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Review

Honey Bee Nutrition: Current Knowledge, Challenges, and Future Research Directions

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Abstract

Honey bees *(Apis mellifera)* play a major ecological role since they are the main pollinators worldwide. In addition, these insects have been managed for commercial purposes for a long time due to the products obtained from their colonies. However, based on the number of published scientific studies, honey bee nutrition is a topic that has received increasing attention during the last years, likely due to land use intensification, which has decreased the diversity and/or quality of pollen available for honey bees, impacting their health. Moreover, there is an increase in inquiries from beekeepers regarding strategies to mitigate nutritional stress, suggesting that the information available is not enough. This gap might be related to the fact that honey bee nutrition is closely dependent on the environment in which the honey bees are. In this revision, we first review the information regarding honey bees' nutritional resources and requirements. Secondly, we analyze the flow of these nutritional resources within the honey bee colony and their effect at the individual and colony level. Thirdly, we analyze the impact of nutritional stress on honey bee colonies, explore the availability of strategies for colony supplementation, and discuss their effects on colonies' strength and productivity. Fourthly, we analyze the interaction between the infection level with pathogens and nutritional stress, considering the *Eucalyptus grandis* plantations, a common scenario in Uruguay in which those stressors interact. Finally, we aimed to identify research directions that could contribute to improving honey bee health through nutrition. Understanding the complex interactions between honey bee colonies, their environment and beekeeping management practices is key to achieving a sustainable productive activity.

Keywords: colony nutritional supplementation, *Eucalyptus grandis*, landscape composition, nutritional value, pollen

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Nutrición de las abejas melíferas: Conocimiento actual, desafíos y perspectivas de investigación

Resumen

Las abejas melíferas *(Apis mellifera)* tienen un rol ecológico sumamente relevante debido a que son los principales insectos polinizadores. Además, han sido manejadas con fines productivos desde hace largo tiempo por los productos que es posible obtener a partir de las colmenas. En los últimos años, los estudios científicos publicados vinculados a la nutrición de estos insectos se han incrementado debido principalmente a la intensificación en el uso del suelo, lo que ha disminuido la diversidad y/o la calidad del polen disponible para las abejas, lo que impacta en su salud. En este sentido, los apicultores cada vez demandan más estrategias para mitigar el estrés nutricional y sugieren que la información disponible no es suficiente. Este vacío de información puede estar relacionado con el hecho de que la nutrición de las abejas está fuertemente asociada al ambiente en el que se encuentran. En esta revisión se presenta, en primer lugar, información disponible sobre los recursos y requerimientos nutricionales de las abejas. En segundo lugar, se analiza el flujo de los recursos nutricionales a distintos niveles de la colonia y su impacto a nivel individual y colonial. En tercer lugar, se analiza el impacto del estrés nutricional en las colonias de abejas, las estrategias de suplementación nutricional disponibles y su impacto en la fortaleza y productividad de las colonias. Tomando como modelo ambiental las plantaciones de *Eucalyptus grandis*, escenario cotidiano dentro de la apicultura uruguaya, se analiza la interacción entre los niveles de infección con patógenos y el estrés nutricional. Por último, con base en los aspectos revisados, se plantean posibles caminos para investigación, buscando contribuir así a la mejora de la salud a través de la nutrición. Comprender las complejas interacciones entre las colonias de abejas, su ambiente y las prácticas de manejo apícola parecería ser clave para lograr una producción sustentable.

Palabras clave: suplementación nutricional colonial, *Eucalyptus grandis*, composición del paisaje, valor nutricional, polen

Nutrição das abelhas: Conhecimento atual, desafios e perspectivas de pesquisa

Resumo

As abelhas melíferas (*Apis mellifera*) desempenham um papel ecológico extremamente importante como os principais insetos polinizadores. Além disso, as abelhas melíferas têm sido manejadas há muito tempo para fins produtivos devido aos produtos que podem ser obtidos de suas colmeias. No entanto, estudos relacionados à nutrição desses insetos têm aumentado nos últimos anos, principalmente devido à intensificação do uso da terra e ao seu impacto na saúde das abelhas. Nesse sentido, os apicultores estão cada vez mais exigindo estratégias para mitigar o estresse nutricional, sugerindo que as informações disponíveis são insuficientes. Essa lacuna de informação pode estar relacionada ao fato de que a nutrição das abelhas está fortemente ligada ao seu ambiente e ao seu impacto na dinâmica da colônia. Esta revisão apresenta, primeiramente, as informações disponíveis relacionadas aos recursos nutricionais para abelhas e suas necessidades nutricionais. Em segundo lugar, analisam-se o fluxo de recursos nutricionais em diferentes níveis da colônia e seu impacto nos níveis individual e da colônia. Em terceiro lugar, analisa-se o impacto do estresse nutricional nas colônias de abelhas melíferas, juntamente com as estratégias de suplementação nutricional disponíveis e seu impacto na força e produtividade da colônia. Utilizando plantações de *Eucalyptus grandis* como modelo ambiental, um cenário comum na apicultura uruguaia, analisa-se a interação entre os níveis da infestação das plagas e o estresse nutricional. Por fim, com base nos aspectos revisados, propõem-se possíveis caminhos para pesquisas relacionadas à nutrição de abelhas, visando melhorar sua saúde. Compreender as complexas interações entre as colônias de abelhas, seu ambiente e as práticas de manejo apícola parece ser fundamental para alcançar uma produção sustentável.

Palavras-chave: suplementação nutricional colonial, *Eucalyptus grandis*, composição da paisagem, valor nutricional, pólen

1. Honey Bee Nutrition

1.1 Natural Nutritional Resources for Honey Bees

Honey bees (*Apis mellifera)* rely on the consumption of honey and pollen. Honey is the main source of carbohydrates. According to the Codex Alimentarius, it is "a natural sweet substance produced by honey bees from the nectar of plants or from secretions of living parts of plants or excretions of plant sucking insects on the living parts of plants, which the bees collect, transform by combining with specific substances of their own, deposit, dehydrate, store and leave in the honey comb to ripen and mature" (Food and Agriculture Organization of the United Nations & World Health Organization, 2019). When honey is produced from the nectar of plants, it is called blossom honey, while when it is produced from excretions of plant-sucking insects, it is called honeydew. Blossom honey has high amounts of fructose and glucose, while honeydew honeys contain high amounts of the oligosaccharides melezitose and raffinose (Doner, 1977; Pita-Calvo & Vázquez, 2017). Salivary enzymes are added by the bees, which, together with the free amino acids, are an important fraction of the 0.2-0.5% protein content of honey dry weight. In addition, the minerals and vitamins content in honey also range between 0.2-0.5% of honey dry weight, depending on its botanical origin, with potassium and sodium being the main minerals found in honeys (Bogdanov et al., 2007). Since carbohydrates are used as an energy source and honey provides low quantities of non-carbohydrate nutrients, this review focuses on pollen nutrition.

Pollen is the main source of proteins, lipids, vitamins, and minerals for honey bees (Brodschneider & Crailsheim, 2010). The pollen is collected from the flowers by the bee foragers, transported in their legs ("corbiculae pollen"), mixed with honey and glandular secretions, and stored in the colony as "beebread". For a long time, it was proposed that pollen in beebread is fermented by microorganisms, increasing its nutritional value in comparison to the corbiculae pollen (Brodschneider & Crailsheim, 2010; Gilliam, 1979; Gilliam & Bee, 1979). However, the advent of molecular techniques and the study by scanning electron microscopy allowed to propose that the pollen from the beebread is not microbiologically modified and the associated microbiota has instead preservative functions (Anderson et al., 2014).

