International Journal of Advanced Biochemistry Research

ISSN Print: 2617-4693
ISSN Online: 2617-4707
IJABR 2024; SP-8(10): 143-149
www.biochemjournal.com
Received: 16-07-2024
Accepted: 19-08-2024

Mounika Jarpla
Department of Entomology, Navsari Agricultural University, Navsari, Gujarat, India

HL Bandhavi
Department of Entomology, Navsari Agricultural University, Navsari, Gujarat, India

Malireddi Prasanna
Department of Entomology, Navsari Agricultural University, Navsari, Gujarat, India

KJ Bhuva
Department of Entomology, Navsari Agricultural University, Navsari, Gujarat, India

AR Prajapati
Department of Entomology, Navsari Agricultural University, Navsari, Gujarat, India

Bhanavathu Sai
Department of Entomology, Navsari Agricultural University, Navsari, Gujarat, India

Corresponding Author:
Mounika Jarpla
Department of Entomology, Navsari Agricultural University, Navsari, Gujarat, India

Role of pheromones and chemical secretion in bees

Mounika Jarpla, HL Bandhavi, Malireddi Prasanna, KJ Bhuva, AR Prajapati and Bhanavathu Sai

DOI: https://doi.org/10.33545/26174693.2024.v8.i10Sb.2427

Abstract
Chemical signals are important in coordinating complex social behaviour within the colony. Pheromones which produced by queens, workers, and larvae, regulate essential colony functions like reproduction, foraging, defense, and communication. Queen pheromones, such as the queen mandibular pheromone (QMP), help maintain colony cohesion, inhibit worker reproduction, and ensure the queen's dominance in the hive. Workers respond to various pheromones to perform tasks such as brood care and hive defense, which are crucial for the colony's survival. Environmental stressors, including pesticides and climate change, affect the production and efficacy of these pheromones, leading to disorganized colony behavior, reduced foraging efficiency, and, in extreme cases, colony collapse. Additionally, pheromones play a key role in hive hygiene by signaling infected brood and promoting disease resistance. The study also explores the potential applications of pheromones in pest management and how synthetic pheromones could be used to enhance agricultural practices.

Keywords: Honey bees, pheromones, colony communication, queen mandibular pheromone, defense, pest control

Introduction

Communication in bees is a vital aspect of their social organization, enabling them to function as highly efficient and cooperative colonies (Seeley, 1989) [51]. Honeybees rely on a combination of physical and chemical communication mechanisms to coordinate their complex social behaviours. Chemical signals primarily pheromones, play a key role in maintaining colony structure and alarm pheromones alerting workers to threats (Schmidt, 2019) [47]. The waggle dance conveys information about the location of distant food sources, while a round dance signals nearby resources (Grüter and Farina, 2009) [18]. Tactile communication through trophallaxis allows bees to exchange food and pheromones, reinforcing social bonds (Sebeok, 1977) [50]. Vibrational signals like the vibration and piping signals help regulate brood care and colony activity (Schneider and Lewis, 2004) [48]. Acoustic cues such as queen piping, are used during swarming or queen replacement (Uthoff *et al.*, 2023) [56]. Together, these methods ensure efficient coordination within the hive.

Hormones in organisms regulate individual physiological processes, while pheromones in superorganisms coordinate group-level behaviors, ensuring social cohesion and survival (Alaux *et al*, 2010) [3]. Both serve as chemical messengers, but at different scales of organization. Pheromones are chemical substances produced and released by bees that trigger specific behavior or physiological response in other members of the colony. It is produced by queens, larvae and workers which regulate colony functions, influencing gene expression, hormones, and behavior (Pham-Delegue *et al.*, 1993; Kocher *et al.*, 2010) [42, 28]. These pheromone levels are dynamic, ensuring the colony adapts to internal and external changes.

Bee swarms locate their queen by fanning their wings to direct pheromones, forming a dynamic communication network. This process involves scenting bees amplifying and propagating the queen signals which guides other bees towards her and maintain a characteristic distance between scenting individuals, ensuring optimal signal transmission. This behavior allows the swarm to solve the challenge of finding the queen efficiently over long distances (Nguyen *et al.*, 2021) [38].

Social and sex pheromones, such as QMP and 9-ODA, are received by antennal olfactory receptor neurons (ORNs), processed in the antennal lobes and modulate gene expression, leading to changes in worker behavior and metabolism (Bortolotti and Costa, 2014) [9].

