The Foraging Honey Bee

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For their feed, nectar and pollen, honey bees depend completely on flowers. The foraging behaviour and preference for crops depend on the needs of the colony and the attractiveness of the crop, and nectar and pollen source. The foraging behaviour is constantly adapted to the availability of the crop and the needs of the colony. Honey bees live in colonies, varying in size of about 7,000 individuals in spring to 20,000–30,000 bees in summer, decreasing in size in autumn. During the active foraging and breeding period approximately 25–30% of the population is potentially a forager bee. In the course of the season roughly 25 kg water, 20–30 kg pollen, 125 kg nectar and small amounts of resins (propolis) are collected and brought back to one central location: the hive. Foraging flights, for water, pollen and nectar respectively are 2–3, 6 and 12km from the hive. However, usually the foraging flights are restricted to less than one kilometre.

As nectar and pollen yield per flower depend on the plant and climatic conditions, only estimations can be made about the number of flowers visited and the potential foraging area. To collect 20 kg pollen and 125 kg nectar, respectively 1,125,000 and 4,000,000 flowers will be visited. When bees collect the feed within a radius of 500 metre, 3 km or 10 km the potential foraging area is 0.8 km² (80 ha), 28 km² (2800 ha) and 314 km² (31400 ha). On average, forager bees go out ten times per day, sometimes for some minutes or up to one hour. Communication by bee dances and trophallaxis directs the bees to the feed sources. Ergo, bees of a colony are not homogeneously divided over the foraging area. This results in convergent flight paths and collection areas, and 'no foraging' or 'much foraging' on a crop is much more common than 'little foraging'. Honey bee colonies of one apiary are not equally foraging on the same feed sources; the colonies will visit some different and some overlapping areas. This means that more than one colony must be sampled to obtain an overview of available feed sources and for bioindication of pollutants and plant pathogens potentially present in a foraging area.

Knowledge about how a honey bee colony organises itself and how it exploits and explores the foraging area is not just a biologically interesting subject. It is in the interest of the beekeeper to understand what he/she sees when watching bees actively foraging at the flight board as well as inside the hive. It is also highly important when sampling bees for pathogens and when setting up and interpreting studies, such as measuring exposure to pesticides, or bioindication and biomonitoring investigations of environmental pollution and plant pathogens. Similarly, it is important when using bees to pollinate general and specific crops. This article presents a description of the honey bee colony with a particular focus on factors determining foraging activities for nectar, pollen and water, including distance from the hive, communication, how honey bees explore and exploit their foraging area and the exchange of forage in the colony. It is a compilation of the article (in Dutch) *Factoren die het foerageergedrag van bijenvolken bepalen* (Factors determining foraging by honey bees) on the website of PRI bijen http://www.wageningenur.nl/nl/Expertises-Dienstverlening/Onderzoeksinstituten/plant-research-international/Over-Plant-Research-International/Organisatie/Biointeracties-Plantgezondheid/Bijen.htm.

The honey bee colony

The honey bee colony consists of one reproductive bee, the queen, thousands of female bees, the workers, and, in summer, hundreds of male bees, the drones. The female worker caste includes four sub-castes: cleaning caste, brood nest caste, food storage cast and foraging caste.[1] A honey bee worker lives in the summer for four to five weeks and in the winter for six to eight months. The colony is actively foraging from April to October, although this period shows variation depending on weather conditions and local circumstances. Facts and figures presented here are about the active foraging period.

The tasks of workers are age-related. Globally, during the first three weeks workers are in-hive bees, cleaning the cells (cleaning caste), nursing the brood, queen, drones and young adult workers (brood nest caste), defending the colony, transferring the incoming feed to the cells and processing the nectar into honey (food storage caste). In the last one to two weeks of her life the worker bee is a forager, collecting food (foraging caste). The honey bee colony is a symbol of an efficient, cooperative community in which every bee is busy, contributing her share to the welfare of the colony. In reality, however, this is not entirely correct; about 10–30% of workers inside the hive show no specific activity; they are the 'resting bees'.[2] This pool of resting bees has a function. They are 'spare' bees. The age-related tasks are not cast in concrete, but show plasticity. The tasks are more related to the need of the colony than to an individual bee's age.[3] If the composition of the worker pool or the tasks to be performed changes dramatically, then, worker bees' activities can be adjusted. For instance, older bees can regenerate their food glands to become nurse bees again if there is a sudden shortage of nurse bees, and young in-hive bees can start foraging activities before they would normally forage if a significant number of foragers were to disappear.[4,5]