Carbohydrates can be found in pollen in concentrations ranging between 24-60% (Thakur & Nanda, 2020). The main carbohydrates are fructose and glucose, but others can also be found in lower concentrations, such as sucrose, melezitose, trehalose, among others (Baky et al., 2023; Oroian et al., 2022). They can also be found in pollen grains as cellulose and hemicellulose, with percentages ranging between 10.3 and 15.9% (Bonvehí & Jordà, 1997; Stanley & Linskens, 1974).

Pollen crude protein content varies according to its botanical origin, ranging between 2.9 and 53.3%. Factors such as air temperature, soil moisture and pH impact the plant physiology and thus affect pollen protein content (Day et al., 1990; Herbert & Shimanuki, 1978; Somerville, 2001). The amino acid composition of pollen is another important variable for describing its quality. Pollen should provide at least ten essential amino acids for bees in the required quantities, being leucin, isoleucine, and valine the most limiting ones (de Groot, 1953). Lipids are the second pollen component: their quantity varies between 0% and 20.3% (Singh et al., 1999; Somerville, 2001), and palmitic, arachidic, stearic, oleic, linoleic and linolenic acid are among the most concentrated fatty acids in pollens (Baky et al., 2023; Bonvehí & Jordà, 1997; Hsu et al., 2021; Manning & Harvey, 2002). Pollen is also rich in water-soluble vitamins thiamine, riboflavin, pyridoxine, pantothenic acid, niacin, folic acid, biotin, inositol, and ascorbic acid, and also has small quantities of non-soluble vitamins (Herbert & Shimanuki, 1978; Nielsen et al., 1955). Finally, pollen is an important source of minerals, including K, Na, P, S, Ca, and Mg, among the most abundant (Bonvehí & Jordà, 1997; Herbert & Miller-Ihli, 1987; Somerville & Nicol, 2006). The quantity of all these components in pollen varies according to the botanical origin (Anjum et al., 2024; Giampieri et al., 2022).

1.2 The Flow of Nutritional Resources within the Honey Bee

Honey bees are eusocial insects that have developed a complex system of organization characterized by a division of labor. In this regard, nutrition is one of the driving forces behind this organizational system (Ament et al., 2008, 2010; Schulz et al., 1998; Toth & Robinson, 2005; Toth et al., 2005).

From an evolutionary point of view, division of labor has allowed honey bees to shelter nutritional resources at the colony level. Adult bees consume pollen, especially during the first nine days of life (Crailsheim et al., 1992). This high pollen consumption of young bees is associated with their nursing activity, which is supported by anatomical and physiological adaptations: nurse bees show well-developed hypopharyngeal glands and fat bodies and produce proteolytic enzymes for the initial pollen digestion (Crailsheim et al., 1992; Moritz & Crailsheim, 1987; Roulston & Cane, 2000). After protein degradation, the amino acids are absorbed by specific transporters, while lipids are processed by lipases in the gut lumen and absorbed into the enterocytes by simple diffusion and specific transporters. Both are transported in the hemolymph by lipophorins and internalized into the fat body cells. Fat bodies are the major site of insect metabolism and nutrient storage, and when nutrient mobilization is required, these reserves are used to synthesize proteins such as the lipoprotein vitellogenin (Vg) (Corona et al., 2007; Crailsheim, 1988; Haszonits & Crailsheim, 1990). Vitellogenin is mobilized in the hemolymph to the hypopharyngeal glands for synthesizing the royal jelly, which is delivered mainly to the larvae (Amdam & Omholt, 2002; Crailsheim et al., 1992). Each worker larvae is fed with about 25-37.5 mg of protein, of which 95% comes from the royal jelly, and only 5% comes directly from pollen (Babendreier et al., 2004; Crailsheim et al., 1992; Hrassnigg & Crailsheim, 2005). If larvae are not visited and fed according to their requirements, the brood population decreases, and future bee generations show more susceptibility to stressors like diseases (Brodschneider & Crailsheim, 2010). Thus, the proteins and lipids ingested at the bee level affect future generations.

Royal jelly is also delivered to adult bees, to the queen, and eventually to the drones by trophallaxis, providing them with processed food which they could not obtain otherwise, since their digestive capacity is reduced (Crailsheim, 1998). Therefore, adult bee nutrition also affects their partners' nutrition. Moreover, at the individual level, pollen feeding increases bee lifespan and its division of labor, since well-nourished bees show a late behavioral maturation (Ament et al., 2010; Corona et al., 2007, 2016; Toth & Robinson, 2005; Toth et al., 2005). Longer lifespans and later onset of foraging increase the foraging capacity of the colony, which allows it to collect and store more food for better colony overwintering and survival. Moreover, the behavioral maturation for foraging is associated with a shift from high to low fat reserves (see Section 1.3) (Toth et al., 2005), and consequently, forager bees have diminished nutritional reserves.

The background presented in this section shows that honey bee colonies have developed mechanisms of nutritional interplay at the brood, adult, and colony level to ensure that nutritional reserves remain within the colonies.

1.3 Nutritional Molecular Physiology

Evolutionary changes have also operated in the nutritional molecular physiology of honey bees. In most organisms, a better nutritional state increases the expression of insulin (-like) peptides (ILPs), thereby stimulating growth, energy storage, and reproduction (Badisco et al., 2013; Nässel & Vanden Broeck, 2016; Simopoulos, 2002, 2008; Wu & Brown, 2006). However, in honey bees, pollen-rich diets decrease the expression of ILP1 in the brain and enhance the activity of the target of rapamycin (TOR) in other tissues (Ament et al., 2008). TOR is a conserved intracellular pathway that integrates information regarding amino acid availability and insulin/insulin-like signaling (IIS pathway) (Kapahi et al., 2010).

In well-nourished worker bees, Vg acts as a central regulator: high Vg levels inhibit ILP1 expression in the brain, and Vg and juvenile hormone (JH) show negative feedback (Amdam & Omholt, 2003; Ament et al., 2008;

Guidugli et al., 2005; Marco Antonio et al., 2008). Low levels of JH are associated with nurse behavior, while high levels of this hormone are associated with foraging (Amdam et al., 2006; Ament et al., 2008; Robinson, 1992). Thus, the expression pattern of highly conserved molecular mechanisms strongly linked to nutrition is modified in honey bees and adapted to allow their connection to the eusociality of this species.

In this extremely simplified molecular explanation of nutrition and sociality, it is important to note that nutrition is not the only driving force of behavioral transition, and social signs are also involved. Among these social signs are some pheromones and trophallactic interaction that modulate ILPs expression in the brain according to the colony demands of foragers (Johnson, 2010; Leoncini et al., 2004).

1.4 Mechanisms of Pollen Foraging Regulation

Pollen collection is shaped by the colony's nutritional requirements (Schmickl & Crailsheim, 2004), since more pollen forager bees are recruited when pollen stores are scarce, and with higher quantities of unsealed brood (Al-Tikrity et al., 1972; Barker, 1977; Fewell & Winston, 1992; Free & Williams, 1971; Rotjan et al., 2002). Thus, pollen foraging activity is regulated by the relationship between pollen stores and pollen demand.