Pheromones in honey bees influence olfactory learning and memory by modulating appetitive motivation rather than directly altering odor processing. Geraniol enhances, while 2-heptanone impairs, these cognitive processes through their effects on motivational circuits (Baracchi *et al*., 2020) [6]. By understanding the chemical communication in bees provides insights into improving beekeeping techniques and conserving bee population.

Effects of the queen signal

Pheromones that cause immediate behavioural response (Releaser effect) in honey bee where mating occurs in specific areas called drone congregation areas (DCAs), where drones gather in anticipation of a queen. The queen releases a potent pheromone 9-ODA (Oxodecanoic acid) which attracts drones from nearby colonies and drones use a combination of olfactory cues and visual orientation to find the queen. Once in flight, drones chase the queen, and multiple matings take place mid-air. After mating, the queen returns to her hive, while the drones die shortly afterward due to the mating process (Mariette *et al.*, 2021) [35]. Retinue behaviour in bees involves worker bees surrounding the queen, attracted by her pheromones like 9-ODA, coniferyl alcohol (CA), and methyl oleate (MO) to care for and attend to her (Carroll *et al.*, 2023) [12]. Swarm clustering is the aggregation of bees into dense, temporary clusters during the swarming process, a natural reproductive behaviour in which a colony divides and a portion of the bees leave with a queen to establish a new colony (Janson *et al.*, 2005) [24].

Another response is Primer effect where it shows long-term changes in physiology or behaviour triggered by chemical signals from the queen (Conte and Hefetz, 2008) [14]. These effects include Queen rearing where the queen pheromones inhibit the development of new queens by suppressing the growth of larvae into queens. These pheromones suppress ovary development in worker bees, preventing them from laying eggs and enhance various worker bee tasks such as comb building, brood feeding, guarding, and foraging (Bortolotti and Costa, 2014) [9].

Pheromone-secreting glands

Mandibular Gland is situated in the head near the mandibles. In worker bees, this gland secretes compound involved in larval feeding and in the production of alarm pheromones. In queen, these glands are responsible for secreting queen mandibular pheromone (QMP) (Table 1), which plays a critical role in maintaining the colony social structure and inhibiting worker reproduction (Tan *et al.*, 2015) [55]. The biosynthesis pathway of honey bee mandibular gland secretion involves differentially expressed genes with varied expression levels between queen and worker libraries, reflecting their roles in pheromone production (Wu *et al.*, 2017) [62]. Tergal glands are located underneath the abdominal tergites and their ducts open through the cuticle in the tergite posterior edge region. These gland cells in queens are more developed and numerous, aiding in pheromone production, which is crucial for colony regulation (Strachecka *et al.*, 2022) [53]. Dufour's gland is in the sting shaft and is found in queens and workers. Extract contains chemicals that can partially mimic the queen's egg-marking pheromone, reducing the likelihood of worker-laid eggs being removed by the colony (Martin *et al.*, 2005) [36]. The worker repellent pheromone from young virgin queens identified as o-aminoacetophenone causes workers to move away, groom themselves, and stay idle, likely preventing interference in queen fights (Bortolotti and Costa, 2014) [9]. Lopez incera *et al.* (2021) [31] bees exhibit response to alarm pheromones, increasing aggression with rising concentrations but reducing it at very high levels. This behaviour modeled through Projective Simulation, highlights a balance between reacting to genuine threats and avoiding false alarms, optimizing aggression to prevent unnecessary worker loss, especially in environments with low predator density.

Different chemicals secreted by bees that may smell differently to humans such as Isoamyl acetate smell like banana indicates attack, Citral as lemon signals for swarming, heptanone as cheesy smell triggers alarm, and an ODA as undetectable scent from queen bees attracts males. The Nasonov gland is located at the tip of a honey bee abdomen. It releases a pheromone that helps bees orient and gather especially during swarming or when locating the hive (Strachecka *et al.*, 2022) [53]. It also serves as a potential source of death cue (Klett *et al*., 2021b) [27] The worker footprint pheromone secreted from the tarsal glands on bee feet helps to mark the hive entrance. Honey bees secrete beeswax from abdominal glands to build the hive, while venom from the sting gland serves as a defense mechanism. Brood pheromone is vital sign attracts hygienic workers which detect the non-volatile death cue upon direct contact with the brood (Alison Mcafee, 2017) [4]. Insects detect odors through olfactory receptors in their antennae, which activate cellular cascades and generate action potentials upon binding with odorant molecules (Bortolotti and Costa, 2014) [9]. Ma *et al.* (2018) [32] observed that both nurse and forager bees detect BP and EBO, with nurses reacting more strongly, and these pheromones act as global signals influencing the entire colony, potentially as parts of a larval needs.

