to be modified because it entailed the use of too many worker bees. The modified method has the additional advantage that the rate the queen lays eggs can be measured under standard conditions. As expected from earlier observations, no correlation between inhibitory power and egg-laying was apparent. The future performance of young, mated queens whose inhibitory and egg-laying abilities have been measured are being recorded. (Butler and Watler)

It is hoped that by using objective methods of selection, such as piping by virgin queens (see above), and the inhibitory and egg-laying powers of young, mated queens, queen evaluation and selection will become quicker and more reliable.

In 1967, Butler (*Proc. R. ent. Soc. Lond.* (*A*) **42**, 71–76) obtained evidence that the 9-oxodecenoic acid contained in the mandibular gland secretion on a queen's body acts as an aphrodisiac and stimulates a drone to mount her when he finds her on her nuptial flight. At that time the evidence obtained suggested that 9-oxodecenoic acid is probably the queen's only aphrodisiac, which is perceived by the drone, while flying close to leeward of her, not only by smell, but also by frequently touching her body with his antennae and sometimes with his front-legs. Additional results this year strongly suggest that there is another aphrodisiac, probably olfactory, but perhaps gustatory, that is produced in gland pockets on the dorsal surface of a queen's abdomen. These glands are most active when the queen is ready to mate (Renner, M. & Baumann, M. *Naturwissenschaften* (1964), **51**, 68–69), and this substance may be an aphrodisiac that is perceived by the drone when he touches the queen's body with his antennae or front-legs. (Butler)

Pheromones of worker honeybees. Worker honeybees (*Apis mellifera*) often open their Nassanoff glands and disperse attractive scent while collecting sucrose syrup, especially when the syrup is free from a floral or other scent (*Rothamsted Report for 1968*, Part 1, 225). We now find that they also sometimes open these glands when collecting water, but usually only when the water is odourless. When water contains decaying vegetation and has a pronounced odour, or when an odour is added to pure water, they disperse scent less often. Presumably, dispersing Nassanoff scent near an odourless food source facilitates its discovery by searching bees.

It seems that foraging workers of *A. mellifera* rarely open their Nassanoff glands except when collecting water. Occasional opening of the Nassanoff gland when collecting nectar from glasshouse crops, and frequent opening on odourless sucrose syrup, is perhaps a response to great abundance of the desired material. (Free and Weinberg)

A pheromone that we have called 'footprint' substance, is distributed around the entrance of the hive by crawling bees, and it attracts other workers and stimulates them to enter the hive (Butler, Fletcher and Watler, *Anim. Behav.* (1969), **17**, 142–147). Bees detect it by smell from a short distance away, and possibly by taste. It is persistent but probably not

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colony-specific, perhaps not even species-specific. Although deposited by the workers' feet and perhaps a little by the tip of the abdomen (as we have recently discovered by making bees leaving and entering their hives crawl over smoked glass plates) it occurs all over the body, but is most abundant on the thorax, and is probably produced by glands on most parts of a bee's body. Worker 'footprint' pheromone persists for at least four hours at 23°C and longer when colder, many times longer than Nassanoff pheromone with which dishes of food are seldom, if ever, contaminated because the feeding bees disseminate this pheromone into the air rather than on to the food or substrate. Bees that were feeding on sucrose syrup from a glass dish and were disseminating Nassanoff scent, were made to stand on, and feed through, large mesh wire-gauze that completely covered the dish. After removing the wire-gauze, through which some of the Nassanoff scent in the atmosphere could be expected to have passed and reached the dish and its contents, these were found to be no more attractive to bees than a clean dish of syrup. The wire-gauze on which these bees had stood attracted other bees but no more than a similar piece of wire-gauze on which the same number of bees had stood for a similar length of time without exposing their Nassanoff glands. Nassanoff pheromone freshly released by bees flying around, or feeding at, a dish of syrup, apparently attracts other bees nearby, but it is the 'footprint' pheromone deposited on a dish that makes such a dish more attractive than a clean one. This is a point that needs to be considered both when planning experiments and trying to interpret their results.

