

The foraging behaviour of honey bees, *Apis mellifera*: a review

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ABSTRACT: Foraging behaviour is one of the distinctive behaviours of honey bees, *Apis mellifera*. This behaviour is the link between the honey bee colony and the ambient environment. Therefore, various in-colony and out-colony factors have an impact on this behaviour, and many studies have been employed to investigate these factors. Foraging behaviour is not advantageous only for the colony and for plant pollination but also has other benefits. In contrast, some disadvantages have also been discovered to be linked with foraging activity. Practically speaking, the control over this behaviour is very important to maximize colony products as well as to increase other agricultural benefits. This paper presents a review on foraging activity including; the regulation of foraging tasks, factors impacting this behaviour, foraging preference, variations between subspecies, monitoring methods as well as the possible methods for controlling this behaviour. As concluded from this review, more work needs to be performed in order to elucidate certain aspects of foraging behaviour.

Keywords: colonies; *Apis mellifera*; flying; workers; ethology

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1. Introduction

Under normal colony conditions, the forager bees are workers with an age of over 21 days, at which time they shift to perform Out-colony tasks including water, nectar, pollen or resin collection. The division of labour and the change of the nurse bees to perform foraging tasks were suggested to be impacted by colony factors (Huang and Robinson 1996), elevated levels of the *foraging* gene (Amfor) (Ben-Shahar et al. 2003) and/or the variations in the abundance of mRNA (Whitfield et al. 2003) in the worker's brain. Also, many other factors were suggested to have a key role in the shifting of worker bees from In-colony tasks to Out-colony

tasks. The anticipation of the commencement of foraging is associated with an increased titre of juvenile hormone (JH) in foragers which is not affected by foraging experience but by diurnal variations (Elekonich et al. 2001). Further, Schulz et al. (2002) found higher octopamine concentrations in the antennal lobes of the bee brain in foragers compared to nurses regardless of the age. They also found that changes in octopamine are modulated by juvenile hormone. The earlier age of foraging activity commencement (shifting to Out-colony tasks) was found to be affected by bovine insulin treatments (Mott and Breed 2012). In another study, and under reduced brood rearing activity a delay in foraging commencement and death was found

to be associated with increased vitellogenin levels (Amdam et al. 2009). Generally, the foraging skills and the number of forager workers are increased with age (Dukas and Visscher 1994). Additionally, the forager bees have different *n*-alkane profiles than the nurse bees with a higher quantity of *n*-alkane which may help the forager bees to tolerate the ambient conditions (Kather et al. 2011). Still more studies are required to elucidate the mechanisms influencing the shifting of the nurse bees to forager bees. After the change to foraging, a worker begins a new part of her life outside the colony in combination with different foraging tasks and interactions with the environment as explained in the next paragraphs.

2. Foraging tasks

The forager bees can be classified into two categories; scout bees which search for the best food resource and the reticent bees which wait in the beehive until the scout bees return and give them information about the food source by dancing. The reticent bees, in general, range from 40–90% of the total forager population (Nest and Moore 2012). This organization is important in saving time and the efforts of the honey bee foragers. Liang et al. (2012) found extensive differences between honey bee food scouts and the other foragers with regard to brain gene expression including catecholamine, glutamate, and γ -aminobutyric acid signaling. Under some ecological conditions, a temporal shift from foraging activity to sleeping (napping) may occur (Klein and Seeley 2011). The night sleep of forager bees is very important and night sleep deprivation may impact the navigation memory of honey bees (Beyaert et al. 2012).

