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RELATIONSHIPS BETWEEN POLLEN, BROODREARING AND CONSUMPTION OF POLLEN SUPPLEMENTS BY HONEYBEES

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SUMMARY

Two field experiments with a commercial pollen supplement provide information on possible relationships between pollen, broodrearing and consumption of the supplement. When colonies were provided with the supplement continuously for one year, the results showed that broodrearing was initiated and maintained by pollen, and that consumption of the supplement varied in direct relationship to the rate of broodrearing. In a second experiment, colonies on a nectar flow, but virtually devoid of pollen, did not consume the pollen supplement, and reared larvae from less than 20 % of eggs laid. When an extract of pollen was added to the supplement, the bees consumed it readily, and eventually reared larvae from 91 % of eggs laid. The extract of pollen induced the bees to eat the supplement and the author suggests that this caused their hypopharyngeal glands to become active so that they could feed more newly emerged larvae. The author also suggests the presence of a chemical or chemicals in pollen which may serve as a trigger to activate the hypopharyngeal glands and that bees secreting larval food would then feed on supplements that do not contain the primary phagostimulants that are contained in pollen.

INTRODUCTION

Development of a complete replacement for pollen in the diet of the honeybee *Apis mellifera* L. is a primary aim of research into the nutrition of honeybees. It has become evident that few of the major problems that have arisen in the development and use of pollen substitutes have their origin in nutritional inadequacies of the synthetic foods. Instead, they appear to be due in the main to the effects of some major factors associated with the behavioural and physiological processes that are involved in feeding and broodrearing by honeybees.

This paper discusses the results of two experiments that provide information on the possible relationships between pollen, broodrearing and the consumption of pollen supplements.

METHODS AND RESULTS

For convenience and clarity of discussion, the two experiments are considered separately.

Experiment 1

In a field experiment to examine the effects of a commercial pollen supplement on honey production (DOULL and PURDIE, 1966) five colonies were provided continuously with the supplement for one year. The hives were moved at intervals to take advantage of a succession of honeyflows, and throughout the year supplies of pollen fluctuated between extreme abundance and extreme scarcity.

Amounts of pollen available to the bees were estimated by measuring areas of pollen stored in the combs (ALLEN and JEFFREE, 1956), and rates of broodrearing by measuring areas of sealed brood. These measurements, together with amounts of the supplement consumed were recorded as nearly as possible at 21 day intervals. Since some slight variations occurred in the intervals between recordings, daily consumption of the supplement was calculated for each interval.

Towards the end of the year, management problems associated with prolonged and exceptionally heavy intakes of nectar and pollen introduced substantial and unexpected variable factors. Results for this period were therefore omitted from the analyses of results for this paper.

Results for the period 8th January to 14th october 1965 are presented in Fig. 1. This shows areas of sealed brood and stored pollen at each of the 14 dates on which data were recorded, together with daily consumption of the supplement for the interval prior to each recording. Data are means per hive for the five hives receiving the supplement.

Correlation co-efficients for the relationships between the three parameters were calculated :

Constant	*Variable*	*r*
Pollen	Brood	.3679
Pollen	Food	.4975
Brood	Food	.3768
Food	Brood	.3770

All values of *r* are significant at the 0.1 % level.

As was to be expected, there was a direct relationship between the amounts of pollen available in the colonies and the rate of broodrearing.

The correlation between the amounts of brood and consumption of the supplement substantiates the author's observations that consumption of this and other pollen supplements is directly influenced by the amount of brood being reared (DOULL, unpub. obs.). The results emphasise the basic role of pollen in initiating and maintaining broodrearing. The supplement on its own does not appear to have done this. However, analysis of results of the whole

