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Context matters: plasticity in response to pheromones regulating reproduction and collective behavior in social Hymenoptera

Margarita Orlova and Etya Amsalem

Pheromones mediating social behavior are critical components in the cohesion and function of the colony and are instrumental in the evolution of eusocial insect species. However, different aspects of colony function, such as reproductive division of labor and colony maintenance (e.g. foraging, brood care, and defense), pose different challenges for the optimal function of pheromones. While reproductive communication is shaped by forces of conflict and competition, colony maintenance calls for enhanced cooperation and self-organization. Mechanisms that ensure efficacy, adaptivity and evolutionary stability of signals such as structure-to-function suitability, honesty and context are important to all chemical signals but vary to different degrees between pheromones regulating reproductive division of labor and colony maintenance. In this review, we will discuss these differences along with the mechanisms that have evolved to ensure pheromone adaptivity in reproductive and nonreproductive context.

Address
Department of Entomology, Center for Chemical Ecology, Center for Pollinator Research, Huck Institutes of the Life Sciences, Pennsylvania State University, University Park, PA 16802, USA

Corresponding author: Amsalem, Etya (eua6@psu.edu)

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Introduction

Social insects perform collectively many types of known animal behaviors, such as search for food and shelter, defense against predators and parasites, reproduction and parental care, but however varied and diverse these social behaviors might be, they all rely on effective communication. The most common and ancient means of communication occurring widely among social insects are pheromones [1]. Ubiquitous and pervasive, pheromones are the equivalent of mass-media in nature and, just as with our own mass media, they have the potential for being adaptive and constructive, but also maladaptive and downright disastrous. For the purpose of this review, we discuss two types of pheromones social insects use to regulate social behavior: reproductive signaling (i.e. when an individual advertises their reproductive status for the purpose of regulating reproduction in other individuals), and maintenance signaling (i.e. when individual uses chemical signaling to induce behavior for the purpose of maintaining colony functions namely foraging, defense, etc.).

The destructive potential of both types of pheromones is rooted in their ability to influence large masses of individuals and to manipulate individuals into seemingly acting against their interests. Indeed, misperception and misinterpretation of signals can (and sometimes do) result in detrimental effects for individuals or colonies. However, the cost of signal misperception to the individual may vary greatly. Here we argue that (1) pheromones regulating reproduction differ from pheromones regulating colony maintenance in the potential cost of erroneous response; (2) honesty and social context are of greater importance to reproductive than to nonreproductive signaling, allowing greater plasticity in response to these signals; (3) the mechanisms underlying the plasticity in response to pheromones evolved to match the function of communication in different contexts and are critical to the evolutionary stability of pheromones.

Conflicts and commonality of interests in insect societies

Social insect colonies are frequently referred to as a super organism – a system consisting of individuals acting in seemingly perfect unison. Unlike a true organism, however, a social insect colony has one domain where conflicts between

individuals persist. The Achilles' heel of social harmony is reproduction [2].

Reproductive division of labor, the signature trait of eusocial insects [3], is regulated by signals that evolved in the absence of a shared optimum between individuals, a situation which calls for additional mechanisms ensuring signal honesty [4]. The gambit of fitness between the reproductive (queen) and her helpers (workers) in insect societies is very similar to that between vertebrate males and females: the latter bear the brunt of costs associated with reproduction and investment in a low-quality partner incurs a significant loss of fitness. Thus, reproductive signaling in social insects likely evolved along the same paths as quality-related sexual signals in vertebrate males, with two chief qualities in common: (1) communication takes place on inter-individual rather than inter-group level; and (2) honesty of signals is of central importance and is regulated both at the level of production and perception. This is often achieved by producing and responding to a signal only when it appears in the proper context. The pervasive use of pheromones for regulating reproduction in social insects highlights a third quality that is unique to chemical signaling. Unlike other types of signals (e.g. acoustic or visual), pheromones have the potential to become ubiquitous and their source may be ambiguous. Therefore, they are predicted to be physically linked to the body of the emitter whose quality they advertise, requiring the receiver to be in close contact to perceive them.

