NEURAL LIMITATIONS IN PHYTOPHAGOUS INSECTS: Implications for Diet Breadth and Evolution of Host Affiliation

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Key Words   specialization, herbivore, plant-insect interactions, neural constraints

■ **Abstract**   This review points out the problem of processing multiple sensory inputs and provides evidence that generalists suffer a disadvantage compared with specialists with respect to efficiency of host plant choice and discrimination. The specialists' mechanisms for improved efficiency are discussed as well as some of the processes that may be selected to increase processing efficiency in generalists. The fitness consequences of differences in efficiency of specialists and generalists are pointed out. One of the major disadvantages for generalists is the increase in vulnerability to ecological risks, especially risks imposed by various natural enemies. Efficiency-related factors are indicated as previously underestimated elements that could influence host affiliations including diet breadth and changes in host plant use.

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INTRODUCTION

Behavior is the link between physiology and ecology of animals. Because behavior is an expression of neural processes modified by physiological and environmental factors, it is central to understanding interactions of organisms; therefore, studies of both the functioning and constraints of the nervous system are important in understanding animal evolution (104). For example, inherent limitations of the nervous system constrain how much information may be processed in a given time (49, 55, 98). This simple fact has major repercussions in ecology, and, in this review, I make the case for neural limitations as a primary factor in phytophagous insects' interactions with plants, including their coevolution with plants.

Rapid, accurate perceptual judgments are relatively easy when choices are strictly limited, but difficulties increase sharply as the perceived choices increase, so that mechanisms for selecting and canalizing information are very important (81). Generalists must make choices among a large number of options, and they must do so with a nervous system that is definitely limited in its capacity to deal with multiple inputs. It is known that, in humans, selective attention to subsets of sensory inputs at any one time is critical for normal behavior (132).

Most experimental studies that demonstrate the constraints on processing sensory information have dealt with vision. For example, animals cannot undertake computations of the inputs across a whole visual field at once. Instead, attention to parts of the visual field changes over time so that the whole can be interpreted over a period (87). There may be sequential attentiveness to different stimuli in order to encompass a large field, or there may be prolonged engagement with a few stimuli in order to evaluate them more fully (48). Paying attention to subsets of the visual field has been demonstrated to be important ecologically in a number of contexts. Thus, the ability of birds to more readily notice cryptic prey with experience indicates that certain visual cues have assumed specific importance, and functionally this allows them to feed at a faster rate on a prey species that is abundant (101, 105, 128). It follows that, if certain elements of the visual field are typically conspicuous, then they should be generally detected more readily than elements that blend into the background. This is the presumed basis for the value of visual "sign stimuli" used by animals in many different contexts, especially intra- and interspecific communication (56, 129).

The need for attentiveness to relevant stimuli at any particular time does involve all sensory modalities, however, and many different levels of the nervous system (81). A generalist must compute a large amount of information from different modalities and, in changing attentiveness to different stimuli, must also retain other inputs in memory for comparison and subsequent evaluation. Animals have extensive capacities for working memory, allowing them to make accurate behavioral selections after some experience. An alternative strategy, however, that might be adaptive in a relatively predictable environment would be to have enhanced sensitivity to a few relevant and important stimuli and thereby simplify the problem of selective attention. Such a strategy should require fewer receptors

and smaller memory capacity. It would involve more fixed responses and perhaps more decisiveness and faster reaction times. Presumably there is a tradeoff between the saving in neural machinery and efficient decision making on the one hand and the flexibility of the broad sensory capacity combined with an ability to switch attentiveness and an extensive use of learning on the other hand. The former describes a specialist, while the latter describes a generalist.

In all animals cognitive decisions are complicated also by the fact that they must be made in the context of a constantly changing internal chemical environment of nutrients (116), toxins (66), hormones, and neuromodulators (2), as well as diverse neural oscillatory processes (28) and complex, even chaotic neural interactions (44). This complexity will influence the final commands issued by the central nervous system for a particular behavior, but, in this report, I focus on sensory inputs from the environment and the importance of attentiveness in achieving efficient behavior under any particular set of internal conditions.

