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Trends in Ecology & Evolution

Review

Evolutionary importance of intraspecific variation in sex pheromones

Chiara De Pasqual,[1,*] Astrid T. Groot,[2] Johanna Mappes,[1,3] and Emily Burdfield-Steel[2]

Sex pheromones in many insect species are important species-recognition signals that attract conspecifics and inhibit attraction between heterospecifics; therefore, sex pheromones have predominantly been considered to evolve due to interactions between species. Recent research, however, is uncovering roles for these signals in mate choice, and that variation within and between populations can be drivers of species evolution. Variation in pheromone communication channels arises from a combination of context-dependent, condition-dependent, or genetic mechanisms in both signalers and receivers. Variation can affect mate choice and thus gene flow between individuals and populations, affecting species' evolution. The complex interactions between intraspecific and interspecific selection forces calls for more integrative studies to understand the evolution of sex pheromone communication.

Highlights

Sex pheromones have traditionally been viewed as species recognition signals and thus are expected to show little within-species variation in composition and amount. Current research, however, reveals a high degree of intraspecific variation in sex pheromone communication channels, suggesting they are molded by multiple selection forces.

Sex pheromone signaling can be costly and plastic, and signals as well as responses may be affected not only by between-species interactions (e.g., communication interference, host plants, and geographic variation), but also by within-species interactions (mate choice) in addition to the genetic architecture, physiological state, and previous experience of individuals.

As variation in sex pheromone communication can be induced by intrinsic factors, its evolution may not only follow ecological speciation, but also be the driver of divergence.

Sex pheromones and their functions

Pheromones are semiochemicals involved in intraspecific communication, where species-specific signals are released by a sender that modify the behavior of a receiver [1]. Sex pheromones signal attraction and selection of potential mates. Sex pheromones are used by a variety of animal species, but the focus of this Review is on insect sex pheromones, as most pheromone research has been conducted on this class of animals. The traditional view is that sex pheromones are important species recognition signals to distinguish between species and thus under **stabilizing selection** (see Glossary) [2]. As closely related species can have similar sex pheromone signals that may only differ in the ratio of the different chemical constituents, the signaler and the receiver need to be finely tuned to recognize each other [3]. Small changes in pheromone release rate or ratio of the chemical constituents can affect attraction of the receiver [4].

Since sex pheromones are also mate-recognition signals acting within species, their roles in reproductive isolation and speciation processes are important. Reproductive isolation can be shaped by **reproductive character displacement** [5]. In sex pheromone communication channels, reproductive character displacement has been found in closely related, sympatrically occurring taxa [6,7], which lessens communication interference between closely related and **sympatric species**, but can generate variation between populations that lead to divergence [5]. Intraspecific variation between geographically distant populations has been described in many species [8–10], suggesting that such communication interference and other environmental factors affect variation in pheromone communication.

Even though intraspecific variation between geographically isolated populations is generally accepted, variation within populations is still thought to be less common. Johansson and Jones [11], however, reviewed the role of sex pheromones in mate choice, showing the possibility of variation in these signals even within populations. We now know that sex pheromones can even be plastic, and this **plasticity** can be translated into quantitative [12,13] or qualitative [14]

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intrapopulational differences. This can take place over an individual's lifespan [12,15], as a consequence of seasonal development [13], or due to the vicinity of heterospecifics during development [14]. Since sex pheromones can provide information on the general condition of the signaler, and the receiver can select based on this variation, intraspecific variation in sex pheromones must be more common than previously assumed.

Why has intraspecific variation been overlooked?

Although chemical communication is considered to be the oldest form of communication [16], humans are mostly visually oriented and thus much of the research focused on sexual signaling has been on variation in visual signaling. Also, it has proven challenging to analyze individual-level variation in chemical extracts. For example, identification of the first moth sex pheromone required thousands of individuals pooled together [17], naturally obscuring any intrapopulation variation. In addition, research on sexual selection and sexual conflict theory is affected by biases of sex roles and assignment to different taxa in sexual selection research [18]. In moths, females are typically thought to be the signalers and release the sex pheromone, while males are the responding sex, which could explain the higher volume of literature on female sex pheromone variation in moths [19–22]. Males, however, also produce and release sex pheromone [23] to which females may respond, but this aspect has been little explored (Box 1). Finally, female-signaling insect systems are well-represented amongst pest species, making them economically important. Sex pheromones are commonly used to monitor the presence and abundance of these pests and to disrupt mating. These applied aspects of insect chemical ecology likely increased the focus on sex pheromones at the species level. Thus, it is possible that, to date, our understanding of sex pheromone evolution, and in particular how intraspecific variation can affect a single species, has been held back by our research focus.