Factors Affecting Pheromone Communication

Impact of pesticides on pheromone production and reception in honey bees and other pollinators is profound. Many pesticides, especially neonicotinoids and organophosphates, interfere with the neurobiological systems of insects, disrupting their ability to synthesize, release, or detect pheromones (Manzoor and Pervez, 2021, Tasman *et al.*, 2021) [34, 55]. Exposure to sublethal doses of pesticides has been shown to impair these processes, leading to disorganized colony behavior, reduced foraging efficiency, and even a diminished ability to respond to alarm signals (Bartling *et al.*, 2023) [7]. This disruption in chemical communication weakens colony cohesion and can contribute to colony collapse, as bees fail to perform essential tasks or communicate effectively with one another.

Climate change also poses a significant threat to the production and reception of pheromones. Shifts in temperature, humidity, and seasonal patterns affect both the bees and the plants they rely on. Warmer temperature can accelerate the breakdown of pheromone molecules in the environment, shortening their active period and reducing their efficacy (Willmer and Stone, 2004) [60]. Additionally, changes in flowering times and plant-pollinator interactions can lead to misalignment between bees reproductive cycles and the availability of critical resources. The stress caused by extreme weather events, such as heatwaves and droughts, can further affect pheromone production, particularly in queen bees, potentially altering reproductive success and colony health (Przybyla *et al.*, 2021) [44].

Habitat changes including habitat fragmentation, urbanization and agricultural expansion limit the availability of diverse floral resources that are crucial for maintaining bee nutrition and pheromone production. The loss of natural habitats reduces foraging options, which directly affects bees ability to gather the necessary nutrients to support pheromone synthesis (Kendall *et al.,* 2022) [26]. Furthermore, habitat fragmentation can isolate colonies, hindering the exchange of chemical signals between individuals and neighbouring colonies. This isolation weakens genetic diversity and can lead to inbreeding, which further impacts the integrity of pheromone systems (Rodriguez, 2021) [46]. The reduction in floral diversity also impacts the production of specific pheromones linked to foraging and mating behaviors, undermining overall colony resilience.

Applications of Bee Pheromones in Pest Control

Bees themselves are not directly used for pest control, pheromones from bees or bee-related technologies have applications in pest management, particularly in Integrated Pest and Pollinator Management (IPPM) systems (Okosun and Reddy, 2022) [40]. Some pheromones produced by bees, especially alarm pheromones can deter herbivorous pests from damaging crops. when bees perceive a threat, they release an alarm pheromone (like isoamyl acetate) which can signal danger, causing certain pests to avoid those areas. Synthetic pheromones are being used to disrupt the mating patterns of parasitic varroa mites (*Varroa destructor*) (Ziegelmann and Rosenkranz, 2014) [64]. Queen mandibular pheromone (QMP) significantly suppresses early-stage *Nosema ceranae* infections, offering potential for improved honey bee disease management (Huang *et al.,* 2024) [23]. Additionally, *Braula coeca* selects host honey bees using olfactory cues primarily mandibular gland pheromones, favoring workers with higher queen-like pheromone levels. This enhances the lice ability to secure food through trophallaxis (Yusuf *et al.,* 2024) [63].

Pollinators like bees can influence the foraging behavior of natural enemies (parasitic wasps) by interacting with the ecosystem chemical signals. Bee foraging activity or pheromone release might indirectly attract beneficial insects that control pests (Pickett *et al*., 2012) [43]. Synthetic pheromones can be designed to mimic those of pollinators like bees to create pheromone traps for monitoring or mass trapping of pest insects. These traps help reduce pest populations by disrupting mating or catching pests before they can harm crops. The presence of pollinators and the pheromones they release can trigger indirect plant defense mechanisms, such as increased volatile emissions that attract pest predators, helping to naturally reduce pest populations (Bezerra *et al.,* 2021) [8].

