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INTRODUCTION: VALUE OF POLLEN TO BEES

POLLEN plays an important part in the life of honeybees, supplying the necessary constituents for the growth and development of these insects.

A number of investigators have chemically analyzed pollen *(1, 6, 7, 30, 38, 39, 44, 48)*. A review of the chemical composition of pollen is given by Paton *(34)* and recently by Svoboda *(45)*. The protein content of pollen varies considerably (8-40 per cent). Lecithin and cholesterol are present. Pollen is rich in the mineral constituents (2.88 to 8.28 per cent), the amount of K and P being especially noticeable. It contains various enzymes. There was some indication *(31)* that pollens from the anemophilous plants contain less nitrogen (4.63 per cent) and phosphorus (1.76 per cent) than that of the entomophilous plants (7.49 and 3.05 per cent, respectively). However, recent analysis by Todd and Bretherick *(50)* did not show such relationship.

The composition of beebread—pollen stored in cells of combs by bees—does not differ appreciably from that of pollen, except that the nitrogen content is lower, that of carbohydrates is higher, and the *p*H is lower *(2, 6, 32, 42)*. It contains the following vitamins: A, thiamine chloride, riboflavin, pyridoxine, ascorbic acid, pantothenic acid, and nicotinic acid *(25, 26, 27)*. Vitamin E is present in insignificant amounts *(24)*. The lactic acid present in beebread is formed during the process of fermentation *(51)*.

Although the larvae are fed a special larval food or royal jelly, elaborated in the pharyngeal glands of the nurse bees, pollen grains in varying amounts are always found in the food given to all stadia *(8)*. The belief that the food of the queen larvae does not contain pollen is unfounded, for recent investigations showed that pollen grains are always found in the digestive tract of the queen larvae and that "the pollen was apparently an

[1] The writers wish to express their appreciation to Dr. W. A. Riley for his helpful criticisms and suggestions during the preparation of the manuscript.

ingredient of the food of queen larvae, because the amount is entirely too large to be explained as an accidental admixture" *(29)*.

Pollen is also needed for the normal development of emerged bees. Haydak *(15)* showed that there is a definite increase in the nitrogen content of bees during the first days of their lives, the greatest increase occurring during the first five days of adult life. This average increase in the nitrogen content of bees five days old over that of newly emerged bees amounted to 92.6 per cent in the heads, 76 per cent in the abdomens, 37.5 per cent in thoraces, and 64.1 per cent in the whole bees.

If pollen is withheld from the diet of emerged bees, they can subsist on a pure carbohydrate diet for a relatively long time but they lose weight and the nitrogen content of their bodies diminishes. Their mortality is very high (60 per cent compared with 12.7 per cent in the control pollen-fed colony). Such bees do not start brood rearing, although the queen lays eggs. When pollen is added to the diet of such bees, their bodies develop and they commence brood rearing normally *(18)*.

Although adult bees can, for a short time, rear brood when fed only sugar solution *(16)*, they do it at the expense of the materials of their bodies. In the experiment cited, the bees lost 6 per cent of nitrogen, the greatest loss being in the abdomens of these bees (18.9 per cent). They can also live for a long time on a food consisting of pure carbohydrates but they decrease in weight because there are no materials available to cover the losses of catabolism. In an experiment *(19)* in which adult bees lived on a diet of sugar solution for 189 days, they lost 33.7 per cent of their dry weight and 22.2 per cent of nitrogen, the greatest loss being in abdomens (72.5 and 44.7 per cent, respectively).

It has been shown that even in winter, pollen is utilized by the bees and the amount of the available pollen present in the hive influences the outcome of wintering and the consequent spring development of the colony. Farrar *(10)* ascertained that those colonies which received 615-626 square inches of pollen cells in the fall had only 6.4 per cent less bees in the spring, while those which received sugar sirup or honey and sugar sirup without pollen had their fall population depleted by 78.2 and 71.5 per cent, respectively. That this was due to the fact that the colonies reared brood during the winter was obvious in those colonies which had their Italian queens replaced by Caucasian. There was a larger number of Caucasian bees in the early spring than in the fall. Examination of the colonies at the University of Minnesota showed that sealed brood was present as early as February. In summing up his investigations, Farrar *(11)* concluded, "Pollen reserves of 300, 600, or 1,000 square inches, depending upon locality, may be considered equally as necessary as large clusters of young bees, vigorous queens, 60 to 70 pounds of honey of good quality, and adequate protection for insuring ideal wintering."

In some locations shortage of pollen during the active season causes a considerable loss in bees and honey crops. Goodacre *(13)* states that during dry seasons such a shortage occurs at the time of heavy honey flows from yellow box, and points out that if supplies of pollen substitutes were available it would result in a heavier crop of the choice "box" honey being extracted. Moreover, colonies become very weak when working yellow box because of a shortage of pollen for brood rearing.

Shortage of pollen in the spring creates the most serious danger for the development of the colonies in the northern countries. When such a shortage occurs, due to either a late frost or a drouth or some other cause, the bees in search of pollen can be seen collecting various powderlike materials such as flour, meals, sawdust, dust on the roads, and rotted woods, fungus spores, etc.

