Original article

Pollen nutrition and colony development in honey bees: part I[1]

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Pollen is the honey bees' main source of several important nutrients. Consequently, an adequate pollen supply is essential to ensure the long-term survival of a colony and to maintain its productivity. Part 1 of this 2-part review focuses on the botanical composition of bee-collected pollen and its protein and mineral content. Further, we discuss the impact of pollen on honey bee physiology and assess the pollen requirements of individual workers and larvae.

In many industrialized countries, modern agricultural practices have led to an impoverishment of the flora over large areas. This might reduce the availability of profitable pollen sources and could have severe detrimental effects on honey bees (*Apis mellifera*).[79] The preservation of healthy colonies, however, is of considerable economic importance as bees not only produce honey but also serve as pollinators of many cultivated plants.[8,20,44] To assess the quality of a given environment for honey bees, a thorough understanding of their pollen nutrition is essential. In this article, we review the literature on the botanical composition of bee-collected pollen, with a focus on European studies from the last five decades (section A). In section B, we investigate the protein and mineral content of pollen from different plant species. It is very possible that differences in the nutritional value of pollen may strongly influence the foraging decisions of honey bees. Finally, we try to estimate the quantity of pollen required per worker and worker larva, and discuss the impact of pollen consumption on the physiological development of honey bees (section C).

A. Botanical composition of the pollen collected by honey bees

Main pollen sources in Europe and northern Africa

Data on the composition of bee-collected pollen was available from one location in Egypt, one in England, several locations in Scotland, three in Italy and 17 in Switzerland.[41,45,57,60,65,71,76–78] As some of these studies reported findings from several colonies and/or several years, a total of 114 data sets could be considered.

Across all investigations, it was apparent that the bulk of the pollen collected generally came from just a few plant species. Thus, the five most common pollen sources yielded on average more than 60% of the total collected pollen. Such an unbalanced pollen composition does not appear to be a recent phenomenon but was also observed in studies from the late 1940s and early 1950s.[65,79] In figure 1, we plotted the number of times a given plant taxon ranked among the five main pollen sources of a colony. We omitted 29 plant taxa, which were among the five main pollen sources in fewer than three of the data sets.

Unfortunately, most authors did not provide any information on the abundance of different plant species in the vicinity of the bee colonies. Nonetheless, it seems safe to conclude that many of the important pollen sources were plants occurring at high densities either naturally or due to



Rape blossoms can be an important pollen source for honey bee colonies.

[1]Dedicated to the memory of Hans Wille, head of the Apicultural Section of the Swiss Federal Dairy Research Station in Liebefeld-Bern, 1957-87. the topic of this research was a crucial part of his work.

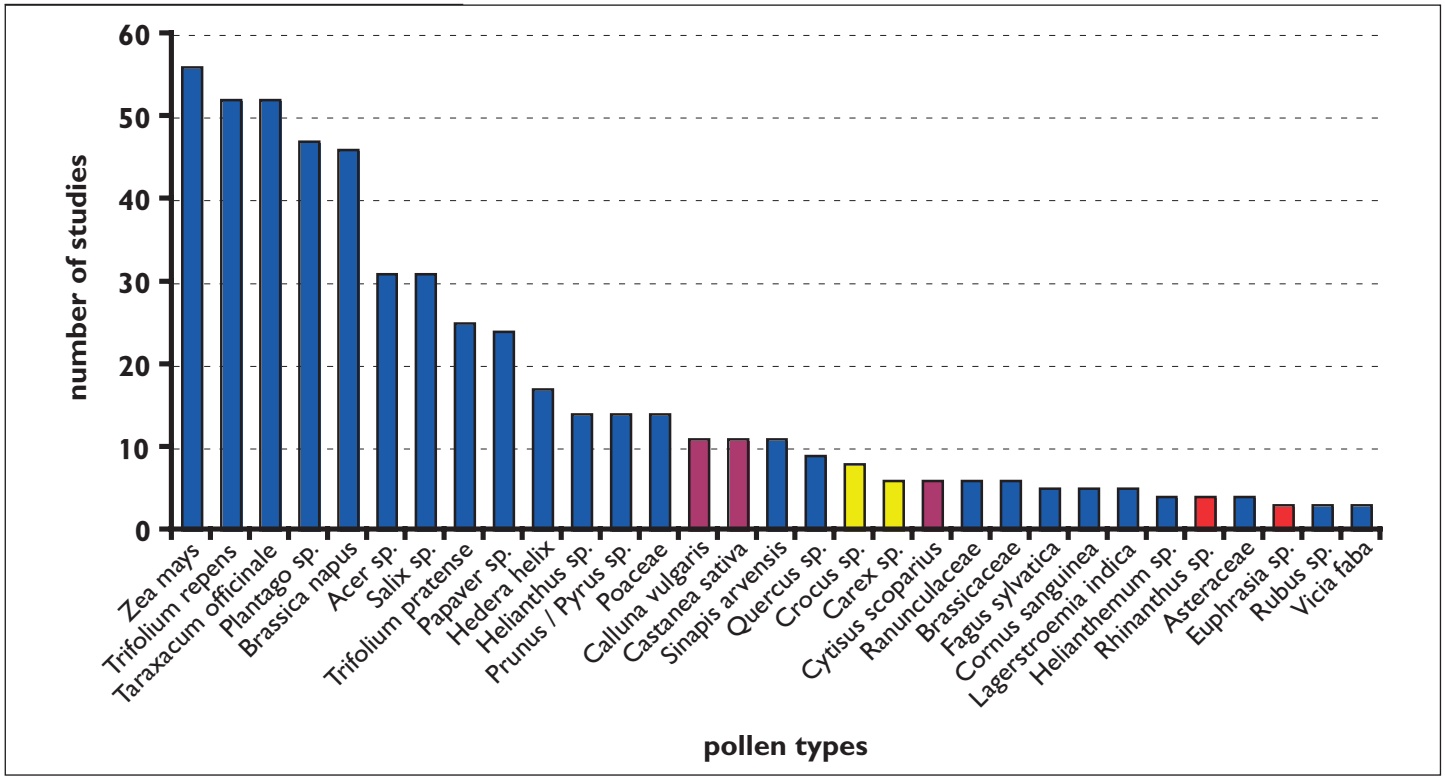


FIG. 1. Number of studies in which a given plant taxon ranked among the five most common pollen sources. A total of 114 data sets were included in the analysis. (blue bars = pollen types found in several locations; mauve bars = pollen types found only at Intragna, Switzerland; red bars = pollen types found only at Schönried, Switzerland; yellow bars = pollen types found only at Schönried and Davos, Switzerland).

