

The role of alarm pheromone in honey bee (*Apis mellifera* L.) colonies

Uloga alarmnog feromona u zajednicama medonosne pčele (*Apis mellifera* L.)

Saša PRĐUN (✉)

University of Zagreb Faculty of Agriculture, Department of Fisheries, Apiculture, Wildlife Management and Applied Zoology, Svetošimunska 25, 10000 Zagreb, Croatia

✉ Corresponding author: sprdjun@agr.hr

Received: September 19, 2024; accepted: February 4, 2026

ABSTRACT

The alarm pheromone of honey bees represents a crucial part of their social system and defense mechanisms. When confronted with a threat, worker bees release this chemical signal to alert other members of the community to the danger. The main component of this pheromone is isopentyl acetate, which is released from specialized glands near the stinger of the worker bee. In addition to isopentyl acetate, other compounds such as octyl acetate can enhance the effect of the alarm pheromone. Bees detect the pheromone using specific receptors on their antennae, enabling a rapid and coordinated reaction to danger. Once other bees detect the presence of this pheromone, they become agitated and undertake defensive actions to protect the nest. This may involve increased buzzing, formation of defensive clusters around the hive entrance, and readiness to fight. Besides serving as a warning against external threats, the alarm pheromone can also serve as a means of communication within the community. Worker bees can use this pheromone to inform other colony members of the need for defense or other urgent situations. Understanding the function of the alarm pheromone and the mechanisms of its action is crucial for studying the biology of honey bees. Researching this pheromone also provides deeper insights into the complex social interactions within the bee community and offers insight into the evolutionary processes that have shaped their behavior.

Keywords: alarm, honey bee colony, defense mechanism, *Apis mellifera*

SAŽETAK

Alarmni feromon medonosne pčele predstavlja ključni dio njihovog zadružnog sustava i obrambenih mehanizama. Kada se susretnu s prijetnjom, pčele radilice oslobađaju ovaj kemijski signal kako bi upozorile ostale članove zajednice na opasnost. Glavna komponenta ovog feromona je izopentil acetat, koji se oslobađa iz posebnih žlijezda u blizini žalca pčele radilice. Osim izopentil acetata, i drugi spojevi poput oktil acetata mogu pojačati učinak alarmnog feromona. Pčele detektiraju feromon pomoću specifičnih receptora na svojim antenama, što omogućuje brzu i koordiniranu reakciju na opasnost. Nakon što i druge pčele detektiraju prisutnost ovog feromona one postaju uznemirene i poduzimaju obrambene radnje kako bi zaštitile gnijezdo. Ovo može uključivati pojačano zujanje, formiranje obrambenih skupina oko ulaza u košnicu te spremnost za borbu. Osim što djeluje kao upozorenje na vanjske prijetnje, alarmni feromon također može poslužiti kao sredstvo komunikacije unutar zajednice. Radilice mogu koristiti ovaj feromon kako bi obavijestile ostale članove zajednice o potrebi za obranom ili drugim hitnim situacijama. Razumijevanje funkcije alarmnog feromona i mehanizama njegova djelovanja ključno je za proučavanje biologije medonosnih pčela. Istraživanje ovog feromona omogućuje i dublji uvid u složene socijalne interakcije unutar pčelinje zajednice te pruža uvid u evolucijske procese koji su oblikovali njihovo ponašanje.

Ključne riječi: alarm, pčelinja zajednica, obrambeni mehanizam, *Apis mellifera*

INTRODUCTION

Different species of insects use different strategies in defending themselves from an intruder or predator. The honeybee is the most extensively studied insect species for social behavior (Hunt et al., 2007). The bee colony is recognized as a superorganism, with each individual performing a specific role at various life stages, collectively forming a highly organized system. However, with sociality comes the challenge of coordinating the actions of thousands of bees to efficiently respond to potential threats without significantly depleting the colony's workforce (Rivera-Marchand et al., 2008). The defensive mechanism of the bee colony is crucial for protecting against potential dangers and enemies (López-Incera et al., 2021). The nest contains essential resources such as honey, pollen, brood, the queen, and the bees themselves. These resources must be defended from a range of predators and parasites (Li et al., 2014). Specialized worker bees, known as guards, undertake this task. They adjust their defensive response based on the nature of the threat and environmental conditions, striving to balance effective defense with the need to maintain foraging activities. By releasing alarm pheromones, guard bees can recruit additional workers to assist in repelling large predators (Nouvian et al., 2016). The honeybee colony (*Apis mellifera* L.) employs a combination of physical, chemical, and social strategies for defense. The primary defense mechanism is stinging, which releases a complex blend of over 40 chemical compounds (Free, 1961). The main component, isopentyl acetate, is particularly effective in eliciting a defensive response from other bees (López-Incera et al., 2021). The sting functions as a mechanical barrier and an offensive tool through which venom is injected, causing pain and often deterring or incapacitating intruders. Furthermore, the structural organization of the hive plays a crucial role, as bees cluster densely and deploy guard bees at the hive entrance to prevent the entry of unwanted intruders (Breed et al., 2004). These chemical signals induce both immediate and long-term behavioral changes in nearby bees, preparing them for a coordinated defense. Chemical defenses are based on the production and release

of complex mixtures of pheromones and other bioactive compounds. Alarm pheromones, such as isopentyl acetate and 2-heptanone, act as danger signals that trigger defensive responses among colony members, including aggressive stinging and heightened vigilance. In addition to eliciting threat responses, some of these chemicals possess antimicrobial properties that protect the hive from pathogens and infections (Slessor et al., 1988; Rybak-Chmielewska, 2009). Social defenses encompass coordinated behaviors among colony members, including alarm signaling, recruitment of guard bees, and allogrooming. Grooming behavior helps remove parasites and foreign particles from the bodies of nestmates, enhancing colony hygiene and health (Moore and Wilson, 1997; Wilson-Rich et al., 2009). The complex social communication network ensures rapid dissemination of threat information, enabling a collective and effective response. Together, these integrated defense strategies enhance colony survival by minimizing damage from predators and parasites while maintaining the internal health and cohesion necessary for colony function.

A deeper understanding of the function of alarm pheromones and their role in colony defense is essential for the development of strategies aimed at preserving honeybee populations and supporting sustainable beekeeping practices. Despite significant advances in the study of honeybee defense mechanisms, substantial gaps in knowledge remain, particularly regarding the interactions between alarm pheromones, environmental factors, and colony health. This review aims to provide a comprehensive synthesis of current knowledge, identify unresolved questions, and highlight priorities for future research.

