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The Evolutionary Importance of Intraspecific Variation in Sexual Communication Across Sensory Modalities

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Abstract

The evolution of sexual communication is critically important in the diversity of arthropods, which are declining at a fast pace worldwide. Their environments are rapidly changing, with increasing chemical, acoustic, and light pollution. To predict how arthropod species will respond to changing climates, habitats, and communities, we need to understand how sexual communication systems can evolve. In the past decades, intraspecific variation in sexual signals and responses across different modalities has been identified, but never in a comparative way. In this review, we identify and compare the level and extent of intraspecific variation in sexual signals and responses across three different modalities, chemical, acoustic, and visual, focusing mostly on insects. By comparing causes and possible consequences of intraspecific variation in sexual communication among these modalities, we identify shared and unique patterns, as well as knowledge needed to predict the evolution of sexual communication systems in arthropods in a changing world.

1. INTRODUCTION

The evolution of sexual communication systems is an important determinant in the speciation process because it contributes to prezygotic isolation (36). Sexual communication in insects can occur through several sensory modalities, but the most common modalities are chemical, visual, acoustic, or a combination thereof (65). Traditionally, sexual communication has been mostly studied for its importance in mate recognition as a major cause of sexual isolation between species. In the past decades, the focus has shifted toward the potential for sexual selection on intraspecific variation. As we show below, research in all three modalities has shown significant intraspecific variation, with plastic and genetic components, in both signalers and receivers (for a review of chemical communication, see 40). However, we lack a cross-modal understanding of the causes and consequences of intraspecific variation in sexual signals and responses, which is the fuel of evolutionary change on short timescales, as well as on the longer timescales of the speciation process. In this review, we identify shared and unique mechanisms underlying intraspecific variation in chemical, acoustic, and visual communication systems in a comparative way. We start with an overview of how the different signals are produced, transmitted, and perceived (**Figure 1**), after

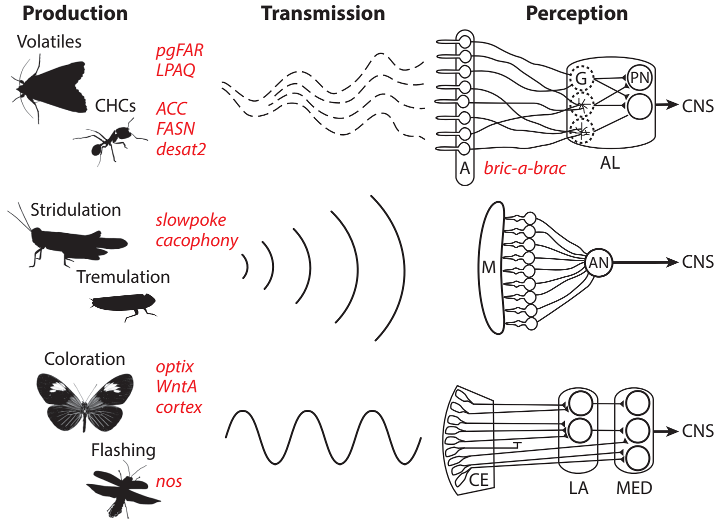


Figure 1

Sexual signaling in chemical, acoustic, and visual sensory modalities. Illustrations show different mechanisms of (*left to right*) production, transmission, and perception of (*top to bottom*) chemical, acoustic, and visual signals. Insect silhouettes are taken from **https://phylopic.org**. From top to bottom: *Autographa gamma*, *Messor capitatus*, *Trimerotropis maritima*, *Orientus ishidae*, *Eueides tales*, *Photinus pyralis*. Structures involved in chemical, acoustic, or visual perception include the antenna (A) (e.g., of a male moth, containing many olfactory receptors), glomeruli (G), projection neuron (PN), antennal lobe (AL), central nervous system (CNS), membrane (M) (e.g., of a grasshopper ear, connected to many scolopidia), ascending neuron (AN), compound eye (CE) (e.g., from *Drosophila*, depicting many ommatidia), lamina (LA), and medulla (MED). Chemical signal genes include *pgFAR* (fatty acyl reductase) (87); *LPAQ* (delta–11-desaturase) (64); and *ACC*, *FASN*, *desat2*, and other genes in the fatty acid biosynthetic pathway affecting cuticular hydrocarbon (CHC) composition in *Drosophila melanogaster* (42, 149). Acoustic signal genes include *slowpoke* and *cacophony* (ion-channel genes) (43, 144). Visual signal genes include *optix* (89), *WntA* (93, 94), *cortex* (104), and *nos* (109). The only currently identified gene for intraspecific variation in signal perception or preference is the transcription factor *bric-a-brac* (see the sidebar titled Importance of Identifying the Genes Underlying Intraspecific Variation in Sexual Signals and Responses). Images taken from PhyloPic and used under CC BY 3.0.

which we review the main identified causes of intraspecific variation in sexual signals and responses in the three modalities. We end by placing the results in an evolutionary context to determine the potential consequences of intraspecific variation in the different sexual communication systems in the light of global changing conditions.