Role of pheromones in Hive Hygiene and Disease Resistance

Pheromones are essential for maintaining hive hygiene and promoting disease resistance in honey bee colonies. One of the most important examples is brood pheromones, which are released by larvae and pupae. These pheromones communicate the health status of developing bees to worker bees. When workers detect abnormal brood pheromones, indicating disease or infection, they perform hygienic behaviors such as uncapping cells and removing infected or dead larvae and pupae (Spivak and Gilliam, 1998) [52]. This targeted removal of unhealthy brood helps prevent the spread of diseases like American Foulbrood (AFB) or chalkbrood, making it a key defense mechanism in hive hygiene (Owen *et al.,* 2023) [41]. E-b-ocimene accelerates the behavioral maturation of worker bees, promoting early foraging to optimize food collection and brood care. It also inhibits worker ovary development, maintaining social harmony and productivity within the hive (Maisonnasse *et al.,* 2010) [3].

Queen pheromones particularly the queen mandibular pheromone (QMP), also play a significant role in disease resistance by maintaining colony harmony and encouraging worker bees to engage in hygiene-related tasks. QMP suppresses the development of egg-laying workers, ensuring that the queen remains the sole reproductive individual. This stability allows worker bees to focus on maintaining the health of the colony, including cleaning tasks, brood care, and disease prevention (Hefetz, 2019) [19]. A strong queen with healthy pheromone production can enhance the overall cleanliness of the hive, reducing the likelihood of pathogen outbreaks.

Role in Colony Defense

Bees particularly honeybees (*Apis mellifera*) use pheromones to coordinate their defense response and aggression toward intruders. Bees use pheromones particularly alarm pheromones to coordinate defense and aggressive responses toward intruders (Nouvian *et al.*, 2016) [39]. When a bee senses a threat, it releases these chemical signals to alert and mobilize the rest of the colony. The main pheromone involved in this process is isopentyl acetate (IPA), which is released from the sting gland when a bee stings (Gong *et al.,* 2017) [17]. This pheromone signals nearby bees to become more aggressive and directs them to the source of the threat. Alongside IPA, 2-heptanone, another pheromone released from the mandibular glands which helps reinforce the alert in close proximity to the intruder (Schorkopf *et al.,* 2009) [49]. These pheromones trigger a coordinated attack, with bees rushing toward the threat and stinging it to neutralize the danger.

Guard bees stationed at the hive entrance are particularly sensitive to alarm pheromones and play a critical role in initiating the colony defense. When alarm pheromones are detected, guard bees become more vigilant and aggressive, while foragers and other worker bees are also recruited for defense (Nouvian *et al.,* 2016) [39]. This pheromone-driven coordination ensures that the entire hive can rapidly respond to threats. The aggressive response is modulated based on factors like the colony's strength and the bees age, with older bees typically being more responsive (Kastberger *et al.,* 2009) [25]. These chemical communication systems allow bees to work collectively to protect their hive, providing an evolutionary advantage by quickly neutralizing predators or intruders.

Table 1: Pheromones in Bees, key compound and their role

Type of pheromone	compound	purpose	reference
Queen Mandibular Pheromone (QMP)	9-oxo-2-decenoic acid (9-ODA) 9-hydroxy-2-decenoic acid (9-HDA) methyl p-hydroxybenzoate 4-hydroxy-3-methoxyphenylethanol (HVA)	Maintains colony cohesion, inhibits worker ovary development, and attracts drones for mating	Carroll *et al.*, 2023 [12]; Walsh *et al.*, 2020 [58]
Brood Pheromone	Ethyl linoleate Methyl linolenate Methyl oleate	Stimulates workers to feed larvae, regulate brood care, and modulate foraging behavior	Hu JingHua *et al.*, 2018 [21]
Nasonov Pheromone	Geraniol Citral (neral and geranial) Nerol Farnesol	Used for orientation and recruitment of workers during swarming or foraging	Adams, 2014 [2]; Deshpande and Naik, 2016) [16].
Footprint pheromone or Trail pheromone	alkanes, alkenes, alcohols, organic acids, ethers, esters and aldehydes	to mark paths and guide others toward food sources or nesting sites	Lensky *et al.*, 1987 [30]
Alarm Pheromone	Isoamyl acetate 2-heptanone Octyl acetate Benzyl acetate	Released by guard bees to signal danger and attract other bees to defend the hive	Costa *et al.*, 1996 [15] Collins and Blum, 1982 [13].
Dufour's Gland pheromone	Alkanes Alkenes Esters	Involved in nestmate recognition and marking the brood cells	Wheeler *et al.*, 1985 [59]
worker repellent pheromone	o-aminoacetophenone	Released from young virgin queens which causes workers to stay away, prevent groom interference in queen fights	Bortolotti and Costa, 2014 [9]
Retinue Pheromone	Coniferyl alcohol (CA) Methyl oleate (MO) (E)-9-oxodec-2-enoic acid	Draws workers to attend the queen, enhancing her grooming and feeding	Lan Keeling, 2001 [29]
Drone Attractant Pheromone	9-ODA (also in QMP) 9-HDA	Attracts drones to the queen during mating flights.	Villar and Grozinger, 2017 [57]
Egg Marking Pheromone	Hydrocarbons such as alkanes and alkenes	Allows worker bees todistinguish between queen-laid and worker-laid eggs	Ayasse *et al.*, 1999 [5]
Wax secretion	Hydrocarbons, Palmitic acid, oleic acid, and myristic acid. Myricyl palmitate, 1-Triacontanol and octacosanol	Beeswax gives its strength, flexibility, and hydrophobic properties essential for honeycomb construction.	Buchwald *et al.*, 2009 [10]
Venom secretion	Mellitin, secapin, apamin, tertiapin, adolapin	Cause pain, defend against microbes, and modulate nerve and muscle activity during defense.	Abd El-Wahed *et al.*, 2019 [1]

