

Pollen nutrition and colony development in honey bees – Part II ¹

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The consumption of high-quality pollen induces the development of the hypopharyngeal glands in young honey bee workers. As protein-rich secretions from these glands are an important component of larval food, a direct relationship between pollen supply and brood rearing can be suspected. Consequently, the availability of pollen is likely to be a central parameter influencing the development of honey bee colonies.

The control mechanisms in honey bee (*Apis mellifera*) colonies are of particular interest not only from a scientific but also from an economic point of view. Thus, a detailed understanding of the causal relationships between different parameters might allow the specific manipulation of a given quantity such as e.g. honey yield or pollen foraging intensity. The latter may be significant in view of the fact that honey bees are important pollinators of some crops.

Estimates of the amount of pollen collected by a colony are generally obtained by means of pollen traps. We will discuss the limitations of this method (section A) and give a survey of the approximate annual pollen intake of honey bee colonies in different

¹ Dedicated to the memory of Hans Wille, head of the Apicultural Section of the Swiss Federal Dairy Research Station in Liebefeld-Bern from 1957 to 87. The topic of this review was a crucial point of his work.

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geographical areas (section B). This data will allow a rough assessment of the pollen requirements of a colony and help to identify potential periods of pollen shortage. Experimental approaches are necessary to detect causal relationships between pollen supply and different demographical parameters (section C).

The impact of pollen consumption on the physiological development of honey bees was discussed in more detail in a first part of this review article ²⁸. This publication also provided a survey of the literature on the botanical and chemical composition of bee-collected pollen.

A. The estimation of pollen intake

Pollen samples are generally collected by means of pollen traps, which also provide quantitative estimates of the pollen intake of a colony. There is a large variety of different trap designs, but all consist of some type of grid, which removes the pollen pellets from some of the returning foragers as they enter the hive. The pollen is collected in a tray and can be easily removed by the researcher. The grid is installed either in front of the hive entrance² or horizontally underneath the entrance to the brood nest (O.A.C. trap design)^{49, 56}.

The percentage of pollen actually retained in a trap may be quite variable, but will always be considerably less than 100%. Extensive observations by Imdorf²¹ showed that the efficiency of a trap at one colony could vary between 3 and 25% during the course of the vegetation period. Still larger variation (15 – 43%) was observed between different colonies, even if the same trap type was used¹⁹. Such discrepancies may stem from small differences in the material used for the individual traps. Alternatively, honey bee colonies may vary in the average size of the workers or may collect a different spectrum of pollen types. The species composition of the collected pollen appears to be of particular importance. Thus, Levin & Loper²⁹ found that the average efficiency of their traps increased from 33% to 60% when they were moved to a different location where different flowers were available, and the foragers collected significantly larger pollen pellets.

From the above discussion it becomes clear that accurate estimates of the actual quantity of pollen collected by a colony are virtually impossible. The situation is further complicated because the colonies might change their behaviour in response to continuous pollen trapping, for example by increasing their foraging effort^{29, 57}. It is also not well understood to what extent honey bee colonies might be harmed by the permanent use of pollen traps. Some studies detected a reduction of the brood area as a response to pollen trapping^{41, 48, 57}, while others did not find such an effect^{29, 41}. The honey yield of a colony may be negatively affected by pollen trapping^{16, 41}, possibly because pollen collection is intensified at the expense of nectar foraging.

Some authors tried to prevent potential negative effects of constant pollen trapping by returning the collected pollen to the colonies¹⁹ or avoiding continuous sampling at the

same beehive^{12, 54, 62}. Imdorf²¹ further described a method of extrapolating the results of weekly pollen samples to the entire vegetation period, taking into account the weather conditions between the sampling days.

In conclusion, pollen traps are useful tools to study different aspects of honey bee behaviour and ecology. However, it is important to bear in mind that accurate estimates of the pollen quantity collected by a colony are virtually impossible due to the above-mentioned problems. Comparisons between locations may be particularly difficult as different studies are likely to vary in some methodological details.