cultivation. Agricultural crops with an important role as pollen sources included white and red clover (*Trifolium repens* and *T. pratense*), corn (*Zea mays*), rape (*Brassica napus*) and sunflowers (*Helianthus* sp.). Several other plants shown in figure 1, such as plantain (*Plantago* sp.), dandelion (*Taraxacum officinale*) and mustard (*Sinapis arvensis*) are generally abundant in meadows and pastures.[7] A third group of important pollen sources included different tree species such as maple (*Acer* sp.), willow (*Salix* sp.), stone fruits such as plums and cherries (*Prunus* sp.) and pome fruits such as pears (*Pyrus* sp.). Of course, this list is strongly influenced by the over-representation of study sites from the Swiss midland, and many other plant species may be important locally.

Even within one geographical area, the composition of the pollen collected by colonies at different locations may vary considerably due to differences in the surrounding vegetation. Thus, 18 pollen types occurred at frequencies of ≥ 5% in a least one of 13 samples collected at three locations in the Swiss midland in 1981.[78] Out of these, only three plant taxa were detected in all three study areas (*Brassica napus*, *Trifolium repens* and *Zea mays*), while the remaining pollen types were found at only one or two of the locations. These differences become even more pronounced if we include colonies from other geographical areas. Thus, pollen from heather (*Calluna vulgaris*), European sweet chestnut (*Castanea sativa*) and scotch broom (*Cytisus scoparius*) was quite dominant in samples from Intragna in southern Switzerland (mauve bars in fig. 1), but was not found at other localities. The study sites Schönried and Davos were located in the subalpine region of Switzerland at an elevation of 1250 and 1560 m above sea level, respectively. Dominant plants at these two locations were crocus (*Crocus* sp.) and sedges (*Carex* sp.). Two other taxa, *Rhinanthus* sp. and *Euphrasia* sp., were found exclusively in samples from Schönried (red bars in fig. 1). Again, no information is available on the vegetation in the vicinity of the colonies. However, many of the above-mentioned plants are known to be common in the respective habitats,[7,16] which further suggests that abundant plants are generally important pollen sources.

Van der Moezel *et al.*[46] compared the composition of bee-collected pollen with the composition of the surrounding flora and found that the bulk of the pollen indeed came from common plants. However, it is likely that the pollen composition does not simply reflect the proportions of different flowers in the surroundings but is, at least to some extent, determined by true preferences. In this case, the proportion of a preferred pollen type should be higher in the bee-collected samples than in the environment.[6] Instead of analysing the actual pollen intake of colonies, Visscher & Seeley[67] assessed the foraging effort directed towards individual plant patches by studying recruitment dances of pollen foragers. They found that on a given day the pollen foragers of a colony indeed showed clear preferences and focused on only a few of the plant patches available within their foraging area. On the other hand, honey bees may also exhibit pronounced dislikes of some pollen types. Workers from colonies placed near cucumber or cotton fields, for example, completely ignored these abundant plants as pollen sources.[48,60] The factors responsible for such preferences or dislikes are largely unknown (see section B of this article for a discussion of the potential role of the nutritive value of different pollen types).

Individual preferences of different colonies can be detected by comparing several hives from one location, where the availability of flowers is likely to be the same for all colonies. Sixteen data sets were available,

where the pollen intake of two or more colonies had been investigated at the same location and in the same year.[41,65,78] We used chi-square tests to investigate if the proportions of the more common pollen types were different between colonies at the same location. A combined probability across all studies[61] indicated that this was indeed the case. Most of these differences were quantitative rather than qualitative. Bees from different colonies often collected pollen from similar plants but sometimes in quite different amounts. Three of the samples obtained from colonies in Galmiz in 1981, for example, contained more than 30% of pollen from white clover (*Trifolium repens*) as opposed to a proportion of only 16% in the fourth sample.[78] Occasionally, the pollen samples also differed in terms of their botanical composition. Thus, three colonies at Intragna (1981) collected around 10% of ivy (*Hedera helix*) pollen, whereas a fourth colony did not use this pollen source at all.[78]

The results of this literature review support the hypothesis that honey bee colonies may differ in their use of the pollen available at a given location. The study of Van der Moezel *et al.*[46] showed that the preferences of a colony were not necessarily fixed but could change from year to year. In their first study year, the authors found that the bees mainly visited one abundant plant, whereas a second common species was ignored. In the following year, this preference was inverted although the availability of both plants was unchanged. This observation could be explained easily if the flower preferences of different colonies were determined largely by chance. Thus, it is conceivable that foragers simply continue to visit the pollen source they happened to encounter first. This would be consistent with behavioural observations, which showed a remarkable constancy of individual foragers with respect to preferred pollen types.[19,70] Alternatively, it is possible that our assumption of equal availability of flowers for different colonies at a given location is false. Synge,[65] for example, observed that one of his study hives was shaded much longer than the other in the mornings, which delayed the start of pollen foraging in this colony. As the available flower spectrum generally varies throughout the day,[41,43] this could lead to differences in the botanical composition of the collected pollen.

