Learning in Insect Pollinators and Herbivores

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Abstract

The relationship between plants and insects is influenced by insects' behavioral decisions during foraging and oviposition. In mutualistic pollinators and antagonistic herbivores, past experience (learning) affects such decisions, which ultimately can impact plant fitness. The higher levels of dietary generalism in pollinators than in herbivores may be an explanation for the differences in learning seen between these two groups. Generalist pollinators experience a high level of environmental variation, which we suggest favors associative learning. Larval herbivores employ habituation and sensitization—strategies useful in their less variable environments. Exceptions to these patterns based on habitats, mobility, and life history provide critical tests of current theory. Relevant plant traits should be under selection to be easily learned and remembered in pollinators and difficult to learn in herbivores. Insect learning thereby has the potential to have an important, yet largely unexplored, role in plant-insect coevolution.

53

INTRODUCTION

Associative learning (classical conditioning): the formation of an association between a neutral stimulus and reward or punishment

Habituation: decreased responsiveness to a stimulus with repeated exposure

Sensitization: increased responsiveness to a stimulus with repeated exposure

The majority of insects inhabit complex environments in which they must make decisions about where to seek food, with whom to mate, and where to rear their young. Learning is an important factor influencing such decisions. For pollinators and herbivores, these decisions not only affect the insect's fitness, but also can have beneficial or detrimental consequences for the plant. We follow Papaj & Prokopy's (111) definition of learning as when an "individual's behavior changes in a repeatable way as a consequence of experience (p. 316)." This intentionally broad definition includes not only associative learning, but also processes such as induction, habituation, and sensitization. All of these are mechanisms by which learning influences behavior, and they have a rich literature in the study of insects (46, 111). There is research on learning about plant traits from a broad diversity of plant-associated insects belonging to different foraging guilds. For example, learning can affect flower visitation (66), the amounts of plant tissue consumed by herbivores (41), and oviposition choices of adult females (31). The evolution of learning in plant-associated insects therefore could have important consequences for the evolution of traits about which insects learn. In this review, we focus on the common themes that unite the evolution of learning in pollinators and herbivores. First we examine the conditions that may favor learning in these different foraging guilds. We then summarize research on learning about different plant traits in pollinators and in herbivores, and finally we discuss the potential for learning in plant-associated insects to be a force of natural selection on plants.

When Does Learning Evolve?

Learning in insects is remarkably common (46, 111) but not ubiquitous (90, 112). A number of general predictions have been made about when we should expect natural selection to favor learning abilities. For example, learning provides little benefit in either static or unpredictable environments. In these cases, animals are best served by making choices based on genetically fixed preferences (80, 136). In contrast, we expect animals to benefit from learning in variable environments with repeating patterns (or predictability), which allow individuals to use information they have previously acquired (34, 103). The temporal and spatial scale of this variation likely determines the degree and type of learning observed in plant-associated insects (**Figure 1**), be they pollinators or herbivores. For example, an animal that encounters large amounts of variation over short temporal or spatial scales may demonstrate associative learning, which allows it to form positive or negative associations with a wide range of neutral stimuli (e.g., colors, odors, shapes). In contrast, an animal that encounters less variation might be more likely to exhibit habituation or sensitization, which are changes in behavioral responses to stimuli that already invoke an innate response (e.g., bitter or sweet taste).

Who Learns? A General Framework

Several life-history attributes may affect the amount and rate of variation that an animal encounters. These factors allow us to formulate hypotheses about the extent of learning in plant-associated insects and the types of learning that different species exhibit. Some of these life-history factors include dietary generalism, mobility, foraging guild, lifespan, and sociality. It has been proposed that individuals that are generalists (38, 113) and highly mobile (85) encounter more variation and therefore should be better learners than ones that are specialists or sedentary. The same explanation based on the extent of exposure to environmental variation has been put forward for why we might expect stronger learning abilities in individuals of longer-lived than
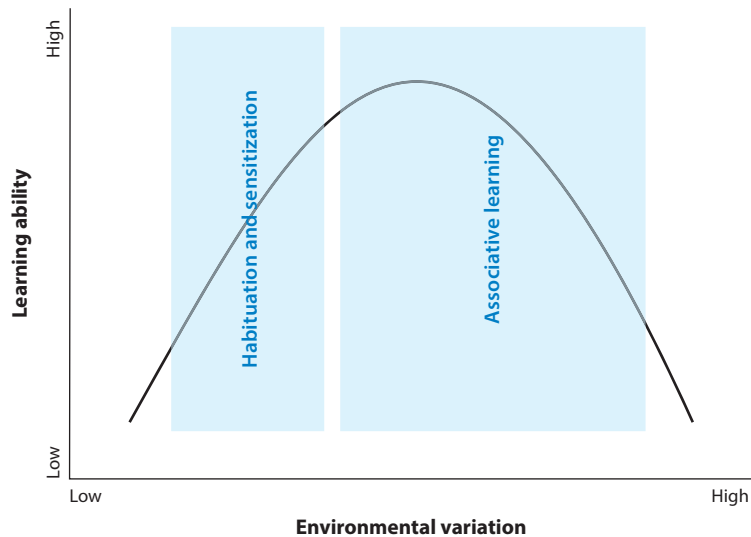
Figure 1