2. SEXUAL SIGNAL PRODUCTION

In general, sexual signals share many similar functions across modalities (e.g., long-range mate attraction, mate quality evaluation). However, the underlying mechanisms of production, transmission, and perception differ substantially. Chemical sexual signals, generally referred to as sex pheromones, consist of blends of volatile or nonvolatile molecules that are attached to or emitted by insects, which is fundamentally different from acoustic and visual signals, where energy, instead of substance, is transmitted between sender and receiver (see **Figure 1**). In chemical signals, a distinction is made between so-called type I and type II pheromones, which are all derived from fatty acids (5, 32). In moths, the majority of identified sex pheromones are classified as type I, which consists of blends of mono- or diunsaturated alcohols, aldehydes, and acetate esters synthesized de novo by females in specialized glands and released into the air by a process known as calling. Moth sex pheromones are species specific due to the presence or absence and relative amounts or ratios of these de novo produced components. Type II sex pheromones are polyunsaturated hydrocarbons synthesized from diet-derived linoleic or linolenic acid and produced in oenocyte cells associated with the integument. These molecules are often referred to as cuticular hydrocarbons (CHCs) and require direct contact (72). Even though the relative importance of the individual CHCs is usually not clear, their role in mate choice has been clearly established in, e.g., cockroaches, beetles, crickets, plant hoppers, and flies (32, 71, 81, 133, 135, 146, 156).

Acoustic sexual signals encompass airborne, water-borne, and substrate-borne vibrations and are widely used by terrestrial and some (semi)aquatic taxa. Acoustic signals are characterized by their intensity; carrier frequency (or pitch); harmonicity; and rhythm, which is typically represented by the rate (modulation frequency) and/or the duty cycle (the duration over a period of pulses or groups of pulses). Most acoustic signals are produced by stridulation or tremulation. Stridulation is the rubbing of various body parts against one another, such as the wings and/or legs of grasshoppers and crickets. Tremulation is the shaking of the body and legs, used by many insects relying on the seismic channel to communicate. Timbal sound production, such as that used by cicadas in their exceptionally loud calls, is produced by specialized skeletal structures. The timbals are rapidly contracted and can produce vastly different sounds, such as the mid-frequency songs in cicadas and the high-frequency clicks in tiger and wax moths. Sound-producing organs often contain resonators to amplify sounds, such as the mirrors and harps on the wings of crickets (13).

Visual signals can encompass a range of signaling styles, from always-on signals, such as color, pattern, or shape, to more punctuated signals, such as flashes of light or specific movements, which are produced dynamically. Visual signals have been measured in many ways. Older studies often simply identified different color or pattern morphs by eye. A rapid increase in the accessibility of both methods to measure color (e.g., multispectral cameras and spectrometers) and methods to analyze it has resulted in various methods of classifying color. Common metrics in visual sexual signals in insects and other invertebrates include pattern, irradiance spectra, UV reflectance, luminance, contrast, and pattern size (46, 80, 140). In addition to pigment-based colorations, visual signals can be produced by specialized structures that diffract and reflect the incoming light. Diffraction and reflection are the basis of blue colorations; iridescence, where the signal properties depend on the viewing angle; and polarization, which is a change in the way light propagates that is invisible to humans but widely used by insects.

3. SEXUAL SIGNAL TRANSMISSION

Chemical signals emitted by the sender are transmitted through molecular diffusion and convection (126). In contrast to acoustic signals, the relationship between chemical signal composition and transmission cannot be reliably estimated and calculated because the process of diffusion of chemical blends is difficult to predict in a natural environment.

For acoustic sexual signals, transmission rates can be reliably calculated. Airborne sounds attenuate by six decibels with every doubling of distance, and they are also affected by atmospheric conditions and the topology of the environment through which sounds propagate (23). Higher sound frequencies attenuate faster due to temperature, humidity, and vegetation density, whereas lower sound frequencies attenuate faster when signalers are close to large reflective surfaces (such as solid rock or stiff leaves) (151). Substrate-borne sounds, such as the vibratory signals of treehoppers (Membracidae) produced on plant stems or the ripples produced by male *Gerris gracilicornis* water striders on the water surface, travel as Rayleigh waves through solid or liquid media (66). These signals suffer from dispersion, or frequency-dependent transmission speeds, such that certain frequencies arrive at the receiver later than others, which could decrease signal quality.