EARLY DATA ON POLLEN SUBSTITUTES

Beekeepers of all times, even though they did not know the real value of pollen, have tried to feed bees with various food materials so as to increase the strength of their colonies in order to secure a better crop of honey. In the time of Aristotle, bees were fed on figs and other fruits which were placed in the hives. Varro describes a method for preparing a mixture from figs, raisins, and grape juice for bee food. The Romans fed their bees with honey and fresh sheep milk for stimulation of brood rearing.

There are notes in beekeeping literature about feeding the following materials to bees: various kinds of flours and meals; chicken and rabbit meat; slices of rye, buckwheat, corn, or wheat bread soaked in brown sugar sirup; milk; paste composed of eggs and honey; milk with sugar and whole egg; powdered casein.

Prominent beekeepers of the past have advised feeding pollen substitutes to bees when the natural pollen resources were lacking. All of them reported beneficial results from the feeding of various foods other than pollen to bees.

Recently several investigators have tried experiments of feeding various pollen substitutes to bees under natural conditions. They fed a patented yeast mixture, milk, yeast, and soya meal and obtained good results.

However, there has always been some opposition to the feeding of bees with foods other than pollen on the basis that they are injurious to the bees and useless, or because the question is not settled yet. Beekeepers have been advised to store pollen or pollen combs for the time of possible shortage of the natural food of bees.

CONTROLLED EXPERIMENTS ON POLLEN SUBSTITUTES

Experiments of Other Investigators

The objection to the outdoor experiments in which various investigations have tried to prove the usefulness of pollen substitutes as food for bees lies in the fact that the bees may have had access to natural pollen.

Root *(40)* was first to try experiments in which bees were fed various food materials under controlled conditions. He kept several colonies of bees in a glass house in winter for four or five months. He produced brood and also prevented its production many different times by feeding bees rye and oat flour and then withdrawing it.

Parker *(35)* fed bees in a greenhouse with finely ground rye, wheat, oats, pea meal, corn, and buckwheat and found they were not beneficial to bees. The feeding of the substitute stimulated the queen to lay eggs, and the nurse bees to feed the young larvae, but the development of the latter was not completed. Later *(36)* he found that "dried egg yolk aided in the production of three generations of bees, but only in small numbers, as has been the case in all of the experimental colonies."

Whitcomb and Wilson *(52)* fed bees under control conditions with rye and wheat flour, both wet and dry, as well as split canned peas. A limited number of young bees was reared. However, control colonies, composed of bees which were shaken on new combs and fed only a sugar solution, also reared approximately the same quantity of brood. They concluded that brood may be reared during the time when such substitutes are given to bees, but that this is not necessarily proof that bees do utilize pollen substitutes in brood rearing.

Soudek *(43)* based his investigations on the fact that the pharyngeal glands in emerging bees are underdeveloped, whereas those of bees five to six days old are well developed and active. He assumed that any food which causes development of these glands in a normal manner might be considered as a pollen substitute. After trying out 15 different pollen substitutes, he decided that fresh egg albumen and dried yeast gave the best results.

At the All Union Bee Culture Institute at Tula (Soviet Union) *(33, 47)* good results were obtained with oat, pea, and soya meals; rye and wheat flour were fed with fair results. Good results were also secured when milk and eggs were substituted for pollen.

Because of a severe shortage of pollen in certain parts of Australia, the Council for Scientific and Industrial Research started an investigation of the value of pollen substitutes. A number of foods was tried and a mixture of pure casein, 25 parts; dried yeast, 1 part; pollard, 6 parts; pea flour, 1 part; and dried milk, 1 part, was recommended *(3, 4)*.

Peterka and Svoboda *(37)* offered soybean flour to newly emerged bees and found that their pharyngeal glands developed as well as those of bees fed pollen. They concluded that soybean flour can be used as a pollen substitute. However, its effectiveness is not equal to that of pollen.

Schaefer and Farrar *(41)* fed a mixture consisting of soybean flour, 3 parts, and dried pollen from pollen baskets, 1 part. This pollen supplement was mixed with a sugar solution to form candy which was offered to bees. They reported very satisfactory results, considerably better than when soybean flour alone was fed to bees.

In the above-mentioned investigations, attention has been paid to one or seldom two phenomena of bee life. Also, except in Soudek's, and Peterka's and Svoboda's experiments, bees of an unknown age have been used.

The suitability of any food in the nutrition of higher animals is determined by feeding it to young experimental individuals which are kept under controlled conditions. The changes in the weight and in the size of these animals are recorded, general health is observed, and their general activity noted. In addition, the quality and quantity of the offspring is determined.

Haydak *(14)* applied these criteria to the study of pollen substitutes. He fed various foods under controlled conditions to young bees which had never eaten pollen, and observed the following phenomena:

1. The changes in the weight and the nitrogen content of young bees fed with various pollen substitutes.
2. The mortality of the experimental bees.
3. The quality, weight, and nitrogen content of the emerging bees reared by the colonies fed with pollen substitutes.
4. The quantity of reared brood.