DEFENSE MECHANISM

The honeybee is a social insect that lays large quantities of protein (pollen) and energy resources (honey) in a stock. The division of labor during colony defense in honeybee colonies is a fascinating aspect of their social organization. This division involves individuals of different ages (>7 days of age) and roles within the colony, each contributing to the overall defense effort in various

ways (Winston, 1987). Besides the pollen and the brood, it is the honey that attracts not only robbers like bears, martins, badgers, birds and insects like wasps, moths, ants, but also bees of their own species. The strength of the defensive instinct directly depends on the breed of the bee, as well as on the individual colony. It is well known that African bees are much more aggressive than European honeybee breeds, especially when compared to *Apis mellifera carnica*, which is considered one of the calmest bee breeds in the beekeeping world. Aggressiveness in bees is a highly heritable trait (Guzmán-Novoa et al., 2002; Arechavaleta-Velasco et al., 2003; Ilyasov et al., 2016), and through continuous selection, efforts are being made to reduce this defensive instinct, allowing beekeepers to receive fewer stings when working with bees. This has been demonstrated in the breeding of calmer lines such as Buckfast bees, as well as in programs aimed at reducing the aggressiveness of Africanized hybrids in the Americas. In tests conducted in the UK and Germany, Buckfast lines exhibited a 2- to 5-fold lower number of bees responding to disturbance compared to local *A. m. mellifera* populations (Adam, 1987). For example, in Mexico, selection for lines with lower defensive tendencies led to a significant reduction in the number of bees flying out in response to disturbance and in the number of stings during standardized tests. The heritability of aggressiveness in these hybrids has been estimated at 0.2 to 0.4, indicating that selection can effectively reduce aggression within just a few generations (Guzmán-Novoa and Page, 1994; Guzmán-Novoa et al., 2005). Additionally, Zakour et al. (2020) estimated the heritability of defensive behavior in Italian honey bees (*A. mellifera ligustica*) at 0.36, indicating moderate heritability. Garcia et al. (2013) reported higher heritability estimates for specific defensive traits: 0.71 for the number of stings, 0.86 for time to first sting, and 0.84 for the time to formation of a "heat-ball" reaction, suggesting a strong genetic basis for these traits. Avalos et al. (2020) found heritability of defensive behavior at the colony level to be 0.63, an unusually high value for behavior, indicating that defensive behavior is strongly inherited at the col-

ony level. These variations in heritability estimates collectively demonstrate a significant genetic component to defensive behavior, enabling effective selection for reduced aggressiveness in honey bee colonies. On the other hand, aggressive bees are in demand in some parts of Africa as crop protectors against elephants (Ngama et al., 2016; Cooke et al., 2017; King et al., 2017).

Large predators

In certain areas and at specific times of the year, bee colonies face larger predators. Guard bees respond to various disturbances occurring near the hive, often triggered by sudden movements, foreign intense odors, or dark colors (Free, 1987). In such situations, a few guards will investigate the disturbance and attack by stinging to drive away the threat (Moore et al., 1987; López-Incera et al., 2021). When the colony is attacked by a large mammal seeking brood to meet its protein needs, a strong response from the guards occurs because such predators usually provoke bees with their sudden movements and vibrations, leading to a pronounced defensive mechanism. In this scenario, the bees attempt to drive the intruder as far away from their nest as possible. Other worker bees inside the hive will retract their stingers, raise their abdomens, and flutter their wings to spread the alarm pheromone within the hive (Collins et al., 1980), releasing alarm pheromones produced by their stingers to alert the colony members to the potential threat. Shortly after the alarm pheromone is released, guard bees and worker bees typically emerge at the hive entrance to assess the source of the disturbance and initiate defensive responses. If the threat persists, additional bees will leave the colony to locate and target the intruder, guided by visual cues such as movement and the olfactory trail of the alarm pheromone deposited by guards during their initial stings. This coordinated defense behavior ensures a rapid and effective reaction to potential threats. Not all bees will sting; in fact, the majority will simply dart at the target (Cunard and Breed, 1998; Millor et al., 1999; Wagner and Breed, 2000; López-Incera et al., 2021).

Insects predators

Insects do not cause as much damage to a bee colony as mammals do, but insect attacks on the hive can be ongoing, which may ultimately lead to the collapse of weaker colonies. Ants, wasps, various night moths, wax moths, and similar insects are generally not major threats to bee colonies. However, insects that feed on proteins, such as European hornets (*Vespa crabro*) and the yellow-legged hornet (*V. velutina*), which appeared in 2004 in the southwest part of France (Rortais et al., 2010), and as such pose an additional threat, can seriously disrupt the population of a bee colony. These insects fly near the entrance and hunt adult worker bees as they return to the hive. In such predation, bees are typically powerless to defend their colony because they cannot sting the hornet due to its tough exoskeleton. However, if a hornet does enter the hive, bees have developed a defense mechanism. The initial defensive behavior of bees involves forming large clusters at the hive entrance. The bees gather and try to grab the hornet with their front legs and mandibles. If successful, they quickly trap the hornet inside a dense ball of bees (Baracchi et al., 2010). In this way, several dozen bees encircle the hornet and, by contracting their flight muscles, raise the temperature around the hornet to 44 °C, ultimately killing it (Ken et al., 2005). Indeed, *A. cerana*, which is likely to have coevolved with *V. velutina* exhibits efficient anti-predator behaviours against this hornet species, whereas *A. mellifera* suffers a higher predation rate due to the inefficiency of its defence (Ken et al. 2005; Tan et al. 2007; Monceau et al., 2014). That is why honeybees developed their typical guarding behavior (Stabentheiner et al., 2002). Their ability to produce endothermic heat by means of their flight muscles plays an important role in colony defence (Ono et al., 1995). To defend their colony properly against other bees, guards are thought to need a higher or at least the same motility than the bees examined by them (examinees). The main parameter influencing the motility of honeybees is the thorax temperature. The guard bees are typically older worker bees (3 weeks old) that specialize in guarding the hive entrance, and after this role, they transition into foragers. In addition, the propensity to sting is regulated

