CHAPTER FOUR

One problem, many solutions: Female reproduction is regulated by chemically diverse pheromones across insects

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Abstract

The reproductive division of labour in social insects is a fascinating phenomenon regulated by diverse chemical signals that vary substantially in structure. Is this diversity an example of one problem (reproductive regulation) and many potential solutions (diverse chemicals)? Or are there hidden shared elements in the pheromonal regulation of reproduction across insects? To address this question, I will first discuss the phenomenon of reproductive division of labour in social insects, particularly, the reproductive conflicts among females and the means by which these conflicts are resolved. I will then focus on the use of pheromones, a mode of communication that has broadly diversified among social insects that live in large complex societies. I will summarize the different approaches to define semiochemicals in the context of the reproductive division of labour and review the state of knowledge of compounds regulating insect reproduction, both solitary and social, demonstrating the structural diversity as well as the potential conservation of the mechanisms regulating signal production and perception. Lastly, I will discuss the different hypotheses underlying the evolution of pheromones regulating reproduction in insects. Our current understanding of reproductive signalling, while extensive within single species, is still limited by the paucity of comparative studies across the Insecta as a whole, and further investigations are sorely needed.

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1. Introduction

The process of producing offspring is a key mechanism of evolution, and animals evolved sophisticated ways to optimize their reproductive success by tuning in to signals from the environment, rivals, predators, cooperators, and even from their own offspring. Insects, both solitary and social, provide a unique opportunity to understand whether there are shared elements in the signals that insects use in order to optimize their reproduction, or whether this is a classic example in evolution for a shared problem with many creative, lineage- or species-specific solutions.

Signalling mechanisms, particularly chemical signalling, diversified in social insects where reproduction in some species is monopolized by one or a few females, and provide a window to understanding the nature and diversity of the signals, and insights into the way that social insects likely evolved from solitary ancestors.

2. Reproductive division of labour in insect societies

The fundamental characteristic of social species is reproductive division of labour (RDOL) between dominant females who largely monopolize reproduction, and subordinate females who become helpers (Wilson, 1971). Subordinate females either forgo reproduction entirely, or substantially reduce their reproductive output in favour of helping the dominant female(s). This phenomenon spans a gradient of conditions ranging from a small reproductive skew in favour of a few dominant females up to the most extreme cases of insect societies where a single female monopolizes reproduction while the remaining females (workers) are functionally sterile.

Sterile workers often specialize in performing tasks supporting the reproduction of the queen such as caring for the brood, cleaning, foraging, and guarding. In some species, workers have lost the ability to mate and/or reproductive organs (e.g., spermatheca). Workers have also developed morphological traits to help them master the helping tasks, such as large mandibles in solider termites which enhance their defensive abilities (Deligne et al., 1981), or a swollen abdomen that turns honeypot ants into living larders (Conway, 1986).

Superficially, RDOL is a puzzling phenomenon because forgoing selfreproduction in favour of another individual seems to negate the basic principles of natural selection. Moreover, at the molecular level, a reproductive skew between females requires the transfer of genetic traits which encode behaviours that seemingly sabotage their own inheritance, raising the question of how such complex behaviours are inherited and maintained in the population. Many theories have been formulated to address these questions, with some of them based on the inclusive fitness that individuals gain from helping relatives (Hamilton, 1964), group benefit (Wilson, 1983), future individual benefit (Smith, 1979), and other characteristics. These are discussed at length elsewhere [for example: (Birch and Okasha, 2014; Kramer and Meunier, 2016; Leigh, 2010; Liao et al., 2015; Wilson and Holldobler, 2005)] and are not the focus of the current review. The evolution of RDOL can be partially explained in the ecological success of social insect species. The ability to compartmentalize

reproduction gave rise to a variety of complex cooperative behaviours which underlie the ecological dominance of social insects in the animal world (Wilson, 1990). Termite queens for example, can lay up to 18,000 eggs per day (Kaib et al., 2001), an extraordinary reproductive output that allows specialization within the sterile caste and higher efficiency in performing tasks. Task specialization in the sterile caste of ant societies is largely responsible for their great diversity and abundance. A few examples of this specialization are temporal polyethism (i.e., the tendency to change task with time/age) in ants and bees (SchmidHempel and Schmid-Hempel, 1984; Seeley, 1982), and polymorphism (i.e., different body sizes and morphologies as a function of task) in many ant species (Wills et al., 2018).

3. Reproduction by female insects

To review semiochemicals regulating reproduction, it is necessary to first define female reproduction. Reproduction is a very broad term that can apply to any behavioural, physiological, and molecular changes that occur in insect females before, during, and after egg-laying. This may include behaviours optimizing reproductive success such as finding a mate, mating, nesting, searching for proteins, or establishing a reproductive hierarchy. It also includes physiological changes related to the production and maturation of eggs (e.g., resource allocation), and regulatory events orchestrating both behavioural and physiological changes such as shifts in levels of hormones and neuro-hormones. For the purpose of this review I will focus on semiochemicals that regulate female oogenesis (ovary activation), ovulation (the release of oocytes from the ovary to the oviduct), and oviposition (egg- laying behaviour). The physiological and molecular mechanisms regulating female reproduction across insects were recently reviewed by (Roy et al., 2018), specifically the role of hormones (juvenile hormone (JH) and ecdysteroids), nutritional signalling pathways (e.g., Amino Acids/Target of Rapamycin and Insulin Pathways), and microRNAs, in regulating reproduction by female insects at the molecular level. Other reviews have covered the hormonal regulation of female reproduction in depth (Raikhel, 2005; Wyatt and Davey, 1996).

Oogenesis, ovulation, and oviposition are relatively simple physiological processes with known regulators, that are typically stimulated by intake of nutrients that leads to the production and release of neurohormones and insulin-like peptides (ILPs) from the brain and several other tissues, such as the gut and the reproductive tract. The role

of ILP's in regulating reproduction in insects is relatively conserved and well established (Raikhel, 2005; Roy et al., 2018; Wu and Brown, 2006). The role of neurotransmitters, neuromodulators, and neurohormones in regulating reproduction has been shown in many insect species (Raabe, 2012). Neural activity is followed by hormonal activity, mostly release of JH and ecdysteroids (Hardie, 2018). JH, the main gonadotropin in insects, is produced and released to the hemolymph by the corpora allata glands (Noriega, 2014) and affects the uptake of vitellogenin (the main yolk protein in females) into the ovaries. Ecdysteroids, steroid hormones that are produced in the prothoracic glands of larvae to control moulting, or in the follicle cells of the ovaries, regulate vitellogenesis and oogenesis in adult females. This includes the transfer of vitellogenin from the hemolymph into the ovary and egg maturation, resulting eventually in egg-laying behaviour. Any of these neural and hormonal mechanisms can become a regulatory switch on which semiochemicals affecting female reproduction can operate.

4. Reproductive conflicts across insects

Reproductive decisions in insects, as in all animals, are shaped by conflict: conflict between sexes, generations, and individuals over access to reproduction or resources. Solitary insects comprise the most simple system to demonstrate this. There, decisions about reproduction are individual and based upon information produced by other individuals with complimentary or conflicting reproductive interests (e.g., males, brood, predators, and competitors) (Billeter and Wolfner, 2018), or information associated with food quality or oviposition sites.

Conflict between males and females is ubiquitous among insects and may occur before mating (over mate choice), during and after mating (over mating frequency and fertilization, number of mating partners, egg production, and the number of offspring) or after reproduction (over relative parental effort and parental care). Both sexes are expected to evolve suites of adaptations that bias the outcome towards their own interests (Chapman et al., 2003).

Conflict between parents and offspring is centered around investment in the existing brood versus future opportunities of the parents to reproduce. Insect larvae that are progressively provisioned often influence food allocation by begging, resulting in females caring for brood at the expense of future reproduction. Such a trade-off has been broadly shown across insects of differentsocial organizations(Bigley andVinson,1975;Ebieetal.,2015;Endler et al., 2004; Engel et al., 2016; Hunt and Simmons, 2004; Kolliker,€ 2007; Maisonnasse et al., 2010;

Tallamy and Denno, 1982; Villalta et al., 2015; Woodard et al., 2013; Zink, 2003). Conflict over parental investment also provides opportunities for sibling rivalry (Trivers, 1972).

Reproduction may also involve conflict over resources, such as food and oviposition sites, with conspecific reproductive females. Multiple studies in diverse solitary species showed that marking by females deters conspecific females from exploiting food resources and oviposition sites (Frankie and Vinson, 1977; Roitberg and Prokopy, 1987; Schoonhoven et al., 1981; Stelinski et al., 2009). Interestingly, competition over scarce oviposition sites is apparently one of the factors driving incipient sociality in some bee species (Rehan et al., 2014; Richards, 2011; Velthuis and Gerling, 1983).

Competition between females reached new levels of complexity in social insects, as compared to solitary insects. At first glance, it seems as though social insects exist in perfect harmony. However, below the surface there are multiple reproductive conflicts among females (Bourke, 1988; Heinze, 2010; Ratnieks et al., 2006), and although decisions regarding reproduction may seem altruistic, they too are shaped by considerations of fitness that ensure their evolutionary stability. Here, reproduction is shaped by conflicts with males, competitors, brood, and over resources, but is also affected, and to some extent intertwined with cooperative behaviour among females. Species exhibiting simple sociality (e.g., sub-social or primitively eusocial) vary greatly in their sociobiology and all females retain the ability to reproduce, but they all share some reproductive skew among females (Michener, 1974). Partial reproductive skew is maintained either throughout the life cycle (i.e., a few dominant females share reproduction, e.g., Ponerine ant species, Polistes wasps), temporarily (i.e., helper daughters remain with their mother, e.g., Ceratina species), or seasonally (i.e., a single queen that monopolizes reproduction for only part of the life cycle, e.g., bumble bees). Access to reproduction in simple social species is often achieved by behavioural means and the establishment of linear dominance hierarchies (Appleby, 1983; Cant and Field, 2005). The establishment of behavioural dominance is often coupled with chemical signalling (Kocher and Grozinger, 2011). If a female is not in a social position to reproduce, she may benefit from responding to cues/signals from a dominant female by postponing her reproduction or benefit indirectly through rearing relatives or groupmates. Many, but not all, simple social species have an annual life cycle which includes a solitary phase for the founding female in relatively small-size colonies (up to 1000 individuals and frequently many fewer than that), limited

morphological differences between castes (or lack of castes), and a weak division of labour among helpers. These factors allow a much less rigid dominance hierarchy, as compared to advanced eusocial species, and the reliance on aggressive behaviours for regulating reproduction.