B. Quantity of pollen collected by honey bee colonies

Total annual quantity of pollen collected by different colonies

The available estimates of the amount of pollen collected per colony and year range between 5.6 kg and 222 kg (Table 1). This maximum value was observed at a location in California and was computed assuming a trap efficiency of 25%. Unfortunately, no estimates of trap efficiency were provided in the original publication, as was also the case for the second Californian study. In spite of this element of uncertainty, the Californian colonies seem to have collected considerably higher pollen quantities than the European ones (Table 1). Thus, the actual pollen yield (left shaded column) observed by Todd & Bishop⁵⁴ is comparable to the values for total pollen quantity obtained in Erlangen and Bern-Liebefeld (right shaded column). In the study by Eckert¹², even more than 50 kg of pollen were actually retained in the traps. Among other factors, the longer vegetation period in California compared to northern and central Europe may lead to a better and more continuous availability of pollen¹⁹. At the other end of the spectrum are the very low pollen quantities of 5.6 – 6 kg collected by colonies in southern England⁵³. The author mentioned the rather unfavorable weather conditions in 1946 as one possible reason for this result. However, many other parameters such as the abundance of pollen sources or the nutritional need of the colony may influence the foraging behavior of the bees. As mentioned above, some discrepancies may also result from differences in experimental conditions between studies.

Comparisons between several colonies at one location are less problematic because they are normally carried out by the same researchers using the same trap type and identical experimental procedures. The results of such analyses are quite inconsistent. In some studies, the pollen yield differed considerably between colonies^{19, 30, 62}, whereas in others it was strikingly similar^{34, 37, 39, 53}. Interestingly, three of the studies reporting comparable pollen yields were based on colonies, which were of similar strength at the beginning of the observation period^{37, 39, 53}. Wille et al.⁶², on the other hand, used colonies of slightly different sizes, whereas Maurizio³⁴ and Hirschfelder¹⁹ did not provide any information

on this parameter. The potential correlation between colony size and intensity of pollen foraging will be discussed in more detail in section C of this article.

Seasonal fluctuations of the pollen yield

At most locations, the pollen intake of honey bee colonies is subject to considerable fluctuations during the course of the year. Very often one or two distinct peaks are observed, which are likely to be associated with the flowering of a locally abundant plant species. Todd & Bishop⁵⁴ studied the pollen yield at three Californian locations during an entire year. At Orange in the southern Californian lowlands, pollen collection did not cease completely during winter but continued at low intensity. A wide peak of the pollen income was observed between May and September. In the southern Californian mountains (Black Star Canyon) and in the Sacramento Valley (Davis), pollen foraging stopped between November and January. At Black Star Canyon, the quantity of collected pollen showed a pronounced peak in June and July. At Davis, on the other hand, the distribution of the pollen yield was rather bimodal with a maximum in March and April and a second considerably lower peak between July and September. A similar bimodal distribution was observed by Eckert¹² for an unspecified Californian location.

Due to the cooler climatic conditions in northern and central Europe, pollen foraging is restricted to a shorter time period than in California. Hirschfelder¹⁹ plotted the pollen quantities collected by a colony in Erlangen (Germany) between April and September in two consecutive years. In 1949, the pollen yield increased steeply during April, reached a peak in July and then almost ceased during late August and September. In 1950, the weather was very unfavorable in April, which resulted in a very low availability of pollen during that period. The amount of collected pollen then increased and remained high between May and the middle of September with a very pronounced peak in June.

Observations carried out at three colonies in Bern-Liebefeld (Switzerland) in 1980 and 1981, also revealed considerable annual differences in the pollen quantities collected at a given time in the course of the season⁶². In the first study year, a maximum was observed in May and early June and a second peak between the middle of July and the middle of September. Such a pattern with a collapse of the pollen income in late June and

early July appears to be quite common for the Swiss midland, although it is not always equally pronounced^{34, 62}. For example, it did not occur in 1981, maybe due to particular weather conditions, which lead to a better staggering of different pollen sources⁶². In an agricultural area in Germany, a similar pollen shortage in mid-summer led to an increase of the average foraging distances of honey bees⁵².

In the subalpine region of Switzerland, the vegetation period is still considerably shorter than in the European lowlands. In Davos (Switzerland), for example, the bulk of the pollen was collected between the middle of April and the middle of July. During the rest of the summer and early fall the pollen yield was very low³⁴.