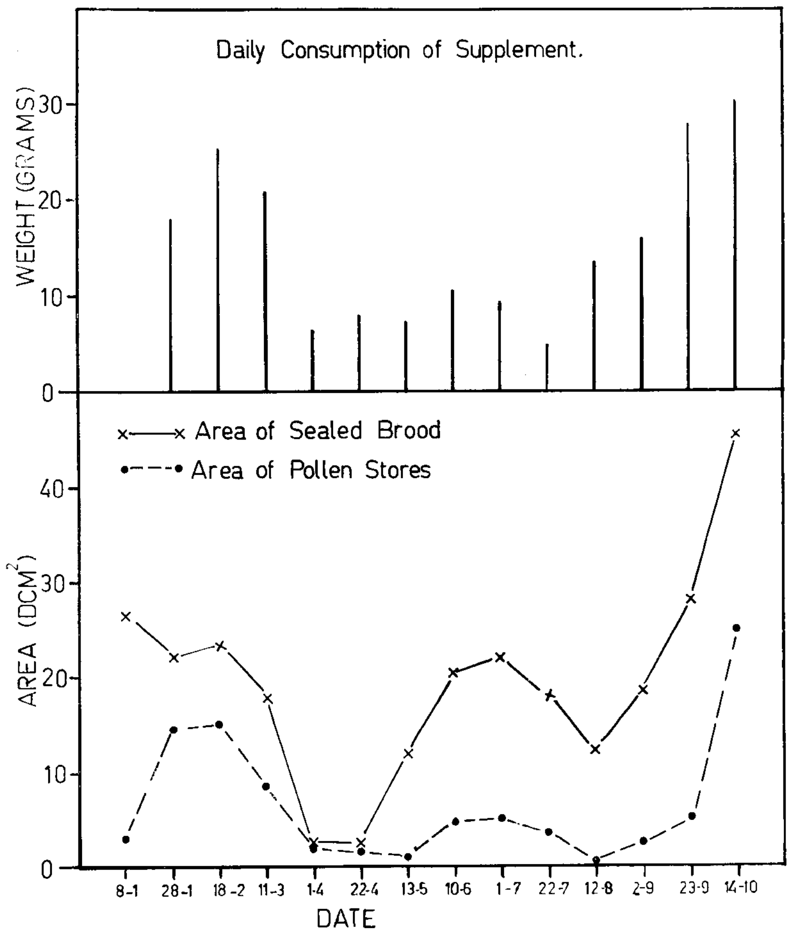

FIG. 1. — *Variations in amounts of stored pollen, rates of broodrearing and consumption of a pollen supplement in colonies continuously supplied with a commercial pollen supplement.*
Means per hive for the five hives in the group

experiment for the period 2nd March to 6th July, when pollen was scarce, shows that the colonies receiving the supplement produced an average for the period of 25.67 dcm² of sealed brood as compared with 16.32 dcm² produced by the control colonies. This difference was significant at the 5 % level and thus presence of the supplement when pollen was scarce enabled the treatment colonies to produce more brood than they might otherwise have done.

Experiment 2

During the summer of 1967 colonies on a pollen deficient honeyflow from *Eucalyptus fasciculosa* presented an opportunity for further study of this problem. With an intake of nectar to stimulate oviposition (CRANE, 1950; CHAUVIN, 1956; STANDIFER *et al.*, 1971) eggs were present in all colonies but there were fewer larvae than would be expected and the commercial supplement was not consumed in measurable amounts.

The n-hexane extract of pollen of the almond *Prunus amygdalus* was added to some of the supplement in amounts equivalent to the addition of 25 % of whole pollen. Ten nucleus colonies each received 250 g of this treated supplement, while a further ten colonies which served as controls, received fresh supplies of the standard supplement.

Numbers of cells containing eggs, larvae, pupae and pollen were recorded every five days. The treated supplement was all consumed after fifteen days, and the experiment was terminated at this point. The control colonies did not consume measurable quantities of the standard supplement at any time during the experiment.

The results are presented in Table 1, which shows numbers of cells containing eggs, larvae, pupae and pollen at each of the four dates on which these data were recorded. Data are means per hive for the ten hives in each group.

TABL. 1. — *Numbers of cells containing eggs, larvae, pupae and pollen in colonies receiving the treated and standard pollen supplements.*

Data are means per hive for the ten hives in each group.

	Date			
	14-4	19-4	24-4	29-4
Eggs :				
Treatment	1066	1916	1950	1430
Control	1332	1319	812	487
Larvae :				
Treatment	262	1882	2405	2177
Control	98	617	747	357
Pupae :				
Treatment	780	832	2184	4095
Control	195	344	942	1597
Pollen :				
Treatment	62	981	975	1384
Control	195	695	390	624

Differences in numbers of eggs and larvae in the two groups were significant at the 5 % level for all except the first recording. For pupae and pollen differences were significant only at the third and fourth recordings.

A feature of the results is the immediate response of the colonies receiving the supplement containing the extract of pollen. Numbers of eggs almost doubled and despite this increase there was a sevenfold increase in numbers of larvae after only five days. The rate of broodrearing in these colonies increased until the last recording, by which time the treated supplement had been consumed and both oviposition and numbers of larvae had begun to decline.

In the control colonies on the other hand, egg laying declined steadily throughout the experiment, but the increase in numbers of larvae may be correlated with an increase in amounts of pollen available.

The effects of the treated supplement may also be demonstrated by comparing expected and actual numbers of larvae. In any colony in which the queen has been laying consistently for 21 days, eggs, larvae and pupae will be present in the proportions of 3:5:13 — the three stages of the bee occupying 3, 5 and 13 days respectively. If the queen is varying her rate of egglaying, the ratios will change (WEDMORE, 1932).