Chronology of the main pollen sources

At the beginning of the vegetation period, a uniform pattern was observed across most available studies with a very pronounced dominance of different tree species as the most popular pollen sources.[30,37,41,59,65,71,76] These included maple (*Acer* sp.), ash (*Fraxinus* sp.) different fruit trees (*Prunus* sp. and *Pyrus* sp.), poplar (*Populus* sp.), oak (*Quercus* sp.), willow (*Salix* sp.) and elm (*Ulmus* sp.). At some Swiss locations, dandelion (*Taraxacum officinale*) was also an important pollen source in spring.[41,71,76] In May and June, the spectrum of pollen types became much more diverse and generalizations across all study sites were hardly possible. In Ireland and England some shrub species such as hawthorn (*Crataegus monogyna*) and elder (*Sambucus* sp.) were important pollen sources,[10, 65] whereas rape (*Brassica napus*) was frequently collected at several of the Swiss locations.[71,76] In midsummer and early autumn, pollen from red and white clover, corn and plantain dominated the samples from all locations from the Swiss midland.[41,71,76] In southern Switzerland, European sweet chestnut and heather were the dominant pollen sources at this time of the year.[71,76] In Ireland, on the other hand, large amounts of pollen were collected from blackberry (*Rubus* sp.) and meadowsweet (*Filipendula ulmaria*).[10] Towards the end of September, ivy became the dominant pollen source at several locations.[10,71,76]

...honey bees may exhibit pronounced dislikes of some pollen types. Workers from colonies placed near cucumber or cotton... completely ignored these abundant plants as pollen sources.

The chronology of the main pollen sources may differ considerably between successive years at a given study site.[71,76] To a large extent, this may be due to changes in the surrounding vegetation, which can be very pronounced for colonies located close to farmland. Further, annual weather differences may influence the phenology of the flora and consequently the period when a given pollen type is available.

If we considered the mode of pollination of the dominant plants, we observed a consistent pattern at different localities. Generally, wind-pollinated plants were dominant pollen sources in spring and were then replaced by insect-pollinated plants.[49,51,59] This was a consequence of the importance of anemophilous trees as early pollen sources. The frequency of pollen from wind-pollinated plants may show a second peak in midsummer at locations where corn (*Zea mays*) was an important pollen source.[59]

B. The chemical composition of the pollen collected by honey bees

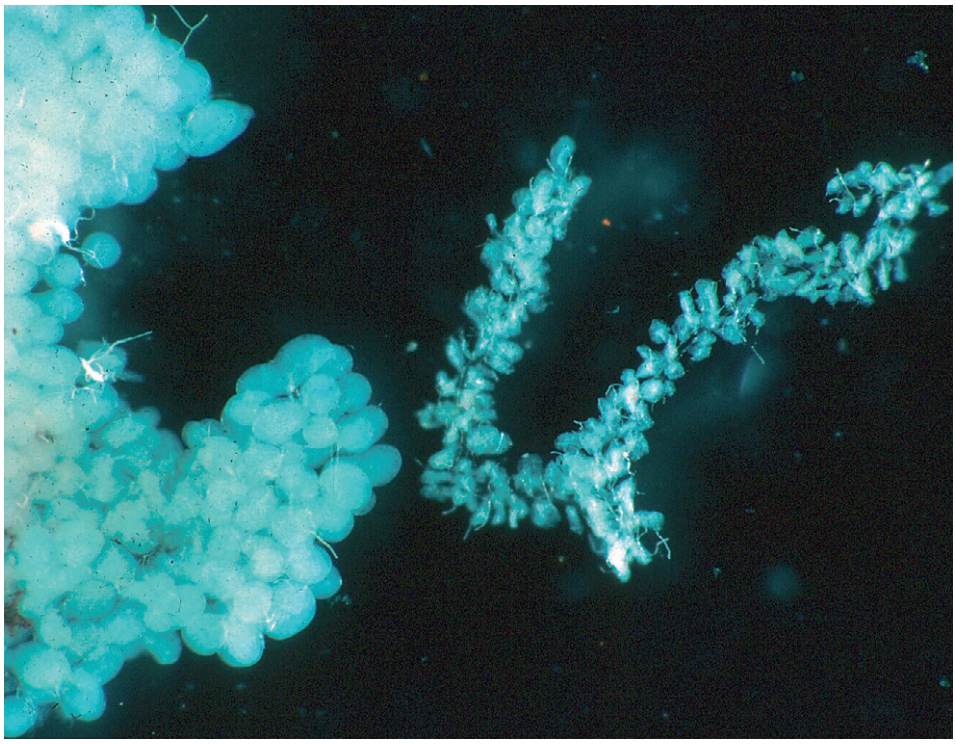
Like all animals, honey bees have to consume certain essential nutrients with their food. Pollen is their main source of proteins, minerals, fats and several other substances, while nectar provides the bulk of carbohydrates.[26] In the following, we will review the literature on the protein and mineral composition of pollen and investigate if honey bees prefer pollen types with a high nutritional value.

Honey bee foragers mix freshly collected pollen with some nectar before packing it into their corbiculae.[50] In the hive, the workers add more nectar and glandular secretions to the pollen, which then undergoes lactic acid fermentation. Consequently, the chemical composition of pollen samples will depend on whether they were obtained directly from flowers, from foragers or from brood combs.[27,66] Whenever possible, we will indicate which type of pollen was analysed.

Protein, amino acid and mineral content of pollen from different plant species

The protein concentrations in hand-collected pollen from 377 plant species from 93 families are given in the extensive review by Roulston *et al.*.[56] Pollen from different species may vary considerably in protein content, with values ranging between 2.3% in the cypress (*Cupressus arizonica*) and 61.7% in *Dodecatheon clevelandii* (Primulaceae). Within plant families, however, protein concentration appears to be highly conserved, except in the species-rich Cactaceae and Fabaceae.[56] On average, animal-pollinated plants do not appear to be richer in pollen protein than wind-pollinated plants.[56]

Ten amino acids are reported to be essential for honey bees, i.e. they cannot be synthesized by the organism but have to be ingested with food.[15] These are arginine, histidine, lysine, tryptophane, phenylalanine, methionine, threonine, leucine, isoleucine and valine. The content of essential amino acids was found to be positively correlated with the total protein content of a pollen.[75] Generally, there appear to be few qualitative differences in the amino acid composition of different pollen types and most of them contain all essential amino acids (see[26,55], and references therein). Wille *et al.*[75] also detected very similar proportions of the different amino acids in bee-collected pollen samples from 99 plant species. There are a few plants such as for example dandilion (*T. officinale*), whose pollen lacks one or several of the essential amino acids.[3,75]



The hypopharyngeal glands are situated on the head of worker honey bees. The developed gland of a nurse bee (left) is shown in comparision to the degenerated gland of a foraging bee (right).

