

Review Article

HONEYBEE NUTRITION: PHYSIOLOGICAL AND ECOLOGICAL INSIGHTS

ABSTRACT

Bees play a vital role in global agriculture through their pollination services; however, their populations have declined over the past three decades due to various stress, including nutritional deficits stemming from habitat loss and alteration. This review emphasizes the critical need for understanding bee nutrition, which is essential for overcoming these declines. With their evolutionary background alongside flowering plants, bees have adapted to a herbivorous diet primarily consisting of floral nectar and pollen. Nectar provides the energy necessary for flight and other metabolic processes, while pollen supplies essential proteins, fats and micronutrients. Foraging behaviors vary among bee species and are influenced by environmental factors and the genetic composition of the colony. Honey bees exhibit complex social structures where worker bees gather nectar, pollen and water, each contributing to the nutritional needs of the colony. The transformation of collected nectar into honey and pollen into bee bread illustrates bees unique food storage strategies, providing vital nutrition to larvae and adult workers. Additionally, understanding the nutritional processes involved in larval development and royal jelly production sheds light on caste differentiation and overall colony health. This comprehensive view on bee nutrition underscores its significance for future conservation strategies.

Keywords: honey bee, nectar, pollen, royal jelly, nutrition, bee bread

Abbreviations

(Gamma-AminoButyric Acid, Major Royal Jelly Proteins)

1. INTRODUCTION

Bees are crucial to global agriculture, primarily due to their role as pollinators. However, over the past three decades, bee populations have faced significant threats from parasites, diseases, pesticide exposure and dwindling food sources. Among the factors contributing to the current decline in bee populations, nutritional stress resulting from habitat change and loss is considered a major contributor. Understanding the nutritional needs of bees is essential for addressing this decline. Bees have co-evolved with flowering plants over the past 90 million years, and most bee species have adapted to a diet that relies heavily on floral nectar and pollen (Michener, 2000). Nectar provides bees with the energy required for flight, thermoregulation and wax production, while pollen supplies them with vital proteins, fats, sterols and micronutrients. The variety of plant species that bees use as floral

hosts varies widely among species, though even generalist bees exhibit some degree of selectivity in the pollen they collect (Minckley and Roulston, 2006).

2. NUTRIENT GATHERING

The majority of bee species are solitary, with female bees independently collecting and storing nectar and pollen to provide for their offspring. In primitively eusocial species like bumblebees, a single queen initially establishes the colony and undertakes all foraging activities to feed the larvae until the first generation of worker daughters matures. Once these daughters are capable, they assume the foraging responsibilities, while the drones (male bees) leave the colony and survive on floral nectar (Goulson, 2003) (Fig. 1).

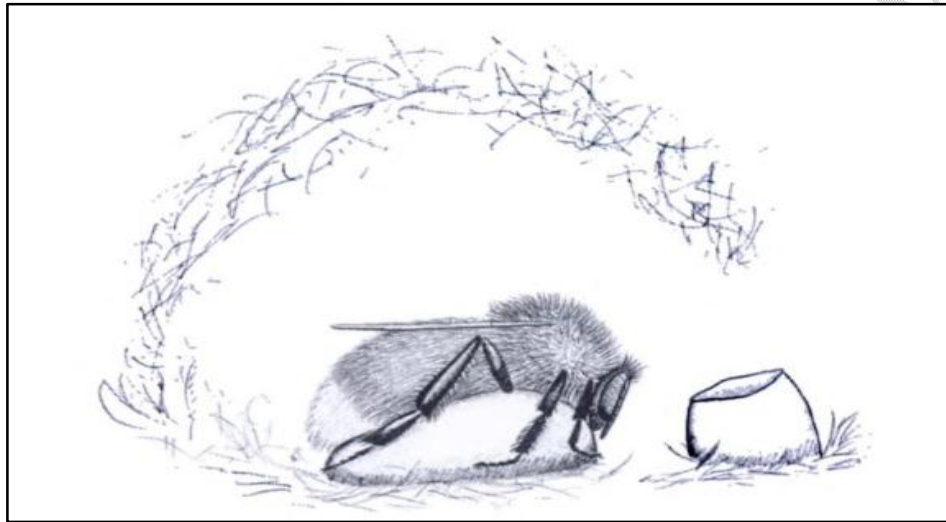


Fig.1 Queen of *Bombus lapidarius* (Linnaeus, 1758) incubating the brood lump

In honeybee colonies, the queen and drones do not forage; instead, this task is exclusively performed by sterile female worker bees. As these workers age, they transition through various roles within the colony, with their behavior being influenced by both genetic and environmental factors (Robinson, 2002) (Fig. 2). Foragers collect various materials, including nectar, honeydew, pollen, water and tree resin (used to produce propolis), adjusting their efforts according to the colony's specific needs. The genetic makeup of the queen and the worker bees influences the colony's pollen-hoarding behavior and the likelihood that a forager will collect pollen versus nectar (Robinson, 1989; Page, 2013). Although honeybee foragers typically specialize in either pollen or nectar collection, they can sometimes gather both simultaneously. Pollen is packed onto specialized structures called corbiculae located on the bees hind legs. During pollen collection, bees often exhibit a temporary preference for the pollen of a single plant species (Gruter and Ratnieks, 2011). Studies have shown that peak pollen-collection times vary by location. The diversity of pollen sources from trapped pollen pellets changes throughout the year, differs between locations, and even varies among colonies within the same site. The number of plant species represented in pollen samples per site per sampling date ranged from 5 to 20, with the most abundant pollen source accounting for 22 to 94 percent of the total pollen collected (Avni et al., 2009). Pollen collection is generally regulated by the