Both queen and drone honeybees also deposit 'footprint' pheromones on surfaces on which they crawl; when tested on food-seeking bees in the field they were indistinguishable from those of worker honeybees—being neither more, nor less, attractive. However, differences were found when comparisons were made in the hive, where the queen's 'footprint' pheromone was much more attractive than the 'footprint' pheromones of workers or drones to worker honeybees. Presumably, the worker, drone and queen honeybee share a common 'footprint' pheromone, but the queen has an additional substance that strongly attracts bees in the hive. (Butler)

Field behaviour

Response to shapes and patterns of flowers. Flat, cardboard models were used to study the responses of honeybees to flower-like shapes and simulated nectar-guides (visual patterns leading towards the nectaries of flowers). Bees preferred models with disruptive outlines (e.g. petaloid or star-shaped) to circular ones, even when they had been trained to collect sucrose syrup from the circles. Radially symmetrical models were preferred to bilaterally symmetrical ones. Adding to models 'nectar-guides', contrasting in colour with their background colours, greatly increased their attractiveness. 'Nectar-guides' consisting of dotted guide lines were more attractive than those consisting of solid lines, and a group of dots was more attractive than a black circle in the centre of a model. Models with both disruptive outlines and 'nectar-guides' were more attractive than those with either one of these attributes.

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Most bees alighted at the periphery of a model, few at its centre even when guide lines radiated from it. However, once bees had learned to collect syrup from the centre of a model with guide lines radiating from its centre, they later used the simulated nectar-guide pattern when seeking the syrup. Although bees showed no innate preference for the region around the point from which the guide lines radiated, they could easily be trained to seek food in this region, whereas they were less easily trained to seek it in places where the guide lines were furthest apart. Attempts were also made to give a three-dimensional illusion to models, but the bees did not respond to these. (Free)

Foraging constancy of bumblebees. The foraging behaviour of bumblebees and their constancy to one species of flower during consecutive trips and from day to day was studied by removing and examining the pollen pellets of marked foragers when they returned to their nests. Nearly all the bees collected only nectar on some trips, and pollen on others. A third of the loads collected by two *Bombus lucorum* colonies and two-thirds of those collected by two *B. agrorum* colonies contained pollen of more than one species. As with honeybees, the bumblebees obtained most of their pollen from a few kinds of plants, but small amounts from many others. Loads of the most frequently collected pollens tended to be the most pure. The most commonly collected pollen was also often a minor constituent of loads consisting predominantly of other pollens. In general, the day-to-day constancy of *B. lucorum* foragers equalled that of honeybees, about 70% keeping to their original sources of pollen throughout the ten consecutive days they were observed.

When a bumblebee deserted one kind of flower for another, it sometimes made the change abruptly but, more often, it visited, and collected food from, both species on several trips before making the change. However, mixed loads of pollen did not necessarily indicate that a bee was in process of transferring its attention from one species to another. Some bees habitually collected the same mixtures of pollens, even in similar proportions, on consecutive trips that sometimes extended over several days. Sometimes, even the proportions of the different species of pollen in the mixed loads remained similar from trip to trip. No regular pattern of change from one species to another during the course of the day was observed; nor did bees that collected pure loads from two or more species of plants each day, collect a load from each species at a regular time of day.

The two *B. lucorum* colonies, at the same time and place, exploited the flora in ways that differed too much to be explained by random foraging by individual bees. Perhaps the odour of the predominant pollens in a nest induces the foragers to seek these pollens when they begin foraging. It seems that the constancy of individual *B. lucorum* foragers is not determined by the flora alone, but also in some way by their colonies. A similar, primitive method of communication may also influence the choice of flowers visited by honeybee foragers. Although introducing a strange odour into the atmosphere of a hive does not induce honeybee foragers to search for it, introducing the odour into their food stores does, even when the bees have been conditioned to visit other food sources. However,

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when their search is unrewarded they soon return to their original sources of food. (Free)