Pheromones governing other aspects of colony life, such as foraging, nest searching, and defense (all of which can be referred to as colony maintenance tasks), often regulate tasks, in which the emitters and receivers of the signal share a common interest. These pheromones serve to optimize the task performance, rather than to solve a conflict, and are predicted to be honest simply because cheating would be detrimental to both the emitter and the receiver [4]. However, the regulation of such collective behaviors has its own challenges – efficiency, flexibility, and robustness of self organized systems. Here, pheromone communication is truly collective rather than inter-individual and allows the use of rather sophisticated governance systems where the resulting behavior of the group depends on numbers and locations of multiple emitters ('situational context' as opposed to 'social context'). In these systems, signals and responses of one individual usually cannot tip the scales. Fitness costs in case of error will be only fractions of an individual's total fitness, since only a critical mass of individuals erring in production or perception of the signal can make a significant impact on fitness.

Below we will review some examples of pheromones responsible for communication in reproductive and maintenance scenarios and discuss the different mechanisms ensuring their adaptivity. Specifically, we highlight the importance of honesty and social context to reproductive signaling, and the importance of situational context to maintenance signaling.

Pheromones regulating reproductive conflicts

Hymenoptera pheromones regulating reproduction include different types of signals such as fertility, caste, dominance, sex, and brood pheromones. However, they all share three main qualities: they are often of low volatility and are linked to the body of the emitter; they contain information about reproductive or dominance status and have low or no impact at all when introduced in the wrong social context. Fertility signals are pheromones correlated with the reproductive capacity of an individual [5], such as esters in the Dufour's gland of the Apis mellifera [6], and cuticular hydrocarbons in many wasps and ants [7,8,9]. A curious development of fertility signaling is found in Bombus species where Dufour's gland esters are produced exclusively by workers and signal sterility [10], and similar compounds in the labial glands correlate with sterility in all females [11]. The theoretical framework underlying the production of fertility signaling is that these compounds regulate reproduction in workers since they provide honest information about the reproductive status of the females producing them [12]. However, the majority of the findings about female fertility signals are correlative in nature. The impact of the synthetic compounds or the extract of the glandular source on worker reproduction was examined only in a handful of species and provide inconclusive results. For example, while the cuticular hydrocarbon 3-methylhentriacontane produced by Lasius niger queens correlates with queen fecundity and inhibits worker reproduction [13], fertility signals of Bombus impatiens queens [14] failed to reduce ovarian activation in workers [15–17].

Queen signals are a subset of caste-recognition signals that distinguish the queen from the workers [5]. Within Hymenoptera, such pheromones were only found in A. mellifera where the composition of the pheromone is known [18], and in Solenopsis invicta where the composition remains elusive [19,20]. The A. mellifera queen mandibular pheromone blend is responsible for maintenance of the queen reproductive monopoly by inducing worker sterility [21,22]. It further increases grooming and feeding of the queen [23] and inhibits the production of new queens [24]. Mating signals, an important subset of fertility and queen signals, provide information about the mating status of females (typically the queen, since workers

of many social species either lost the ability to mate or do not mate) and exist in different ant and bee species. For example, homovanillic alcohol and methylparaben in the honey bee queen mandibular pheromone correlate with the queen mating status [25,26], and in bumblebees, expression levels of the gene for vitellogenin (the main yolk protein in the ovary) are reduced in the presence of newly mated compared to virgin same-age queens, although both queens have inactive ovaries [17]. Mating signals, as fertility or sterility signals, are correlative in nature but are frequently necessary for the full inhibitory effect of the queen's pheromone.