needs of the colony, with an average colony maintaining around 1 kg of stored pollen (Brodschneider and Crailsheim, 2010). Nectar collection fluctuates with the availability of floral nectar, showing significant daily and seasonal variations, with storage sometimes reaching tens of kilograms (Seeley, 1995). Water is mainly collected to cool the brood nest through evaporation, with collection increasing in response to rising hive temperatures. Additionally, research indicates that a colony's water collectors can adapt to meet current water demands and prepare for future water stresses by storing water in their crops and combs (Ostwald et al., 2016). Propolis, a resinous substance collected from plants, is used by bees to enhance hive hygiene and acts as a form of social immunity. This behavior, which reduces parasite load within the colony, demonstrates social immunity in action. For example, honeybees gather plant resins to use in their nests, which can reduce the need for individual bees to activate their immune responses. Studies have shown that colonies increase resin foraging rates following exposure to fungal pathogens such as *Ascophaeraapis*, the cause of chalkbrood disease (Simone et al., 2012).

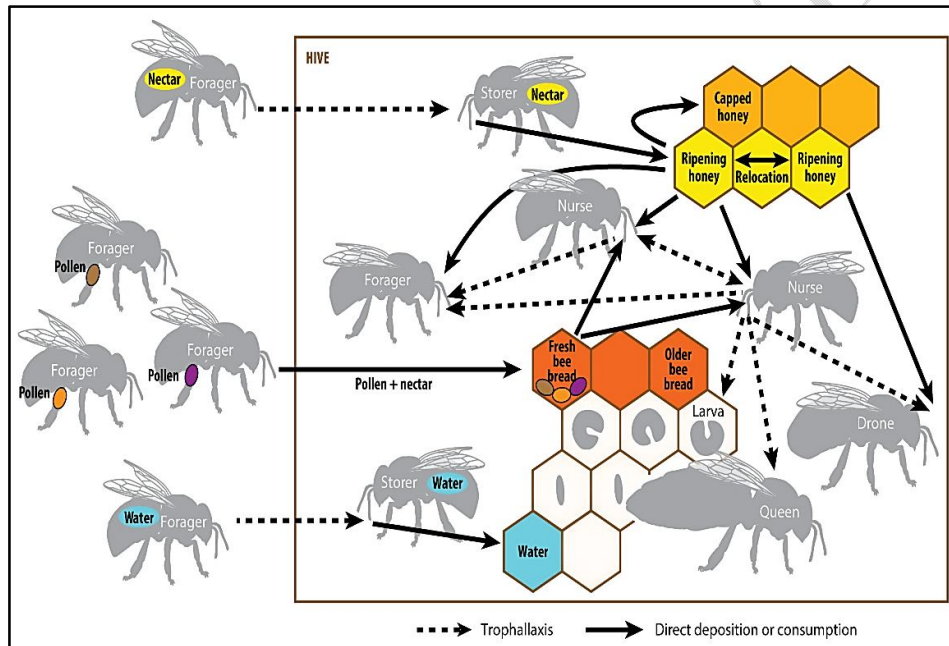


Fig.2 The flow of food and water in a honey bee colony

a) Nectar

Nectar characteristics often show similarities among plants that attract the same types of pollinators. Much of the knowledge on nectar chemistry has been gathered in the study of pollination syndromes, which describe the relationships between floral traits and the types of animals that pollinate them. The primary nutritional value of nectar comes from three simple sugars: sucrose, glucose and fructose. The specific ratio of these sugars varies depending on the plant species producing the nectar, with total sugar concentrations ranging from approximately 10 - 70% w/w (Nicolson et al., 2007). Honey bees generally prefer nectar with a sugar concentration of 30-50%, showing a preference for sucrose over fructose, and fructose over glucose (Waller, 1972). However, in natural settings, bees collect nectar with varying water content, depending on the availability in their

environment. The optimal concentration for energy intake in honey bees is around 60 per cent, beyond which nectar becomes too viscous for efficient consumption (Roubik and Buchmann, 1984).

Sucrose is particularly favoured by foraging bees due to its higher metabolic value per unit of weight. Regardless of the glucose concentration, worker bees require more sugar per meter flown and per unit of body and thorax weight than the significantly heavier drones and queens. Nevertheless, the specific composition of nectar sugars—whether sucrose, glucose, or fructose—might not be critically important since bees can rapidly digest sucrose, and nectar sugars are efficiently assimilated (Gmeinbauer and Crailsheim, 1993). Many homopteran insects, such as aphids (Aphididae), coccids (Coccidae), and membracids (Membracidae), engage in mutualistic relationships with ants. These insects excrete "honeydew," a sweet byproduct of their sugar-rich but amino acid-deficient diet of plant sap. The sugar composition of honeydew plays a crucial role in ant-homopteran interactions, with ants showing a strong preference for honeydew that contains high levels of melezitose, a trisaccharide synthesized in the aphid's gut from two glucose units and one fructose unit. Other sugars, such as those in the honeydew of phloem-feeding homopterans, are also collected by bees. This honeydew typically contains sucrose, fructose, and glucose, along with the metabolizable trisaccharide melezitose, with the proportions varying depending on plant-aphid-ant interactions (Fischer and Shingleton, 2001).