Mechanisms underlying intraspecific sex pheromone variation

Both sender and receiver are involved in the process of mate attraction, and intraspecific variation in pheromone communication can either arise as a consequence of physiological variation in the signaler (sender-specific driver of variation) or the receiver (receiver-specific driver of variation). To

Box 1. Visual versus chemical signals

In butterflies, mate attraction is typically determined by visual cues, while sex pheromones are usually involved in short-range attraction. Current research is uncovering many aspects of sex pheromone roles in butterflies, suggesting that chemical signals are much more involved than previously expected in diurnal species that commonly rely on visual cues. *Heliconius* butterflies (see Figure 1C,D in main text) are well known for exhibiting Müllerian mimicry, in which unrelated and chemically defended species mimic each other warning signal to more efficiently advertise their unpalatability to predators. When two species share identical wing pattern, such as *Heliconius timareta* and *Heliconius melpomene* in Peru, chemical signals are important to discriminate against heterospecifics [103]. Sex pheromones have a great importance in conspecific recognition, act as premating barriers and affect mate choice [104]. As male pheromones and female preference have been found to be heritable at least in some *Heliconius* butterfly species [105], pheromone communication may play a role in their speciation process. Thus, even in the visually-orientated butterflies, pheromones and other chemical signals, are used as premating barriers in addition to wing patterns, making these species multimodal signalers [106].

In *Bicyclus anynana*, the male sex pheromone can provide a wealth of information on the signaler, from the male's age to individual identity [100]. This pheromone is also a plastic trait as a consequence of a more or less climatic favorable season for their reproductive success [38], which has implications in their mating success [13]. Their sex pheromone can be more variable within populations than between populations and possibly acts as precursors of an ongoing speciation process [8].

In both *Heliconius* and *Bicyclus* study systems, short-range chemical signals are thus involved in species recognition and therefore under natural selection, but have also been shown to act in intraspecific mate assessment and thus under sexual selection. These examples show that in a male-signaling, female responding system, the progress of our understanding of the roles of pheromone signals seems to run counter to that in the more commonly studied females-signaling systems.

Glossary

Assortative attraction or assortative mating: individuals with similar phenotypes are attracted and mate with one another more frequently than expected under random mating.
Cuticular hydrocarbons (CHCs): molecules on the surface of adult insects, generally serving as antidesiccation compounds. In a number of species, CHCs have also be found to play important roles in insect communication. One of these roles is attraction and selection of potential mates.
Ecological speciation: a form of speciation that arises as a consequence of reproductive isolation due to a change in ecological factors (e.g., change in the host plant, presence of predators or parasites and, in general, any environmental factor).
Genetic correlation: two or more sets of genetic loci expected to covary as a consequence of, for example, linkage disequilibrium or pleiotropy.
Mating disruption: a pest management technique which prevent individuals to successfully locate potential mates through the release of a synthetic sex pheromone that mimics the species sex pheromone.
Plasticity: the phenomenon for which organisms with the same genotype manifest alternative phenotypes in response to environmental conditions, experienced usually during developmental time.
Preference function: along a continuous range of a signaling trait values, most receivers express a preference for intermediate values, while few show preference towards extreme values.
Reproductive character displacement: selection to avoid hybridization between species. When two species have overlapping habitats and (signaling) traits, divergence in one or more traits evolves in response to unfavorable interactions, such as cross-species attraction. When the divergence is due to selection to avoid hybridization between races/strains within species, the term reinforcement is used.
Runaway selection: due to genetic correlation between the sender and receiver's trait, changes in the sender's signal are inherited together with changes for the preference for that signal. This leads to a positive feedback loop, whereby both signal and

add another layer of complexity, both the sender and the receiver experience physiological changes within their lifetime, adding within-individual variation to the between-individual variation at the population level. In addition, senders may become receivers and vice versa.