Reproductive dominance is further maintained through worker policing, a phenomenon known from different species of social Hymenoptera, and can manifest as aggression towards individuals challenging the reproductive monopoly or as destruction of eggs laid by such individuals [27]. In various Ponerine ant species, the reproductive monopolist marks her lower-ranking opponent with the secretion from her Dufour's gland, consisting mostly of hydrocarbons, which elicits aggression from low-ranking workers [28,29]. In different wasp species, worker-laid eggs are distinguished from queen-laid eggs by their surface chemical profile and devoured by other workers [30–32]. Fertile A. mellifera workers are detected by the content of esters in Dufour's gland secretions and attacked in addition to worker-laid eggs being devoured [33,34]. Similar mechanism was suggested for Bombus terrestris, where worker-laid but not queen-laid eggs are devoured soon after they are laid [35].

The brood may be another source for pheromones regulating reproduction in social Hymenoptera [36], eliciting behavioral responses related to both maintenance (brood care) and reproductive division of labor in ants [37] and bees [38]. The regulation of reproduction by brood may be simply due to a tradeoff between brood care and reproduction [36], but also due to potential information embedded in the brood signal. Brood is often the ultimate testimony that the queen is mated, reproductive and productive, an information that can be used by workers as a social signal to refrain from reproduction. Several aliphatic esters and E-b-ocimene produced by A. mellifera larvae suppress reproductive physiology in workers [38,39,40]. Brood also suppresses worker reproduction in Ooceraea biroi [41], Camponotus floridanus [42], and B. impatiens [43], though the specific mechanisms of such a suppression in the later cases are not yet known. Interestingly, there is conflicting evidence for larvae discrimination by sex or relatedness. There are some species, in which discrimination of brood was demonstrated [44,45] but other species with the opposite findings [43,46]. The reason for this might be that such a discrimination happens at the egg stage and the vast majority of emerging larvae are queen's progeny.

Ic all your bluff: the importance of honesty and context in reproductive signaling

Honest signals in the absence of a shared optimum between the emitter and the receiver are predicted to evolve through one of two pathways precluding faking [4,47]. Index signals are linked to the condition they advertise and are physically impossible to produce otherwise. Handicap signals are prohibitively costly to produce and maintain, and faking them would result in a significant reduction in fitness [48]. In line with the index hypothesis, insect pheromones were hypothesized to have evolved from non-communicative cues that are a by-product of physiological processes [9,49]. However, experimental studies in support of this within Hymenoptera are scarce. Studies on wasps corroborate this idea showing that cuticular hydrocarbons serving as queen signals are physiologically linked to fertility [50]. In A. mellifera, mating alters the pheromone profile of different glands [26] and only fully fertile mated queens are able to produce the complete mandibular pheromone blend that produces the complete range of effects [51]. Existence of viable brood is often a testimony to the queen's reproductive abilities and of fitness gains incurred by workers who help her. The ability to distinguish between queen's and worker's progeny is thus critical to maintenance of reproductive skew in species where workers can potentially become fertile. Both A. mellifera and B. terrestris workers are clearly able to discriminate between queen laid and worker-laid eggs [35,52]. Similar ability was shown in ants [42]. The mechanism of such discrimination is likely chemical but the substances involved and their sources have not yet been identified [53,54].

Stable function of reproductive signals is maintained not just by their intrinsic honesty, that is, their ability to convey qualitative information about reproduction, but also by their structure and their dependency on social context. Signals related to an individual's quality must be inextricably linked to the signaler's identity rather than being omnipresent. This is apparent in a peacock tail and deer antlers, but in the case of pheromones requires specific physical properties. Most Hymenoptera fertility-signaling and caste-signaling compounds have very low volatility. This includes cuticular hydrocarbons in wasps and ants, esters and hydrocarbons in Bombus, and esters and hydroxy fatty acids in A. mellifera. Low volatility poses a particular challenge for pheromone transmission within very large colonies such as honeybees. In A. mellifera, a system of messenger workers transmit the pheromone among colony members [55]. Such an indirect

transmission system however seems not very efficient. Indeed, crowding, increased distance from the queen and spatial differences increase selfish behavior in workers [56,57]. This system illustrates the importance of honesty in the trade-off betweenhonestyandefficiency.

