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The multifaceted role of brood communication in wasp societies

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ABSTRACT

The family Vespidae represents a key group to understand the evolutionary trajectory of social behavior in insects, as these wasps display the entire spectrum of social behaviors, from solitary to highly eusocial. The evolution of eusociality likely depended on a coordinated communication system, with chemical communication being suggested as the most commonly used among social insects. Chemical communication provides information about colony identity and an individual's identity, sex and caste, and can help resolve intracolonial conflicts. Parallel to the communication observed in adult-to-adult interactions, several reports have highlighted that the brood (eggs, larvae or pupae) can also act as direct or indirect sources of chemical compounds that can convey information. For example, eggs are covered with chemical substances that provide information about egg maternity and the queen's fertility. Given the increase in the past years of studies aiming to understand how brood can contribute to social dynamics, we reviewed the literature about the information conveyed by brood in wasp's nests across different levels of sociality. The main goal of this review was to synthesize the current knowledge and provide new venues of research. We addressed five main subjects (1) brood mediated conflicts and underlying mechanisms, (2) brood parasitism, (3) hydrocarbon cues covering brood, (4) juvenile hormone influencing brood scent and (5) other modes of communication used by brood.

Introduction

Cooperation and division of labour are critical for colony success in eusocial insects. Social wasps from the Vespidae family provide fascinating models for understanding the evolution and maintenance of such behaviours. These wasps vary in social organization, from primitively to highly eusocial species, and exhibit intricate communication systems that coordinate colony dynamics (Hunt 2007). While many studies have been done on adult-adult communication, the role of brood (eggs, larvae, and pupae) in influencing colony dynamics has received less attention. Highlighting the involvement of brood in social interactions can reveal critical processes that contribute to colony success and motivate future research beyond adult-centric studies.

Adult-adult communication in social wasps primarily involves chemical signaling, with cuticular hydrocarbons (CHCs) playing a central role in mediating these interactions. CHCs serve a dual function: they act as a physical barrier, preventing desiccation and protecting against infections by microorganisms (Gibbs 1998; Gibbs & Rajpurohit 2010), and they also facilitate complex social interactions such as nestmate recognition, reproductive regulation, and caste determination (Van Oystaeyen et al. 2014; Cini et al. 2019). These hydrocarbons are critical for maintaining colony cohesion, as they enable individuals recognise nestmates and regulate task behaviours within the colony. While CHCs have been extensively studied in adult wasps, their potential role in brood recognition and brood-adult interactions has received little attention, despite their importance for colony dynamics. Although brood are immobile and do not engage in active communication, they can produce hydrocarbons that help adults recognize them, influencing interactions such as queen-worker and worker-worker relationships (Schultner et al. 2017). In Polistinae and Vespinae subfamilies, which include primitively eusocial and highly eusocial wasp species, workers retain functional ovaries and are capable of laying male-destined eggs. This reproductive flexibility leads to potential conflicts over male production, especially in species with high levels of worker reproduction, where workers may challenge the queen's reproductive monopoly (West-Eberhard 1978; Strassmann 1985; Wenseleers et al. 2020).

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Efficient brood maternity recognition is important not only for brood care but also for mediating reproductive conflicts. Proper identification of brood is critical for colony success, as brood care represents a substantial investment in the colony's future (Schultner & Pulliainen 2020).

Historically, research on wasp brood has concentrated on morphology, systematics, and production dynamics (Giannotti & da Rocha 2021; Strassmann 1985; Solis & Strassmann 1990). Studies have also looked into defensive behaviors related to brood presence, such as ant-repellent glandular secretions produced by adult females (Jeanne 1970; Jeanne 1975) and defensive responses observed in swarm-founding wasps (Strassmann et al. 1990). However, these studies largely emphasize brood protection rather than the potential active role of brood in colony dynamics. More recently, interest in communication strategies has led researchers to explore whether brood actively contribute to colony behavior through signals or cues. Furthermore, physiological mechanisms, such as the pleiotropic effects of juvenile hormone (JH)—well studied in adults—have received little attention in brood, but it is likely that similar physiological pathways regulate both adult and brood traits. Understanding these mechanisms could fill knowledge gaps.

