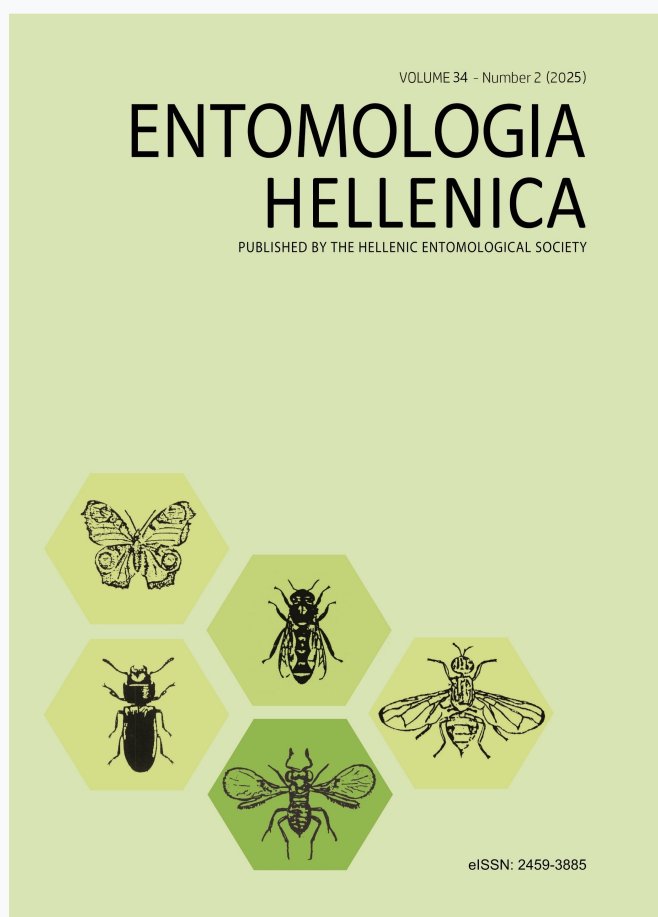


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A mini review on the abiotic factors that disrupt honeybee behavior and impede plant pollination

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ABSTRACT

Honeybees, *Apis mellifera*, play a crucial role in pollinating various plants. During their foraging age, many stressors can directly disrupt their ability to collect food from flowers. These behavioral disruptions can hamper the foragers' ability to perform round trips between the hive and the flowers, and to visit flowers for collecting food, leading to pollination failure. Stressful environments with poor air quality, pesticide contamination, microplastics, high electromagnetic fields, high wind speeds, and temperature extremes can affect foraging round trips and flower visitation ability. Despite the importance of successful flight trips until landing on flowers for pollination, no specific studies have comprehensively discussed these environmental stressors in the light of behavioral disruptions. Therefore, this mini-review considers abiotic stressors with or without human interference that can cause such behavioral disruptions in the context of recent studies, and suggests new avenues for future research, which are crucial for pollination studies and global food security. Understanding pollination failure due to behavioral disruptions in forager honeybees caused by abiotic factors, even when the bees are seemingly healthy, is emphasized. This article provides a synthesis of important bodies of work related to the foraging ecology of honeybees.

KEY WORDS: floral, ecology, pollinators, abiotic, behavior, foraging.

Introduction

Honeybees, *Apis mellifera*, are kept in colonies worldwide for their valuable products and their crucial role in pollination to enhance agricultural production (Paudel et al., 2015; Eeraerts et al., 2020; Fei et al., 2021; Ferenczi et al., 2023). Floral resources serve as the primary food sources for colonies, with the availability of nectar and pollen being essential for their development and survival (Tsuruda et al., 2021; Paray et al.,

2021), and variations in food sources can impact honeybees (Lan et al., 2021). Healthy foragers are expected to visit flowers and successfully collect food, although learning abilities may vary among bees (Tait et al., 2019). The selection of floral resources depends on various factors, including colony strength and requirements for nectar or pollen (Weidenmuller & Tautz, 2002; Amdam et al., 2009; Abou-Shaara et al., 2013). Flower selection is also influenced by factors such as flower shape, odor, color (Kheradmand et

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al., 2020; Mas et al., 2020; Romero-González et al., 2020; Ma et al., 2021; Bisrat & Jung, 2022; Su et al., 2022; Liga et al., 2024), flower position, sugar content, and nectar viscosity (Peter & Johnson, 2008; Horna Lowell et al., 2019; Shi et al., 2020; Cruz et al., 2024).