A conceptualization of when particular types of learning are predicted to occur in plant-feeding insects. In low to medium levels of environmental variation, habituation and sensitization may be beneficial, whereas associative learning is predicted to be beneficial under greater spatial or temporal variation.

shorter-lived species (99). None of these propositions are a hard-and-fast rule, however. For example, a generalist may encounter more variation than a specialist does in some cases, but if the phenotype of a resource a specialist searches for (e.g., flower color, leaf shape, or chemotype) is variable (i.e., polymorphic) depending on the habitat or community in which it is embedded, learning may be as advantageous to a specialist as to a generalist (109). Similarly, although mobile animals may typically encounter more environmental variation than sedentary animals do, some long-lived sedentary animals may experience large variation over their lifetimes.

In vertebrates, feeding guild has been proposed as a factor influencing learning abilities (26). The theory behind this prediction is that members of guilds that locate their food in places with high spatiotemporal complexity may be better learners than individuals that forage in less complex environments. For example, voles that feed on resources that are spatially and temporally predictable, such as plant roots, perform spatiotemporal learning tasks more poorly than do voles that feed on more variable foods, such as insects and seeds (76). Similarly, in insects, it has been proposed that parasitoids might be better learners than members of other insect guilds are because the parasitoid lifestyle requires finding a highly specific food amid tremendous environmental complexity (52). In summary, we predict that species that encounter large amounts of variation over their lives—because of environmental complexity, dietary generalism, mobility, or lifespan—should benefit from the ability to learn, whether they are a pollinator or an herbivore.

There is, however, a final and somewhat more contentious life-history trait that has been proposed to influence learning abilities: the level of sociality. One theory is that sociality per se favors the evolution of learning in order to remember interactions with individual nestmates (the social brain hypothesis) (21, 48). Although this has been suggested as an explanation for the impressive learning abilities of the eusocial Hymenoptera, some of which do learn to recognize nestmates (130), alternative explanations (such as the ancestral history of parasitoidism) have also been proposed (52). There is an additional path by which sociality could select for learning

Induced preference:
increased preference
for a host plant after
exposure

abilities. Membership in a social group allows individuals to specialize in space or time on different resources, as has been demonstrated for bees (77). Sociality may thus simultaneously select for high foraging efficiency and performance to feed the entire colony and for learning for short-term specialization.

Testing these theories on when we should expect the evolution of learning abilities poses a number of methodological issues. One approach has been to compare learning abilities of species that differ in one of these life-history traits. This has been attempted for a number of pollinators with comparisons of species that differ in traits such as level of sociality (8, 48), environmental complexity (29), and mobility (85), as discussed below. To our knowledge, no such comparisons have been conducted in herbivores. Caution should be exercised in interpreting such comparisons, however, as the initial studies employed low sample sizes (i.e., a comparison of two species) and did not control for confounding factors that also vary with the life-history trait in question. Another approach has been experimental evolution of learning in the laboratory, as has been demonstrated with oviposition site learning in *Drosophila melanogaster* (88, 102). This approach opens the door for studies to manipulate animal environments and directly test hypotheses about the evolution of learning. Although life-history traits are far from perfect predictors of learning abilities, they are starting points for testing hypotheses and developing alternatives about which species should be better learners and the type of learning they may exhibit.

Why Study Learning in Plant-Associated Insects?

There is a long history of research on learning in plant-associated insects (46, 110). Not only are insects tractable study organisms, but learning in insects can have significant implications for agriculture (35, 115). Pollinators and herbivores have important relationships with plants, and for both groups, learning has been documented in many species (23, 111). Making a comparison between pollinators and herbivores, however, is problematic, as pollinators and herbivores are often distantly related taxa or different life stages; therefore, such comparisons are confounded by many factors. An important issue complicating comparisons of learning in pollinators and herbivores is the degree of dietary generalism, which has been discussed above as an important axis in the evolution of learning (38, 113). Overall, insect pollinators are more generalized than insect herbivores are, with herbivores interacting with fewer and more closely related species (54). What further exacerbates this difference is that the pollinators for which learning is the best studied are the generalist social hymenopteran bees, for which there is a large literature on associative learning (101), and the herbivores for which learning is arguably the best studied are the more specialized larval Lepidoptera, for which there is a substantial literature on habituation and induced preferences (111). Comparative issues arising from inherent differences between pollinators and herbivores are thereby accentuated by traditions of how these areas of research have developed. Nonetheless, these two foraging guilds are often learning about traits of the same plant resource.