The building activity of the experimental bees was followed at the beginning but later this was discontinued, since young bees fed only sugar solution drew foundation normally.

Value of Pollen Substitutes in the Nutrition of the Honeybee

The procedure in this series of experiments in general was as follows: Young bees were allowed to emerge during six- and ten-hour periods in a constant temperature chamber adjusted to about 33° C. and 75 per cent relative humidity. During three consecutive days, they were brushed in a small three-frame nucleus, provided with a freshly drawn comb filled with sugar solution and the experimental food. Such a nucleus was located in an isolated compartment of a greenhouse or, in later experiments *(17, 20)*, in a screen cage 50 x 40 x 15 inches in size, kept in a heated basement. On the third or, in the last experiment of this series, on the second day a fertile laying queen was added to the colony. On the fourth day the sugar solution and water were offered to the bees. A frame of foundation was hung alongside the comb already present in the nucleus on the fifth day and in the last experiment it was placed in the hive before the bees were brushed. On the seventh day young bees which emerged during a one-hour period were marked and brushed into the nucleus. Changes in the dry weight and the nitrogen content of the thoraces of these bees were determined in two-day intervals during the first eight days of their lives. The thoraces of 20 bees were used for each sample. Starting from the seventh day, the brood-rearing activity of the colony was observed. Ten days after the first sealed cell was noted, the combs with brood were photographed, the number of sealed cells and larvae just to be sealed was counted, and the combs were placed in a constant temperature chamber. The dry weight and the nitrogen content of the emerging bees were determined. The colonies which did not rear brood or reared their brood inefficiently were kept in the experiment a longer time and the queens were removed from them in order to stimulate a normal brood-rearing activity. Those which did rear brood were discarded after their brood combs were removed to the constant temperature chamber.

Dead bees were not counted during the first six days of the experiment. Afterwards a daily count of dead bees was continued for a period of 21 days. At the end of the experiment the colonies were killed and the number of bees in each of them was ascertained. The mortality of bees in percentage of the total population of each experimental colony was calculated.

The following food materials have been tested: dried yeast, fresh whole milk, dry skim milk (spray process), whole egg, egg yolk, egg white, meat scrap, ground dried blood, digested tankage, fish meal, whole wheat flour, whole oat flour, whole rye flour, corn flour, pea flour, cottonseed meal, commercial casein, soybean flour, soybean meal, peanut meal, linseed meal; cottonseed meal, soybean meal, and linseed meal each mixed with 20 per cent of dry skim milk by weight. The foods were mixed with honey in a proportion suitable to obtain a paste of such consistency that it did not harden in the cells of the comb to which it was distributed by means of a spatula.

The results of the experiment are presented in table 1.

Table 1. Value of Foods Other Than Pollen in the Nutrition of the Honeybee

Food	Data on bees used in experimental colonies				Data on bees reared by experimental colonies							
					Dry weight in mgm.				Nitrogen content in mgm.			
	Dry weight of thoraces of bees 6-8 days old, mgms.	N. content of thoraces of bees 6-8 days old, mgms.	Mortality, per cent	Number of sealed cells and larvae before sealing	Heads	Thoraces	Abdomen*	Whole	Heads	Thoraces	Abdomen*	Whole
Control	13.2	1.61	17.4	1,439	2.6	9.1	5.0	17.9	0.27	1.08	0.45	1.89
Dried yeast	13.2	1.59	15.47	922	2.4	8.5	4.7	15.6	0.27	1.04	0.47	1.78
Meat scrap	11.5	1.49	18.7	170	2.3	8.2	7.0	17.5	0.27	0.98	0.67	1.92
Cottonseed meal	12.1	1.40	27.8	191	2.4	8.5	5.5	16.4	0.23	0.95	0.52	1.70
Cottonseed meal and dry skim milk	13.5	1.65	28.2	244	2.8	9.3	3.2	16.8	0.28	1.07	0.31	1.90
Soybean flour	13.3	1.61	30.2	248	2.4	9.2	2.7	17.2	0.26	1.09	0.26	1.96
Soybean meal and dry skim milk	12.4	1.49	42.6	351	2.3	7.8	2.8	......	0.25	0.88	0.23	......
Fresh whole milk	12.6	1.48	28.89	376	2.2	8.6	6.8	17.6	0.27	1.01	0.56	1.84
Dry skim milk	12.8	1.46	40.58	336	2.4	7.9	5.4	15.7	0.25	0.94	0.51	1.69
Whole egg	13.1	1.53	31.31	163	2.9	8.0	7.2	18.1	0.29	1.05	0.95	2.29
Egg yolk	13.7	1.59	40.09	169	2.7	9.4	7.6	19.7	0.30	1.16	0.95	2.41
Egg white	13.8	1.56	48.61	17	......	......	......	......	......	......	......	2.30
Commercial casein	12.4	1.49	49.7	0	Reared from one day to sealed larvae							
Linseed meal	12.3	1.45	18.1	0	Hatched to 2½ days old larvae							
Linseed meal and dry skim milk	12.6	1.57	20.3	0	Hatched to sealed larvae							
Peanut meal	12.2	1.50	28.6	0	Hatched to half a day old larvae							
Soybean meal	13.6	1.60	44.5	0	Hatched to sealed larvae							
Whole oat flour	10.3	1.27	42.0	0	Hatched to 3½ days old larvae							
Whole wheat flour	10.8	1.30	43.6	0	Hatched to 2 days old larvae							
Whole rye flour	11.6	1.31	52.1	0	No brood rearing attempted							
Corn flour	10.1	1.17	44.0	0	No brood rearing attempted							
Pea flour	9.9	1.14	92.9	0	No brood rearing attempted							
Digested tankage	11.9	1.36	43.9	0	Hatched to 2½ days old larvae							
Ground dried blood	11.3	1.41	45.3	0	Hatched to 1½ days old larvae							
Fish meal	10.5	1.26	96.6	0	No brood rearing attempted							