Nectar also contains amino acids, although they are present in low concentrations (ranging from micromolar to millimolar levels), with non-essential amino acids often dominating the profile. While the nutritional significance of these amino acids is not fully understood, their presence may influence the taste of nectar and could affect how bees learn and recognize floral traits (Simcock et al., 2014). Free-flying honey bees tend to prefer essential amino acids over non-essential ones, though there are exceptions, such as methionine. Pollinator preferences significantly influence nectar composition, with phenylalanine being a key compound that attracts nectar consumers, especially long-tongued bees like those in the Megachilidae family. Gamma-aminobutyric acid (GABA) also has a strong influence on both long-tongued bees (e.g., Anthophoridae and Andrenidae) and flies (e.g., Syrphidae), while asparagine and tryptophan generally act as repellents. Phenylalanine is often the most phagostimulatory amino acid and is typically found at high concentrations in the nectar of plants frequented by bees (Petanidou et al., 2006). Research shows that bees collect water from sources with a wide range of salt concentrations, although most collected water had relatively low salt content, except for seawater and swimming pools, which contained more than 0.6 per cent sodium, with potassium chloride (KCl) being aversive to them (Lau and Nieh, 2016). Secondary metabolites in nectar, such as alkaloids and phenolics, are common and have diverse effects: they can deter (e.g., alkaloids, coumarins, and saponins), attract (e.g., terpenes), or be toxic (e.g., cardiac glycosides and cyanogenic glycosides) (Detzel and Wink, 1993). Some metabolites, though undetectable by bees, can still influence bee behavior, as evidenced by the role of caffeine in enhancing honey bee memory of floral traits (Wright et al., 2010; Wright et al., 2013).

b) Pollen

Pollen analysis typically involves studying the pollen collected by honey bees using pollen

traps. Honey bees collect powdery pollen by moistening the grains with nectar, honey, and salivary secretions before packing it into their corbiculae. This process can result in sugar levels in bee-collected pollen reaching up to 50 per cent of the dry mass, although the exact proportion is often unknown (Nicolson, 2011). The protein content of pollen in angiosperms can range from 10 – 60% of the dry mass. For instance, research has shown that crude protein levels in analyzed pollen pellets range from 9.2% in *Hypochoerisradicata* to 37.4% in *Echium plantagineum*, with an average of 25.9% (Somerville and Nicol, 2006).

Beyond crude protein levels, the quality of pollen is also assessed based on its amino acid composition. The quantity of protein is less significant than the proportion of essential amino acids relative to what bees require (de Groot, 1953). Similar to nectar, pollen tends to have a higher proportion of non-essential amino acids, such as proline, compared to essential amino acids. Deficiencies in certain essential amino acids have been identified; for example, low histidine concentrations in maize pollen can lead to reduced brood rearing and lifespan, making maize pollen a less suitable food source for bees due to its lower protein and essential amino acid content (Hoehler et al., 2012).

In addition to proteins, pollen provides bees with other macronutrients, including carbohydrates and lipids. Carbohydrates in pollen include starch, with starchy pollens typically containing less oil than starchless pollens. Insects that consume pollen may be deterred by starchy pollens due to their inability to digest starch or may be more attracted to oily pollens because of their higher caloric content (Roulston and Buchmann, 2000). Pollen also contains fibres in the indigestible cell wall and sugars from nectar added during collection. Lipids, which are present in both the pollen grains and their outer coating (pollenkitt), vary in composition. Studies have shown that neutral lipids, which serve as energy storage and essential oil constituents, are most diverse in pollenkitt, while polar lipids, which are primarily membrane constituents, are found almost exclusively within the internal pollen fraction. The composition of neutral lipids suggests that pollenkitt may provide pollen with species-specific odors (Dobson, 1988). Total lipid content in pollen ranges from 2% to 20% of the dry mass (Roulston and Cane, 2000). The fatty acid composition of pollen varies significantly, with palmitic, linoleic (omega-6), and alpha-linolenic (omega-3) acids being the most common, together comprising 60-80 per cent of all fatty acids. A shift in available forage toward a higher omega-6:3 ratio has been associated with declines in managed colonies (Arien et al., 2015). These three fatty acids, along with oleic and stearic acids, are the main fatty acids found in honey bee bodies (Avni et al., 2014). The two essential fatty acids, linoleic and alpha-linolenic acid, are of particular nutritional importance, with a deficiency in alpha-linolenic acid impairing cognitive function (Arien et al., 2015). Linoleic acid concentrations are higher in bee bodies than in their brains, while the reverse is true for alpha-linolenic acid. Pollens high in lipids and dominated by linoleic, linolenic, myristic, and dodecanoic acids likely play a key role in inhibiting the growth of spore-forming bacteria such as *Paenibacillus larvae* (American foulbrood), *Melissococcus pluton* (European foulbrood), and other microbes inhabiting brood combs. Pollens rich in oleic and palmitic acids are likely more important for honey bee nutrition (Manning, 2001).