Using this ratio and disregarding changes in the rate of oviposition, the expected number of larvae can be calculated from the numbers of eggs present at any time. Table 2 presents actual and expected numbers of larvae per hive for the two groups at each date on which records were taken.

TABL. 2. — *Differences between expected and actual numbers of larvae in colonies receiving the treated and standard supplement.*

Data are means per hive for the ten hives in each group.

Date	Treatment Hives			Control Hives		
	Expected larvae	Actual larvae	%	Expected larvae	Actual larvae	%
14-4	1775	262	14,76	2220	98	4,45
19-4	3190	1882	58,99	2195	617	28,10
24-4	3250	2405	75,03	1350	747	55,03
29-4	2380	2177	91,47	811	357	44,07

Differences between the two groups were not significant at the start of the experiment but were significant at the 5 % level at all other times.

It is clear that bees were rearing larvae from only a small proportion of eggs present in the colonies at the start of the experiment. In the control colonies the rates of egglaying declined steadily, and under these circumstances the proportion of cells containing eggs would fall below the expected one-seventh. In the treatment colonies on the other hand when egglaying increased, the proportion of cells containing eggs would be greater than one-seventh. Thus the calculated expected numbers of larvae cannot be completely accurate.

Nevertheless the results indicate that the consumption of the pollen supplement containing the extract of pollen enabled the bees in the treatment colonies to rear larvae from a higher proportion of eggs laid. In the control colonies, although a small increase in amounts of pollen available led to a corresponding increase in numbers of larvae, the proportion of larvae reared would actually have been lower than that calculated since there was a steady decline in the rates of oviposition by the queens in these colonies.

DISCUSSION

Observations and records of experimental and commercial hives supplied with a variety of pollen supplements have shown that bees in broodless colonies will not accept any synthetic food, nor will they begin broodrearing when pollen is completely absent (DOULL, unpub. obs.).

The results of Experiment 1 substantiate these observations for they show that pollen is essential for the initiation and maintenance of broodrearing in honeybee colonies. They also show that consumption of pollen supplements varies in direct relationship to the amount of brood in the colony.

The probable role of pollen in broodrearing will become more apparent after discussion of the results in Experiment 2.

LINEBURG (1924, 1925) and NELSON and STURTEVANT (1925) showed that bees place food in the brood cells shortly after the eggs hatch and that virtually all the food necessary to sustain the larva for the first two days of its life is placed in the cells within a few hours of hatching. In addition, DU PRAW (1961) showed that larvae die unless they are fed within a few hours of hatching. Thus it is reasonable to assume that discrepancies between actual and expected numbers of larvae in the colonies used in this experiment were due to the inability of the bees to feed all newly hatched larvae. The improvement in broodrearing in the treatment colonies would then have been due to the fact that consumption of the supplement containing the extract of pollen would have enabled bees in these colonies to produce more larval food and to feed more newly hatched larvae.

The behaviour of bees feeding newly hatched larvae has been described by LINDAUER (1953) and SMITH (1959), and their descriptions of this behaviour leave no doubt that the food given to newly hatched larvae is entirely glandular in origin. Larval food does not normally appear in cells until shortly after the eggs hatch (LINEBURG, *loc. cit.*) and it follows that the provision of this food is a response by nurse bees to some stimulus provided by the presence of newly hatched larvae. However, if the hypopharyngeal glands of nurse bees in colonies at the start of this experiment were inactive, they would not be capable of responding to this stimulus, and thus many larvae would have died because they were not fed within an hour or two of hatching.

The extract of pollen provided phagostimulants that were lacking in the supplement and the addition of the extract induced the bees to feed on the treated supplement. It may well be that this consumption of proteins and other essential nutrients in the treated supplement was sufficient to activate the glands of nurse bees in the treatment colonies.

However, it should be noted that SHEESLEY and PODUSKA (1968) reported an increase in broodrearing in colonies receiving Drivert sugar with only 1 % of pollen. It is possible therefore that pollen contains some components which exert the specific function of activating the fully developed hypopharyngeal glands of nurse bees. Further investigation of this possibility is warranted.