The decision-making process within a colony may be influenced by the need for pollen and the availability of suitable floral resources (Quinlan et al., 2021). Honeybees can balance their nutrient requirements by adjusting foraging allocation at the colony level and modulating nutrient preferences at the individual level (Hendriksma et al., 2019). A deficiency in essential dietary amino acids can stimulate the collection of more pollen (Bonoan et al., 2020). Furthermore, insufficient storage space within the colony can have a negative impact on foraging activity (Kietzman & Visscher, 2021). The quantity of pollen collected is closely tied to colony strength, which is influenced by the availability and nutritional quality of pollen sources (Ghosh et al., 2020). Physiologically, foragers with a lower metabolic rate tend to visit more flowers compared to those with a higher metabolic rate (Cassano & Naug, 2022). Octopamine (OA) may play a role in regulating pollen and nectar foraging, as providing colonies with OA-treated food can increase the number of pollen foragers (Arenas et al., 2021).

The interaction between flowers and forager bees is highly intricate and can be disrupted by various factors (Abou-Shaara, 2014). Apart from factors that related to bee colonies, this review focuses on forager-flower interactions. The successful pollination of a particular floral resource depends on foragers capable of completing enough round trips (RoT) from hives to flowers (requiring skills such as navigation, learning, and memory) and effectively visiting flowers (VoF) (requiring skills like landing on flowers, spending adequate time per flower, and visiting a suitable number of flowers per foraging trip). Disruptions in these two behavioral sets (RoT and VoF) may arise due to various abiotic factors. Recent studies, particularly those conducted after 2020, have been scrutinized and evaluated concerning their impacts on these be-

haviors, marking a unique approach to comprehending the influence of abiotic factors on the foraging ecology of honeybees. This review focuses exclusively on abiotic factors (e.g., pollutants, climate), excluding biotic factors such as habitat loss. The effects of biotic factors, though significant, have been documented elsewhere, for example, by Abou-Shaara (2025).

Poor air quality

Poor air quality serves as a stress factor for honeybees that can have adverse effects on foragers during their trips, causing disruptions to RoT and VoF. In terms of RoT, urban air pollution containing diesel components can hinder learning and memory in honeybees (Leonard et al., 2019a). Diesel exhaust has been found to modify floral volatiles, negatively impacting the learning abilities (Girling et al., 2013; Lusebrink et al., 2015) and memory of honeybees (Leonard et al., 2019b). However, the revisitation of food resources has not shown alterations following exposure to air pollution from diesel exhaust (Lusebrink et al., 2023). Exposure of foraging bees to carbon dioxide can adversely affect their memory, reducing their ability to return to their colonies (Stec & Kuszewska, 2020). The use of carbon dioxide to narcotize forager bees can lead to negative impacts on homing success (Okubo et al., 2020). Air pollution containing ozone (O₃), originating from both human activities and specific chemical reactions, can also impact honey bee foragers. Elevated levels of ozone can disrupt plant-pollinator interactions, diminishing the honey bees' capacity to respond to floral volatile compounds and affecting their olfactory memory (Agathokleous et al., 2022; Démares et al., 2022; Langford et al., 2023; Démares et al., 2024). Additionally, exposure of honey bees to ozone at field-realistic concentrations has been demonstrated to have negative effects on their memory (Démares et al., 2023). Concerning VoF, the duration of foraging can be adversely affected by airborne particulate matter, indicating poor air quality (Cho et al., 2021). Air pollutants such as ozone and diesel exhaust can lead to a reduction in the number of pollina-

tors visiting flowers (Ryalls et al., 2022). Future studies should delve into the effects of different air pollutants on honeybee foraging abilities to enhance our current understanding. Additionally, poor air quality in terms of ozone and Air Quality Health Index has been linked to the risk of increased honeybee mortality (Coallier et al., 2025), a point that worth consideration together with behavioral changes.