Despite the significance of brood-adult communication, there is no existing synthesis of brood roles in wasp societies. By addressing this gap, this review aims to compile the literature on brood-adult interactions in Vespidae wasps, with an emphasis on chemical communication and its effects on adult behavior. Specifically, we explore the following topics: (1) brood mediated conflicts, (2) brood as mediators of parasitism, (3) hydrocarbons covering brood, (4) juvenile hormone influencing brood scent, and (5) other modes of communication used in brood-adult interactions. We conclude by identifying knowledge gaps and future directions for research on brood-adult communication in social wasps. We frame the main aspects covered in each of the five topics, including the gaps in knowledge and future testable hypotheses (Table 1):

Table 1
Topics covered in this review of role of brood in communication in social wasps, followed by what is currently known, gaps and future testable hypotheses.

Topics covered	What is known	Gaps and testable hypotheses
1) Brood-mediated conflicts	Eggs and larvae have hydrocarbons related to caste and sex.	G: Identify compounds driving egg recognition, especially in Neotropical wasps. H: Test experimentally if specific brood compounds (volatile and non-volatile) drive recognition.
2) Brood mediating parasitism	Brood hydrocarbons are species-specific, but parasitized brood lacks those recognition odors.	G: Strategies that enable nest parasitism in Neotropical wasps. H: Parasite eggs mimic host species chemically.
3) Hydrocarbons covering brood	Brood odors have endogenous production, deposited by adults or external sources (e.g., nest material).	*G:* Investigate if adult saliva transfers chemical cues to brood; Mechanisms of endogenous production H: Brood odour production are similar to adults.
4) Juvenile hormone influencing the brood scent	JH affects larval body odor. JH influence adult Dufour's gland composition, consequently those chemicals are deposit into egg surface.	G: Explore links between JH and Dufour's gland composition; Study JH variation across different brood castes.
5) Other modes of communication used by brood	Vibrational and visual communication used in larvae-adult interactions. Larvae signal hunger through noise; adults use tactile cues to regulate feeding, development, and caste fate. Absence of brood influences adult caste determination and reflects queen quality.	G: Lack experimental evidence that brood noise induce worker foraging. H: Amplitude of the noise correlated with colony size.

(1) Brood-mediated conflicts

In colonies of social wasps, reproductive interests of the queen and workers can be in conflict, especially in species where the queen mates with multiple partners. This results in workers sharing less genetic material with offspring from different paternal lineages, which contributes for workers to reproduce for their own fitness gain (Wenseleers et al., 2020). However, from the colony's perspective, reproductive workers can be costly as they may neglect essential colony tasks (e.g., foraging or nest construction) (Wenseleers et al., 2004).

A central element in resolving these conflicts – directly or indirectly - involves the brood, which includes individuals at different developmental stages—eggs, larvae, and pupae. Brood mediates colony dynamics such as queen-worker reproductive conflict resolution and nestmate recognition (Table 2). This is because hydrocarbons found on the brood's cuticle, convey important information about maternity, enabling workers to recognize whether the brood belongs to the queen or to other workers. Those hydrocarbons are used to recognize brood from the same nest.

For example, in *Vespula vulgaris*, workers use hydrocarbon signals (e.g. 3-MeC29) on eggs to discriminate between queen-laid and worker-laid eggs, and they will remove the latter to maintain the queen's reproductive dominance (Oi et al., 2015). Similarly, in *Polistes dominula*, eggs laid by subordinate females are distinguishable from queen-laid eggs based on distinct hydrocarbon signatures, which include a variety of alkanes and alkenes (Dapporto et al., 2007). These chemical cues facilitate the recognition process and help maintain reproductive hierarchy within the colony.

In addition to egg recognition, brood scents may also influence the care given to different stages of brood. In *Polistes chinensis antennalis*, for instance, queen-laid eggs are recognized by their specific hydrocarbon profile, which helps prioritize their care over worker-laid eggs (Tsuchida et al., 2020). Moreover, in species like *Vespa crabro*, egg recognition is critical in regulating worker reproduction, as queen-laid eggs are more likely to survive, while worker-laid eggs are often removed, particularly in queen-right colonies (Foster et al., 2002).