Pollen is also a crucial source of micronutrients for bees, including minerals, vitamins, and essential sterols. Pollen sterols are diverse, encompassing compounds such as β -sitosterol, stigmasterol, avenasterol, and 24-methylene cholesterol (Villette et al., 2015). Iron is one of the important minerals derived from pollen and accumulates in the periphery of the bee's abdomen, partially as magnetite, which is suspected to play a role in bee navigation (Wang et al., 2013). However, high iron concentrations in pollen, such as those from heavily fertilized crops, may lead to lipid peroxidation and reduced bee longevity (Jumarie et al., 2017). Secondary metabolites, such as toxins and polyphenols, tend to be present in higher concentrations in pollen than in nectar, and are least concentrated in honey (London et al., 2003). Polyphenols, such as the flavanol quercetin, are commonly found in pollen (Bonvehi and Jorda, 1997).

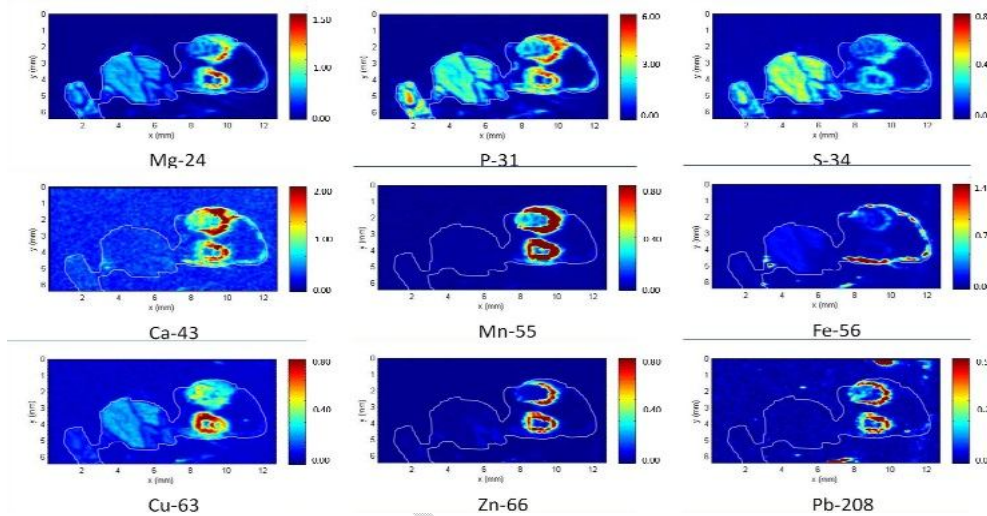


Fig.3. Spatial distributions of inorganic elements in a honeybee, measured using LA-ICP-MS. The unit shown in the figure is ng/mm².

3) Food Storage

Honey bees process the food they collect, altering it from its original state before storage. They mainly store two forms of food: honey, which is derived from nectar, and bee bread, which is produced from pollen. This stored food is kept in combs made from wax that is secreted by the wax glands of adult worker bees.

a) Honey

In a honey bee colony, a distinctive pattern of storage develops on the combs, creating three concentric zones: a central area where the brood is reared, a surrounding layer where pollen is stored, and an outermost region that contains honey. When nectar foragers return to the hive, they transfer their nectar loads to specialized food-storer bees through a process known as trophallaxis.

These food-storer bees then regurgitate the nectar into cells distributed throughout the comb (Camazine, 1991) (Fig. 4).

