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Host Plant Effects on Sexual Selection Dynamics in Phytophagous Insects

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Abstract

Natural selection is notoriously dynamic in nature, and so, too, is sexual selection. The interactions between phytophagous insects and their host plants have provided valuable insights into the many ways in which ecological factors can influence sexual selection. In this review, we highlight recent discoveries and provide guidance for future work in this area. Importantly, host plants can affect both the agents of sexual selection (e.g., mate choice and male–male competition) and the traits under selection (e.g., ornaments and weapons). Furthermore, in our rapidly changing world, insects now routinely encounter new potential host plants. The process of adaptation to a new host may be hindered or accelerated by sexual selection, and the unexplored evolutionary trajectories that emerge from these dynamics are relevant to pest management and insect conservation strategies. Examining the effects of host plants on sexual selection has the potential to advance our fundamental understanding of sexual conflict, host range evolution, and speciation, with relevance across taxa.

1. INTRODUCTION

Sexual selection occurs within ecological contexts (27, 45, 92, 125). Environmental conditions can change rapidly within these contexts—for example, food, temperature, predation risk, and social factors are rarely static. What these changes mean for sexual selection can be striking (e.g., 20, 117). Documenting and testing such dynamics are critical for understanding how evolution occurs in nature, especially how it will change as the planet becomes increasingly dominated by humans. Yet the consequences of varying environments for sexual selection can be difficult to uncover and measure.

Studies that focus on the interactions between phytophagous insects and their host plants can yield profuse insights into the effects of ecological dynamics on sexual selection and the resulting evolutionary outcomes. This is because host plants, as discrete living, growing, and changing resources, often dominate the ecological niche of phytophagous insects. The resources provided by the host plants often change starkly across the seasons and with, for example, water stress and temperature change. Furthermore, numerous insects, including many crop pests, use multiple host plants and must therefore tolerate very different ecological conditions within, and across, generations. Ecological conditions can have swift as well as long-term effects on the processes and outcomes of sexual selection, as we describe in this review. In our rapidly changing world, insects commonly encounter new potential host plants as either the insects or the plants (or both) find themselves transported to new locations. Feeding upon a new host plant early in the process of adaptation might, for example, lead to stunted size and altered pheromone composition, with negative consequences for mating success. Indeed, the processes of natural selection and sexual selection can easily become entwined for phytophagous insects. Our goal in this article is to review the diverse mechanisms by which host plants can influence sexual selection, provide guidance for future research, and show the enormous potential of research on phytophagous insects to yield evolutionary insights in our changing world.

2. PREMATING SEXUAL SELECTION

2.1. Intrasexual Selection

Intrasexual selection occurs when members of the same sex, often males, compete for mating opportunities. Intrasexual contests have led to the evolution of sexually selected weapons, including some of the most exaggerated morphological traits in the natural world (43). For example, males in the hemipteran superfamily Coreoidea have large hind femurs that they use to fight one another for territories on host plants (39, 89, 93), and male stag beetles (Coleoptera: Lucanidae) have enlarged mandibles that are used in fights for access to tree sap wounds from which females feed (70). In this section, we focus on how the host plant on which an individual develops influences the expression of, and selection on, the morphological weapons of sexual selection.

2.1.1. Nutrition. Sexually selected traits typically have heightened condition dependence (13, 14, 28); thus, variation in the quantity or quality of resources to which males have access during development can impact the size and shape of male sexually selected weaponry. Weapons typically scale with body size in what is known as an allometry; individuals that have had more resources or higher-quality resources are larger and have larger weapons. Early instars often lack the ability to disperse widely, and so the host plant where they hatch influences their body size during development (88). Host plant species typically differ in their nutrients, and this can lead to developmental plasticity in the morphology of insect weapons.