In social wasp species, most available knowledge is based on correlational data, which, while useful, does not confirm the existence of specific signals driving queen-worker or worker-worker reproductive conflicts.To make progress in the field, systematic assays must be performed to identify biologically active chemical compounds emitted by the brood, whether volatile or non-volatile.

(2) Brood-mediated parasitism

Brood scents play a crucial role in avoiding nest parasitism by social parasites and unrelated/alien species. In social parasite wasps, females have lost the ability to build their own nests and rely on laying their eggs in the nests of host species to achieve reproductive success (Cervo 2006; Cervo et al. 2008; Elia et al. 2018). However, this parasitic strategy can fail when host females can detect and prevent parasitic eggs from hatching or being raised.

Two primary hypotheses have been proposed to explain why host females may unknowingly raise alien eggs. The first is that the parasitic eggs or larvae are chemically insignificant, meaning they are not detected by the host. The second hypothesis is that brood parasites might use chemical mimicry, matching the chemical profile of the host species to avoid detection (Cervo 2006; Cervo et al. 2008). For example, the larvae of the social parasite *Polistes sulcifer* exhibit chemical profiles

Table 2
A comprehensive review of the literature on the roles of brood (eggs, larvae, and pupae) in conflict and conflict resolution in vespid wasps. This summary highlights the key findings from the cited studies, categorizing them by the type of evidence—either correlational or experimental. The findings are further organized based on their context: (1) intracolonial, (2) intercolonial, and (3) interspecific interactions.

Level	Context of Interaction	Resolution	Evidence type	Species	References
Intracolonial	**Male Parentage**: Workers increase fitness by laying eggs in queen-right conditions	Queens and policing workers rely on chemical/visual info to selectively destroy worker-laid eggs	Experimental: Egg-marking compounds linked to caste, behavioral data	*Vespula vulgaris; Vespula rufa; Polistes dominula*	Oi et al. 2020; Wenseleers et al. 2005a; Wenseleers et al. 2005b; Kovacs & Goodisman 2007; Saigo & Tsuchida 2004; Tsuchida et al. 2020; Cotoneschi et al. 2009
	Breeding Role: Subordinate workers attempt reproduction instead of brood care	Foundresses/dominant females distinguish eggs using cell screening and egg-marking	Correlational: Egg-marking linked to female breeding role	*Polistes dominula*	Dapporto et al. 2010; Dapporto et al. 2007
Intercolonial	**Caste Fate**: Females lay eggs in unrelated nests	Females recognize natal eggs over alien eggs and remove gyne-destined eggs	Experimental: Egg recognition based on caste fate	*Polistes biglumis*	Lorenzi & Filippone 2000
	Nestmate Recognition: Workers lay eggs in unrelated nests in high-density populations	Workers use cell screening to distinguish natal eggs from non-nestmates	Correlational: Chemical cues covering eggs reflect nest identity	*Polistes dominula; Polybia paulista; Polistes biglumis; Mischocyttarus cerberus*	Cotoneschi et al. 2007; Kudô et al. 2017; Turillazzi et al. 2008; Lorenzi & Filippone 2000; da Silva et al. 2023a
	Kin Recognition: Females share reproduction with kin	Females tolerate kin's brood more than non-kin	Correlational: Chemical cues linked to kin recognition	*Polistes fuscatus*	Klahn & Gamboa 1983; Panek & Gamboa 2000
Interspecific	**Nest Usurpation**: Primitively eusocial wasps' nests are usurped by different species	Resident females recognize alien eggs through chemical cues	Experimental & Correlational: Egg recognition by chemical cues	*Polistes dominula; Polistes metricus; Mischocyttarus cerberus*	Wright et al., 2019; Ferreira et al. 2022; da Silva et al. 2023a; da Silva et al. 2023b
	Social Dumping: Nests are usurped by social parasites	Brood recognition by host females occurs, though parasite eggs may be chemically similar to host eggs	Experimental & Correlational: Recognition depends on chemical cues	*Polistes dominula; Polistes atrimandibularis; Vespa crabro*	Elia et al. 2018; Cervo et al. 2008; Martin et al. 2008