Conveying honest information about individual's quality is key inreproductivesignalingandwasextensively reviewed[12,58]. It was amply demonstrated in A. mellifera queen's signals that change according to her mating status and quality and exerting different effects on workers and males [26,59,60]. Honest fertility signaling was also demonstrated in different ant species [61,62] as well as in social wasps [63]. The honesty of queen signals has been debated at length and the view of queen pheromones as manipulative agents was frequently challenged and mostly abandoned [5,8,9,15]. One notable example, however, is the homovanillic alcohol component in the honeybee queen's mandibular glands that has been shown to modulate dopamine signaling pathways in workers and thus can beconsideredmanipulative[64].

Asanadditionalmeanstoavoidmisinterpretation,social context (i.e. the identity and behavior of individuals participating in communication)playsanimportantrole intheresponsivenessto reproductive signaling. Indeed, this idea is supported by a growing body of evidence [24,65,66,67,68]. In some species, isolated fertility-signaling compounds like 3-methyl-hentiracontane in L. niger, or 3-methylnonacosane in Vespula vulgaris elicit grooming and suppress worker reproduction [13,69], butthisis notthecaseinmost socialHymenoptera [70]. In Odontomachus brunneus the queen fertility signal (Z)-9-nonacosene is perceived as such only when presented on a familiar chemical background [71]. In B. impatiens, chemical signals produced by the queen fail to achieve their full effect on workerswithoutthebehavioralcontextprovidedbyherpresence [16,17,72]. In A. mellifera, fertility-signaling esters attract workers when secreted by the queen (concomitantly with the QMP) but elicit aggression when secreted by selfish workers [73]. Arguably, the presence of brood also provides a social contexttofertilityandqueensignals.Aqueen-rightA. mellifera colony is more effective at inducing worker sterility than the queen by herself [22]. An interesting interplay between fertility signalsandnest-materecognitionsignalsoccursinponerineants [74,75] where foreign fertile queens are clearly identified as a threat, while foreign sterile workers are welcomed as additional workforce. In this case, fertility signals provided a valuable contextfornest-materecognitionandviceversa.

Chemicalcommunicationincolony maintenance

Pheromonesregulatingmaintenancetasks suchasforaging, nest search and defense have several features in common: they all direct large masses of individuals to locations where their activity is needed, they are often volatile or semivolatile, are not directly linked to the body of the emitter and depend on a situational rather than a social context. The activity in question can however be of quite different nature: food collection, brood care, aggression, or escape. Pheromones regulating foraging effort have been studied extensively in A. mellifera, where foraging behavior is agedependent and foraging effort is regulated through acceleration or delay of the behavioral transitionfromnursetoforagerbees[76].Pheromonesproduced by young larvae and workers (a blend of methyl esters, E-b-ocimene and possibly other, yet unknown, compounds) accelerate the transition to foraging and decrease the receiver's lifespan and reproductive capacity, with larvae of different age regulating pollen and nectar foraging differentially and ethyl oleate produced by old foragers inducing the opposite effect [38,77–81]. In the clonal raider ants O. biroi, brood signals both inhibit worker reproduction and increase foraging activity in a dose-dependent manner [41]. Unfortunately, glandular sources or mechanisms of production of these pheromones are not currentlyknown.