In this section, we discuss the plant traits that pollinators learn and we review species comparisons in learning ability. We also highlight avenues of research unique to each of these groups, including social learning in pollinators and the potential for learned information to cross-metamorphic stages in herbivores. Whereas our discussion of learning in pollinators is focused on nectar and pollen foraging, our discussion of herbivores includes the role of learning in oviposition because it is a critical decision with important consequences for the insect and its plant resource. Additionally, oviposition by adult Lepidoptera, which are nectar feeders as adults but herbivores as larvae, links pollinators and herbivores, as individuals may be simultaneously learning in nectar foraging and oviposition decisions. Given pollinators' and herbivores' intimate relationships with

plants, side-by-side discussions of learning in these two groups may provide important insights into the evolution of learning and the role of learning in community ecology more generally.

Given the commonness of learning in insects and potential effects of this learning for plant fitness, learning may have a prominent role to play in the reciprocal adaptation (or coevolution) between species. It has been proposed (158) that the positive relationship between pollinators and plants favors floral traits that are easy for pollinators to learn. Learning of floral traits increases visits to that plant species through flower constancy, thereby increasing pollen transfer and, theoretically, seed set (24). Traits that could increase pollinator learning are ones that are honest indicators of nectar or pollen quality and consistent within a species but variable between plant species (158). Multimodal plant signals can also make flowers easier to learn (93) and could be under similar selection. We might therefore expect a feedback between learning in pollinators due to their life-history traits selecting for plant traits that are easier to learn, which further favors the evolution of learning. By extension, we predict plant traits that are under selection by herbivorous insects to be difficult to learn. Dishonest signals of plant quality (127) or high variability within species (118) could potentially thwart the evolution or application of learning abilities in herbivores. In the sections below, we review the learning abilities and mechanisms described for pollinators and herbivores.

POLLINATORS

The majority of research on learning in pollinators has been conducted with bees, but wasps, adult Lepidoptera, beetles, and flies are also important pollinators for many plant species (151). We focus here on associative learning in bees and Lepidoptera, as these are the groups with the most research and they make an interesting contrast. Within each of these groups, we discuss the plant traits about which insects learn, discuss what factors may drive learning abilities, and conclude with speculation about the consequences of pollinator learning for selection on plant traits.

The range of floral traits learned by bees is extraordinary. Honey bees, *Apis mellifera*, and bumblebees, *Bombus* sp., can learn to associate flower colors, odors, shapes, patterns, electric fields, textures, and locations with nectar rewards (27, 59, 66, 91, 101, 131). Not only do bees learn to associate floral traits with nectar, but bees also learn how to extract pollen (117), learn how to associate pollen rewards with floral colors (106), and can even simultaneously learn to associate pollen rewards with one flower color and nectar rewards with another color (105). Reviews on learning in bees (46, 101) indicate that learning of associations between floral traits and rewards is generally rapid, occurs in many sensory modalities, and likely is important for plant reproduction through the process of flower constancy (see below). The learning abilities of bees have been attributed to a number of factors, including that colonies are large and long lived and must therefore take efficient advantage of ephemeral resources (67), they are central-place foragers that navigate through space to and from resource patches (8), and they are social animals with potentially long-term and complex social interactions (21). As discussed above, one method to test each of these hypotheses is to compare closely related species that differ in one of these traits.

Three studies have compared learning abilities of bees that differ in life history traits. Africanized honey bees, *A. mellifera scutellata*, because of their tropical habitats, do not store as large honey reserves as do European honey bees, *A. mellifera*, and more frequently move nest sites. The reduced need for honey production and reduced central-place foraging may result in Africanized honey bees being under reduced pressure to learn new stimuli to maximize honey storage. This has been proposed as an explanation for the slower learning and shorter memories of Africanized honey bees (29). The second study addressed the role of sociality in the evolution of learning by comparing honey bees and solitary blue orchard bees, *Osmia lignaria*. Honey bees were

SOCIAL LEARNING IN POLLINATORS

The best-known example of social learning is the waggle dance of the European honey bee, *Apis mellifera* (58), but simpler forms of social learning such as learning of floral scents from nectar brought back by others in the hive have also been demonstrated for honey bees and bumblebees (13, 44, 51, 57). As a mechanism to recruit more individuals to visit flower types or patches, social learning in pollinators may benefit plants by increasing visitation rate and pollen transfer. It is therefore possible that plants could evolve traits that enhance social information use by pollinators (69). Although social learning was historically believed to be unique to social animals, recently, it has been proposed that social learning is no more complicated a cognitive task than second-order conditioning (40). Social learning may therefore occur not only in bee pollinators. Tropical *Heliconius* individuals that share the same roosts appear to nonrandomly forage at the same food sources, raising the possibility of social learning (147, but see 53). For other adult Lepidoptera foraging over wide areas and feeding from a range of floral sources (e.g., during migration), social learning could be a beneficial source of information about which food sources are high quality and needs further investigation.

