# HONEY BEE NUTRITION[1]

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In discussing honey bee nutrition, one has to differentiate, as with many other insects, between the nutrition of adults and that of the immature instars.

## Nutrition of Adult Bees

The food of adult worker bees consists of pollen and nectar or honey. The nutritive value of pollen from different plants varies considerably (61, 72, 108, 117). Mixed pollens brought into the hives have a high nutritive value (115) and supply all the necessary materials for proper development of young animals (4, 6, 68, 109). When dried, pollen quickly loses its nutritive value on storage at room temperature (42, 73, 112), therefore, in studying the nutritive value of pollens for bees, pollens of the same age, preferably freshly collected, should be used to preclude erroneous interpretations of results.

When bees don't have access to pollen, they may be offered a pollen supplement—foods mixed with pollen (18) or pollen substitutes—foods intended to replace pollen completely. The most widely used substitute consists of a mixture of soybean flour, dried brewers' yeast, and dry skim milk. When commercial casein and dried egg yolk are added, the nutritive value approaches that of mixed pollens brought fresh to the hive by bees (36, 111, 117, 118). Such pollen substitutes do not adversely influence the quality of larval food produced (41), nor do they have any deleterious influence on the activity of the enzymes of the midgut (27).

Nectar and honey contribute mostly mono and oligo saccharides (75, 101, 102, 123) to the food of bees.

*Criteria in studying honey bee nutrition.*—1. The longevity of emerging bees kept in cages and offered the food being tested is compared with controls (71). 2. The development of various internal organs of emerged bees fed the diet tested is observed or measured (79, 88). 3. Growth (changes in weight and N content), the building activity of bees, the quality and quantity of reared bees (weight and N content), and the mortality of the bees are ascertained (28).

*Nutrition of worker bees.*—After emerging, some worker bees begin con-

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suming pollen during the first 1 to 2 hours of their presence in the colony. At 12 hours after emergence, 50 per cent or more of the workers have started eating pollen in small amounts (13, 26). However, mass consumption begins when bees are 42 to 52 hours old (26) and reaches a maximum when they are five days old (81, 88). The mandibles are used in crushing clumps of pollen or bee bread (52). For reliable results in experimental feeding, pollen or pollen substitutes should be fed separately as such or in candy form, and not added to a sugar solution (88). Growth begins when emerging bees commence eating pollen. Simultaneously, their hypopharyngeal glands, fat body, and other internal organs develop (72, 83). The degree of these changes, however, depends on general conditions, such as the state, the requirements, and strength of the colony, brood rearing, presence of queen, incoming nectar and pollen, weather (19, 60, 93). Proper nutrition is one of the most important factors influencing the longevity of emerged bees (10, 70, 73, 114). However, the presence of the queen (98) and group rather than isolated living (104) also increases the life span, other conditions being equal.



When bees are 8 to 10 days old, their pollen consumption diminishes (66). This can also be determined by the diminishing weight and N content of their digestive tracts (29). Under abnormal conditions, such as when they are forced to rear brood continuously, proteinaceous food is consumed for a longer period (43, 44).

In addition to feeding themselves, bees feed each other. This is called "food transmission" (21, 87, 90) and is observed only over the brood area (17). Workers may also obtain food from the queen (90); drone food is acquired by ingesting material regurgitated by drones (22, 53), but only in some cases is direct feeding observed (12). Such food transmission is believed to play an important role in maintaining cohesion of the colony.

*Nutrition of drones.*—The study of nutrition of drones has been neglected and only recently have some observations and analyses been made. Young drones (1 to 8 days old) are fed mainly by younger workers with food which resembles modified worker jelly—a mixture of glandular secretions, pollen, and honey. In some cases, food for drones is derived from the honey stomach of feeding workers. This type of feeding is followed by a period in which the drones feed themselves on honey from the combs, with occasional feeding by workers. The food of flying drones (12 to 26 days old) consists mostly of honey which they take from cells. Only rarely do they receive it from the workers (22, 80).