Foragers

In summer, there can be up to 35,000 worker bees in the colony. As a consequence, the number of foragers depends on the colony size. On one dm² (square decimetre) there are 125 bees when they are close to each other and no comb is visible.[6] Based on this, every apiculturist can easily assess the total number of bees in a hive (Table 1).

The Simplex frame:
- Measures 3.40 x 1.98 dm = 6.7 dm² per side and 13.5 dm² per two sides
- Per 1 dm² = 125 bees
- Number of bees per fully occupied Simplex frame is: 13.5 x 125 = 1683 bees

Table 1. Number of bees in a Simplex hive (inner frame measures 340 x 198 mm)

Frames: 2-sided, fully occupied	dm^2	Number of bees
1 frame	13.5	1683
5 frames	67.3	8415
10 frames	134.6	16830
15 frames	202.0	25245
20 frames	269.3	33660

Inside the hive, on the brood frames and the frames next to the brood frames, bees of all age cohorts are present in the same ratio: about 25% one week-old bees, 25% two week-old bees, 25% three week-old bees and 25% four and five week-old bees. On the frames with emerging brood, the very young bees, and on the storage frames the older bees are over-represented.[7] The percentage of foragers (four to five week old bees) in a colony is maximally 40%. In a strong colony this is approximately 10,000 foragers, but not all foragers are constantly foraging.

The lifespan of a forager is, on average, seven to eight days with a minimum of about five and a maximum of nineteen days.[8] In this period the bee can fly 800 km or so.[9] The bees forage for nectar up to 13 km, for pollen up to 6 km and for water up to 2–3 km.[10–12] Results of studies on the flight speed range from 4.9 to 8.2 meter per second.[13–15] The flight altitude is one to two metres.[16] A forager makes about ten foraging flights per day, being away for ten minutes for nectar and thirty to eighty minutes for pollen.[17] The collection process is the result of three sub-processes:

- Scout bees find new sources and recruit foragers to exploit these sources.
- Scout bees only recruit foragers for profitable sources.
- Foragers stop collecting nectar and pollen on sources that are no longer profitable.[18–20]

A strong colony can make up to 35,000 flights per day.[21] It is obvious that the data presented are estimates and, depending on food availability, weather circumstances and structure of the landscape, great variation can be seen. The distance bees forage for nectar and pollen depends on the availability of the food sources and on the energy it costs to collect the food. Bees go for the most efficient way and 'calculate' the benefit, taking into account the flight costs and the profit.[22] For instance Garbuzov *et al.* (2014)[23] found that in an urban area the majority of foragers collected food within 1 km from the hive, although further away, profitable sources, were available. As honey bees have only small energy stores in the body, they depend on the amount of sugar in the honey sac. This honey is transferred to the ventriculus and across the ventricular cell wall into the haemolymph down a concentration gradient. Ergo, the sugar concentration in the honey sac determines how far a bee can fly.[24,25]

Newly collected nectar is distributed among all workers and the larvae, and the major part is stored to be converted into honey.[26–29] Foragers fuel their foraging trip with recently collected nectar complemented by nectar from other foragers.[30,31] So the sugar concentration in the honey sac of the departing bees depends on recent forage trips.