better at learning nectar concentration tasks, but the two species performed equally well at volume learning tasks (8). A third study compared a eusocial bumblebee, *Bombus bimaculatus*, and a semisocial carpenter bee, *Xylocopa virginica*. The eusocial bumblebees learned rewarding flower colors faster than carpenter bees learned, but memory retention overnight was equal between the two species (48). These experiments compared two species (often distantly related) that varied in multiple traits beyond the one in question. Regardless, these studies do support the hypothesis that the requirements of long-term central-place foraging and sociality are involved in the evolution of the remarkable learning abilities recorded for honey bees and bumblebees. It is possible that social bee species may be better learners not only because of selection imposed by sociality, but also because they have access to additional sources of information from the experience of their nestmates (i.e., social learning; see the sidebar titled Social Learning in Pollinators). Future work that compares several lineages of honey bees, or multiple congeners of bees with different ecologies, will be important as tests of hypotheses about learning.

Lepidopterans are generally herbivorous as larvae and pollinating flower visitors as adults. There is substantial research on associative learning of flower colors and odors in adult lepidopteran flower visitors (151). Learning of floral colors has been demonstrated in multiple species of papilionid (92, 150, 152), pierid (68), and nymphalid butterflies (18, 137, 149), and the diurnal moth *Macroglossum stellatarum* learns flower colors and sizes (89). Olfactory learning occurs in cotton bollworm moths that learn associations with individual floral volatiles (32, 33), and the hawk moth *Manduca sexta* is becoming a model system for learning. *M. sexta* has both innate and learned responses to floral colors and odors (37, 72, 123), and in the case of olfaction, there appear to be different neurological channels through which learned and innate responses operate (124). In parallel with the literature on herbivores discussed below, *M. sexta* also exhibits aversion learning when floral odors are paired with nectar containing plant defensive toxins (36). Comparative studies in Lepidoptera are limited, but there is some evidence that larger (also more mobile) and longer-lived species are better learners, potentially because of the variety of habitat types and plant species they are exposed to (85). There are a number of other species comparisons that could be informative to our understanding of the evolution of learning in pollinators, including comparisons of the learning abilities of generalists and specialists as well as pollinators that forage in environments of different spatiotemporal complexity.

Aversion learning:
the formation of an association between a stimulus and malnutrition or sickness
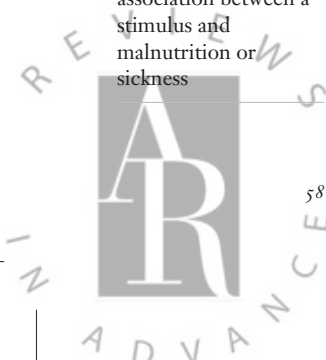
Learning in both bee and lepidopteran flower visitors manifests in a phenomenon referred to as flower (or floral) constancy, in which a flower visitor repeatedly visits one flower type even amid rewarding alternatives (25). Flower constancy was noticed by Aristotle (74) and Darwin (39) and has been recorded in the field for honey bees (55), bumblebees (56, 156), and butterflies (70) and in seminatural field arrays for hoverflies (71). The neuroethology of flower constancy remains poorly understood, but it is generally believed to increase foraging efficiency of flower visitors as a result of reduced search or handling times (63, 73). From the plant's perspective, learning can result in insects making sequential visits to the same flower type, thereby increasing intraspecific pollen transfer and reduced deposition of heterospecific pollen (22, 83). As flower-visiting insects learn many different flower stimuli, flower constancy can be affected by differences in color, scent, pattern, nectar chemistry, or combinations of multimodal traits (62, 64, 116). Given that flower constancy increases conspecific pollen transfer, certain flower stimuli (or combinations of stimuli) may be under selection to increase flower constancy. Although the majority of research on flower constancy has focused on flower color and visual learning (24), there is a developing focus on how floral scents influence pollinator-plant interactions (122) and some tantalizing evidence that nectar secondary metabolites can affect flower constancy in pollinators. In particular, the presence of caffeine in floral nectar increases honey bees' memories for olfactory stimuli (157), and there is more pollen transfer by bumblebees to flowers with caffeine in their nectar (139). Because learning in pollinating insects should benefit plants, learning may be an agent of selection on multiple floral traits with important consequences for both insect foraging efficiency and plant reproduction.

It has been proposed that traits that make flowers easier to learn include high interspecific variation, low intraspecific variation, and signal honesty (158). High interspecific variation and low intraspecific variation would make flowers more distinctive from others in a plant community, potentially allowing pollinators to better identify them once they have learned a particular flower type. At the same time, coexisting plant species can sometimes benefit from sharing pollinators, as a community that shares pollinators can support a larger number of pollinating insects (104). In this case, it could be advantageous for a flower to resemble its sympatric species enough that pollinators willingly visit both plant species. Flower traits, therefore, could be under conflicting selection pressure to be both distinctive from and similar to the flowers of their sympatric heterospecifics or to evolve alternative tactics such as depositing pollen on different pollinator body parts from where it is deposited by heterospecific plants (20).