Pesticides

Pesticides can significantly impact bee round trips. Research has shown that the navigation and homing abilities of honeybees can be compromised when exposed to certain pesticides, such as the insecticides imidacloprid (Colin et al., 2019) and sulfoxaflor (Capela et al., 2022). These insecticides have also been linked to other adverse effects, including disruptions in foraging frequencies in bees exposed to imidacloprid (Ohlinger et al., 2022) and a decrease in the number of flights in bees exposed to sulfoxaflor (Barascou et al., 2022). Conversely, the insecticide clothianidin has been found not to impact homing success or flight duration (Tison et al., 2020). Thiamethoxam, another insecticide, has been shown to affect the learning abilities of honey bees (Ludicke & Nieh, 2020; Mustard et al., 2020), leading to inefficient foraging (Mustard et al., 2020). Exposure to the acaricide amitraz and the insecticide thiacloprid can have detrimental effects on the learning and memory of honeybees (Begna & Jung, 2021). Additionally, the herbicide glyphosate has been found to negatively affect the learning processes of foragers (Farina et al., 2019).

Foraging activity can be influenced not only by adult exposure to pesticides but also by larval exposure. Research indicates that exposure to the insecticide clothianidin can reduce foraging activity (Morfin et al., 2019), while the insecticide flupyradifurone does not impact foraging activity but does decrease survival rates (Guo et al., 2021). Glyphosate herbicide has been shown to delay brood development, resulting in adverse effects on foraging behavior (Farina et al., 2019). It appears that insecticides have

received more attention in studies compared to other types of pesticides concerning their effects on the navigation, learning, and memory of forager bees, highlighting the need for further comprehensive research involving various pesticide types.

Microplastics

Microplastics pose a pervasive environmental challenge that also impacts forager bees. Plastic finds its way into beekeeping practices using plastic tools, beehives, microfiber sheets, and various sources of contamination like polluted soil, water, and floral resources (Koelmans et al., 2019; Conti et al., 2020; Rahman et al., 2021; Buteler et al., 2023). Microplastics can infiltrate bee bodies, larvae, wax, and honey via contaminated feeding (Alma et al., 2023). Although microplastics have low acute toxicity to honeybees (Deng et al. 2021; Buteler et al. 2022), they can mildly affecting cognitive abilities (Balzani et al. 2022). Oral exposure to microplastics (including polystyrene, plexiglass, and their combinations) can detrimentally affect the learning and memory of honey bees, with notable consequences observed for polystyrene, where 1-5 μm particles accumulate in the brains of exposed bees after 72 hours of exposure (Pasquini et al., 2023). This evolving research area still lacks comprehensive understanding, particularly concerning the effects of different types of plastic particles on RoT.

Temperature, relative humidity, wind speed, and light

The VoF by bees can be influenced by fluctuations in temperature and relative humidity. For instance, air temperature (up to 27 °C) can impact flower visitation by pollinators, showing a positive correlation between the frequency of honeybee visits to *Megaleranthis saniculifolia* and hourly air temperature (Lee and Kang, 2018). Temperature can positively affect foraging time on oilseed rape while being negatively impacted by relative humidity (Pătruică et al., 2019). Wind speed acts as a limiting factor for successful flower visitation, as increas-

ing wind speed can decrease the number of flowers visited by bees (Hennessy et al., 2020; 2021). Furthermore, flower movement caused by wind can influence the time spent searching for nectar (Hennessy et al., 2020) and handling time (Hennessy et al., 2021). Moreover, a combination of factors such as temperature extremes, precipitation, humidity, and wind strength significantly contribute to honeybee visitation of sunflower hybrid flowers, with optimal conditions being 20-25°C and 65-75% relative humidity, while heavy rainfall and strong winds have negative effects (Puškadija et al., 2007). Similarly, high visitation to watermelon occurs during the early morning when there are low temperatures and high relative humidity, as well as low solar radiation and wind speed (Di Trani et al., 2022). There remains a dearth of comprehensive new studies on the interactions between temperature, relative humidity, wind speed on one side, and flower visitation ability on the other. At the same time, the future challenge of climate change, expected to result in elevated temperatures, may impact the foraging behavior of honeybees. Some studies have predicted adverse effects of climate change on beekeeping (Le Conte & Navajas, 2008; Landaverde et al., 2023; Neumann & Straub, 2023). However, further research on this topic deserves more attention, particularly focusing on the foraging behavior of honeybees.