The pollen ash content of 33 North American plant species was estimated at 0.9 to 6.4% of the dry weight.[66] However, very little data is available on the different minerals and trace elements making up pollen ash and on how their composition varies between plant species. Todd & Bretherick[66,68] found that their bee- and hand-collected pollen samples contained potassium, phosphorus, calcium, magnesium, iron and surprisingly high levels of copper. More recent pollen analyses have also detected sulphur, sodium and the trace elements manganese, zinc and selenium.[14,62] The concentration of a given substance appears to differ considerably between plant species.[66]

In their study at 11 Swiss locations, Wille *et al.*[73] found that the protein content of bee-collected pollen was subject to considerable temporal variation due to differences in its botanical composition. Generally, the protein content was low in early spring and then reached a maximum of 25–30% in May. Low pollen protein concentrations were sometimes observed in June, but then the values remained relatively constant around 20% for the rest of the vegetation period. The yearly average appeared to be around 20% although there was some variation due to location, year and colony.[73] The mineral levels in pollen were also found to vary considerably in the course of the year due to differences in the floral origin of the pollen.[28] This was true for potassium, magnesium, calcium, manganese and iron, while the zinc and copper content of pollen appeared to be more constant.

Assessment of pollen quality by honey bees

As discussed above, the pollen produced by different plant species may differ considerably with respect to protein and maybe also mineral content. Such qualitative differences might have a strong impact on the foraging decisions of honey bees and could possibly explain preferences for certain pollen types. However, due to our insufficient understanding of the nutritional requirements of honey bees, it may be very difficult to determine which pollen types actually have a high nutritive value for the animals. Most researchers used somewhat arbitrary criteria such as the content of essential amino acids to determine pollen quality.

It has been shown that honey bee foragers may indeed exhibit preferences for certain pollen types (see also section A). Even when pure pollen was offered to eliminate visual signals of the flowers, honey bee foragers gathered higher quantities of some pollen types than of others.[35] However, it remains to be seen if such preferences are really associated with pollen quality or if they are due to other factors such as, for example, smell or visual signals of the pollen itself.[38]

In choice experiments, honey bees were offered pollen from rape (*Brassica napus*) and broad bean (*Vicia faba*).[11] Rape pollen was considered to be of higher nutritional value because it contained a greater proportion of essential amino acids. The bees showed no consistent preferences, except for colonies which had been fed rape pollen before the experiment. When offered a choice between rape and bean pollen, these colonies continued to collect significantly higher quantities of the former. The authors argued that this behaviour might be a consequence of the supposedly higher quality of rape pollen. However, they acknowledge that the two pollen types probably also differed in many other respects.

Waddington *et al.*[69] found that honey bees that had collected pure pollen were more likely to perform a recruitment dance than animals that had been presented with a mixture of pollen and cellulose powder, which had a lower nutritive value. However, Pernal & Currie[53] argued that it was not possible to attribute these behavioural differences to pollen quality as the test foods used by Waddington *et al.*[69] were not standardized for pollen odour concentrations. In their own study, Pernal & Currie[53] found that foragers responded to such olfactory cues, whereas their behaviour was not affected by changes in the protein content of the soyabean flour they were offered.

In conclusion, no experimental study has so far provided conclusive evidence of preferences for high-quality pollen in honey bees. The main difficulty of such studies consists in finding adequate test diets, which differ only with respect to the property that is to be investigated.



The abdominal fat body is well developed in nurse bees as well as in winter bees (right) in contrast to foraging bees (left).

Some indirect evidence is provided by the observation that, on average, animal-pollinated plants do not have higher pollen protein contents than wind-pollinated plants.[56] This would not be expected if pollinators preferred protein-rich pollen. Indeed, it is possible that honey bees are not able to assess the nutritive value of pollen because they do not consume it directly but transport it to the hive in their pollen baskets. This could also explain why honey bees may readily collect toxic pollen.[39,47] In conclusion, it is well possible that colonies regulate the quantity rather than the quality of the pollen that is collected. In a natural environment, this may suffice to ensure an adequate supply with all essential nutrients.

C. Pollen nutrition and honey bee physiology

The bulk of the pollen available to a colony is consumed by the workers, which then feed queens, drones and larvae with caste-specific food jellies.[25] The high protein contents of these jellies are derived from secretions of the hypopharyngeal glands of the nurse bees.[25,26] Worker and drone jellies may also contain some pollen, which constitutes an additional source of protein.[25] However, this pollen fed directly to the larvae was estimated to contribute less than 5% to the total protein necessary for larval development.[4]

Influence of pollen on the physiological development of worker honey bees

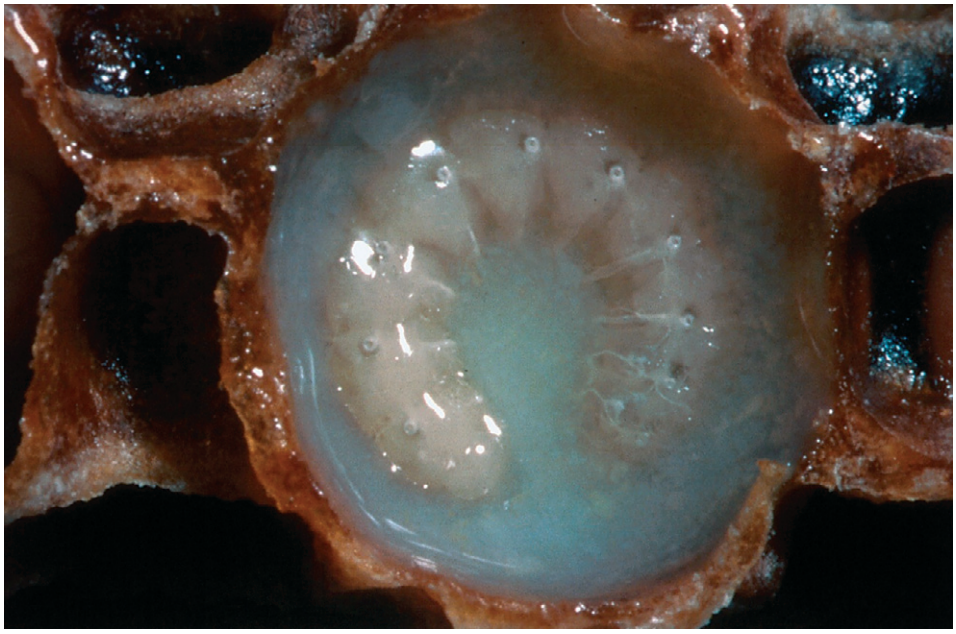
Worker honey bee start to consume large quantities of pollen within the first 42 to 52 hours after emergence.[21] The pollen content of the gut reaches a maximum in 8–9-day old workers and then decreases to very low levels in individuals older than *c.* 20 days.[13,36] Older individuals, which perform foraging tasks, mainly consume nectar but may also be fed with protein-rich jelly by nurse bees.[12]