Techniques to detect pheromones from bees

Detecting bee pheromones require sensitive techniques with Gas Chromatography-Mass Spectrometry (GC-MS) being one of the most used methods. It separates and identifies chemical compounds with high accuracy, though it is slow for real-time monitoring (Hites, 1997) [20]. Another method Electroantennography (EAG), measures the electrical response of a bee antenna to pheromones, providing real-time data specific to what bees can detect, but not quantifying pheromones in the environment (Mas *et al.*, 2020) [37]. Solid-Phase Microextraction (SPME) paired with GC-MS is non-invasive and ideal for field studies, collecting airborne pheromones, though it's less precise in real-time (Wilson *et al.*, 2018) [61]. Artificial Neural Networks (ANNs) handle large datasets from methods like GC-MS or EAG to classify pheromones, although they need extensive training data (Butcher *et al.*, 2013) [11]. Electronic noses (e-Noses), which mimic the olfactory system, provide real-time detection but can be sensitive to environmental conditions (Hu *et al.*, 2019) [22].

An olfactometer is an essential tool for studying how bees respond to pheromones, which are critical for their communication and social organization. This device allows to create controlled environments where bees can be exposed to specific odors while their behaviors are observed and recorded. By analyzing how bees move toward or away from these pheromones, can determine the effectiveness and significance of various chemical signals. Olfactometers can also help validate the biological activity of pheromones identified through chemical analysis methods. (Pham-Delegue *et al.*, 1993; Reichle *et al.*, 2013) [42, 45].

Conclusion

Pheromones play a crucial role in honeybee colony functioning, affecting reproductive control, foraging, defense, and communication. External factors like pesticides and climate change significantly impact pheromone production and reception, potentially leading to colony collapse. Understanding these chemical signals opens opportunities for enhancing pest control and disease management in beekeeping.

Future thrust

Bees rely on a complex communication system, primarily through pheromones, to coordinate activities such as foraging and responding to threats. When signal-sending bees are removed, the colony may struggle to effectively communicate about food sources, potentially disrupting foraging efficiency. Introducing artificial pheromones can either mimic or interfere with natural signals, allowing researchers to study how bees adjust to abnormal cues. Wind interference presents a challenge by dispersing pheromones, making it harder for bees to locate food or alert others to danger. Future studies should focus on how bees react to predators, particularly by analysing alarm pheromone release and mapping neural circuits associated with threat responses. Additionally, understanding how bees balance the risk of predation while foraging can reveal trade-offs, they make between gathering resources and ensuring colony safety.