According to the resource forager bees collect, foraging activity can be classified into water, nectar, pollen or resin foraging. On rare occasions, forager bees can also collect wax from scale insects, *Ceroplastes* sp. (Dimou and Thrasyvoulou 2007). The type of foraging, whether for pollen or nectar, is a colony-level trait with a genetic component (Hunt et al. 1995), and is affected by the genotype of bee strain (Pankiw et al. 2002). Also, these tasks depend on collective and individual decisions of forager bees. The prior experience at a feeding place plays a role during collective foraging (Fernandez and Farina 2005). For more details about the collective foraging of honey bees see Vries and Biesmeijer

(1998). In this publication the authors developed a model based on individual behaviour roles (e.g. previous information about food sources). Another important factor for the type of foraging task is sucrose response thresholds. Pankiw and Page (2000) found differences between honey bee workers in their thresholds to sucrose; the lowest threshold was found in water foragers, then pollen foragers, then nectar foragers followed by foragers of both pollen and nectar. They correlated these differences with the division of labour of forager bees. Simone-Finstrom et al. (2010) found that the sucrose response thresholds of the resin foragers were lower than pollen foragers. Thus, honey bee workers with low sucrose response thresholds start foraging behaviour for water and pollen earlier and at younger ages than workers with high sucrose response thresholds which forage for nectar (Pankiw 2005). The correlation between foraging behaviour and sucrose response thresholds (foraging behaviour syndrome) was reviewed by Pankiw (2005). The sucrose concentration response threshold is affected by rearing environment (Pankiw et al. 2002) and responds positively to bovine insulin treatments (Mott and Breed 2012).

Also, the change to pollen foragers is related to the colony conditions and foragers use their experience in trophallactic contacts to assess the pollen need of their colonies (Weidenmuller and Tautz 2002). Under shortages of pollen or in conditions of poor pollen quality, honey bee colonies increase the proportion of pollen foragers without increasing foraging rate (Pernal and Currie 2010). The foraging choice between pollen (protein) and nectar (carbohydrate sources) is influenced by insulin receptor substrate (IRS) as demonstrated by Wang et al. (2010). It seems that the foraging tasks are under the control of many factors and detailed studies on these factors are required.

3. Foraging time

It is known that the foraging activity of honey bees is initiated in early morning and finishes in the evening. In some studies, honey bee workers started foraging activity at 6.17 am (Joshi and Joshi 2010) but this commencement time can be greatly impacted by the region. Under desert conditions, Alqarni (2006) found that a higher number of foragers left the colonies at 8 am than at 10 am. In general, the foraging activity fluctuates during the day

from the morning until the evening. Reyes-Carrillo et al. (2007) found high pollen collection in the early morning while low amounts of pollen were collected in the afternoon. Pernal and Currie (2010) reported a higher foraging rate mean during the afternoon period (36.02 foragers/min) than during the morning period (17.66 foragers/min). Yucel and Duman (2005) found that honey bee workers visited onion flowers from 8.15 to 16.30 h and the peak foraging was between 11.00 to 12.00 h. Foragers have the ability to remember the time of the day at which the higher food resources are available as found with *Sysirinchium palmifolium* plants (Silva et al. 2013) and such ability may correlate with foraging activity peaks. In general, the normal foraging interval at the same feeding site is less than 5 min (Yang et al. 2008) and bees spend different times per flower depending on the plant species. The time spent per flower was 6.92, 6.50 and 5.54 s for Chinese cabbage, broccoli and kohlrabi, respectively (Sushil et al. 2013). There are numerous factors that may impact foraging activity (e.g. onset and end time, foraging interval and peaks) as explained in the next paragraphs.

4. Foraging distance

The energy hypothesis which suggests that foragers estimate the feeder distance (food resource) based on the spent energy during foraging flight is now considered to be incorrect and another hypothesis based on optical flow was suggested (Esch and Burns 1996). Both hypotheses can be considered as integrated explanations inasmuch as the energy spent during flight as well as the speed motion of the ground image received by the retina are both essential for estimating distance as well for distance calculation. The mean foraging distance for *A. m. carnica* was 1526.1 m while foraging distances of pollen-collecting bees had a mean of 1743 m in simple landscapes and 1543.4 m in complex landscapes (Steffan-Dewenter and Kuhn 2003). The mean of foraging distances for small colonies of *A. m. mellifera* was 670 m and for large colonies it was 620 m in July, while the values were 1430 m for small colonies and 2850 m for large colonies in August (Beekman et al. 2004). Hagler et al. (2011) found that the foraging range of honey bees ranged from 45 m to 5983 m. Under desert conditions, water foragers can fly up to 2 km from their colonies to collect water (Visscher et al. 1996). It seems that the foraging distance for colonies in the

same region is impacted by race, colony strength, food resource, month and the time of the day.