Natural sunlight and moonlight typically do not have detrimental effects on insect activity and behaviors, unlike solar or lunar eclipses (Juddin et al., 2023). During a partial solar eclipse with a 39% coverage of the solar disk, the round trips of honeybees gradually increased up to the peak of the eclipse, followed by a gradual decrease back to normal levels as the eclipse resolved (Hains & Gamper, 2017). Total solar eclipses can reduce foraging activity without coming to a complete halt, but during a total eclipse of the sun, the homing behavior of honey bees is negatively impacted (Waiker et al., 2019). Such an eclipse can lead to a decrease in sunlight and air temperature by 10-15°C; however, the intensity of light, especially total darkness, can significantly impede flying activity (Galen et al., 2019).

Longer flight durations are also noted during partial eclipses (Galen et al., 2019). Partial solar eclipses can alter the microenvironment of colonies without a corresponding increase in bee flight activity (Choudhary et al., 2021). Given the transient effects of solar eclipses on honeybee activities, long-term impacts on RoT are not anticipated. Nevertheless, further attention is warranted in studies examining variations in sunlight intensity on an hourly, daily, and seasonal basis to understand their implications for honey bee foraging activities.

Electromagnetic and magnetic field

Electromagnetic and magnetic fields have been observed to influence the behavior of various organisms (Toribio et al., 2021; Balmori, 2022), impacting activities such as navigation, mating, and migration (Xu et al., 2017; Dreyer et al., 2018; Odemer & Odemer, 2019). In honeybees, the presence of magnetite in their abdomens allows the detection of changes in magnetic fields (Lambinet et al., 2017). Studies have demonstrated that placing mobile phones in beehives can have a negative impact on the foraging behavior of honeybees (Favre, 2011). Furthermore, fluctuations in magnetic fields have been shown to affect the homing abilities of honeybees (Ferrari, 2014). Research indicates that extremely low frequency electromagnetic fields can modify the learning capabilities of honeybees (Shepherd et al., 2018) and exposure to such fields can lead to disruptive symptoms in honeybee behaviors (Migdal et al., 2022), causing physiological and behavioral changes that disrupt honeybee pollination activities (Molina-Montenegro et al., 2023). The impact of electromagnetic and magnetic fields on RoT in conjunction with other stressors warrants further investigation.

Other factors

The learning and memory of honeybees can be either positively or negatively influenced by exposure to specific factors. Heavy metals can influence honeybee feeding behavior. For instance, the ingestion of lead at cer-

tain concentrations may diminish bees' sensitivity to sucrose, while the ingestion of cadmium and copper did not appear to affect sucrose sensitivity (Burden et al., 2019). Such heavy metals can originate from open dump leachate, which can be considered chronic sources of pollution. Bees may be exposed to these pollutants during their foraging activities. Additionally, compounds like caffeine and tea polyphenols found in nectar typically enhance learning and memory (Gong et al., 2021). Learning can be adversely impacted by high concentrations of ethanol (Black et al., 2021). Certain contaminants like heavy metals and other compounds in nectar can induce detrimental effects on RoT. Our understanding of the impacts of these contaminants on behavioral disruptions in honey bees remains limited.