Sender's perspective

Diet, age, mating status, and vicinity to conspecifics are among the mechanisms that can produce physiological changes and contribute to the maintenance of intraspecific variation in pheromone production. These changes can lead to both within- and between-individual variation. When considering intraspecific sex pheromone variation, it is important to first consider how they are produced. In some species, pheromone components and precursors are sequestered from the diet, while in others they are produced *de novo* within the animal [24]. Although both forms of pheromone production rely on the resources available, pheromones derived from the diet will be more vulnerable to environmental and host-related effects, and thus to external conditions. In contrast, species that produce their pheromones *de novo* are probably less susceptible to externally induced variation, but may exhibit variation due to internal processes. This is especially likely if there are costs to pheromone production, as this could result in trade-offs with other processes. Sex pheromones can indeed be costly: nutritional state influences the amount of pheromone produced in cockroaches [12], smaller female moths have lower fitness when they are stimulated into pheromone signaling [25] and pheromone composition predicts the fitness of female moths [26]. The **signaling sex** may communicate its nutritional state to the receiver [27]. There is also ample evidence that sex pheromones are affected by suboptimal diet at the larval stage [15,28], in adults [12], or at both life stages [15]. Pheromone production can be recouped if a higher nutritional diet is obtained [12], resulting in a dynamic environment–individual interaction. Regardless of how sex pheromones are produced, their variation can also be a consequence of the internal physiological state and its changes, such as mating status [29,30] or aging [31,32]. Generally, a greater investment in pheromone signaling is expected in older unmated females [33]. Older females may also call earlier in the night to avoid competition with more attractive young females [34].

Other mechanisms that can affect pheromone production and release are pathogens [19], volatiles from host plants [31], conspecifics [35,36], or prey [37]. Verheggen *et al.* [37] recently found that pheromone production in the Asian lady beetles (*Harmonia axyridis*) (Figure 1A) is conditioned by the presence of prey, as exposure to volatiles of the prey initiated pheromone production. Also, the female calling behavior of the gregarious beet webworm moth (*Loxostege sticticalis*) is affected by the vicinity to male conspecifics [38]. Pheromone release can also be increased by crowding and sexual competition; for example, in the American grasshopper (*Schistocerca americana*) [35]. It remains unclear if any of these changes represent adaptive strategies, that is, changes in resource allocation depending on individual status, or are simply nonadaptive responses to environmental triggers. Examples that do suggest a level of adaptive response to the environment are developmental plasticity due to the chemical environment, when individuals have been exposed to the chemical signals of heterospecifics [14], as a consequence of environmental temperature [39], seasonal variation [13], or nocturnal light pollution [40].

Finally, genetic and behavioral mechanisms may contribute to within-population pheromone variation. For example, a point mutation identified in the tobacco budworm (*Heliothis virescens*) (Figure 1B) translates to a sex pheromone signal with a higher or lower ratio of two pheromone components [41]. The different ratios of the two components affect the signal's attractiveness to males, and females releasing a signal with a higher ratio of the two components are less attractive than females releasing pheromone signal with a lower ratio [36]. Unattractive females can obtain matings while in close proximity to attractive females and, therefore, unattractive

preference for the signal become exaggerated over time.
Saltational event: evolutionary event which generates greatly or completely different phenotypes in a few generations, due to a mutation with major phenotypic effect. For example, a mutation in an enzyme that changes the stereochemistry of a pheromone component.
Signaling sex: the sex releasing a sexual communication signal to attract a potential mate.
Stabilizing selection: a form of selection in which the population mean trait converges to intermediate values, for example, when the mean pheromone signal is preferred over signals deviating from the mean.
Sympatric species: species with overlapping geographic ranges that are close enough to regularly interact.