that are qualitatively similar to those of the host *Polistes dominula*, suggesting that the parasitic larvae have evolved the ability to mimic the host's chemical signals (Cervo et al. 2008). Alternatively, social parasite brood may survive in host nests by producing chemical compounds that have appeasing effects on the host females. For example, although the eggs, larvae, and pupae of the social parasite *Polistes atrimandibularis* differ chemically from its host species, *Polistes biglumis*, the larvae and pupae of the parasite contain a high proportion of the alkene 9-nonacosene. This compound likely plays a key role in promoting the survival of the parasite brood by influencing host females' behavior (Elia et al. 2018).

Though not extensively studied, it is possible that parasite brood may acquire the chemical cues of the host colony indirectly through trophallaxis, the exchange of liquid food between colony members. In ants, trophallaxis enriches the exchanged liquids with various chemical compounds, including hydrocarbons (Leboeuf et al. 2016). Since wasps also engage in frequent trophallaxis, parasite brood could potentially acquire host chemical cues in a similar manner. Kudô et al. (2017) demonstrated that female wasps lick their brood, which could allow the brood to acquire the colony's chemical profile. However, more research is needed to fully characterize the chemical composition of the saliva released by adult wasp females, which may provide insights into whether this is a viable route for modulating brood chemical composition in social wasps. Being able to synthetize specific compounds that ensure parasite brood to succeed is also another option that should not be discarded and addressed in the future.

From an evolutionary standpoint, if nest usurpation events are frequent, females with the cognitive ability to recognize their own brood are likely to be favored by natural selection. The ability to recognize and preferentially care for one's own brood might be particularly beneficial for the colony, especially if alien eggs could negatively affect colony performance. For instance, in *Polistes biglumis*, females seem to have evolved the ability to distinguish between worker-destined and gyne-destined eggs, with worker eggs being more likely to be accepted, as they contribute to the workforce of the colony (Lorenzi & Filippone 2000).

Brood parasitism is observed in *Mischocyttarus* and *Polistes* wasps, nests can be attacked by various parasitoid wasps or other females of the same species attempting to parasitize the nest (Cervo et al. 2008; Montagna et al. 2012; da Silva et al. 2019). In *Mischocyttarus consimilis*, which acts as a social parasite by usurping nests of *Mischocyttarus cerberus*, the eggs of the two species are chemically distinct. Eggs of *M. consimilis* are covered with fewer hydrocarbons compared to those of *M. cerberus*, which suggests that *M. consimilis* may succeed reproductively because their eggs go unnoticed by the host (Montagna et al. 2012). However, further studies are needed to confirm this hypothesis.

In both *Polistes dominula* (host species) and *Polistes sulcifer* (social parasite), brood scent alone does not entirely prevent parasitism. Parasite larvae develop more quickly than the host larvae, and adult parasites may chemically mimic the host species (Sledge et al. 2001). This highlights the sophisticated ways in which brood parasites manipulate host care behavior for their benefit (Cervo et al. 2004). For example, eggs of the brood parasite *Vespa dybowskii*, which invades both *V. crabro* and *V. simillima* nests, are likely not removed because they are chemically insignificant. The host eggs contain a high proportion of hydrocarbons, while parasite eggs have almost no methyl-branched compounds. This chemical divergence may help the parasite eggs avoid detection, particularly if the host species relies on methyl-alkanes for brood recognition (Martin et al. 2008).

At the intraspecific level, *Polistes fuscatus* females can recognize their own larvae, but they are unable to distinguish between larvae from different nests of the same species. This suggests that the chemical cues facilitating brood recognition are colony-specific, but not necessarily kin-specific (Klahn & Gamboa 1983; Panek & Gamboa 2000). In contrast, *Parischnogaster mellyi* may exhibit nestmate recognition through brood chemical cues, which reflect their nest origin (Turillazzi et al. 2008). Similarly, in the swarm-founding wasp *Polybia paulista*, chemical cues covering the brood convey nest identity information, and females provide more care to larvae from their own nest (Kudô et al. 2017).