There is a distinct growth of drones after emergence, an increase amounting to 28 per cent in dry weight, and 38 to 62 per cent in N content for drones four days old (11). Thoraces of nine-day-old animals increase as much as 53 per cent in dry weight and 57 per cent in N content (40).

*Nutrition of queens.*—There is no clear-cut knowledge of the nutrition of the queen bee. It was previously assumed that during the active season her food consists of royal jelly given by nurse bees, and honey during the winter period. However, chromatographic analyses of the contents of honey stomachs and of ventricular lumina of wintering queens have shown the presence of 17 amino acids but only traces of glucose and fructose. Apparently, wintering queens are fed larval food by workers, and neither feed themselves on honey nor are fed honey (20). Isolated queens kept in cages without workers can feed themselves on sugar-honey candy, provided water is available to them. Under these conditions, most of the queens live more than two weeks but some continue to feed for more than 48 days (122).

Queens also grow after emergence. The greatest increase in thoracic dry weight (47 per cent) and in N content (52 per cent) occurs in queens two years old (40).

## Food Requirements of Adult Bees

*Water requirement.*—Water plays an important role in the life of bees. The form of food has little influence on the longevity provided water is available (71). Isolated queens kept in cages and offered sugar candy and water are known to live on an average of two weeks or more; kept without water they survive only three or four days (122). Water economy in bees is influenced by secretions from the corpora allata and corpora cardiaca, the first increasing water consumption, the latter decreasing it (2). It is a well-known fact that a colony of bees utilizes large amounts of water during the active season to dilute honey and to regulate temperature in the brood nest (63).

*Protein requirement.*—Under natural conditions, pollen supplies the necessary proteins for bees. As mentioned earlier, growth begins when emerging bees start eating pollen. Within five days the N content increases by 93 per cent in the head, by 76 per cent in the abdomen, and by 37 per cent in the thorax (29). Simultaneously, the hypopharyngeal glands, fat body, and other organs also develop (72). The dry weight and N content of heads and thoraces of queens and drones increase, reaching a peak at certain periods of the life of these castes (queen—2 years, drones—14 days) and then decline (40). Under adverse conditions, when supplies of pollen are lacking for long periods, bees use honey (mostly carbohydrate) as their only food. Under experimental conditions, a colony of bees kept on a pure carbohydrate diet will start rearing brood. However, for this the bees utilize materials of their own bodies, with a consequent loss of weight and diminished N content which is greatest in the abdomen. The resulting young bees have less body nitrogen than do normally reared bees, with the greatest decrease also occurring in the abdomen (19 per cent) (30). Such bees have 62 per cent less thiamine than do normal emerging bees (35). These results are significant in that they suggest that food components can be stored in body tissues during immature development, and demonstrate the importance of an abundant, balanced diet of nurse bees to the well-being of the colony.

When freshly emerged bees are kept on a pure carbohydrate diet, the N content of their bodies diminishes and mortality greatly increases. However, when, even after 30 days on a pure sugar diet, protein-starved bees are offered pollen normal development is re-established and the young bees reared by them are normal (31). When the diet consumed by emerged bees is inadequate, weight and N content increases very slightly. If these bees, even after 60 days on such a ration, receive a proper diet, their growth becomes normal (28). This phenomenon is of great importance. It indicates the tremendous ability of a colony of bees to adjust itself to adverse circumstances and to recover when normal conditions return.

This raises the question of nutrition and aging. Older bees have considerably smaller amounts of vitamins of the B group in muscular tissues than do emerging bees—a condition similar to that found in other animals (50). A colony consisting of bees 47 days old kept on pure sugar diet for 189 days, maintained normal flying activity; but the bees lost 33 per cent of body weight and 22 per cent of N, the greatest N loss (44.7 per cent) occurring in the abdomen (32). Apparently, older bees need only a supply of carbohydrate for energy, deriving all the necessary materials for repair of vital organs by catabolizing the body stores deposited during earlier periods of growth.