An adequate pollen supply is indispensable for the development of some of the internal organs of worker bees. Substantial amounts of protein are needed as a consequence of the increase in protein content of the hypopharyngeal glands and the fat body at the beginning of the adult stage.[18] If newly emerged bees are kept on a pure carbohydrate diet their hypopharyngeal glands remain undeveloped.[42] Pollen-feeding, on the other hand, induces the growth of these glands and of the fat body. Generally, the size of the hypopharyngeal glands showed a similar age dependence as the intensity of pollen consumption, i.e. it reached a maximum in *c.* 10-day old bees.[13] Not surprisingly, it is the animals in this age group which perform most of the brood rearing duties in a colony.[31] Different pollen types were found to vary considerably in their effectiveness, with some low quality pollen types having as little impact on physiological development as a pure carbohydrate diet.[40,42] Standifer[63] reported that pollen quality did not appear to be associated with total protein content. Other than that, little information is available on the chemical components determining the physiological effectiveness of a given pollen type. The vitamin and mineral requirements of honey bees, for example, are virtually unknown, although these substances play a significant role in the growth and development of all living organisms.[26]

Pollen quantity required per adult bee or per larva

Based on analyses of the gut contents of adult honey bees from two colonies, Crailsheim *et al.*[13] estimated that a worker consumed on average 3.4 to 4.3 mg of pollen per day. In a different colony, Schmidt & Buchmann[58] found that the pollen–sucrose mixture consumed per bee and day contained 0.11 mg of nitrogen. This means that each worker consumed *c.* 3.1 mg of pure pollen, assuming a nitrogen to protein conversion factor of 5.6[54] and an average pollen protein content of 20%.[73] Thus, the two studies gave very similar estimates of the daily pollen consumption of workers although the between-colony variability would need to be investigated in more detail. Further, it is unclear if these results apply to more natural conditions. For example, it is conceivable that the mixture of pollen and sugar solution used by Schmidt & Buchmann[58] would also attract foragers which would not normally eat pure pollen.[17]

Some of the pollen protein consumed by worker honey bees will be used for the production of proteinaceaous food jelly, which is then fed to larvae. To our knowledge, the amount of protein required to raise one queen or drone larva has not been investigated so far. Caged colonies provided with a mixture of pollen and honey used on average 140 mg of pollen to rear one



Honey bee larvae consume the protein rich food jelly produced by the hypopharyngeal glands

worker.[1] Haydak[23] showed that groups of bees without access to pollen used 3.21 mg of their body nitrogen to rear one worker. If we assume a nitrogen to protein conversion factor of 6.25, a pollen protein content of 20% and a digestive efficiency of 80%[58] this would be equivalent to about 125 mg of pollen per individual (note that the two different nitrogen to protein conversion factors used in this section result from differences in the nitrogen content between pollen and animal protein[54]).

More accurate estimates of the protein requirement of larvae can be obtained by examining their nitrogen content. Pupae and newly emerged adults contained between 1.73 and 1.87 mg of nitrogen.[22–24,29] This would indicate a consumption of 68–73 mg of pollen per worker larva, if we assume the same conversion factors as above. This estimate will be somewhat too low because the animals defecate before pupation. Consequently, the nitrogen content of larvae will be higher than that of pupae or emerging adults. Indeed, the feeding experiments of Alfonsus[1] and Haydak[23] indicated that the amount of pollen needed could be twice the amount mentioned above.

The average nitrogen content of workers without the intestinal tract increased by 0.86 mg during the first five days after emerging (from 1.74 to 2.60 mg N), that of whole bees by 1.27 mg (from 1.98 to 3.25 mg N).[22] After the fifth day, no further increase in worker nitrogen content was observed.[22] If we assume that, on average, the nitrogen content per bee increases during the first five days after emergence by about 1 mg and if we apply the same conversion factors as above, 39 mg of pollen are required for one worker. Adding this amount of pollen to the 125 to 140 mg that are needed to rear one worker,[1,23] approximately 160 to 180 mg are required for the nutrition of one worker bee during its entire life. Based on estimates of the yearly pollen supply, pollen protein content and number of brood cells in 59 colonies, Wille & Imdorf[72] found that *c.* 180 mg of pollen were needed to rear one bee, which would be in good agreement with the requirements estimated above. In central European regions healthy colonies without brood interruptions raise about 100 000 to 200 000 bees per year.[75] Consequently, about 17 to 34 kg of pollen may be required per colony and year.

It is essential to bear in mind that all of the above results depend on various assumptions and should not be considered as more than rough estimates of the pollen requirements of honey bees. Further, we know very little about the between-colony variation of factors such as the pollen quantity collected per larva or the nitrogen content of larvae before pupation. At least the former has been reported to vary considerably between colonies.[2,74] Among other factors, the botanical composition of the pollen may determine the number of bees reared with a certain pollen quantity.[9]

Pollen digestion

Of course, the value of pollen will be determined to a large extent by the efficiency with which it can be digested by an organism. Pollen digestion may be quite difficult due to the several cell wall layers that surround the nutrient-rich cytoplasm. The innermost of these layers is known as the intine and consists mainly of cellulose and pectin. The next layer, the exine, is composed of sporopollenin and is generally perforated by so-called germination pores. The exine is covered by the semi-solid pollenkitt, which is made up of lipids, proteins and sugars.[55]

The crop of honey bees is mainly a storage organ but it may also be involved in pollen digestion. Thus, Klungness & Peng[32] reported that most of the pollenkitt layer of dandelion pollen was separated from the exine in the crop. Peng *et al.*,[52] on the other hand, suggested that the pollenkitt was not removed until the midgut.