Seasonal changes of the amount of stored pollen

The amount of pollen available for consumption at any given point in time is determined not only by the intensity of pollen collection but also by the pollen stores of a colony. In an extensive survey of Scottish colonies, Jeffree & Allen²⁶ found that the amount of stored pollen was very low between September and April, averaging ca. 75 g. Although not very large, these pollen reserves may be important for the survival of overwintering colonies. Thus, Farrar¹³ detected a positive correlation between the extent of pollen stores and the colony size in spring expressed as a percentage of the fall population. In Scotland, the average pollen stores reached a maximum of ca. 650 g between June and August, indicating an excess of pollen collection over pollen consumption during that period²⁶. However, even under optimal foraging conditions we will not observe an unconfined increase of the pollen stores. In fact, the size of the pollen reserves seems to serve as an important stimulus in the regulation of foraging behaviour. In experimental colonies, the intensity of pollen foraging could be decreased by adding and increased by removing pollen stores. If stores were added, the colonies used up this additional pollen until the size of the pollen reserves reached the pre-experimental level¹⁴.

Table 1: Annual quantity of pollen collected by colonies of *Apis mellifera* at different locations. Pollen traps were installed continuously during the specified period except in the study by Wille ⁶², where the results of weekly samples were extrapolated as described in Imdorf ²¹. Colony = name of the study colony as used in the original publications; Yield = quantity of pollen collected in traps; Eff. = trap efficiency assumed in calculating the total (an efficiency of 25% was assumed if no estimates were provided in the original publication = values in italic); Total = estimate of the total amount of pollen collected by a colony.

Study	Location	Year	Trapping period	Colony	Yield	Eff.	Total
Todd & Bishop ⁵⁴	Orange, CA, USA	1938-39	Feb - Jan	several ^a	15.54	25%	62.16
	Black Star Canyon, CA, USA	1938	Feb - Dec	several ^a	13.64	25%	54.56
	Davis, CA, USA	1938-39	Jun - Jun	several ^a	17.98	25%	71.94
Eckert ¹²	CA, USA (no details given)	1940	Feb - Oct	several ^a	55.45	25%	221.79
		1941	Mar - Oct	several ^a	50.65	25%	202.62
Synge ⁵³	Rothamsted, UK	1946	Feb - ?	E4	1.48	25%	5.92
		1946	Feb - ?	K5	1.39	25%	5.56
Louveaux ³⁰	Bures-sur-Yvette, F	1950-55	Mar - Sep	average ^b	2.3 - 3.3	10%	23 - 33
Hirschfelder ¹⁹	Erlangen, D	1949	Apr - Sep	1	2.33	15%	15.56
		1949	Apr - Sep	6	8.92	31%	28.77
		1950	Apr - Sep	1	2.58	15%	17.17
		1950	Apr - Sep	6	7.39	31%	23.86
		1950	Apr - Sep	14	9.11	34%	27.61
		1950	Apr - Sep	55	9.19	43%	21.37
Wille et al. ⁶²	Bern-Liebefeld, CH	1980	Apr - Sep	7		14%	23.59
		1980	Apr - Sep	9		14%	20.31
		1980	Apr - Sep	10		14%	13.94
		1981	Apr - Okt	7		14%	9.97
		1981	Apr - Okt	9		14%	26.98
		1981	Apr - Okt	10		14%	15.01

^a The pollen trap was installed consecutively at several different colonies. ^b Average values across several colonies.

C. Influence of pollen supply on colony development

If beekeepers want to control the development of their colonies with a view to maximizing certain quantities such as for example honey yield, it will be fundamental for them to understand the causal relationships between different factors. Given the importance of pollen for brood-rearing^{17, 18} and physiological development of workers³², it is obvious to take pollen supply into consideration as an essential parameter influencing the development of honey bee colonies. We will start this section with an survey of studies that have investigated how different demographical parameters covary with pollen supply. In a second part, we will discuss experiments, which tried to establish actual causal relationships between different variables.

Correlations between pollen supply and different demographical parameters

We will summarise the results of studies investigating correlations between pollen supply and the number of bees after overwintering, the amount of brood, bee longevity and, finally, colony size.

During winter, honey bee colonies may use their honey and pollen stores to rear small amounts of brood²⁵. Even in non-breeding colonies, the overwintering animals will consume and digest small quantities of pollen⁵. These observations indicate that the size of a colony in spring might, to some extent, be influenced by the availability of pollen to the overwintering animals. Indeed, Farrar¹³ found that the size of the spring population expressed as a percentage of the fall population was positively correlated with the extent of the pollen stores. Colonies with larger pollen reserves also grew faster in spring and produced more honey during the first nectar flow period. However, due to the lack of further studies the generality of these findings is unknown.