Different genotypes often exhibit different levels of developmental plasticity: One genotype might develop a large weapon when reared on one host plant but a smaller weapon on a different

Sexual selection: selection arising from fitness differences associated with nonrandom success in the competition for access to gametes for fertilization

Phytophagous: plant feeding

Natural selection: selection arising from fitness differences associated with nonrandom survival and reproduction of different phenotypes within a population

Sexually selected weapon: a morphological or chemical trait that has evolved to function in intrasexual physical conflict over access to mates; may retain other functions as well (e.g., predator defense, locomotion, feeding)

Allometry: the scaling relationship between body size and a trait of interest

Developmental plasticity: the property of a single genotype to express different phenotypes depending on the developmental conditions

host plant, whereas a different genotype might be insensitive to the host plant and develop the same sized weapon on both plants. When these reaction norms of male weaponry for individual genotypes reared across a range of host plants are not parallel, there is evidence for genotype-by-environment interactions (GEIs) (32). GEIs are crucial to consider when investigating sexual selection more broadly because they influence the evolvability of sexually selected traits in an environmentally dependent manner (71, 146). GEIs are ubiquitous in nature and therefore are relevant to the topics addressed throughout this review.

Many insects can use multiple host plant species for development. Experiments have revealed extensive plasticity in weapon morphology. For example, Allen & Miller (2) reared *Narnia femorata*, a species of leaf-footed bug (Hemiptera: Coreidae), on two different host plants (*Opuntia mesacantha* and *Opuntia robusta*), one of which (*O. robusta*) was completely novel to the population. They then measured the body and weapon (hind femur) sizes of the adults. The novel host plant led to complete reduction in sexual size dimorphism of male weapons: Allometric intercepts were lower on the novel host plant, indicating smaller (both shorter and thinner) weapons relative to the individual's body size (2).

Even when populations of insects use the same host plant species for development, nutrition may vary predictably, or unpredictably, across generations. *N. femorata* has several generations per year, and in North-Central Florida, populations only use one species of host plant, *O. mesacantha* ssp. *lata*. Each generation of *N. femorata* emerges to find their host plant in a different phenological state. Early in the year, *Opuntia* cacti flower, and then fruits mature gradually over the spring and summer. The size and shape of male weaponry is influenced by cactus fruit phenology (127). In fact, sexual dimorphism is eliminated when cactus fruit is removed by competitive herbivores during juvenile development (90). The presence of fruit also affects the narrow-sense heritability (h^2) by altering the relationship between additive genetic variance, V_A, and overall phenotypic variation, V_P (127). Thus, the evolvability of the population should fluctuate seasonally—at some times of year, the population may more readily respond to selection than at other times.

Importantly, the effect of nutrition on sexually selected weapons extends beyond external size. Male *N. femorata* reared on cacti with early season, unripe fruits have exoskeletons that are much more easily injured than those reared on cactus fruit that is more mature (151). Injury resistance is related to the thickness of endocuticle layers deposited during juvenile development and early adulthood, and the thickness of these layers is tied to nutrition. In addition to its roles in locomotion and preventing desiccation, which may be subject to natural selection, the exoskeleton also serves both sexually selected defensive and offensive purposes, and a robust cuticle likely leads to not only effective armor, but also a robust weapon.

Host plants can change the expression of sexually selected traits through size or structure, and they can alter the strength of selection on these traits. High-quality cactus plants with ripe fruit induce greater levels of intrasexual competition for territories (56, 101). Sexual selection is therefore likely weaker on unripe plants and stronger on high-quality plants; the strength of sexual selection in insect populations likely varies throughout the year, and some of this variation is due to the phenology of their host plants. Consequently, the strength of sexual selection might vary more for multivoltine species than for univoltine species. A complete picture of intrasexual selection dynamics must therefore incorporate the expression of, and selection on, sexually selected traits and how these traits change over space and time.

2.1.2. Host plant structure.
Across taxa, sexually selected weapons are highly variable in structure, shape, size, and location on the body, even within groups of closely related species (44, 92, 147). The shape of weapons is often associated with specific fighting styles (19, 43, 83, 86, 107). Behavior is highly plastic and can lead the evolutionary process (149): Fighting in a new

Reaction norms: quantify how a phenotype belonging to a single genotype changes across a range of environments