From the crop, the pollen is transported through the proventriculus, where it is formed into a lump or so-called bolus before entering the midgut (see[5] and references therein). Kroon *et al.*[34] argued that differences in osmotic pressure between crop and midgut might cause the pollen grains to burst and expose the nutrient-rich cytoplasm. This hypothesis was not supported by other studies, which detected a high proportion of intact pollen grains in the anterior part of the midgut.[33,52] In the midgut, the pollen bolus is encased in several membrane layers, which probably protect the gut from injury and may also release digestive enzymes (see[5] and references therein).

In the anterior midgut, the protoplasm of dandelion pollen appeared to be gradually removed through the germination pores.[52] In the median and posterior midgut, an increasingly high proportion of the pollen grains was characterized by ruptured cell walls and a strong reduction of the protoplasmic volume.[33,52] The exine of the cell wall was found to be undigestible, in contrast to the intine from which the polysaccharide components were partially removed.[32,33]

Most of the above mentioned investigations focused on dandelion pollen, while little meaningful data is available on other pollen types and the efficiency of pollen digestion in general. Crailsheim *et al.*[13] found that the percentage of empty grains in the rectum was higher for pollen from *Castanea* than from *Trifolium*. Further, the efficiency of pollen digestion appeared to decrease with the age of the bees.[13] In agreement with this result, the lipase activity was found to be highest in the gut of 3–12-day old workers,[36] but we do not know if similar patterns exist for other digestive enzymes. Schmidt & Buchmann[58] carried out a detailed analysis of food intake

and excretion in a honey bee colony. They found that 83% of the nitrogen ingested with pollen was indeed utilized by the animals, which would indicate a very efficient pollen digestion. Although larvae consume only very little pollen directly (see above), they also appear to be very efficient at digesting this food source. Thus, analyses of the gut contents of larvae fed with corn pollen showed that 98% of the pollen grains were at least partially digested.[4]

Perspectives

Studies from different countries showed that the bulk of the pollen was collected from a limited number of plants, which were often common species such as agricultural crops. This result indicates that honey bees may not necessarily suffer from an impoverishment of the flora in agricultural areas, although some periods of pollen shortage may occur, which might not be observed in a more diverse environment.[64]

Plant abundance was clearly not the only factor determining the foraging decisions of honey bees and some true preferences seemed to exist. Several studies suggested that such preferences were probably not based on assessments of the nutritive value of a given pollen type. However, it remains unclear which factors actually do determine the current value of a food resource for honey bees.

High-quality pollen is necessary to induce the development of the hypopharyngeal glands in young worker bees. These glands secrete the food jelly which is fed to the larvae. During its entire life, one worker bee requires an estimated 160 to 180 mg of pollen with an average nitrogen content of 20%. This implies that a colony rearing 150 000 bees in one season has to collect about 25 kg of pollen. A direct relationship between pollen availability and colony development can be expected. This topic will be covered in the second part of this review to be published in the next issue of *Bee World*.

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References

1. ALFONSUS, E C (1933) Zum Pollenverbrauch des Bienenvolkes. *Archiv für Bienenkunde* 14: 220–223.
2. AL-TIKRITY, W S; BENTON, A W; HILLMAN, R C; CLARKE, W W J (1972) The relationship between the amount of unsealed brood in honeybee colonies and their pollen collection. *Journal of Apicultural Research* 11: 9–12.
3. AUCLAIR, J L; JAMIESON, C A (1948) A qualitative analysis of amino acids in pollen collected by bees. *Science* 108: 357–358.
4. BABENDREIER, D; KALBERER, N; ROMEIS, J; FLURI, P; BIGLER, F (2004) Pollen consumption in honey bee larvae: a step forward in the risk assessment of transgenic plants. *Apidologie* (in press).
5. BARKER, R J; LEHNER, Y (1972) A look at honey bee gut functions. *American Bee Journal* 112: 336–338.
6. BEGON, M; HARPER, J L; TOWNSEND, C R (1996) *Ecology: individuals, populations and communities*. Blackwell Science; Oxford, UK; 1068 pp. (3rd edition).
7. BINZ, A; HEITZ, C (1990) *Schul- und Exkursionsflora für die Schweiz*. Schwabe & Co AG; Basel, Switzerland; 659 pp. (19th edition).
8. CALE, G H J (1968) Pollen gathering relationship to honey collection and egg-laying in honey bees. *American Bee Journal* 108: 8–9.
9. CAMPANA, B J; MOELLER, F E (1977) Honey bees: preference for and nutritive value of pollen from five plant sources. *Journal of Economic Entomology* 70: 39–41.
10. COFFEY, M F; BREEN, J (1997) Seasonal variation in pollen and nectar sources of honey bees in Ireland. *Journal of Apicultural Research* 36: 63–76.
11. COOK, S M; AWMACK, C S; MURRAY, D A; WILLIAMS, I H (2003) Are honey bees' foraging preferences affected by pollen amino acid composition? *Ecological Entomology* 28: 622–627.
12. CRAILSHEIM, K (1990) Protein synthesis in the honeybee (*Apis mellifera* L.) and trophallactic distribution of jelly among imagos in laboratory experiments. *Zoologisches Jahrbuch Physiologie* 94: 303–312.
13. CRAILSHEIM, K; SCHNEIDER, L H W; HRASSNIGG, N; BÜHLMANN, G; BROSCH, U; GMEINBAUER, R; SCHÖFFMANN, B (1992) Pollen consumption and utilization in worker honeybees (*Apis mellifera* carnica): dependence on individual age and function. *Journal of Insect Physiology* 38: 409–419.
14. DAY, S; BEYER, R; MERCER, A; OGDEN, S (1990) The nutrient composition of honeybee-collected pollen in Otago, New Zealand. *Journal of Apicultural Research* 29: 138–146.
15. DEGROOT, A P (1953) Protein and amino acid requirements of the honey bee (*Apis mellifera* L.). *Physiologia comparata et oecologia* 3: 197–285.
16. DELARZE, R; GONSETH, Y; GALLAND, P (1999) *Lebensräume der Schweiz - Ökologie - Gefährdung - Kennarten.* Ott Verlag; Thun; 413 pp.
17. DOULL, K M (1980) Relationships between consumption of a pollen supplement, honey production and broodrearing in colonies of honeybees *Apis mellifera* L. I. *Apidologie* 11: 361–365.
18. FLURI, P; BOGDANOV, S (1987) Age dependence of fat body protein in summer and winter bees (*Apis mellifera*). *In* Eder, J; Rembold, H. (eds) *Chemistry and biology of social insects*. Verlag J Peperny; Munic, Germany; pp. 170–171.
19. FREE, J B (1963) The flower constancy of honeybees. *Journal of Animal Ecology* 32: 119–131.
20. FREE, J B (1970) *Insect pollination of crops*. Academic Press; London, UK.
21. HAGEDORN, H H; MOELLER, F E (1967) The rate of pollen consumption by newly emerged honey bees. *Journal of Apicultural Research* 6: 159–162.
22. HAYDAK, M H (1934) Changes in total nitrogen content during the life of the imago of the worker honeybee. *Journal of Agricultural Research* 49: 21–28.
23. HAYDAK, M H (1935) Brood rearing by honeybees confined to a pure carbohydrate diet. *Journal of Economic Entomology* 28: 657–660.