* Intestines were removed from the abdomens before determinations were made.

Table 1 shows that the substances fed to the experimental bees can be roughly divided into two groups:

1. Those foods which the bees could utilize for their own development and for the production of new generations. These were: beebread, dried yeast, meat scraps, cottonseed meal, cottonseed meal mixed with dry skim milk, soybean flour, soybean meal mixed with dry skim milk, fresh whole milk, dry skim milk, whole egg, egg yolk, and egg white.

2. Those which did not give satisfactory results, though the bees could utilize some of them for the development of their bodies. On none of these foods could the experimental bees produce a new generation of young bees: commercial casein; linseed meal, both plain and mixed with skim milk powder; peanut meal; soybean meal; whole oat, whole wheat, whole rye, corn, and pea flours; digested tankage; ground dried blood; and fish meal.

Mortality in the second group was, on an average, higher than that of the first group.

Comparative Value of Pollen Substitutes

In the previous series of experiments attention was paid almost exclusively to the question of whether any given food substance could replace pollen as a food for bees. One could not draw an exact comparison between pollen and a pollen substitute since the former was given in a natural undiluted state as stored by the bees in cells of the combs and the latter was offered diluted with honey in a proportion 1:4 to 1:7.

Under such circumstances the qualitative and quantitative differences which were observed in the experiments might have been due to the fact that the bees fed pollen actually consumed more proteinaceous food per volume intake than did the bees fed pollen substitutes and therefore showed a better physiological performance.

For an evaluation of the nutritive value of any food substance the food intake of the experimental animals must be equalized. In the case of bees where any restriction in food brings a certain reaction of the colony as a whole (restriction of egg-laying, change in the rate of the brood-rearing activity), such equalization may involve additional factors which may make very difficult the interpretation of the results obtained.

Therefore, it was decided to feed the experimental colonies *ad libitum,* but to equalize the percentage of food per volume intake.

The method and the procedure in this series of experiments did not substantially differ from those described for the first series. However, a fertile laying queen was introduced during the first day of the experiment simultaneously with the second addition of emerged bees, because such an early introduction tended to quiet the bees and made the whole procedure of an addition of new bees simple and easy. Young bees were not brushed directly into the hive but into a glass container through a bee funnel, similar to that which is used in the bee package industry. The container with the bees was then weighed and the bees poured into the hive. An approximately equal number of ounces of bees was hived in each nucleus. In this way the number of bees in the colonies was practically equalized. Since it has been established that the growth curves representing an increase in the dry weight and the nitrogen content for adequate foods follow each other quite closely *(20)*, only the dry weights of thoraces of the experimental bees were ascertained.

In this series only those substances which can be used in beekeeping practice were examined. In selecting a pollen substitute for general use by beekeepers, one has to take into consideration the fact that the food must be easily available and it must be cheap.

Judging from these viewpoints the following pollen substitutes were used: cottonseed meal mixed with skim milk powder in the ratio 1:4 and a similar mixture of various brands of soybean flour and dry skim milk.

Beebread and pollen substitutes were mixed with honey in such a proportion as to contain the same amount of the material tested in a unit of food *(21, 23)*.

The results of these series of experiments, presented in table 2, show that cottonseed meal mixed with skim milk powder and soybean flour, expeller-processed or solvent-extracted and heated, mixed with dry skim milk, can be favorably compared with the natural food of bees.

In order to show numerically the efficiency of foods investigated, a system of indices was used. The poorest performance in each category (highest mortality, lowest brood-rearing activity, respectively) was accepted as a basis of measurement. The number of points for each performance in other colonies was found by the division of the corresponding values, the poorest performance serving as a dividend in the case of mortality percentages and as a divisor in the case of brood rearing. The sum of the quotients gave an index of the food efficiency.