Genotype-by-environment interaction (GEI): situation in which the expression of a trait of different genotypes is dependent on the environment

environment could require a different fighting style that then imposes selection on weapon morphology to best match the new behavior. Yet we know little about why male fighting style changes, initiating changes in morphology. For many insect species, selection on weapon shape may differ according to the structural context in which fights occur. For example, competitions that occur in flat open spaces should take a different form than competitions that occur in tight tunnels or amid dense foliage (43). Phytophagous insect groups wherein males fight in a variety of structural contexts provide powerful opportunities to investigate the role of structural context in the dynamics of fighting behaviors. Some species of hemipterans fight on the stem of a smooth and firm surface, such as the shaft of bamboo (94), whereas others fight on leafy, unstable legumes (138). The surfaces on which males fight likely influence grip and the space available for combat maneuvers. Importantly, expansions onto new host plant species are common and contemporary in many groups of phytophagous insects (51, 128). It would be valuable to test selection on weapon form when insect fights are induced on a variety of ecologically relevant host plants. In our rapidly changing world, insects now frequently encounter potential host plants that are novel to them and may start to utilize them as host plants. Such new hosts may differ in architecture and structure from ancestral host plants, and such spatial changes may influence the likelihood of individuals interacting and engaging in intrasexual selection. Using experimental evolution, Tomkins et al. (142) found that complex three-dimensional environments change the size at which males invest in weaponry: When certain arthropods, such as male *Rhizoglyphus echinopus* mites, evolved in more complex environments in the lab, only larger males developed weapons. This fascinating discovery likely reflects a change in the balance between the costs and benefits of growing a weapon. For example, a more complex environment, like a more architecturally complex host plant, should lead to greater mobility costs associated with weaponry and a decreased likelihood of needing to fight to be able to mate (142).

Different host plants may have different characteristics that also influence the spatial distribution of defensible resources. Rhinoceros beetle (*Trypoxylus dichotomus*) males exhibit large horns for fighting over wounds in oak (*Quercus* spp.), ash (*Fraxinus griffithii*), and bay (*Machilus thunbergi*) trees. Del Sol et al. (34) studied five populations of *T. dichotomus* and found population-level differences in horn length. The two northern populations have the longest horns because the males defend wounds in oak trees, which have thick bark that they cannot chew into. Thick bark therefore reduces the number of defensible sites, increasing the competition for mates. The three southern populations feed on wounds in ash and bay, which have thinner bark and more wounds, resulting in a reduction in sexual selection and smaller horns (34). It would be interesting to better understand whether colonization of a novel host plant only occurs when selection on weapons is similar to selection imposed by ancestral host plants. Future work should compare selection gradients on weaponry between species that have recently adopted new host plants and sister species that have remained upon their ancestral host plants.

2.2. Intersexual Selection

Mate choice can be a powerful force of sexual selection (5, 124). Yet we still know little about the forces that shape the evolution of mating preferences (76) or why mate preferences are not always consistent across females or even within a single female over time (20). Differences in mate choice can be influenced by the past or present ecological contexts (18), and so can the many varied ornaments produced by males to entice females to mate. In this section, we outline some intriguing ways in which host plants can alter mate choice decisions by changing pheromones and other ornaments used to attract mates and also by altering mate preferences. Phytophagous insects provide excellent opportunities to address these phenomena. In a review of ecological effects on

sexual selection, the host plant of phytophagous insects was determined to be the ecological factor driving divergent mate choice in nature in 27% of cases (130), suggesting that host plant effects on mating decisions may be common.

2.2.1. Nutrition.
Nutrition during development and even adulthood can affect the expression of sexually selected ornaments, just as it affects the expression of weapons (96). Butterflies have provided useful insights in this area. Even if butterfly species can feed on multiple species, the larvae are generally restricted to a single host plant. The available resources, which vary across host plants, are then used to develop colors and patterns that inform mate choice decisions (e.g., 73). For example, the common blue butterfly (*Polyommatus icarus*) has wing patches that are comprised of flavonoids, pigments that absorb ultraviolet radiation. These pigments are obtained by the larvae during development (77). Male common blue butterflies prefer females with flavonoid-rich wings. Because different species of host plant contain different concentrations of flavonoids, male preference for females is linked to the female developmental host plant. Host plants can also influence wing scale microstructure: Ultraviolet-reflecting wing scales are affected by host plant species in the butterfly *Zerene cesonia* (50). Male cabbage white butterflies (*Pieris rapae*) with more colorful dorsal wings are preferred by females (97). Tigreros (140) manipulated the nitrogen within the diets of larval cabbage white butterflies, paralleling the variation in nitrogen across its host plants. High nitrogen resulted in brighter male wing color and, interestingly, a longer latency to first mating (140).