by both genetic factors and age, with older bees being more likely to sting (Giray et al., 2000). They patrol the entrance, inspecting incoming bees and other potential intruders (Paxton et al., 1994). The number of guard bees at the hive entrance is relatively small compared to the total colony size, typically representing only a minor fraction of the population. This limited number of guards is sufficient to effectively monitor and defend the hive entrance. Additionally, since guard bees only serve in this role for a few days, their guarding duty typically lasts only one to two days (Moore et al., 1987). When a colony is under attack or if such attacks are recurring, the bee colony usually deploys a greater number of guards at the hive entrance (Arechavaleta-Velasco and Hunt, 2003; Guzman-Novoa et al., 2004). When a foraging bee or a bee from another colony lands at the entrance, the guard bees quickly approach and check whether the bee belongs to their own colony. Their recognition process is based on interpreting chemical signals exchanged between the guard bee and the foraging bee (Dani et al., 2005; Pradella et al., 2015). The task of the guards is thus to compare the chemical profile of incoming bees with that of their own colony. Since the colony odor can change - such as when a new queen takes over or during swarming - guards continuously update their internal template and accept other bees based on their chemical similarity (Breed et al., 2004; d'Ettorre et al., 2006; Nouvian et al., 2016). In cases where a beekeeper transfers frames with bees and comb from one colony to another, there is a sudden mixing of pheromones. Consequently, guard bees adopt the scent directly from the comb, as confirmed by Couvillon et al. (2007). The duration for which a guard bee inspects a bee that has landed at the hive entrance depends on many factors. Stabentheiner et al. (2002) describe that this process usually takes a few seconds but can sometimes last up to half a minute. Guard bees display aggressive behavior towards threats, such as predatory insects or animals, and may engage in defensive maneuvers to protect the colony. While the term "soldier bees" is occasionally used, it is important to note that all worker bees are capable of stinging (Breed et al., 2004). However, some individuals may exhibit

more aggressive behavior and are more likely to engage in stinging attacks against intruders. These bees may also participate in defense outside the hive, attacking threats in the surrounding area.

Although nurse bees and foragers are not directly involved in guarding the colony entrance, their roles are essential for maintaining colony health and resource availability, which indirectly support the colony's defense capabilities. Nurse bees care for the brood and maintain the hive's internal structure, ensuring the colony remains strong and vital. Foragers collect nectar, pollen, and water, providing the necessary resources for colony survival and function. By sustaining the overall well-being and productivity of the colony, these groups enable the guard bees to effectively perform their defensive tasks. The division of labor during colony defense is dynamic and adaptable, with individuals performing roles based on age, experience, and colony needs. This flexibility allows honeybee colonies to balance defense with other vital activities, maintaining cohesion and resilience against threats.

AGGRESSION OF HONEY BEES

Sting apparatus

Aggressive behavior plays a significant role in the fitness of animals, and it is widespread in the animal kingdom. Animals use aggression to defend themselves and their progeny from attack by predators, to fight for females, to feed, and to maintain the social hierarchy (Popova, 2006). The sting apparatus of the honey bee represents a highly specialized defensive system, the morphology of which is the result of evolutionary adaptation to various types of threats, including both invertebrate and vertebrate enemies. It consists of a modified ovipositor, two barbed lancets, and a central stylet, forming a functional unit connected to paired venom glands (Snodgrass, 1956). If a bee stings another bee, she can retrieve her sting without any problem. That later in evolution, animals such as the mammals appeared with tissues from which the sting, with its barbs, could not be extracted was "unpredictable" for bees, and may be seen

instead as an evolutionary "mistake" on their part. Should the sting, with the attached poison gland, small muscles, and nerve cells, be ripped out of the bee, the stinger will die from the massive wound in its abdomen. This morphology represents a clear evolutionary adaptation primarily to interactions with invertebrate antagonists. The fatal consequence for the bee following a sting in a vertebrate is an evolutionary side effect that has not led to the loss of the sting barbs, as their presence provides a collective advantage for colony defense that outweighs the cost at the individual level. The number of bees that lose their lives in this way is, nevertheless, so small that there has been no selection toward a barbless sting. The small muscles of the detached sting system are still highly active and continue to operate the different parts of the sting that move relative to one another. Their barbs drive into the tissue, and an alarm pheromone, released into the air from a gland beneath the sting, rallies the bees' hive comrades to attack (Tautz, 2011).

The functional anatomy of the worker honeybee sting apparatus has been thoroughly analyzed by Ramirez-Esquivel and Ravi (2023). Their research demonstrates that during stinging, the lancets of the sting apparatus alternately move forward and backwards relative to the central stylet, enabling the stinger to penetrate tissue with minimal resistance. During lancet retraction, penetration is believed to be aided by the rearward-facing barbs on the lancets, which anchor into the tissue and allow the remaining components to advance deeper. As the stinger penetrates the tissue, venom is discharged from the canal between the lancets. Only the distal portion of the sting apparatus enters the tissue during stinging. This mechanism reduces the force required for penetration and allows the stinger to embed even in relatively firm tissue, such as vertebrate skin. The extent of penetration appears to be limited by the expansion of the stylet into the bulbous base. Das et al. (2018) report that the stinger of *A. cerana* enters tissue almost perpendicularly and that the total stinger length is 1.62 mm, while Ramirez-Esquivel and Ravi (2023) report an average stinger length of 2.5 mm in *A. mellifera*, with an average penetration depth of 1.3 mm. In human skin, this would be sufficient

for the stinger to pierce the epidermis and inject venom into the underlying dermal layer, but not into the subcutaneous tissue.

These biomechanical properties of the sting apparatus have been evolutionarily optimized for defense under conditions where the honeybee faces various types of attackers. The dynamics of venom injection are also part of this evolved functional adaptation. Once the stinger becomes embedded in tissue, the muscles associated with the sting apparatus continue to autonomously inject venom through pulsatile movements, independently of the bee itself. This process can persist for up to a minute after stinging. Such autonomous activity enables the maximal delivery of venom even when the bee is already dead or immobilized, thereby enhancing the defensive efficiency against vertebrate predators.

In this way, the functional role of the sting apparatus extends beyond morphology to the level of social behavior. Thus, the sting alarm pheromone potentially carries information about the presence and location of a threat, but also about the magnitude of the attack already mounted against it (Lensky et al., 1995; Nouvian et al., 2016). Furthermore, Alaux et al. (2009) and Chandrasekaran et al. (2011) established that there is a transcriptional signature of aggression in the bee brain. These adaptations of the sting apparatus, combined with the coordinated social responses of honey bees, represent a unique example of an evolutionarily shaped defense system, with a clear functional differentiation between vertebrate and invertebrate targets. A systematic presentation of these features is essential to understand how individual behavior and morphology contribute to the collective defense of the colony, and how such mechanisms have been shaped by selective pressures throughout evolution.