IN PART TWO

Part two of this literature review focuses on the relationship between pollen supply, brood rearing and colony development. The following aspects will be discussed:

- the methods for estimation of the amount of pollen collected by honey bee colonies
- the annual pollen yields including the geographical, seasonal and colony-dependent fluctuations as well as the storage
- the correlations between pollen supply and some demographical parameters e.g. the amount of brood, the number of adult bees and bee lifespan

24. HAYDAK, M H (1959) Changes with age in weight and nitrogen content of honeybees. *Bee World* 40: 225–229.
25. HAYDAK, M H (1970) Honey bee nutrition. *Annual Review of Entomology* 15: 143–156.
26. HERBERT, E W J (1992) Honey bee nutrition. *In* Graham, J E (ed.) *The hive and the honey bee*. Dadant & Sons Inc.; Hamilton, Il, USA; pp. 197–233.
27. HERBERT, E W J; SHIMANUKI, H (1978) Chemical composition and nutritive value of bee-collected and bee-stored pollen. *Apidologie* 9: 33–40.
28. HERBERT, E W J; MILLER-IHLI, N J (1987) Seasonal variation of seven minerals in honey bee collected pollen. *American Bee Journal* 127: 367–369.
29. IMDORF, A; RICKLI, M; KILCHENMANN, V; BOGDANOV, S; WILLE, H (1998) Nitrogen and mineral constituents of honey bee worker brood during pollen shortage. *Apidologie* 29: 315–325.
30. JAXTHEIMER, R (1949) Die Ausnutzung der heimischen Flora durch die Bienen. *Archiv für Bienenkunde* 25: 17–30.
31. JOHNSON, B R (2003) Organization of work in the honeybee: a compromise between division of labour and behavioural flexibility. *Proceedings of the Royal Society London, Series B* 270: 147–152.
32. KLUNGNESS, L M; PENG, Y S (1984) A histochemical study of pollen digestion in the alimentary canal of honeybees (*Apis mellifera* L.). *Journal of Insect Physiology* 30: 511–521.
33. KLUNGNESS, L M; PENG, Y S (1984) Scanning electron microscope observations of pollen food bolus in the alimentary canal of honeybees (*Apis mellifera* L.). *Canadian Journal of Zoology* 62: 1316–1319.
34. KROON, G H; PRAAGH, J P V; VELTHUIS, H H W (1974) Osmotic shock as a prerequisite to pollen digestion in the alimentary tract of the worker honeybee. *Journal of Apicultural Research* 13: 177–181.
35. LEVIN, M D; BOHART, G E (1955) Selection of pollens by honey bees. *American Bee Journal* 95: 392–393.
36. LOIDL, A; CRAILSHEIM, K (2001) Free fatty acids digested from pollen and triolein in the honeybee midgut. *Journal of Comparative Physiology B* 171: 313–319.
37. LOUVEAUX, J (1958) *Recherches sur la récolte du pollen par les abeilles (*Apis mellifica *L.).* PhD thesis, University of Paris, France; 206 pp.
38. LUNAU, K (2000) The ecology and evolution of visual pollen signals. *Plant Systematics and Evolution* 222: 89–111.
39. MAURIZIO, A (1941) Über ein Massensterben von Bienen, verursacht durch Pollen von *Ranunculus puberulus* Koch. *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft* 149–150.
40. MAURIZIO, A (1950) The influence of pollen feeding and brood rearing on the length of life and physiological condition of the honeybee: preliminary report. *Bee World* 31: 9–12.
41. MAURIZIO, A (1953) Weitere Untersuchungen an Pollenhöschen. *Beihefte zur Schweizerischen Bienen-Zeitung* 2: 486–556.
42. MAURIZIO, A (1954) Pollenernährung und Lebensvorgänge bei der Honigbiene (*Apis mellifica* L.). *Landwirtschaftliches Jahrbuch der Schweiz* 68: 115–193.
43. MAURIZIO, A; KOLLMANN, H (1949) Beobachtungen an PollenhÜschen. *Schweizerische Bienen-Zeitung* 72.
44. McGREGOR, S E (1976) *Insect pollination of cultivated crop plants*. Agricultural Research Service; Washington, DC, USA.
45. MCLELLAN, A R (1976) Factors affecting pollen harvesting by the honeybee. *Journal of Applied Ecology* 13: 801–811.
46. MOEZEL, P G van der; DELFS, J C; PATE, J S; LONERAGAN, W A; BELL, D T (1987) Pollen selection by honeybees in shrublands of the northern sandplains of Western Australia. *Journal of Apicultural Research* 26: 224–232.
47. MORGENTHALER, O; MAURIZIO, A (1941) Die 'Bettlacher Maikrankheit', eine Vergiftung durch Hahnenfuss-Pollen. *Schweizerische Bienen-Zeitung* 64: 538.
48. OLSEN, L G; HOOPINGARNER, R; MARTIN, E C (1979) Pollen preferences of honeybees sited on four cultivated crops. *Journal of Apicultural Research* 18: 196–200.
49. O'NEAL, R J; WALLER, G D (1984) On the pollen harvest of the honey bee (*Apis mellifera* L.) near Tucson, Arizona (1976–1981). *Desert Plants* 6: 81–109.
50. PARKER, R L (1926) The collection and utilization of pollen by the honeybee. *Memoir Cornell University Agricultural Experiment Station* 98: 3–55.