References

1. Abd El-Wahed AA, Khalifa SA, Sheikh BY, Farag MA, Saeed A, Larik FA, *et al*. Bee venom composition: From chemistry to biological activity. Studies in Natural Products Chemistry. 2019;60:459-484.
2. Adams JA. The effect of Nasonov-based dispensers on honey bee behavior and on pollination in blueberry, apple, and cherry [PhD dissertation]. East Lansing (MI): Michigan State University; c2014.
3. Alaux C, Maisonnasse A, Le Conte Y. Pheromones in a superorganism: from gene to social regulation. Vitamins and Hormones. 2010;83:401-423.
4. McAfee A. Mechanisms of hygienic behavior: It's all about the necromones. American Bee Journal. 2017;157(4):1-9.
5. Ayasse M, Birnbaum J, Tengö J, van Doorn A, Taghizadeh T, Francke W. Caste-and colony-specific chemical signals on eggs of the bumble bee, *Bombus terrestris* L. (Hymenoptera: Apidae). Chemoecology. 1999;9:119-126.
6. Baracchi D, Cabirol A, Devaud JM, Haase A, d'Ettorre P, Giurfa M. Pheromone components affect motivation and induce persistent modulation of associative learning and memory in honey bees. Communications Biology. 2020;3(1):447.
7. Bartling MT, Brandt A, Hollert H, Vilcinskas A. Current insights into sublethal effects of pesticides on insects. International Journal of Molecular Sciences. 2024;25(11):6007.
8. Bezerra RHS, Sousa-Souto L, Santana AEG, Ambrogi BG. Indirect plant defenses: volatile organic compounds and extrafloral nectar. Arthropod-Plant Interactions. 2021;15(4):467-489.
9. Bortolotti L, Costa C. Chemical communication in the honey bee society. Neurobiology of Chemical Communication. 2014;1:585-593.
10. Buchwald R, Breed MD, Bjostad L, Hibbard BE, Greenberg AR. The role of fatty acids in the mechanical properties of beeswax. Apidologie. 2009;40(5):585-594.
11. Butcher JB, Moore HE, Day CR, Adam CD, Drijfhout FP. Artificial neural network analysis of hydrocarbon profiles for the ageing of *Lucilia sericata* for post mortem interval estimation. Forensic Science International. 2013;232(1-3):25-31.
12. Carroll MJ, Brown NJ, Ruetz Z, Ricigliano VA, Anderson KE. Honey bee retinue workers respond similarly to queens despite seasonal differences in Queen Mandibular Pheromone (QMP) signaling. PLOS ONE. 2023;18(9)
13. Collins AM, Blum MS. Bioassay of compounds derived from the honeybee sting. Journal of Chemical Ecology. 1982;8:463-70.
14. Le Conte Y, Hefetz A. Primer pheromones in social hymenoptera. Annual Review of Entomology. 2008;53(1):523-542.
15. Costa H, Talora DC, Palma MS, Chaud-Netto J. Chemical communication in *Apis mellifera*: temporal modulation of alarm behaviors. Journal of Venomous Animals and Toxins. 1996;2:39-45.
16. Deshpande PV, Naik DG. Attractants for Honey Bees. In: Ramawat KG, Mérillon JM, editors. Mutualistic Interactions between Flowering Plants and Animals. Manipal Universal Press; c2016. p. 106.
17. Gong Z, Wang C, Dong S, Zhang X, Wang Y, Hu Z, *et al*. High concentrations of the alarm pheromone component, isopentyl acetate, reduces foraging and dancing in *Apis mellifera Ligustica* and *Apis cerana Cerana*. Journal of Insect Behavior. 2017;30:188-198.
18. Grüter C, Farina WM. The honeybee waggle dance: can we follow the steps?. Trends in Ecology & Evolution. 2009;24(5):242-247.
19. Hefetz A. The critical role of primer pheromones in maintaining insect sociality. Zeitschrift für Naturforschung C. 2019;74(9-10):221-231.
20. Hites RA. Gas chromatography mass spectrometry. In: Settle FA, editor. Handbook of Instrumental Techniques for Analytical Chemistry. Prentice Hall PTR; c1997. p. 609-625.
21. Hu JH, Zhang LZ, Liao CH, Jiang WJ, Zeng ZZ, Yan WY. Effects of mixtures of brood pheromone esters on the reared queen quality of the Chinese honeybee, *Apis cerana cerana* (Hymenoptera: Apidae). Zoological Research. 2018;39(2):112-118.
22. Hu W, Wan L, Jian Y, Ren C, Jin K, Su X, *et al*. Electronic noses: from advanced materials to sensors aided with data processing. Advanced Materials Technologies. 2019;4(2):1800488.
23. Huang WF, Safo-Mensa A, Palmer-Young E, Evans JD, Chen Y. The effects of queen mandibular pheromone on *Nosema* (*Vairimorpha*) *ceranae* infections in caged honey bees. Journal of Invertebrate Pathology. 2024;206:108167.
24. Janson S, Middendorf M, Beekman M. Honeybee swarms: how do scouts guide a swarm of uninformed bees? Animal Behaviour. 2005;70(2):349-358.
25. Kastberger G, Thenius R, Stabentheiner A, Hepburn R. Aggressive and docile colony defence patterns in *Apis mellifera*. A retreater-releaser concept. Journal of Insect Behavior. 2009;22:65-85.
26. Kendall LK, Mola JM, Portman ZM, Cariveau DP, Smith HG, Bartomeus I. The potential and realized foraging movements of bees are differentially determined by body size and sociality. Ecology Letters. 2022;25(10):1935-1947.
27. Klett K, Zhang JJ, Zhang YY, Wang Z, Dong S, Tan K. The Nasonov gland pheromone as a potential source of death cue in *Apis cerana*. Journal of Insect Physiology. 2021;131:104238.
28. Kocher SD, Ayroles JF, Stone EA, Grozinger CM. Individual variation in pheromone response correlates with reproductive traits and brain gene expression in worker honey bees. PLOS ONE. 2010;5(2)
29. Keeling CI. The honey bee (*Apis mellifera* L.) queen retinue [Doctoral dissertation]. Burnaby (Canada): Simon Fraser University; 2001.
30. Lensky Y, Finkel A, Cassier P, Teeshbee A, Schlesinger R. The tarsal glands of honeybee (*Apis mellifera* L.) queens, workers and drones—chemical characterization of footprint secretions. Journal of Insect Physiology. 1987;33(10):849-856.
31. López-Incera A, Nouvian M, Ried K, Müller T, Briegel HJ. Honeybee communication during collective defence is shaped by predation. BMC Biology. 2021;19(1):1-16.