Invasive species, such as *Polistes dominula*, have been shown to alter brood parasitism dynamics. In areas where *P. dominula* is invasive, females tend to be more tolerant of alien brood, likely because they are not highly related to one another and are less focused on brood policing (Wright et al. 2019). In contrast, in areas where *Polistes metricus* is native, females tend to start nests alone and are less tolerant to unrelated eggs (Wright et al. 2019). This suggests that invasive species can change the dynamics of brood recognition and parasitism in ways that are not seen in native populations.

Studies on host-parasite interactions in Neotropical species are scarce but essential to determine whether parasitic wasps in the region adopt strategies similar to those in Temperate zones. Evidence of obligatory social parasite wasps, such as those in the *Polistes* clade, remains limited and often anecdotal. The resource disparity between Tropical and Temperate zones likely displays a role as an environmental pressure shaping host-parasite interactions. Exploring this topic could clarify the factors driving these interactions in wasps.

(3) Hydrocarbons covering brood

The different types of chemical compounds covering brood in social wasps originate from different endogenous and exogenous sources and are critical for coordinating the colony life, such as brood recognition and nestmate discrimination. Below an overview on the potential sources and functions of these compounds:

3.1. Endogenous sources

Endogenous sources of chemical compounds are produced within the brood itself or by adult females and secondarily transmitted to them. During larval and pupal development, several glands may contribute to the production of chemical substances used in chemical recognition. Larvae and pupae produce their own chemical compounds, as they possess oenocytes responsible for molting and waterproofing of the tracheal system (Makki et al. 2014). Similarly, oenocytes are also known to synthesize cuticular hydrocarbons in adult insects, important for desiccation and communication (Wang et al 2025). Hydrocarbons and other compounds produced by glands are important cues to recognize colony members. In this section, we will focus on the gland secretion as endogenous sources in brood.

The accessory gland that is part of the female reproductive apparatus, *Dufour's* gland, is a potential direct source of hydrocarbons covering eggs. This is an exocrine gland that displays distinct functions across Hymenoptera (Mitra 2013), and usually has a big role on communication in social insect colonies (Mitra 2013). During egg laying, the *Dufour's* gland releases chemical compounds that help the egg to remain attached to the wall surface and that cover the eggs (Mitra 2013). Hydrocarbons usually present in the *Dufour's* gland are also detected over the surface of eggs in wasps with different levels of social organization (from primitively eusocial to highly eusocial wasps) (Ferreira et al. 2022; da Silva et al. 2022; Bonckaert et al. 2012; da Silva et al. 2023c). In Stenogastrinae, female wasps also use the *Dufour's* gland as a reservoir of a gelatinous substance (pap) that is secreted over the eggs to help egg adherence to the substrate (Turillazzi & Pardi 1982). In *M. cerberus* and *Mischocyttarus cassununga*, considerable overlap of chemical compounds exists between the contents of *Dufour*'s gland and egg-marking compounds (Ferreira et al. 2022). In these societies, egg marking occurs when the females are alone (Ferreira et al. 2022) or in the presence of nestmates (da Silva et al. 2023a). In nests of *Mischocyttarus metathoracicus* and *Polistes versicolor*, egg marking cues are more similar to the contents of the *Dufour*'s gland than to females' CHCs (da Silva et al. 2023b). The next step will be to track whether the *Dufour*'s gland in Neotropical social wasps contain nestmate information.

Interestingly, in ants, cephalic secretions are enriched by several compounds, including hydrocarbons (Leboeuf et al. 2016), and in social wasps these secretions are probably deposited on the nest or transferred to the brood during grooming. The saliva produced by larvae of different social species (*Vespula vulgaris, V. germanica, V. maculata, V. maculifrons, Vespa crabro, V. orientalis, Polistes annularis, P. carolina, P. exclamans* and *P. fuscatus*) have been shown to be enriched with several amino acids (Hunt et al. 1982), however, it is still unknown if wasp larval saliva also contains hydrocarbons, which should be investigated for both Vespinae and Polistinae wasps.