Pollen is consumed in large quantities by nurse bees⁶, which then feed larvae with protein-rich glandular secretions¹⁸. Against this background, it is quite obvious to suspect a connection between brood production and pollen supply. Indeed, all but one of the available studies detected a significant positive correlation between the two variables

(Table 2). McLellan³⁷ found that the brood area was not correlated with the amount of pollen collected or available as stores on the same day. The author argued that larger colonies might collect relatively less pollen because nutrient imbalances were reduced with greater intakes of different dietary components. However, it is also possible that the non-significant correlations were a result of estimating the two quantities on one single day. Depending on the causal relationship between the two parameters, they will not change synchronously. If, for example, the number of eggs laid by the queen changes in response to the amount of pollen brought into the hive, the brood area will lag behind changes in pollen supply. In most other studies in Table 2, the estimates were based on longer time periods^{1, 3, 10, 55, 61}, which also alleviated the effects of daily fluctuations of foraging intensity.

At all six locations investigated by Al-Tikrity et al.¹, the pollen intake was positively correlated with the area of unsealed brood in a colony. Between locations, however, there were large differences in the quantity of pollen collected by colonies with a given brood area (see fig. 1 in Al-Tikrity et al.¹). Such local differences would blur correlations between pollen supply and amount of brood if data from several locations were pooled. This could be another possible reason for the non-significant correlations obtained by McLellan³⁷. Wille et al.⁶¹ combined data from eight Swiss locations and five different years (fig. 1A). They also detected considerable differences in the amount of pollen collected by colonies with a given number of brood cells but there was still a significant positive correlation between the two variables across all data sets. In all other studies listed in Table 2, the analyses were based on colonies from one location.

Little data is available on the potential association between pollen supply and average worker longevity. In a survey of 102 free-flying colonies in Switzerland, a significant negative correlation was detected between annual pollen intake and average life expectancy of workers (fig. 1B; Spearman correlation coefficient = -0.283; $p = 0.004$)⁶¹. However, this correlation disappeared if the pollen intake per bee was considered ($p = 0.145$)⁶¹.

Few studies investigated the association between pollen supply and colony size (i.e. worker population size). It is evident that changes in worker population size cannot occur

instantaneously due to the egg and larval stages that precede the emergence of adult honey bees. Depending on the actual causal relationships, population size might therefore respond with a certain delay to changes in other variables. Indeed, McLellan³⁷ found no significant correlations between the number of bees and the amount of pollen retained in traps on any of six study days. Similarly, Wille⁵⁹ reported that the two quantities did not change synchronously during the course of the season. However, it is clear that generalisations are not possible given the scarcity of the data.

In conclusion, pollen supply appears to be associated at least with brood area. However, this was also the most intensively studied pair of variables, while little data was available on other demographical parameters. It is important to bear in mind that the studies discussed above are all correlative, i.e. they solely investigate if two factors vary together and do not allow any conclusions about causal relationships between them³⁸. If we detect a positive correlation between pollen supply and the number of brood cells, for example, it is possible that the amount of brood regulates the intensity of pollen foraging.

Alternatively, it is just as possible that the quantity of pollen collected by the foragers determines the number of larvae the colony will rear. A third option would be that the two factors covary because they both depend on a third, hidden variable⁵⁰. For example, the intensity of pollen collection and brood rearing might both be determined by day length. To establish actual causal relationships it is indispensable to perform experiments³⁸. The studies discussed above clearly indicate that such experiments would be worthwhile as they have confirmed the existence of associations between pollen supply and at least some demographical parameters.

Experimental evidence for causal relationships between pollen supply and demographical parameters

The control mechanisms in honey bee colonies are likely to be very complex. Thus, the amount of pollen collected by a colony could potentially be influenced by as many as ten or more other variables (e.g. worker population size, number of larvae, surrounding vegetation, weather conditions etc.). As a consequence of this intricacy, the following

overview is by no means exhaustive and leaves out important aspects such as e.g. the genetic basis of foraging behaviour^{20, 42}.

Impact of the number of larvae on pollen stores and pollen collection. Eckert et al.¹¹ manipulated the amount of brood in colonies, which were initially similar with respect to pollen reserves, honey stores and adult population size. One week after the manipulation, the pollen stores were significantly lower in colonies with high brood levels as compared to colonies with little brood indicating increased pollen requirements in the former. In a different experiment, a frame with mainly unsealed brood was exchanged with a frame of sealed brood between pairs of colonies⁹. The number of pollen foragers was found to be significantly reduced in colonies with a low brood stimulus, i.e. with more sealed brood that did not need to be fed.