When adult bees are forced to rear brood they continue to consume pollen well past the normal nurse age. Under these conditions, as high as 70 per cent of the hypopharyngeal glands of bees 75 to 83 days old may remain fully active (44, 82). However, larval food produced by such bees is of a watery, rather than the usual milky consistency, and contains considerably smaller amount of vitamins of the B group (43). The intestines of emerging bees produced by nurses 50 days old and older are very fragile and the longevity of such bees diminishes as the age of the nurse bees increases (44). The weight and N content of queens produced under similar conditions is considerably lower than that of queens reared by young bees (49).

The amount of protein necessary for a certain growth rate is dependent on the quantitative amino acid composition of the protein concerned and on the requirement of the organism for each of the amino acids. The following amino acids and their proportional ratio are essential for growth of adult honey bees: arginine (3.0), histidine (1.5), lysine (3.0), tryptophan (1.0), phenylalanine (2.5), methionine (1.5), threonine (3.0), leucine (4.5), isoleucine (4.0), and valine (4.0)—the same 10 which are essential for normal growth of rats. Serine, glycine, and proline, though not essential for growth, exert a stimulating effect at suboptimal growth levels. In the study of quantitative requirements for essential amino acids, it was demonstrated that there is a nutritional surplus of each of the essential amino acids in the natural food of bees (11).

*Carbohydrate requirement.*—Carbohydrate requirements of honey bees have been determined by feeding various sugar solutions to bees and comparing their longevity with that of those receiving pure water. In case of "unsweet" sugars, the latter were mixed with a certain quantity of sucrose solution which is barely enough to sustain bees longer than on pure water alone, but which imparts taste to the "unsweet" sugars and makes the bees consume it. By this method it was found (116) that bees can utilize the following "sweet" sugars: glucose, fructose, saccharose (sucrose), maltose, trehalose, melezitose; those unsweet: arabinose, xylose, galactose, cellobiose, raffinose, mannitol, sorbitol. They cannot utilize rhamnose, fucose, mannose, sorbose, lactose, melibiose, dulcitol, erythritol, or inositol. Mannose is decidedly poisonous to honey bees (110). However, it is found in royal jelly bound in glycopeptide form (100). These findings are supported by results of study of the enzymes of the hypopharyngeal glands and the midgut (73, 74, 76). Bees can utilize dextrins well but only those starches which are biologically important to them (pollen starches). Intact starch grains are not affected by the bee's diastase, because they are protected by a shell of amylopectin (65).

The requirements of adult bees for lipids, vitamins, and minerals have not been studied to any great extent. Although lipase is secreted by the ventriculus of honey bees (125), apparently for growth and development of the hypopharyngeal glands, adult bees do not need extra lipids (47). Nor do they need extra vitamins (5, 11, 47, 72) or minerals (47). It is possible that the minute quantities of these materials in test diets are sufficient for normal adult growth, or that they are stored in sufficient quantity during the immature stadia and can be utilized for growth of adults, provided the diet of emerged bees contains enough good quality proteins for the task (117). The significance of Fe deposited in various tissues of pollen-fed bees (66) is unknown.



## Nutrition of Larvae

Larvae of honey bees are fed a special food. Several intensive reviews of analyses of this food are available (3, 9, 46, 55, 56, 94, 95, 113) and interested readers are referred to these sources. It may be stated here that this food supplies all the necessary materials for complete development of all three castes of honey bee larvae.

*General.*—Upon hatching the bee larva begins to feed on food supplied by nurse bees. Actual observations (62) showed that each feeding is preceded by an inspection during which the nurse bee makes sure where the head of the larva is located. She then turns herself in such a way that the points of her mandibles lie very near the head of the larva. The mandibles open and start to vibrate with minute motions. After one or two seconds a drop begins to appear between the mandibles and is left near the larva. The drop is generally spread out slightly with the mandibles forming a little pool around the larva. The time taken for one feeding, including inspection, is variable, usually from one-half to two minutes.