Foraging for nectar, pollen and water

Bees collect nectar and pollen for their own direct needs and store the surplus for winter survival. Annually, a colony needs 60–80 kg honey.[22] To collect this amount, minimally 125 kg nectar must be collected, which will cost about 4,000,000 foraging trips. The frequency of the visits is determined by the time it takes foragers to unload their harvest to the bees inside the hive. A forager bringing in nectar with a relatively high concentration of sugar will more quickly find a bee of the food storage cast that is willing to accept her nectar load. The food collection caste consists of 18–28 day-old bees.[2,32] In this way colonies focus more on rich foraging sites.[33,34] During a nectar foraging trip, bees visit hundreds of flowers collecting 25–40 mg nectar (21–33 µl) per trip. The amount collected during a trip depends on the distance between the hive and the nectar source and on the nectar sugar concentration. The closer the nectar source the less nectar is collected per trip and the same is true for low sugar containing nectars. When foraging time and energy profitability are equal, the energy profitability determines where to forage.[35] On foraging sites of equal nectar value, the nearest site is preferred.[36] A forager will use up around 1–1.5 mg (0.85–1.25 µl) nectar to fly 1 km.[22]

Annually, a colony needs 15–30 kg pollen. Per trip 10–30 mg pollen is collected from 1–500 flowers. Assuming that per foraging trip, an average of 20 mg pollen is collected on 250 flowers, it takes 1,125,000 pollen trips to collect 22.5 kg in which per trip 12–13 flowers are visited. On average a pollen pellet weighs 6–11 mg.[37] The amount of pollen collected depends on the amount of brood in the colony and the season. In spring more pollen is collected than in autumn and the amount of pollen collected is positively related to the amount of brood. The regulation is based on a feed-back system via trophallaxis; high protein content in the jelly, fed to the pollen collectors by the nurse bees, incites the bees to decrease foraging for pollen and to switch to nectar.[5,38,39]

In the same way as for nectar, bees focus on profitable pollen sources. Most pollen has an incomplete essential amino acid content. Honey bees need pollen diversity to fulfil their need for a complete protein diet.[40–42] In general, four pollen sources daily are visited intensively and 10–14 are visited less intensively or only by the foragers looking for new pollen sources.[21]

Annually, a honey bee colony collects 25 kg water for dilution of the larval feed and for cooling the brood nest.[43,44] As water has no energy input for the return flight, bees return from these trips on their energy reserves, which restricts the flight distance to 2–3 km.[11]

During a foraging trip bees show flower constancy and location constancy. Flower constancy means that during a trip, the bee restricts herself to one plant species and keeps on doing this until the resources are 'dry' or a better alternative shows up. A bee can remember a good source for months.[45] The flower constancy is not absolute; up to 11% of pollen foragers collect pollen from different sources.[46,47] Also the division between pollen and nectar collectors is not absolute. In a study conducted by Ribbands (1949)[48] 58% of the bees collected only nectar, 25% collected only pollen and 17% collected both.

Communication: a means to efficient foraging

Honey bee colonies are highly efficient in collecting their feed. This is achieved by effective communication systems which are geared toward the benefit of the colony rather than toward the individual bee. The communication systems are the well known bee dances and trophallaxis (food exchange) in which the location of, direction of and distance to nectar, pollen and water sources are communicated to the forage collectors by the scout bees, whose job is to locate potential sources. Not all recruited foragers will

find the source that has been communicated, but approximately one third will find the source immediately.[49] It takes a bee around 2.4 and 4.8 trips to locate a source at 200 metres and 1000 metres respectively.[1]

Exploring and exploiting the foraging area

Theoretically the maximum foraging area for nectar is 450 km^2, for pollen is 113 km^2 and for water is 28 km^2. Bees prefer to collect as close to the hive as possible (>1 km) because of the link between distance and profitability, so the maximum distance will only be flown for very profitable sources or if no other sources are available in the proximity. It is obvious that, given the focus on profitable nectar and pollen sources and the effective communication systems, foragers of a colony do not forage homogeneously over the foraging area. In fact only a relatively small part of the theoretically available foraging area is exploited. This area can change daily or even over a few hours.[18,22,48] Colonies in one apiary can forage on similar, different and overlapping sites. In an orchard, a forager will restrict herself to one or two flowering trees in the same row.[50,51] On rich sources a bee exploits 10–40 m^2, on less profitable sources the distance between visits increases and the bees become more restless.[48,52,53,54]

A food source is effectively exploited by considering direction and distance; the less sugar in the nectar and the less time spent on a flower, the less change in direction is observed, ergo the richer the source and longer the time spent on one flower, the more bees change direction. Decreasing direction to less profitable sources helps the bee to spend less time on these sources.[55,56]