Complex or advanced eusocial insect groups, as compared to solitary and simple social insect groups, display extreme reproductive skew where one or a few fecund females are heavily outnumbered by subordinate helpers. In these species another dimension of conflict is added – a conflict between subordinate helpers and reproductives. Some subordinates may strive to challenge the reproductive hierarchy and act selfishly (as in simple social species), while others benefit most from preserving reproductive monopoly of the dominant and will police pretender females who challenge the dominant, ultimately discouraging individuals from acting selfishly (Wenseleers et al., 2004). In many advanced eusocial insects, helper workers reached "a point of no return" (Wilson and Holldobler, 2005) and will not reproduce even in the absence of the queen. Some of these conflicts stem from the haplo-diploid mechanism for sex determination which creates asymmetries inrelatednessbetweencolonymembersand,therefore,intheirinterestinself reproduction vs. helping behaviour (like in ants, social bees and wasps, and social aphids) but are not limited to haplodiploid species (e.g., termites, social ambrosia beetles). The main challenge in these advanced eusocial societies is thus to keep the social structure cohesive by preventing unproductive competition between egg layers and new reproductive females, and by regulating task allocation and division of labour to support the reproductive output of the dominant female.

It is important to note that reproduction in both solitary and social species is often regulated concurrently by multiple factors, rather than by a single one. In some eusocial insects, for example, reproduction is often regulated indirectly, at multiple levels, by multiple factors and members of the colony. Bumble bees (Bombus impatiens, Bombus terrestris) and honey bees (Apis mellifra) are perhaps the best-known examples. In bumble bees, the queen inhibits worker ovary activation and egg-laying (Amsalem et al., 2017; Duchateau and Velthuis, 1988; Padilla et al., 2016), the workers regulate each other's reproduction (Amsalem and Hefetz, 2010; Amsalem and Hefetz, 2011; Bloch and Hefetz, 1999), and the presence of the brood also regulates worker egg-laying (Orlova et al., 2020a; Starkey et al., 2019a). The queen, workers, and brood use a combination of physical coercion and chemical signalling to regulate reproduction (Amsalem et al., 2009, Amsalem and Hefetz, 2010; Ayasse

and Jarau, 2014; Orlova et al., 2020a,b; Starkey et al., 2019a, 2019b), and the regulation by the different colony members is limited to specific phases during the colony life cycle (Amsalem et al., 2015a; Duchateau and Velthuis, 1988). On top of that, it was recently shown that different members of the colony target different aspects of reproduction in workers. While B. impatiens queens inhibit both ovary development and egg-laying in workers, young larvae can only reduce worker's egg-laying (but not ovary activation), while the presence of pupae increases egg-laying behaviour in workers (Orlova et al., 2020a; Starkey et al., 2019a,b).

The types of conflicts between females in social species vary greatly (Ratnieks et al., 2006, Heinze, 2010), but undoubtedly the main conflict between females is over production of males (Hammond and Keller, 2004). Hymenopteran workers in societies with a single, singly-mated queen are often incapable of mating, but nevertheless are able to lay haploid eggs that develop into males, and while their reproductive interests align with the queen in rearing females to which they are highly genetically related due to the haplo-diploid mechanisms for sex determination (relatedness of 0.75 to other females if the queen is singly mated), they do not benefit as much from rearing the queen's or their sisters' sons (relatedness of 0.5 and 0.38 to brothers and nephews, respectively) (Hamilton, 1964).

Another potential conflict between workers and queens arises from the timing of production of sexuals. In species with an annual life cycle where worker reproduction occurs towards the end of the season and caste is determined by the queen (e.g., bumble bees), workers may be forced to postpone reproduction until the queen starts producing sexuals, specifically gynes. To reduce the time window available for worker reproduction, queens have an incentive to produce gynes for only a short period and towards the end of the season, preventing workers from initiating reproduction of males (Alaux et al., 2006). In species where there is unequal relatedness between workers and future gynes, such as the honey bee where the queen mates multiple times with numerous different males (Kraus et al., 2005), workers may be conflicted about gyne rearing, are able to detect developing gynes from the same father, and exhibit nepotism towards rearing gynes of their own paternal line (Noonan, 2010; Page et al., 1989).

Workers and queens may also conflict over the preferred sex ratio (Trivers and Hare, 1976). Even in species where the workers are fully sterile and the queen produces both sexes, the genetic relatedness of workers to brothers and sisters is not equivalent. In societies with a single,

singly mated queen, workers are three times more related to sisters (r ¼0.75) than to brothers (r ¼0.25), therefore their reproductive interests dictate an optimal sex ratio that is skewed 3:1 in favour of sister gynes. This however conflicts with the queen's best interest, which is to have a sex ratio close to 1:1 because she is equally related to both sons and daughters. As a result, both sides may try to bias the sex ratio in their favour by, for example, eliminating males or by manipulating female caste determination.

These are only some of the examples for reproductive conflicts within insect societies because numerous factors contribute to these conflicts, such as a species' life history (e.g., whether they are perennial or annual), their sociobiology (e.g., the number of queens in the colony and the number of times they mate), their ecology (e.g., temperate vs tropical species), as well as on other factors (e.g., colony size, level of sociality). However, whatever these conflicts are, the ways by which they are resolved provides insights into the maintenance and evolution of insect societies, and the regulation of reproduction in social species as compared to solitary ancestors. A detailed comprehension of these conflicts and their resolution is key to understanding the dynamics of social insect societies.

5. Resolution of reproductive conflicts

Reproductive conflicts are often settled by means of communication. The most common means of communication is aggression. For example, B. impatiens queens use aggressive behaviour as their primary means of monopolizing reproduction in relatively young colonies with low numbers of individuals (Orlova et al., 2020b), and groups of workers without a queen in both B. impatiens and B. terrestris use aggression to establish a reproductive hierarchy (Amsalem and Hefetz, 2010; Amsalem and Hefetz, 2011; Amsalem et al., 2013a; Duchateau and Velthuis, 1989; Orlova and Amsalem, 2019; Padilla et al., 2016; Van Doorn, 1989). Ants, such as Diacamma species, where there is no queen, use physical aggression to claim dominance and monopolize reproduction (Monnin, 1999), and social wasps use aggression to determine reproductive and dominance hierarchies (Jandt et al., 2013). These behaviours translate into physiological changes in the reproductive status of the dominant female which are mediated by hormone and/or biogenic amine levels (Okada et al., 2015; Tibbetts and Huang, 2010). Aggression is a simple and honest way to communicate reproductive and behavioural superiority, but it is also costly and requires physical interactions with every female in the

colony, which becomes increasingly less feasible as colony size increases (Kocher and Grozinger, 2011; Orlova et al., 2020b). Thus, it is not surprising that aggression as a means of regulating RDOL is characteristic of societies with a low level of complexity, where the interactions between individuals are frequent and the number of individuals in a group is relatively small, ensuring that the dominant female(s) have access to each potentially subordinate female and is/are capable of reinforcing the dominant behavioural signal over time.

Other modalities of communication to resolve reproductive conflicts include visual, auditory, chemical, and contact signals. Visual signals, either static or dynamic, are fairly common in insects. They are simple to exhibit and perceive for both the producer and receiver of the signal and provide honest information because they are hard to fake. For example, courtship and mating behaviours in Drosophila melanogaster are largely mediated by visual signals (Spieth, 1974). In the social wasp Polistes satan, where nests are founded by 1–18 females, the dominant female uses facial markings as visual signals that transmit information on fertility and social dominance to subordinate nestmates which function as helpers (Tannure-Nascimento et al., 2008). In the congener Polistes fuscatus, females have highly variable yellow markings on their faces that allow recognition of individuals (Tibbetts, 2002). It was shown that helper females are rewarded with a fraction of the colony reproduction and the dominant female monitors and punishes cheaters that try to exceed their share in reproduction (Reeve and Nonacs, 1992; Reeve et al., 2000).

Auditory signals and hearing were described in many insect species such as grasshoppers, crickets, katydids, beetles, moths, bees and mosquitoes (Greenfield, 2016). The honey bee waggle dance is perhaps the best known example for auditory (and visual) communication, and a recent study also demonstrated that honey bee gynes use toot and quack signals during swarming to ensure that the parental colony is always left with at least one mature gyne after a swarm (headed by the old queen) has departed (Ramsey et al., 2020). However, compared with other modalities of communication, little is known about the use of auditory signals in the context of reproductive signalling. More common is vibrational communication in insects, i.e., the ability of some species to produce and detect substrate-borne vibrations. These were described mainly in the context of mating behaviour and reproductive conflicts between parents/caregivers and offspring (Cocroft and Rodrı´guez, 2005; Yack, 2016). For example, late instar larvae of Vespa orientalis wasps signal to adult workers for food via a rhythmic hunger signal (Ishay and Landau,

1972). Whether these signals also affect worker reproduction is unknown but brood care trades off with reproduction in many insect species (Schultner et al., 2017; Starkey et al., 2019a).

Beside aggression, chemical signals are by far the most common signals in insects and are particularly common for resolving reproductive conflicts in social insects. In many insect species, females often produce volatile pheromones indicating their readiness to mate while males produce pheromones attracting the females (Jacobson, 1972). Multiple insect orders provide ample examples for such reproductive signalling, particularly Lepidoptera, Coleoptera and Hymenoptera (Jacobson, 1972). Reproductive status of females in insects is also communicated via their cuticular hydrocarbon composition which differs in quantity and sometimes also in quality between reproductive and non-reproductive females (Blomquist et al., 2018). For example, in the blowfly Chrysomya putoria, age is communicated via cuticular hydrocarbons (CHCs) (Braga et al., 2016), and in D. melanogaster, mate quality, presence, and identity are communicated to the opposite sex via CHCs (Billeter and Wolfner, 2018). Such signals have been shown not only in many solitary species, but also in social ant, wasp, and bee species (Blomquist and Bagne`res, 2010; Blomquist et al., 2018). Queen pheromones and signals, as well as worker specific-signals, were shown to regulate worker reproduction in several social species (Hefetz, 2019; Le Conte and Hefetz, 2008). More information about these signals, their chemical structure and diversity is discussed in Sections 6–8.