There are at least three mechanisms that regulate pollen collection. During trophallaxis between nurses and foragers, bees communicate to each other the nutritional demands of the colony: high-protein food is transferred between them when there is an excess of pollen in comparison to the brood demand, inhibiting pollen foraging behavior, and vice versa (Camazine et al., 1998). Forager bees can also screen directly the cells containing pollen and brood, modifying their collection behavior accordingly (Dreller & Tarpy, 2000; Vaughan & Calderone, 2002). Finally, brood can induce pollen collection directly through the secretion of the brood pheromone (Pankiw et al., 1998).

On the other hand, bees can distinguish different pollen based on a combination of olfactory, visual, and chemotactic cues (Arenas et al., 2021; Cook et al., 2005; Ruedenauer et al., 2018). In this sense, some pollen species are preferred over others (Cook et al., 2005; Ruedenauer et al., 2018). However, which pollen components make the bees prefer one pollen over another is a question still unanswered. Pollen cues do not seem to inform honey bees about their nutritive quality, since forager bees cannot distinguish pollen types based on their protein or essential amino acid content (Leonhardt et al., 2012; Pernal & Currie, 2001), and nurse bees cannot discriminate the pollen quality based on their protein lipid ratio (Corby-Harris et al., 2018). This behavior contrasts with that observed in bumblebees, which have shown significant preferences for higher nutritive pollens (Leonhardt et al., 2012; Vaudo et al., 2016). Thus, if pollen nutritional quality does not shape the collection behavior of honey bees, but honey bees prefer to collect some pollen over others, it seems that pollen foraging preferences are mainly driven by the presence of specific components. In this regard, there is emerging evidence that lipids could act as phagostimulants (Singh et al., 1999), while repellent components could exert rejection (Schmidt et al., 1987).

1.5 Effects of Honey Bee Nutrition at the Individual and Colony Level

One of the most challenging aspects of bee nutrition is identifying which pollens offer higher nutritional value. Pollen differs widely in protein concentration and its amino-acid composition (Day et al., 1990; de Groot, 1953; Somerville, 2001). Pollen also differs in the quantity and specific composition of lipids, and in the content and types of sugars and micronutrients (Herbert & Shimanuki, 1978; Manning, 2001a; Singh et al., 1999; Stanley & Linskens, 1974). As a result, pollen quality depends on the nutritional parameters considered. In this regard, different studies have addressed the effects of feeding bees with different pollen on bee lifespan and other physiological parameters, characterizing these pollens considering some of those parameters.

Bees fed with diverse pollen and with high protein content have increased lifespan but also have a better ability to respond to pathogen infection, since they present greater expression of genes associated with the individual humoral and social immune response (Alaux et al., 2010; Castelli et al., 2020). Furthermore, pollen feeding decreases bees' sensitivity to pesticide poisoning, probably due to greater activation of genes linked to the detoxification of these compounds (Schmehl et al., 2014). Schmidt et al. (1987) fed caged bees with 25 different pollens. Bee lifespan increases according to the protein concentration in the pollen, but mainly with the total amount of pollen protein consumed, and this consumption depends on how attractive the pollen was to the bees (Schmidt et al., 1987). In this study, the authors highlighted that some observed deviations deserve future attention for understanding the effects of different pollen feeding on honey bees. In addition, bees fed with spring protein-rich pollens show higher protein hemolymph titers, higher hypopharyngeal glands (HG), and higher expression levels of genes related to bee nutrition (vitellogenin and hexamerin 70a) than bees fed with fall pollens. However, fall pollen was consumed in higher amounts and was better digested, which might be associated with the preparation of the bees for periods of confinement (DeGrandi-Hoffman et al., 2021). On the other hand, different studies proposed that specific amino acid and fatty acid concentrations are better predictors of the HG growth size, as a marker of the nutritional status of the bees in comparison to the protein content (Corby-Harris et al., 2018; DeGrandi-Hoffman et al., 2018).

Recent studies have shown that the amount of lipids and the omega-6:3 ratio in the honey bee body depend on the composition of the diet on which they were fed (Arien et al., 2020). The quantities of these components in the honey bee diet affect their learning abilities, since bees fed with diets with 4% of total lipid concentration and with an omega-6:3 ratio of 1 achieved the best learning performance (Arien et al., 2015, 2018). Moreover, diets with 4 and 8% of lipids and with an omega 6:3 ratio lower than 1 extended bee lifespan in comparison to diets with lower lipid contents and higher ratios, and these better nourished bees reared more brood (Arien et al., 2020), demonstrating that the quantity and quality of lipids in the diet affect the colony performance.

The impact of pollen protein nutrition at the colony level has also been studied, mainly by Australian researchers. In 1976, a non-peer-reviewed Australian journal specialized in beekeeping published an article that classified pollens based on their protein content as having poor quality (<20%), average (between 20 and 25%), or good quality (≥25%) for honey bee colonies (Kleinschmidt, 1976). These values have been considered in later studies to the present day as a reference to categorize pollens and to predict their effect at the colony level. However, since the recently available information has shown that other pollen components affect honey bee nutrition, these values should be revised (Black, 2006; Invernizzi et al., 2011; Somerville, 2001; Somerville & Nicol, 2006).

Probably the most challenging aspect in analyzing nutrition at the colony level is the difficulty in manipulating and controlling colony pollen intake under field conditions. However, it is evident that to understand the effects of the consumption of different pollens on honey bee colonies, it is necessary to study their composition deeply and focus not only on protein concentration but also on other nutritional components, such as amino acid composition, lipid content, lipid quality, micronutrients, the amount of pollen consumption, and its digestibility. The development of the analytical methodologies for analyzing the pollen composition and its nutritional properties will hopefully allow for the near future to study their potential effect on different parameters of honey bees at the individual and colony level.

2. Nutritional Stress

2.1 Impact of Landscape Composition on Honey Bee Colonies

During the last years, high percentages of colony losses have been reported worldwide, and nutritional stress has been proposed as one of the driving forces associated with these losses (Clermont et al., 2015; Goulson et al., 2015). In natural and harmonic conditions, pollen quantity and quality support colony development, maintenance, reproduction, and overwintering. However, land use management modifies natural processes, implying that the environment can or cannot provide what colonies need, depending on what flourishes in different periods. Thus, nutrition and colonies might be phase-shifted. Considering the global agricultural production scenario, it is evident that this situation is more the rule than the exception. The intensification of land use associated with the increase in areas of monocultures provides bees with pollen from one or a few major sources (Naug, 2009), and does not necessarily provide all the nutritional requirements for the bees (de Groot, 1953; Naug, 2009; Somerville, 2001). Moreover, land use intensification is associated with extensive herbicide, fungicide, and pesticide use, which reduces floral resources and contaminates nectar and pollen (Cappellari et al., 2024; Knapp et al., 2023). Finally, this disequilibrium might be intensified with extreme climatic events such as droughts, irregular rainfall, and frosts, among others (Descamps et al., 2021; Frigero et al., 2025; Phillips et al., 2018).