*Nutrition of queen larvae.*—Queen larvae, reared in special cells, are supplied throughout their larval life with an abundance of royal jelly. Even after they are sealed in the cells they have food to consume. Nurse bees feeding the larvae deposit two types of secretions: watery-clear and milky-opaque, the former, secreted by nurses averaging 17 ± 2 days of age, while the latter by those of 12 ± 2 days of age. The ratio of these components is approximately 1:1. However, this ratio is dependent on the age of the nurses, the older nurses providing less of the white component. The number of feedings per hour is increased as larvae grow older (1 day old—13 feedings; 3rd day—16; and on the 4th day—25 feedings). The average length of individual feeding also increases with the age of the larva. Total number for the whole larval period is 1600 feedings, lasting 17 hours. In a normal colony, larvae one-fourth to one-half day old receive about 1.13 mg of clear and 0.81 mg of milky white components per feeding. The total amount of food provided one larva is about 1.5 g (57). There is relatively little variation in the composition of royal jelly fed to younger and older larvae (51, 99). However, one analysis showed a considerable difference in vitamin content (64). Only traces of pollen are found in royal jelly (33, 105).

Queen larvae, up to the age of three days, are fed more of the white secretion, while those four days and older, receive more of the clear component. Judging from the pH of these secretions it may be concluded that the clear substance is a mixture of hypopharyngeal gland secretion and honey, while the milky-white mixture is the secretion of the mandibular glands. The milky-white secretion gives a light blue fluorescence on chromatographic analysis as do the secretions of the mandibular glands. Paper chromatographic separations showed that both secretions contained ninhydrin-positive substances (57). It was established (89) that the proteins of royal jelly are derived from the secretion of the hypopharyngeal glands. The protein content of the clear component is 110.5 mg/g and that of the white 140.5 mg/g. Consequently, the milky-white secretion is a mixture of the secretion of the mandibular and the hypopharyngeal glands (57). These conclusions are supported by the fact that when the secretion of the mandibular glands comes in contact with the lobules of the hypopharyngeal glands, the latter become milky-opaque, condensation appearing inside the cells (38). During the first three or four days of their lives, queen larvae grow more slowly than do the worker larvae of corresponding age (16, 119). They then increase their rate of growth and overtake the worker larvae, and reach a weight of 300 to 322 mg. However, there is considerable variation in the weight of larvae of the same age. The differences in rate of growth may be found between colonies, as well as between individual larvae within a colony (105).

*Nutrition of worker larvae.*—Young (newly hatched to 2.5 days old) larvae are always surrounded by, or even float on an excessive amount of food material which is uniformly grayish-white and of pastelike consistency (worker jelly). Although a certain amount of penetration of dissolved substances may take place through the body wall (105), the amount absorbed is very small and is not enough to account for increase in the weight of larvae. The food consumed by larvae is the most important factor. Young worker larvae receive, as do queen larvae, two different food components—water-clear and milky-white, the proportion being about 3:1 or 4:1. Only worker larvae from which emergency queens are reared receive the food components in a 1:1 proportion (57). The number of feedings is considerably fewer than in the case of queen larvae, only 143, lasting 1 hour, 50 minutes for the whole larval period (62). Older (over 3 days old) larvae receive, in addition to the clear secretion, a yellowish, pollen-containing food (modified worker jelly). Feeding with the white secretion is seldom observed. The ages of the nurses feeding young and older worker larvae do not show any significant differences, being, on an average, about 11 to 13 days (57).

The significance of the addition of pollen to the modified worker jelly is not known. Pollen does not supply more than about one tenth of the N requirement of larvae (103). Furthermore, pollen is not an essential constituent of the food of worker larvae because normal colonies, deprived of pollen for a short period of time, can rear worker brood if given only sugar solution (30), or when fed a number of pollen substitutes (36). Pollen grains are probably incorporated into modified worker jelly when the nurses add to it the sugary material from the honey stomach. This material could be contaminated with pollen grains (103). However, royal jelly, although containing an admixture of honey from the honey stomach, shows only traces of pollen (105) and older drone larvae usually have considerably more pollen in their food than worker larvae of the same age. Nurse bees apparently recognize the sex (39) and the caste (120) of larvae and may exercise some choice in feeding pollen to larvae of different castes.