HERBIVORES

Herbivores make a striking contrast to pollinators in the type of relationship they have with plants. It has been proposed that the antagonistic relationship between plants and herbivores may favor the evolution of specialization, in contrast to the mutualistic relationships of pollinators that may favor generalization (140). This is a potential explanation for the higher prevalence of specialism in herbivores when compared to pollinators (54). The increased frequency of specialism may also be an explanation for the paucity of research on associative learning in herbivores. Research on learning in herbivores is instead dominated by studies of aversion learning and induced preferences through habituation and sensitization (111). These types of learning will be more common when animals are encountering lower amounts of environmental variation (**Figure 1**), such as might be the case for specialists. Although these explanations remain speculative, the literature on learning in herbivores differs substantially from learning in pollinators.

Herbivores learn about many different plant traits including leaf color (135), leaf shape (118), and both olfactory (102) and gustatory (47) plant chemical cues. There are some herbivores, such as grasshoppers and locusts (Acrididae, Orthoptera), that are mobile generalists for which we

might expect associative learning to be advantageous because of the large amount of environmental variation they encounter. Other herbivores, such as the larvae of most holometabolous insects (e.g., Lepidoptera), are relatively immobile and/or typically specialists, for which we expect learning to be less advantageous or habituation and sensitization to predominate. In this section, we discuss these two avenues of research on learning in herbivore foraging and then turn our attention to the role of learning in oviposition. Information that influences oviposition decisions can be acquired through previous oviposition experience and also through foraging experience either as larvae (although this has long been contentious) or as adults. The influence of adult foraging is particularly interesting in the case of lepidopterans, which are simultaneously pollinating nectar feeders and ovipositing herbivores. Finally, we evaluate the potential for herbivore learning to be an agent of natural selection on plant traits.

Highly mobile generalist herbivores, such as grasshoppers, encounter large amounts of environmental variation, and we might expect learning abilities similar to those of highly mobile pollinators (i.e., associative learning). Whereas the associative learning we have discussed in the pollinator section above has been focused on learning of positive associations between stimuli and rewards, for feeding herbivores there is a large literature on aversion learning (15, 16, 42), or associating a cue with a negative unconditioned stimulus such as bitter taste, poor nutrition, or illness. Given that leaves benefit from deterring herbivores, in contrast to flowers that attract and reward pollinators, this difference in research tradition perhaps matches the ecological interaction. Aversion learning can refer both to learning to avoid food that is nutritionally deficient, and to learning to avoid food that induces illness (61, 75). *Schistocerca americana* grasshoppers learn to avoid nutritionally deficient foods such as spinach (94), and given the opportunity to learn associations between odors and nutritionally complete foods versus incomplete foods, they have higher growth rates than *S. americana* that were not given the opportunity to learn such associations have (47). This study (47) is one of the few (in any taxa) to show an increase in fitness components with the opportunity to learn. Aversion learning has also been demonstrated in lepidopteran larvae; for example, woolly bear caterpillars learn to avoid innately preferred nonhost petunia after it causes acute illness (42). It should be noted that grasshoppers do also learn positive associations between odors and food nutrition. For example, desert locusts, *S. gregaria*, learned to pair odors with food rewards (133), and *Locusta migratoria* learned positive associations between odors and protein-rich diets (134). Learning to avoid plants that cause illness, and to prefer nutritious species, may be particularly important for polyphagous species, as they may be more likely to sample a range of plant species.

The oldest and most extensive literature on learning influencing diet choices of herbivores is on induced preferences, or an increased preference for a particular host plant after feeding experience when compared to naïve individuals (82). There are a number of mechanisms by which induced preferences could potentially occur (17), including habituation to feeding deterrents (41), sensitization (111), and the production of enzymes to detoxify plant defensive compounds (4). Induced preferences by habituation are a means by which an herbivore can alter its behavior with experience, but in some cases it is a one-time only process (87). Induced preferences have been demonstrated for Homoptera, Coleoptera, Hemiptera, Phasmatodea, Acari, and many Lepidoptera species (3, 81). Because different host plants often require slightly different physiological means of processing (or avoiding toxins), when the herbivore runs out of food or is otherwise moved (e.g., falls off the plant), induced preferences may allow insects to behaviorally adapt, which should make the insect more efficient in accessing and utilizing that resource (81).

Induced preferences, and the habituation and sensitization by which they occur, are predicted to be most common in environments with fairly low amounts of variation, in contrast to associative learning, which should evolve in more variable environments when individuals need to learn many

different stimuli (**Figure 1**). The more specialized diets of larval herbivores, in contrast to adult pollinators (54), may create a difference in environmental variation that favors different types of learning. Given the fast and flexible associative learning demonstrated for adult nectar-feeding Lepidoptera, the predominance of research on induced preferences in larval Lepidoptera makes a striking contrast. There are, however, a few examples of associative learning in lepidopteran larvae, such as learning to associate odors with electric shock in *M. sexta* (19) and both appetitive and aversive conditioning between odors and taste in *Spodoptera littoralis* (125). The prevalence of associative learning in larval Lepidoptera is unclear, and studies of its ecological relevance would be an important contribution.

