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Honey Bee Nutrition

Honey bees are the most economically valuable pollinators of agricultural crops worldwide (Free, 1993). One third of the total human diet is dependent on plants pollinated by insects; predominately honey bees (McGregor, 1976). Yet, honey bee populations are in jeopardy as evidenced by the dramatic loss of approximately 33% of overwintered colonies each year since 2007 (vanEngelsdorp 2010). Since 1987 with the introduction of *Varroa destructor*, problems related to pathogens and pests of honey bees have risen dramatically (Delfinado-Baker, 1989). Additionally, residues of miticides and fungicides are the most frequently detected compounds in foundation and comb beeswax, pollen and honey (Mullin, 2010; Ostiguy, submitted). With the detection of various chemistries associated with honey bee forage, i.e. nectar and pollen, what is the effect of these chemistries on the health of honey bees? First we need to understand the nutritional requirements of honey bees and what plants produce the optimal supply of these essential nutrients. So the first question should be, what do bees eat? The answer to this question may be quite different from what they actually forage on and collect. Just like humans, bees require carbohydrates, proteins, fats, sterols, minerals, vitamins and water in order to live a long and healthy life.

Carbohydrates

Carbohydrates are required by both the adult and larval stage for normal growth and development. They generate energy for muscle activity and are absolutely essential for fueling flight muscles. Carbohydrates also are the primary energy source for maintaining the required body and nest temperature. The elevated intake of carbohydrates in the form of honey is correlated with proper wax gland function and secretion. A classic study reported estimates of close to nine pounds of honey needed to make one pound of wax (Whitcomb, 1946). Both nectar and pollen are the primary sources of carbohydrates. Carbohydrates encompass a large group of compounds (sugars, starches, celluloses etc…) that can easily be broken down to provide energy at the cellular level.

Nectar

Nectar is a plant-made liquid primarily produced in the flowers, but other sources include extrafloral nectaries. Plant feeding insects also produce honeydew as an excretory product that is also collected by foragers and has a similar chemical composition to flower-produced nectar. Nectar is the main source of carbohydrates for a colony, and the primary sugars identified in nectar are sucrose, glucose and fructose. Not all nectars are made equal and the sugar content can vary greatly with reports of 4% to 60 maximum collection response.

Honey bees robbing sugar syrup from a petri dush

Honey

Honey is nectar that has been enzymatically converted via the addition of enzymes from the hypopharyngeal gland, mainly diastase, sucrase and glucose oxidase. During this process most of the sucrose is changed to fructose and glucose and the nectar then goes through a ripening and evaporation stage that protects it from fermentation by yeasts and bacteria. Once fully ripened and capped under beeswax 99.9% of the solids in honey are sugars.

Nectar and honey requirements

The amount of nectar and honey that is needed for optimal colony health and longevity depends on many variables. The size and the strength of a colony determine the amount of nectar and honey the developing brood and adults will need to sustain themselves. The weather directly affects the timing of flower bloom and the availability and amount of different types of plants and nectars. Other environmental variables also affect nectar production from soil to temperature and humidity, and finally sunlight. On average a colony will require from 150 to180 pounds of honey annually. Broken into seasons a colony requires anywhere from 50 to 80 pounds of honey from the time brood rearing ends in the fall until the first flowers open in the spring. Summer requirements range from 90 to 100 pounds depending on the length and severity of the season.

Honey bees ripening nectar into honey

As we can see from observing bees forage on different plants not all nectar is equally enticing; sugar concentration is one of the main factors influencing foraging decisions. Early studies by Von Frisch (1967) also show that bees prefer certain sugars over others. In fact honey bees recognize only a few sugars as being sweet: glucose, fructose, sucrose, melizitose and maltose. Early studies (Waller, 1972) also show that bees actually show a preference, when given a choice, to sucrose followed by glucose, maltose and fructose. This preference, not surprisingly, transfers over to a higher nutritive value as well. Studies by Barker and Lehner, (1974; 1978) reveal that bees fed sucrose lived longer and developed better than bees fed diets composed of other sugar sources.