Since Levins & MacArthur (83) first suggested that generalist insect herbivores may find it relatively difficult to choose among alternative host plants, a number of authors have proposed that neural limitations have greater significance among generalists than among specialists (29, 47, 53, 54, 62, 64, 78, 82). Others have pointed to the likelihood of neural constraints in insect herbivores as a reason for various observed limits in insects' behavioral repertoires (84, 95, 103). However, few attempts have been made to make a synthesis of these ideas and to draw together the available relevant material on phytophagous insects.

Identifiably different issues need to be considered in the context of neural limitations. They are not mutually exclusive, and their relative importance varies from one insect group to another and also in relation to the degree of specialization of the insect being studied.

Detection of Relevant Information

For a predator, detecting cryptic prey is a major issue and requires attentiveness to fine details of prey features that may vary at different times, and for herbivores, detection of both visual and olfactory cues can be important. Visually, shape or reflectance pattern matter to some species, whereas chemically there may be particularly attractive mixtures of common green plant chemicals and chemicals that occur in particular host taxa (19, 112). From work on humans, it is certainly known that detection of "targets" becomes significantly more difficult as the target becomes similar to alternative aspects of the visual field, the "distracters" (81). Host-specific characters that are conspicuous to the particular herbivore and stand out from nonhost characters would be an advantage, particularly for specialists.

Discrimination and Choice Among Alternatives

This problem has been studied extensively in humans, and it is well known that the more items there are to choose from, the longer it takes to make the choice. It is in this context perhaps that herbivores have the greatest challenge. For them,

one of the environmental complexities is that communities of plants display an unparalleled array of different volatile and nonvolatile chemicals (69), many if not most of which are detectable by insect sensory systems, and many are potentially noxious. Furthermore, nutritionally, plants demonstrate extreme variation so that decisions should involve some evaluation of nutrient quality. Ideally, the best choices for food or oviposition must be made in a minimal amount of time.

It is likely that optimizing both host quality and time taken for the decision is difficult. The individual may make very good decisions with respect to host quality but take time to make them, or the individual may make rapid decisions, perhaps compromising on host quality. Such alternatives have been demonstrated often in other animals (52, 99). For small animals such as insects that often use odor-conditioned upwind movements to locate food, decisions must be made first at a distance and then in the proximity of the plant or at contact. Finally, there may be decisions concerning the precise plant part to utilize. For less than ideal foods, a further decision may involve when to stop feeding (or when to leave a host without laying a full complement of eggs). When comparing insect herbivores with different diet breadths, efficiency may be measured in either quality (relative fitness value of the host selected, proportion of errors made, etc) or time taken to make decisions.

Task Attentiveness

When a final host choice has been made, attentiveness to the task of egg laying or feeding must ensue rapidly and be maintained long enough to ensure that these behaviors are completed without delay, so that predator avoidance behaviors and full attention to all environmental risks can be quickly resumed. A generalist, with a choice of similarly attractive hosts, may be more readily distracted by competing sensory information about such alternatives than is a specialist, whose sensory input or attentiveness is dominated by the specific host cues.

Vigilance Against Risk

The attention to host cues should not be so demanding of neural effort that potentially more important inputs, such as the presence of a predator, are not noticed. An inability to attend to danger during decision making while foraging has been demonstrated to increase predation risk in fish (89), birds (85), and other animals (115). Unlike vertebrates, insect herbivores are faced with a bewildering diversity of predator and parasitoid types (124). The problem for them is potentially much greater, because the cues associated with risk are extremely diverse, and the numbers of natural enemies are also commonly large, so that a specialist, with less host-related sensory information to process, may have an advantage in this context.