Visual signal transmission in terrestrial environments is not greatly influenced by climatic conditions, such as temperature or humidity, but is heavily impacted by light (68). This is particularly true for signals that rely on reflectance, which are the majority of visual signals, as without light they will be imperceptible, and the wavelengths of the light that falls on them will greatly impact their appearance. The light falling on a visual signal can vary with the time of day and season and is affected by vegetation structure, which can also create physical barriers blocking the transmission of visual signals (121).

4. SEXUAL SIGNAL PERCEPTION

To define sexual signals, it is crucially important to understand how they are perceived and what part of the variation affects mate choice and/or intrasexual competition, given that beauty is in the eye of the beholder. For example, there is considerable variation among insect species in how signals are actually perceived (140). Variation in color discrimination, as well as visual acuity, between insects and humans (86) means that features of visual signals visible to researchers may be invisible to their study species, and vice versa, which holds true for all of the senses (157).

Chemical perception of sex pheromones occurs through fast-evolving olfactory receptors (11, 100), usually located on antennae, although olfactory receptors can also be located on the legs, abdomen, or ovipositor (16, 29, 53, 150, 160). Chemical odorants first transverse the hydrophobic sensillar lymph with odorant binding proteins, after which they bind to olfactory receptors expressed in the membranes of olfactory receptor neurons (129). These neurons project into the macroglomural complex, from which projection neurons connect to the mushroom body (6) (**Figure 1**).

Acoustic signals are received and evaluated by hearing organs (setae, antennae, tympana) in the periphery, which are connected to the central nervous system by one or a few ascending neuron(s), with auditory neurons connected to abdominal, thoracic, and head ganglia in the central nervous system (56, 58). Acoustic processing in the periphery is mostly mechanosensory, combined with tuning to specific carrier frequencies due to frequency-dependent amplification (58). The signal is transmitted to the brain through ascending neurons, where integrative neurons weigh temporal patterns in the signal (56, 58, 127). Interestingly, the organization of peripheral evaluation of carrier frequency and central evaluation of rhythm presents the potential for serial processing (60), which has been shown in field crickets (Gryllinae): Species-specific carrier frequencies and pulse rates of male songs are evaluated first, after which mate quality is evaluated by more variable, condition-dependent higher-order temporal patterns integrated in the brain (19, 60, 127).

Visual signals are perceived by the eyes, of which insects have two main types, simple ocelli and more complex compound eyes (**Figure 1**). Ocelli are often positioned on the top of the head and can play roles in light perception, phototaxis, and circadian rhythms, as well as in flight orientation (88). Their role in perception of sexual signals is unclear, although they have been shown to be sexually dimorphic in some groups (78). Compound eyes are often able to detect a greater variety of wavelengths, and thus play an important role in color perception (130). Perception of different wavelengths of light occurs through opsins, rhodopsins, and cryptochromes, and variation in these pigments affects color perception in different insect species (111, 140). The visual environment, i.e., ambient light spectra and levels, likely determines receptor sensitivity (103). Visual signals are then first processed in the optic lobe, which includes both the lamina and the medulla, before being transmitted to the central brain (106).

Chemical, acoustic, and visual senses are thus similarly organized by peripheral filtering, followed by evaluation in the central nervous system. In addition, the physiology underlying between-species variation is related to the presence or absence of pheromone components, song carrier frequency, or pigments, while the physiology underlying within-species variation is related to fine tuning of the signal, i.e., compositional variation in the pheromone blend, song rhythm, or visual patterning. These findings suggest that the serial processing that was shown in the acoustic perception of field crickets (60) could be widespread across sensory modalities, but this has not been tested.

5. GENETIC ARCHITECTURES OF SEXUAL SIGNALS AND RESPONSES

Whether and how quickly sexual communication channels may evolve depend at least partly on the genetic architectures of sexual signals and responses. First, the number and genomic distribution of loci likely affect the evolutionary rates and potential of sexual signals and responses (7). Both polygenic and major effect loci architectures have been identified in all modalities. However, the qualification of polygenic versus major effect loci depends mostly on effect size expressed as a percentage of the total variance of the population (e.g., 7). As a result, if intraspecific variation in a signal is limited, then detecting small effect loci requires unfeasibly large sample sizes, and major effect genetic architectures may be spuriously inferred. Second, linkage among signal and preference genes is important because, where genes underlying variation in sexual signals and responses are coupled or linked, Fisherian runaway selection is possible. Such coupling has been found for chemical (95, 101), acoustic (18, 154), and visual (84, 97) systems. In acoustic communication, the similar neurobiological underpinnings of signal rhythm and preference suggest that the same genes may underlie variation in both (56). Correspondingly, in Hawaiian sword-tail crickets (Gryllidae: *Laupala*), very tightly linked quantitative trait loci (QTLs) have been found for song and preference (154), while in lesser waxmoths (Pyralidae: *Achroia*), there is no colocalization of genetic loci underlying ultrasonic signal and response traits (2). In contrast, functionally different genes are likely involved in signal and preference variation when the underlying physiological pathways are different. This is the case for song carrier frequency, which depends on morphometrics of the sound-producing organs (13), while ears are usually tuned to a specific carrier frequency due to the resonant properties of hearing organs and neurons involved in frequency-dependent amplification (58). In addition, in visual communication systems, variation in rhodopsin proteins determines the extent of color vision across species (111), while neural processing genes appear to determine visual preference within species (120). In moths, chemical signal and response QTLs have not been found to be linked either (62), which means that genetic correlations among