Alarm pheromone

Defensive behaviour is partly induced and modulated by pheromones (Trhlin and Rajchard, 2011). If they detect a threat, guard bees can disperse the sting alarm pheromone actively by raising their abdomen, extruding their stinger and fanning their wings. Alternatively, since the sting alarm pheromone is carried on the stinger itself, it is automatically released upon stinging (Wright et al., 2018). The alarm pheromone of honeybees is one of the most crucial communication mechanisms within the hive (Verheggen et al., 2010), particularly for defense and responding to threats. Bees are highly social animals, and their coordination within the colony is vital for survival, leading them to develop complex communication methods. The alarm pheromone is a chemical signal released by bees when they feel threatened or are under attack (Baumann, 2018; Wang and Tang, 2019), with the primary function of mobilizing other colony members to confront the danger collectively.

Typically, the alarm pheromone is emitted through the stinger, especially when a bee stings a threat. When a bee uses its stinger for defense, it simultaneously releases a pheromone with a distinctive odor, often described as a banana-like scent. This pheromone is crucial for activating collective defense, with worker bees taking an active role in protecting the nest or food sources. The pheromone is primarily secreted from specialized glands near the bee's stinger, known as Koschevnikov's glands (Shearer and Boch, 1965; Hunt, 2007; Kannan et al., 2022), and becomes active when the bee uses its stinger in an attack or defense. When a bee stings an intruder, it often sacrifices its life because the barbed stinger remains lodged in the target's skin, leading to the bee's death shortly thereafter. During this attack, the pheromone disperses through the air, marks the predator and signals other bees that there is danger. Nearby bees become agitated and prepare to defend, displaying a collective defensive response (Urlacher et al., 2010). One of the most important aspects of this defensive response is that the pheromone not only mobilizes the bees but also precisely directs their attacks. The scent

of the pheromone is localized at the sting site, allowing other bees to concentrate their attacks on the same target. This synchronized reaction is incredibly effective against predators, especially those that attack the hive directly, such as bears, wasps, or humans. In this way, the pheromone becomes fundamental to the collective intelligence and organized response of the bee colony. In addition to being secreted from the sting, the alarm pheromone in honeybees can also be released from the mandibles (Papachristoforou et al., 2012).

Chemical structure and components of the honeybee alarm pheromone

The chemical composition of alarm pheromones has long been the subject of research. Specific compounds of the pheromone blend vary in their effects on chemotaxis, flying and stinging (Pickett et al., 1982; Wager and Breed, 2000; Hunt, 2007). The alarm pheromone components are usually small in molecular size and have high volatility, so they can reach the receivers fast and are cleared quickly after the disturbance (Kannan et al., 2022). Early studies showed that the main component of honeybee alarm pheromones is isopentyl acetate (Collins et al., 1989; Wagner and Breed, 2000; Akongte et al., 2023), a compound with a sharp, distinctive banana-like odor. However, further research has revealed that this pheromone actually contains a complex mixture of various compounds, including 1-butanol, hexyl acetate, 2-heptanone, and octanol, among others (Lensky and Cassier, 1995; Scheiner et al., 2003; Hunt, 2007; Urlacher et al., 2010). The role of 1-butanol is still not well understood, but it is suggested that it contributes to aggressive behavior in bees when present in high concentrations, especially near the hive. Conversely, 2-heptanone, which was previously known as a component of the bees' pheromonal system, has been shown in recent studies to play a specific role in calming aggression among worker bees (Couvillion et al., 2010; Papachristoforou et al., 2012). It is produced by the mandibular glands of worker bees and mainly consists of volatile compounds, such as alcohols and ketones (Ali and Morgan, 1990), including 2-heptanone. This compound may also act as a warning signal

to cease defensive reactions or reduce aggression when the threat is no longer considered acute. Furthermore, Papachristoforou et al. (2012) in their study investigated the role of 2-heptanone on intruders in the bee community, such as *Varroa destructor* and the greater wax moth (*Galleria mellonella*). These intruders are too small for the bees to sting, so they bite them with their mandibles, releasing a certain amount of 2-heptanone, which then has a short-term paralytic effect. Guard honeybee behaviour was normal at low doses of 2-heptanone, and they noted no other defensive responses, such as stinging behaviour. Although 2-heptanone is traditionally considered an alarm pheromone eliciting defensive behavior in honey bees, its role in grooming behavior has not been directly investigated. Some studies suggest that 2-heptanone may exert different effects depending on its concentration and context. In the study by Collins and Blum (1982), bees exhibited increased sensitivity to electric shocks following exposure to 2-heptanone, indicating its involvement in defensive responses but not necessarily in grooming behavior. Furthermore, Vallet et al. (1991) suggested that 2-heptanone may function as a food-marking pheromone, deterring bees from flowers recently visited and depleted of nectar. This behavior may contribute to more efficient foraging but is not directly linked to grooming behavior among honey bees. Although evidence exists that 2-heptanone plays multiple roles in honey bee behavior, including defense and food marking, there are currently no direct studies confirming its specific role in grooming behavior among worker bees.

Hexyl acetate and octanol have also been identified in alarm pheromone mixtures and are thought to have specific functions in modulating bee behavior. For example, hexyl acetate may act as a secondary signal, enhancing the effect of isopentyl acetate, while octanol may be associated with increasing the bees' sensitivity to other chemical signals (Collins and Blum, 1983; Wang and Tan, 2019). It can be concluded that this mixture of chemical signals acts synergistically, creating a complex effect that can have different functions depending on the context. One of the important functions is distinguishing be-

tween types of threats. For example, bees may respond differently to threats from small predators like wasps compared to larger predators like various mammals. The combination of specific chemical compounds can signal different levels of danger and cause varying degrees of aggression among the bees. Additionally, the presence of other types of pheromones within the colony, such as those produced by the queen, can modulate the intensity of the bees' response to the alarm pheromone. Depending on the intensity of the attack and the size of the predator attacking them, honeybees can release the mandibular alarm pheromone to defend against other insects, as compared to releasing the sting alarm pheromone to defend against predators, such as different mammals (Millor et al., 1999; Bortolotti and Costa, 2014). These pheromones sometimes also occur in tandem with the secretion of the same or different glands, thus exhibiting a combined attack force in their alarm-defense system.