Body size often affects both morphology and behavior. Sexually selected traits scale with body size through allometry; larger males may be more aggressive in male–male competition and may be preferred by females (6). Insect body size is often dramatically affected by the host plant used during development (e.g., 108). Host plant quality can lead to larger males that are more successful in contests (131) and better at mate searching through greater locomotor performance (106), and larger females may obtain more matings (56). Thus, sexual selection can indirectly select upon the oviposition behaviors of mothers seeking to place their offspring on the best hosts (91, 118).

2.2.2. Chemical signals.
The primary modality of signaling associated with sexual selection in phytophagous insects is chemical. Herbivores use chemicals from their host plant as essential precursors to synthesize signaling molecules—or they may even use the compounds directly without alteration. Interestingly, both plants and insects can use the same volatile chemicals for defense, while insects may also use volatiles for finding and attracting mates (129, 152). Sexual selection can act on a range of systems, such as sensory and locomotion systems for mate location, and when mating occurs on host plants, even finding a host plant may be a form of scramble competition (133). For example, *Heliconius* butterflies exhibit pupal-mating behavior: Males emerge first and locate female pupae on a host plant, where they guard the female and mate with her when she emerges (47). Competition for mates therefore rests on the ability of a male to quickly locate a suitable host plant. This ability in *Heliconius charithonia* depends on the host plant on which the male developed and the host plant on which the female resides (75). Females are more likely to oviposit on the *Passiflora* species on which they developed, and males are more likely to search for female pupae on the same species, with some evidence for assortative mating between individuals based on their host plants. The location of potential mates via host plant volatiles has also been seen in bees (1), cockchafers (122), mirid bugs (49, 95), and gall wasps (143), a broad range of taxa indicating that this is a general pattern worthy of further study, especially for its evolutionary consequences.

The chemical signals of phytophagous insects are derived from host plant compounds. Short-range cuticular hydrocarbons (CHCs) (37) and sex pheromones are used to locate or attract the opposite sex (80). CHCs are hydrocarbons on the surface of insects that serve as antidesiccants (and

Sexually selected ornament: a trait that is expressed by the chosen sex and is a direct target of selection from mate choice by the choosier sex; can be of multiple modalities (morphological, acoustic, chemical, behavioral)

Assortative mating: situation in which individuals with similar phenotypes or genotypes prefer to mate with one another

thus have a naturally selected purpose; e.g., 21), as well as playing a role in conspecific recognition and communication over short distances. Variation in CHCs has a considerable genetic basis (e.g., 11, 68), and they are also phenotypically plastic, changing with abiotic and biotic environmental factors (105). For example, the CHC profile of the mustard leaf beetle (*Phaedon cochleariae*) changes depending on whether it developed on Chinese cabbage (*Brassica rapa* ssp. *pekinensis*) or watercress (*Nasturtium officinale*) (54), or even on the quantity of fatty acids that is present in artificial diets (104). Changes in CHC profiles can modify the mating choices of the opposite sex. Male mustard leaf beetles prefer to mate with females that developed on the same host species that they did, with some evidence to suggest that they base this decision on the CHC profile (54; but see 104). The genetic component of CHC profiles means that they have the capacity to evolve, which is why different populations have different CHC profiles. CHC profiles are important for mate discrimination in the cactus-feeding *Drosophila mojavensis*. A Baja California population uses the agria cactus (*Stenocereus gummosus*) as a host plant, while a mainland (Sonora, Mexico and Arizona) population uses the organ pipe cactus (*Stenocereus thurberi*) (48, 63). Multiple genes contribute to the evolution of CHC differences between the two host plants, and there are complex interactions that occur between loci and host plants that affect male mating success (48). The extent of plasticity in CHC profiles has also evolved to be different between populations using the different host plants. The Baja population has evolved reduced plasticity in CHCs in response to the species of cactus; in this case, the CHC profiles are not measurably different across the host plants on which individuals developed (63). It is therefore important to understand when host plants induce plastic changes in sexually selected traits, but also, crucially, when they do not, as the extent of plasticity induced by host plants will result in drastically different evolutionary predictions (149).