IMPORTANCE OF IDENTIFYING THE GENES UNDERLYING INTRASPECIFIC VARIATION IN SEXUAL SIGNALS AND RESPONSES

The two sex pheromone strains of the European corn borer, *Ostrinia nubilalis* (Lepidoptera, Crambidae), have together been used as the model system to understand the evolution of pheromone divergence ever since their discovery (82). Females of both strains produce a volatile pheromone consisting of (*Z*)-11-tetradecenyl acetate (Z11–14:OAc) and (*E*)-11-tetradecenyl acetate (E11–14:OAc), but in opposite ratios, 97:3 Z:E ratio in the Z-strain and 1:99 Z:E in the E-strain. This ratio variation was long thought to be due to variation in a desaturase. However, by combining QTL analysis with a candidate gene approach, a pheromone gland–specific fatty acyl reductase (pgFAR) on chromosome 31 was finally identified to underlie the variation in the pheromone signal (87). The variation in male preference was mapped to the Z chromosome, and the candidate genes were pheromone receptors located on this chromosome (45, 117). However, fine-scale QTL studies showed that the response locus did not coincide with the receptor cluster (45, 83). Ultimately, by combining behavioral and electrophysiological phenotyping, expression profiling and gene editing, and genomic scans of assortative mating and associations with preference in nature, *bric-a-brac* was identified as the gene controlling male choice (139). This transcription factor probably modifies the neural architecture of the olfactory sensory neurons in antennal sensilla, leading to saltational shifts in sex-pheromone preference in males. This example shows that physical linkage between signal and response genes is not necessary for coevolutionary divergence of signal and response genes as long as diverged preferences are strong enough to facilitate assortative mating and mate choice divergence (139). It also shows that the identification of the genes underlying intraspecific variation in sexual signals and responses is necessary to discover both the mechanisms and the evolutionary trajectories underlying intraspecific variation of sexual communication.

signal and preference loci are likely to be easily lost, increasing the possibility of signal–preference mismatch.

Which genes underlie intraspecific variation in sexual signals and responses is still largely unknown in all of the three modalities. The few genes that have been identified to control signal variation encode enzymes that change the saturation or convert among terminal groups of fatty acids of chemical signals, ion channels that change the rhythmicity of acoustic signals, or scale-specific expression of pigments used in visual signals (see **Figure 1** for references). On the perception side, the only identified gene to date affects chemical communication: *bric-a-brac* has been found to underlie male preference in *Ostrinia nubilalis* (see the sidebar titled Importance of Identifying the Genes Underlying Intraspecific Variation in Sexual Signals and Responses). More knowledge of preference genes is needed to determine whether variation in perception is caused by genes coding for sensory properties in the periphery or neuronal processing in the central nervous system and whether changes in preferences first occur in the periphery or centrally in the different modalities.

6. CAUSES OF INTRASPECIFIC VARIATION IN SEXUAL SIGNALS AND RESPONSES

Throughout an insect's life, an individual may encounter different environments that can affect the health and/or resources available for developing, producing, and/or maintaining an attractive signal. This is generally referred to under the framework of condition-dependent signaling. In addition, the community composition may also drive variation in how, when, and where to signal for mates. Below, we discuss the main factors that have been found to be associated with intraspecific variation in sexual signals and preferences across modalities, summarized in **Figure 2**.