Table 2. Comparative Value of Pollen Substitutes

Food	Mortality	Number of sealed cells and old larvae	Indices of food efficiency	Remarks
	per cent			
Beebread	18.5	334	3.9	
Cottonseed meal and dry skim milk	33.6	391	3.2	
Soybean flour I	21.7	195	2.9	Soybean flour produced by expeller method, low fat content (5.0-7.5 per cent)
Soybean flour II	35.7	0	1.1	Soybean flour from steamed dehulled beans with 22 per cent fat content
Soybean flour I and skim milk powder	11.9	576	6.4	Soybean flour produced by expeller method, 7 per cent fat
Soybean flour III and skim milk powder	27.8	532	4.2	Soybean flour produced by solvent method, heated afterwards. Fat content 1.5 per cent
Soybean flour IV and skim milk powder	31.0	409	3.4	Soybean flour produced by solvent method, not heated. Fat content 1.3 per cent
Soybean flour V and skim milk powder	40.4	200	2.0	Soybean flour produced by solvent method, not heated. Fat content 0.8 per cent
Soybean flour III and skim milk powder and crude oil extract	19.8	621	5.2	Fat content 5.5 per cent
Soybean flour III and skim milk powder and crude oil and dry egg yolks	18.1	1,318	8.9	Fat content 5.5 per cent and dried egg yolk 10 per cent

Reference to table 2 shows that the highest mortality was 40.4 per cent. The lowest number of sealed cells and old larvae was 195. Using these figures, the efficiency of beebread as represented by decreased mortality (40.4:18.5) was 2.2. The production of brood in this same colony was 1.7 greater than that in the colony with the lowest performance. Adding these two values (2.2 and 1.7) gave the index of food efficiency, 3.9.

Value of Pollen Substitutes in Queen Rearing

In this series of experiments a somewhat modified method was applied. Dead bees were weighed and the mortality was established by a comparison with the original weight of bees added to nucleus minus the weight of those which died during the first six days of the experiment. Since the development of bees on the pollen substitutes studied has already been established *(21, 23)* no data on the development of the experimental bees were taken. Neither were the weights of the bees reared by these colonies ascertained.

After the combs with brood were photographed the bees from these combs were permitted to emerge in the original nucleus. At the same time the queen was removed from the colony and the bees were allowed to rear a new queen. Seven days after emergence the queen was weighed and the colony discarded.

Beebread (stored in a refrigerator for one year), sifted cottonseed meal with 20 per cent dry skim milk, expeller-processed soybean flour with 20 per cent dry skim milk, dry skim milk, and dry skim milk with 20 per cent dried nonirradiated yeast were used in this experiment. The pollen substitute was at least one year old. Thirty-five gms. of food were mixed with 200 gms. of honey, adding water to compensate for the difference in the moisture content of the beebread and the pollen substitutes.

The experiment showed that soybean flour mixed with dry skim milk was the most satisfactory inexpensive bee food (table 3).

Discussion of the Results

The chemical composition of pollen substitutes *(14, 17, 20)* shows that, in general, those foods in which all the elements essential for the development of young animals are well represented were able to cause a normal development of emerged bees

Table 3. The Value of Pollen Substitutes in Queen Rearing

Food	Strength of colony	Mortality	Number of sealed cells and larvae before sealing	Weight of queens	Indices of food efficiency
		per cent		mgms.	
Beebread					
1	700	26.4	594	158.3	
2	720	21.0	792	144.7	
Average	710	23.7	693	151.0	6.0
Cottonseed meal and dry skim milk					
1	731	31.0	161	146.2	
2	730	24.1	227	160.6	
Average	730.5	27.5	194	153.4	3.2
Soybean flour and dry skim milk					
1	700	28.7	1,422	142.5	
2	708	32.0	1,546	did not rear	
Average	704	30.4	1,484	142.5	9.6
Dry skim milk	692	28.2	366	did not rear	2.9
Dry skim milk and dried yeast	814	25.3	1,652	172.0	10.9

and to enable the bees to rear brood. On the contrary, foods which contained a large percentage of indigestible materials, such as starch in oats, wheat, corn, and rye flour, and the protein and mineral content of which was low, did not produce a normal development and brood rearing. The apparent discrepancy in the case of ground dried blood, digested tankage, peanut meal, linseed meal, and fish meal can be explained by an assumption that the availability of the food constituents for bees might have been impaired by the processes used in the preparation of these foods in the factory. As a matter of fact, the consumption of the fish meal food was negligible, the food being repellent to bees. There was very poor consumption of the pea flour food and the development of bees was far below normal.

When we exclude these foods we may see that the development of bees and their brood-rearing activity, like that of other animals, closely corresponds to the richness of the foods in the utilizable food constituents, particularly proteins and minerals. Foods like rye or corn flour contain a small percentage of proteins. The main representatives of these proteins, gliadin of rye and zein of corn, lack one and two essential amino-acids, respectively. Both rye and corn flour caused a very slight development of the bodies of the bees subjected to these diets and the bees fed on these foods did not even attempt to rear brood. Proteins of the rest of the experimental foods contained all the essential amino-acids and in all cases the bees fed them attempted brood rearing.

