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Food transmission within the honeybee community

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Six bees were trained to a dish, from which they collected 20 ml. of sugar-syrup containing radioactive phosphorus. The distribution of radioactivity among the bees and larvae of their colony of 24 500 bees was then studied.

62 % of the foragers and 16 to 21 % of all the bees in the hive were radioactive within 4 h. 76 % of the foragers and 43 to 60 % of all the bees were radioactive within 27 h. The nurse bees were significantly less radioactive than the house bees and the foragers significantly more so. Within 48 h all the large larvae in unsealed cells were radioactive. These results are attributed to widespread food transmission.

Food transmission is suggested as the foundation of the division of labour within the honeybee community and of the similar odour produced by the members of each colony, which serves for mutual recognition.

Food transmission would enable slow-acting insecticides contained in their food to be widely distributed among the members of a honeybee colony.

Introduction

Experiments which form the subject of the preceding paper (Ribbands 1952) showed that the division of labour among the honeybee community was not controlled by the ages of the worker bees. These results suggested that the duties of any individual are the resultant of the requirements of the colony and the age of that individual, and that the requirements of the colony are determined by its food supply and play the predominant role.

The present experiments were designed to discover whether there is a widespread food transmission which could serve as a means of communication between members of a colony and thus provide a basis for their social organization. A few marked bees from known colonies were fed with small quantities of syrup containing radioactive phosphorus, and the distribution of the radioactivity within the colonies was then studied.

Choice of radioactive element

^{32}P was selected because of its suitable half-life, easily measured radiation and general convenience in handling. The choice of a non-specific tracer clearly makes it impossible to draw from our results any conclusions about the metabolism of the sugar-syrup used. It can only be justified when the measurements are to be made soon after the administration of the tracer and when qualitative indications of the presence of radioactivity are sufficient. The only possible specific tracer element would have been ^{14}C, and this was rejected because of difficulties in detecting and measuring the very weak β-radiation.

Radioactive dose received by the bees and the possibility of radiation damage

Apart from the trained and marked individuals which actually carried the radioactive syrup into the hive and which were subsequently rejected from the samples drawn for detection, the very few bees with the highest activities contained about 10^{-3} μC. Assuming that about three-quarters of the radiation was absorbed in the bodies of these individuals, the dose they received was at the rate of about 0·2 röntgen equivalent physical per 24 h. Most of the bees received very much less than this, and we have no evidence that any effects attributable to radiation damage played any part in this experiment.

Experimental methods

The experiments were made when the carbohydrate requirements of the colonies were in excess of supplies available from the field, so that little of the radioactive syrup was stored.

The syrup was administered by training a number of bees to take sugar-syrup from a dish placed a short distance from the hive. During the training period the dish contained no radioactive material. When the bees had been trained, marked, and the weather was suitable, the dish was replaced by another which contained syrup together with radioactive phosphorus in 0·01 M-NaH_2PO_4. During the feeding of the radioactive syrup all newcomers were removed and killed. When all the radioactive syrup had been carried into the hive the empty dish was removed.

Samples of bees were then withdrawn from the hive at intervals. Each bee in each sample was later examined for radioactivity, using an end window-counter tube attached to a rate-of-count meter. The background count was about 20 to 30 counts/min with an unshielded tube, and bees were scored as radioactive when the count was greater than 150 counts/min with the bee almost touching the counter window. It is therefore inevitable that our results underestimated the amount of food transfer which took place, because all those individuals which had not received activity sufficient to give at least 150 counts/min (equivalent to about 40 μg of syrup in the second and third experiments) are recorded as 'inactive'. At the outset it was considered desirable for the error to be in this direction rather than in the other, because some bees might have received traces of syrup by external contact. In experiment 3 the possibility of any such transfer was checked by making separate examinations of dissected legs, wings and heads from twenty-five radioactive bees. No activity was detectable on these parts, which would clearly have become contaminated had external contact been important in spreading radioactivity in the colony.

At the conclusion of each experiment all the bees in the colony were shaken off their combs and weighed. A sample was then weighed and counted, so that the population of the colony could be calculated.