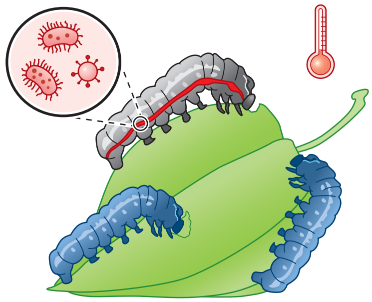
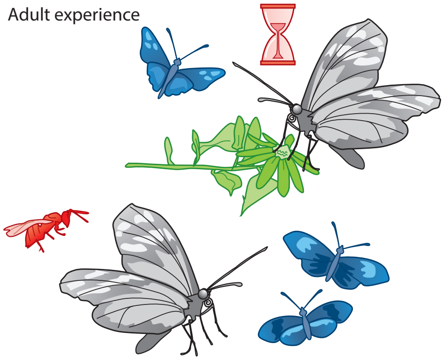
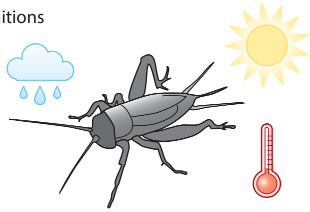
Sources of variation	Topic	Chemical	Acoustic	Visual
Larval development 	**Temperature**	?	✓	✓
	Diet	✓	✓	✓
	Conspecific interactions	✓	✓	?
	Microbiome	✓	?	?
	Parasites	✓	✓	✓
Adult experience 	**Age and mating status**	✓	✓	✓
	Conspecific interactions	✓	✓	✓
	Host plant interactions	✓	✓	?
	Heterospecific interactions	✓	✓	✓
	Parasitoids/predators	✓	✓	✓
Abiotic conditions 	**Light**	✓	✓	✓
	Humidity	✓	?	?
	Temperature	✓	✓	✓

Figure 2

Summary of the sources of variation in the three signaling modalities, which can influence signal development and preferences, at either the larval or adult stage, or directly impact signal production and reception through the ambient abiotic environment.

6.1. Larval Behaviors and Experiences

The extent to which signal variation is affected directly by diet differs among signaling modalities. Even though most chemical sexual signals are generally produced de novo and fatty acid derived, sex pheromones or their precursors can also be plant derived. This is the case, for example, for male sex pheromones of butterflies, which are released from androconia on the wings or in so-called hair pencils surrounding the aedeagus (16). Interestingly, bark beetle pheromones were originally thought to be plant derived but turned out to be also mostly produced de novo (21). Conversely, type I lepidopteran pheromones were always thought to be produced de novo, but recently, Fujii et al. (54) found that larval diet significantly affects lipid content and thus fatty acid precursors. Acoustic signals are produced by neuromuscular processes that involve dedicated morphological structures and thus do not directly depend on dietary metabolites. Similarly, acoustic preferences are independent of dietary metabolites. Visual signals can be directly affected by early life diet, particularly in terms of nitrogen and protein content, as this may affect the production of pterin- and melanin-based patterns. For example, nitrogen availability has been shown to influence male color, through the production of pterins, in the cabbage white butterfly, *Pieris rapae* (48). In stalk-eyed flies, the size of male eye stalks is diet dependent, and females prefer to mate with males with larger eye stalks, although high-quality males can maintain their signal even under dietary stress (38).

In contrast to direct dietary effects, indirect effects of larval diet are shared among all signal modalities and likely extend to effects on preferences. The nutritional quality of the larval diet influences body size across animals (30), and larger animals spent more time signaling with chemical (20), visual (75), and acoustic (56) signals. Larger animals produce signals with higher intensities, i.e., higher pheromone titers (20, 136), louder calls with lower carrier frequencies (24, 131), and larger wings (91). Compositional aspects of smells, songs, and displays may also depend on body size. For example, larger *Chloridea subflexa* (Noctuidae) females produce signals with different ratios of components important for mate choice (20), and larger males of the European field cricket, *Gryllus campestris*, produce songs with higher duty cycles (124). Larger animals are likely also more sensitive to directional information, given that directional information depends on differences in the magnitude of excitation between left and right sensory organs in all signal modalities. Body size may also be the basis of assortative mating, thus influencing preferences for signal traits that inform about signaler body size (76, 161). In animals that duet, such as grasshoppers, or in taxa where mate localization by the choosing sex is energetically costly, diet and size constrain the resources available for interaction with potential mates (35). Such interactions may result in correlations between body size and discrimination in sexual signal preferences, as found in frogs (105), although to our knowledge this has not been tested in insects.

Effects of larval population density on adult sexual communication have also been found. For example, in the *Uraba* moth, larval densities affect adult male wing and antenna size (77). In Hawaiian *Teleogryllus oceanicus* field crickets, silencing mutations have spread due to parasitoid selection pressure, and late-instar exposure to songs makes adult females more discriminatory (9).

In summary, dietary effects seem to mostly affect signalers and responders in the same direction, which may cause assortative mating. The positive correlation among body size, fitness, and sexual attraction indicates that most sexual signals in insects are, at least to some extent, honest signals.

6.2. Microbiota

Microbiota can affect sexual communication in several ways. For example, the gut microbiome may affect sexual signals or preferences, although such effects have to our knowledge not been explored yet in visual and acoustic communication systems. Engl et al. (47) found that a disruption of the microbiota through an antibiotic treatment with tetracycline affects CHC profiles and mate choice in the tsetse fly, *Glossina morsitans*, and both female and male flies preferred nontreated flies over tetracycline-treated flies in choice assays (47). Another example comes from diet-induced mating preferences in *Drosophila melanogaster*. These preferences resulted in assortative mating, were found already after one generation, and lasted for 37 generations (128). However, when flies were treated with antibiotics prior to diet change, mating preference was lost; it was restored when the commensal bacterium *Lactobacillus plantarum* was added (128).