The bees on commercial casein diet started their brood rearing normally, but the larvae were afterwards removed by the bees. Those larvae which reached the stadium before sealing were unhealthy in appearance. There was an abundance of larval food of normal color and consistency in the cells with larvae. Some of the older larvae were sealed but they died in the cells either in the prepupal stadium or in the earliest pupal stage. When the queen was removed, the queen larvae, which the bees started to rear, were supplied with an enormous amount of food. Nevertheless they looked unhealthy and died. Currie *(4)* found that on casein alone the young bees reached the pupal stage but failed to emerge as adults although, as he stated previously *(3)*, "casein alone can lead to development of pharyngeal glands."

This finding emphasizes that in the study of bee nutrition it is necessary to follow more than one factor. The development of the pharyngeal glands alone cannot serve as an indication of the suitability of any food as a pollen substitute since such developed glands may secrete a product that is deficient in a factor or factors essential for a normal development of growing individuals.

The best results were obtained when dried yeast, cottonseed meal, or soybean flour mixed with dry skim milk were used as pollen substitutes. Soybean flour produced by the expeller method, containing less fats (5-7 per cent), and the solvent-extracted flours, containing 6-7 per cent fat, and heated after extraction should be used in feeding bees since they have better food value than that prepared from untreated beans. Solvent-extracted soybean flours with a low fat content should not be used as pollen substitutes because the mortality of bees fed those flours was higher and the brood-rearing activity was lower than when flours of medium fat content were fed to them. Possibly the supply of some essential lipids is inadequate in the low-fat solvent-extracted flours. That this is probably the case is indicated by the fact that an addition of the crude oil extract caused a considerable reduction in the percentage of mortality and an increase in the brood-rearing capacity of the experimental bees. An incorporation of 10 per cent dried egg yolk into the diet caused still further improvement.

Although the brood-rearing activity of bees in the third series of experiments was considerably higher than that in the second one, the ratio of the indices for soybean flour and the beebread was the same in both cases (1.6).

An interesting biological phenomenon has been observed during these experiments. On several occasions bees fed adequate foods, even natural beebread, did not start brood rearing. It is hard to explain such behavior of bees by any known causes brought out by the study of animal nutrition.

VALUE OF POLLEN SUBSTITUTES FOR SPRING PACKAGES

In order to test the advisability of giving pollen substitutes to early packages in the spring under Minnesota conditions, a number of packages were hived outdoors between March 30 and April 2 (in 1936, because of the unfavorable weather conditions, the packages were hived on April 9) on pollen-free combs. Pollen substitutes and sugar solution were supplied to them in quantity. Control colonies received only sugar solution. The experimental colonies were protected on top by newspaper and balsam wool. In order to follow the development of the colonies the amount of brood present in the hives was ascertained every month beginning May 15. The record of honey production of the colonies was kept.

A total of 123 packages was used in the experiment during a seven years' period (1934-1940), three-pound packages being used in the experiment except in 1935 and 1937 when two-pound packages were installed. Convenient methods of giving pollen substitutes in the hives were tested. The review is presented below.

1934. Dry pollen substitute was mixed with four parts of powdered sugar. A candy was prepared using glycerin. The candy was given on the top bars of the hive.

1935. Candy was made as in the preceding year. However, one part of pollen substitute to three parts of powdered sugar was used.

1936. Pollen substitutes were placed dry in cells or given as candy. When given dry, in some cases pollen substitutes restricted brood rearing. Bees removed pollen substitutes and the cell walls to the midribs. The candy was eaten eagerly.

1937. The pollen substitutes were offered to the bees in several ways: in the cells as a paste, as candy on the top of the frames, or as a paste in paper dishes placed on the top bars of the frames. The pollen substitutes placed in cells restricted the brood rearing in some colonies. Fresh skim milk was mixed with sugar in proportion 2:1 by volume. It was changed every other day. For the fresh milk and egg mixture, one egg was added to a quart of milk and mixed thoroughly.

1938. Pollen substitutes were given as candy. One part of dry pollen substitute was mixed with two parts of powdered sugar by weight. Commercial invert sirup was used in preparing candy.

1939. Pollen substitutes were given by Farrar's method *(22)* in cells. In some colonies bees were biting out pollen substitute to the midrib of the comb. To test the advisability of hiving packages very early in the spring, six packages were installed in the bee cellar on March 22. Pollen substitutes were provided by Farrar's method. Sugar solution was poured in combs. These colonies were taken out on April 22.

October 16 of the same year, six 5-pound packages were hived in the apiary. They were divided into three groups: one was offered cottonseed meal and dry skim milk, another soybean flour and dry skim milk mixture, and the third received combs with pollen. They were fed enough sugar solution and the stores were sealed normally. The colonies were protected for winter. March 30, 1940, all of them except the one fed the cottonseed meal and dry skim milk mixture were found dead, with indications of a severe dysentery. Microscopical examination showed nosema spores present both in the feces and the dead bees. No conclusions as to the value of pollen substitutes were drawn from the experiment.

1940. Pollen substitutes were given as honey candy. Dry food was directly mixed with honey and offered to the bees. No molding occurred when enough candy was left on the top of the frames to last for two or three weeks. Four packages were hived on combs containing pollen.