This review is an examination of the potential importance of neural limitations in host plant choice by phytophagous insects. I first provide evidence for the difficulty

they have in making decisions and for advantages accruing to specialists in each of the four categories discussed above. I then discuss mechanisms by which specialists may deal with informational complexity and the ways in which generalists may improve their handling of potential sensory overload. I then survey the adaptive significance of efficient decision-making processes, including obvious benefits of choosing high-quality food, the ways in which time may be limiting, and the subtle but highly significant role of improved decision making in attentiveness, vigilance, and escape from natural enemies. I argue that these ecological benefits provide a strong case for the evolution and maintenance of restricted diets by insect herbivores. I further suggest that evolution of phytophagous insect diversity and the coevolution of insects and plants are directly related to neural limitations and can be seen as a product of adaptations of nervous systems for channeling information and making efficient decisions.

EVIDENCE FOR LIMITED BEHAVIORAL EFFICIENCY AMONG GENERALISTS

Data from a variety of herbivorous insect species now indicate that there are indeed limitations on efficiency of the decision-making process. These data involve time spent making a decision, ability to make the best choice among hosts of variable quality, and levels of distraction during a host-related activity. Where comparisons between specialists and generalists have been specifically tested, the specialists have the advantage.

Little data are available on relative abilities of herbivores with different diet breadths to detect host plants, because it is difficult to determine what has been detected before the insect approaches or reaches a plant, but a few observations point to a problem and suggest that further work would be instructive. For example, Papaj (96) showed that ovipositing females of the pipevine swallowtail *Battus philenor* tend to specialize on one species of host plant at any one time and that, if they do not, then host plants are found at a lower rate. At different times, however, these butterflies might focus on alternative species. Focusing attention on one leaf shape or developing a "search image" for a specific leaf shape apparently made detection easier, and may be called an attentional shift (52a).

An interesting contrast is seen between the generalist species of *Heliothis* moths and the closely related specialist, *Heliothis subflexa*. Many plants are highly attractive to the generalists but are unsuitable for oviposition (61), but *H. subflexa*, is strongly and solely attracted to its only host, *Physalis* spp. (131), suggesting that the specialist is superior at detecting the appropriate host. Another suggestive contrast is between the generalist aphid *Myzus persicae*, which lands indiscriminately on hosts and nonhosts (76), and the specialist aphid *Cavariella aegopodii*, which is specifically attracted by host monoterpenes (39). In the realm of actual detectability, however, no experimental contrasts between insects with different diet breadths have been undertaken.

Ability to choose plants that are suitable hosts has been examined among butterflies with contrasting diet breadths. In a group of species and populations of species that all utilize the nettle *Urtica dioica*, experiments were conducted to compare those specific to nettle with those that also use a range of additional plant species. The butterflies were given a choice of healthy green nettle plants and senescing ones that were less suitable for growth of the caterpillars. The species or populations of species with the greatest dietary restriction to nettle chose to lay eggs on the healthy plants over the senescing ones, whereas the species or populations with broader host ranges did not distinguish between them, even though, for all species, the healthy plant was the best choice for their offspring (74). This difference is consistent with the notion that the generalists were less efficient in choosing accurately, perhaps because of neural limitations.

Experiments with four species of generalist larval Lepidoptera and four of Hemiptera showed that, when a choice was available, individuals commonly did not select the most favorable host or the best mixture for growth and development (26, 119). Although there may be various functional explanations for this apparently suboptimal behavior, the data are consistent with the notion that making the most appropriate choices incurs some difficulty. Detailed observations on one of the lepidopterans, *Grammia geneura*, showed that, although decisions were made quickly, they tended to be poor decisions with respect to what was known to be best choices for growth.

A comparative study of different populations of the aphid *Uroleucon ambrosiae* with different diet breadths demonstrated that, during a 24-h choice test, the relative generalists remained on unsuitable hosts long after the specialists had moved on to the *Ambrosia trifida*, the superior host for both populations (22). These limited data so far suggest that the specialists have an advantage with respect to accuracy (i.e. fitness value) of the choices made.