5. Foraging preference

Forager bees prefer the collection of water, nectar, pollen or resin from some resources over others. There are many examples of foraging preference; only a few examples are presented here. Water foragers were noticed to prefer continuous water sources than stable ones as well as large water containers than small ones (Abou-Shaara 2012). Also, forager bees have a preference to collect water from some unusual sources (e.g. cow dung) over clean water (Butler 1940). Nectar foragers sometimes prefer one food source over another as well as the specific position of one flower over another. Sushil et al. (2013) found that more honey bee foragers visited broccoli followed by kohlrabi and finally Chinese cabbage with 6.05, 5.35 and 5.05 bees/plant, respectively. Mayer and Lunden (1988) found more nectar foragers on the top of the flowers of Manchurian crabapple than red delicious apple. Fohouo et al. (2008) found the highest number of forager workers was on *Syzygium guineense* var. *guineense* and the lowest number on *Psorospermum febrifugum*. Also, Weaver (1965) detected differences in honey bee foraging behaviour on hairy vetch (*Vicia vitifolia* Roth) flowers; some bees used the flower base while others use the flower mouth. Honey bees have a preference for apple tree branches located in the middle of trees rather than for those branches located higher up or lower (Mattu et al. 2012). Similarly, pollen and resin foragers prefer some resources over others. More studies are required to fully uncover the preference behaviour of forager bees.

6. Foraging behaviour of honey bee subspecies

Differences between foraging activity as the number of bees leaving the hives were found between three honey bee subspecies; Yemeni, Italian and Carniolan honey bees, with a higher foraging activity of Yemeni then Italian and finally Carniolan honey bees under desert conditions (Alqarni 2006). Also, Ali (2011) found a higher foraging rate for Yemeni honey bees than Carniolan honey bees during June and August and at different monitoring times; 6–7 am, 11–12 am and 4–5 pm. The

same trend was found by Abou-Shaara et al. (2013), where Yemeni honey bees had higher foraging activity than Carniolan honey bees under desert conditions. In contrast, no clear impact of bee race was found for ARS Russian or Italian honey bees with respect to the percentages of pollen foragers or flight activity (Danka et al. 2006). The differences between the foraging activity of honey bee subspecies can be explained partly by the variations in their morphological characteristics. Bees with large wings were reported to have higher flying ability than small ones (Mostajeran et al. 2006). Higginson et al. (2011) found that bees with damaged wings had less foraging trips and flew closer to the hive than healthy ones. Positive correlations were found between foraging activity and sealed brood area as well as bee number (Abou-Shaara et al. 2013). Also, the adaptation of honey bee subspecies to certain environmental conditions may influence the foraging activity (Alqarni 2006). Forager workers of Yemeni and Carniolan honey bee subspecies, under laboratory conditions, showed different abilities to tolerate different temperatures and relative humidity gradients (Abou-Shaara et al. 2012). However, until now only relatively few studies have been performed on honey bee subspecies.

7. Factors impacting foraging activity

There are many factors that can impact foraging activity. These factors can be divided into two major groups: in-colony factors and out-colony factors. The first group (in-colony factors) include: queen presence and case (virgin or mated). Higher foraging activity with less pollen collection was found in colonies headed by virgin queens than colonies headed by mated queens while lower foraging activity and pollen collection were found in queenless colonies than in colonies with a mated or virgin queen (Free et al. 1985b). Also, foraging activity is impacted by colony strength and brood rearing activity (Amdam et al. 2009; Abou-Shaara et al. 2013), and the degree of pollen need (Weidenmuller and Tautz 2002). Beehive type also has an impact on the foraging activity of honey bees (Abou-Shaara et al. 2013). The infection of honey bee foragers with diseases and parasites such as *Nosema* sp. or *Varroa destructor* may result in the inability of foragers to return to their colonies or increased time to return (Kralj and Fuchs 2006; Kralj and Fuchs 2010). The genotype of honey bee strains (e.g. high and low

pollen-hoarding bees) strongly affected foraging behaviour for nectar or for pollen (Pankiw et al. 2002). The inheritance of high pollen-hoarding behaviour is a recessive trait unlike honey storing behaviour, which shows a more dominant pattern (Page et al. 1995). Beside these factors, ovariole number can influence nectar collection by honey bee workers (Siegel et al. 2012).