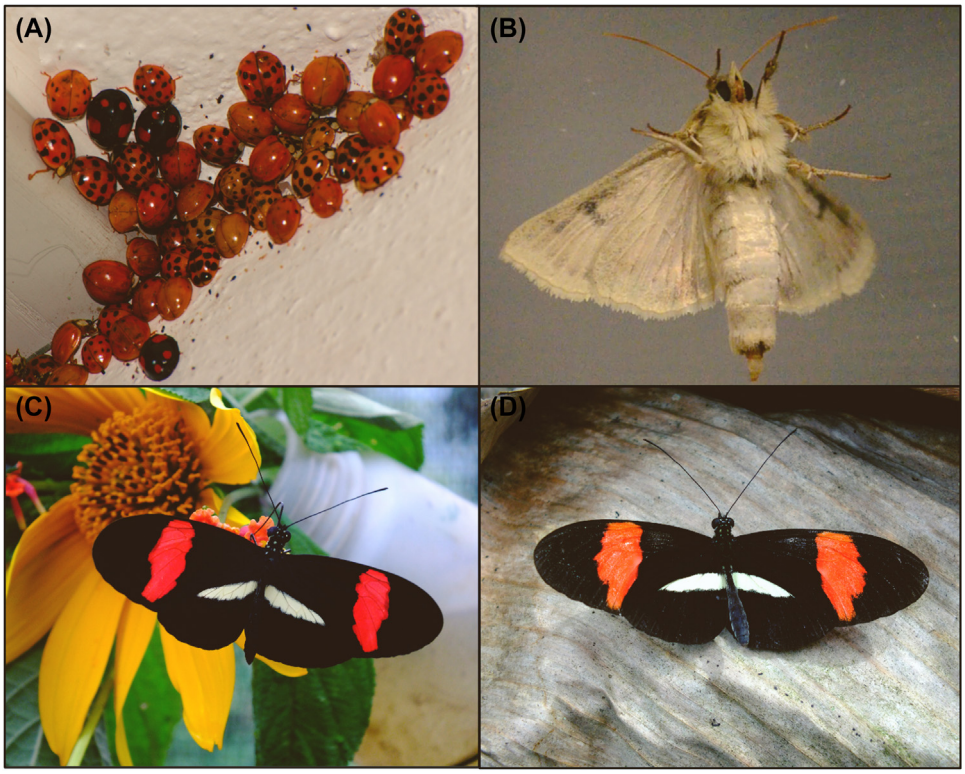

Figure 1. Examples of some species for which intraspecific variation in sex pheromone has been described in the literature. (A) Asian lady beetle (*Harmonia axyridis*) (Photo: Chiara De Pasqual). (B) Tobacco budworm (*Heliothis virescens*) (Photo: Jan van Arkel/IBED/UvA). (C) *Heliconius erato* and (D) *Heliconius melpomene* (Photo: Melanie Brien).

females are maintained in the population [36]. Similarly, in the European corn borer (*Ostrinia nubilalis*), two genetically identified sex pheromone strains [42] are maintained because males assortatively mate with females of their own pheromone strain [43].

Receiver's perspective

The traditional view holds that signalers and receivers are finely tuned, where the predicted shape of the receiver's **preference function** corresponds to the distribution of the female pheromone signal in the population. Experimental evidence from the 1970s and 1980s suggested that female pheromone signals experience stabilizing selection [3] and there is a lack of variation in male responses, because of optimal tuning to specific component ratios [2,4]. Variation in either the signaler or receiver, however, can introduce novelty in the communication channel even in established sender–receiver systems. For example, the rare receivers in the population that track changes in the pheromone signal [44], which might be possible through a **saltational event** [45]. New compounds in the signal may remain unperceived initially and only later do receivers evolve the preference for the new signal [46]. This scenario is known as the asymmetric tracking hypothesis [47]. An alternative and new conceptual model proposes that the preference trait evolves first in the receiver as a veiled preference, before the preferred trait is evolved in the signaler, and the receiver starts to select individuals with the newly preferred trait as soon as the trait arises [48].

Variation in receivers can take place at different levels, such as between and within individuals, and at different life stages, as a consequence of plasticity in the olfactory system [49]. In some

species, population density can contribute to variation in the morphological structures of the receiver as a consequence of developmental plasticity. For example, gum-leaf skeletonizer male moths (*Uraba lugens*) develop longer and more elaborate antennae to locate females in sparse populations [50]. This plasticity depends on the population density during the developmental stage and suggests that individuals can be more or less sensitive to pheromone signals.

Within the lifespan of an individual, plasticity in behavioral responses is well demonstrated in relation to circadian rhythms, as males of many moth species actively respond to pheromone sources at restricted times in the photoperiod [51]. A difference in gene expression in odor receptors seems to be at the base of this behavioral plasticity, linked to both the physiological state [52] and circadian rhythms [53] with, for example, effects on antennal sensitivity [54]. Responses to sex pheromones can also be modulated by experience, where pre-exposure to sex pheromones increases long-term sensibility and responsiveness [55,56]. The olfactory system dynamically adjusts to optimally perceive the surroundings [57] and differential receptor expression characterizes, for example, mated and unmated individuals [58]. After matings, some insects become less sensitive to sexual signals and cues for mating sites [59], either through a reduction in antenna sensitivity [54] or differences in pheromone processing in the central nervous system in the brain [60]. In other instances, environmental stress can have an effect on the receiver olfactory system. Sublethal pesticide doses was shown to increase the peripheral sensitivity of cotton leafworm (*Spodoptera littoralis*) males and increase their mating success [61]. A recent review [49] reports that the plasticity of the olfactory system occurs at all levels of the olfactory pathway. When studying the insect sensory system, it is challenging to integrate information from the periphery to the brain, therefore, we have just begun to understand these interactions. As the olfactory system can plasticly respond to, for example, changes in the environment, physiological state, social interactions and experience, variation in the olfactory system among individuals is likely to lead to differences in sensitivity and responses.