Distribution of the radioactivity

In experiment 1 five individually marked bees were used as carriers. On 22 March 1950 they took home 10 ml. sugar-syrup containing *ca.* 20 μC of ^{32}P in 201 loads. The colony contained 12800 bees. A sample of 350 bees was taken from the colony 24 h after treatment and 64 % were radioactive. The sample was drawn by shaking half the nucleus into a container, shaking the container and then transferring the required number of bees into a tin, which was then placed in a refrigerator at 0° C until the bees were dead.

In experiment 2 nine marked bees were used as carriers. Between 11.05 and 12.05 h B.S.T. on 25 April they took away 20 ml. of sugar-syrup, which contained 100 μC of ^{32}P, in 271 visits. The colony contained 2500 bees. The first sample was collected at 15.45 h on the day of the experiment and the second 24 h later. The samples were taken in the same manner as in experiment 1.

The first sample contained 240 bees, 92 % of which were radioactive. 73 % had received 40 to 250 μg of the syrup and 19 % had received more than this amount. There were 338 bees in the second sample: 98 % were radioactive, 85 % had received 40 to 250 μg syrup and 13 % had received more than 250 μg.

In experiment 3 six marked bees acted as carriers. Between 12.30 and 15.45 h B.S.T. on 21 August 1951 they took away 20 ml. sugar-syrup, containing 100 μC of ^{32}P, in 379 loads. The colony contained 24600 bees and occupied a National brood-chamber and two supers. The upper super was filled with honey, while the lower super and the brood-chamber contained honey and brood.

The first sample of bees was collected at 17.30 h on the day of treatment and the second at the same time 24 h later. Each bee was collected in a separate specimen tube, so that external contamination with syrup could not occur after the bees were collected. The entrance to the hive was blocked and the returning foragers were collected. The hive was then opened and either six, twelve or twenty-four worker bees collected at random from each comb. The drones were collected from wherever they could be found, mainly from the brood chamber. The results are shown in table 1.

TABLE 1. DISTRIBUTION OF RADIOACTIVITY AMONG ADULTS

type of bees	first sample (*ca.* $3\frac{1}{2}$ h)		second sample (*ca.* $27\frac{1}{2}$ h)	
	no. of bees	% radioactive	no. of bees	% radioactive
top super	63	21	134	60
bottom super	69	16	132	53
brood chamber	135	18	255	43
foragers	71	62	144	76
drones	—	—	95	27

The foragers became radioactive much more quickly than the rest of the colony. Even in the second sample the difference between the proportion of radioactive foragers and that of the next highest group, the bees in the top super, was highly significant ($\chi_c^2 = 7{\cdot}5$, $P = 0{\cdot}007$). In the same sample the difference between the bees in the top super and those in the brood chamber was also significant ($\chi_c^2 = 6{\cdot}1, P = 0{\cdot}013$). Foragers had the highest proportion of radioactive individuals, and idle foragers congregate around the brood nest. Nearly all the foragers were present at the time of sampling, and they must therefore have helped to obscure the observed difference between the bees in the brood chamber and the bees in the supers.

In this experiment the distribution of radioactivity among larvae and in honey was also studied, in a count of brood taken from the hive 48 h after the treatment. The larvae were divided into three groups—those in recently sealed cells, and large and small ones in unsealed cells—and each larva was separately examined for radioactivity. The groups were then weighed, digested in sulphuric acid, and the activity of each group determined by counting in a liquid counter attached to a scaling unit. The results, expressed in terms of μg of the original radioactive syrup received by each larva, are shown in table 2. The radioactivity in the 'inactive' groups was measurable when a number of larvae were taken together and counted with the liquid counter and scaling unit, even though individuals forming the sample had been 'inactive' within the definition previously given, i.e. had given less than 150 counts/min when tested with the rate of count meter.

Every one of the eighty-five large unsealed larvae was radioactive, so that food had been disseminated throughout this group. The 'inactive' unsealed larvae were very small ones, which were for the most part still receiving a diet of pure brood food. The sealed larvae were taken from cells in the vicinity of unsealed larvae, and so were the youngest members of this group. Those which were radioactive must have been unsealed at the time of the treatment.