The bees do recognize the quantity of food present in the cells, which is evident by the fact that all larvae of approximately the same age and position on the comb have about the same amount of food at all times. In spite of such care and feeding, there are great individual variations in the daily rate of growth as manifested in the differences between weight of individuals of the same age in the same lot. Differences between the smallest and the largest individual amount to nearly 100 per cent (86).

In addition to more sugar, modified worker jelly has considerably more dry matter and considerably less proteins, lipids, minerals, and vitamins (51, 99). An addition of pollen appears to be relatively unimportant, but the addition of honey has an important dilution effect (99).

*Nutrition of drone larvae.*—Drone larvae grow larger (384 mg versus 159 mg for worker larvae) (107) and receive considerably more food during their development than do worker larvae (avg. 9.6 mg versus 1.7 mg per cell) (92). The food of young drone larvae (drone jelly = DJ) is milky-white. Microscopic examination shows no pollen, or the presence of occasional single grains (37). As in the case of queen and worker larvae, DJ consists of the mixture of water-clear and milky-white components (57). Its composition is similar to that of other jellies. The food of older drone larvae (modified drone jelly = MDJ) is a dirty-yellow-brown color. Numerous pollen grains are present. The changes in the composition of MDJ follow closely those occurring in modified worker jelly. (37). Actually, normal drones can be produced by feeding drone larvae with the food of worker larvae of corresponding age. This would indicate that both foods are physiologically equivalent (96).

## Food Requirements of Larvae

Little work has been done to ascertain the fundamental requirements for growth of honey bee larvae. Up to the present no chemically defined diet which can be used for rearing larvae from hatching to the adult stage has been developed. One can, to a certain extent, judge the requirements of larvae from the results of various laboratory brood rearing experiments.

*Water and mineral requirements.*—Water is indispensable for growth and development of living organisms. That the requirement of water for growth of honey bee larvae is specific is obvious from the results of those investigators who reared honey bee larvae under laboratory conditions. Larvae grow and are more likely to pupate successfully and become adults on jellies that are diluted with water (91, 105). There is a gradual decrease in the percentage of water in the food of older worker and drone larvae (33, 37, 105). In royal jelly this change is opposite: the moisture content increases in the food of older larvae. These gradual opposite changes in the moisture content of food of worker and queen larvae could be related to the different character of growth of those larvae and may be instrumental in initiating the caste differentiation in honey bees (15). Thus, the influence of moisture changes in the food or larvae may be very significant.

Practically nothing is known about the mineral requirements of larvae. There are some indications (8) that cobalt added to sugar solution fed to colonies of bees increases the growth rate of the larvae reared.

*Protein requirements.*—Larval food of the early stages of all three castes of the honey bee is abundant in proteins. The food of the young worker larva is especially rich. Undoubtedly, proteins play an important part in the nutrition of larvae. Calculations from feeding experiments indicate that between 4 and 6 mg of N is used to rear one larva, depending on the diet fed to the nurses (1, 34). When bees are forced to utilize the stores of their own bodies only 3.1 mg of N is used (30). However, even starved larvae can develop into smaller, but still normal-looking adult individuals (54). This would indicate a considerable adaptability of naturally growing larvae to adverse conditions. The proteins in larval food contain all the essential amino acids necessary for the development of emerging bees (10, 121). That larvae also need complete proteins for their development is suggested by the fact that colonies of newly emerged bees fed two-year-old pollen do not start normal brood rearing until 30 days after the beginning of an experiment. They begin to rear brood several times but the larvae are eaten by adult bees when they reach two or three days of age. Those offered fresh pollen start normal brood rearing in six days (45). The nutritive value of old stored pollen can be restored to the quality of fresh pollen by the addition of lysine and arginine (14). This suggests that these two amino acids are required by larvae.

The results of studying utilization of sugars uniformly labeled with $^{14}C$ showed that cystine, aspartic acid, asparagine, isoleucine, leucine, phenylalanine, methionine, tryptophan, valine, threonine, taurine, thyrosine, lysine, histidine, and arginine are essential for the growth of honey bee larvae. In this case, amino acids in the haemolymph of larvae which had become labeled with $^{14}C$ from the sugars ingested were considered nonessential and those not so labeled as essential (67). However, until a method is devised to rear honey bee larvae on synthetic diets in which the presence or absence of certain amino acids can be regulated, the exact protein requirement of larvae cannot be established.