Information about the location of food resources and potential nest sites is transmitted by trail pheromones that have been studied extensively in ants and identified in stingless bees. The necessityofforagingisself-evident,whilenest migrationmaybe initiated for a variety of reasons such as degradation of the existingnestorcolonyfissionduetohigh density.Migrationmay evenbeadefiningpartofspecies ecology,asinarmyantsthatare constantly on themove. Ant trail pheromones frequently serve both for foraging and nest searching [82,83] and are mainly produced in the Dufour's, pygidial, orvenom glandwhich allows the worker to deposit them by touching the tip of the abdomenonthe surface[84].Trailpheromonesinstinglessbees are produced in the labial glands and include mostly long-chain esters [85]. Trail pheromones of ants are extremely structurally diverse and represent virtually all classes of organic substances including alcohols, ketones, esters, terpenes, pyrazines, and many more [84]. Pheromone trails are often complex systems withquorum-dependenteffectsanddifferentcomponentsacting asroad-signswithdifferent meaning[86–88].

Flying species that cannot deposit a trail on solid surfaces use a volatile pheromone to mark forage and nest sites. Hornets, bumblebees, and stingless bees leave pheromone marks on food sources that are subsequently detected by their nest-mates [89–

91]. There is also some evidence of food-marking in honeybees, with different studies attributing attractive or repellent qualities to it [92–94]. Hornets have been shown to use 1-methylbutyl 3-methylbutanoate to mark food sites while bumblebees leave 'footprints' of alkanes and alkenes. Contrary to these species, however, stingless bee food marking pheromones have not been yet identified [89]. Swarming A. mellifera searching for a new nesting cavity will mark potential nesting sites with the Nasanov gland pheromone, which attracts workers at a long range, containing (Z)-citral, nerol, geraniol, nerolic acid, geranic acid, and (E,E)-farnesol. A. mellifera queen mandibular pheromones complement the Nasanov blend as a very short range orientation aid [95,96].

Collective colony defense from outside threats is most commonly orchestrated by alarm pheromones, though the specific effects produced by alarm pheromones may differ between species [97]. In social species with very small colonies, alarm pheromones mostly trigger escape behavior, but in species with large colonies, that are able to mount a significant defense, alarm pheromones elicit aggression and produce a coordinated attack [98]. In these species, guard or soldier workers move toward the source of the pheromone and attack any foreign object near which a high concentration of the pheromone is detected [98,99,100]. Alarm pheromones are usually produced in or near organs and structures associated with defense, such as mandibular or venom glands in ants or Koschevnikov gland on the sting sheath in A. mellifera [101]. They are structurally diverse and represent different classes of chemicals, mostly volatiles such as the isopentyl acetate in A. mellifera [102], formic acid that doubles as chemical weapon in the Formica genus, [103] or ketones and pyrazines in other ants [104–106].

All for one and one for all: efficacy and robustness of maintenance signals

The ultimate challenge for maintenance signals, unlike reproductive signals, is to reach large numbers of individuals at the right time and in the right place. The right time is different for different activities. Alarm pheromones, adapted to eliciting a quick, pervasive, and short lived response are usually volatile and made of multiple components that are quickly distributed throughout colonies. These pheromones can potentially reach a great number of individuals in a short time, but once the threat is dealt with, they dissipate quickly, and alarm is not sustained beyond necessity. In multi-component alarms, pheromone substances with different volatilities are responsible for different components of aggressive behavior [107]. Trail pheromones are semi-volatile compounds that remain on the surface for enough time to allow the next worker to follow the trail but will eventually dissipate if the trail is not maintained, preventing workers from following unrewarding trails.

While the social context for reproductive signaling sets the scene, responses to maintenance signals are shaped by situational context – the time and place, in which communication occurs. In Pogonomyrmex badius oleic acid is treated according to the work environment. Objects treated with oleic acid were regarded as corpses and taken to the midden when found within the nest, but were brought into the nest as food items when found outside the nest [108]. Similarly in B. terrestris, the nutritional state of the colony modulates the perception of foraging-related signals [109]. Situational context also plays a role in pheromone regulation of defense. In A. mellifera, workers only react to isopentyl acetate, the main component in the alarm pheromone, when they are in groups, and they are most sensitive when they are close to the colony entrance [110]. In Camponotus aethiops, an odor presented on nonnestmate ant elicited aggression even though the same odor was previously associated with a reward and learned as a positive stimulus [111]. Temnothorax rugatulus reject a new nest marked with 2,5-dimethylpyrazine, their alarm pheromone, but move towards it near their home nest [112]. Atta capiguara workers respond more strongly to alarm pheromone near nest entrance than to the same pheromone away from nest entrance, and the response depends on 'ant traffic' conditions on the trail [113].