Some chemical signals require physical contact in order to be perceived, which introduces an additional level of "cheat-proofing." For example, both B. terrestris and B. impatiens workers form a reproductive hierarchy only if physical contact with nestmates, either the queen or other workers, is allowed. Workers' reproduction is inhibited by the presence of the queen or other dominant workers, however, in experiments where workers were separated from other workers (Amsalem and Hefetz, 2010) or from the queen via a mesh (Padilla et al., 2016), worker reproduction was not affected, showing that actual physical contact is required. Worker egg-laying in B. impatiens is also inhibited by the presence of brood. However, visual or chemical cues from the brood were not enough to induce the inhibitory effect, and the key factor for the regulation of female reproduction by brood is still under investigation (Starkey et al., 2019b).

All modalities of reproductive signals have one requirement in common—they all have to be honest. Honesty is a basic requirement for any signal to become stable over evolutionary time because dishonest

signals are putting their receiver at a disadvantage and will eventually go extinct— together with the gullible receivers (Heinze and D'ettorre, 2009; Smith and Harper, 2003; Van Zweden, 2010; Zahavi, 1975). Honesty is especially important in signals regulating reproduction in social insects (Orlova and Amsalem, 2019), due to the fundamental conflict between the sender (who wants to manipulate the receiver's reproduction) and receiver (who will forgo reproduction only if it enhances its own fitness), and the potential loss of fitness associated with cheating (Riehl and Frederickson, 2016). That being said, cheating is not rare, and cheaters were described in every insect order. Workers of the cape bee, A. mellifera capensis lay eggs despite the queen's presence (Jordan et al., 2008), lower quality cricket males mate despite avoiding costly reproductive signalling by adopting satellite strategies (Cade, 1980), and slave making ants exploit honest signalling by mimicking the host cuticular profile when invading the host (Brandt et al., 2005). These examples may suggest that despite the importance of honesty, under some conditions cheating may be advantageous, and chemical signalling is shaped by an arms race between the signal producer and the receiver (Heinze and d'Ettorre, 2009).

6. Insect semiochemicals: historical perspectives and definitions

Semiochemicals broadly refer to two types of signals: allelochemicals (such as kairomones, allomones and synomones, Table 1) that are produced by one species and typically perceived by members of another species, or pheromones that are both produced and received by members of the same species (Nordlund and Lewis, 1976), although eavesdropping by heterospecifics may occur. The original definition of 'pheromone' was proposed by Karlson and Luscher (1959) as a chemical signal that carries a message to another organism of the same species and elicits a response. These signals presented an extraordinary opportunity to gain some understanding as to how social behaviour is maintained and evolved. However, the more we learned about the signals' identity, regulation, and mode of action, the more it was necessary to refine the basic definitions to account for their diverse meanings. The first refinement relevant to the definition of pheromones was made between cues and chemical signals, and was based on the question of which organism is likely to benefit from the message (Otte, 1974). Cues, like signals, convey information to another organism (and elicit a response), but, unlike signals, they were not shaped by natural selection for that purpose and do not benefit the signal producer (Bradbury and

Vehrencamp, 2001; Wyatt, 2010). Instead, they are being exploited by individuals which may benefit from the information they carry.

In contrast to cues, chemical signals have been shaped by natural selection for the purpose of mutually beneficial communication, and the response to a signal must result in fitness consequences that, on average, enhance the fitness of both the signaler and the recipient. Signals are thus expected to be specific to the message they convey, and to be reliable and honest so as to protect them from potential cheaters (Dawkins and Krebs, 1978). The problem of honesty yielded another set of refinements: signals were divided based on the type of information they convey (either about self or about others) (Hasson, 1994), the reliability of the signal as expressed by its cost (minimal signal vs. cost-added signal), and the type of relationship the signal has with the object it represents (symbol, icon, and index, Table 1) (Smith and Harper, 1995). These refinements may sound like a semantic argument but in fact hold a deep significance to the way these different signals evolved. Index, for instance, suggests that the signal is inherently linked to a physiological process and is thus honest by nature, while a symbol does

Table 1 Definitions of selected semiochemicals.

Cue	A chemical in the environment that provides information to a receiver.
Pheromone	A chemical signal that conveys information and elicits a response in recipients of the same species. On average, both sender and receiver benefit.
Kairomone	A chemical signal that benefits a recipient of a different species.
Allomone	A chemical signal that elicits a response in a recipient of a different species and benefits the sender.
Synomone	A chemical signal that elicits a response in a recipient of a different species and benefits both the sender and recipient.
Self-reporting signal	A chemical signal that provides information about some property of the sender.
Other-reporting signal	A chemical signal that conveys information about an object or organism other than the sender.
Minimal signal	A chemical signal whose cost is as low as it can be while still conveying information.

Cost-added signal	A chemical signal that is more costly to produce than the minimum required to transmit the information.
Index	A chemical signal that is physically associated with the information it conveys.
Icon	A chemical signal whose form is similar to the content it represents.
Symbol	A chemical signal whose form is arbitrarily linked to the object it represents.
Queen control/queen pheromone	A chemical signal produced by the queen or dominant female for the purpose of inhibiting reproduction in subordinates.
Fertility signal; Queen signal	A chemical signal produced by the queen or dominant female that honestly reflects her physiology and advertises her fecundity, and elicits a response in subordinates (not to be confused with compounds that correlate with reproductive status but which have not been shown to induce a response in the receiver).
Worker signal	A chemical signal produced by workers that varies with their physiology and advertises their fertility or sterility.
Signature mixture	A variable chemical mixture learned as a template by other conspecifics and used to recognize an animal as an individual or as a member of a particular social group.

not hold such a meaning. Honesty can be achieved also by the cost of the signal, dictating that only capable individuals can produce an optimally effective signal, while a minimal signal does not hold a cost (Zahavi, 1975).

Another subtle distinction that applies specifically to chemical signals used by social insects was offered by Keller and Nonacs (1993) who divided chemicals produced by the queen (or the dominant female) that regulate worker reproduction into two categories: queen control and queen (fertility) signals based on the type of effect that they induce in workers (coercive vs. information, Table 1). Distinguishing between queen control and queen fertility signals in this context can be difficult because both evolutionary scenarios lead to similar outcomes, namely reproductive inhibition in the subordinates. One confusion arising from this distinction is the potential interpretation of these two scenarios. Certain studies interpret the term “queen pheromones” as control substances that do not necessarily honestly reflect the physiology of the female, and “queen

fertility signals" as honest signalsthatreflectthequeen'sphysiology.Bothtypesofsignalsinducereproductive inhibition in workers (Amsalem et al., 2015b; Amsalem and Grozinger, 2018). However, others studies use the term "queen pheromones" for any chemical correlating with reproductive status in females regardless of its mechanism of action (i.e., whether it is coercive or provide information and whether it is able to induce a response in workers or not) (Holman, 2018a). Keller and Nonacs (1993) noted that a manipulative queen pheromone is unlikely to evolve because it would put workers at a disadvantage in terms of fitness and set off an arms race between the queen and the workers, a condition that is not likely to be stable over evolutionary time (Smith and Price, 1973). Indeed, experimental data mostly support the queen signal over the queen control hypothesis (Smith and Liebig, 2017; Villalta et al., 2018).

Finally, the most recent debate about the potential of CHCs to function as manipulative queen pheromones (Amsalem and Grozinger, 2018; Amsalem et al., 2015b; Holman, 2018b; Smith and Liebig, 2017; Smith et al., 2018; Van Oystaeyen et al., 2014) resonates with another refinement made by Wyatt (2010) regarding the composition of the signal, drawing the line between a "pheromone," which elicits innate responses (but can also be conditional on development, context, experience, and internal state) and a "signature mixture," which is a variable subset of molecules of an animal's chemical profile that are learned by other animals. A recent paper by Smith and Liebig (2017) suggested an evolutionary framework for the transition of reproductive communication from cue-like signature mixtures to learned fertility signals to innate queen pheromones as a function of the size of the social colony (Smith and Liebig, 2017). While these different approaches refine the definition of a pheromone/chemical signal, it is important to note that its original meaning has not changed and thus can be discussed across insect species based on three simple assumptions: (1) a signal is a compound or a blend produced by signalers, which evolved for the purpose of conveying information to recipients; (2) a signal elicits a response in recipients (either immediate or delayed), and (3) a signal results in fitness consequences that are valuable to both the signaler and the recipient [modified from (Laidre and Johnstone, 2013)].

7. Diversity and conservation of cues and pheromones regulating reproduction in insects

Chemical signals in insects have been extensively studied, and numerous reviews and books have summarized our knowledge of chemical signalling in animals. However, signals regulating reproduction were mostly reviewed within social insects (Hefetz, 2019; Oi et al., 2015), in Hymenoptera (Le Conte and Hefetz, 2008) or within a subfamily of bees (Caliari Oliveira et al., 2015), and none of these reviews focused exclusively on reproductive cues and signals across insect species. Separately, there are many reviews on the cues and signals involved in regulating the reproduction of solitary insects, particularly of oogenesis, ovulation and oviposition behaviour. The missing link is, thus, the comprehensive examination of reproductive signals in both solitary and social species.

In solitary insect species, semiochemicals regulating reproduction are likely to provide information about availability of food and oviposition sites (e.g., environmental derived cues), as well as presence or absence of competitors and mates (e.g., sex and aggregation pheromones). In species exhibiting simple social systems (mostly hymenopteran) where several females share a nest and compete over limited resources and access to reproduction (Michener, 1974), signalling is likely to be centered around the dominance hierarchy between females, dictated by the availability of resources, as well as the presence, quality, and fecundity of potential rivals, and their readiness to cooperate. In advanced eusocial species, where a single female monopolizes reproduction while the rest of the females function as sterile helpers, chemical signals reflect the fecundity and superiority of the reproductive female, to limit or prevent oogenesis and oviposition by subordinate females and to maintain acohesivesocialstructure.Tounderstandtheevolutionofthelatter and to draw meaningful conclusions about pheromone conservation and diversity, it is necessary to expand our investigation beyond social species and trace the origin of signals in solitary insects.