Bee diseases and pests

Paralysis. Tests were made with the antibiotic fumagillin, often used to control infection by *Nosema apis*, following a report from a drug manufacturer that beekeepers had found it cured paralysis. Bees fed chronic paralysis virus mixed with antibiotic at twice the suggested concentration in syrup and subsequently fed *ad lib.* on the same antibiotic concentration were as susceptible to paralysis as bees fed plain syrup. Similarly, bees injected with only few infective doses of virus were not protected when fed the antibiotic. Many spontaneous recoveries of colonies with paralysis have been observed at Rothamsted, and the recoveries noticed by beekeepers probably resemble these rather than being related to any common treatment. (Bailey)

Nosema apis. Samples of drones and of worker bees were collected simultaneously from the same colonies in spring, and the infected individuals of each kind of bee counted. Many fewer drones were infected than workers. Nevertheless, the median infective dose for newly emerged drones in laboratory tests—about ten ingested spores—was no more than that for workers of similar age. These results support previous conclusions that natural infection is not carried primarily in food but that comb-cleaning worker bees become infected when they ingest faeces deposited by infected bees. As drones do not clean combs, they are less likely to become infected than workers. Those that become infected probably had been fed by workers that just previously had been cleaning up infected faeces. (Bailey)

Sacbrood. Sacbrood virus multiplies in adult drones, much of it in their heads, when injected into their haemolymph. According to electron microscopy and serology, about 10^{11} or 10^{12} particles of sacbrood virus developed in the head of an infected drone—about a thousand times the number of particles that develop in similarly infected adult worker bees—and most were in the brain. This was unexpected because the infection caused no overt symptoms. Moreover, the lives of infected drones, kept in cages at 35°C with uninfected workers, was shortened only slightly, although significantly, from 25 days to about 21 days, and much virus was still in infected drones at the end of their lives. By contrast, acute bee-paralysis virus, which has particles the same size and shape as those of sacbrood virus and which multiplied about as much and as quickly as sacbrood virus in the brains, killed drones within six days. Sacbrood virus multiplied most in the youngest drones, which contained most particles within three days of infection. The median infective dose of sacbrood virus by injection for drones is between 10^5 and 10^6 particles—about one hundred times as much as for workers. By mouth, the dose is between 10^8 and 10^9 particles, about the same as for workers and about ten times that for larvae. The susceptibility of drones to infection by mouth decreases

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rapidly with age, as with workers, until they are seemingly immune when about seven days old. Sacbrood virus was readily detectable by serology in extracts of the heads of infected drones, which makes them both more convenient and sensitive for bioassay than larvae. For example, injecting drones with extracts of the heads of two laying queens, which had been injected with sacbrood virus three weeks and six weeks previously, showed that the virus had multiplied in the queens. As previous tests suggested, but then without the knowledge that the virus had multiplied when injected, queens infected with sacbrood virus did not transmit sacbrood to their offspring. Similarly, newly emerged queens that were successfully infected by mouth with sacbrood virus did not transmit sacbrood, but only two out of ten queens that were fed virus and later mated produced much worker brood.

Although sacbrood virus can multiply in adult worker bees and become especially concentrated in their hypopharyngeal glands (*Rothamsted Report for 1968*, Part 1, 229), there is no direct evidence that larvae become infected from this likely source. Attempts to obtain such evidence were made by twice establishing colonies during late summer that contained a normal, laying queen and about one thousand worker bees, each of which was infected by injection with sacbrood virus. However, most of the very few larvae that were reared were healthy and developed into apparently normal workers. Possibly infected adult bees transmit sacbrood virus more during spring, when sabrood affects most larvae in nature, but it seems remarkable that they can, under some circumstances at least, feed larvae with secretions from their hypopharyngeal glands, which are rich in virus, without infecting the larvae. The only unusual behaviour of the infected worker bees in the small colonies, except for their reluctance to rear many larvae, was the so-called 'washboard dance', regularly performed by many individuals when it could not be observed in similarly small, uninfected colonies. (Bailey)

European foulbrood. Virus-like particles isolated from larvae that apparently died of European foulbrood (EFB) in France were pathogenic, and the suggestion has been made elsewhere that EFB is caused by a virus and not by any of the several kinds of bacteria associated with the disease. Preparations of the virus received at Rothamsted and examined by electron microscopy contained particles resembling those of sacbrood virus. They multiplied when injected into drones and were serologically indistinguishable from those of sacbrood virus. As this virus was not detected in preparations of larvae with EFB from several sources in Britain, it can be concluded that sacbrood and EFB are independent; the common occurrence of sacbrood makes it probable that both diseases will occur simultaneously in some colonies.