Ecological consequences of intraspecific variation: effect on attractiveness and mating success

Intraspecific variation in sex pheromones can have important consequences in attractiveness, mating success, and mating behavior, even when the source of the variation is entirely environmental. Furthermore, these consequences can be sex specific.

Volatiles produced by host plants can affect the production and response to sex pheromones. This can in turn affect mate location by increasing the calling behavior of signalers, for example by augmenting the frequency and calling duration [62], or increasing pheromone release/production [63]. Alternatively, host plant volatiles can enhance receivers' attraction to pheromone signals [62,64], by attracting a higher number of individuals [62,64] or by reducing the time to locate the pheromone source [64]. Finally, host plant volatiles can alter the response to ratios of pheromone components [65]. Thus, in general, host plants can influence species reproductive success during different stages of the insect lifespan, through both resource acquisition at the larval stage, and the interaction of plant volatiles with adult signals and behavior. Oxidative stress and pathogen infections can also affect sex-pheromone based mate location [66,67]. Curiously, challenged immune systems and pathogen infections have been found to increase rather than decrease attraction in some insects, suggesting either terminal investment [67] or a strategy of pathogens to spread through populations via host manipulation [19]. Immune system challenges can also lead to sex-specific differences; for example, only female mating success might be affected [68]. As populations vary in parasite load [69], variation in immune challenge could thus impact the dynamics of both pheromone signaling and sexual selection. In addition to host plants and pathogens, sex pheromone production and mating success can be affected by seasonal

fluctuations. A good example is the squinting bush brown butterflies (*Bicyclus anynana*), in which males that emerge in the wet season produce more pheromone and have higher mating success than those that emerge in the dry season [13].

Mate assessment is based on intraspecific variation in sexually selected traits. Sex pheromones can be under sexual selection when used as indicators of mate quality. Variation in sex pheromone composition can be used to avoid mating with siblings [70], which increases genetic variability and decreases the impact of deleterious alleles. For example, in *B. anynana*, females avoid mating with inbred males, which is assessed solely on the male-produced sex pheromone [71]. Sex pheromones are also used as signals to avoid matings that would lead to a lowered fitness and thus reduce the cost of matings. For example, sexually immature females of the cotton bollworm (*Helicoverpa armigera*) inhibit male attraction by temporarily releasing a repellent component in their pheromone signal [72]. Another example is the haplodiploid parasitic wasp, *Nasonia vitripennis*, in which females are more attracted to males with more pheromone, which correlates to a full sperm load [73]. As unfertilized eggs develop into males, this selection thus affects the population sex-ratio.

Sexual conflicts often arise over mating frequency. For example, in the parasitoid wasp families Pteromalidae and Braconidae, females tend to mate only once [30,74], while males mate multiple times. After mating, *Spalangia endius* (Pteromalidae) females actively resist males by increasing the release of a specific pheromone component, which prevents or terminates male courtship behavior [74]. Mated *Cotesia glomerata* (Braconidae) females stop releasing their attractive pheromone component in favor of the repellent only. These changes likely help mated females to avoid male harassment by reducing the attraction of males, and are also thought to help males locate virgin females, as their pheromone is distinct from mated females [30].

To conclude, intraspecific sex pheromone variation can have important consequences for the attractiveness and mating success of individuals, regardless of the source of this variation. If variation in signals and responses is heritable, there is the potential for different investment or responsive strategies to evolve.

Evolutionary consequences of intraspecific sex pheromone variation

Evolution in sexual communication systems can occur when heritable differences in signals and/or responses increase the survival and reproductive output of the individual (Figure 2 and Table 1). Below, we explore whether and how such evolution can occur in response to **ecological speciation** or as a driver of population divergence.