BEHAVIOR AND ROLE IN THE ECOSYSTEM

The behavior of bees in the presence of alarm pheromones has been extensively studied through ethological experiments. When bees detect the pheromone, they become agitated, raise their abdomens to expose their stingers, and show an increased propensity to attack. Interestingly, not all bees are equally sensitive to the pheromone. Guard bees, which are responsible for defending the hive, react most aggressively, while younger bees performing tasks inside the hive do not exhibit the same level of agitation. Alarm pheromones also play an important role outside the hive (Wang and Tan, 2019). Foraging bees may encounter predators during their activities away from the nest. If a predator attacks while a bee is foraging, the pheromone is released and signals the presence of danger to nearby bees. This form of communication allows for rapid and effective protection of other colony members and contributes to reducing the risk for plant pollination. An intriguing aspect of the role of alarm pheromones is their interaction with plants. There is evidence that some plant species have evolved to mimic the chemical signals of bee pheromones. This

phenomenon, known as chemical mimicry, allows plants to attract pollinators or even their predators to enhance pollination. For example, certain orchid species produce scents that mimic bee pheromones to attract male bees (Schiestl and Cozzolino, 2008), thus ensuring pollination without rewarding the bee with nectar. This strategy illustrates how bee alarm pheromones have become a significant factor in the co-evolution of plants and their pollinators.

Evolutionary adaptation

Considering that pheromones are chemical signals that have evolved over millions of years, they represent one of the oldest forms of communication in the animal kingdom (Free, 1987; Bortolotti and Costa, 2014). Evolutionary pressures that shaped the function of alarm pheromones in bees can be viewed through predator-prey relationships. Bees that developed more sophisticated warning and collective defense systems had a greater chance of survival and of ensuring offspring. As a result, alarm pheromones have become one of the key factors in the evolutionary success of honeybees. On the other hand, bee predators, such as wasps or birds, have also developed adaptations that help them avoid or suppress the bees' response to alarm pheromones. Some predators have learned to recognize the scent of the pheromone and quickly leave the area to avoid attack, while others have developed resistance to bee stings or even specific tactics for attacking hives.

Defensive mechanisms and the use of alarm pheromones in honeybees are the result of long-term evolution of social behavior and chemical communication within the colony. As social insects with a complex hierarchy, honeybees have developed sophisticated ways to detect and respond to threats that endanger the survival of the community. Evolutionary pressures, such as the presence of numerous predators and competition for resources, have driven the development of pheromone systems as a fast and efficient means of warning and coordinating defense. Alarm pheromones enable bees to trigger protective behavior almost instantly, thereby increasing the survival of the colony. Collins et al. (1980),

Free (1987), Winston (1987), and Koeniger et al. (2010) report that different species and subspecies of *Apis* exhibit variations in the chemical composition and strength of alarm pheromones, reflecting adaptations to local conditions and specific threats. This variability may be key to understanding how defensive mechanisms have evolved in different ecological niches. Furthermore, the evolution of defensive mechanisms also involves the development of a complex division of labor, where different groups of bees (guards, workers, foragers) have specific roles in maintaining and protecting the colony. This division allows the colony to be flexible and efficient in facing changing threats. Understanding the evolutionary background of these mechanisms not only enriches our knowledge of honeybee behavior but may also have practical implications for beekeeping and the conservation of bees in changing environmental conditions.

CONCLUSION

The defensive mechanisms of the bee colony, combined with alarm pheromones, are a highly effective means of defense against various predators. The bee colony is an organized system that reacts strongly to external and/or internal signals when they pose a direct threat to the hive. Overall, the division of labor during colony defense is dynamic and adaptable, with individuals taking on different roles based on their age, experience, and the current needs of the colony. This flexible system allows honeybee colonies to effectively protect themselves against a wide range of threats while maintaining their productivity and cohesion as a social unit. As research advances at the molecular, behavioral, and ecological levels, we are getting closer to a deeper understanding of how bee alarm pheromones contribute to the stability and sustainability of natural systems.