Insect collective behavior is renowned for sophisticated coordination. It includes use of different pheromones regulating different elements or stages of the task. In Oecophylla longinoda, alarm pheromones consist of multiple components with different compounds eliciting different behavioral elements of the defensive reaction from alertness to physical attack [107]. In Leptogenys distinguenda, different components produced by two different glands direct workers from the nest toward food and back to the nest from a foraging trip [114]. An even more striking example of multi-component pheromones is activator-repressor systems where one substance activates a certain behavior and the other one suppresses it. A prominent example comes from Monomorium pharaonis that mark rewarding and unrewarding trails with attractant and repellent pheromones respectively [86,87]. The interplay between attraction and repellence allows for flexibility and maximum efficiency in foraging. A similar activator–repressor effect on a longer time scale is observed in A. mellifera colonies where brood and nurse pheromones activate foraging behavior and physiology while forager pheromones repress maturation of new foragers [115]. Brood effect on worker reproduction in B. impatiens follows the same principle, with inhibition of egg laying in the presence of young larvae and stimulation of egg laying in the presence of

pupae [43]. Such a system maintains a balance of supply and demand of food and allows flexibility when either demand or supply changes.

Spying and propaganda: exploitation of chemical signals

Though the regulatory mechanisms described above may be robust, they are by no means perfect. Different social Hymenopteran species are entangled in predator–prey or host–parasite relationships with each other and have developed abilities to exploit each other's pheromones. Vespa mandarina use alarm pheromones of their prey (honeybees and smaller Vespa species) as a food-indicating cue, while those prey species eavesdrop on the predators' food marking pheromone and use it as a cue to mount a defensive reaction [116,117]. Slave-maker ants Formica sanguinea use alarm pheromones of their victims as propaganda substances to lure as many workers as possible out of the nest and make a raid within the nest an easier task [118]. Leptothorax kutteri, Bombus psithyrus, and A. mellifera capensis workers mimic the fertility and queen signals of their host species to parasitize their nest and usurp the privilege of reproduction [119–121]. As our knowledge of chemical signaling expands, we are sure to discover new ways in which pheromones play a role in ecological relationship between colonies and species of social insects.

Conclusions

Regulatory mechanisms ensuring the adaptivity of pheromones are fascinating not only because of their diversity and sophistication, but also because they are uniquely suited to fitness costs and consequences of the situation in which they are employed. Pheromones regulating reproduction were designed to solve a conflict between individuals with different interests. They are often nonvolatiles, depending on direct contact between the emitter and receiver and correlate with individual quality. As such, they are predicted to rely heavily on mechanisms insuring honesty and compatibility between the social context and the signal. Unfortunately, studies examining the role of social context in the perception and responsiveness to pheromones are still limited. Pheromones regulating maintenance tasks often bear no conflict and aim at optimizing the performance of a task between individuals with shared interests. They rely on the synchronized action of many individuals, and erroneous response of one or few individuals is not likely to result in a great loss of fitness. These signals are not predicted to rely heavily on mechanisms ensuring honesty or social context, but instead rely on compatibility with the situational context and require efficiency and flexibility, that can be achieved using mechanisms such as activator– repressors that allow quick and accurate responses. Finally, regulatory mechanisms of pheromones provide an excellent example of selection acting on multiple levels and continuing evolution and refinement of both individuals and collective behavior.

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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