The number of larvae in the colony is probably assessed directly by pollen foragers, whereas indirect cues, e.g. through trophallactic interactions between nurse bees and foragers, appear to be less important. As mentioned above, the number of pollen foragers was significantly increase in colonies with artificially enlarge brood areas⁹. When the researchers inserted a screen, which kept the foragers out of the brood nest but still allowed trophallactic interactions with nurse bees, this significant difference between high and low brood treatments disappeared. Among other factors, pheromones produced by the larvae were found to provide a direct stimulus affecting pollen foraging behaviour. Thus, the experimental addition of glass plates treated with brood pheromone led to a similar increase of the number of pollen foragers as the addition of brood⁴³. In both of these treatments, the number of pollen foragers was significantly higher than in colonies where all larvae had been removed. In a second experiment, Pankiw et al.⁴³ provided honey bee colonies either with 1000 larvae plus four glass plates treated with pheromone extracts or with the same number of larvae and four control glass plates. The number of pollen foragers was significantly higher in colonies with pheromone supplements than in colonies containing brood only.

Impact of pollen collection on the number of larvae. As we have seen above, the amount of brood present in a colony appears to have a direct influence on pollen foraging intensity. Several studies have tried to ascertain the existence of a causal relationship in

the opposite direction by manipulating the pollen intake of honey bee colonies rather than the amount of brood. Fewell & Winston ¹⁴ compared the amount of brood reared by colonies, which were initially similar in terms of number of adults, extent of the honey stores, open and capped brood and empty combs but were manipulated to contain either large or small pollen reserves. Brood production increased significantly when colonies were given more extensive pollen stores. Interestingly, the differences in pollen reserves due to the manipulation did not persist. After 16 days, the extent of the pollen stores had returned to the pre-experimental level in both treatments. If honey bee colonies were kept from pollen foraging by placing them under a wire mesh tent they reduced and finally stopped brood rearing ²⁴. As a consequence, the number of workers became significantly lower in these colonies than in colonies, which were allowed to forage freely. These results clearly indicate that honey bees respond to the availability of pollen by adjusting brood production. In the case of pollen shortage, this may happen either through a decrease of the number of eggs laid by the queen, a reduction of the pollen quantity used per larvae or the destruction of parts of the brood. Anecdotal evidence from one colony showed that fewer larvae survived until the capping stage during periods of artificial pollen shortage probably because they were cannibalised by adult workers ⁴⁴. Similar observations were made by Imdorf et al. ²⁴.

Impact of worker population size, pollen stores and empty storage space on pollen collection. The presence of brood is probably not the only factor influencing the amount of pollen collected by a honey bee colony. Eckert et al. ¹¹ manipulated the size of the worker population with the ratio between number of adults and number of larvae held constant. They found that the proportion of pollen foragers was significantly higher in small colonies than in large ones. Further, they found a significant increase in the brood area of small colonies until it had reached a level similar to that in large colonies. Eckert et al. ¹¹ suspected that it might be the best strategy for small colonies to invest in population growth to ensure successful overwintering, and consequently pollen should have a high value for them.

We already saw that an experimental increase of the brood area could cause a reduction of the pollen stores ¹¹. In such a situation, we might expect the bees to try and replenish the reserves by intensifying pollen foraging. Animals from colonies with large pollen

stores, on the other hand, might reduce their foraging activities. Indeed, a negative relationship between pollen stores and foraging effort was found in colonies where the extent of the pollen reserves had been manipulated^{9, 14}. Dreller et al.⁹ experimentally changed the pollen stores in a part of the hive that was accessible only to foragers but not to nurse bees. With this setup, they were able to demonstrate that the extent of the pollen stores was assessed directly by the foragers.

Finally, the foraging effort was also found to be regulated by the amount of empty storage space in the colony⁹. Thus, the number of pollen foragers was significantly increased if an empty comb was placed inside the brood nest.