*Carbohydrate requirements.*—For most insects carbohydrates serve as a convenient source of energy. The addition of sugars (glucose and fructose mixture) to worker jelly also increases larval weight, probably due to an increased synthesis of fats (16). The suitability of various carbohydrates in the nutrition of insects is assessed by comparing the average length of life of the insect fed the carbohydrate in question with that of an insect fed water alone. By this technique it was established (7) that larvae are able to utilize the following carbohydrates, named in order of their apparent value: sucrose, fructose, maltose, melizitose, glucose, trehalose, dextrins, galactose, and lactose.

*Lipid requirement.*—Little is known about the lipid requirement of honey bee larvae. Larvae can synthesize fats from carbohydrates (16). Ether-extracted royal jelly supported larval growth remarkably well. However, mortality was high on pupation, and there was a reduction in the amount and quality of silk spun. Many larvae failed to spin silk at all. There was very little difference in the amount of fat laid down by the larvae on the ether-extracted diet as compared to normal jelly and the fats were found to be identical in structure. The ether-extractable lipids in the diet do not appear to be essential for fat synthesis in the tissues, or to affect the composition of the fats laid down (106). Honey bee larvae do not need acetone-extractable lipids for their growth and development into adults. However, when acetone- and ether-extracted royal jelly is fed, the larvae grow normally and some change to pupae, but the latter die one or two days before emergence at the time when they are already well pigmented (91). More controlled experiments are needed to solve these problems.

*Vitamin requirement.*—Again, we can judge larval needs for vitamins only from inference. On vitamin-free casein, minerals, and invert sugar diet, emerging bees develop their bodies and their hypopharyngeal glands normally. However, although the food in their cells is abundant and of normal color and consistency, the larvae do not grow beyond two to three days of age (according to their size) and then disappear. When the B vitamins and cholesterol are added to this diet, four 10-day cycles of normal brood are produced (47). These findings emphasize that in the study of bee nutrition it is necessary to follow more than one factor. The development of the hypopharyngeal glands alone cannot serve as an indication of suitability of any food for brood rearing, since such well-developed glands may secrete a product that is deficient in a factor or factors essential for normal development of growing individuals. Of those vitamins studied pyridoxine (48) and inositol (85) appear to be definitely required for normal brood rearing.

Not only the proper nutritional balance of food elements is essential for growth of honey bee larvae (16) but the proper balance of certain unknown substances is important. This can be demonstrated from the fact that it is impossible to rear larvae to pupation using only the food of young queen or worker larvae (97, 105). There are also indications of improved brood rearing when the food of nurse bees contains heteroauxins (23), oil growth factor, antibiotics, cobalt (24), or giberellic acid (84).

In conclusion, another aspect of larval nutrition should be mentioned. Experiments in the Soviet Union indicate that larval food secreted by the nurse bees has an influence on the hereditary characteristics of bees produced. The food is supposed to have a direct influence on the larvae reared by the nurse bees, as well as through the laying queen fed the same food (59). In this manner the nurses, through their brood food, influence the type of cappings placed over honey (25), the orientating ability of bees produced (58), or morphological characters (78). It is of interest to note that some of these changes are claimed to be hereditary (77). And even the sex of larvae is changed by the nurse bees (79). The latter investigators explained these results by qualitative differences in the composition of the food secreted by the nurses for feeding queens and drone larvae. However, in this latter case no evidence is given that the authors took into consideration the possibility of haploid females (69) or diploid males (124) appearing in the colony.

The study of larval nutrition is still in the beginning stages and much more work is needed to solve the problem. Further valuable information on the subject of honey bee nutrition can be found in chapters written by a number of research workers in *Traité de Biologie de l'Abeille,* published under the editorship of R. Chauvin, Masson & Cie., Paris, 1968.



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