The counter detected radioactivity wherever it was placed over portions of the comb which contained unsealed honey (it covered about twenty cells at any one time). Honey samples were then taken at random from seven unsealed cells scattered over the surface of the comb. The honey was removed on a small tuft of cotton-wool held in tweezers and the activity of a suitably diluted sample determined with the liquid counter and scaling unit. The method was unsatisfactory because it was difficult to extract all the honey without breaking into adjoining cells. All the cells examined had received some radioactive syrup, but the amounts varied widely (3·3, 4·2, 11·7, 20·2, 25·3, 34·4 and 100 μg syrup per cell).

TABLE 2. DISTRIBUTION OF ACTIVITY AMONG LARVAE

third sample, 48 h after feeding

larvae type	no.	% 'inactive'	% radio-active	mean wt. of a larva (g)	μg radioactive syrup per larva to give observed activity
sealed	86	40	60	0·146	65
				0·144	19
large unsealed	85	0	100	0·119	167
small unsealed	214	74	26	0·047	66
				0·028	1·6

UNIMPORTANCE OF FOOD DISSEMINATION FROM DANCING BEES TO RECRUITS

Von Frisch (1946) reported that, before and during intervals between dancing, successful foragers distributed small quantities of nectar to potential recruits.

Experiment 4 was designed in order to determine whether radioactivity was rapidly transmitted among the foraging population because they received small amounts of syrup from dancing bees. On 25 August 1951 twelve marked bees were trained to a dish of dilute sugar-syrup; concentrated syrup which contained radioactive phosphorus was then substituted, and recruits began to arrive. The weather was very unfavourable, so recruits came very slowly. Sixteen were collected during the next 40 min; four were radioactive and twelve inactive.

One of the radioactive bees had received about 5000 μg syrup; the other three from 50 to 150 μg. The inactive bees had received less than 45 μg. This result indicates that dissemination of small quantities of nectar may not be an essential preliminary to successful recruitment. Such distribution would certainly be insufficient to explain the widespread food transmission which is now recorded.

THE EXTENT OF THE FOOD TRANSMISSION

The results of the first two experiments are valuable in so far as they confirm that the results obtained in the third experiment were not exceptional. In all three experiments a high proportion of the bees became radioactive within 28 h. This radioactivity is attributed to food transmission, because analyses of the heads, wings and legs of radioactive bees in experiment 3 showed that external contamination was not responsible.

Experiment 3 shows that incoming nectar was rapidly passed round among the foragers. The proportion of radioactive individuals in the top super was second only to that of the foragers, indicating that a proportion of the syrup was handed on to house bees, which then took it up into the supers for ripening and storage. The proportion of radioactive individuals among the bees in the brood chamber, most of which must have been nurse bees, was significantly less than in any other group of workers. The diet of nurse bees must be different from that of the other members of the community; they utilize much larger quantities of protein and possibly smaller quantities of carbohydrate; this could account for the lower proportion of radioactive individuals found.

All larvae of appropriate age obtained a share of the incoming syrup, and they must have received this from the nurse bees. The activity was more evenly distributed among the larvae than among the nurse bees, presumably because each larva was visited by many different nurses.

The lowest proportion of radioactivity was found among the drones. The diet of drones within the hive has not been investigated. If they lived upon nectar they might be expected to share incoming supplies and to show a higher proportion of radioactive individuals than the foragers, because they are larger. The present results are consistent with the supposition that they are fed upon brood food; the proportion of radioactive individuals among them might then be expected to be even lower than that among the nurse bees. The results of Alpatov & Saf'yanova (1950) would support such a hypothesis.

The economic importance of the food transmission

These results also illustrate the ease with which any slow-acting insecticides which might be contained in their food could become distributed through a honeybee colony. They could explain some of the phenomena associated with parathion poisoning of honeybees (Palm 1951).

Similar food transmission among ants would explain the success of thallium sulphate as an ant eradicator (Popenhoe 1926), and it is likely that some method of poison-baiting would be effective against other noxious social insects.