51. PEARSON, W D; BRAIDEN, V (1990) Seasonal pollen collection by honeybees from grass/shrub highlands in Canterbury, New Zealand. *Journal of Apicultural Research* 29: 206–213.
52. PENG, Y S; NASR, M E; MARSTON, J M; FANG, Y (1985) The digestion of dandelion pollen by adult worker honeybees. *Physiological Entomology* 10: 75–82.
53. PERNAL, S F; CURRIE, R W (2002) Discrimination and preferences for pollen-based cues by foraging honeybees, *Apis mellifera* L. *Animal Behaviour* 63: 369–390.
54. RABIE, A L; WELLS, J D; DENT, L K (1983) The nitrogen content of pollen protein. *Journal of Apicultural Research* 22: 119–123.
55. ROULSTON, T; CANE, J H (2000) Pollen nutritional content and digestibility for animals. *Plant Systematics and Evolution* 222: 187–209.
56. ROULSTON, T; CANE, J H; BUCHMANN, S L (2000) What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs* 70: 617–643.
57. SABATINI, A G; VECCHI, M A; WILLE, M; WILLE, H (1987) Sulla raccolta del polline da parte delle api analizzata in tre diverse località nel 1981–1982 e nel 1982–1983. *Apicoltura* 3: 113–156.
58. SCHMIDT, J O; BUCHMANN, S L (1985) Pollen digestion and nitrogen utilization by *Apis mellifera* L. (Hymenoptera: Apidae). *Comparative Biochemistry and Physiology* 82A: 499–503.
59. SEVERSON, D W; PARRY, J E (1981) A chronology of pollen collection by honeybees. *Journal of Apicultural Research* 20: 97–103.
60. SHAWER, M B (1987) Major pollen sources in Kafr-El-Sheikh, Egypt, and the effect of pollen supply on brood area and honey yield. *Journal of Apicultural Research* 26: 43–46.
61. SOKAL, R R; ROHLF, F J (1995) *Biometry*. W H Freeman & Co.; New York, USA; 887 pp.
62. SOMERVILLE, D C; NICOL, H I (2002) Mineral content of honeybee-collected pollen from southern New South Wales. *Australian Journal of Experimental Agriculture* 42: 1131–1136.
63. STANDIFER, L N (1967) A comparison of the protein quality of pollen for growth-stimulation of the hypopharyngeal glands and longevity of honey bees, *Apis mellifera* L. (Hymenoptera: Apidae). *Insectes sociaux* 14: 415–426.
64. STEFFAN-DEWENTER, I; KUHN, A (2002) Honeybee foraging in differentially structured landscapes. *Proceedings of the Royal Society London, Series B* 270: 569 – 575.
65. SYNGE, A D (1947) Pollen collection by honeybees (*Apis mellifera*). *Journal of Animal Ecology* 16: 122–138.
66. TODD, F E; BRETHERICK, O (1942) The composition of pollens. *Journal of Economic Entomology* 35: 312–317.
67. VISSCHER, P K; SEELEY, T D (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63: 1790–1801.
68. VIVINO, A E; PALMER, L S (1944) The chemical composition and nutritional value of pollens collected by bees. *Archives of Biochemistry* 4: 129–136.
69. WADDINGTON, K D; NELSON, C M; PAGE, R E (1998) Effect of pollen quality and genotype on the dance of foraging honey bees. *Animal Behaviour* 56: 35–39.
70. WELLS, H; WELLS, P H (1983) Honey bee foraging ecology: optimal diet, minimal uncertainty or individual constancy ? *Journal of Animal Ecology* 52: 829–836.
71. WILLE, H (1979) Pollensammeln 1978. *Schweizerische Bienen-Zeitung* 102: 1–31.
72. WILLE, H; IMDORF, A (1983) Die Stickstoffversorgung des Bienenvolkes. *Allgemeine Deutsche Imkerzeitung* 2: 37–50.
73. WILLE, H; IMDORF, A; WILLE, M; KILCHENMANN, V (1984) Jahreszeitlicher Verlauf des Polleneiweissgehaltes an einigen schweizerischen Beobachtungsstationen. *Schweizerische Bienen-Zeitung* 107: 407–417.
74. WILLE, H; IMDORF, A; BÜHLMANN, G; KILCHENMANN, V; WILLE, M (1985) Beziehung zwischen Polleneintrag, Brutaufzucht und mittlerer Lebenserwartung der Arbeiterinnen in BienenVÜlkern (*Apis mellifica* L.). *Mitteilungen der schweizerischen entomologischen Gesellschaft* 58: 205–214.
75. WILLE, H; WILLE, M; KILCHENMANN, V; IMDORF, A; BÜHLMANN, G (1985) Pollenernte und Massenwechsel von drei *Apis mellifera*-VÜlkern auf demselben Bienenstand in zwei aufeinanderfolgenden Jahren. *Revue suisse de zoologie* 92: 897–914.
76. WILLE, M; WILLE, H (1980) Pollensammeln 1978/1979 - Vergleichende Untersuchungen. *Schweizerische Bienen-Zeitung* 103: 285–293.
77. WILLE, M; WILLE, H (1981) Die Pollenversorgung der Bienenvölker in den Jahren 1978–1980. Vergleichende Untersuchungen, botanische Aspekte. *Schweizerische Bienen-Zeitung* 104: 227–242.
78. WILLE, M; WILLE, H (1983) Vergleichende pollenanalytische Untersuchungen des Rückbehaltes in Pollenfallen, Ermittlungsjahre 1981 und 1982. *Schweizerische Bienen-Zeitung*
79. WILLE, M; WILLE, H (1984) Was hat sich in der Pollenversorgung der Bienenvölker in den letzten 35 Jahren verändert? *Schweizerische Bienen-Zeitung* 107: 463–472; 504–511.

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