Ecological speciation

Many herbivore species use chemicals from their host plants as precursors for compounds that make up the pheromone signal. Thus, host plant shifts can directly affect pheromone composition. If this is followed by changes in responses, leading to **assortative mating** and reproductive isolation, ecological speciation can occur [75]. Changes in mating signals following a host plant shift has been experimentally shown in the mustard beetle (*Phaedon cochleariae*) [76], where **cuticular hydrocarbons** used as mate recognition cues differ depending on the host plant on which they feed. Similar changes are hypothesized to have contributed to the speciation process between two parental species of flea beetles (*Altica fragaria* and *Altica viridicyanea*) [77]. Pheromone divergence between populations linked to differences in host plants has also been hypothesized in the pine and larch strain of larch budmoth (*Zeiraphera diniana*) [78] and the chestnut tortrix (*Cydia splendana*) [79], and may represent the initial step towards reproductive isolation in these species. Changes in host plants, however, do not automatically lead to differences in sex

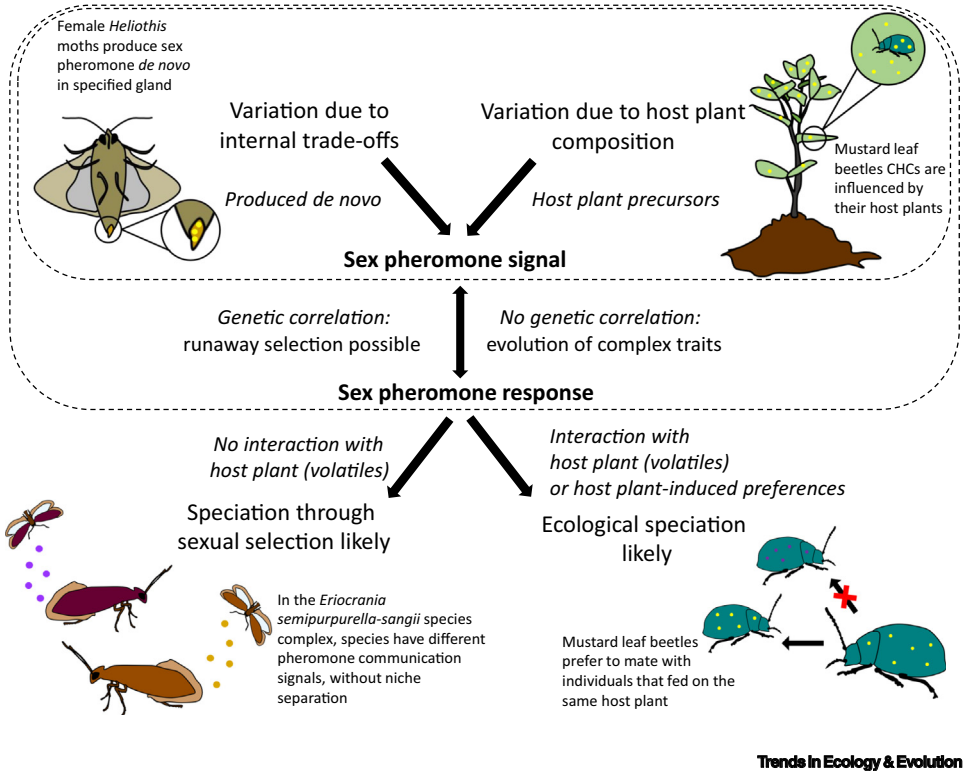

Figure 2. Some possible routes to speciation through variation in pheromone production and perception in herbivorous insects. Arrows indicate two of the possible alternative routes in the evolution of sex pheromone signals and responses. Pictures indicate examples discussed in this paper, clockwise from top left: *Heliothis* spp. [24]; mustard leaf beetle (*Phaedon cochleariae*) [76]; and *Eriocrania semipurpurella–sangii* [84].

pheromones [80] or to host shift [81], suggesting that other processes are also involved in speciation events.

Plants damaged by conspecific herbivores can negatively affect the premating and mating behavior in the moth species *S. littoralis* [82]. Host plant volatiles released as a result of herbivory can decrease the calling behavior of the signaler and negatively impact the mating success. This interaction may result in an avoidance of egg laying on a suboptimal plant that has high competition for resources or is attractive to the enemies of the herbivore [82]. Thus, interactions between host plants and pheromone signals and/or responses are complex and not straightforward, and how these interactions are involved in ecological speciation likely depends on the plants and insects involved.