6.3. Parasite Infections

In contrast to the effects of the gut microbiome, parasite infections have been found to affect all three signal modalities. For example, in burying beetles (*Nicrophorus vespilloides*), parasite load affected the ratio of the two pheromone components in males that are important in attracting females (28). In *Tenebrio molitor*, females were less attracted to the odor of males infected with a tapeworm than to that of healthy males (152). When *Helicoverpa armigera* was infected with the apicomplexan parasite *Ophryocystis elektroscirrha*, the female pheromone signal did not differ in quality or quantity, but her reproductive output was negatively affected, and infected females mated more with uninfected than infected males in choice experiments (55). In acoustic sexual communication, parasite infections can result in song and preference changes. For example, when parasitoid flies develop in the pupae of crickets, the crickets reduce their singing activity and gain more mass, which is likely due to host control by the parasitoid (12). Moreover, parasites have been found to induce behavioral fever to fight off infection in the house cricket, *Acheta domesticus* (1). Behavioral modulation of ambient temperature likely influences not only the immune system, but also song rates and preferences, as crickets have temperature-coupled signals and preferences in response to both developmental and ambient temperature (59, 112). Whether visual signals are affected by parasites or the microbiome is to our knowledge unexplored to date, although nonsexual color traits have been found to be impacted. For example, color in pea aphids changes depending on the types of symbionts that they carry (113), while parasite infections in *Danaus plexippus* did not impact wing color (39). Thus, parasite infections have mostly been found to decrease sexual attraction, which suggests honest signaling. Exceptions to these findings can be explained in view of terminal investment (132) and/or behavioral manipulation by the parasites (142).

6.4. Adult Age and Mating Status

Age and mating effects are among the best-known factors affecting sexual signals and/or responses (15, 156). For example, *Bicyclus anynana* females prefer chemical signal profiles correlated with mid-aged rather than younger males (107), while *D. melanogaster* males prefer younger over older females, largely determined by age-related cuticular lipid profiles (156). Acoustic signals are also affected by age. For example, younger males of the Mediterranean field cricket, *Gryllus bimaculatus*, have higher duty cycles (long chirp duration, short interchirp pause) (143), and virgin *T. oceanicus* field cricket females respond faster to playback than do mated females (137). Changes in butterfly color with age have been found in the red bands of *Heliconius* females, although it is unclear if this influences their sexual attraction, as females typically mate shortly after eclosion (41). Age also affects the structural coloration of *Colias eurytheme* males, which may aid females in selecting younger mates (79). Finally, some female damselflies change color when they are mature enough to mate (73).

6.5. Conspecific Interactions

Learning, experience, and social environment may affect variation in sexual signals and responses in all three modalities. The role of learning in sexual trait evolution in insects and spiders, with olfactory, visual, and acoustic examples, has recently been reviewed (44) and is not discussed in this article. Experience can affect sexual communication in several ways. For example, in S*podoptera littoralis*, pre-exposure to female sex pheromone increases male sensitivity, and this effect lasts at least 27 hours (3) and thus changes over time (4). In addition, female moths may vary in their time spent calling (138), and pheromone calling effort in the moth *Lobesia botrana* was found to depend on the presence of other calling females (67). In the burying beetle *Nicrophorus vespilloides*, breeding females generally emit only trace amounts of methyl geranate but emit high amounts when males are present, which indicates that breeding females can assess their social environment, i.e., whether they reproduce alone or with a male partner (134).

Late-instar and adult acoustic experience mimicking high rates of calling males also makes female field and bush crickets more discriminatory and increases male calling effort, although male song traits were not affected (8, 115). Preferences in field cricket females can also be learned by observing mating interactions in conspecifics (10). In *Schizocosa floridana* spiders, courtship structure in the substrate-borne vibratory call of males changes depending on social context, i.e., whether females are present or absent (119).

In visual signals, perhaps the most striking example of social influence comes from *Photinus* fireflies, which call synchronously in large groups (122). This synchronous calling possibly facilitates female recognition of species-specific flash patterns and reduces visual noise (102). It is also worth mentioning that female fruit flies have been found to prefer to mate with males of the same color as those they previously observed copulating with another female (98), and this preference can be passed across multiple generations, potentially leading to cultural evolution of color preferences within insect populations (37).

Plasticity through learning and experience in sexual signals and responses thus occurs in all three modalities. Whether such plasticity enhances or impedes the evolution of sexual communication systems depends to a large extent on the spatial structure of populations, i.e., how much gene flow there is between populations with different social experiences, and whether mate preferences are reinforced by or averse to previous experiences (44).