Long-distance pheromonal communication is also influenced by host plants. The synthesis of most pheromones has a large genetic contribution (61), yet pheromones in different taxa are often reliant on resources sequestered from larval and adult host plants (30; for a detailed review, see 80). Some female arctiid moths choose males using a pheromone derived from pyrrolizidine alkaloids that is obtained from developmental host plants (*Crotalaria* in the family Fabaceae). The pheromone appears to be an honest signal to the females of the male's ability to protect the female and her eggs via high levels of pyrrolizidine alkaloids in his spermatophore, a package of sperm and nutrients that males give to females (38). After mating, the female imbues her eggs with this defensive compound, protecting them from parasitism (12). These chemicals are also used by the female as protection from spider attacks (25, 57), a direct benefit of choosing males that originate from a high-quality host plant.

Finally, perfumes are chemicals that are not synthesized but are taken from a plant to assist in attracting a mate. For example, male *Euglossa* bees pollinate orchids and harvest fragrant compounds, which they store in baskets in their modified hind tibias (36). The perfumed compounds are used by males in ritualized behaviors to attract females (64). The scent is highly variable across species (41, 114, 119, 148), suggesting that the strong stabilizing selection maintaining these perfumes is species specific. Yet habitat differences, seasonality of flowering plants, and microclimate lead to intraspecific variation in the perfumes (31, 114, 119).

Plant chemicals can also act as synergists with insect-derived chemicals, such that both volatiles from the plant and insect pheromones need to be experienced at the same time to elicit a response (33). For example, males of the agricultural pest *Spodoptera littoralis* are more attracted to female sex pheromone when it is combined with the volatiles of the host plant on which the male developed (3), and there is evidence that this mechanism maintains species boundaries (16). These synergisms are widespread in phytophagous insects (8, 103, 154), and understanding them is crucial for mating disruption tactics that can be used in integrated pest management strategies (74). Different ecological contexts, like the phytochemicals released by a host plant species, can change the

costs and benefits of mate choice, altering the selective regime on preferences and signals (141). An interesting approach would be to use individual-level pheromone profiles in combination with different plant volatiles to assess the importance of this mechanism in influencing population-level sexual selection dynamics.

2.2.3. Vibrational signals. Vibrational communication is taxonomically widespread in insects (22). The best-studied insect group that vibrates to attract mates is the *Enchenopa binotata* species complex of treehoppers. The males drum on their host plant, and the females choose the males based on qualities of the drum, especially drumming frequency. Each treehopper species uses only one host plant species in nature. Drumming frequency is species specific. Drumming has greater transmission efficiency or attenuation on a species' host plant versus other plants, suggesting a history of selection to match frequency with host plant structure (87). There are strong GEIs in the male signal; male genotype influences drumming frequency, and males of different genotypes have different drumming frequencies depending on the individual plant on which they are drumming. This mechanism maintains variation in drums and also means the host plant on which a male drums is crucial in determining his mating prospects (123). Genes are also part of the environment in which these males are drumming, as their host plants also harbor genetic variation that determines the structure of the plant. Plant structure and substrate determine vibrational transmission and, therefore, how male treehopper signals are received. Indeed, different plant genotypes influence the sexual selection dynamics of the treehoppers; male and female treehoppers reared on different clone lines of their host plant showed variation in male signals (121) and female preference for those signals (120).