Just as there are sugars that increase the quality and longevity of the honey bee there are also sugars that are toxic to bees. These toxic sugars are mannose, lactose, galactose and raffinose. Generally these sugars are from non-floral sources and not secreted in nectar. However, bees fed these sugars have reduced longevity and sub-optimal development.

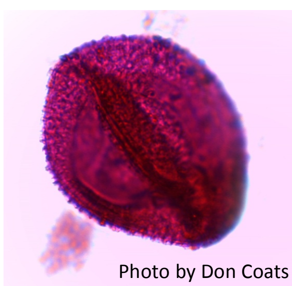
The second major nutritional requirement for honey bees is protein. Protein is essential for the development of body tissue, muscles and glands. Proteins are the building blocks of cells and therefore life. All organisms require adequate protein levels in order to ensure proper development.

Pollen

Honey bees foraging for pollen produced by the flower's male sex organ also known as the basal tassel.

One of the main sources of protein in a honey bee diet comes from pollen. Just as nectar is converted to a storable energy source in the form of honey, pollen is processed via fermentation to a storable protein source called bee bread. Pollen is the male gamete or sex cell that is produced by the male sex organ of a flower also known as the basal stamen and anther. During pollen collection bees inadvertently transfer these male gametes to the receptive female organ of a flower, which generally results in pollination. Early binges on bee bread during larval development aids in the formation of fat bodies, internal organs and glands. High consumption of bee bread also promotes egg laying in queens. Factors that affect the nutritive value of pollen are largely environmental such as temperature and soil moisture and pH, but protein levels also vary widely depending on the plant type. Protein levels from pollen of different plants range from 8 to 40%. Follow -up studies focused more on protein content and amino acid composition (Standifer, 1967) and how pollen converts to brood (Loper and Berdel, 1980). From these studies they found that pollen not only varies from species to species but from season to season and that bees seem to prefer mixed pollen sources.

Pollen requirements



Light microscopy photo of a stained watermelon pollen grain.

Various studies have looked at the amount of pollen that a colony would need to reach healthy, productive population numbers. Most of the research estimates that a honey bee colony requires an average 40-140 pounds annually. This is a large range but it is dependent on the length of the season, the protein value of the local pollen sources and also the genetics of the bees themselves. A study by Haydak (1935) found that each larva needed 100 mg of pollen to complete development from the larval stage to the pupal stage on through to adult emergence.

Building blocks of protein: amino acids

Different pollens can have different mixtures and quantities of amino acids. A study by de Groot (1953) showed that most pollen contains all the essential amino acids: arginine, histidine, lysine, tryptophan, phenylalanine, methionine, threonine, leucine, isoleucine and valine. Amino acid composition is a major factor in the nutritive value of different pollens. However, the predominant amino acids in mature fermented pollen are isoleucine and proline. Proline is found in high levels in all insects and is an essential substrate for the citric acid cycle. Proline is extremely important as a substrate for flight metabolism. One question that many beekeepers are asking now is whether stored pollen or bee bread loses its nutritive value

and found that the honey bees could not develop properly. However when lysine and arginine were added back into the pollen it restored its biological value.

Lipids, fats and sterols

Lipids and fatty acids are the building blocks of phospholipids which are a major component of cell membranes. These complex lipids are the precursors to important hormones involved in the molting process during the insect's life cycle and serve as a primary energy store for insects in their fat bodies. These fatty acids also are used for the derivation of different defensive secretions in some insects and they also aid in the lubrication of food. The loss and depletion of fatty acids is linked to the desiccation of many insects. Pollen contains a fair amount of lipids and sterols. The lipid content just like the carbohydrate and protein content varies depending on the pollen (Todd and Bretherick, 1942; Standifer, 1966). Studies have shown that lipid content can range from 13% in mustard pollen and up to 20% in stored pollen mixtures.