Pheromone differentiation as driver of speciation

Reproductive isolation can also take place without ecological differentiation, through divergence in mate preference [83]. For example, in the primitive moth *Eriocrania semipurpurella–sangii* species complex, the ratios of components in the female pheromone do not only reflect geographic differences between populations, but also identify different species [84]. Since all the species share the same host plant, this is a case in which reproductive isolation likely has evolved as a result of divergence in sexual communication [84]. Such divergence could happen if some individuals of the choosing sex have a preference for a specific pheromone signal and

Table 1. Examples of intraspecific sex pheromone variation for which causes and/or consequences of the variation has been described and genetic basis or heritability is known

	Level of variation[a]					
Species name	Quantitative[b]	Qualitative[c]	Cause of variation	Consequences of the variation	Genetic basis known or heritability calculated	Refs
Tobacco budworm (*Heliothis virescens*)	—[d]	Yes	Single point mutation	Female attractiveness and mating success affected	Genetic basis known	[21,36,41]
	Yes	Yes	Pathogen infection boosted immune system	Sex specific: females mating success affected		[68]
Subflexus straw (*Heliothis subflexa*)	—	Yes	Phenotypic plasticity	Increase in **assortative attraction**	Genetic basis known	[14,100]
Squinting bush brown (*Bicyclus anynana*)	Yes	—	Seasonal polyphenism or age	Mating success affected	Heritability known	[13,101]
Parasitic wasp (*Nasonia vitripennis*)	Yes	—	Sperm limitation (highly correlated with pheromone titer)	Attractiveness and mating success affected	Genetic basis known	[73]
Burying beetle (*Nicrophorus vespilloides*)	Yes	Yes	Diet or age, or parasite load	Male attractiveness affected	Unknown	[102,103]

[a]Variation in sex pheromones can take two forms: quantitative and qualitative.
[b]Quantitative when the variation is referred to the total amount of the components.
[c]Qualitative when the variation is referred to the relative amounts and/or ratio of the components.
[d]Refers to not tested or not reported.

choose those signalers. A good example comes from *B. anynana*, in which females developed a mating bias towards the pheromone signal they were exposed to, even when this was a new signal. As this mating bias can be transmitted to the next generation without the offspring being exposed to the new pheromone signal [85], such heritable learning can drive the evolution of assortative mating and speciation. The potential of sex pheromones as drivers of speciation has been hypothesized for some *B. anynana* populations in which sex pheromone differentiation was found to be higher than genetic differentiation, suggesting that pheromone divergence precedes genetic divergence [8] (Box 2).

Potential mechanisms that can introduce variation and novelty in sex pheromones lie in the sequence variability of the genes involved in determining component ratios in pheromone signals [86], such as gene duplication and amino acid substitution in genes coding for specific enzymes in the pheromone pathways [87]. Variation in response and preference for pheromone signals may be due to divergence and evolution in olfactory receptors [88]. For example, chemosensory divergence in odorant receptors in the peripheral nervous system associated with reproductive isolation, have been found in two rarely hybridizing *Heliconius* species [58]. In *O. nubilalis*, however, genetic differences in the central nervous system (i.e., neurogenesis), instead of the

Box 2. Ecological and evolutionary consequences in the burying beetle (*Nicrophorus vespilloides*)

A comprehensive example of intraspecific sex pheromone variation that merges ecological and evolutionary consequences of its variation comes from burying beetles (*Nicrophorus vespilloides*). Intraspecific differences in sex pheromone have been shown to reflect males' condition, with males being more attractive when they are in better nutritional condition, of older age, have a larger body size and bear less parasites [101]. Burying beetles start to attract females once they have found a carcass suitable for reproduction, by releasing a sex pheromone. Both parents are known to feed on the carcass, so it is beneficial to both the parents and the offspring to mate only after a carcass has been found. Interestingly, males that have already performed brood care produce and release a higher amount of sex pheromone, and attract more females. Because of this positive loop, in which individuals that perform parental care produce more sex pheromone and become more attractive to females, the interplay between food source and heightened expression of secondary sexual trait (sex pheromone) has been suggested to have contributed to the evolution of parental care [102].

odorant receptors, were recently found to be primarily responsible for the differential male response [89]. The discovery of the genetic architecture underlying variation in sexual signals and responses has just recently begun, and so far mostly focused on Lepidoptera [90]. Recent studies suggest that phenotypic variation in sex pheromones can be the result of single gene [42] or locus [91] variation or due to a number of loci [92]. In the moths species studied so far, the genomic regions involved in signaling and response are unlinked. This makes **runaway selection** unlikely and the lack of **genetic correlation** favors the evolution of complex traits [90]. Thus, how phenotypic variation in pheromone communication may lead to reproductive isolation and, ultimately, to speciation is still an evolutionary mystery.