Combs from colonies with EFB and that had been subsequently irradiated with gamma radiation by Canadian workers were received at Rothamsted where the surviving bacteria were identified and counted. Almost as many colonies of *Streptococcus pluton* could be cultivated in agar from extracts of the combs that had been exposed to most irradiation (0·8 M rad) as there were cocci + clumps of cocci to be seen microscopically. Thus,

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S. pluton seems especially resistant to gamma radiation. The irradiated combs again caused EFB when they were placed in uninfected honeybee colonies in Canada. (Bailey)

Pathology of other insects

Wax moth. Tests were made with non-occluded virus—'dense-nucleus' virus—of *Galleria mellonella* after reports from elsewhere that the virus effectively protects honeybee combs against wax moth larvae. Enclosed cultures of wax moths on honeybee combs died out eventually after infected wax moth larvae had been placed in them, but not until after unacceptable damage had been done to the combs. Attempts to protect combs were made also by dusting them with powdered preparations of the dried remains of caterpillars killed by the virus. Such caterpillars still contained much infective virus many weeks after drying. Apparently up to about 10^5 median lethal doses by mouth for young larvae should have been in each desiccated larva according to previous feeding and injection tests with preparations of partially purified virus. However, about 35 desiccated larvae had to be dusted on to one British standard brood comb to prevent serious damage by new infestations: the virus from one desiccated larva was enough to kill sufficiently quickly only about one hundred larvae. There seems no simple and effective way of controlling wax moth with the virus, which seems to lose infectivity quickly when it is thinly dispersed, and its use will depend on finding a way to maintain its infectivity. Similar tests with a polyhedrosis virus of *G. mellonella* (*Rothamsted Report for 1963*, 167) showed that the larvae are not susceptible enough to this persistent virus to make it a simple and adequate means of control. (Bailey)

Entomophthoraceae on Wheat Bulb fly. About one hundred Wheat Bulb flies per week were collected from the beginning of July to the middle of September in Stackyard field, to estimate the incidence of infection by fungi of the family Entomophthoraceae. One fly of each sample collected on 23 July, 7 August and 13 August, respectively, died infected with *Entomophthora muscae*. On these flies, conidiophores and conidia developed, but one collected on 20 August died later with its abdomen full of resting spores of *E. muscae*. One fly collected on 27 August was infected with *E. dipterigena*.

Female Wheat Bulb flies were collected from Brent Pelham, Hertfordshire, in July. The percentage of flies dying infected with *E. muscae* were 8% of 200 collected on 24 July, 0% of 200 collected on 29 July and 2% of 270 collected on 30 July. Many flies collected at Barton Bendish, Norfolk, on 14 July were also infected with *E. muscae*.

E. muscae was consistently transmitted from infected Wheat Bulb flies, scatophagid flies and syrphid flies to healthy individuals of the same host or host family, but never, under identical conditions, from one of these hosts, or host families, to another. This supports the conclusion that the fungus exists in strains adapted to specific hosts.