Previous studies have shown that colonies located in uncultivated forage lands show annual colony mortality within the acceptable range of beekeepers' expected losses and significantly lower than those experienced by the colonies located in agriculturally dominated landscapes (corn, soybeans, wheat, and oats) (Smart, Pettis, Rice et al., 2016). This lower survival was associated with less pollen quantity rather than the diversity (Smart, Pettis, Euliss et al., 2016; Smart, Pettis, Rice et al., 2016). The nutritional characteristics of the pollen available in these environments seem to be more suitable for bees, since the protein content of beebread decreases with higher levels of arable and horticultural farmland and increases with the cover of natural grasslands and broad-leaf woodlands (Donkersley et al., 2014). In addition, healthy honey bees kept in lower cultivated areas exhibited higher lipid levels than those kept in areas of high cultivation (Dolezal et al., 2016), providing a link between landscape and the nutritional ecology of socially foraging insects.

In this interaction between landscape composition and honey bee nutrition, the sanitary status of the bees is playing an important role. In this regard, the presence of the widely distributed ectoparasite *Varroa destructor* unbalances this relationship (Alaux et al., 2011; Dolezal et al., 2016). This occurs probably because the mite sucks the fat body and hemolymph content of the bees, diminishing the nutrient stores (Ramsey et al., 2019) and inhibiting the bee protein metabolism (Alaux et al., 2011). Thus, the benefits of foraging in improved landscapes can be lost because of inadequate mite control strategies. On the other hand, pollen feeding helps honey bee colonies to diminish the negative consequences of *Nosema ceranae* infections, a microsporidian that infects the bee digestive tract, causing gut disorders (Botías et al., 2013; Branchiccela et al., 2019; Di Pasquale et al., 2013; Higes et al., 2013). Probably, the strengthening of the bees' immune system due to adequate nutrition helps the bees to overcome the infectious process of this intracellular pathogen (Alaux et al., 2010; Corona et al., 2023; Di Pasquale et al., 2013).

Finally, landscape composition might also impact the bee gut microbiota. Like other animals and plants, honey bees are not autonomous entities, but rather holobionts, parts of a complex network composed of the individual and its associated microorganisms (Bordenstein & Theis, 2015). They possess a relatively simple and stable gut microbiota, dominated by five bacterial genera that constitute the core and include Bombilactobacillus (former Lactobacillus Firm-4), Lactobacillus Firm-5, Snodgrassella, Gilliamella, and Bifidobacterium, together with other bacteria including Bartonella, Commensalibacter and Frischella (Motta & Moran, 2024). This community is acquired after emergence through social interactions and contact with hive surfaces (Powell et al., 2014; Raymann & Moran, 2018). However, its abundance and composition might be altered by honey bee nutrition (Castelli et al., 2020; Maes et al., 2016; Ricigliano et al., 2022; Saraiva et al., 2015). Considering that the gut microbiota plays important roles in nutrition and detoxification of toxic compounds, growth, development, immunity, and defense against pathogens (Motta & Moran, 2024), this dysbiosis can potentially impact honey bee health, highlighting the need to consider the microbiota in studies of bee nutrition and health.

2.2 Diagnosis of the Nutritional Status of Honey Bee Colonies

At the individual level in controlled assays, the protein hemolymph content, the size of HG acini, and the expression of genes related to nutrition, such as *vg* and major royal proteins, are among the nutritional indicators most widely studied (Azzouz-Olden et al., 2018; Cremonez et al., 1998; Danihlík et al., 2018; DeGrandi-Hoffman et al., 2010, 2021; Di Pasquale et al., 2013; Watkins de Jong et al., 2019). However, as was previously mentioned, at the colony level, the nutritional status of honey bees affects their task transitioning (Ament et al., 2010; Toth & Robinson, 2005; Toth et al., 2005). Therefore, choosing the most suitable type of sample and the most informative indicator of the nutritional status of the colony can be challenging.

In order to study the effect of different nutritional regimens at the colony level, the bee and brood populations, the bee hemolymph protein titers, and colony infection level with different pathogens are among the chosen parameters (Branchiccela et al., 2019, 2023; García-Vicente et al., 2024; Lamontagne-Drolet et al., 2019; Matilla & Otis, 2006; Peirson et al., 2024; Tapia-Rivera et al., 2025). However, different studies have failed to prove that nutritionally manipulated colonies performed better than those that did not receive any supplementation. Contradictory results have been obtained when analyzing brood quantity, bee protein content, and bee lifespan in supplemented and non-supplemented colonies (DeGrandi-Hoffman et al., 2021; Lamontagne-Drolet et al., 2019). In addition, it has been shown that supplemented colonies located in a nutritionally stressed environment were stronger in terms of bee and brood population and healthier considering the infection level with *Nosema* spp., but no differences in the bee crude protein were found (Branchiccela, 2020; Branchiccela et al., 2019). In later studies and with a great sampling effort, it was confirmed that in these environments, bees from supplemented colonies were better nourished since they showed higher expression levels of *vg* than bees from non-supplemented colonies (Viera López, 2021). To arrive at more generalized conclusions, extensive field studies across heterogeneous environmental conditions concluded that it is important to measure multiple colony and individual bee parameters to test the suitability of a diet, as honey bee nutrition evaluation is complex to measure (Lamontagne-Drolet et al., 2019). Also, it has been shown that some of the nutritional parameters are under the control of the nutritional manipulations, but also the environmental factors play major roles (Matilla & Otis, 2006). Therefore, from a beekeeping point of view, the return of extra feeding is highly contextually dependent (Peirson et al., 2024). In this sense, as one of the most impactful variables influencing colony performance, nutritional management represents a crucial aspect of modern beekeeping, and beekeepers should be able to ascertain the nutritional status of the colonies and the potential contribution of the surrounding environment to the colonies to adjust the nutritional colony manipulations and achieve the productive goals. From the current scientific knowledge, it seems that this decision-making is neither simple nor intuitive. Initiatives such as identifying indicators of nutritional status of the colonies, such as their protein levels, can be valuable to diagnose and perform precise nutritional manipulations (Rudelli et al., 2024).

2.3 Strategies for Nutritional Stress Mitigation

Since the consequences of nutritional stress are difficult to determine and mitigate (Branchiccela et al., 2023), one of the most important challenges in honey bee nutrition is to predict the potential colony nutritional stress in a timely manner, to avoid its negative consequences. Once nutritional stress is potentially possible, there are two main management practices to be carried out. The first one is to relocate the colonies to areas where beneficial flowering periods for bees occur. This strategy needs the availability of a suitable place, can stress the colonies in the short term, and can be economically costly (Pavlin et al., 2025; Pilati & Prestamburgo, 2016). Besides, the relocation of the colonies is not a productive strategy for honey producers, since on some occasions, nutritional stress due to low quality/quantity pollen occurs simultaneously with the nectar flow (Manning, 2018). The second option, and the most widely implemented, implies the provisioning of the colonies with supplements that provide bees with nutrients that the environment cannot provide (Haydak, 1945, 1970; Haydak & Tanquary, 1943; Manning, 2018; Spencer-Booth, 1960; Tsuruda et al., 2021).