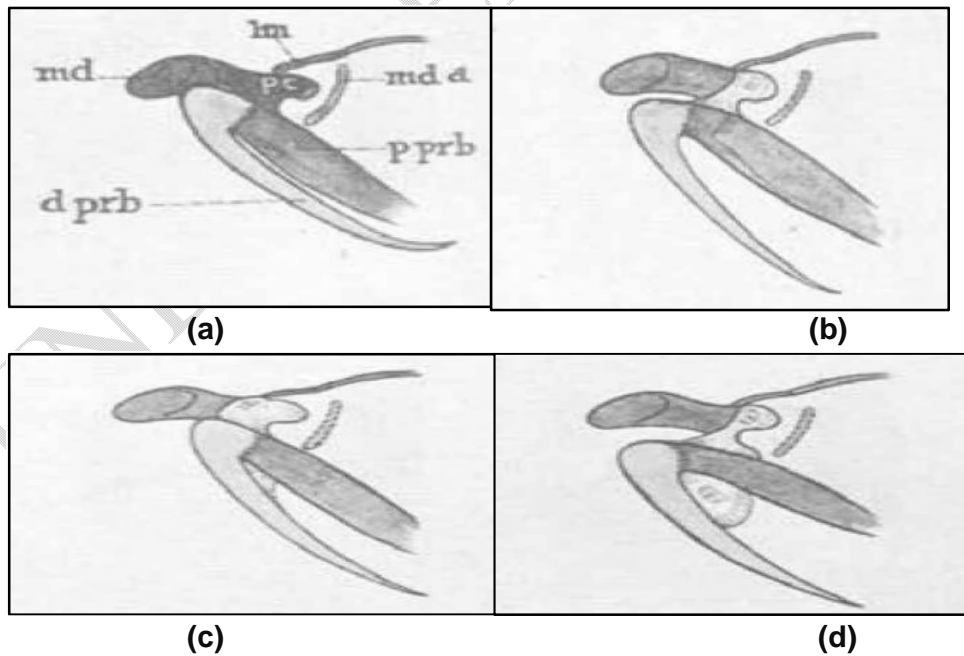
The transformation of nectar into honey begins with the active reduction of its water content. Foragers regurgitate the nectar and hold it between their mandibles to facilitate water evaporation (Park, 1925) (Fig. 5). Additionally, passive evaporation occurs within the cells as the nectar ripens. Research indicates that moving the nectar between different cells before final storage is crucial for proper honey maturation, contributing to honey's inhomogeneous matrix (Eyer et al., 2016). Water removal can also start during the transport of nectar to the hive (Nicolson and Human, 2008). Another critical part of this process is the hydrolysis of sucrose into glucose and fructose, which occurs when the enzyme invertase is added to the nectar in the bee's crop during collection (Oertel et al., 1951).



Fig.4a. Nectar being transferred from a loaded nectar-carrier to a house-bee

b. House bee ripening

c. House-bee depositing honey



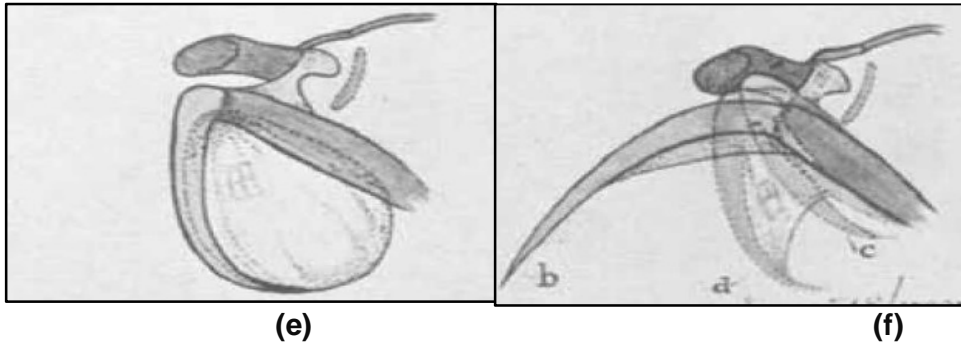


Fig. 5. Figures depicting the mouthparts of a bee engaged in honey ripening.

The stored honey is characterized by a low water content of less than 20%, coupled with a high sugar concentration exceeding 80%, primarily composed of the monosaccharide glucose and fructose. Fructose is present in higher amounts due to the lower solubility of glucose, which tends to crystallize. At the temperature within the hive, the solubility of glucose increases with the concentration of fructose, leading to a highly concentrated sugar solution that effectively inhibits microbial growth (Doner, 1977).

Honey also contains free amino acids, with proline being the most abundant, partly added by bees during the honey-making process. Additionally, enzymes such as glucose oxidase, which converts a small portion of glucose into gluconic acid and hydrogen peroxide, are introduced by the salivary glands of bees. Other enzymes include diastase (α -amylase), which breaks down starch, and invertases that convert sucrose into fructose and glucose. The high osmotic concentration, coupled with hydrogen peroxide and a low pH, significantly enhances honey's antimicrobial properties (Kwakman et al., 2010). Furthermore, minor compounds like phenolics contribute to the distinct colour, aroma, and flavour of different types of honey and may also play a role in bee health (Mao et al., 2013). Honeydew honey is distinguishable from floral honey by its content of melezitose and other oligosaccharides (Bogdanov et al., 2004).

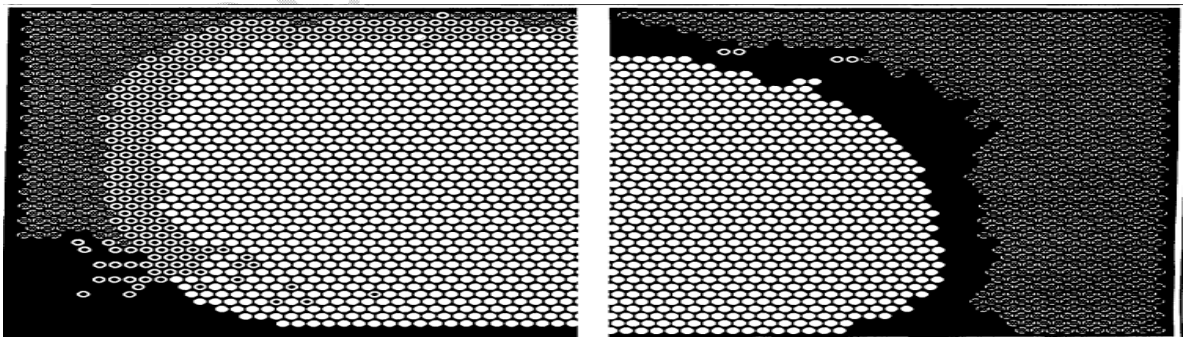


Fig.6a. A characteristic pattern of comb consisting of brood, pollen, and honey area.