REFERENCES

- Adam, B. (1987) Search of the Best Strains of Bees. Hebden Bridge, UK: Northern Bee Books.
- Akongte, P. N., Park, B. S., Kim, D. W., Choi, Y. S. (2023) Honey Bee Colonies (*Apis mellifera* L.) Perform Orientation Defensiveness That Varies among Bred Lines. *Insects*, 14, 546. DOI: <https://doi.org/10.3390/insects14060546>
- Alaux, C., Sinha, S., Hasadsri, L., Hunt, G. J., Guzman-Novoa, E., De Grandi-Hoffman, G., Uribe-Rubio, J. L., Southey, B. R., Rodriguez-Zas, S., Robinson, G. E. (2009) Honey bee aggression supports a link between gene regulation and behavioral evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 15400-15405. DOI: <https://doi.org/10.1073/pnas.0907043106>
- Ali, M. F., Morgan, E. D. (1990) Chemical communication in insect communities: A guide to insect pheromones with special emphasis on social insects. *Biological Reviews*, 65, 227-247. DOI: <https://doi.org/10.1111/j.1469-185X.1990.tb01425.x>
- Arechavaleta-Velasco, M. E., Hunt, G. J. (2003) Genotypic variation in the expression of guarding behavior and the role of guards in the defensive response of honey bee colonies. *Apidologie*, 34, 439-447. DOI: <https://doi.org/10.1051/apido:2003028>
- Avalos, A., Fang, M., Pan, H., Ramirez Lluch, A., Lipka, A. E., Zhao, S. D., Giray, T., Robinson, G. E., Zhang, G., Hudson, M. E. (2020) Genomic regions influencing aggressive behavior in honey bees are defined by colony allele frequencies. *Proceedings of the National Academy of Sciences of the United States of America*, 117 (29), 17135-17141. DOI: <https://doi.org/10.1073/pnas.1922927117>
- Avalos, A., Rodríguez-Cruz, Y., Giray, T. (2014) Individual responsiveness to shock and colony-level aggression in honey bees: evidence for a genetic component. *Behavioral Ecology and Sociobiology*, 68, 761-771. DOI: <https://doi.org/10.1007/s00265-014-1689-8>
- Baracchi, D., Cusseau, G., Pradella, D., Turillazzi, S. (2010) Defence reactions of *Apis mellifera ligustica* against attacks from the European hornet *Vespa crabro*. *Ethology Ecology & Evolution*, 22, 281-294. DOI: <https://doi.org/10.1080/03949370.2010.502323>
- Baumann, K., Vicenzi, E. P., Lam, T., Douglas, J., Arbuckle, K., Cribb, B., Brady, S.G., Fry, B.G. (2018) Harden up: Metal acquisition in the weaponized ovipositors of aculeate hymenoptera. *Zoomorphology*, 137, 389-406. DOI: <https://doi.org/10.1007/s00435-018-0403-1>
- Bortolotti L, Costa C. (2014) Chemical Communication in the Honey Bee Society. In: Mucignat-Caretta C, ed. *Neurobiology of Chemical Communication*. Boca Raton (FL): CRC Press/Taylor & Francis. Chapter 5. Available at: <https://www.ncbi.nlm.nih.gov/books/NBK200983/>
- Breed, M. D., Diaz, P. H., Lucero, K. D. (2004) Olfactory information processing in honeybee, *Apis mellifera*, nestmate recognition. *Animal Behavior*, 68, 921-928. DOI: <https://doi.org/10.1016/j.anbehav.2003.10.033>
- Breed, M. D., Guzmán-Novoa, E., Hunt, G. J. (2004) Defensive behavior of honey bees: organization, genetics, and comparisons with other bees. *Annual Review of Entomology* 49, 271-298. DOI: <https://doi.org/10.1146/annurev.ento.49.061802.123155>
- Chandrasekaran, S., Ament, S. A., Eddy, J. A., Rodriguez-Zas, S. L., Schatz, B. R., Price, N. D., Robinson, G. E. (2011) Behavior-specific changes in transcriptional modules lead to distinct and predictable neurogenomic states. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 18020-18025. DOI: <https://doi.org/10.1073/pnas.1114093108>
- Collins, A. M., Blum, M. S. (1982) Bioassay of compounds derived from the honeybee sting. *Journal of Chemical Ecology*, 8, 463-470. DOI: <https://doi.org/10.1007/BF00987794>
- Collins, A. M., Rinderer, T. E., Daly, H. V. (1989) Alarm pheromone production by two honey bee (*Apis mellifera*) types. *Journal of Chemical Ecology*, 15, 1747-1756. DOI: <https://doi.org/10.1007/BF01012262>

PRĐUN: The role of alarm pheromone in honey bee (*Apis mellifera* L.) colonies...