3.2. Exogenous sources

Exogenous sources may contribute to the overall brood smell. Brood may acquire chemical compounds indirectly from nest material due to direct contact (Soares et al. 2021; Sguarizi-Antonio et al. 2022). For example, studies targeting larval stages of wasps and focusing on their morphological characteristics have reported that as the larvae molt and grow, they will be attached to the nest (Rocha et al. 2016; da Silva et al., 2020). The wasp nest is composed of woody fibers, plant trichomes mud and secretions released by wasp cephalic glands (Jeanne 1975; Brown et al. 1991). The nest material is enriched with several hydrocarbons (Brown et al. 1991; Silva et al. 2016; Soares et al. 2021; Sguarizi-Antonio et al. 2022). In nests of *V. germanica*, the nest material is covered in hydrocarbons that resemble those found over the body surface of mature workers (Brown et al. 1991). However, after being used over several generations to stock brood, the nest material hydrocarbons become more closely related to those found covering the pupae (Brown et al. 1991). In *Polistes,* females stroke their gaster into the nest which could potentially be used as a way to deposit hydrocarbons (Dani et al., 1992). As the nest contains chemical compounds and the brood is in the cells, brood can acquire the same smell due to the close contact with the nest material; in *Protopolybia exigua,* for example, the chemical composition of brood and nest material overlaps (Silva et al. 2016). The chemical composition of brood and the nest material of *P. exigua* comprises a total of 49 peaks, which range from the linear alkane n-C14 and n-C36 (Silva et al. 2016).

The main unresolved question is the origin of the brood's chemical composition. While anecdotal evidence suggests passive acquisition from nest material, however the nest alone is unlikely to be the sole external source. Adult females, frequently in contact with the brood, may transfer chemical compounds through interactions like saliva exchange. Additionally, brood may produce their own compounds, indicating that their chemical profile could result from a combination of endogenous production and secondary acquisition.

(4) Juvenile hormone influencing the brood scent

Juvenile hormone (JH) plays a central role regulating several processes in social insects, such as behavioral maturation and physiological processes in social insects, including social wasps (Hartfelder 2000; Huang, 2020). JH titers affect ovary activation levels in adult females (Barth et al. 1975; Agrahari & Gadagkar 2003; Giray et al. 2005; Neves et al. 2020; Walton et al. 2020; Oi et al. 2021; Ferreira et al. 2022; Prato et al. 2021; Prato et al. 2022; da Silva et al 2022). In principle, JH impacts the transcription of a vitellogenin gene, which induces the production of vitellogenin, a key protein that is up taken by the growing oocytes in reproductive females (Hartfelder 2000). Its influence surpasses developmental and the reproductive aspects listed above and affects chemical communication (e.g. adult and brood scent) (Prato et al. 2021; Prato et al. 2022; da Silva et al. 2022). Below, we outline how JH can potentially affect brood aspects linked to the formation of their own scent and, hence enabling chemical communication.

The primary function of JH in brood is controlling the molting and metamorphosis, but it can also affect brood in other ways. In *M. consimilis,* for example, JH is probably involved in determining the fate of larvae (Montagna et al. 2015; Neves et al. 2020), as third instar larvae topically treated with JH emerge as adult females having a greater body size, they do not leave the nest frequently, they are less attacked by other females, and they have CHCs that differ from other females (Montagna et al. 2015; Neves et al. 2020).