b. Pattern of comb during early August

The majority of honey is consumed by the colony, with a preference for less concentrated honey, while only a small portion is stored (Eyer et al., 2016). Despite this, the honey storage area

within the comb can be substantial, often weighing several tens of kilograms. Typically, the storage pattern features brood at the center, surrounded by a thin strip of pollen, with honey stored in the outermost region (Camazine, 1991) (Fig. 6). Water reserves within the colony are relatively small and are mainly found in the crops of water foragers and in-hive reservoir bees, to which water collectors transfer their load; some water may also be stored in the combs (Ostwald et al., 2016).

b) Bee Bread

When pollen-collecting foragers return to the hive, they deposit their pollen loads directly into cells dispersed throughout the comb (Camazine, 1991). These cells often already contain pollen from previous collections, which may originate from different floral sources. Young worker bees further process this pollen by tightly packing it and adding regurgitated honey, which possesses antimicrobial properties that help preserve the stored pollen (Anderson et al., 2014). Bees tend to consume fresh pollen, typically preferring pollen that has been stored for less than three days. Initially, newly collected pollen contains few bacteria, but these levels decrease significantly after the pollen has been stored for more than 96 hours. Consequently, most of the stored pollen is found in a narrow strip surrounding the brood cells (Camazine, 1991).

The pollen packed into cells for storage is referred to as bee bread. The nutritional profile of bee bread differs from that of floral pollen, with protein content ranging from 10 to 30 percent, while lipids are present within a narrower range of 3 to 8 percent (Human and Nicolson, 2006; Nicolson and Human, 2013). In contrast, pollen lipids can constitute up to 20 percent of the dry weight (Roulston et al., 2000). The carbohydrate content of bee bread falls between 25 and 50 percent of dry weight, which includes additional carbohydrates from honey or nectar (Nicolson and Human, 2013).

During pollen collection, lactic acid bacteria from the bee's crop are introduced into the pollen, leading to microbial activity that may result in predigestion or the addition of essential nutrients (Gilliam, 1997). The bee gut harbors a unique microbial community composed of about nine bacterial species clusters, each adapted to specific niches and spatial locations within the gut. This microbial community is transmitted between bees through social interactions, similar to the transmission of gut microbes in mammals. Honey bee gut bacteria are known to synthesize B vitamins (Kwong and Moran, 2016), which could potentially enhance the B vitamin content of bee bread or help degrade complex polysaccharides in the pollen's outer layer (Lee et al., 2014).

4) BEE NUTRITION

Honey bees exhibit distinct behavioral phases throughout their adult life, transitioning from tasks such as nursing to foraging. This behavioral shift is accompanied by significant physiological changes, particularly in their nutritional needs. Unlike many other insects, adult nurse bees are capable of producing royal jelly—a glandular secretion that is essential for larval development, much like mammalian milk provides critical nutrients for young mammals.

a) Nutritional Processes: Pollen Digestion by Nurse Bees and Larval Nourishment

Bee species nourish their larvae either through mass provisioning or progressive feeding (Michener, 2000). In solitary bee species, larvae develop independently, relying on the nectar and pollen provisioned by their mothers at the time of egg-laying. This method contrasts with social bees, such as honey bees, where nurse bees engage in progressive feeding, a process that has had a significant impact on their nutritional requirements and methods.

Nurse bees play a pivotal role in feeding all colony members. They accomplish this by directly providing honey and bee bread or by producing glandular secretions such as royal jelly, which are produced after consuming these food sources. The consumption of pollen triggers the development of the mandibular and hypopharyngeal glands in young nurse bees, with glandular development peaking between six and ten days after the bees emerge from their cells (Pernal and Currie, 2000). These hypopharyngeal glands are unique to the Hymenoptera order, and in honey bees, they are particularly well-developed in nurse bees, enabling them to produce jelly for larval nourishment (Moritz and Crailsheim, 1987). Additionally, the transfer of gut bacteria among colony members, which occurs partly through trophallaxis, plays a crucial role in digestion and defence against pathogens (Billiet et al., 2017).

As the primary consumers of pollen within the colony, nurse bees exhibit higher levels of pollen consumption and midgut protease activity compared to foragers (Crailsheim et al., 1992). The development of their hypopharyngeal glands is closely linked to the protease activity in the midgut (Moritz and Crailsheim, 1987). The pollen grain's exine serves as a barrier to nutrient extraction, and the size and surface area to volume ratio of pollen grains can influence their nutritional value and the ease with which nutrients are extracted (Rourke and Buchmann, 1991). Osmotic shock is proposed as a mechanism for pollen digestion in bees; the exposure to lower osmotic concentrations in the midgut compared to the crop may cause the grains to rupture and release their contents (Kroon et al., 1974).

b) Royal Jelly

Honey bees are unique among bee species in their ability to convert their food intake into royal jelly, a highly nutritious substance used to feed their brood. This jelly is secreted by the mandibular and hypopharyngeal glands in the heads of nurse bees. It is then deposited into the cells of both worker and queen larvae, with queen larvae receiving significantly more jelly than workers, who receive smaller quantities and are fed on demand during later developmental stages (Haydak, 1970). Worker larvae are initially fed exclusively on royal jelly for the first three days before their diet is supplemented with a mix of glandular secretions, honey, and pollen (Crailsheim, 1990). Larval starvation, whether due to food scarcity or other stressors, can lead to weakened colonies. Insufficient feeding during development can result in smaller, less robust adult bees, and in some cases, young larvae may be cannibalized by adult workers (Brodschneider and Crailsheim, 2010).