Honey bee foraging for pollen from *Phacelia tanacetifolia*

Unlike humans and many plants, insects (honey bees included) cannot synthesize sterols and therefore require a dietary source. Sterols are also components of cell membranes and many exterior surface waxes on the bee's exoskeleton.. Honey bees use sterols acquired from plant sources as precursor molecules for the production ecdysteroids which are essential in the molting process, from instar to instar and from larva to pupa and finally from pupa to adult. There are two types of sterols that are predominantly detected in pollen: 24-methylene cholesterol and B-sitosterol and both of these are the precursor molecules used for the production of ecdysteroids in honey bees.

Honey bees require cholesterol or 24-methylene cholesterol, found in many plants, for normal growth and development. It is a precursor for the production of hormones that initiate molting. Diets supplemented with cholesterol or 24-methylene cholesterol supported large amounts of sealed brood (Herbert et al. 1985).

Vitamins and minerals

Nectar and pollen both contain many vitamins and minerals. The variation in these nutrients is as varied as the plant species themselves, but there are certain consistencies within these two resources that can be described from previous research. Pollen contains the B-complex vitamins (thiamine, riboflavin, pyridoxin, pantothenic acid, niacin, folic acid and biotin). These vitamins are crucial for hypopharyngeal gland development (Herbert and Shimanuki 1978). Pantothenic acid is now known to play a critical role in queen/worker differentiation. Riboflavin, nicotinic acid and pyridoxine have also been correlated to brood rearing. Anderson and Dietz (1976) found that 5.4 µg of pyridoxine was needed to rear 1 larva to the capped stage. Like the other essential nutrients pollen contains all of the essential minerals: sodium, potassium, calcium, magnesium, chlorine, phosphorus, iron, copper, iodine, manganese, cobalt, zinc, and nickel. Many of these minerals are important components in enzymatic metabolism and also nervous system polarization and depolarization. To emphasize this point, the minerals identified in the three main body regions of the honey bee and in royal jelly are potassium, sodium, magnesium and phosphorus. These minerals are crucial in honey bee metabolism and also in proper nervous system functioning. Just as with other

Water

Without water bees will die within a few days if not sooner. Water loss and desiccation is the biggest obstacle most insects must overcome due to their large surface to volume ratio. Water carries dissolved nutrients to all parts of the body and aids in the removal of waste from the body. Water also aids in ingestion and digestion as a lubricant and carrier. Water is used to dilute thick honey and nectar and larval food may contain up to 66% water. As important as all these dietary functions of water are to honey bee survival at the individual level, at the colony level water is also crucial. Hive bees must maintain an optimal humidity of 90 to 95% in order for brood to hatch normally (Doull, 1976). Water collection is essential to thermoregulating the colony during the dry and warm seasons.

Larval Nutrition

Honey bee larvae

A healthy honey bee colony will begin to expand in numbers in the early spring, where a feedback loop occurs; the foraging bees bring in nectar and pollen which are cues for the queen to start laying eggs. These eggs develop into larvae and require carbohydrates in the form of bee milk (a mixture of honey and glandular secretions) and bee bread which serves as the main protein source for developing bee larvae. Bee milk or worker jelly is a mixture of hypopharyngeal secretions which are clear and contain mostly protein and mandibular gland secretions which are white and high in lipids. Just as in adult honey bee foragers who prefer nectars with a higher sugar concentration, higher sugar contents in larval food directly correlates to a faster or higher consumption rate. It has been shown that larvae chosen to become queens are fed diets with a higher sugar concentration, which causes there consumption rate to increase. This higher consumption rate has been implicated as trigger for hormone release that causes the physiological switch from worker to queen development.

Future Work

Although there is much research to date on the nutritional requirements of bees much of this work is dated and does not represent the modern foraging environment honey bees are subject to. The landscape is becoming more and more fragmented with limited monocultures of forage. With the detection of various chemistries in hive matrices and the constantly changing landscape new studies are focusing on understanding the roles microflora play in nutrient assimilation and food processing in the conversion of pollen to bee bread.

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Participants in MAAREC also include state beekeeper associations, and State Departments of Agriculture from Delaware, Maryland, New Jersey, Pennsylvania and West Virginia.

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