3. POSTMATING SEXUAL SELECTION

When females mate multiple times, competition can occur between male gametes for the opportunity to fertilize (109). Until the 1970s, sperm competition was a hidden part of sexual selection, but as research into postmating sexual selection has grown, so has our understanding of how it drives the evolution of a diversity of male adaptations (135). In many species, investment in premating sexually selected traits, like weapons or ornaments, requires a trade-off with investment in postmating sexually selected traits, like testis size and the related trait, ejaculate size, a key component in sperm competition (136). The developmental host plant can influence this allocation trade-off. The weapons of male leaf-footed cactus bugs are dependent on nutrition, but the seasonal quality of their host plant, even within a single host species, changes the allocation patterns between weapons and testes. Males raised on high-quality fruit have larger weapons and larger testes, but individuals on a medium-quality diet invest relatively more in their weapons than in their testes (127). Investment patterns can also differ by host plant species. Somjee et al. (137) reared the heliconia bug *Leptoscelis tricolor* on two different species of *Heliconia* host plants and found a complete reversal of investment in testis and weapon size: Testes were larger and weapons smaller in individuals reared on *Heliconia mariae*, whereas weapons were larger and testes smaller in individuals reared on *Heliconia platystachys* (137), and courtship rates were higher (88). Is such a pattern adaptive, i.e., does one host plant require contests to obtain matings, while sperm competition is more important on the other plant? Regardless of the answer, the dynamics of sexual selection are likely to be different for males raised on the two different heliconia species, with males raised on *H. platystachys* likely to be more successful in precopulatory sexual selection via male–male competition, while males raised on *H. mariae* may be more successful in sperm competition.

Host plant quality influences the investment that males make into spermatophores. Poor diets may influence protein content and sperm number in spermatophores (53, 140). The consequences can substantially influence fitness because females may assess spermatophore size and choose only

Sperm competition: competition between the sperm of two or more males for fertilization of a female's eggs after mating

males providing the best or the biggest spermatophores, as she uses the nutrients to invest in main-
tenance or egg provisioning. For example, Cook & Wedell (26) show that, in *Pieris rapae*, the size of
the first spermatophore was smaller when males were reared on *Tropaeoleum majus* than when they
were reared on *Alliaria petiolata*, although the total sperm numbers within the spermatophores
were the same. This suggests that males on a poor host plant maximize fertilization potential
per mating while minimizing the direct benefits to the female. Male European grapevine moths
(*Lobesia botrana*) that develop on Mourvèdre grapevines have smaller spermatophores and fewer
numbers of eupyrene sperm (those capable of fertilizing an egg) (99). Interestingly, female moths
can discern the host plant of the male, and they lay fewer eggs when paired with a Mourvèdre
male (100), suggesting that cryptic female choice may be occurring. More studies are needed to
know how females are able to bias fertilization based on the host plants of males. Understanding
these mechanisms holds promise for integrated pest management strategies, including attempts
to produce sterile males that are appealing to females (134). Studying postmating sexual selection
is well worth the effort, despite the difficulties, because so much remains to be discovered in this
area, and deeper understanding will provide benefits to both basic science and applied entomology.

4. SEXUAL CONFLICT

A consequence of sexual selection is divergent selection between the sexes, which has the potential
to put them in evolutionary conflict (78). The two sexes largely share the same genome, so each
sex is constrained in the direction in which it can evolve by the other. In addition, the sexes may
have different optima for trait expression. The costs and benefits of adaptations to sexual conflict
are sensitive to local ecological conditions (111), of which host plants have been an understudied
part. The sexes might differ in which host plants they prefer to visit (139), which may reflect
sex-specific adaptations to various host plant species. Alternatively, the sexes may have different
resource requirements that are best obtained from separate plant species (55). For example, males
of many species of butterfly release host plant–derived antiaphrodisiacs to prevent females from
remating (4, 98)—an adaptation arising from sexual conflict. The loss of sexual dimorphism on a
certain host plant may be a good indication that at least one sex developed on a host plant that is
unable to provide the resources required to develop important secondary sexual traits (2). Different
host plants may lead to sex-specific selection, as stressful environments, such as a novel host plant,
may increase or decrease the variance in fitness separately between the sexes (84). Delcourt et al.
(35) estimated the genetic basis for fitness for both sexes in the fly *Drosophila serrata* across two
diet environments: the laboratory yeast diet on which they had evolved and a novel corn diet.
The intersex genetic correlation in both ancestral and novel environments was negative, meaning
genes in the populations that benefited males were deleterious in females and vice versa, a clear
sign of sexual conflict that could be present across different host plants.