Impact of pollen supplements on colony development

As discussed above, several experimental studies detected a causal relationship between pollen supply and brood production. It is conceivable that this relationship could be exploited in apiculture to manipulate colony development through supplemental feeding. In view of the potential economic implications, considerable research efforts have been directed towards this issue. In spite of this, it has not been possible so far to develop pollen substitutes, which could completely replace natural pollen^{7, 51}. Generally, honey bees are offered additional pollen or an artificial, protein-rich diet to complement the pollen intake of the colony (i.e. pollen supplements). We will not delve into the merits or disadvantages of different artificial diets as these aspects have been treated in some detail by Johansson & Johansson²⁷. We will also not discuss the influence of different pollen types or artificial diets on the physiological development and longevity of honey bee workers, issues that were intensively studied by Maurizio^{31, 33, 35, 36}. Rather, we will focus on studies that investigated the impact of supplemental feeding on parameters directly related to colony size and productivity, i.e. amount of brood, worker population size and honey yield.

The results in Table 3 show that supplementary feeding does not always have the desired effect. If pollen supplements were offered in spring (first four studies) the amount of brood was generally higher in fed than in unfed colonies. A similar effect was observed in only one of the studies where the supplementary food was provided at other times of

the year⁶⁰. In this case, the authors explicitly state that the substitute feeding occurred during a period of pollen dearth. It is conceivable that honey bees may benefit from supplementary feeding when the natural pollen supply is critically low, as is sometimes the case in spring⁵⁸ or, in some areas, also in June^{34, 60}. However, any beneficial effects of pollen supplements on colony development appear to be rather transient, as no significant increase in worker population size was detected in any of the studies (Table 3). Cook & Wilkinson⁴ argued that supplementary feeding might not so much influence the number of workers but rather the age structure in the colonies. They hypothesised that fed colonies might contain a higher percentage of young adults than unfed ones. Finally, the availability of pollen supplement significantly increased the honey yield in two out of three studies^{8, 40}. This aspect should be of particular interest from an economic point of view but it would need to be studied in more detail. Among other things, it would be important to investigate if the financial gain from an increased honey yield really exceeds the costs of supplementary feeding.

In future experiments, more emphasis should also be put on choosing appropriate controls so that positive results can really be attributed to the impact of the pollen supplement. In several of the experiments listed in Table 3^{8, 15, 22, 23}, the treatment group received a pollen supplement mixed with sugar, whereas the control group was not fed at all. In such a design, any differences between treatment and control can be due to the pollen supplement and/or the better sugar supply³⁸. Indeed, Doull⁸ emphasised that the supplementary food might have been consumed mainly by older workers that were attracted by its high sugar content. He hypothesised that this could increase the average life span of foragers and lead to the observed boost of the honey production.

The rather conflicting results of the different studies may indicate the difficulty of manipulating such a complex system in a predictable manner. As discussed above, there is convincing experimental evidence for a causal relationship between pollen supply and brood production, for example. Nonetheless, it may be difficult to anticipate how brood rearing will be affected in the long term by an artificial increase of the food supply. It may be essential to provide pollen supplements at the correct time of the year (see above). Feeding measures may also be unsuccessful due to much more trivial reasons. Thus, it is by no means guaranteed that an artificial diet will be consumed by the bees, as

they may ignore high quality food if it does not contain certain phagostimulatory substances¹⁸. The acceptance of artificial diets can be enhanced by adding some pollen⁵¹ or pollen extracts⁴⁵. If feeding measures are supposed to induce population growth, it may be essential that the pollen supplement is actually consumed by the nurse bees involved in brood rearing and not by foragers only. The exact placement of a food source within the hive may determine how attractive it will be to a given segment of the worker population⁴. Although such factors can reduce the beneficial impact of pollen supplements, it is, in principle, possible to adapt the feeding method in an appropriate way. Other colony responses, however, may be much more difficult to influence and may render feeding measures completely ineffective. For example, some colonies may react to supplementary feeding by reducing their own foraging efforts^{22, 23}. Goodwin et al.¹⁵, on the other hand, did not detect a decrease of foraging intensity associated with the provision of pollen supplements.

In conclusion, the regulatory mechanisms in honey bee colonies are so complex that it is, at present, hardly possible to anticipate how a given parameter will change in response to a certain manipulation. Therefore, it is difficult to give general recommendations as to whether pollen supplements might be economically advantageous and if so in which particular situations.