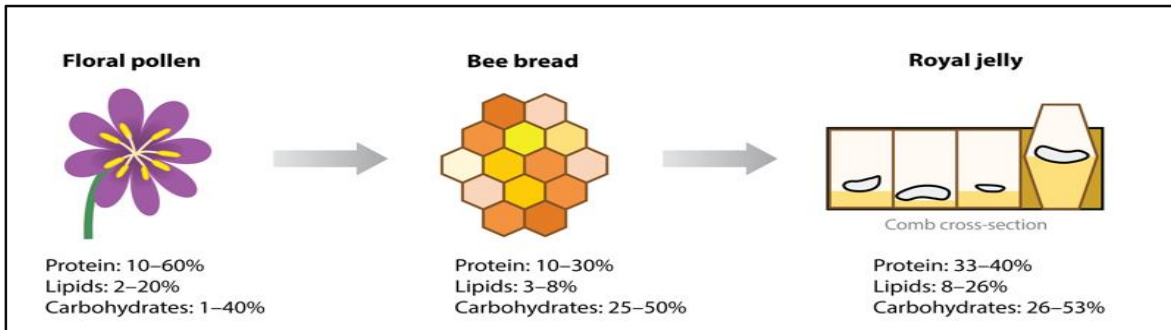


Fig. 7 The refinement of floral pollen into royal jelly by adult worker honey bees

Royal jelly is a specialized nutritional product produced by nurse honey bees, derived from the honey and bee bread they consume (Fig. 7). Despite being collected from colonies in various geographical regions, royal jelly exhibits a remarkably consistent chemical composition.

Royal jelly generally contains about 63% water, 14% protein, 18% carbohydrates, and 6% fats. The carbohydrate profile of royal jelly is similar to that of honey, primarily consisting of glucose and fructose in nearly equal amounts, with only trace levels of other sugars, such as sucrose (Wang et al., 2016). The proteins found in royal jelly, known as major royal jelly proteins (MRJPs), are produced exclusively by nurse bees. These proteins are secreted by the hypopharyngeal and mandibular glands of the nurse bees and provide larvae with essential amino acids. While MRJPs are also found in other hymenopterans, honey bees produce a specific set of nine MRJPs. These proteins are likely digested and then used to synthesize other proteins in the bee's body, suggesting that they are optimally suited for the nutritional needs of developing honey bees (Buttstedt et al., 2014).

In terms of fat content, royal jelly contains up to 10% fat by wet weight, with a significant proportion of these fats being uncommon free fatty acids, such as hydroxyl and dicarboxylic fatty acids (Plettner et al., 1996). Notably, royal jelly includes two key compounds—10-HDA [(E)-10-hydroxy-2-decenoic acid] and 10-HDAA (10-hydroxy-decanoic acid)—which are related to components of queen mandibular pheromone but originate from different oxidation pathways (Plettner et al., 1996). 10-HDA, constituting up to 73% of the fatty acid profile and up to 2–4% of the total wet weight of royal jelly, acts as an epigenetic modulator by inhibiting histone deacetylases (Spannhoff et al., 2011). This function suggests a potential role in caste differentiation within the hive.

In addition to macronutrients, royal jelly contains approximately 2% micronutrients, including sterols, vitamins, minerals, and phenolic compounds (Ciulu et al., 2013). The predominant sterol in royal jelly is 24-methylene cholesterol, with other sterols such as cholesterol, stigmaterol, and isofucosterol also present, deriving from the plant sources of the pollen collected by the bees (Lercker et al., 1982). Since honey bees cannot synthesize sterols themselves, they rely on the sterols from their pollen sources for their nutritional needs.

The exact mechanisms by which specific compounds in royal jelly influence caste differentiation in honey bees remain unclear. Recent research suggests that floral pollen might affect

caste development, as it contains microRNA molecules that can interfere with primary metabolic pathways. When these pollen-specific microRNAs were administered with royal jelly, the resulting adult bees exhibited characteristics typical of worker bees, such as smaller size, fewer ovarioles, and slower development (Zhu et al., 2017) (Fig. 8).