6.6. Host Plant Interactions

Host plants can affect sexual signals and responses in several ways in all three modalities.

In chemical sexual communication, host plant odors can interact with sex pheromone odor negatively or positively. For example, in the moth *Agrotis ipsilon*, the flower volatile heptanal reduces responses to sex pheromones in the macroglomerulal complex but also results in improved temporal resolution of pheromone pulses by output neurons (70). Host plant odors can also affect sex pheromone calling and responses. For example, in *S. littoralis*, fewer females called in the presence of cotton plants damaged by larvae compared to undamaged plants, while males showed delayed activation and reduced attraction toward female sex pheromones when damaged plants were present (158). Host plant–dependent plasticity has also been found in male substrate vibration signals of *Enchenopa binotata* treehoppers and contributes to reproductive isolation among host races (74, 123). The attractiveness of visual signals is also influenced by the background against which they are viewed, and visual signals can be made more, or less, detectable by altering the light or visual environment in which they are situated. For example, in flies and butterflies, males were found to prefer backgrounds that enhanced the appearance of their markings, either through increased contrast with the background (147) or through increased UV brightness, visible area, and flash effect due to the viewing angle (148). The interaction between sexual signals and host plants likely contributes to the evolution of host races, especially when mating occurs on plants (14).

6.7. Heterospecific Interactions

Other species in the same environment may cause communication interference, e.g., in signaling between closely related species, or eavesdrop, e.g., by predators and parasitoids. Communication interference in chemical communication may be the reason that several species produce not only attractive sex pheromone components, but also chemicals that repel closely related species (31, 63, 155). Such interference can be reduced by species-specific timings of sexual activities at night (61). In some insect species, competition due to masking interference promotes divergence of the acoustic space, i.e., the spectral and temporal features of the signal, as well as the time and place of the signal (125). Visual signals are also often easily detectable by heterospecifics. As a result, visual appearance can play an important role both in antipredator strategies (such as crypsis, mimicry, or aposematism) and when hunting other visually oriented species (27). It has been suggested that mimicry of antipredator warning signals in *Heliconius* trades off with efficient mate recognition, as accurate mimicry among species can lead to failures of species recognition (92). The use of chemical signals in combination with visual ones can help males direct their courtship attempts to conspecific, rather than heterospecific, females (96), and one study suggests that the optimal color pattern for mate attraction was also the most effective at deterring predation (51). Parasitoids and predators may also home in on the sexual signals, as has been found for the sex pheromone signals of moths (49, 69, 153) and in water striders, where the male ripple signals attract predators, pressuring the females into allowing the male to mount and mate quickly (66). Eavesdropping predators and parasitoids also use song signals to localize their prey, as for example in bats (50) and in acoustically orienting parasitoids, such as *Ormia* flies (25). In the tiger moths, song signals have been coopted to jam echolocation signals by bats. Incidentally, the high duty cycle that makes the song attractive also makes it more efficient in signal jamming (50). Visual sexual signals are also at risk of being hijacked by predators, i.e., via aggressive mimicry. One striking example is female *Photuris* fireflies, which mimic the flash patterns of other species to attract heterospecific males, which they then eat (90). The homing in of parasitoids and predators on insect sexual signals thus causes natural selection pressures that may cause significant shifts in these signals, depending on the relative strength and direction of natural and sexual selection pressures.

6.8. Abiotic Interactions

Abiotic factors, such as temperature and light, can affect sexual signals and responses in all three modalities in several ways. For example, as CHCs are important for desiccation resistance, several studies have shown interaction effects between temperature and CHC mating signals in, e.g., *D. melanogaster* (22) and *Osmia* bees (34).

Acoustic signals are also highly temperature dependent (52, 145) due to (*a*) temperature-dependent movement of wing muscles and tymbals and (*b*) temperature-dependent latencies in the nervous system. Temperature also affects acoustic sexual vibration signals in *S. floridana* wolf spiders (118). Temperature may have similar effects on signal and preference (116), as, for example, in temperature-dependent latency in neurons involved in signal rhythm and signal evaluation or temperature-dependent active amplification in tree cricket ears (99). Various cricket species are known to have temperature-coupled signals and preferences in response to both ambient and developmental temperature (59, 112). However, signalers and receivers may also respond differently to temperature, which then leads to signal–preference mismatch, as was found for the *Drosophila montana* courtship song (116).

Temperature effects on visual signals are less known. One exception is the flash rates of fireflies, where temperature has been shown to affect not just the flash rate, but also the peak wavelength of the light produced, likely due to denaturation of the producing enzymes (114). The amount of melanin can also vary according to temperature during development (57), as has been found in many species; this effect may be adaptive (either for sexual selection or processes such as thermoregulation) or simply a side effect of the difficulties of producing melanin-based patterns at higher temperatures.