Table 2: Correlations between pollen supply and brood production in *Apis mellifera*. The significance of the correlation coefficients is given as specified in the original publications, except for the values marked with *, which were computed using the Statistical Tables Calculator (<http://faculty.vassar.edu/lowry/tabs.html>). See footnotes for methodological details of the different studies. N = sample size; Corr. coeff. = correlation coefficient; n.s. = non significant.

Study	Timeframe	N	Corr. coeff.	Significance	Footnote
Cale ³	late spring and summer	?	0.660	highly significant	^a
Cale ³	late spring and summer	?	0.580	highly significant	^a
Cale ³	late spring and summer	?	0.810	highly significant	^a
Todd & Reed ⁵⁵	20 days	170	0.598	P < 0.0001*	^b
Al-Tikrity et al. ¹	1 - 12 May	6	0.925	P < 0.05	^c
Al-Tikrity et al. ¹	17 June - 4 July	6	0.851	P < 0.05	^c
Al-Tikrity et al. ¹	18 - 26 July	9	0.952	P < 0.05	^c
Al-Tikrity et al. ¹	25 May - 5 June	9	0.984	P < 0.05	^c
Al-Tikrity et al. ¹	23 June - 10 July	6	0.974	P < 0.05	^c
Al-Tikrity et al. ¹	23 June - 11 July	6	0.931	P < 0.05	^c
McLellan ³⁷	6 individual days	16	1 value / day	all n.s.	^d
McLellan ³⁷	6 individual days	16	1 value / day	all n.s.	^e
Wille et al. ⁶¹	entire vegetation period	102	0.580	P < 0.001	^f
Dustmann & von der Ohe ¹⁰	March - June	13	0.889	P < 0.0001*	^g

Footnotes

^a Pollen supply = yield of pollen traps; brood = number of eggs laid; the three rows give the results obtained at three different locations; no further methodological details are given in the original publication.

^b Pollen supply = yield of pollen traps; brood = brood area at end of study period; measurements at 170 colonies at one location in two years.

^c Pollen supply = yield of pollen traps; brood = average of unsealed brood area based on estimates at start and end of study period; each row gives the correlation coefficient for one particular location as estimated based on N colonies.

^d Pollen supply = yield of pollen traps; brood = estimates of brood area; a correlation coefficient is estimated for each study day based on 16 colonies from four locations.

^e Pollen supply = area of pollen stores; brood = estimates of brood area; a correlation coefficient is estimated for each study day based on 16 colonies from four locations.

^f Pollen supply = yield of pollen traps; brood = sum of three-weekly estimates of brood area; measurements at 102 colonies at eight location in five years.

^g Pollen supply = number of returning pollen foragers; brood = estimates of unsealed brood area; correlation coefficient computed using the means of four colonies at 13 time points.

Table 3: Impact of supplemental feeding on amount of brood, worker population size and honey yield. Pollen supplement was offered in spring (first four studies), summer (following two studies), or year-round (last study).

Study	Supplement	Control	Brood	Worker population	Honey yield
Cook & Wilkinson ⁴	pollen	unfed	fed > controls	fed ≈ control	—
Imdorf et al. ²³	pollen + sugar solution	unfed	fed > control ^a	fed ≈ control	—
Goodwin et al. ¹⁵	64% sucrose, 12% lactalbumin, 24% yeast	unfed	—	—	fed ≈ control
Nabors ⁴⁰	Bee Pol + sugar solution	sugar solution	fed > control	—	fed > control
Wille & Schäfer ⁶⁰	pollen substitute + sugar solution	sugar solution	fed > control ^b	—	—
	pollen substitute + sugar solution	sugar solution	fed ≈ control ^c	—	—
Imdorf et al. ²²	pollen + sugar solution	unfed	fed ≈ control ^d	fed ≈ control	—
	Protivy 50 + sugar solution + 4% pollen	unfed	fed ≈ control ^d	fed ≈ control	—
Doull ⁸	commercial pollen supplement + sugar	unfed	fed ≈ control	—	fed > control