Learning and Oviposition

Herbivores make foraging decisions not only for themselves, but also for their offspring through oviposition choices. Learning can influence oviposition decisions through multiple mechanisms. Information acquired from oviposition itself could influence future oviposition decisions, or experience foraging either as a larva or as an adult could influence later oviposition choices. The frequent demonstrations of learning during oviposition from adult Lepidoptera (see the section titled Learning from Oviposition Experience below) may be surprising given the fairly limited learning demonstrated for larval Lepidoptera (see the introduction to the section titled Herbivores above). Nonetheless, this difference could be explained by the increased mobility of adults in comparison to larvae that potentially exposes individuals to more environmental variation, increasing the advantages of learning. Differences in learning between adults and larvae are particularly interesting from an evolutionary perspective, as selection would be acting differently on different life stages of the same organism. This is an area in need of further theoretical and empirical investigation.

Learning from oviposition experience.   Oviposition experience itself frequently influences later oviposition choices (96, 111). For example, in the moth *Helicoverpa armigera*, experience ovipositing on a host plant influences later host selection and host acceptance behavior (31, 35). The evolution of learning in oviposition has best been studied with the fruit fly, *D. melanogaster*, in which female flies learn to associate fruit juices (orange or pineapple) with an aversive taste stimulus (quinine). Artificial selection of eggs from females that learned the association resulted in populations of flies with improved learning and memory after multiple generations (102). This research highlights the capacity for learning in oviposition to evolve under strong selection.

Unlike the focus on induced preferences in larval lepidopteran learning, there are multiple examples of associative learning in adult lepidopterans making oviposition choices. In pipevine swallowtails, *Battus philenor*, females learn associations between leaf shape and the chemical compositions required for oviposition (108, 118). Similarly, in cabbage white butterflies, females can learn associations between colors of oviposition substrates and the chemical oviposition stimulants (143). These cases of associative learning in oviposition could be compared to learning of associations between floral traits and nectar rewards by pollinators (of the same or different species) and may be indicative of the ovipositing females searching for host plants under variable conditions.

We earlier discussed the role of social information in pollinator learning (see the sidebar titled Social Learning in Pollinators), but it is also possible for social information to influence oviposition choices, as exposure to the offspring of other individuals is another source of information for an ovipositing female. If there are larvae on a host plant, this may be informative about the quality of that host plant species for oviposition. The best evidence for this type of social influence on

A BRIEF HISTORY OF HOPKINS HOST SELECTION PRINCIPLE

Hopkins host selection principle (HHSP) is attributed to Andrew Delmar Hopkins, an entomologist at the US Department of Agriculture who studied the effects of bark beetles on western conifers. In the Program of Work for the USDA in 1917, Hopkins referred to what he called the "selection principle" that "a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted" (78, p. 353). Hopkins's original statement implies that he was referring to evolutionary adaptation, but since then, perhaps starting in 1921 with Craighead (30), HHSP has come to refer to within-generation plasticity and in particular preimaginal conditioning. Early studies that did find evidence for HHSP attributed it to preimaginal conditioning and did not eliminate other possible explanations, particularly chemical legacy (97, 141, 142). HHSP went through an unpopular phase (1970s–1990s), because of considerable doubt as to whether preimaginal conditioning could occur given the extensive reorganization of the neural system during metamorphosis (14). More recently, however, an increasing number of studies have shown preimaginal conditioning to be possible—for example, in moths (19) and wasps (60), as well as in fruit flies (144) and houseflies (119).

oviposition choices also comes from *D. melanogaster*. Female flies prefer to lay eggs on patches where larvae are feeding, opposed to on patches with no larvae (49), and oviposition substrate flavor can be learned from exposure to other females ovipositing (126). In fruit flies, larval aggregation has an advantage in generating a larger inoculum of wild yeasts (154) and also potentially decreasing the risk of parasitism to any one indi (153). For many other insects, however, females are deterred from ovipositing by the presence of conspecific larvae. For example, there are many cases of herbivore-induced plant volatiles deterring oviposition by females (7, 120). The deterrence from ovipositing by the presence of conspecifics may be due to avoidance of competition or cannibalism (45). Plants even appear to have mechanisms that thwart this type of social influence on oviposition sites. In a particularly striking example, some *Passiflora* and *Steptanthus* spp. have egg-mimicking vegetative structures that deter oviposition by butterflies (155). It is therefore unclear when social information will predictably result in positive versus negative cues for oviposition, but this is an important frontier. As with social learning in pollinators, there is the potential for these types of social information uses in herbivores to impact selection on plant traits.