Sexual conflict plays out differently depending on the structural components of the environ-
ment in which males and females interact. For example, male purple-edged copper butterflies
(*Lycaena hippothoe*) defend territories of nectar-rich plants and harass any females that fly by, so
much so that females will avoid ovipositing on these plants to avoid harassment, even if the host
plant is of desirable quality (144). Harassment could also be mitigated at a microhabitat scale
with different host plant architectures. In *Drosophila melanogaster*, Yun et al. (155) found that the
complexity of the environment within which male harassment took place altered the ability of
the female to escape such harassment. Similarly, the more complex the host plant, the greater the
opportunity that females may have to escape harassment, and this may reduce sexual conflict. As
a large component of the environment that phytophagous insects experience, differences in host
plant characteristics can dramatically alter the form and outcomes of sexual conflict (111). Females

may have more control over the resolution of sexual conflict over host plant use, as they choose on which plant to oviposit eggs. Female oviposition patterns could therefore be dynamic in response to the sex-specific effects of host plants on offspring: If they have recently mated with a high-quality male, females may choose to oviposit on a host plant that is most beneficial for males, for example, a currently untested possibility. One way to investigate this is to expand existing meta-analyses (for example, 60) to include sex-specific effects on offspring and get a better grasp on the extent of such a pattern in nature.

5. THE BROADER IMPLICATIONS OF HOST PLANTS AND SEXUAL SELECTION IN PHYTOPHAGOUS INSECTS

In this review, we discuss the multiple ways in which host plants influence sexual selection dynamics in phytophagous insects. To what extent are these patterns important to consider if we want to better understand adaptive evolution and speciation in insects and other taxa? Phytophagous insects provide outstanding opportunities to understand changes in the rate of adaptation to new environments, as many pest species feed on, and may adapt to, economically important agricultural crops. In addition, the diversity of phytophagous insects is linked to their relationships with host plants, so asking questions about host range evolution and the factors that might influence it can tell us about broad patterns of niche evolution and speciation (62, 102).

5.1. Changes in the Rate of Adaptation

Sexual selection can increase the rate of adaptation to a new environment, as shown by a recent meta-analysis (17). However, in some cases, sexual selection can hinder adaptation, especially when its operation induces sexual conflict (15, 23, 112). In *N. femorata*, the developmental host plant can influence sexual dimorphism (2), a hallmark of sexually antagonistic selection (29) and potential maladaptation (85). Developing on the novel *O. robusta* shrinks weapon size, reduces sexual dimorphism, and likely also dampens the strength of sexual selection acting on males (2). It is as yet unknown whether this novel host plant influences female fitness-related traits too, and the strength and sign of the genetic correlations for fitness between males (e.g., in terms of winning contests) and females (e.g., fecundity) also remain unclear. Negative intersex correlations for fitness, while rare (113) and not always a consequence of sexually antagonistic selection (24), can dramatically slow adaptation to novel environments (35) and should be considered when predicting short-term evolutionary dynamics.

Theory and data suggest that sexual selection can aid adaptation in circumstances in which a population is far away from a fitness peak (17, 81), as should be common with species introductions or host shifts. Sexual selection can increase population mean fitness in at least two circumstances. In the first case, population mean fitness can improve when there is a positive genetic correlation between sexually selected traits and other fitness-relevant traits, like parental care or survival (72). In other words, when natural and sexual selection align, rapid adaptive evolution is possible (126). This idea can be applied to the long list of examples provided in this review. For example, sexual selection and natural selection have aligned in male *Utetheisa ornatrix* moths: Females choose males based on their sex pheromones, which signal their ability to defend their partner's eggs from parasitoids with pyrrolizidine alkaloids, both of which are derived from the same host plant, *Crotalaria* (12). In the second case, sexual selection may purge deleterious alleles from the population at a greater rate than natural selection alone (66, 150; but see 7, 67). This may be especially true when traits under sexual selection are condition dependent; that is, individuals that possess alleles that enable them to better feed or survive early life are more likely to succeed in the competition for gametes. This good genes idea tightly aligns the processes of natural selection with those of

Host range:
the diversity of plant species that can be utilized by an insect population

sexual selection, which, theoretically at least, would lead to rapid adaptation (82, 115, 116). These ideas can be perfectly tested in phytophagous insects. We have seen that host plants influence the expression of traits used in intrasexual (e.g., 2) and intersexual (e.g., 77) selection, so we encourage future experiments explicitly designed to disentangle host plant effects on natural and sexual selection simultaneously.