Colonies supplementation can be achieved by providing pollen, pollen substitutes, or pollen supplements (Haydak, 1970; Spencer-Booth, 1960). The main difference between pollen substitutes and pollen supplements is that supplements include pollen in their formulation, while substitutes do not (Haydak, 1970; Spencer-Booth, 1960). Pollen or pollen supplements are preferred over the substitutes (Lamontagne-Drolet et al., 2019; Watkins de Jong et al., 2019), and all options have advantages and disadvantages. Pollen is the natural source of nutrients for bees and the pollen needs of the colony can vary between 13-50 kg annually, depending on the size of the colony and the availability of pollen in the environment (Crailsheim et al., 1992; Somerville, 2000). Despite preferring freshly stored pollen, bees store the pollen for consuming it in periods of pollen shortage (Carroll et al., 2017; Pernal & Currie, 2000). Thus, one beekeeping strategy to supplement the colonies is to take out the pollen using traps, or the beebread, during periods of abundant availability and provide it to the colonies when they need it, but its availability is scarce. However, this strategy should be implemented with caution since storage conditions must be optimal to avoid nutrient degradation and formation of toxin (Anjos et al., 2019; Van Bilsen et al., 1994). Moreover, since pollen might transmit diseases, it should be collected from healthy own colonies to ensure good beekeeping management and sanitary practices from these source colonies (Chen et al., 2006; Flores et al., 2005). Previous studies have shown positive effects of this supplementation on colony strength and health, mainly in summer, fall, and early spring (Table 1) (Branchiccela et al., 2019; DeGrandi-Hoffman et al., 2020; Invernizzi et al., 2011; Moayed Saffari, 2008; Viera López, 2021). However, also neutral and negative effects have been reported for colony pollen supplementation, considering different physiological parameters of the honey bee colony strength and health (Table 1) (DeGrandi-Hoffman et al., 2020; Invernizzi et al., 2011; Matilla & Otis, 2006; Mortensen et al., 2019; Viera López, 2021).

The development of pollen substitutes was addressed more than 300 years ago (Johansson & Johansson, 1977). Historically, the first substitutes were made with rye and pea flour, egg white, milk, and even chicken meat and bone ash (Johansson & Johansson, 1977). During the first half of the 20th century, North American and Australian beekeepers started preparing their substitutes mainly with wheat soybean flour and several brewer's yeast products (Haydak & Tanquary, 1943; Manning, 2018; Oertel, 1980), while in the subsequent years, the development of pollen substitutes has stopped using some components that have been identified to have negative or neutral effects for bees, and also those that risk the honey quality. Nowadays, the main protein sources are different vegetable flours (soybean, chick pea, mung bean, corn gluten meal), dried skim milk, yeast extract, commercial casein, dried egg yolk, and albumin, among others (Manning, 2018; Noordyke & Ellis, 2021). Since lipids and fatty acids contribute to the attractiveness of natural pollens (Singh et al., 1999), their presence in pollen substitutes is important for ensuring their consumption. The coconut, linseed, almond, and evening primrose oils are among the most preferred by the bees (Manning, 2018). On the other hand, pollen substitutes must avoid toxic substances for honey bees, including lactose, galactose, stachyose, pectins, protease inhibitors such as pepsin inhibitors, tannins, and highly concentrated minerals. Some of them are in the protein sources, and, thus, they should be pre-processed to remove these toxic compounds (Black, 2006). In a recent study, Noordyke and Ellis (2021) reviewed the available literature, which aimed to characterize the effect of different combinations of ingredients, and found that 133, 59, and 15 studies reported positive, neutral, or negative effects, respectively, on a wide range of parameters related to colony productivity, physiological, and pest and pathogen response (Noordyke & Ellis, 2021). One alternative is to use commercial substitutes, which, despite their formulations being confidential, their main ingredients are animal or vegetable flours, according to their labels. The most studied formulations are the Feed-Bee® and Bee-Pro®, which have shown positive but also neutral and negative effects on individual and colony responses (Table 1) (Amro et al., 2016; DeGrandi-Hoffman et al., 2016; Matilla & Otis, 2006; Moayed Saffari, 2008; Mortensen et al., 2019; Watkins de Jong et al., 2019). Moreover, in some studies, contradictory results have been reported considering the same parameter analyzed under similar experimental design, but in different years (Matilla & Otis, 2006), and also in the same experiment, some nutritional parameters showed positive effects while others showed the opposite response (DeGrandi-Hoffman et al., 2016; Lamontagne-Drolet et al., 2019).

Table 1. Published studies analyzing the impact of pollen supplementation, or pollen supplements and substitutes (commercial formulations), on honey bees and at colony level

Commercial supplements with no scientific basis are not included.

Type of product	Name of the product/composition	N/group	Period of administration	Form of administration	Control group	Effects on bees (supplemented vs. control)	Effects on colonies (supplemented vs. control)	Reference
Pollen patty	**polyfloral corbicular pollen** 33.3%, 33.3% granulated sugar, and 33.3% Drivert sugar	8	Summer to fall	454 g/dose weekly	non-supplemented colonies	↑ expression level of vg	↑ adult population ↑ brood population ↑ winter survival = infestation rates with *Varroa* in adult and brood = number of virus and infection level with DWV	Haydak (1945)
Commercial substitute	**BeePro®** (Mann Lake, Hackensack, MN, USA); premade patty	10	Summer (2014) and fall (2013)	113 g/dose, weekly	non-supplemented colonies	↓ pollen digestion = hemolymph protein titers in nurse bees	= colony size ↑ levels of BQCV ↑ levels of *Nosema* ↑ queen losses	Somerville (2000)
Commercial substitute	**MegaBee®** (Dadant, Chico, CA, USA) (granulated sucrose with water (2:1) and MegaBee® powder at a 1:1 weight ratio)	10		113 g/dose, weekly	non-supplemented colonies	↓ pollen digestion = hemolymph protein titers in nurse bees	= colony sized ↑ levels of BQCV ↑ levels of *Nosema* ↑ queen losses	
Pollen patty	wildflower pollen; granulated sucrose with water (1:1)	≤ 11	Summer to fall (2015)	weekly, 4 weeks	non-supplemented colonies	-	= colony strength = levels of *Nosema* spp.	Haydak and Tanquary (1943)
Commercial substitute	**MegaBee®** (Dadant & Sons, High Springs, FL)	≤ 11		453.5 g/dose, weekly, 4 weeks	non-supplemented colonies	-	= colony strength = levels of *Nosema* spp.	

Type of product	Name of the product/composition	N/group	Period of administration	Form of administration	Control group	Effects on bees (supplemented vs. control)	Effects on colonies (supplemented vs. control)	Reference
Commercial substitute	**BeePro®** (Mann Lake, Hackensack, MN, USA)	≤11		453.5 g/dose, weekly, 4 weeks	non-supplemented colonies	-	= colony strength = levels of *Nosema* spp.	
Commercial substitute	**Utra Bee®** (Mann Lake Ltd, Hackensack, MN)	≤11		453.5 g/dose, weekly, 4 weeks	non-supplemented colonies	-	= colony strength = levels of *Nosema* spp.	
Commercial substitute	**Brood Builder** (Dadant & Sons, High Springs, FL)	≤11		453.5 g/dose, weekly, 4 weeks	non-supplemented colonies	-	= colony strength = levels of *Nosema* spp.	
Commercial substitute	**Feed-Bee®**; premade patty	20	Fall	91 g/dose, 5 doses each, every 15 days	non-supplemented colonies	= dry weight of heads	↑ adult population ↑ brood population = levels of *Nosema* ↑ honey production ↑ levels of DWV	Alarcón et al. (2026)
Pollen patty	polyfloral pollen; 15:1 beebread pollen and granulated sucrose with water (2:1)	20	Fall	250 g/dose, 5 doses each, every 15 days	non-supplemented colonies	= dry weight of heads	↑ adult population ↑ brood population = levels of *Nosema* ↑ honey production ↑ levels of DWV	Alarcón et al. (2026)
Pollen patty	polyfloral pollen; 15:1 beebread pollen and granulated sucrose with water (2:1)	31	Fall	500 g/dose, 5 doses, every 15 days	non-supplemented colonies		↑ adult population ↑ brood population ↓ levels of *Nosema* ↑ levels of DWV and ABPV = honey production	Smart, Pettis, Rice et al. (2016)