With regard to out-colony factors, the availability of suitable plant resources has a great impact on foraging activity, and forager bees have a preference for some resources over others (see, preference of honey bees paragraph). Moreover, Fulop and Menzel (2000) found that the reward volume (e.g. sucrose solution or nectar) has an impact on foraging activity and that bees can perceive the amount of reward from the feeding source.

With respect to environmental factors which influence foraging activity, *A. mellifera* bees were observed to commence their foraging activity at ambient temperatures with a mean of 6.57 °C (Tan et al. 2012) while in another study this value was found to be 16 °C (Joshi and Joshi 2010). At ambient temperatures of about 20 °C, the highest activity was recorded (Tan et al. 2012) while at 43 °C the lowest foraging activity was found (Blazyte-Cereskiene et al. 2010) as well as at or below 10 °C (Joshi and Joshi 2010). Further, a significant negative correlation ($r = -0.09$) was found between foraging activity and temperature (Abou-Shaara et al. 2013). Thus, it is expected that foraging activity is influenced passively by elevated temperature as found by Cooper and Schaffer (1985) with pollen foragers. In contrast, relative humidity had less of an effect on flight activity (Joshi and Joshi 2010). Further investigations are required in order to elucidate these phenomena.

It was also found that other environmental factors can have an impact on foraging activity. Collins et al. (1997) found no impact of solar ultraviolet-B (UV-B) on the foraging activity of honey bees on two species of mustard, *Brassica nigra* and *B. rapa* grown under controlled conditions. However, Mattu et al. (2012) reported that altitude influenced foraging commencement and cessation time, duration of foraging activity and trips as well as the number of flowers visited per minute. Further, Sharma and Kumar (2010) found a negative effect of an electromotive field on foraging behaviour. Surprisingly, diesel exhaust can diminish the foraging efficiency of honey bee workers by reducing the ability of worker bees to recognize floral odours (Girling et al. 2013).

Foraging behaviour can also be influenced by natural enemies of honey bees. In the United Kingdom Kirk et al. (1995) found that the pollen beetle *Meligethes aeneus* (Nitidulidae) influenced the foraging behaviour of honey bees on oilseed rape flowers: forager bees preferred fully open flowers without beetles on them. Foraging activity can also be affected by the presence of predators (e.g. hornets) and a reduction in the foraging visits by 55–79% and residence times by 17–33% was previously reported (Tan et al. 2013). Also, the presence of bee-eaters impacted passively on foraging activity (Ali and Taha 2012).

Insecticides may also influence foraging behaviour. Yang et al. (2008) reported effects of sublethal doses of imidacloprid on the foraging behaviour of honey bees which manifested as a delay in their visit to the feeding site. The delay depended on the imidacloprid concentration. Schneider et al. (2012) found a significant reduction in foraging activity as well as longer foraging flights at doses of two neonicotinoid insecticides; 0.5 ng/bee or more for clothianidin and 1.5 ng/bee or more for imidacloprid during the first 3 h after treatment. In contrast, the presence of residues in the nectar and pollen of oilseed rape and maize due to seed treatment with thiamethoxam was reported to represent a low risk to honey bees (Pilling et al. 2013). More investigations on these factors are urgently required especially since neonicotinoids are so widely used.

Other factors may also have an impact on foraging behaviour. For example, foraging distance was found to be affected by the time of year (Steffan-Dewenter and Kuhn 2003; Beekman et al. 2004). Pearce et al. (2013) found no considerable effects of moving beehives from their location to another location as far as 26 km from their original site on honey bee foraging activity. Sushil et al. (2013), meanwhile, found that foragers spent less time in a flower under open conditions than in net house conditions. Brittain et al. (2013) observed alterations in honey bee foraging behaviour in California almond orchards due to the presence of other bee species communities. Picard-Nizou et al. (1995) found no effects of oilseed rape (*Brassica napus* L.) genetically modified by the introduction of a chitinase gene to enhance disease resistance on the foraging behaviour of honey bees (*Apis mellifera* L.). In general, the time of the year, the presence of other bee species and the study conditions should be taken into consideration in study of foraging behaviour. Clearly, moreover, more studies on genetically modified plants are required.