5.2. Host Range Evolution

Sexual selection has the capacity to affect host range evolution of phytophagous insects, a factor that has been ignored to date (62). The number of host plants that a species of phytophagous insect can utilize—its host range—can evolve, resulting in either greater host plant generalism or greater specialism. Whether an insect is a specialist or a generalist is important to know for forecasting invasion likelihood (110) or conservation concern (69). The evolution of a mate-finding system dependent on volatiles from host plants tightly links host plant use to finding mates (46). For generalist species, this may require searching many different plant species, which may lead to accrual of search costs that a specialist species may not incur. Theory suggests that, if female preference for host plant–derived pheromones in males becomes genetically linked with female oviposition behavior for that same host plant, then sexual selection can drive the evolution of a more specialized niche (118).

Developmental effects of natal host plants have been widely documented to contribute to assortative mating. When this occurs, it is predicted to result in the formation of a host race that uses a single host plant, due to the positive feedback mechanism of females preferring males that developed on the same host plant as they did themselves. This mechanism often relies on the ingestion of pheromone precursors or host plant effects on CHC composition (40, 42, 52, 54, 59, 65, 131, 153). The evolution of reproductive isolation can occur swiftly under these conditions and ultimately result in speciation (58, 68), especially when a condition-dependent trait is an honest indicator of local adaptation (145). To truly understand how common host plant–induced assortative mating is, however, studies must publish negative results, which are critical to understanding more broadly when host plant–induced plasticity induces assortative mating and when it does not (e.g., 9).

Sexual selection could also contribute to expanding a population's host range, rather than narrowing it down, as described above. Sexual conflict might be resolved by sex-specific host plant preferences through sex-biased dispersal or adult feeding choices (55), preventing the population from adapting to a single plant species. Different host plants might offer individuals a wide range of phytochemicals that are used in a range of natural selection (e.g., defense) and sexual selection (e.g., mate attraction) functions that prevent specialization. Indeed, a poor-quality host can still be favored by males if it contains pheromone precursors that aid them in acquiring mates. Male *Batrocera dorsalis* flies that were fed a poor diet have little to no mating success, but this was reversed if their poor diet was supplemented only with methyl eugenol, a pheromone precursor (132). Studying host plant effects on sexual selection dynamics in phytophagous insects should provide priceless insights for use in integrated pest management strategies for pest species (e.g., 10, 74) and into the evolution of phytophagous insects in urban environments (79).

6. CONCLUSIONS

In this review, we highlight the range of mechanisms by which host plants can influence the sexual selection dynamics of the insects that live and feed on them. If we try to understand an insect's ability to adapt to a host plant independently of how that host plant affects the dynamics of sexual selection, then we may get an incomplete idea of how adaptation and host range evolution will

unfold. Our review showcases other areas that would be fruitful for future research. First, there is a dearth of work on how postmating sexual selection is affected by host plants, knowledge of which is fundamental for the complete understanding of sexual selection. Second, understanding of the intersection between the host plant and the generation or resolution of sexual conflict is lacking, even in existing systems. Third, we encourage researchers to investigate which scenarios are most likely to lead to host plant–induced assortative mating. This question can only be answered with more mate choice experiments and the publication of null results. Furthermore, developmental host plants are known to affect insect attractiveness, but less is known about how they influence mate choice and male–male competition. Host plants may affect both the targets and agents of selection, leading to fascinating evolutionary dynamics. Future work on the myriad of ways that host plants can affect sexual selection is likely to provide vast insights into insect ecology and evolution. Moreover, the results of this work will undoubtedly inform numerous subfields of entomology and help to guide strategies used in pest management, insect conservation, and beyond.

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