32. Ma R, Villar G, Grozinger CM, Rangel J. Larval pheromones act as colony-wide regulators of collective foraging behavior in honeybees. Behavioral Ecology. 2018;29(5):1132-1141.
33. Maisonnasse A, Lenoir JC, Beslay D, Crauser D, Le Conte Y. E-β-ocimene, a volatile brood pheromone involved in social regulation in the honey bee colony (*Apis mellifera*). PLOS ONE. 2010;5(10)
34. Manzoor F, Pervez M. Pesticide impact on honeybees declines and emerging food security crisis. In: Manzoor F, editor. Global Decline of Insects. Intech Open; c2021. p. 1-13.
35. Mariette J, Carcaud J, Sandoz JC. The neuroethology of olfactory sex communication in the honeybee *Apis mellifera* L. Cell and Tissue Research. 2021;383(1):177-194.
36. Martin SJ, Dils V, Billen J. Morphology of the Dufour gland within the honey bee sting gland complex. Apidologie. 2005;36(4):543-546.
37. Mas F, Horner RM, Brierley S, Butler RC, Suckling DM. Selection of key floral scent compounds from fruit and vegetable crops by honey bees depends on sensory capacity and experience. Journal of Insect Physiology. 2020;121:104002.
38. Nguyen DMT, Iuzzolino ML, Mankel A, Bozek K, Stephens GJ, Peleg O. Flow-mediated olfactory communication in honeybee swarms. Proceedings of the National Academy of Sciences. 2021;118(13)
39. Nouvian M, Reinhard J, Giurfa M. The defensive response of the honeybee *Apis mellifera*. Journal of Experimental Biology. 2016;219(22):3505-3517.
40. Okosun OO, Reddy GV. Holistic management of pollinators and pests: Integrating semiochemicals with on-farm pesticides. Annals of the Entomological Society of America. 2022;115(1):56-68.
41. Owen R, Scheerlinck JP, Stevenson M. Honey Bee Pests and Diseases: A Complete Guide to Prevention and Management. Auckland, New Zealand: Exisle Publishing; c2023.
42. Pham-Delegue MH, Trouiller J, Caillaud CM, Roger B, Masson C. Effect of queen pheromone on worker bees of different ages: behavioural and electrophysiological responses. Apidologie. 1993;24(3):267-281.
43. Pickett JA, Aradottir GI, Birkett MA, Bruce TJ, Chamberlain K, Khan ZR, *et al*. Aspects of insect chemical ecology: exploitation of reception and detection as tools for deception of pests and beneficial insects. Physiological Entomology. 2012;37(1):2-9.
44. Przybyla K, Michez D, Zambra E, Anselmo A, Hennebert E, Rasmont P, Martinet B. Effects of heat stress on mating behavior and colony development in *Bombus terrestris* (Hymenoptera: Apidae). Frontiers in Ecology and Evolution. 2021;9:748405.
45. Reichle C, Aguilar I, Ayasse M, Twele R, Francke W, Jarau S. Learnt information in species-specific 'trail pheromone' communication in stingless bees. Animal Behaviour. 2013;85(1):225-232.
46. Rodriguez M. Review on Honey Bee Colony Collapse: Problems, Consequence and Solutions. International Journal of Science and Research. 2021;10(8):1190-1195.
47. Schmidt JO. Mass action in honey bees: alarm, swarming and the role of releaser pheromones. In: Landolt PJ, Phillips TW, editors. Pheromone Communication in Social Insects. Boca Raton (FL): CRC Press; c2019. p. 257-290.
48. Schneider SS, Lewis LA. The vibration signal, modulatory communication and the organization of labor in honey bees, *Apis mellifera*. Apidologie. 2004;35(2):117-131.