The relationship between the presence of larvae and of pollen and the consumption of the pollen supplement in Experiment 1 may also be explained in terms of the physiological state of nurse bees and of the role of stimulus and response in their feeding behaviour. FREE (1961) indicates that activity of the hypopharyngeal glands requires both the presence of larvae and the consumption of protein. Possibly the presence of newly hatched larvae stimulates nurse bees to seek protein foods and the consumption of pollen would then result in the activation of their hypopharyngeal glands. Bees that were actively secreting larval food or royal jelly would experience an internal stimulus arising from their need for essential nutrients from which to elaborate these foods. The effect of this internal stimulus would probably be to reduce the bees' thresholds of response to the sugars, proteins and vitamins they needed, and they would then feed on pollen supplements, even though these did not contain the primary phagostimulants that induce them to move towards and feed on pollen. The pollen supplement in Experiment 1 was placed on the top bars of the brood combs directly above the brood cluster, so that the bees would make direct contact with it as they moved about the combs. They would then respond to phagostimulation from water, sugars and other essential nutrients in the supplement (DOULL, 1973). They would continue to feed on the supplement as long as there were larvae present to provide the initial stimulus, and as long as there was pollen present to activate their brood food glands. The rate of consumption of the supplement would therefore be directly affected by the number of larvae to be fed, and the amounts of pollen in the hive.

These experiments make it clear that pollen is not simply a source of essential nutrients for honeybees. It appears to play other important roles in feeding behaviour, and in the process of elaboration and secretion of larval food and royal jelly. No artificial protein food can completely replace pollen in the diet of the honeybee unless it fulfills completely all the roles of pollen. Further research in this field should be directed towards identifying all the roles of pollen and the specific compounds appropriate to the performance of these roles.

Future field trials with pollen supplements should also provide more information on the quality of the artificial foods if numbers of eggs, larvae and pupae and amounts of pollen stored in the experiment hives are recorded.

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RÉSUMÉ

RELATIONS ENTRE POLLEN, ÉLEVAGE DU COUVAIN ET CONSOMMATION DES SUCCÉDANÉS DE POLLEN CHEZ LES ABEILLES

Dans le but d'étudier les effets d'un succédané de pollen du commerce sur la production du miel, cinq colonies d'abeilles ont été approvisionnées de façon continue pendant un an avec ce produit. Durant cette période les colonies ont été déplacées de temps en temps de façon à pouvoir bénéficier d'une série de miellées. Les quantités de pollen disponibles dans la nature ont varié d'un extrême à l'autre. Les surfaces de couvain operculé, de réserves de pollen ainsi que la consommation du succédané ont été mesurées à intervalles de 21 jours pendant toute l'année. Pour les besoins du présent travail, les données recueillies entre le 8 janvier et le 14 octobre 1965 ont été analysées afin de déterminer les corrélations éventuelles entre pollen, élevage du couvain et consommation du succédané.

Dans une seconde expérience, 20 colonies placées dans les conditions d'une miellée abondante pendant laquelle les ressources en pollen étaient très faibles n'ont pas consommé le succédané commercial et n'ont transformé en larves qu'une faible proportion des œufs pondus. La partie extractible par le n-hexane du pollen d'amandier a été ajoutée à une partie du succédané de pollen et donnée à 10 colonies, les autres recevant le succédané commercial frais. Le nombre des cellules contenant des œufs, des larves et du pollen a été enregistré à intervalles de 5 jours jusqu'à la consommation complète du succédané traité.

ZUSAMMENFASSUNG

BEZIEHUNGEN ZWISCHEN POLLEN, BRUTAUFZUCHT UND VERZEHR VON POLLENERSATZMITTELN BEI DER HONIGBIENE

Um den Einfluss handelsüblicher Pollenersatzmittel auf die Honigerzeugung zu untersuchen, wurden fünf Bienenvölker während eines Jahres fortlaufend mit Pollenersatz versorgt, wobei mit diesen Völkern von Zeit zu Zeit in neue Nektartrachtgebiete gewandert wurde. Das den Völkern zur Verfügung stehende Pollenangebot reichte von äusserster Knappheit bis zu extremem Überfluss. Die Flächen mit verdeckelter Brut und mit Pollenvorräten sowie der Verbrauch an Pollenersatz wurden das Jahr hindurch alle drei Wochen registiert. Für die vorliegende Arbeit wurden die Daten vom 8. Januar bis 14. Oktober 1965 analysiert, um etwaige Zusammenhänge zwischen Pollen, Brutaufzucht und Verzehr von Pollenersatz festzustellen.

In einem zweiten Versuch nahmen 20 Bienenvölker, denen Nektartracht zur Verfügung stand, die aber wenig Pollenvorräte hatten, keinen Pollenersatz an und zogen nur einen geringen Prozentsatz von Larven aus den vorhandenen Eiern auf. n-Hexan-Extrakt aus Mandelpollen wurde einem Teil des Pollenersatzes zugesetzt, der dann an die Völker verfüttert wurde. Die übrigen Völker erhielten frische Vorräte an normalem Pollenersatz. Die Anzahl der Zellen mit Eiern, Larven und Pollen wurden in Abständen von fünf Tagen registriert, bis der behandete Pollenersatz verbraucht war.

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