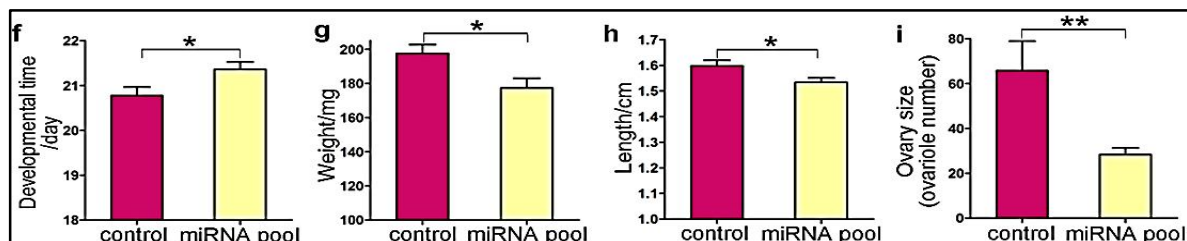


Fig. 8 Effect of plant miRNA pool on honey bee phenotypes

c) Nutritional Needs of Adult Workers Honey Bees

In honey bees, the dietary intake preferences are skewed towards carbohydrates due to their nectar-based diet, as reflected in their protein: carbohydrate ratio (Stevenson et al., 2017). This ratio varies with the age of the worker bees: when essential amino acids (EAA) are the primary protein source, the EAA ratio shifts from 1:50 to 1:75 during the first two weeks of adulthood, and further decreases to 1:250 in caged foragers (Paoli et al., 2014). Research indicates that a high-protein or high-EAA diet significantly impacts survival, aligning with observations in other species where elevated protein intake is associated with reduced lifespan (Simpson and Raubenheimer, 2012). Honey bees show a preference for salty water sources, particularly those with sodium (Lau and Nieh, 2016). It is suggested that bee-associated microbes might synthesize essential vitamins not provided by pollen. Moreover, while the specific sterol requirements of honey bees are not fully understood, it is known that they need pollen-derived sterols like 24-methylene cholesterol (Svoboda and Lusby, 1986).

Foraging in honey bees demands advanced cognitive and flight capabilities. When nurse bees transition to foragers, their physiology undergoes significant changes. This shift includes a reduction in hypopharyngeal gland size, alterations in brain structure and function, changes in neurochemistry and gene expression, as well as adjustments in flight muscle biochemistry that enhance metabolic and aerodynamic efficiency (Roberts and Elekonich, 2005). Nurse bees exhibit well-developed hypopharyngeal glands, higher levels of blood proteins, and increased lipid reserves in their fat bodies compared to foragers. Lipid reserves are depleted just before the onset of foraging, which can be accelerated by severe colony starvation (Toth et al., 2005). The presence of foragers in the colony can delay the initiation of foraging behaviour in nurses, suggesting that foragers may exert a social influence rather than directly affecting the nutritional state of nurse bees through trophallaxis.

d) Colony-Level Nutrition

Research has shown that feeding honey bee colonies for extended periods on either of two commercial artificial diets or pollen does not significantly impact hemolymph protein levels in nurse bees or the overall size of the colony population. Nevertheless, colonies that were sustained on artificial diets displayed poorer health outcomes, including increased rates of queen loss and *Nosema* infections (DeGrandi-Hoffman et al., 2016). A diet consisting of a variety of floral sources typically offers superior nutrition compared to a single-floral diet, enhancing bee health, immune function, and lifespan. However, the specific composition of pollen constituents also plays a crucial role (Alaux et al., 2010). On a colony-wide scale, foraging behavior tends to focus on resources that address nutritional gaps (Hendriksma and Shafir, 2016). For instance, Zarchin et al. (2017) observed that foragers performed more vigorous dances to attract pollen sources that helped alleviate the colony's essential fatty acid deficiencies.

5) IMPORTANCE

Honeybee nutrition plays a pivotal role in the scientific community, as it is essential for comprehending bee health and ensuring agricultural productivity, especially in light of the global decline in bee populations. The health of honeybees is integral to pollination, which in turn sustains biodiversity and supports food production. As environmental stressors increasingly threaten bee populations, understanding their impact on honeybee nutrition is crucial for developing effective conservation strategies. Advancements in nutritional science, particularly in the study of nutritional physiology, are key to optimizing bee diets, thereby enhancing colony resilience and productivity. This research necessitates interdisciplinary collaboration, bringing together various scientific fields to explore the complex interactions that influence bee health. Additionally, insights gained from nutrition studies are instrumental in refining beekeeping practices, leading to better management of colonies for improved health and productivity.

6) CONCLUSION

In summary, the intricate relationship between bee nutrition and colony health is critical to understanding the ongoing decline of bee populations. Bees, as vital pollinators, rely heavily on a diverse diet of floral nectar and pollen to meet their energy and nutrient requirements. This nutritional strategy is shaped by their evolutionary journey over millions of years, leading to specialized foraging behaviors that address their specific dietary needs. The interplay of factors such as seasonal availability, pollen quality, and nectar composition plays a significant role in their survival.

Furthermore, the processing of food into honey and bee bread not only serves as a reserve for nutrient storage but also enhances the nutritional value through fermentation and microbial digestion. The production of royal jelly, which is critical for larval development and caste determination within the hive, emphasizes the nuances of honey bee nutrition. As threats from environmental changes and agricultural practices increase, enhancing bee nutrition through habitat restoration and dietary diversity can help mitigate population declines and ensure the sustainability of these essential pollinators in our ecosystems.

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