49. Schorkopf DLP, Hrncir M, Mateus S, Zucchi R, Schmidt VM, Barth FG. Mandibular gland secretions of meliponine worker bees: further evidence for their role in interspecific and intraspecific defence and aggression and against their role in food source signalling. Journal of Experimental Biology. 2009;212(8):1153-1162.
50. Sebeok TA. Communication in Social Hymenoptera. In: Sebeok TA, editor. How Animals Communicate. Bloomington (IN): Indiana University Press; c1977. p. 418-471.
51. Seeley TD. The honey bee colony as a superorganism. American Scientist. 1989;77(6):546-553.
52. Spivak M, Gilliam M. Hygienic behaviour of honey bees and its application for control of brood diseases and Varroa: Part II. Studies on hygienic behaviour since the Rothenbuhler era. Bee World. 1998;79(4):169-186.
53. Strachecka A, Chobotow J, Kuszewska K, Olszewski K, Skowronek P, Bryś M, *et al*. Morphology of Nasonov and Tergal Glands in *Apis mellifera* Rebels. Insects. 2022;13(5):401.
54. Tan K, Liu X, Dong S, Wang C, Oldroyd BP. Pheromones affecting ovary activation and ovariole loss in the Asian honey bee *Apis cerana*. Journal of Insect Physiology. 2015;74:25-29.
55. Tasman K, Rands SA, Hodge JJ. The power of *Drosophila melanogaster* for modeling neonicotinoid effects on pollinators and identifying novel mechanisms. Frontiers in Physiology. 2021;12:659440.
56. Uthoff C, Homsi MN, von Bergen M. Acoustic and vibration monitoring of honeybee colonies for beekeeping-relevant aspects of presence of queen bee and swarming. Computers and Electronics in Agriculture. 2023;205:107589.
57. Villar G, Grozinger CM. Primer effects of the honeybee, *Apis mellifera*, queen pheromone 9-ODA on drones. Animal Behaviour. 2017;127:271-279.
58. Walsh EM, Sweet S, Knap A, Ing N, Rangel J. Queen honey bee (*Apis mellifera*) pheromone and reproductive behavior are affected by pesticide exposure during development. Behavioral Ecology and Sociobiology. 2020;74:1-14.
59. Wheeler JW, Shamim MT, Ekpa O, Eickwort GC, Duffield RM. Exocrine secretions of bees: VI. Unsaturated ketones and aliphatic esters in the Dufour's gland secretion of *Dufourea novaeangliae* (Hymenoptera: Halictidae). Journal of Chemical Ecology. 1985;11:353-361.
60. Willmer PG, Stone GN. Behavioral, ecological, and physiological determinants of the activity patterns of bees. Advances in the Study of Behavior. 2004;34:347-366.
61. Wilson AE, Sparks DL, Knott KK, Willard S, Brown A. Implementing solid phase microextraction (SPME) as a tool to detect volatile compounds produced by giant pandas in the environment. PLOS ONE. 2018;13(12).
62. Wu Y, Zheng H, Corona M, Pirk C, Meng F, Zheng Y, *et al*. Comparative transcriptome analysis on the

synthesis pathway of honey bee (*Apis mellifera*) mandibular gland secretions. Scientific Reports. 2017;7(1):4530.
63. Yusuf A, Pirk C, Crewe R. A Hitchhiker's Ride: The Honey Bee Louse *Braula coeca* (Diptera: Braulidae) Selects its Host by Eavesdropping. Journal of Chemical Ecology. 2024;50(1):1-8.
64. Ziegelmann B, Rosenkranz P. Mating disruption of the honeybee mite *Varroa destructor* under laboratory and field conditions. Chemoecology. 2014;24(4):137-144.