^a different amounts of brood in April only

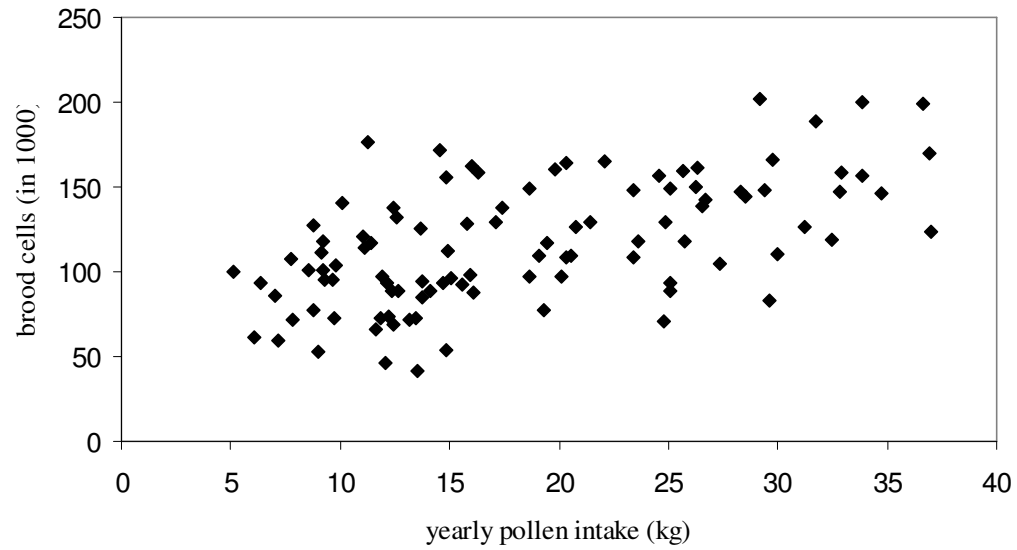
^b supplementary feeding from end of May to early July during period of pollen dearth

^c supplementary feeding in July

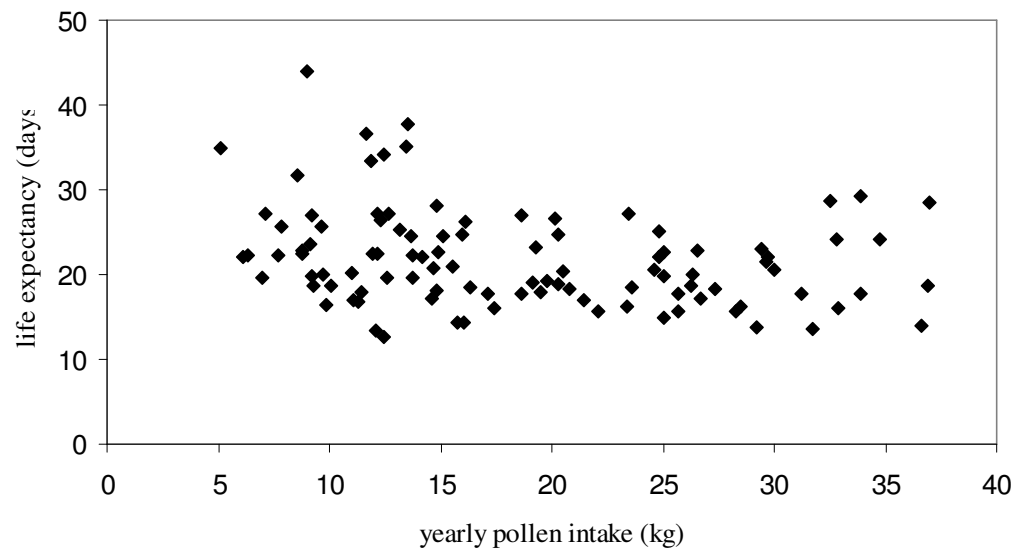
^d all pollen-fed and some Protivy-fed colonies were infested with chalk brood

FIG. 1: Yearly pollen intake and number of brood cells (A) or life expectancy (B) at 102 colonies of *Apis mellifera* in Switzerland. Data from Wille et al.⁶¹.

(A)



(B)



Perspectives

Several experimental studies have found causal relationships between different pairs of variables associated with pollen supply and colony demography. However, the regulatory mechanisms in honey bee colonies appear to be very complex and a given quantity may be regulated by several others. As a consequence, it may still be impossible to predict the outcome of a given manipulation such as supplemental feeding.

It also has to be kept in mind that the beekeepers' interests may differ considerably from those of the animals. Beekeepers will mainly want to maximize the long-term productivity of their colonies. However, producing excessive amounts of honey will probably not be an adaptive strategy for honey bees, which should rather be interested in maximizing their reproductive fitness^{46, 47}. Such issues should be considered even in a species such as the honey bee whose behaviour has been influenced through selective breeding.

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