Type of product	Name of the product/composition	N/group	Period of administration	Form of administration	Control group	Effects on bees (supplemented vs. control)	Effects on colonies (supplemented vs. control)	Reference
Pollen patty	polyfloral pollen; 160-180 g commercial pollen and granulated sucrose with water (2:1)	11	Fall	300 g/dose, 5 doses, every 10-11 days	non-supplemented colonies	= body protein	= brood population	Kleinschmidt (1976)
							= honey production	
							↓ levels of *Nosema*	
Pollen patty	polyfloral pollen; 160-180 g commercial pollen and granulated sucrose with water (2:1)	20	Fall	500 g/dose, 5 doses, every 15 days	non-supplemented colonies	↑ expression levels of vg	↑ adult population	DeGrandi-Hoffman et al. (2010)
						↑ expression levels of glucose oxidase	= brood population	
						= expression levels of prophenoloxidase	= levels of *Nosema* spp.	
							= honey production	
Commercial substitute	**ApiHerb®** (Chemicals Laif S.p.A., Italy)	6	Fall	4 g in 50 ml/dose (prepared in sugar syrup 50%), 3 doses, every week	non-supplemented colonies		↓ levels of *N. ceranae*	Cilia et al. (2020)
Pollen patty	polyfloral pollen; 15:1 beebread pollen and granulated sucrose with water (2:1)	11	winter	500 g/dose, 4 doses, every month	non-supplemented colonies		= adult population	Maes et al. (2016)
							= brood population	
							= levels of *Nosema*	
							= levels of ABPV, BQCV, DWV and SBV	
Commercial substitute	Diet 1	20	Fall (2005) to Winter (2007)	454 g/dose; 3-week intervals	HFCS (negative control)		↑ brood population	DeGrandi-Hoffman et al. (2016)
							= adult population	
Commercial substitute	Diet 2; premade patty	20		454 g/dose; 3-week intervals	HFCS (negative control)		↑ adult population	
							↑ brood population	
Commercial substitute	Diet 3 - liquid	20		226 g powder in 3.8 l of HFCS; 3-week intervals	HFCS (negative control)		↑ adult population	
							↑ brood population	

Type of product	Name of the product/composition	N/group	Period of administration	Form of administration	Control group	Effects on bees (supplemented vs. control)	Effects on colonies (supplemented vs. control)	Reference
Commercial substitute	Diet 2; premade patty	6	Summer (2007)	454 g/dose; 2-week intervals	pollen (positive control)		= adult population	
							= brood population	
Commercial substitute	Diet 3 - prepared patty	6		454 g/dose: the patty was prepared by mixing 226 g powder with 3.8 l of HFCS; 2-week intervals	pollen (positive control)		= adult population	
							= brood population	
Pollen patty	pollen and granulated sucrose with water (2:1)	7	Spring 2002	500 g/dose, 7-10 days, 5 doses	non-supplemented colonies and pollen deprived colonies	↑ lifespan in 2002		Antúnez et al. (2015)
						↓ dry weights and protein contents		
Pollen patty	pollen and granulated sucrose with water (2:1)	7	Spring 2003	500 g/dose, 7-10 days, 5 doses	non-supplemented colonies and pollen deprived colonies		↑ brood-related tasks	
							↓ foraging effort	
Commercial substitute	**BeePro®** (Mann Lake, Hackensack, MN, USA)	7	Spring 2003	500 g/dose, 7-10 days, 5 doses	non-supplemented colonies and pollen deprived colonies	↓ lifespan in 2003	↑ brood-related tasks	
						= dry weights and protein contents	↓ foraging effort	
						= dry weights and protein contents		
Commercial supplement	**Global Patties®** (Airdrie, AB, Canada)	10 (assigned to 3 sites)	Summer to Fall (2016)	*ad libitum,* during 2 months in summer	non-supplemented colonies	↑ protein content in nurse bees	= brood population	Raymann and Moran (2018)
						↓ lifespan	= foraging effort	
							= *Nosema* spp. and *V. destructor* levels	
Commercial substitute	**Utra Bee®** (Mann Lake Ltd, Hackensack, MN)	10 (assigned to 3 sites)			non-supplemented colonies	= protein content in nurse bees	= brood population	
						↓ lifespan	= foraging effort	

Type of product	Name of the product/composition	N/group	Period of administration	Form of administration	Control group	Effects on bees (supplemented vs. control)	Effects on colonies (supplemented vs. control)	Reference
							= *Nosema* spp. and *V. destructor* levels	
Commercial supplement	**Global Patties®** (Airdrie, AB, Canada)	5	Summer to Fall (2017)	*ad libitum,* during 2 months in summer	non-supplemented colonies	↓ lifespan	= *Nosema* spp. and *V. destructor* levels	
Commercial substitute	**Utra Bee®** (Mann Lake Ltd, Hackensack, MN)	5			non-supplemented colonies	↓ lifespan	= *Nosema* spp. and *V. destructor* levels	
Pollen patty	pollen	7	Early spring (2004)	*ad libitum*	non-supplemented colonies		↑ adult population ↑ brood population ↑ honey production	Johnson (2000)
Commercial substitute	**Feed-Bee®**	7			non-supplemented colonies		↑ adult population ↑ brood population ↑ honey production	
Commercial substitute	**BeePro®** (Mann Lake, Hackensack, MN, USA)	7			non-supplemented colonies		= adult population = brood population = honey production	
Commercial substitute	**ApiHerb®** (Chemicals Laif S.p.A., Italy)	5	Spring	4 g in 50 ml/dose (prepared in sugar syrup 50%)	non-supplemented colonies		↓ levels of *Nosema* spp.	Michalczyk et al. (2016)
Commercial substitute	**BeePro®** (Mann Lake, Hackensack, MN, USA)	5 (in enclosed flight area)	Spring	*ad libitum*	pollen (positive control; in enclosed flight area)	= hemolymph protein concentration ↓ protein digestion ↓ hypopharyngeal gland size ↑ infection levels with *Nosema* spp.		Bordenstein and Theis (2015)

Type of product	Name of the product/composition	N/group	Period of administration	Form of administration	Control group	Effects on bees (supplemented vs. control)	Effects on colonies (supplemented vs. control)	Reference
						↑ infection levels DWV		
Commercial substitute + pollen	**BeePro®** (Mann Lake, Hackensack, MN, USA)	5 (in enclosed flight area)			pollen (positive control; in enclosed flight area)	= hemolymph protein concentration		
						↓ protein digestion		
						↓ hypopharyngeal gland size		
						= infection levels with *Nosema* spp.		
						= infection levels DWV		
Commercial substitute	**Feed-Bee®** and pollen deprived	3	not mentioned	100 g/dose, every 6 days, 6 weeks	allowed to forage	↓ fresh weight in 6-day old larvae and newly emerged bees	↓ brood population	Tsuruda et al. (2021)
						↓ dry weight in 6-day old larvae and newly emerged bees		
						↓ total protein in 6-day old larvae and newly emerged bees		
Commercial substitute	**HiveAlive™** (Advance Science, Ireland)	3	not mentioned	2,5 ml/l in sugar syrup, 15 ml per comb, every 4 weeks	sugar syrup		↓ levels of *N. ceranae*	Garrido et al. (2024)
Commercial substitute	**HiveAlive™** (Advance Science, Ireland)	20	2-year period	2,5 ml/l in sugar syrup, or 5 ml/kg of candy. Trickled at 0,5 ml in 50 ml, twice per week for 2 weeks 15 ml per comb, every 4 weeks	sugar syrup		↑ adult population	Charistos et al. (2015)
							↓ levels of *N. ceranae*	