How easily can pheromone communication channels evolve?

As insect pheromones are used for pest management tactics, we have some knowledge on the evolution of sex pheromones in response to anthropogenically induced selection, which shows that pheromone communication channels can evolve relatively rapidly. Techniques such as pheromone trapping and **mating disruption** are attractive alternatives to pesticides, but the continuous use of artificial sex pheromones as disruptants may exert selective pressure on pest species to change their sexual signals and evolve resistance to it [93], meaning that males are no longer disrupted by the artificial pheromone composition. Cases of such emerging resistance can be viewed as natural field experiments showing that sexual communication systems can sometimes evolve quickly. The first field case of male resistance to pheromone-based traps was reported in Japan, where males of the smaller tea tortrix (*Adoxophyes honmai*) stopped responding to synthetic lures after about 10 years of treatment, causing the efficacy of mating disruption to drop from >96% to <50% [94]. The strong selective pressure exerted on this species resulted in the evolution of a resistant population, in which females changed their pheromone composition and males broadened their pheromone response [95,96]. This is unlikely to be an isolated case, as intraspecific variation observed in the cosmopolitan pest, codling moth, *Cydia pomonella*, shows the same potential for a shift in female sexual signal in response to mating disruption [20].

The continuous use of artificial pheromones can have an effect on both signalers and receivers. The signaling sex may evolve a different pheromone signal [95,97] and/or modify their behavior, by releasing pheromone for a longer time [98]. Pre-exposure to sex pheromones can affect gene expression of chemosensory genes and olfactory sensitivity [53] and result either in enhanced [55,56] or reduced [99] receiver sensitivity. All these factors can contribute to the evolution of resistance to artificial pheromones, and suggest that signaler and receiver can evolve and change in short time periods. Such quick evolutionary responses to selection indicate that there is a high level of standing genetic variation in populations on which selection can act.

Concluding remarks and future perspective

There is an increasing awareness that intraspecific variation in sex pheromone communication channels, both in the signaler and the receiver, is more common than previously assumed. There is also an increasing number of studies that point to the existence of within-population variation, as these signals are used for mate assessment and choice. Thus, sex pheromone signals and responses can be under multiple selection forces (see Outstanding questions) and seem able to evolve relatively quickly. This is particularly well represented by the fact that wild populations have been found to evolve resistance to synthetic sex pheromone composition, which suggests a high level of standing genetic variation within species on which selection can act. Finally, it is important to realize that individuals in nature can be affected simultaneously by several external factors (e.g., pathogens, vicinity to conspecifics, and predators), which can trade off with the physiology of the individual, so that populations always show some degree of

Outstanding questions

How do interspecific and intraspecific selection forces interact and cause population divergence? Individuals often are under multiple selective pressures resulting from abiotic and biotic sources, which may act in opposite, similar or complex ways.

Is only one sex the signaler and the other sex the receiver, or is there mutual mate choice? As signalers may become receivers in different phases of mate assessment, it is important to determine which signals are being used by which sex at the different phases, and how these signals may interact or evolve separately.

How much of the intraspecific variation is determined by genetic factors and how much plasticity occurs in pheromone signals and responses? Since both sex pheromone signals and responses have been found to be plastic, and plasticity can accelerate as well as impede evolution, we need to gain more knowledge on the fitness consequences and heritability of this plasticity.

When using artificial pheromone blends for mating disruption, could resistance development be delayed by using variable pheromone lures? Knowledge on the level of intraspecific variation in the pheromone signal may be used to develop lures with different pheromone blends to reduce evolution of resistance to pheromone artificial traps.

variation. We therefore need to deepen our understanding on how variation in pheromone communication channels affects and is affected by the interaction between the internal state of signalers and receivers, their mutual mate choice and their environment. We also need a better understanding of the mechanisms behind this variation, whether these are genetic or plastic, and which molecular pathways are involved. With all this information it will be possible to move the field forward and better understand how the evolution of chemical communication between the sexes affects speciation.

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Declaration of interests

The authors declare no conflict of interests.

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Update

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Correction

Evolutionary importance of intraspecific variation in sex pheromones

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The introduction of a late reference during the proof stage led to errors in the reference numbers in Boxes 1 and 2. All numbers, except for [8,13], need to be increased by 1. The authors and publisher apologize for any confusion caused by this oversight.

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