Tables 2A and 2B list examples for compounds that have been found to have a role in regulating female oogenesis, ovulation, and oviposition in various insect taxa, both social and solitary. Table 2A focuses on insect produced signals while Table 2B focuses on environmental cues. Oogenesis, ovulation, and oviposition in this context included changes in the following parameters: ovary size (a numeric value representing the size of the oocyte in the ovaries), ovary development (a categorial value representing whether ovaries were developed or undeveloped), and egg

laying behaviour. The parameter "oocyte regression" (reabsorption of the oocyte after it is fully developed) was also included, although it is unclear if it is a form of reproductive inhibition because it was observed in most egg-laying females in several bumble bee species (Amsalem et al., 2015b; Amsalem and Grozinger, 2018; Duchateau and Velthuis, 1989). Some of the compounds listed in Tables 2A and 2B do not regulate ovary development or egg laying directly (e.g., n-C21 in termites). Instead, they regulate social behaviours in the sterile caste of social insects, such as recognition of queens and males (kings), and inhibition of rearing of new reproductives. These were included because in these species, the sterile caste does not reproduce even in the absence of royals, and these signals maintain the social structure as a whole.

The list of compounds in Tables 2A and 2B is only a representative sample of the studies conducted on the regulation of reproduction in insects, but it exemplifies the diversity of cues and signals, as well as the different classes of chemicals that are involved in regulating female oviposition and egg laying behaviour. Complimentary information about semiochemicals exploited by egg parasitoids of Heteroptera was reviewed by Conti and Colazza (2012), oviposition pheromones in haematophagous insects was reviewed by Seenivasagan and Vijayaraghavan (2010), and chemical cues for oviposition site selection by malaria vectors were reviewed by Himeidan et al., (2013). In social insects, there are many studies showing correlations between cuticular chemicals (mostly hydrocarbons) and the reproductive status of females. These correlations suggest that a chemical may be providing an information that can be used as a signal by members of the same species but are not sufficient to demonstrate their communicative role. CHCs primary function is to maintain water balance and prevent desiccation. Subsets of these compounds have been coopted to serve as signals denoting information about individual species, sex and physiology. Thus, they may not necessarily have a communicative role. These chemicals were not

Table 2A Some examples for insect-produced signals regulating reproduction in female insects.

Order	Species	Signal/cue	Class	Producer	Function	References
Hymenoptera	Apis mellifera	9-Oxo-2-decenoic acid (9ODA), cis- and trans-hydroxydec-2-enoic acid (9HDA), methyl hydroxybenzoate alcohol (HOB) and 4-hydroxy3-methoxy phenyl ethanol (HVA)	Ketoacid, hydroxy acid, 9-aromatic methyl ester, aromatic p-	Queens	Inhibited ovarian activation in workers and the rearing of new gynes, attracted workers, attracted males during mating, regulated division of labour	Butler and Fairey (2015), Hoover et al. (2003), and Slessor et al. (1988)
	Apis mellifera	Ethyl palmitate and methyl linolenate and the brood pheromone, E-β-ocimene	Ethyl/methyl esters, Monoterpene	Brood	Stimulated brood care, inhibited ovarian activation, prevented gyne rearing and regulated division of labour in workers	Le Conte et al. (1990, 2001)
	Bombus terrestris	Pentacosane	Hydrocarbon	Females and males	Increased worker egg regression, but not ovary development. Study in B. impatiens showed no effect of c25 on worker ovary size or egg laying	Van Oystaeyen et al. (2014) and Amsalem et al. (2015b)
	Lasioglossum malachurum	18-Octadecanolide, 20-eicosanolide, 22-docosanolide, 24-tetracosanolide	Macrocyclic lactones	Females	Reduced ovary development and increased submissive behaviour by workers	Steitz and Ayasse (2020)

	Vespula vulgaris	Heptacosane, octacosane, nonacosane, 3-methyl-nonacosane	Hydrocarbons	Females	All but octacosane reduced ovary development. All increased ovary regression	Van Oystaeyen et al. (2014)

Continued

Table 2A Some examples for insect-produced signals regulating reproduction in female insects.—cont'd

Order	Species	Signal/cue	Class	Producer	Function	References
	Dolichovespula saxonica	Nonacosane, 3-methylnonaco-sane, triacontane, hentriacontane 3-methylhen-triacontane	Hydrocarbons	Females	Reduced the percentage of workers with activated ovaries	Oi et al. (2016)
	Cataglyphis iberica	Heptacosane, 3-methyl-heptacosane, nonacosane, 3-methyl-nonacosane	Hydrocarbons	Females	All reduced ovary development. All but C29 increased oocyte regression	Van Oystaeyen et al. (2014)
	Lasius niger	3-Methylhentriacontane	Hydrocarbon	Females	Reduced ovarian activation and aggression in workers	Holman et al. (2010)
	Telenomus podisi	A blend of (E)-2-hexenal, terpineol, and benzyl alcohol	Aldehyde, Alcohols	Podisus maculivent-ris males	Egg laying attractant	Bruni et al. (2000)

Isoptera	Reticulitermes speratus	n-Butyl-n-butyrate and 2-methyl-1-butanol	Ester, Alcohol	Female neotenics (secondary queens)	Suppressed the differentiation of new female neotenics; attracted workers, elicited tending behaviours, such as allogrooming and egg care	Matsuura et al. (2010)
	Reticulitermes flavipes	Heneicosane	Hydrocarbon	Queens and kings	Regulated royal recognition behaviours in workers	Funaro et al. (2018)
Coleoptera	Nicrophorus vespilloides	Methyl geranate	Monoterpene ester	Brood	Regulated male copulation, alter JH in females	Engel et al. (2016)
Diptera	Drosophila melanogaster	(Z)-9-tricosene	Hydrocarbon	Males	Oviposition attractant	Lin et al. (2015)
	Drosophila melanogaster	Sex peptide proteins	Proteins	Males	Increased females JH production and stimulated oogenesis	Wolfner (1997) and Kubli (2003)
	Musca domestica	Tricosane and (Z)-9tricosene	Hydrocarbons	Gravid female ovary	Oviposition attractant	Jiang et al. (2002)
	Lutzomyia longipalpis	Dodecanoic Acid	Carboxylic acid	Gravid female accessory glands	Oviposition attractant	Dougherty and Hamilton (1997)

	Culex tarsalis C. pIpIens molestus C. quinquefasciatus	Erythro-6-acetoxy-5-hexadecanolide	Cyclic ester (lactone)	Gravid female (found in eggs)	Oviposition attractant pheromone	Laurence and Pickett (1982)
	Simulium vittatum	(Z)-9-tetradecen-1-ol, 1-pentadecene, and 1-tridecene	Alcohol, Hydrocarbons	Eggs	Oviposition attractant	McGaha et al. (2015)
	Ae. aegypti	Heneicosane	Hydrocarbon	Larvae	Oviposition attractant	Mendki et al. (2000)
	Glossina morsitans morsitans Glossina morsitans centralis	n-Pentadecane and n-dodecane	Hydrocarbons	Larvae	Oviposition attractant	Saini et al. (1996)
	Phlebotomus papatasi	Dodecanoic acid	Carboxylic acid	Egg and larvae	Oviposition attractant	Kowacich et al. (2020)
Lepidoptera	Pectinophora gossypiella	Oleic, linoleic and palmitic acids	Carboxylic acid	Larval faecal pellets	Oviposition repellent	Shah et al. (2020)

Included in the table are compounds that have been chemically identified and were shown to inhibit, reduce, increase, or delay female oogenesis, ovulation, and oviposition, as explained in the text.

Table 2B Some examples for environmental cues regulating reproduction in female insects.

Order	Species	Signal/cue	Class	Producer	Function	References

Lepidoptera	Spilosoma obliqua	Blend of (1) pentacosane, heptacosane, nonacosane, hexatriacontane, palmitoleic acid, linolenic acid; (2) stearic acid, a synthetic blend of pentacosane, hexatriacontane and stearic acid, and (3) a synthetic blend of hexatriacontane, linolenic acid and stearic acid	Hydrocarbons, Carboxylic acids	Leaf surface waxes of three Vigna radiata cultivars, on which the females lay eggs	Egg-laying, short range attractants	Mobarak et al. (2020)
	Trichoplusia ni	Dialkoxybenzene and dialkoxyallylbenzene	Alkoxybenzenes	Plants	Oviposition repellent	Akhtar et al. (2010)
	Ostrinia nubilalis, Spodoptera exigua	Cucurbitacin	Triterpenes	Plants	Oviposition repellent	Tallamy et al. (1997)
	Pieris napi	Glucocapparin, sinigrin, gluconapin. Progoitrin, glucoerucin, glucoiberin, glucosinalbin, glucotropaeolin, gluconasturtiin, glucobrassicin	Glucosinolates	Plants	Oviposition repellent	Du et al. (1995)
Diptera	Drosophila melanogaster	Acetic acid	Carboxylic acid	Overripe fruits	Oviposition attractant	Silbering et al. (2011) and Eisses (1997)
	Drosophila melanogaster	Ethylphenol	Phenol	Yeast produced	Oviposition attractant	Dweck et al. (2015)

Drosophila melanogaster	Lobeline	Alkaloid	Diverse species of Lobelia plants	Oviposition attractant	Yang et al. (2008)
Drosophila melanogaster	Limonene	Monoterpene	Citrus fruits	Oviposition attractant	Dweck et al. (2013)
Drosophila melanogaster	Geosmin	Sesquiterpene	Microbes	Oviposition deterrent	Stensmyr et al. (2012)
Culex quinquefasciatus	3-Methylindole	Indole	Habitat-derived chemical cue	Oviposition attractant/ repellent	Millar et al. (1994)
Culex quinquefasciatus	Egg albumin, lactalbumin hydrolysate, casein hydrolysate and yeast hydrolysate	Protein degradation products	Microbial derived chemical cues	Oviposition attractant	Beehler et al. (1994)
Stomoxys calcitrans	β-Citronellene and carvone	Acyclic monoterpenoids	Donkey and sheep dung	Egg laying attractant	Baleba et al. (2019)
Ceratitis capitata	Linalool	Alcohol	Plants	Oviposition deterrent	Papanastasiou et al. (2020)
Musca domestica	Ethyl palmitate, ethyl linoleate, methyl linoleate, and linoleic acid	Esters, Carboxylic acids	Fermented wheat bran	Oviposition attractant	Tang et al. (2016)

Hemiptera	Aphis craccivora	Blend of pentadecane, tridecanoic acid, and linoleic acid; and blend of pentadecane, docosane, pentacosane, heptacosane, tritriacontane, and linoleic acid	Hydrocarbons, Carboxylic acids	Leaf surface waxes of two cultivar of Llathyrus sativus on which the females lay eggs	Short range oviposition attractants	Mitra et al. (2020)

Included in the table are compounds that have been chemically identified and were shown to inhibit, reduce, increase, or delay female oogenesis, ovulation, and oviposition, as explained in the text.

included in Tables 2A and 2B unless they were shown to affect female reproduction in a controlled bioassay. Additionally, there are many more studies showing attraction or repelling of females to chemical extracts (either signals derived from conspecifics or cues derived from the environment), however, the exact compounds eliciting the effect were not identified. These studies too, were not included in the Tables.