Probably the most convenient way of giving pollen substitute to outside colonies is to offer it in a dry state. The substitute should be placed in shallow trays (made by cutting down the sides of corrugated paper boxes) and offered to the bees in some sunny and protected place in the apiary. Bees eagerly collect the substitute and carry it to their hives. In the spring the stored substitute is quickly consumed and apparently does not harden in the cells. Some of the mixture is wasted by the bees around the collecting place, especially on windy days. This loss can be minimized by spreading a canvas where the trays are located.

Another method of giving pollen substitutes in the apiary is to offer them in the form of sugar candy. The sugar solution is made of two parts of crystal sugar to one part of hot water by volume. The candy is prepared by a thorough mixing of four quarts of hot sugar solution with five pounds of the dry pollen substitute. Then the candy is covered, in the container in which

Table 4. Value of Pollen Substitutes in the Spring to Installed Packages

Year	Brood count (frames of brood)					Production
	May 15	June 15	July 15	Aug. 15	Sept. 15	
Sugar solution (controls)						pounds
1934	3.0	2.5	6.0	5.3	.....	—15
1935	0.7	2.2	6.2	5.0	3.7	7
1936	2.1	4.8	4.4	5.2	5.3	49
1937	2.0	5.5	6.0	4.3	0.8	18
1938	2.0	4.0	5.9	3.9	3.3	245
1939	3.7	7.3	5.6	4.5	3.3	119
1940	2.3	4.3	5.6	4.8	3.8	50
Average	2.3	4.4	5.7	4.7	3.4	79
Cottonseed meal and dry skim milk						
1936	1.5	4.8	4.8	5.1	5.8	36
1936	1.3	3.8	4.9	4.3	4.8	11
1937	1.8	3.7	4.8	4.9	1.1	10
1938	1.9	4.1	6.6	3.8	2.9	251
1939	5.3	9.0	8.0	6.8	4.3	142
1940	2.8	5.7	7.2	5.9	5.2	51
Average	2.4	5.2	6.0	5.1	4.0	98
Soybean flour and dry skim milk						
1937	1.2	2.9	4.5	4.0	0.8	—19
1938	1.7	3.7	7.2	4.3	4.5	193
1939	4.1	6.3	5.4	4.2	3.5	123
1940	2.7	5.7	6.5	4.3	2.7	73
Average	2.4	4.6	5.9	4.2	2.9	92
Dry skim milk						
1934	3.0	3.5	5.5	6.3	.....	8
1935	1.4	3.0	6.0	4.8	3.8	12
1936	2.1	4.9	5.1	4.5	5.2	24
1938	1.9	4.3	7.6	3.9	3.1	238
1940	2.3	5.3	6.0	5.3	4.0	110
Average	2.1	4.2	6.0	5.0	4.0	78

it was mixed, with waxed paper, making the latter adhere to the surface of the candy. Next day, the pollen substitute can be distributed to the colonies. By means of a wide scraping knife, the candy is spread over a piece of waxed paper in a layer about one quarter to half an inch thick and placed directly over the top bars of the hive, leaving the wax paper covering the candy.

The results of the experiment with those pollen substitutes which have been used for several years are presented in table 4.

Even a superficial examination of the table shows the tremendous variability of the results from year to year. This is not surprising since there are so many factors influencing the development and production of a bee colony. If we compare the average brood-rearing activity and the production of the first three groups of the experimental colonies we can see a slight tendency in favor of the pollen substitute group. However, for a proper evaluation we have to compare the results of those years in which all three groups were represented. This is done in table 5. In this case the value of various foods will be in the sequence: cottonseed meal-dry skim milk, sugar solution, and soybean flour-dry skim milk. Such ranking would be justified on the basis of the average yearly results.

The difficulty of interpreting such data on the basis of averages is shown by the results for the year 1939 (table 6). It will be seen that there were four colonies lost in the cottonseed meal-dry skim milk group, and an average is represented by the results of one colony. In the control group, colony No. 13, having a fair brood-rearing activity, gave only 75 pounds of surplus honey, while No. 5 brought 149 pounds. Still more striking difference is in the soybean flour-dry skim milk group. Here colony No. 14 netted 7 pounds while No. 3 gave 220 pounds production. Or, in the group hived in the bee cellar, colony No. 17, fed soybean flour-dry skim milk, had a loss of 2 pounds, while No. 18 gave 138 pounds surplus. Of course, in some cases of the low-production

Table 5. Value of Pollen Substitutes in the Spring to Installed Packages (Seasons of 1937-1940)

Food	Average brood count (frames of brood)					Average production
	May 15	June 15	July 15	Aug. 15	Sept. 15	
						pounds
Sugar solution (controls)	2.5	5.0	5.8	4.4	2.8	108
Cottonseed meal and dry skim milk	2.9	5.6	6.6	5.4	3.4	113
Soybean flour and dry skim milk	2.4	4.6	5.9	4.2	2.9	92

Table 6. Value of Pollen Substitutes in the Spring to Packages Installed in 1939 (Five Colonies for Each Type of Food)