Manipulating JH levels in adult foundresses of two *Mischocyttarus* species (*M. cerberus* and *M. cassunuga*) ultimately affects their *Dufour*'s gland content and the hydrocarbons that are deposited over the egg surface (Ferreira et al. 2022). This indicates that JH levels can alter chemical signals used in brood recognition and policing. For *M. cerberus*, methoprene treatment (JH-analog) induces the production of eggs which positively correlates with the relative peak area of three hydrocarbons found over their eggs (3-MeC29, n-C31 and n-C33) (Ferreira et al. 2022). In *Vespula vulgaris*, the application of methoprene (JH analog) causes workers to lay eggs that are less likely to be policed by other colony members. The eggs of JH-treated workers closely resemble those of the queen in terms of chemical composition, making them harder to differentiate (Oi et al. 2020). This suggests that JH influences chemical identity in both adults and brood and impacts reproductive success by influencing the policing behavior of other colony members. Thus, in both cases the maternal JH levels have an implication on the chemical deposited over their brood and hence it may affect their reproductive success.

The studies discussed in this topic indicate that JH plays a critical role in regulating the chemical profile of the brood, affecting both the chemical cues on eggs and the overall chemical identity of the brood. However, there is still gaps to understand about the biosynthesis of these compounds and the genetic mechanisms underlying JH's influence on brood chemical profiles. Further studies are needed to investigate how JH levels are regulated during brood development and how they interact with other factors, such as environmental signals and nestmate recognition. Additionally, it is yet to be covered whether the JH circulating levels in the brood ultimately impact the production of any queen-like compounds that may already indicate their caste fate as previously reported in the ant species *Harpegnathos saltator* (Penick & Liebig 2017).

(5) Vibrational and visual communication used in larvae-adult interactions

In wasp societies, larvae communicate with adults not only through non-volatile chemical cues but also via vibrational, acoustic, and visual signals, which are crucial for colony dynamics. In some cases, larvae may not produce these signals themselves but respond to stimuli initiated by adult females. We discuss both brood-generated signals affecting adults and adult-generated signals affecting brood.

Larvae from the genus *Vespa* produce sounds when hungry by bending their bodies and scraping their mouthparts against the cell wall (Ganor et al. 1986), known as "scraping noise" or "hunger signals" (Schaudinischky & Ishay 1968). This can act as an incentive for workers to forage and take care of brood, contributing to colony cohesion. Larvae scrape the wall in a specific beat and only stop when an adult female approaches with food (Ishay & Schwartz 1973). Sounds are produced differently by worker, male and queen-destined larvae, which means that adult workers likely react according to this variation (Ishay & Schwartz 1973).

More recently, it has been shown in *P. dominula* that abdominal movements performed by adult females, known as abdominal waggling, create substrate-borne vibrations that are likely perceived by larvae, which respond with increasing body movement (Pepiciello et al. 2018). In nests of *P. fuscatus* the lateral abdominal vibration movements performed by adult females during the feeding time may signal to the larvae to stop secreting saliva (Savoyard et al. 1998). Adult females also perform "antennal drumming" in the nest, which causes vibrations that potentially affect larval caste-fate in *P. dominula* (Suryanarayanan et al. 2011). Gyne-destined larvae raised in nests with antennal drumming emerge as adults with less fat storage, a trait that is characteristic of non-diapausing females (Suryanarayanan et al. 2011). Antennal drumming has also been described as displaying another role in *Polistes* societies, during the moments that adult female wasps are feeding the brood and this behavior leads to a decrease of saliva release by larvae (Pratte & Jeanne 1984; Suryanarayanan & Jeanne 2008). However, in many other species, including primitively and highly eusocial ones, the vibration produced by adult females with other body parts may be involved in the processing of feeding the larvae per se (e.g. warning that they are about to be fed) (Jeanne 1972; Darchen 1976; Greene et al. 1976; Jeanne 1977; Hook & Evans 1982; Ishay et al. 1974).

Visual cues can also affect interactions between brood and adults in wasps. In *P. exclamans*, the lack of brood (removed experimentally) in the nest induces caste changes in newly emerged females (Solis & Strassmann 1990). Following emergence, females that can engage in brood care acquire a worker-like phenotype, whereas females emerging in nests that are brood-deprived acquire a gyne-like phenotype (Solis and Strassmann, 1990). A similar phenomenon was observed in nests of *P. metricus*, in which females emerging in experimental nests with brood possessed behavioral traits and nutritional profiles matching those of workers (e.g. colony maintenance and low energy stores) (Judd 2018).