Differences in the results obtained in the previously mentioned studies may lie in the type of supplement/substitute analyzed, the variable used to determine its effect, the experimental design, or the conditions in which the assays were performed. An important point that emerges from reviewing the available literature is that the amount of pollen, supplement, or substitute provided to the colonies is a minor fraction considering the colony's requirements, and thus, environmental factors play a major role in the colony responses analyzed. In foraging periods, colony demands increase, and the environment should provide these requirements. If this does not happen, nutritional supplementation will probably have positive effects on the colonies, while in periods in which the environmental factors are closely aligned to the colony requirements, then the supplementation will show neutral or detrimental effects on the colonies. Finally, another important factor that should be considered is the number of colonies used in the studies of nutrition, which is highly variable (Table 1). Colonies located in the same apiary tend to collect different amounts of pollen from different botanical origins (Antúnez et al., 2015), which affects the nutrient composition available for each colony. Thus, colonies' response to the supplementation strategy might be different. Under these conditions, maximizing the number of colonies per experimental group is necessary to ensure statistically robust and reliable conclusions about the impact of nutritional supplementation.

2.4 The *Eucalyptus* spp. Plantation Scenario

Eucalypt species include trees from the genera *Eucalyptus*, *Corymbia*, and *Angophora*, which were formerly all grouped under the genus *Eucalyptus* (Brooker, 2000; Johnson, 2000; South et al., 2024). These trees are economically important mainly for hardwood plantations but also for beekeeping. Given that certain eucalypt species supply abundant nectar to honey bee colonies, beekeeping activities have developed in close association with their flowering periods (Branchiccela et al., 2020; Invernizzi et al., 2023; White & Day, 2022). The botanical origin of most of Australian honey is from eucalypt species, as well as 40% of Uruguayan honey (Branchiccela et al., 2020; White & Day, 2022). However, despite that some colonies produce as much as 100 kg of *Eucalyptus grandis* honey in a short period of time (Branchiccela et al., 2020), it has been proposed that they do not provide nutritionally rich pollen (Invernizzi et al., 2011; Manning, 2018; Somerville, 2001).

In Uruguay, colonies are relocated to *E. grandis* plantations at the beginning of the fall, which is their flowering period. In these environments, colonies collect and store large amounts of pollen (Juri et al., 2025). Depending on the plantation area, the pollen available is mainly from *E. grandis* (≥85%) and can be accompanied by pollen from *Baccharis* spp. and *Solidago chilensis* (Branchiccela et al., 2019; Invernizzi et al., 2011; Viera López, 2021). During the first period of the flowering period, the pollen crude protein content is higher than 25%, being this value supportive for the colony development and maintenance, and it is even protein-richer than the pollen available in other regions of the country in this period of the year (Branchiccela et al., 2019; Invernizzi et al., 2011; Kleinschmidt, 1976; Santos et al., 2009). However, protein value decreases towards the end of this season to values lower than 20% (Branchiccela et al., 2019; Invernizzi et al., 2011; Kleinschmidt, 1976).

Most of the *Eucalyptus* spp. pollen provides bees with most of the essential amino acids that they require, except for isoleucine, which has been shown to be deficient in most of the *Eucalyptus* spp. pollen analyzed (Somerville, 2001; Somerville & Nicol, 2006). *Eucalyptus* spp. pollen generally contains less than 2% lipids, which ranks among the lowest lipid concentrations recorded in pollen across plant species. Particularly, *E. grandis* pollen has shown lipid levels of 1.44% (Branchiccela et al., 2019; Manning, 2001b; Somerville, 2000). These lipid levels are below those reported to achieve the best bee performance in terms of associative learning, bee lifespan, and brood rearing (Arien et al., 2018, 2020). Moreover, *Eucalyptus* spp. pollen is poor in omega-3 and high in omega 6:3 ratio, a condition that has been associated with an increased risk of disease incidence in humans (Simopoulos, 2002). It has therefore been hypothesized that a similar imbalance could negatively affect honey bees, potentially contributing to nutritional stress when this pollen constitutes a major component of their diet (Arien et al., 2015). In fact, all colonies located in *E. grandis* plantations get high infection levels of *Nosema* spp., they depopulate, and most of them die if they are not relocated to a more favorable environment immediately after the *E. grandis* flowering period ends (Branchiccela, 2020; Branchiccela et al., 2019; Invernizzi et al., 2011; Mendoza et al., 2012, 2014). Even though about 40% of the colonies that produce honey during the *E. grandis* harvest usually perish during the winter (Branchiccela et al., 2019, 2020; Viera López, 2021).

Given the background outlined in the previous sections, this scenario of colony weakening and high losses due to nutritional stress and high infection levels with *Nosema* spp. should be examined within its broader ecological and management context through a theoretical model. In the original environment and prior to relocation to *E. grandis* plantations, physiological and nutritional changes take place at the individual and colony levels for overwinter preparation (DeGrandi-Hoffman et al., 2018; Steinmann et al., 2015). At this critical time, colonies are moved to the *E. grandis* plantation, where a strong nectar flow is available (Figure 1). Consequently, colony organization is abruptly altered: bees that had developed adequate nutritional reserves to survive the winter within the hive are now forced to forage and store food. Over time, the nutritional quality of the available pollen declines (Branchiccela et al., 2019; Invernizzi et al., 2011), leading to weakened colonies, poorly equipped to face winter conditions (Branchiccela et al., 2019; Invernizzi et al., 2011; Juri et al., 2025; Viera López, 2021). Simultaneously, infection levels of *Nosema* spp. increase, reducing bee survival and colony strength (Branchiccela et al., 2019; Invernizzi et al., 2011; Mendoza et al., 2014). When the *E. grandis* flowering period ends, colonies are relocated back to their original environments, where they must suddenly face the winter conditions, having lost all their physiological and social preparation during the *E. grandis* season. As a result, colonies enter winter in a physiological and sanitary weakened state. These factors, together with disrupted social organization, undermine colony resilience, compromising their ability to overwinter successfully and recover adequately in the following spring (Figure 1).