- Collins, A. M., Rinderer, T. E., Tucker, K. W., Sylvester, H. A., Lockett, J. J. (1980) A model of honeybee defensive behavior. *Journal of Apicultural Research*, 19, 224-231.
DOI: <https://doi.org/10.1080/00218839.1980.11100029>
- Cook, R. M., Parrini, F., King, L. E., Witowski, E. T. F., Henley, M. D. (2017) African honeybees as a mitigation method for elephant impact on trees. *Biology Conservation*, 217, 329-336.
DOI: <https://doi.org/10.1016/j.biocon.2017.11.024>
- Couvillon, J. M., Barton N., S., Cohe, A. J., Fabricius K. O., Karcher, H. M., Cooper, L. S., Silk, M. J., Helanterä, H., Ratnieks, F. L. (2010) Alarm pheromones do not mediate rapid shifts in honeybee guard acceptance threshold. *Journal of Chemical Ecology*, 36: 1306-1308.
DOI: <https://doi.org/10.1007/s10886-010-9881-4>
- Couvillon, J. M., Caple, J. P., Endsor, S. L., Karcher, M., Russell, T. E., Storey, D. E., Ratnieks, F. L. (2007) Nest-mate recognition template of guard honeybees (*Apis mellifera*) is modified by wax comb transfer. *Biology Letters*, 3, 228-230.
DOI: <https://doi.org/10.1098/rsbl.2006.0612>
- Cunard, S. J., Breed, M. D. (1998) Post-stinging behaviour of worker honey bees (Hymenoptera: Apidae). *Annals of the Entomological Society of America*, 91, 754-757.
DOI: <https://doi.org/10.1093/aesa/91.5.754>
- Dani, F. R., Jones, G. R., Corsi, S., Beard, R., Pradella, D., Turillazzi, S. (2005) Nestmate recognition cues in the honey bee: differential importance of cuticular alkanes and alkenes. *Chemical Senses*, 30, 477-489. DOI: <https://doi.org/10.1093/chemse/bjj040>
- Das, R., Yadav, R.N., Sihota, P., Uniyal, P., Kumar, N., Bhushan, B. (2018) Biomechanical Evaluation of Wasp and Honeybee Stingers. *Scientific Reports*, 8, 14945.
DOI: <https://doi.org/10.1038/s41598-018-33386-y>
- d'Etorre, P., Wenseleers, T., Dawson, J., Hutchinson, S., Boswell, T., Ratnieks, F. L. W. (2006) Wax combs mediate nestmate recognition by guard honeybees. *Animal Behavior*, 71, 773-779.
DOI: <https://doi.org/10.1016/j.anbehav.2005.05.014>
- Free, J. B. (1961) The stimuli releasing the stinging response of honeybees. *Animal Behaviour*, 9, 193-196.
DOI: [https://doi.org/10.1016/0003-3472\(61\)90008-2](https://doi.org/10.1016/0003-3472(61)90008-2)
- Free, J. B. (1987) Pheromones of social bees. Chapman and Hall. London, UK, pp 218
- Garcia, R. C., Oliveira, N. T. E. D., Camargo, S. C., Pires, B. G., Oliveira, C. A. L. D., Teixeira, R. D. A., Pickler, M. A. (2013) Honey and propolis production, hygiene and defense behaviors of two generations of Africanized honey bees. *Scientia Agricola*, 66 (1), 74-81.
DOI: <https://doi.org/10.1590/S0103-90162013000200003>
- Giray, T., Guzman-Novoa, E., Aron, C. W., Zelinsky, B., Fahrbach, S. E., Robinson, G. E. (2000) Genetic variation in worker temporal polyethism and colony defensiveness in the honey bee, *Apis mellifera*. *Behavioral Ecology*, 11, 44-55.
DOI: <https://doi.org/10.1093/beheco/11.1.44>
- Guzman-Novoa, E., Hunt, G. J., Page, R. E. Jr., Uribe-Rubio, J. L., Prieto-Merlos, D., Becerra-Guzman, F. (2005) Paternal effects on the defensive behavior of honeybees. *Journal of Heredity*, 96 (4), 376-80. DOI: <https://doi.org/10.1093/jhered/esi038>
- Guzmán-Novoa, E., Hunt, G. J., Uribe, J. L., Smith, C., Arechavala-Velasco, M. E. (2002) Confirmation of QTL effects and evidence of genetic dominance of honey bee defensive behavior: Results of colony and individual behavioral assays. *Behavioral Genetics*, 32, 95-102. DOI: <https://doi.org/10.1023/A:1015245605670>
- Guzman-Novoa, E., Hunt, G. J., Uribe-Rubio, J. L., Prieto-Merlos, D. (2004) Genotypic effects of honey bee (*Apis mellifera*) defensive behavior at the individual and colony levels: the relationship of guarding, pursuing and stinging. *Apidologie* 35, 15-24.
DOI: <https://doi.org/10.1051/apido:2003061>
- Guzmán-Novoa, E., Page, R. E. (1994) The impact of Africanized bees on Mexican beekeeping. *American Bee Journal*, 134 (12), 845-848.
- Hunt, G. J. (2007) Flight and fight: a comparative view of the neurophysiology and genetics of honey bee defensive behavior. *Journal of Insect Physiology*, 53, 399-410.
DOI: <https://doi.org/10.1016/j.jinsphys.2007.01.010>
- Ilyasov, R. A., Poskryakov, A. V., Petukhov, A. V., Nikolenko, A. G. (2016) Molecular genetic analysis of five extant reserves of black honeybee *Apis mellifera mellifera* in the Urals and the Volga region. *Russian Journal of Genetics*, 52, 828-839.
DOI: <https://doi.org/10.1134/S1022795416060053>
- Kannan, K., Galizia, C. G., Nouvian, M. (2022) Olfactory Strategies in the Defensive Behaviour of Insects, 13, 470.
DOI: <https://doi.org/10.3390/insects13050470>
- Ken, T., Hepburn, H. R., Radloff, S. E., Yusheng, Y., Yiqiu, L., Danyin, Z., Neumann, P. (2005) Heat-balling wasps by honeybees. *Naturwissenschaften*, 92, 492-495.
DOI: <https://doi.org/10.1007/s00114-005-0026-5>
- King, L. E., Lala, F., Nzumu, H., Mwambingu, E., Douglashamilton, I. (2017) Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conservation Biology*, 31, 743-752. DOI: <https://doi.org/10.1111/cobi.12898>
- Lensky, Y., Cassier, P. (1995) The Alarm Pheromones of Queen and Worker Honey Bees, *Bee World*, 76, 3, 119-129.
DOI: <https://dx.doi.org/10.1080/0005772X.1995.11099258>
- Lensky, Y., Cassier, P., Tel-Zur, D. (1995) The setaceous membrane of honey bee (*Apis mellifera* L.) workers' sting apparatus: structure and alarm pheromone distribution. *Journal of Insect Physiology*, 41 (7), 589-595. DOI: [https://doi.org/10.1016/0022-1910\(95\)00007-H](https://doi.org/10.1016/0022-1910(95)00007-H)
- Li, J., Wang, Z., Tan, K., Qu, Y., Nieh, J.C. (2014) Giant Asian honeybees use olfactory eavesdropping to detect and avoid ant predators. *Animal Behavior*, 97, 69-76.
DOI: <https://doi.org/10.1016/j.anbehav.2014.08.015>
- López-Incera, A., Nouvian, M., Ried, K., Mueller, T., Briegel, H. (2021) Honeybee communication during collective defence is shaped by predation. *BMC Biology*, 19 (106), 1-16.
DOI: <https://doi.org/10.1186/s12915-021-01028-x>
- Millor, J., Pham-Delegue, M., Deneubourg, J. L., Camazine, S. (1999) Self-organized defensive behavior in honeybees. *Proceedings of the National Academy of Sciences*, 96, 12611-12615.
DOI: <https://doi.org/10.1073/pnas.96.22.12611>
- Monceau, K., Bonnard, O., Thiéry, D. (2014) *Vespa velutina*: a new invasive predator of honeybees in Europe. *Journal of Pest Science*, 87, 1-16. DOI: <https://doi.org/10.1007/s10340-013-0537-3>
- Moore, A. J., Breed, M. D., Moor, M. J. (1987) The guard honey bee: ontogeny and behavioral variability of workers performing a specialized task. *Animal Behavior*, 35, 1159-1167.
DOI: [https://doi.org/10.1016/S0003-3472\(87\)80172-0](https://doi.org/10.1016/S0003-3472(87)80172-0)
- Moore, D., Wilson, M. E. (1997) Parasite-induced changes in honey bee (*Apis mellifera*) grooming behaviour. *Behavioural Processes*, 41 (3), 271-278. DOI: [https://doi.org/10.1016/S0376-6357\(97\)00061-0](https://doi.org/10.1016/S0376-6357(97)00061-0)
- Ngama, S., Korte, L., Bindelle, J., Vermeulen, C., Poulsen, J. R. (2016) How bees deter elephants: Beehive trials with forest elephants (*Loxodonta africanaclyotis*) in Gabon. *PLoS ONE*, 11, e0155690.
DOI: <https://doi.org/10.1371/journal.pone.0155690>