8. Monitoring of foraging activity

Foraging activity is measured by employing different parameters including, the foraging commencement or/and cessation time (Joshi and Joshi 2010; Mattu et al. 2012; Tan et al. 2012); the number of bees returning to the beehive (Beekman et al. 2004; Pernal and Currie 2010; Ali 2011) or leaving beehives (Alqarni 2006) or both (Abou-Shaara et al. 2013); the peak and fluctuations of foraging over time (Malerbo-Souza 2011); foraging speed and foraging distance (Steffan-Dewenter and Kuhn 2003); or estimation of foraging distance by decoding of the waggle dance (Pearce et al. 2013).

Other parameters related to foraging activity and the visiting of plants include, the number of foragers per flower (Sushil et al. 2013); the number of visited flowers per forager (Mattu et al. 2012); and time spent per flower (Sushil et al. 2013); nectar and pollen collection method from the blooms (Mackenzie 1994); the position of the forager bees on or at the side of the flower (Mayer and Lunden 1988; Mattu et al. 2012); the position of visited branches and flowers (Mattu et al. 2012); the proportion of pollen or nectar foragers relative to total foragers; foraging type; the load of pollen and pollen type; concentration of crop nectar sucrose (Pearce et al. 2013); and competition with other pollinators (Mackenzie 1994; Brittain et al. 2013).

Also, some studies monitor foraging activity under net conditions (Sushil et al. 2013). Marking and recapturing forager workers has been used in certain studies (Akinwande and Badejo 2009). Hagler et al. (2011) used self-marking devices for studying the foraging range of honey bees on an alfalfa seed production field. Colin et al. (2004) developed a method to quantify the foraging activity of small colonies of honey bees confined in insect-proof tunnels using video recording. Pollen foraging activity can be monitored with pollen traps (Reyes-Carrillo et al. 2007). In some studies, syrup foraging rate was investigated (e.g. Paleolog 2009). Harmonic radar can also be used in recording the flight paths of foraging honey bee workers (Riley and Smith 2002; Riley et al. 2007). A standard protocol for monitoring foraging behaviour was presented by Scheiner et al. (2013) and other protocols for studying plant pollination by honey bees were reported by Delaplane et al. (2013). However, according to the objectives of a given study, any of the previously mentioned parameters can be used.

During the monitoring of foraging activity there are some important factors that should be taken into consideration including, the equal strength of the studied bee colonies especially the number of brood and pollen frames; the presence of any diseases in the studied colonies; the time of day and year; temperature and relative humidity as well as the presence of bee competitors or predators. Forager bees can be collected from the hive entrance by using forceps in front of the colonies as well as using an aspirator (Yucel and Duman 2005). Also, specific devices (e.g. Bee scan) can be used for counting forager bees (Scheiner et al. 2013).

9. Importance of foraging activity

Beside of the basic importance of foraging activity for honey bee colonies in collecting pollen, nectar, water and resin there are numerous reports of its importance for plant pollination (e.g., Young et al. 2007) especially for plants where honey bees are the primer pollinator. A vast number of species were found to be honey bee-pollinated plants including, highbush blueberry; apple and pears; almonds; Cantaloupe; rape varieties; and others (e.g. Boylan-Pett et al. 1991; Mayer and Lunden 1988; Reyes-Carrillo et al. 2007; Blazyte-Cereskiene et al. 2010). In a study by Sushil et al. (2013) honey bees were found to have a key role in increasing the seed production of three crops: broccoli, kohlrabi and Chinese cabbage. Also, an increase in the seed quality and quantity of onion, *Allium cepa*, cultivar Valencia was found (Yucel and Duman 2005). Mishra et al. (2013) found other benefits besides pollination to be mediated by foragers; namely the deposition of nitrogen (in faeces) on plants during visits. They found about 2.27 to 2.69 g nitrogen per month as the mean production rate of bee frass by a 5000-bee colony. Forager bees also have the ability to distribute certain biocontrol agents including *Erwinia herbicola* Eh252 of fire blight onto apple flowers as well as onto nashi flowers (Cornish et al. 1998). To maximize the benefit of forager bees in spreading biocontrol agents, a new high-performance 'Triwaks' dispenser was developed (Bilu et al. 2004).