8. Many solutions for the same problem: diverse chemical structures, shared elements, or both?

The compounds in Tables 2A and 2B display substantial chemical diversity, including hydrocarbons, esters, fatty acids, indoles, phenols, alcohols, and alkaloids, and these represent but a small subset of the total chemical space that encompasses chemical cues and signals used by insects. Even within the small group of compounds that have been identified as pheromones regulating reproduction in social insects, compounds vary substantially. Hydrocarbons were repeatedly highlighted in recent years for their conserved role as reproductive signals (Oi et al., 2015; Oi et al., 2016; Smith and Liebig, 2017; Van Oystaeyen et al., 2014). However, the relatively high representation of hydrocarbons within social insects may be attributed to the ease of experimental procedures involving hydrocarbon extraction and identification, rather than to hydrocarbons being over represented as reproductive signals, which may explain the sheer amount of studies focusing on their role. Additionally, even within the limited examples of the hydrocarbons in Tables 2A and 2B, the diversity is large. While most of the examples are of simple straight chain or monomethyl branched compounds (likely due to biosynthetic considerations), they differ in the chain length and methyl branch points, as well as in the role they play in different species.

The diversity of reproductive signals may stem, in part, from their diverse glandular sources (Bru€ckner and Parker, 2020). While cues can be derived from multiple sources such as the habitat, microorganisms, and other species, pheromones are typically produced in exocrine glands. Gland type can explain patterns of chemical usage in one of two ways: on one hand, gland-specific biosynthesis pathways may be optimized for manufacturing specific secretions, but on the other hand, the diversity of glands, the assembly of new enzyme pathways, the combination of different cell types within a gland and repeated loss of glands can all

contribute to diverse secretions (Bru€ckner and Parker, 2020). In most cases, except the honey bee queen mandibular pheromone, the glandular source of reproductive signals in social insects is unknown. For example, pheromones produced by royals in termites have been identified and their effects on the worker caste are well established (Matsuura et al., 2010). However, these pheromones are volatile, and were extracted from the headspace of fully developed female neotenics and their glandular origin remains unknown. In Bombus species, pentacosane (n-C25) was extensively examined for its role in regulating worker reproduction (Amsalem et al., 2015b; Holman, 2014; Orlova et al., 2020b; Princen et al., 2019; Van Oystaeyen et al., 2014,), and while the results across species are still inconclusive (Amsalem and Grozinger, 2018; Holman, 2018b), the glandular source is unclear. Hydrocarbons are typically synthesized in oenocytes cells associated with the fat body or epidermis and are later transported by lipophorins to different glands. However, n-C25 was shown to be present inmultiple exocrine glandssuchasthe mandibular,Dufour's, and labial glands (Amsalem et al., 2009; Amsalem et al., 2015b; Derstine et al., 2020; Hefetz et al., 1996; Orlova et al., 2020b), and is also present on the cuticle of queens (Sramkova et al., 2008), both virgin and mated, young and old (Orlova et al., 2020b), workers of allages and social conditions (Derstine etal., 2020; Orlova et al., 2020b) and also in males (Valterova et al., 2019). Unlike CHCs, compounds such as wax esters were shown to be synthesized within the gland where they are found (Katzav-Gozansky et al., 1997a). In a recent study showing the effect of macrocyclic lactones (i.e., type of esters) on worker reproduction in the halictid bee Lasioglossum malachurum, the authors not only showed increased amounts of these compounds on the cuticle of queens compared to workers and their effect on reproduction, but also conducted a bioassay showing that the glandular origin of these compounds is likely the Dufour's gland (Steitz and Ayasse, 2020). Although this is only one study on one type of social insect, this is a welcome contribution, that further emphasizes the diversity of reproductive signals and their glandular origins. Overall, because only a handful of conclusively identified pheromones have been shown to regulate social insect reproduction, any general conclusion about the chemical classes of compounds that may be used as social signals is likely to be premature at best.

Examination of reproduction-related semiochemicals across different insect species may provide us with two important insights. First, it will be

instructive to determine whether chemical signals regulating reproduction in social insects are structurally related to cues used by solitary females for making reproductive decisions. While a similar structure, by its own, cannot lead to any conclusions about the evolution or conservation of these signals, it may suggest that the underlying biosynthetic mechanisms are conserved. Second, it would be useful to examine whether the mechanisms of action of these compounds are conserved at the level of production and/or perception. Clearly the conservation at the level of perception is easier to demonstrate as the mechanisms for perception of any types of olfactory or gustatory stimuli are highly conserved within Insecta and beyond. Thus, the mechanisms of pheromone production are likely better candidates to explore for their conservation across insects.

The decision of when and where to lay eggs is important for all insects but is crucial for solitary insects, especially ones lacking parental care. While there are many behavioural studies showing that gravid females lay eggs in response to cues or signals (Honda, 1995; Navarro-Silva et al., 2009; Renwick, 1989), only a few of these compounds have been identified. These compounds seem to derive from multiple sources: some are produced by conspecifics or heterospecifics, some are found in the habitat, produced by plant species, or derived from the food on which the female lays her eggs, and some are produced by microbes providing information about the suitability of a substrate to support larval development (McCall and Cameron, 1995; Seenivasagan and Vijayaraghavan, 2010). In tsetse flies, for example, while the pheromone attracting gravid females has not been identified (and therefore was not included in Tables 2A and 2B), females were shown to be attracted to semiochemicals from anal exudate of larvae (Leonard and Saini, 1993). Conversely, in other species larval faecal matter or other larval-derived or female-derived cues deterred gravid females from ovipositing at sites that were already occupied by conspecifics (Renwick and Radke, 1980). Oviposition attractants and deterrent cues/ signals were described in many other solitary species (for references see Tables 2A and 2B). Similar studies have been conducted in social insects. The best example is perhaps in the fire ant Solenopsis invicta, where several studies showed that a putative queen pheromone inhibits wing-shedding and ovary development in virgin queens and is likely produced in multiple exocrine glands including the poison sac, the mandibular glands and possibly other glands (Robert, 1983; VanderMeer and Alonso, 2002; VanderMeer et al., 1980;

Vargo, 1999; Vargo and Hulsey, 2000; Vargo and Laurel, 1994). However, the actual pheromone was never identified. The main question to be answered is, thus, whether we can draw a link between solitary insect reproductive cues/signals and social insect reproductive pheromones.

The biosynthesis of these various chemicals may shed light on how social insect pheromones evolved (Treanore et al., 2020). Despite their diversity, social insect pheromones regulating reproduction are dominated by several classes, namely, fatty acids, hydrocarbons, esters, and alcohols. The biosynthetic pathways that produce these compounds are largely conserved across species. Fatty acids are formed in the fat body from two or three carbon units (acetyl-CoA or malonyl-CoA) in the presence of NADPH and are catalysed by fatty acid synthases, elongases, and desaturases, resulting in long-chain acyl-CoA thioesters. Unbranched fatty acids are formed from acetyl-CoA whereas malonyl-CoA is incorporated to introduce a methyl branch. The most common fatty acids in insects, 16:0, 18:0, and 18:1, can be synthesized de novo in all insects via the activity of lipogenic enzymes. Long chain fatty acids can be shortened to specific chain length, and double bonds (turning saturated fatty acids to unsaturated) are introduced via desaturase enzymes (Stanley-Samuelson and Nelson, 1993; Stanley-Samuelson et al., 1988). Fatty acids are stored as triglycerides in the fat body, and then mobilized as diacylglycerols to other locations. Hydrocarbon synthesis takes place in oenocyte cells associated with the epidermis or fat body (Makki et al., 2014). Hydrocarbons can be broadly divided into three groups: saturated and unsaturated hydrocarbons (n-alkanes and n-alkenes, respectively), and methyl-branched components (Ginzel and Blomquist, 2016). All of these are formed by fatty acyl-CoAs that are elongated to produce very long-chain fatty acids. These are then converted to alcohols by fatty acyl-CoA reductases and ultimately to hydrocarbons by oxidation of the alcohol to an aldehyde and decarbonylation by a cytochrome P450 (MacLean et al., 2018; Qiu et al., 2012). Unsaturated hydrocarbons can be produced from unsaturated fatty acid precursors and then elongated to longer chain fatty acids followed by removal of the carboxy carbon (Millar, 2010). The hydrocarbons are then shuttled to the epicuticle, exocrine glands, and other parts of the insect body, by lipophorin carrier proteins in the hemolymph (Lucas et al., 2004; Makki et al., 2014). Fatty acids can also be reduced to alcohols by fatty acyl-CoA reductases. Wax esters are formed from fatty acids and alcohols and includes the elongation of fatty acids and

conversion of fatty acyl-CoAs to fatty alcohols (Cane, 1983; Esteves et al., 2017). Various enzymes catalyse further steps prior to reduction to selectively shorten or modify the fatty acid chain (by desaturases or transferases), to add a group (by hydroxylases), or to elongate, cleave, or hydrolyze the chain (Cane, 1983; Ginzel and Blomquist, 2016). The final step is typically catalysed by wax synthase. Previous studies demonstrated that fatty acyl-CoA reductase and wax synthase are the key enzymes in the biosynthesis of wax esters (Cheng and Russell, 2004; Li et al., 2008; Teerawanichpan and Qiu, 2010), and that the biosynthesis of wax esters is taking place in the Dufour's gland in at least one case (KatzavGozansky et al., 1997a).