In *P. dominula,* females can assess the queen's quality based on her reproductive performance, as the experimental removal of eggs triggers ovary activation in subordinate females (Liebig et al. 2005). These findings indicate that workers possibly pick up on and respond to these cues, but also use the presence of brood as direct evidence of queen quality (Liebig et al. 2005).

Future studies should investigate whether larvae produce hunger chemical cues that trigger worker foraging behavior or function in synergy with vibrational signals observed in specific contexts.

Concluding remarks

The present review highlights the different communication roles brood display in wasp societies, mainly related to chemical communication which contributes to colony cohesion and resolution of conflicts. Internal conflicts, involving females within the same nest, and external conflicts, such as nest usurpation by parasites, can be mediated by the brood, once they have a cuticular surface coated with compounds that allow recognition to happen. We focused on chemical communication on brood surface that are produced endogenously or that can be acquired exogenously through possibly grooming and with the contact of nest surface. The identification of chemical cues enabling egg recognition are concentrated on correlative evidence to indicate compounds that differ between brood. There is support for the *Dufour's* gland to be a source of compounds that cover eggs. In this sense, brood odors are ultimately a combination of what they can produce plus what is integrated – passively or actively - over them via their adult nestmates. Empirical studies aiming at determining the specific chemical compounds driving egg recognition should receive more attention, especially for the Neotropical species. For example, the methyl alkane 3-MeC29, which signals maternity in *V. vulgaris*, is commonly found in the blend of compounds coating the eggs and larvae of many Neotropical species. However, it remains unclear whether this chemical compound plays a conserved role in signaling egg maternity across different species. Although the most part of the literature available suggests that the communication between larvae and adult individuals in wasp societies is mainly driven by chemical compounds, other types of cues (vibrational, acoustic, and visual) can also influence the overall social dynamic depending on the species, reinforcing that brood can actively contribute for the social environment. Lastly, different cues produced by brood, probably work in synergy, play a key role in driving social dynamics.

This review has mainly focused on high molecular weight compounds (hydrocarbons) involved in chemical communication; however future investigations should tackle the existence of volatile brood pheromones in social wasps. Justification for this can be found in the honeybee *Apis mellifera*, in which larvae release a volatile compound E-β-ocimene, which is involved in the regulation of social dynamics (it induces workers to start foraging earlier) (Maisonnasse et al., 2010). The same compound increases foraging activity for nectar (Ma et al. 2016). Another aspect is if the compounds released by the brood can affect hygienic behavior. In honeybees, larvae infected with the bacterium *Melissococus plutonius* produce chemical compounds that are linked with their poor health status (e.g. compounds such as oleic acid and γ-octalactone) and hence can be the responsible for triggering hygienic behavior (Kathe et al. 2021). Future research might investigate whether adults transfer non-volatile hydrocarbons through trophallaxis, which can be incorporated into the eggs and larvae. If this is the case, trophallaxis would work as an effective mechanism for homogenizing the colony smell from brood to adult. In the literature, studies involving wasp brood remain scarce, and one reason for that is the challenges to manipulate and raise wasp brood in laboratory conditions. More studies are necessary integrating chemical and cognitive ecology to understand in better details the type of brood-adult interactions that are established in wasp societies. So far, most studies are performed at the behavioral level, meaning that the assays are used to check whether adult female wasps can distinguish between their brood and those heterospecific or conspecific. However, there still a lack of effort in terms of trying to understand which specific compounds (or combination of them) are detected and then integrated in adult female brains (e.g. Do different compounds trigger different glomeruli activity at the antennal lobes of adult females? Do mushroom bodies store information that allow brood recognition to happen? Do adult females emerge with an innate ability to recognize their brood over non-nestmate brood?). In summary, conducting more studies that integrate multiple techniques and communication pathways is crucial for fully understanding the social role of brood in wasp colonies and advancing our knowledge of social wasp societies.

CRediT authorship contribution statement

Rafael Carvalho da Silva: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Fabio Santos do Nascimento:** Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. **Cintia Akemi Oi:** Funding acquisition, Project administration, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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