Pollen substitute used	Colony No.	Brood count (frames of brood)					Production
		May	June	July	Aug.	Sept.	
							pounds
Sugar solution (controls)	5	3.0	8.75	5.0	4.25	3.75	149
Sugar solution (controls)	8	5.0	7.0	5.75	4.0	3.25	132
Sugar solution (controls)	13	3.0	6.0	6.0	5.25	3.0	75
	Average*	3.7	7.3	5.6	4.5	3.3	119
Cottonseed meal and skim milk powder	12	5.25	9.0	8.0	6.75	4.25	142
	Average†	5.3	9.0	8.0	6.8	4.3	142
Soybean flour and dry skim milk	3	5.25	6.5	4.25	4.75	3.75	220
Soybean flour and dry skim milk	6	4.25	7.0	6.25	4.25	2.75	146
Soybean flour and dry skim milk	14	2.75	5.0	5.75	5.0	3.25	7
	Average‡	4.1	6.3	5.4	4.2	3.5	123
HIVED IN BEE CELLAR							
Cottonseed meal and dry skim milk	15	2.75	7.0	....	5.25	4.0	102
Cottonseed meal and dry skim milk	16	4.0	7.25	4.75	5.25	3.25	96
	Average	3.4	7.1	4.8	5.3	3.9	99
Soybean flour and dry skim milk	17	0.75	2.25	5.25	4.25	3.25	—2
Soybean flour and dry skim milk	18	2.5	6.5	5.5	5.0	4.0	138
	Average	1.6	4.4	5.4	4.6	3.6	68
Pollen combs (controls)	21	4.75	7.0	4.0	3.75	4.25	129
Pollen combs (controls)	22	5.5	7.25	5.25	4.0	3.75	143
	Average	4.1	7.1	4.6	3.9	4.0	136

* Two colonies became queenless and were not counted in the average.
† Four colonies were discarded from the experiment on account of various factors.
‡ Two colonies were discarded from the experiment on account of various factors.

colonies, their failure can be explained on the basis of a poorer early brood-rearing activity as compared with that of good producers. By no means, however, can this be attributed to the food offered to the bees since the packages installed and handled in the same way gave very good results. Probably conditions in the colony itself brought about these striking differences. In the recent literature, the importance of the queen in the development and production of the colonies has been emphasized *(5, 12, 28, 41, 46)*.

The differences in the egg-laying ability of the queen and the character of the offspring were most likely the causes of the unevenness in the results of the single groups. Nevertheless, the results of these experiments show that there is no particular advantage in giving pollen substitutes to the early April packages under Minnesota conditions. While the number of trials does not permit a final conclusion, installation of packages on pollen combs seems to give better results. In case of a late cold spring when the development of vegetation is retarded, colonies fed pollen substitutes or offered pollen in combs will show better brood-rearing activity than those given sugar solution only (compare the results of 1939). However, the question as to whether they will yield more honey is still problematic, because this depends upon the working ability of the bees themselves.

SUMMARY

Pollen plays an important role in the life of a colony of bees, because it is the main source of materials necessary for bodily growth and development. During pollen shortage, bees collect various kinds of powderlike materials. Observing this, beekeepers have offered flours and meals to bees at such times. However, controlled experiments showing the value of these pollen substitutes were lacking.

In this bulletin past experiments are reviewed and three series of controlled experiments are reported. In the first series, 24 various foods were tried as pollen substitutes and their utilization by bees ascertained by observing colony development, mortality, and the quantity and quality of the offspring. Only those colonies which were fed beebread, dried yeast, meat scrap, cottonseed meal plain or mixed with dry skim milk, fresh whole milk, dry skim milk, whole egg, egg yolk, and egg white produced a new generation of bees. In the second series of experiments the value of foods most suitable from the economic standpoint was quantitatively compared with that of beebread. Soybean flour, expeller-processed or solvent-extracted and heated, mixed with 20 per cent of dry skim milk proved to be superior to beebread, while cottonseed meal mixed with dry skim milk in the same proportion was of somewhat lower value than the natural food of bees. In the third series of experiments the value of these pollen substitutes for queen rearing was determined. Soybean flour mixed with dry skim milk was found to be the most satisfactory inexpensive pollen substitute for bees.

It was found that pollen substitutes may best be given to bees either dry or in the form of candy.

The value of supplying pollen substitutes to early spring packages was studied under Minnesota conditions. Experiments conducted in the field for seven years showed considerable variations in the results obtained.

These variations could be explained only by the differences in the makeup of the colonies themselves rather than by the differ-

ences in the value of foods: the colonies in each group were exposed to the same conditions and received the same food, but they gave strikingly different results.

Thus it appears that offering pollen substitutes to the spring packages established under favorable conditions is not necessary because the supply of the natural pollen available at that time usually covers the needs of the bee population.

However, in event of pollen shortage or adverse weather conditions the addition of a suitable substitute is essential for the proper development of the colonies. A soybean flour and dry skim milk mixture can be advantageously used in such an emergency.

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