Theenzymessynthesizingpheromonesandthegenescodingforthemare likely conserved, but their diverse combination within a pathway may create diverse pheromone molecules. Several recent studies have demonstrated this principle. For example, insects use a P450 enzyme of the CYP4G family to produce hydrocarbons from aldehydes via oxidation and decarbonylation. Drosophila melanogaster lacking CYP4G1 or NADPH-cytochrome P450 reductase results in flies unable to synthesize CHCs and thus, highly susceptible to desiccation(Qiu et al., 2012). CYP4G sequences and active sites have been highly conserved across insects (Feyereisen, 2020). In addition to the biosynthetic pathways for CHCs being conserved, the mechanisms for their perception are also conserved, and not only among insects but also in many other animal taxa. For example, comparisons of olfactory circuits across insects and mammals show striking similarities in their sensory physiology and neuroanatomy(Benton, 2006), and thenumber and typesof CHCodorant receptors (ORs) were found to have expanded under positive selection (Engsontia et al., 2015). Another interesting example comes from bumble bee males that use diverse unsaturated components (fatty alcohols) in their marking pheromones (which they use to attract females for mating), and these compounds were shown to be synthesized by a conserved family of fatty acyl reductases that has expanded in the Hymenoptera (Bucek et al., 2013; Tupec et al., 2019). And finally, likely the best studied example is from the caste specific compounds produced in the mandibular glands of several honey bee species. These are produced by cytochrome P450 enzymes which regulate the site of hydroxylation, acting on a stearoyl-CoA, a precursor common to caste specific substances of both workers and queens (Hasegawa et al., 2009; Malka et al., 2014; Mumoki et al., 2019;

Plettner et al., 1998; Wu et al., 2017). Overall, while compounds acting as reproductive cues and signals in insects are diverse, there is tantalizing evidence suggesting conservation of mechanisms for their production and perception across insect species, thus opening promising avenues to study the evolution of main classes of signals on a broader scale.

9. The evolution of reproductive signals in insects

Examining the chemical structure of pheromones that regulate reproduction, and their origin, production, or perception across insects can provide insight into the evolution of chemical signals. Comparative studies of pheromone production and perception across insects flourished with the emergence of genomic tools allowing the investigation of the genes involved in these processes. However, these studies mostly focused on social insects. Comparative data on reproductive signalling across both solitary and social insects might be especially useful for tracing the evolution of reproductive signals in general, providing a glance into the origin of these signals and the way they evolved.

Two major hypotheses have been proposed for the evolution of chemical signals in insects (Bradbury and Vehrencamp, 2001; Stokl and Steiger, 2017; Wyatt, 2014a). According to the sender–precursor hypothesis, chemical signals evolved from compounds with no communicative function. Thus, the compound evolved prior to the ability to detect it and/or to elicit a behavioural response. In contrast, the sensory-exploitation hypothesis proposes that signals evolved due to exploitation of a sensory bias to a signal by the sender. Thus, the signal function evolved to match a pre-existing detection ability. Empirical data (not including the wealth of studies on moth sex pheromones) in support of either hypothesis is scarce, but most current data support the sender-precursor theory (Stokl and Steiger, 2017), suggesting that many insect pheromones, including those related to reproduction, evolved from precursors that were byproducts of other physiological processes. Such compounds could be compounds lacking communicative role that are produced by conspecifics. For example, compounds serving as a dessication barrier such as cuticular lipids and wax esters were suggested to evolve communication roles such as sex and nestmate recognition pheromones (Blomquist and Bagne`res, 2010) and reproductive signalling (Amsalem et al., 2009; Derstine et al., 2020; Steitz and Ayasse, 2020;

Steitz et al., 2018). Such evolutionary origin of signals links the signal to the physiology (and thus the quality) of individuals, ensuring inherent signal honesty, robustness, and reliability.

Compounds that are released by the sender and that exploit a preexisting sensory bias in the receiver (the sensory-exploitation hypothesis) can also be selected to become a pheromone. Such compounds could be cues produced by conspecifics but can also be found in the natural environment (e.g., food items for larvae or adults that attract egg laying and repellent components in the substrate such as products of decomposition produced by microbes and fungi; Table 2B). Insects, for instance, may develop perception mechanisms to identify environmental cues and to reproductively respond to them. These perception mechanisms can then be exploited by conspecifics for regulating reproduction. Cues were not shaped by natural selection to serve a communicative function, but if they benefited both the receiver and the producer, they may have been selected for, and evolved, to serve as signals between conspecifics. Some examples for this can be found in pollination systems. Araceae plants, for example, evolved floral volatile organic compounds (VOCs) that attract pollinator scarab beetles. These VOCs were found in non-pollinating beetle groups that are ancestors of pollinating scarabs, suggesting that VOCs may have evolved in Araceae to fit preexisting preferences in the scarabs (Schiestl and Dotterl,€ 2012). Other examples are found in deceptive orchids which mimic the sex pheromones of their pollinators (Schiestl, 2005), and in the orchid, Dendrobium sinense, that exploits another insect signal (Z-11-eicosen-1-ol, serving as the alarm pheromone in the honey bee) to attract hornets for pollination. The hornet (Vespa bicolor) is attracted to both the orchid pollen and to honey bees which she captures as a prey for feeding her larvae (Brodmann et al., 2009). In all of these examples, the perception of the signal evolved earlier than the signal itself. Several more examples are described in Stokl and Steiger (2017), however they are rare and only a few relate directly to reproductive signalling. An interesting example is the ability of the honey bee queen mandibular pheromone (QMP) to inhibit reproduction in distantly related species, mostly D. melanogaster (Carlisle and Butler, 1956; Camiletti et al., 2013; Galang et al., 2019; Lovegrove et al., 2019; Nayar, 1963). Since Drosophila and honey bees do not share the same habitats and are separated by 340 million years of evolution (Lovegrove et al., 2019), it is unclear if the phenomenon is an example of a sensory bias

exploitation (Princen et al., 2019), a unique case where QMP compounds may have evolved to target conserved pathways to repress reproduction, or simply a coincidence. Along the same lines the female Asian elephants release (Z)-7-dodecenyl acetate in their urine, to signal that they are ready to mate. The same compound is the fifth most common attractant for Lepidoptera and serves as a sex pheromone in the turnip looper and the cabbage looper moths (Kelly, 1996).

At the molecular level, chemical regulators of females' reproduction in social insect species are more likely to exploit the well-conserved mechanisms regulating female ovulation/oogenesis rather than to invent new regulatory pathways (Rubinstein and Wolfner, 2014). Such exploitation has been demonstrated in various systems (Leonhardt et al., 2016; Steiger et al., 2011). For instance, one of the queen pheromone compounds in the honey bee, homovanillyl alcohol, is a dopamine mimic (Beggs et al., 2007), able to manipulate worker reproduction, and possibly evolved by exploiting an existent and critical dopamine pathways in worker brains.

Several hypotheses describing solitary species cues that could potentially be hijacked by social species are discussed below. These hypotheses are not mutually exclusive and may have taken place concurrently in the evolution of different species.

9.1 Reproductive signals evolved from oviposition attractants and repellents compounds in the environment

Most insect females lay eggs, and most eggs are laid on top of or inside of the food source which sometimes doubles as an egg cell (Gullan and Cranston, 2004). Attractant cues are useful for finding suitable sites for reproduction among many unsuitable ones, while repellents are useful for identifying unsuited sites to rearing brood. Thus, cues associated with larval food or oviposition sites that function as attractants or repellents for oviposition are likely to be among the most ancient and common regulators of female egg laying behaviour in solitary insects. Mechanism for perception of these cues could be exploited by conspecifics to regulate reproduction in nestmates in social species. Adopting the perception mechanisms for such attractant or repellent cues to mitigate reproductive conflicts and adjust reproductive output in social species can be advantageous, since these cues are physically associated with information valuable to the receiver. Behavioural responses to cues and signals

reflecting the composition and quality of the food/habitat have been demonstrated in multiple species. Cues regulating egg laying have been described in almost every order of insects, suggesting they are widely common. For example, volatile fermentation products in yeasts increase attraction and oviposition in D. melanogaster females (Becher et al., 2012) (more examples below and in Tables 2A and 2B). However, surprisingly, we know very little about their chemical identity in solitary insects and, even less, in social insects. Among the chemical classes in Table 2B, are examples of hydrocarbons,carboxylicacids,alcohols,andesters,butalsomanyothercomp ounds, suggesting that the perception mechanisms to many of these major classes are already in place in solitary insects and possibly also in solitary ancestors. Whether the perception mechanisms for reproductive signals in social insects have evolved from the perception mechanisms for these cues is unknown. Interestingly however, a recent paper found evidence of adaptive evolution withinP450lineagesassociated withfoodprocessinginthe eusocial florivorous Bombus and Apis species but no evidence in the eusocial carnivorous Polistes species (Johnson et al., 2018).