The foraging behaviour of honey bees shows seasonality. In spring, bees will dance to indicate nectar sources of about 30%, in summer it takes higher sugar concentrations and in autumn lower. Also in spring the foraging distances are shorter than in summer and autumn. In spring, bees have a thorax temperature of 35.7°C and in summer 26.6°C. The higher thorax temperature in spring costs more energy at the expense of the foraging distance.[57]

Exchange of pollen and plant pathogens in the colony

Bees collect particles of pollen. Fine dust particles and plant pathogens are collected along with the pollen and, accidentally, along with nectar collection in the branched hairs. Some of these particles are brushed from the hairs and end up in the pollen pellets and some remain in the hairs. These materials are exchanged inside the hive among all bees due to physical contact. A bee leaving the hive has on average 6,706 pollen grains in the hair and even bees that have never left the hive have pollen in the hairs.[58,59] This in-hive exchange of pollen is crucial for cross-pollination.[60] On the other hand, plant pathogens, such as *Erwinia amylovora*, the bacterium that causes fire blight, are transferred from diseased flowers to healthy flowers during a flight or, indirectly, via in-hive exchange of the bacteria. On a bee inside the hive *E. amylovora* remains viable for some days[61–63] and so contamination and spread of disease are potential 'negative' consequences of foraging.

Implications for sampling bees for bee pathogens

The sampling location in the hive will depend upon the bee pathogen under investigation; not all pathogens are detectable at all bee ages. For instance *Nosema apis* is not microscopically detectable in very young bees and the bees cleaning the cells may carry spores of *Paenibacillus larvae* (AFB).

Bioindications of plant pathogens

Because of the risk of transferring flower-borne plant pathogens, a 'hive retention time' should be built into the schedule when translocating colonies for pollination purposes to plants of the same crop. Bioindication of plant pathogens can best be studied in colonies placed in the proximity of crops for pollination. As colonies from one apiary visit overlapping and different areas, more than one colony must be sampled to obtain an overview of available pollen and nectar sources.

Bioindications of atmospheric deposition of heavy metals and exposure to pesticides

Honey bees can be used to detect increased levels of heavy metals in the environment. It is an additional usage of honey bee colonies. At the moment there is no knowledge of a link between (increased) heavy metals in the environment and honey bee health. Atmospheric deposition from combustion and traffic, the main source of heavy metals in and on bees, goes on in large areas; probably all colonies in an apiary have, on average, the same exposure.

Some definitions:

A bioindicator is an organism (or part of an organism or a community of organisms) that contain information on the quality of the environment (or part of the environment).
A biomonitor is an organism (or part of an organism or a community of organisms) that contains information on the quantitative aspects of quality of the environment (or part of the environment). A biomonitor is always a bioindicator, but a bioindicator does not necessarily meet the requirements for a biomonitor.
Active bioindication is the exposure of a bioindicator in a standardized form for a defined period.
Passive bioindication is the study of the impact of materials in the environment on organisms occurring naturally in the environment.

Exposure of honey bee colonies to pesticides

Depending on the scale and diversity of agricultural areas, pesticides are applied on relatively small or bigger areas within the foraging areas of a colony. As foraging distances in spring are shorter than in summer, the risk of exposure to pesticides is lower in spring than in summer or autumn, but on the other hand, pesticides are applied more in spring. Based on an annual colony need of about 125 kg of nectar, 25 kg of pollen and 25 kg water which have all about the same weight per trip, overall the ratio of foragers for nectar, pollen and water is 5:1:1. This indicates that exposure to pesticides is more likely for nectar collecting bees than the ones that forage on pollen and water. A worker consumes, in her 'in-hive' period, 400–500 mg sugar and 65 mg pollen,[64] which is mostly consumed by the nurse bees. Therefore, exposure of honey bees to pesticides via nectar is theoretically seven to eight times higher than via pollen. Due to the efficiency and mass collection of a colony on a profitable food source 'low exposure' or 'high exposure' to pesticides are more likely than 'little exposure'.

References

The reference list is too long to include in the space available for this article. However, for those who are interested, details of the full references are available from the editor at sharon.blake@bbka.org.uk