Larval foraging and oviposition decisions. There is a substantial body of research and much debate on the influence of larval experience on adult oviposition choices (30). This may be in part because the conditions under which learning from larval experience is advantageous are particularly limited, as they require experience from the larval environment to be better-quality information than the combination of genetically determined preferences and the current adult environment (80). Temporal heterogeneity must therefore be low enough that the larval environment is a good predictor of adult oviposition environment but high enough that genetically fixed preferences are not as strong a predictor (80). It is unclear how often this is likely to be the case. Regardless, changes in oviposition due to larval experience [generally referred to as Hopkins host selection principle (HHSP)] (30) have a long and contentious history in the literature (see the sidebar titled A Brief History of Hopkins Host Selection Principle). HHSP is the phenomenon by which insects prefer to oviposit on the host plant (or variety) they consumed as larvae. The mechanisms by which HHSP could occur include (*a*) preimaginal conditioning, or the retention of a learned association or preference through metamorphosis, (*b*) chemical legacy, by which chemicals from the larval environment remain in the hemolymph through metamorphosis or in and around the pupa (28), and (*c*) imaginal conditioning, or neo-HHSP, by which the adult learns an association

THE SPECIAL CASE OF PARASITOIDS

Although not a central part of our review, the remarkable case of learning in parasitoid wasps requires mention. The parasitoid lifestyle has been discussed as one with an important role for cognition because parasitoids are mobile animals searching for hosts amid complex environmental cues (52, 146). Accordingly, there is a substantial literature on associative learning in parasitoids (145). Parasitoids can learn host and nonhost cues to increase search efficiency. Hopkins host selection principle has even been demonstrated in parasitoids that oviposit in multiple host species (142). In general, however, adult learning is believed to be more important for host finding than larval learning is (145).

To increase host-finding efficiency, parasitoids learn odors associated with plants (12) and host feces (95). Parasitoids can also learn to visually recognize colors (148) and habitat patches (11). As associative learners, the many parasitoids that are solitary Hymenoptera could provide an interesting comparison with the learning abilities of pollinating solitary Hymenoptera to examine how foraging niche may drive differences in learning abilities.

as it emerges on the host plant (79, 159). The majority of the studies that have tested HHSP have been unable to distinguish among these mechanisms (5, 121). Although conditioning is the term most frequently used to describe the mechanisms behind HHSP, in many of the cases (see below), induced preference through habituation or sensitization might be a better descriptor of the change in behavior observed. Interestingly, there is also a literature on HHSP in parasitoid wasps, making a noteworthy contrast to this review on pollinators and herbivores (see the sidebar titled The Special Case of Parasitoids).

Three studies have shown effects of larval diet on host plant species preferences in the generalist noctuid moth, *S. littoralis*. Female *S. littoralis* prefer to oviposit on the host species they were raised on whether it was cotton, clover, cowpea, maize, or alfalfa (10, 138). The effects of rearing plant on oviposition, however, are not always positive. Rearing on low-quality cabbage reduced oviposition on cabbage in comparison to females reared on artificial diet, even when females from both rearing environments had experience mating on cabbage (114). Larval experience may therefore be an important source of information about host-plant quality. In another system, the pyralid almond moth (*Ephestia cautella*) females that were raised on a larval diet of nut-containing chocolate prefer to oviposit on nut-containing chocolate in comparison to moths raised on a wheat-based diet (107). Similarly, leaf-mining flies raised on potato showed a preference to orient toward potato in olfactometer tests, whereas leaf miners raised on tomato showed no preference (50).

HHSP can also take the form of reduced response to oviposition deterrents with experience. For example, *S. littoralis* is typically deterred from ovipositing on potato, but females raised through the entire larval development on potato were no longer deterred (9). Granary weevils, *Sitophilus granarius*, showed reduced deterrence to maize in olfactometer tests when they were raised on maize compared to weevils raised on wheat (121), and cabbage looper moths, *Trichoplusia ni*, when exposed to latex from the succulent *Hoodia gordonii* as larvae, did not show the normal oviposition deterrence to *H. gordonii* latex as adults (25, 132). In many of these studies, it is unclear how much of the shifts in oviposition behavior were dictated by preimaginal conditioning versus by chemical legacy. The extent to which HHSP is common, its function in nature, mechanisms by which it occurs, and any adaptive role in insect biology all need further testing.

Adult foraging and oviposition decisions. In insects for which the adult and immature diets are similar, oviposition decisions may be influenced by current foraging information because the