Food and host related chemical cues have been studied mostly in the context of parasitic wasps [e.g., (Tamiru et al., 2015)] and phytophagous insects (Renwick, 1989; Renwick and Chew, 1994) that respond to herbivore-induced plant or host volatiles to locate oviposition sites. A substantial number of studies have focused on dipteran gravid females that locate suitable oviposition sites using various signals, including chemical and tactile cues (Bentley and Day, 1989). These cues vary substantially across species in both their function and chemical structure. They may function as oviposition attractants and/or repellents. For example, volatiles of a wild crucifer (Brassica nigra) are released following oviposition by a generalist moth (Mamestra brassicae), and these volatiles attracted two species of parasitic wasps but repelled the specialist cabbage butterfly (Pieris brassicae) (Fatouros et al., 2012). The chemical structures vary as well: in the parasitic wasp, Cotesia sesamiae, three plant volatiles (E)-4,8-dimethyl-1,3,7-nonatriene, (E)-β-farnesene, and (E,E)-4,8,-trimethyl-1,3,7-tridecatetraene) elicit a behavioural response when tested individually at a natural dose, but many more compounds were active as a blend (Tamiru et al., 2015). Volatiles produced by plants also play a major role in the attraction and landing of gravid lepidopteran females on host

plants, but the induction of oviposition is actually achieved by contact pheromones perceived through the tarsal sensilla after landing (Renwick, 1989). Several such compounds have been identified. For instance, the n-butanol soluble fraction from the crucifer Erysimum Cheiranthoides contains two active compounds (erysimoside and erychroside) that are a strong deterrent to the cabbage white butterfly Pieris rapae (Sachdev-Gupta et al., 1990). In many other cases however, the active compounds remain unknown (Renwick, 1989; Renwick and Chew, 1994).

In Diptera, oviposition is stimulated by cues associated with nutrition (Schwartz et al., 2012) and microbial composition (Ponnusamy et al., 2008) or deterred by cues associated with parasitoids (Dweck et al., 2013). Drosophila melanogaster females are attracted to various infochemicals emanating from suitable larval food such as acetic acid, ethylphenol, lobeline, and limonene (Billeter and Wolfner, 2018).

Food-relatedcuesaffectingfemalereproductionremainlargelyunexplored in social insects, with the one exception of CHCs, which evolved in some social species as reproductive and nestmate recognition signals. Variation in CHC composition occurs through a combination of factors, including, but not limited to, the food items being consumed by the colony, gut microbes, and nest-site material (d'Ettorre and Lenoir, 2010). In the Argentine ant, Linepithema humile, for example, CHCs are modified by diet (Liang and Silverman, 2000). Ants reared on different diets acquired different CHC profilesanddisplayhigheraggressiontowardsnestmatescomparedtoantreare don a shared common diet. CHCs in this species are also used by workers to selectively execute the less fertile queens in the colony (Abril et al., 2018).

The link between food- and habitat-related cues and reproduction is intuitive not only because it provides useful information for places suitable to lay eggs (and rear larvae), but also for the purpose of oogenesis, as many insect females require a protein source (available to them either externally or internally) in order to activate their ovaries. This requirement is naturally attributed to the nutritional value of the food, which directly affects the amino acid-target of rapamycin and insulin pathways that control biosynthesis and secretion of JH and ecdysone. These hormones, in turn, initiate vitellogenesis and egg maturation (Smykal and Raikhel, 2015). The link between nutrients and insulin and hormonal levels is also straightforward (Badisco et al., 2013). However, these pathways may be

activated not only in response to food intake but also in response to cues in the food. For example, in the burying beetle, Nicrophorus orbicollis, JH increases in females within an hour of their discovery of a carcass (Scott et al., 2001). Additionally, exposing D. melanogaster to nutrient-derived odorants from live yeast was shown to reduce lifespan (and therefore reproductive output) and the same effect was achieved when the flies were allowed to consume yeast paste (Libert et al., 2007). In the majority of studies, while nutritional intake and its quality were found to increase ovarian activation in females [e.g., (Bitondi and Simo˜es, 2015; Duchateau and Velthuis, 1989)], no attempts were made to isolate the active compounds that attracted females to a nutritional source, to study the downstream mechanisms in response to food cues, or to separate between the nutritional value of the food and the physiological and behaviour changes stimulated by its odours.

9.2 Reproductive signals evolved from defence related cues

It is hypothesized that some compounds regulating complex social behaviour may have evolved from compounds regulating basal behaviours such as alarm anddefence,whichcanbefoundinsolitarylineagesofwasps,bees(Blum,1969; Wittwer et al., 2017), and aphids (Abbot et al., 2018). This could explain the evolutionofsocialityinspecieswherethesterileindividualsfunctionassoldier s, leading to a potential association between defence related signals (e.g., alarm signals) and sterility (i.e., signals regulating reproduction). Indeed, defence related signals are hypothesized to be the primary route to sociality in aphids, where RDOL involves the production of sterile soldiers, defending their reproductivekinfrompredators(Abbotetal.,2018;SternandFoster,1996).

Alarm pheromones are volatile compounds that cause stereotypical reactions among individuals in the target population and are fairly common across social insect species. Alarm pheromones may function as repellents inducing dispersion, or as attractants in large groups of social insect species with well-organized defences (Blum, 1969). Besides social insects, chemical alarm systems are best developed in aphids, treehoppers and true bugs (Demirel, 2007; Nault and Phelan, 1984), in two of these groups sociality has evolved and is attributed to the evolution of defence-

related cues (Stern and Foster, 1996). While this has been poorly studied and experimental data are scarce, a recent study has shown that aphid soldiers translocate either plant-derived or aphid-derived fatty acids to their adversary when they attack, suggesting a bottom-up, trophic movement of plant-derived metabolites from host plant to aphids to predators that demonstrates how host plant chemistry may shape social traits (i.e., soldiers) in aphids (Abbot et al., 2018).

9.3 Reproductive signals evolved from signals used in the competition between male and females

Female-male conflicts are common in insect species. A particularly important class of chemical signals within this group are sex and aggregation pheromones that are typically species- and sex-specific and are produced to attract a conspecific mate (Wyatt, 2014b). Other signals can be transmitted to the female during mating to affect her reproduction. Drosophila melanogaster males, for instance, produce a set of sex peptides that are delivered to the female during mating and have tremendous effects on her behaviour and physiology, including increased JH levels, decreased female receptivity, and stimulation of oogenesis (Avila et al., 2011; Billeter and Wolfner, 2018).

Sexual selection has long been viewed as a form of social selection (Lyon and Montgomerie, 2012; West-Eberhard, 1979), suggesting that reproduction-related signals in social insects may have evolved from chemical signals originally used for mate choice. The role of sexual selection and mate choice in the chemical communication systems of insects has been recently reviewed by Steiger and Stokl (2014). For instance, many studies published to date, mostly in flies and crickets, have found evidence for sexual selection acting on CHCs (Ferveur, 2005). Sexual conflicts were extensively studied in insect species, providing numerous examples of male-produced substances that manipulate female reproduction (e.g., anti-aphrodisiacs, sex pheromones, semen and nuptial gifts). For example, Drosophila females show increased egg development and reproduction related behaviours following copulation, during which seminal fluid proteins are transferred from males to females along with sperm (Avila et al., 2011; Gillott, 2003). These changes are accompanied by a transfer of several RNAs from males to females and dramatic changes in gene expression in the female reproductive tract following mating (Alfonso-Parra et al., 2016). Anti-aphrodisiacs exist in many species of

insects and are transmitted by the male to the female during mating to render her unattractive to subsequent males (Malouines, 2017). Tephritid males transfer nuptial gifts to females during or after courtship and/or copulation. These nutrients function as either paternal investment or mating effort, leading to increased egg production and maturation in females (Vahed, 1998).

Sex pheromones in insects evolved to serve multiple functions. In some social insects they were suggested to evolve into reproductive signals. The most famous queen pheromone identified so far is in A. mellifera. There, the queen produces a multi-component pheromone in her mandibular glands (Gary, 1962; Gilley et al., 2006; Plettner et al., 1998), inducing multiple primer and releaser effects in workers (Table 2A). The main component of this pheromone (9-ODA) doubles as a long-distance sex pheromone to attract males (Brockmann et al., 2006). Another example is from termites (Nasutitermes takasagoensis), where the queen-specific volatile 2-phenylethanol was suggested to be involved in regulating caste differentiation (Himuro et al., 2011). 2-Phenylethanol, identified in several other insect species, serves as part of the sex pheromone blend of male cerambycid beetles (Lacey et al., 2008) and is also part of the queen-specific compounds of A. mellifera (Gilley et al., 2006), potentially serving as a sex pheromone in gynes. In both examples, whether the signal first function as sex pheromone and only later evolved to regulate worker reproduction is unknown, but the likelihood is high given that complex social behaviours such as worker sterility are an advanced trait of insects.

9.4 Reproduction signals evolved from compounds associated with brood or brood cell lining

Insect larvae that are progressively provisioned by adult conspecifics frequently beg for food and may manipulate the parent reproductive status to accommodate their needs (Mas and Kolliker,€ 2008; Schultner et al., 2017; Trivers, 1972). Numerous studies have shown a tradeoff between maternal care and female reproduction. For example, in earwigs, females caring for larvae lay additional eggs 1 week later, compared to mothers that did not care for brood (Kolliker,€ 2007). Similar tradeoffs between maternal care and reproduction have been shown in treehoppers, between caring for current offspring (egg guarding) and the number of future offspring (Zink, 2003). In B. terrestris, a tradeoff was shown between the

number of times the queen fed the larvae and the number of eggs she laid (Woodard et al., 2013). The tradeoff between care for offspring and the production of new eggs was shown to be regulated by JH in several species, including earwigs, burying beetles and honey bees (Hartfelder and Engels, 1998; Rankin et al., 2008; Scott and Panaitof, 2004; Vancassel et al., 1984).

While the behavioural effects have been extensively studied, the active compounds produced by the brood to manipulate caregivers have been identified in only a handful of species. Culex quinquefasciatus females use a volatile pheromone ((5R,6S)-6-acetoxy-5-hexadecanolide), released by mature egg rafts, to assist in locating suitable oviposition sites (Laurence and Pickett, 2009). In burying beetles, the presence of larvae induces temporary infertility in females that is communicated to the male via a pheromone (methyl geranate) which inhibits further copulation. A shared biosynthetic pathway for the pheromone and JH ensures the reliability of the signal, exemplifying the hormonal and physiological changes that brood may induce in females (Engel et al., 2016). The other examples of brood pheromones are known from advanced eusocial insects, mostly in hymenopteran species (Schultner et al., 2017). In the honey bee, A. mellifera, two pheromones produced by the brood have been identified (Le Conte et al., 1990; Le Conte et al., 2001). The first is a highly volatile compound ((E)-b-ocimene) that is produced by young larvae (and also by queens) and inhibits worker ovarian activation, and the second is a less volatile group known as ester brood pheromones (EBP) composed of ten esters (methyl palmitate, methyl oleate, methyl stearate, methyl linoleate, methyl linolenate, ethyl palmitate, ethyl oleate, ethyl stearate, ethyl linoleate, and ethyl linolenate) that are produced by older larvae. EBP induces several physiological and behavioural effects in workers, such as the delay of behavioural maturation, induction of cell capping, and stimulation of the hypopharyngeal glands, in addition to inhibiting workers' ovary activation (Maisonnasse et al., 2010). In ants, there are several indications for the existence of a brood pheromone (Ebie et al., 2015; Morel and Meer, 1988), but the only major brood-tending pheromone that has been identified is triolein in the fire ant, Solenopsis invicta (Bigley and Vinson, 1975). Triolein is a non-volatile, symmetrical triglyceride with a relatively high molecular weight compared tothe honey bee brood pheromone.