Most Wheat Bulb flies infected and killed by conidia discharged from

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flies infected with *E. muscae* become annulated, with dense growths of conidiophores between the abdominal segments, but some developed symptoms, described previously from field-collected flies (*Rothamsted Report for 1967*, 218), in which the abdomen became ventrally distended and contained many spherical resting spores, each about 37·5 μ in diameter. Clearly these are, as was then suspected, the resting spores of *E. muscae*. (Wilding)

Entomophthoraceae on aphids. Two samples, each of 50 pea aphids (*Acyrthosiphon pisum*), were taken from lucerne each week for 13 weeks, from two sites on Fosters field to estimate the incidence of *Entomophthora* spp. From May to July, a small percentage of aphids, up to 10% on 28 May, were consistently found infected with *E. thaxteriana* but none was found with *E. aphidis*, which was a common pathogen of pea aphids on lucerne on Highfield in 1968. On 22 July, one aphid was found infected with *E. planchoniana*, not previously recorded from pea aphids during three seasons of sampling at Rothamsted. Pea aphids were scarce after the end of July when the percentage parasitised by Hymenoptera was large. The population of aphids failed to increase again until October, when none was found infected with *Entomophthora* spp.

Entomophthora spp. were noted on bean aphids (*Aphis fabae*) at the beginning of August. Six samples, each of 50 aphids, were taken from field beans on an area of Little Hoos field not treated with insecticide. Table 1 shows the percentages of these dying infected with *Entomophthora* spp. (Wilding)

TABLE 1

The incidence of Entomophthora *spp. on bean aphids*

Sampling date	% infected with*				% parasitised by Hymenoptera
	E. aphidis	*E. freesnii*	*E. planchoniana*	*E. thaxteriana*	
4.8.69	4	28	2	20	0
5.8.69	2	26	14	6	2
6.8.69	2	62	6	6	4
7.8.69	4	46	12	4	0
8.8.69	6	52	4	4	0
11.8.69	8	74	0	0	0

* More than one species of *Entomophthora* rarely occurred on one aphid and when it did only the dominant one was counted.

Effect of light and humidity on conidial discharge. In laboratory experiments at 15°C in constant light, conidia of neither *E. aphidis* nor *E. thaxteriana* on pea aphids were discharged below 90% relative humidity. Eleven times more of *E. aphidis* and seven times more of *E. thaxteriana* were discharged at 100% than at 95% relative humidity. Twice as many conidia of *E. aphidis*, and 1·2 × as many of *E. thaxteriana*, were discharged when the infected aphids were placed on a wet substrate in a saturated atmosphere as in a saturated atmosphere only. Preliminary observations showed that many conidia of *E. muscae* on infected scatophagid flies were discharged at 80% but more were discharged at 100% relative humidity.

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At 20°C, conidia of *E. thaxteriana* began to be discharged 6–9 hours after the pea aphids died and discharge was most 9 hours later, when in constant light or dark. However, in the dark the most conidia discharged per hour was 2×10^3/aphid, one quarter as many as in light, but the maximum rate in the dark was maintained for 10 hours whereas in light discharge rapidly declined after reaching the maximum; 26 hours after the death of the host, and thereafter, the discharge rate was similar in light and dark. The total number of conidia discharged in the dark 5×10^4, was about half that in light. When light was alternated in 12 hourly periods with darkness, the number of conidia discharged was intermediate between that in the light and dark. Rate of discharge was doubled two hours after light was admitted and halved two hours after the light was excluded. Previous results (*Rothamsted Report for 1968*, Part 1, 231) from experiments in dim light were intermediate between those recently obtained in constant darkness and constant light.

Entomophthora conidia were counted on slides from a Hirst spore-trap that had been operated constantly from May to September 1958 at Silwood Park, Berkshire, for other studies on air-borne particles. During the period from 25 June to 24 July, when the average concentration of conidia was 114/m³ (maximum 2964/m³), as calculated from hourly samples, the largest aerial concentration of each of five 'types' of *Entomophthora* conidia typically occurred at 05.00–07.00 h and was associated with humid air and sunrise. The smallest concentration occurred between 14.00 and 17.00 h when relative humidity was small. These observations correspond with the results from experiments in the laboratory. (Wilding)

Staff

Mrs. L. M. Hossack, J. Schmid, T. Scott-Hibbert and Clare I. Pearce left and L. K. Graham, Mrs. F. Hornby, Sally A. Jennings, P. Read and Cheryl White were appointed.

C. G. Butler attended the VI Congress of the International Union for the Study of Social Insects in Berne and J. B. Free the XXII International Beekeeping Congress in Munich.

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