An overview and outlooks

The presence of apparently healthy honeybee foragers in the field does not ensure successful pollination of plants, as various stressors can impede their ability to conduct fruitful trips to flowers. It appears that the examined abiotic factors can impact skills associated with RoT, such as navigation, learning, and memory, more significantly than those related to VoF – including landing on flowers, spending sufficient time per flower, and visiting an adequate number of flowers per foraging trip. This implies that foraging bees exposed to these stressors may lose their way to the floral resource or back to their colonies, resulting in detrimental outcomes for the colonies such as inadequate food supply and a decline in the adult population. Bees that successfully complete RoT may encounter challenges in VoF due to adverse air temperature, relative humidity, solar radiation, poor air quality, or wind speed. Adverse effects on RoT and VoF can lead to pollination failures by honey bees. The two primary categories of behavioral disruptions outlined in this article can significantly contribute to comprehending the underlying reasons for pollination failures by honeybees.

There are some strategies that can help in mitigating the negative effects of the re-

viewed abiotic factors on bee foraging. Firstly, utilizing modern technology to monitor the foraging behavior of honeybees and assess the effectiveness of pollination represents a crucial approach that merits exploration to proactively anticipate any issues concerning pollination. To accomplish this, the continual advancement of automated monitoring systems (Ngo et al., 2021) and the refinement of detection and tracking algorithms for individual honeybees within wildflower clusters (Ratnayake et al., 2021) should be actively pursued. Secondly, the utilization of geographical information systems and remote sensing can be considered a beneficial strategy to aid in identifying regions suitable for beekeeping activities while avoiding those with elevated levels of contaminants (Abou-Shaara, 2019). Given the significance of the identified behavioral disruptions, it is essential to develop straightforward and cost-effective methodologies to monitor such disruptions in forthcoming research endeavors. This approach will incentivize researchers to conduct more extensive behavioral assessments in their studies. The development of biomarkers to serve as indicators of exposure to stressful environments is crucial. For instance, heat shock proteins like heat shock protein 70 can be employed as stress indicators (Nicewicz et al., 2021; Abou-Shaara, 2024). Early exploration of the exposure of honey foragers to stressful environments can assist in making decisions about relocating beehives to less stressful environments.

One area that requires further investigation to fill the current knowledge gaps is considering the interactions among stressors that contribute to behavioral disruptions in honeybees, as their effects may intersect. For example, the interactions between temperature extremes and exposure to other environmental pollutants like ozone, or between exposure to pesticides and heavy metals, which require further pairwise investigations. Meanwhile, foragers may be exposed to several stressors simultaneously, such as temperature extremes, pesticides, heavy metals, and microplastics, which require further detailed examination in both field and laboratory settings. The repetition of such experiments under various geo-

graphical conditions is strongly encouraged to have a better understanding of how these factors can affect honey bee foraging ecology and plant pollination.

Conclusion

The study underscores two primary behavioral disruptions induced by abiotic factors that can impede successful plant pollination: I) the inability of foragers to complete successful round trips (RoT) between flowers and hives, and II) unsuccessful visitation of flowers (VoF). The concept of utilizing RoT and VoF to evaluate the impact of environmental factors on the foraging ability of honeybees can significantly aid in comprehending the hidden adverse effects on pollination. Unforeseen elements like ozone levels, carbon dioxide, diesel exhaust, solar radiation, and microplastics may contribute to these disruptions. This review stresses that seemingly healthy colonies with ample foragers can not guarantee successful plant pollination due to hidden behavioral disruptions. Consequently, the study strongly advocates for considering the behavioral disruptions of honeybee foragers as a critical stress-related parameter when evaluating the detrimental impacts of abiotic stressors, alongside traditional metrics such as survival rates, longevity, and physiological/genetic biomarkers. The article illustrates how various environmental stressors can interactively influence the dynamic between bees and flowers. Despite the crucial role of pollination in global food security, our understanding of the correlation between behavioral disruptions and pollination failures amid contemporary environmental pollutants and climate change challenges remains insufficient. Thus, further studies on the effects of abiotic factors, either each factor separately or in combination with other factors, on foraging behavior and plant pollination should be considered. Meanwhile, developing strategies that can help in mitigating the negative effects of abiotic stressors on honeybee foragers should be considered.

This can include developing early prediction methods to monitor the exposure of bee foragers to stressors, as well as using satellite image analysis technologies to select suitable foraging areas for honeybees.

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