Other brood cues are not directly produced by the brood but may be associated with the brood cells. Long chain hydrocarbons, for example, have waterproofing properties that decrease the loss of water through the cuticle in adults as well as in eggs, when deposited into the egg-cell (Gibbs, 1998). In B. terrestris, the wax from which egg cells are made (composed of hydrocarbons, wax esters, aldehydes, ketones, acetates and others) mirrors the cuticular secretion of the queen and reflects the phases during the colony life cycle (Rottler-Hoermann et al., 2016). These phases are the pre-competition phase where the queen is the sole reproductive and the competition phase where worker reproduction and aggression are common (Amsalem et al., 2015a). When workers were grouped with a queen and wax from the competition phase, they exhibited more defensive and aggressive behaviours and increased ovarian activation compared to workers that were grouped with a queen and wax from the pre-competition phase (Rottler-Hoermann et al., 2016).

The use of CHCs and wax esters as waterproof barriers in association with oviposition and egg-cells can explain their function as fertility signals in many insect species (Caliari Oliveira et al., 2015; Smith and Liebig, 2017). Such fertility signals have been suggested for both solitary and social insect species (Abbot et al., 2018; Billeter and Wolfner, 2018; Dani and Turillazzi, 2018; Korb, 2018; Villalta et al., 2018), supposedly providing information on the female's fecundity (Howard and Blomquist, 2005; Kather and Martin, 2015; Smith and Liebig, 2017) to either nestmate, workers or males. However, in the majority of the cases, no bioassays were conducted and so it is unknown whether these compounds only correlate with female reproduction, or actually serve as a signal.

In several species, hydrocarbons seemed to alter female reproduction only when provided in the correct context (Orlova and Amsalem, 2019). For example, context seemed to play a major role in Odontomachus ant species that form relatively small colonies (Smith and Liebig, 2017). Worker ants of Odontomachus brunneus perceived the fertility signalling compound (Z)-9-nonacosene as such only when it was provided together with the proper chemical background, while the isolated compound failed to inhibit worker ovarian activation (Smith et al., 2015). The importance of context suggests that CHCs are either a byproduct of female fertility, holding no signalling role to workers in social species, or, in the best case scenario, function as informative rather than manipulative signals, providing workers with information on other females' physiology so as to

regulate their own reproduction. Hydrocarbons are abundant and conserved across species (Kather and Martin, 2015) and in some cases have been shown to regulate worker reproduction (Holman et al., 2010; Smith and Liebig, 2017; Van Oystaeyen et al., 2014), but whether they are conserved as fertility signals is still under debate. For instance, in a comparative study of 21 stingless bee species, no associations were found between worker reproductive behaviour and queen CHCs (Nunes et al., 2017). Furthermore, in a meta-analysis of hydrocarbons in Hymenoptera, social and solitary insects showed no difference in the complexity of their CHCs. In fact, some of the most complex CHC profiles were found in the Parasitica (Kather and Martin, 2015), suggesting hydrocarbons' evolution in social insects was limited and that their conservation should be attributed to the physical properties they are associated with.

Finally, brood cell lining compounds are also secreted from the Dufour's gland. In both solitary and social bees, the gland contains mostly hydrocarbons and esters, but in social species (e.g., bumble bees and honey bees) the compounds are caste-specific and are selectively produced by females according to their reproductive status. A group of six octyl esters (octyl dodecanoate, octyl tetradecanoate, octyl hexadecanoate, octyl linoleate, octyl oleate, and octyl octadecanoate) are produced in sterile workers of B. terrestris (Amsalem et al., 2009), whereas another group of esters, mostly dodecyl esters, are produced in workers of B. impatiens (Derstine et al., 2020). In both species, esters are not produced by the queen, and in workers, ester quantity either negatively (B. terrestris) or positively (B. impatiens) correlates with ovary size (Amsalem et al., 2009; Derstine et al., 2020). They are also produced in higher amounts by foragers than by house bees (Amsalem et al., 2013b) and negatively correlate with the aggression received by the dominant nestmate in a pair system (Amsalem and Hefetz, 2010). This suggests that workers produce esters to advertise sterility in order to avoid aggression. In the honey bee, A. mellifera, a group of wax esters are produced by fertile females (Katzav-Gozansky et al., 1997b). These esters were suggested to communicate fertility state to other nestmates as they are produced by both the queen and the workers when they transition to reproduction (Dor et al., 2005; Katzav-Gozansky et al., 1997b). Sterile females that participate in helping behaviour have an interest in supporting the most fecundfemalesovertheircompetitors,givingrisetophenomenalikepolicing, aimed at preventing reproduction by any non-queen female. Indeed,

Dufour's gland secretion in ester-producing workers is used to target and police workers with activated ovaries in the honey bee (Malka et al., 2008; Ratnieks, 2015) and ants (Monnin et al., 2002). Lactones and esters, like hydrocarbons, have water-proofing properties that decrease the loss of water from the brood cell, but may also be used as cues marking the nest entrance or to recognize kin (Cane, 1983). A comparative examination of the chemical profile of halictid bees has shown that chemical dissimilarity between castes is higher in obligate than in facultative eusocial species, especially with regard to macrocyclic lactones (Steitz et al., 2018), and a recent study has shown that lactones (cyclic esters) serve as a queen pheromone in a primitively eusocial halictid bee (Steitz and Ayasse, 2020).

10. Future challenges and directions

RDOL is a hallmark of sociality, and the semiochemicals regulating reproduction in these societies have received much attention in the past hundred years for their potential to shed light on the mechanisms regulating social organization (Beshers and Fewell, 2001; Holldobler and Wilson, 2008). While excellent studies about the identity and nature of these semiochemicals are accumulating, there are key questions that have received little empirical attention: how did these signals evolve? Are their chemical structures conserved across insects? To what extent have the compounds used for communication in social species evolved from these reproductive cues/ signals in non-social species? (Amsalem et al., 2015b; Leonhardt et al., 2016; Steiger and Stokl, 2014; Stokl and Steiger, 2017; Van Oystaeyen et al., 2014). Recent reviews have mostly focused on the evolution of these semiochemicals within social insects exhibiting different levels of social organization (Caliari Oliveira et al., 2015; Mas and Kolliker,€ 2008; Oi et al., 2015; Smith and Liebig, 2017; Symonds and Elgar, 2008), but solitary insects were left out. The challenge in addressing these questions stems not only from the need to take an interdisciplinary approach to identify similarities across a broader range of taxa, a task that might be complex due to the diversity of life histories, ecological constraints, and individual differences among species, but also due to the controversy in defining these semiochemicals and their potential roles in regulating social organizations in social insects.

Social behaviour is characterized mainly by RDOL between females. Identifying shared regulatory mechanisms of reproduction across different

insect species has the potential to generate simple predictions about the potential sources and chemical structures of semiochemicals regulating social behaviour. Several potential sources for these compounds were listed in this review: food, defence, brood, and male-derived cues and signals. Progress in understanding how each of these cues evolved to function as a signal, exploited or adopted by social species, if they did, would be highly useful to start mapping the evolution of insect reproductive signals and pheromones in general.

While the sources associated with signals regulating reproduction and the physiological pathways they target in females may be shared across different taxa, there is great diversity in the chemical structures of these compounds. Insect pheromones encompass a multitude of different chemical classes, and, since our knowledge of pheromones regulating reproduction is still limited, we would be wise to assume the same versatility for these compounds until we gather sufficient data to determine otherwise.

To understand how signals evolved, we also need to map the mechanistic link between potential sources of cues/signals and the resulting physiological processes that regulate females' reproduction. The link may be provided by examining how signals evolved when insect species transitioned from solitary to simple sociality to complex sociality, with an emphasis on (1) semiochemicals regulating mother-offspring interactions, (2) oviposition attractants in the food and in the physical environment, (3) female-male interaction vs. female-female interaction, and (4) female interaction with defence-related cues. Examining the impacts that semiochemicals have on ILPs, neurohormones, and reproduction-related insect hormones may close the gap between the communicative role of signals and their additional roles in inducing physiological changes.

Another gap is in our understanding of the mode of action of reproduction-related semiochemicals in simple vs. advanced social insect species. A few studies have pointed out the importance of context (Orlova and Amsalem, 2019; Smith and Liebig, 2017; Smith et al., 2015), but studies examining context are still scarce. Some hydrocarbons were shown to have a primer effect on worker physiology (Holman et al., 2010; Van Oystaeyen et al., 2014), whereas others showed a lack of such effect (Amsalem et al., 2015b, 2017). A recent study in termites has shown that hydrocarbons (particularly n-C21) function as a releaser pheromone,

affecting worker shaking and antennation behaviours, both of which are elevated in the presence of royals and indicate royal recognition (Funaro et al., 2018). On one hand, the diversity of CHCs allows for the generation of multiple unique messages, but on the other hand, the fact that CHCs are so ubiquitous may explain why it is dangerous for them to affect physiology or to function as primer pheromones. Behaviour, on the other hand, is often context-dependent so that the information obtained through the signal can be examined more carefully before further action is taken (one likely exception are behaviours that confer high fitness cost if not performed immediately, such as response of males to femalesexpheromone).Achangeinbehaviourcaneventuallyleadtoachange in physiology, but such a change is much slower and constitutes a lower risk. This, as well as the physiological mechanisms underlying such a releaser effect by hydrocarbons, needs to be broadly studied across a wide range of insects to better understand the diversity and evolution of pheromones.

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