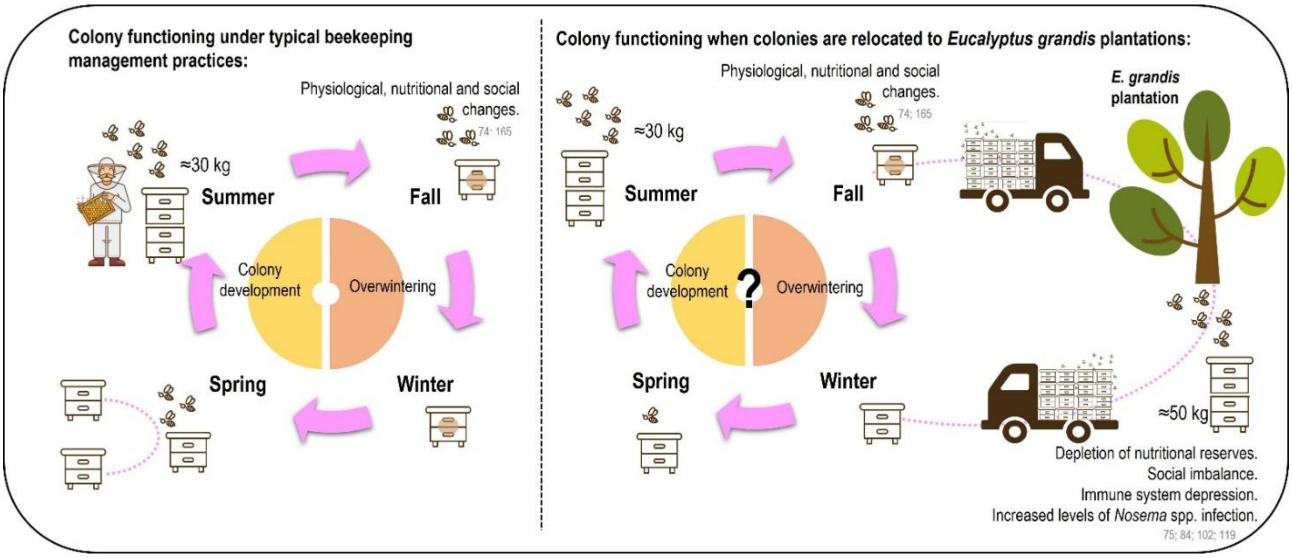

Figure 1. Theoretical model explaining the consequences of *N. ceranae* infection and nutritional stress on honeybee colonies

A schematic overview of the theoretical model explaining the consequences of the infection with high levels of *Nosema* spp. and nutritional stress of colonies relocated to *Eucalyptus grandis* plantations. The natural dynamic of honey bee colonies accompanied the seasonal dynamic: colony population increases during the spring, they reproduce (or are divided into two colonies under beekeeping management), and/or store and produce honey. After that, physiological, nutritional, and social changes occur to prepare the colony for overwintering. However, when colonies are relocated to *E. grandis* plantations, they are abruptly placed in an environment that offers a great nectar flow, forcing the colony to work in the field in a period of time in which they are physiologically and socially prepared to overwinter. Thus, all the changes associated with overwintering are invested in the new environmental scenario, depleting their body nutritional reserves, promoting social imbalance, immune system depression, and weakening the health status of the colony due to high infection levels with *Nosema* spp. When the *E. grandis* flowering period ends, colonies are relocated again to their original site, with extreme winter conditions and no floral resources available to prepare the colony for overwintering. Consequently, colony homeostasis is altered, overwintering is threatened, and those colonies that survive start the next season weakened.

Interestingly, the colony supplementation with nutritive polyfloral pollen increases the nutritional bee reserves and immune functions (Viera López, 2021), reduces the infection level with *Nosema* spp., and increases colony strength (Branchiccela et al., 2019; Invernizzi et al., 2011). However, it is important to note that besides high amounts of pollen being provided to the colonies (up to 500 g, every 15 days), supplementation helps to mitigate the negative effects of nutritional and sanitary stress, but it does not fully prevent them. Colonies that remain in their original environments, without being relocated to *E. grandis* plantations, do not experience the same degree of depopulation or losses as those colonies that are relocated. This suggests that the environment and beekeeping practices play a major role, and the strategies that could be implemented to reverse the negative nutritional scenarios are a management and scientific challenge.

3. Nutritional Research Directions to Support Honey Bee Health

The information presented in the previous sections provides an overview of the current knowledge regarding honey bee nutrition at the individual and colony levels, as well as the beekeeping management practices that can be currently implemented to mitigate the impact of nutritional stress. Despite years of research on honey bee nutrition, the anthropogenic effects associated with changes in landscape composition show that there is still a long way to go to fully understand the biological processes associated with bees' interactions with their environment. This is essential for later adapting beekeeping management practices and maximizing the colony's productive capacity.

Firstly, the botanical origin of bee-collected pollen in some beekeeping regions of Uruguay is unknown, and their nutritional value is limited and scarce (Santos et al., 2009). Moreover, growing data show that the protein content of these pollens is not a sufficient parameter to describe this nutritional value, since other pollen components shape individual and colony responses (Branchiccela, personal communication). Thus, it is necessary to develop available methodologies to characterize these pollens in terms of nutritional value but also regarding the presence of toxic or deterrent compounds. Secondly, how these pollens interact with the honey bees is another chapter, since not all pollens are equally attractive to bees, nor equally digested. In this direction, the deep characterization of pollen species together with the advances in nutritional molecular physiology will give insight into this interaction. The above information will help to model the colony-level responses to honey bee nutrition and nutritional stress at physiological, behavioral, and demographic levels. In this regard, another road ahead is the identification of suitable parameters to describe the colony's nutritional status. The fat body and hypopharyngeal gland development, bee or head dry weights, bee crude protein content, and the expression of molecular markers associated with nutrition, such as Vg, are among the most commonly used parameters at the individual level (Amro et al., 2016; Black, 2006; DeGrandi-Hoffman et al., 2018). However, as bee nutritional status varies according to the age and drastically to task transition, their analysis at the colony level can be challenging considering time, human, and economic resources. At the colony level, the parameters associated with their nutritional status, such as adult and brood population or honey production, are widely used. Nevertheless, although they can provide valuable information about the colony response to nutritional manipulations, they are indirect parameters of the nutritional status of those colonies. Other colony parameters, like royal jelly or queen quality, provide limited information about their nutritional status (Noordyke & Ellis, 2021). Thus, to understand the impact of nutrition on colony response, an integrative approach should be implemented involving the analysis of parameters associated with nutrition at the individual and colony levels. Considering also that colonies located in the same environment can show different responses to pollen nutrition and nutritional manipulations, and, consequently, the parameters to be analyzed can show different results, a large number of colonies should be included to be confident about the obtained results, and this experimental design should be aligned accordingly with the parameters to be analyzed. For example, fewer colonies are needed for analyzing parameters at the individual level with age-controlled bees, while more colonies should be included if the response variable is bee or brood populations, or honey production. Considering the Uruguayan experience and in line with some Canadian reports, no less than ten colonies should be included for analyzing colony populations, and no less than twenty colonies when analyzing honey production, accounting for a ten percent of colony losses at the end of the assays.

Once a comprehensive knowledge of nutritional status in relation to the environmental conditions is fully understood, it will be possible to develop targeted nutritional supplements that compensate for pollen deficiencies. Based on the available information, such supplements should be attractive enough to ensure adequate consumption by the bees, and formulated with plant-based ingredients free from potentially harmful compounds. Finally, this nutritional supplementation should be implemented as part of an integrative management strategy that considers the timing and quality of floral resources as well as the resulting behavioral responses of the colonies. In a climate change context characterized by large climatic variations and their impact on plant phenology and flowering patterns, this integrative strategy is a challenge. In this sense, a multidisciplinary and systemic approach incorporating ecological, scientific, and practical biological knowledge appears to be a strategic direction for the future improvement of honey bee nutrition and health.

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Available data: The entire data set that supports the results of this study was published in the article itself.

Author contribution statement

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Conceptualization			
Writing – original draft			
Writing – review and editing			

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