The function of food transmission

Roubaud (1916) showed that there was reciprocal feeding between some wasps and their larvae, and emphasized the social significance of this process. Wheeler (1918, 1928) elaborated the view that reciprocal feeding, or 'trophallaxis', was the 'social medium' of termites, ants and wasps, and possibly of all other social insects. Brian & Brian (1952), however, have produced evidence that the larval secretions of wasps are not attractive to adults.

Reciprocity of these transactions, which Wheeler postulated, is not essential, although it may have played an important part in the evolution of the habit and may still exist.

Lineburg's (1924) observations on the feeding of honeybee larvae are complementary to the present results. He found that nurse bees made more than 10000 visits to each larvae during its 5 days of development and suggested that this very large number of visits was circumstantial evidence of food exchange. King (1928), however, reported that nurse bees placed food at random in the cells and not into the mouths of the larvae, so that reciprocal feeding was impossible. The very large number of visits seems at first sight to be unnecessary, but they do ensure that each larva is fed by many different nurse bees; thus the diet which each receives is almost identical, and this distribution could enable all the larvae to be affected by any major change in the food supplies of the colony.

An observation of food dissemination by adult honeybees was made by Park (1923). In spring, when bees gather water for brood rearing, Park filled the feeder of a small nucleus (2600 bees) with coloured water. The following morning the abdomens of about half the bees were coloured and distended, and most of them contained a mixture of honey and water. In temperate climates honeybees do not store water in combs, and Park considered that they were using their honeysacs as reservoirs.

The present results involve only very small quantities of syrup, the widespread transmission of which cannot be related to storage requirements. It is considered that the dissemination has a more important function, in that the efficient organization of the community life depends upon it; food supply determines what proportion of the colony will be required for each task, and the ages of the individuals helps to decide which of them will respond to these requirements (Ribbands 1952). In these circumstances an efficient and adaptable division of labour can ensue as a consequence of widespread food transmission, which ensures that all the bees appreciate any changes in the food supply.

Other experiments have since shown that the honeybees of each colony produce a characteristic colony odour, which its members can distinguish from other colony odours and which serves as a means of communication between them (Kalmus & Ribbands 1952). These distinguishable odours are not inherited, but acquired. They can be explained by the hypothesis that all the foraging bees in a colony receive a similar food supply, which gives rise to similar waste products when it is consumed, and that the aromatic portions of these waste products are utilized to produce similar odours. The present results agree with this hypothesis by showing that food is rapidly and thoroughly shared among foragers. It is therefore suggested that in the honeybee community food transmission is the foundation of both division of labour and mutual recognition.

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The origin of the odours by which honeybees distinguish their companions

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Groups of 20 to 50 foragers from two different honeybee colonies were trained, in turn, to syrup in two dishes 1 to 3 ft. apart. Both groups were then allowed to visit their dish at the same time, and newcomers were then found to be preferentially attracted to the dish visited by members of their own colony.

This preferential attraction was shown to be a consequence of distinguishable odours emitted by the workers. These odours were not genetically inherited but were derived from metabolic differences between their colonies. These differences were produced by changes in food supply, and probably also through differences in breeding rhythms. They would develop between queenless halves of colonies.

Uniform and distinguishable colony odours are a consequence of widespread food transmission among the foragers of each colony. The role of olfactory recognition in the social life of the bee is discussed.

Introduction

The existence of different colony odours, distinguishable by honeybees but not by man, used to be assumed by many beekeepers and naturalists (Bethe 1898; v. Buttel-Reepen 1900) and many methods of queen introduction are still based on this belief (Snelgrove 1940). However, conclusive evidence for the existence of such odours has been lacking and honeybee behaviour towards robbers and towards strange queens, formerly expressed in terms of colony odour, appeared capable of other explanations, so the belief in distinguishable colony odour has dwindled. Current opinion on this subject was adequately reflected by Brother Adam (1951) at the 14th International Beekeeping Congress, thus: 'By the term "colony odour" it is assumed that each bee emits a scent which imparts to every member of a colony a uniform and distinctive odour, and that this odour varies from colony to colony. However, no positive evidence has ever been brought forward to warrant this assumption....There may be such a thing as "colony odour", but all the evidence seems to disprove its existence.'

Little attention has been paid to the work of v. Frisch & Rösch (1926), which showed that foraging honeybees preferentially attracted bees from their own