- Nouvian, M., Reinhard, J., Giurfa, M. (2016) The defensive response of the honeybee. *Journal of experimental biology*, 219 (22), 3505–3517. DOI: <https://doi.org/10.1242/jeb.143016>
- Ono, M., Igarashi, T., Ohno, E., Sasaki, M. (1995) Unusual thermal defence by a honeybee against mass attack by hornets. *Nature*, 377, 334–336. DOI: <https://doi.org/10.1038/377334a0>
- Papachristoforou, A., Kagiava, A., Papaefthimiou, C., Termentzi, A., Fokialakis, N., Skaltounis, A., L., Watkins, M., Arnold, G., Theophilidis, G. (2012) The Bite of the Honeybee: 2-Heptanone Secreted from Honeybee Mandibles during a Bite Acts as a Local Anaesthetic in Insects and Mammals. *PLoS ONE*, 7 (10), e47432. DOI: <https://doi.org/10.1371/journal.pone.0047432>
- Paxton, R. J., Sakamoto, C. H., Rugiga, F. C. N. (1994) Modification of honey bee (*Apis mellifera* L.) stinging behavior by within-colony environment and age. *Journal of Apicultural Research*, 33, 75–82. DOI: <https://doi.org/10.1080/00218839.1994.11100853>
- Pickett, J. A., Williams, I. H., Martin, A. P. (1982) (Z)-11-eicosen-1-ol, an important new pheromonal component from the sting of the honey bee, *Apis mellifera* L. (Hymenoptera, Apidae). *Journal of Chemical Ecology*, 8, 163–175. DOI: <https://doi.org/10.1007/BF00984013>
- Popova, N. K. (2006) From genes to aggressive behavior: the role of serotonergic system. *Bioessays*, 28, 495–503. DOI: <https://doi.org/10.1002/bies.20412>
- Pradella, D., Martin, S. J., Dani, F. R. (2015) Using errors by guard honeybees (*Apis mellifera*) to gain new insights into nestmate recognition signals. *Chemical Senses*, 40, 649–653. DOI: <https://doi.org/10.1093/chemse/bjv053>
- Ramirez-Esquivel, F., Ravi, S. (2023) Functional anatomy of the worker honeybee stinger (*Apis mellifera*). *iScience* 26, 107103. DOI: <https://doi.org/10.1016/j.isci.2023.107103>
- Rortais, A., Villemant, C., Gargominy, O., Rome, Q., Haxaire, J., Papachristoforou, A., Arnold, G. (2010) A new enemy of honeybees in Europe: the Asian hornet *Vespa velutina*. In: Settele, J., ed. *Atlas of biodiversity risks—from Europe to the globe, from stories to maps*. Pensoft, Sofia, p. 11
- Rybak-Chmielewska, H. (2009) Chemical compounds of the honeybee sting and their role in defence. *Apidologie*, 40 (3), 325–334. DOI: <https://doi.org/10.1051/apido/2009033>
- Scheiner, R., Pluckhahn, S., Oney, B., Blenau, W., Erber, J. (2002) Behavioural pharmacology of octopamine, tyramine and dopamine in honey bees. *Behavioural Brain Research*, 136, 2, 545–553. DOI: [https://doi.org/10.1016/S0166-4328\(02\)00205-X](https://doi.org/10.1016/S0166-4328(02)00205-X)
- Schiestl, F. P., Cozzolino, S. (2008) Evolution of sexual mimicry in the orchid subtribe orchidinae: the role of preadaptations in the attraction of male bees as pollinators. *BMC Evolutionary Biology*, 8, 27. DOI: <https://doi.org/10.1186/1471-2148-8-27>
- Shearer, D., Boch, R. (1965) 2-Heptanone in the mandibular gland secretion of the honey-bee. *Nature*, 205, 530. DOI: <https://doi.org/10.1038/206530a0>
- Slessor, K. N., Kaminski, L. A., King, G. G., Borden, J. H. (1988) Semiochemical basis of the alarm pheromone in honeybees. *Nature*, 332, 6160, 651–652. DOI: <https://doi.org/10.1038/332651a0>
- Snodgrass, R. E. (1956) *Anatomy of the honey bee*. Ithaca: Cornell University Press.
- Stabentheiner, A., Kovac, H., Schmaranzer, S. (2002) Honeybee nestmate recognition: the thermal behaviour of guards and their examinees. *The Journal of Experimental Biology*, 205, 2637–2642.
- Tan, K., Radloff, S.E., Li, J.J., Hepburn, H.R., Yang, M.X., Zhang, L.J., Neumann, P. (2007) Bee-hawking by the wasp, *Vespa velutina*, on the honeybees *Apis cerana* and *A. mellifera*. *Naturwissenschaften* 94:469–472. DOI: <https://doi.org/10.1007/s00114-006-0210-2>
- Tautz, J. (2011) *The buzz about bees. Biology of a superorganism*. Berlin, Spektrum Akademischer Verlag, Springer.
- Trhlin, M., Rajchard, J. (2011) Chemical communication in the honeybee (*Apis mellifera* L.): a review. *Veterinarni Medicina*, 56, 6, 265–273. DOI: <https://doi.org/10.17221/1543-VETMED>
- Urlacher, E., Francés, B., Giurfa, M., Devaud, J. M. (2010) An alarm pheromone modulates appetitive olfactory learning in the honeybee (*Apis mellifera*). *Frontiers in Behavioral Neuroscience*, 4, 157. DOI: <https://doi.org/10.3389/fnbeh.2010.00157>
- Vallet, A., Cassier, P., Lensky, Y. (1991) Ontogeny of the fine structure of the mandibular glands of the honeybee (*Apis mellifera* L.) workers and the pheromonal activity of 2-heptanone. *Journal of Insect Physiology*, 37, 11, 789–804. DOI: [https://doi.org/10.1016/0022-1910\(91\)90076-C](https://doi.org/10.1016/0022-1910(91)90076-C)
- Wager, B. R., Breed, M. D. (2000) Does honey bee sting alarm pheromone give orientation information to defensive bees? *Annals of the Entomological Society of America*, 93, 1329–1332. DOI: [https://doi.org/10.1603/0013-8746\(2000\)093\[1329:DHBSAP\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[1329:DHBSAP]2.0.CO;2)
- Wang, Z., Tan, K. (2019) Honey Bee Alarm Pheromone Mediates Communication in Plant–Pollinator–Predator Interactions. *Insects*, 10, 366. DOI: <https://doi.org/10.3390/insects10100366>
- Wilson-Rich, N., Spivak, M., Fefferman, N.H., Starks, P. T. (2009) Genetic, individual, and group facilitation of disease resistance in insect societies. *Annual Review of Entomology*, 54, 405–423. DOI: <https://doi.org/10.1146/annurev.ento.54.110807.090443>
- Winston, M. L. (1987) *The Biology of the Honey Bee*. Cambridge, MA: Harvard University Press.
- Wright, M. G., Spencer, C., Cook, R. M., Henley, M. D., North, W., Mafrano, A. (2018) African bush elephants respond to a honeybee alarm pheromone blend. *Current Biology*, 28, R778–R780. DOI: <https://doi.org/10.1016/j.cub.2018.06.008>
- Zakour, M. K., Ehrhardt, K., Bienefeld, K. (2018) First estimate of genetic parameters for the Syrian honey bee *Apis mellifera syriaca*. *Apidologie*, 43:600–607. DOI: <https://doi.org/10.1007/s13592-012-0130-4>