Light effects on sexual signals and responses have also been found in all three modalities. For example, the sex pheromone composition of *Mamestra brassicae* differed under different light conditions (141), although it is not clear whether this variation affects male response. In *S. floridana* spiders, the courtship structure in the substrate-borne vibratory call of males changed depending on whether the environment was light or dark (119). In *P. rapae*, lower light levels resulted in reduced male visual signals (in the form of brightness—typically favored by females) and an increased investment in pheromones (159).

In summary, changes in temperature and light can affect sexual signals and responses in similar ways, which may result in assortative mating in different localities, thus enhancing the evolution of geographically distinct populations.

7. VARIATION IN SEXUAL COMMUNICATION CHANNELS IN RELATION TO GLOBAL CHANGE

Human activities can alter many habitats, thereby influencing the local densities of predators and parasites, as well as rivals and mates. Biotic processes related to these demographic changes can have a strong impact on sexual communication through changes in either natural (e.g., eavesdropping predators) or sexual (e.g., operational sex ratio) selection pressures. Abiotic conditions altered by human activities can influence sexual communication in many different ways, ranging from direct effects on the production side, often resulting in plastic responses, to an impact on the sender's side, which can indirectly alter sexual selection pressures on chemical, acoustic, or visual communication. Especially if the genetic loci underlying signals and preferences are coupled, plasticity in preference could result in selection on the signal, which would then result in indirect selection on the preference. For example, axes of divergence and axes of temperature-related plasticity in song rate are aligned among populations of the Hawaiian cricket *Laupala cerasina*, suggesting that plastic and adaptive effects will reinforce one another (108). However, our knowledge of the effects of global change on invertebrate sexual communication channels is still very limited. The sounds of traffic and industry could possibly overlap in frequency with the sounds of many acoustic signalers, from orthopterans to spiders, which may alter important information used for mate choice (26, 33). For example, bow-winged grasshoppers change their pulse under high levels of traffic noise (85). Different light regimes at night have been shown to affect the sex pheromone composition in *M. brassicae* (141), although the effects of this variation on male response are not yet clear. In fireflies, artificial light has been found to influence both the brightness and the rate of male flashes (110), although in this case, it is not clear if this influences female preference. Sensory pollutants may also hinder mate choice altogether by completely blocking signal access to the sensory receptor cells (e.g., through chemical binding or perceptual masking). For example, male glow worms fail to respond to the visual signals of females under artificial light (17). These limited examples show that much research still needs to be done to assess how chemical, acoustic, and light pollution affect sexual signals and responses in an evolutionary context.

8. CONCLUDING REMARKS

The above sections show that intraspecific variation in sexual signals and responses is found on many different levels in all three modalities. The evolutionary history of sexual communication systems can only be reconstructed when the underlying genes in both signal and response have been identified, which has to date only been accomplished in the two pheromone strains of the European corn borer (87, 139). In all modalities, genetic linkage has been found between signals and responses, which would allow evolution to occur relatively easily. The evolutionary potential of sexual communication systems seems comparable across the three modalities, even though signals and responses are produced, transmitted, and perceived in different ways. Interestingly, in all three signal modalities, plastic responses have been found to the same environmental factors, such as indirect diet effects during development, host plant effects during sexual signaling, communication interference by other species, and eavesdropping by predators and/or parasitoids. Abiotic environmental effects, such as temperature and light, also affect all three modalities. Thus, we have identified several commonalities and differences in how and which environmental factors can affect sexual signals and responses in the three modalities. However, to predict the evolutionary potentials and possible paces of evolution of invertebrate sexual communication systems, we will need to investigate in much greater detail how chemical, acoustic, and light pollution affect sexual signals and responses.

FUTURE ISSUES

1. As sensitivity and acuity of the senses vary among and within species, it is important to determine and account for variation in perception among individuals and species.
2. To reconstruct the evolutionary history and predict the evolution of sexual communication signals and responses, identification of actual genes underlying sexual signals and preferences in all three modalities is needed.
3. When assessing variation in sexual signals and responses, it is important to consider population densities at larval and/or adult stages, as these can affect sexual communication.
4. To what extent microbial communities may affect sexual signals and responses in all modalities is still an open question.
5. Communication interference between closely related species and eavesdropping by predators and parasitoids are likely important drivers of selection in all modalities.
6. As global changes affect species compositions at multiple trophic levels, it will also be important to assess the effects of host plants on sexual signals and responses, e.g., how volatiles interact with chemical signals, what plant characteristics affect acoustic vibrations, and which and how host plant colors and structures affect visual reflectance and/or conspicuousness.
7. Since all modalities are affected by abiotic factors, such as light, noise, and temperature, that are currently changing at a rapid pace, it is important to assess their evolutionary impact on sexual communication in arthropods.

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