adult can taste the food its offspring will eat. Although there is little research on the role of learning in this process, we propose that learning could be playing an important role in these choices and needs to be considered. There are examples of adults preferring to oviposit near food sources for themselves—for instance, in the grass mining fly *Chromatomyia nigra* (128, 129). In this case, adults preferentially oviposit on hosts that are the highest quality for their own fecundity rather than on hosts that have the highest larval performance (128, 129). Adults ovipositing near food sources for themselves has even been demonstrated for insects with very different larval and adult diets. This is particularly interesting in the case of adult nectar-feeding pollinators making oviposition decisions. For example, when *Datura stramonium* flowers are supplemented with additional nectar, adult *M. sexta* lay more eggs on those plants than on unsupplemented plants or plants with nectar removed (1). In this case, the floral nectar may provide information about the suitability of leaves for larvae (1). Similarly, in tobaccos, nicotine concentrations are positively correlated across tissues; therefore, nectar may provide information about leaf defenses (2). There is also evidence for this phenomenon from monarch butterflies, *Danaus plexippus*, in which the presence of toxic cardenolides in flower nectar affects oviposition decisions (84), and there is a positive correlation between nectar and leaf cardenolide levels in milkweeds (98). The role of learning in such oviposition decisions is in need of further investigation, but this influence of adult foraging on oviposition choices is particularly relevant to our discussions of pollinators and herbivores. As we generally consider flower nectar to have evolved as a reward for learning pollinators, its influence on ovipositing herbivores raises important questions about the potential for conflicting selection on nectar chemistry.

There is at least one case in which foraging adult lepidopterans are simultaneously learning leaf and nectar stimuli. For example, *B. philenor* can learn to associate one color with oviposition substrates and a different color with the presence of sucrose for nectar feeding (152). When females made so-called mistakes in one behavioral context, the mistakes tended to be selecting the color that was associated with reward in the other behavioral context. This supports the notion that associative learning of stimuli in foraging and oviposition occurs through the same channels. The linking of behavior in these two contexts is important for our understanding of the evolution of learning because its evolution in one context may make it available for other behavioral contexts, and in terms of potential consequences for the plant because similarities in leaf and floral traits could impact both pollination and herbivory. Future research in this area may be particularly exciting in systems in which the pollinator and the herbivore are the same species.

Learning in Herbivores and Selection on Plant Traits

We have discussed a range of conditions under which learning can affect foraging and oviposition decisions in herbivores. Each of these mechanisms could have consequences for the plants. Most plants exhibit diverse induced responses to herbivory (43, 86, 100), and accordingly, it would be interesting to examine how induction or aversion learning interacts with induced defenses. It is possible that induced preferences would be less common when the plant chemistry is capable of changing or if plants could alter their chemistry to generate aversion learning.

In cases in which herbivorous insects exert strong selection on plants, any means by which a plant could evolve to be harder for an ovipositing female to learn (or provide exposure to a deterrent) could be to the plant's advantage. For example, in the case of pipevine swallowtail butterflies that learn leaf shape to recognize host plants (6), host plants may be under selection to be less distinctive from other species and more variable within species in order to be difficult for butterflies to learn and recognize. This has been proposed for passionflower vines, which possess remarkable within-species diversity in leaf shape; similarities between passionflower leaves and

those of nonhost plants may be due to *Heliconius* butterflies learning the shape of host plant leaves (65). Such research provides an interesting contrast to discussions of how learning in pollinators may select for easily learned and remembered floral traits (158).

CONCLUSIONS

We have reviewed a number of axes of variation that predict learning abilities in plant-visiting insects. These include dietary generalism, mobility, lifespan, foraging guild, and sociality. We propose that the learning abilities of pollinators and herbivores are affected by the degree of environmental variation they encounter, the relationship they have with plants, and the requirements of sociality. Research on pollinators has contributed greatly to our understanding of the cognitive underpinnings of learning and decision making about different flower stimuli. Research on immature herbivores, in contrast, has a long and important history of examining habituation and sensitization in the form of induced preferences. Research with herbivores also allows us to study the role of learning in oviposition decisions and to compare how learning in foraging and oviposition differ. An important distinction between the roles of learning in foraging and oviposition is that an animal directly experiences the consequences of a foraging decision, whereas its offspring experience the effects of an oviposition choice. It could be predicted therefore that learning is unlikely to influence oviposition, but as we have discussed, there is a substantial body of evidence on learning in oviposition decisions. The extent to which this learning is adaptive is unclear.

To better understand how and when animals evolve better learning, we suggest comparative studies between closely related species that differ in life-history traits hypothesized to be important to the evolution of learning, such as lifespan, mobility, or sociality. Although some of these studies have been conducted with bees, such comparative work on learning abilities is largely lacking from other taxa and would contribute to our understanding of when learning evolves. Research on multiple species for which there is phylogenetic information would be the most informative. We also advocate for more studies on experimental evolution of learning in laboratory populations. In-depth investigations into how learning abilities and corresponding neurobiology change between larval and adult Lepidoptera would be fruitful. Are these two life stages of the same species inherently different in how they learn, or have they just been subject to a research bias in how learning is studied? Finally, there is the potential for learning in insects to have important consequences for selection on plant traits. Even with floral constancy, for which there is a long history of theoretical discussions, there is relatively little empirical research linking insect learning to plant reproductive success. In particular, the hypothesis that plants may be under selection to have their flowers be easily recognized, learned, and remembered, whereas leaves of the same plant species may be under selection from herbivores to be difficult to learn, awaits testing.

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