The foraging activity of honey bees is very important as a bioindicator for indirect studies of environmental contamination with pesticides (e.g. Balayiannis and Balayiannis 2008). Foraging bees can even be trained using proboscis extension reflex conditioning for the detection of TNT. The foraging activity of honey bees has also been used to help monitor flowering plant

species in an area. Foraging bees can also be used in the identification of pest infestation (e.g. fruit flies; Chamberlain et al. 2012). Beekeepers can benefit from the foraging behaviour of their colonies by fixing pollen traps or venom collection boards in front of hives to collect pollen or bee venom, respectively.

Foraging behaviour also has importance in computer science. It is known that forager bees can select their food sources in an optimal way although many food resources may be available (Thuijsman et al. 1995). Thus, honey bee foraging behaviour and related skills in food scouting and collection (Swarm intelligence) was used in computer science to solve many optimisation problems. Swarm intelligence is currently an important field in Artificial Intelligence (Kumar and Govindaraj 2013). Baig and Rashid (2007) presented an algorithm based on the swarming of honey bees called Honey Bee Foraging (HBF), which they proposed as useful for multimodal and dynamic nature optimisation problems.

10. Disadvantages of foraging activity

Despite the great importance of foraging behaviour there are also some disadvantages associated with this activity. Honey bee foragers are able to transmit the bacteria *Erwinia amylovora*, the cause of fire blight of apple and pears (Keitt 1941). Also, as found by Boylan-Pett et al. (1991) forager bees play a key role in the transmission and spread of pollen-borne blueberry leaf mottle virus (BBLMV). This virus has the ability to remain infectious within honey bee colonies for at least 10 days. Honey bees are not effective pollinators of some plants; for example, Mackenzie (1994) found that bumble bees were better than honey bees in cranberry pollination (*Vaccinium macrocarpon* Ait). Bee-to-bee contact can also result in the transmission of bee parasites from one forager to another. Moreover, honey bees can transmit different mite species from plant to plant or even to their colonies. Foragers can also collect the poisonous pollen of some plant species and subsequently store these pollens in their colonies with harmful consequences for the colony's health.

11. Controlling foraging activity

It has been found that treatment with certain chemicals can enhance foraging activity. Pankiw (2004) found, using a suspended glass plate con-

taining synthetic brood pheromone in isopropanol that colonies treated with this brood pheromone had higher ratios of pollen to non-pollen foragers entering colonies 1 h after the treatment. Mott and Breed (2012) found that bovine insulin treatments increased the threshold of the bees' sucrose response and significantly decreased the age at which foraging activity commenced for winter worker bees and summer nurse bees, respectively. Also, Schulz et al. (2002) found an earlier commencement of foraging in young bees in colonies treated with octopamine. Additionally, the pollination mediated by honey bees, *A. mellifera*, can be improved by the presence of other bee species in the orchards as found by Brittain et al. (2013) in California almond orchards. In addition, the use of modified beehives as demonstrated by Abou-Shaara et al. (2013), can improve foraging activity.

In contrast, Free et al. (1985a) found that treatment of oil-seed rape, field beans and sunflower heads with 2-heptanone and isopentyl acetate (honey bee alarm pheromones) were repellent to honey bee foragers. Kirk et al. (1995) found that the simulation of adult beetles using black spots on flower petals deterred nectar-foraging honey bees from landing on the flowers. Also, certain pesticides are repellent to honey bees.

12. Conclusion

Although the importance of foraging activity is generally recognised, foraging activity in some honey bee subspecies is not yet well elucidated. Further studies are required on both the in-colony and out-colony factors that affect foraging activity. In addition, possible methods for reducing the passive impact of foraging activity on plants and their colonies need to be investigated.

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