More comprehensive studies were undertaken to examine the question of time taken to make decisions. Experiments with the generalist grasshopper *Schistocerca americana* showed that individuals reared as specialists with a choice of identical artificial foods made feeding decisions threefold more quickly and fed with one-tenth of the amount of interruption compared with individuals reared with a choice of similar artificial foods having different flavors (11). In contrast to the available studies on Lepidoptera, grasshoppers appear to make decisions about eating particular foods that are generally good for growth (16, 116), although they may often reject plants that could enable them to grow well because of the presence of deterrent compounds (6, 7, 41). However, grasshoppers take time to make the decisions, the decisions being longer for developmental generalists than for developmental specialists. Non-food-related sensory inputs can also interfere with the food choice behaviors, because, in the experiments described above, the grasshoppers were tested a second time in a novel environment (a differently shaped cage) and the differences between those with diverse foods and those with identical foods became more marked. Recently, studies with the same species of grasshopper feeding on one or two different host plants have provided similar results, with

the individuals that have a choice of two foods taking longer to make decisions and spending protracted times foraging (14).

A variety of experiments with the aphid *U. ambrosiae* demonstrated benefits in foraging efficiency for relatively specialized individuals (22). Populations of this species differ in diet breadth although, for all of them, *A. trifida* is the most acceptable host. Comparisons were made among these populations with respect to some host-related behaviors in both choice and nonchoice situations. For example, alates were tested in a wind tunnel with a single plant of *A. trifida* located upwind. Those from the relatively specialized populations found the favored host in a wind tunnel more quickly than did those of the relatively generalized populations, even though there were no other plants present. It is not known whether this represents a difference in detectability, or decisiveness, or some other factor, but no variables relating generally to size or activity level of the aphids were observed. Experiments with apterae that had a choice of *A. trifida* and various nonhosts provided in close proximity, demonstrated that the specialists found *A. trifida* significantly sooner than did the generalists. Also, apterae placed on the favored hosts all probed quite quickly, but the specialists reached the phloem, on average, hours sooner than did the generalists. These data not only demonstrate a strong contrast between the insects with different diet breadths but suggest that the specialists are more highly stimulated or aroused by the host cues than the generalists when the stringency on host acceptance has also apparently become relaxed. In all experiments, aphids from the more specialized populations were relatively more efficient.

Other observations are suggestive, although they do not provide definite evidence. For example, Carey (36) showed that in the blue butterfly *Glaucopsyche lygdamus*, those individuals that specialized their oviposition activity on one of the available hosts were more likely to lay an egg in the limited landing time than those that alternated among hosts. To evaluate the relative time taken to make decisions by butterflies with different diet breadths would be worthwhile. Certainly, some butterflies may make many lengthy visits to alternative individual host plants, spending ≥ 30 min in the process, before finally deciding on one (117), and, with such times involved, differences would be relatively easy to monitor.

With respect to task attentiveness, it is clear from the results on grasshoppers described above that part of the problem for individuals reared as generalists was that meals were interrupted relatively more frequently and for longer periods, suggesting that these generalists were being distracted, and observations showed that individuals in this food treatment were more likely to antennate alternative foods during their meals. In a different study, detailed observations on the highly polyphagous *Bemisia tabaci* showed conclusively that adults with a choice of potential foods spent less time on any single food than those with only one food plant present. Indeed, individuals were highly likely to move away from the best food plant if additional plant species were present, but they were most likely to stay on the food plant if only conspecific plants were in the vicinity (12). These data suggest that individuals were distracted when there was additional relevant

food-related information present, which may have complicated their sensory processing.

Further studies are required to enable us to generalize, but to date specialization appears to be associated with measurable and significant advantages. These benefits vary with the insect taxon but include the amount of time taken to reach the host plant, the time taken to make decisions to accept or reject potential food, the time taken to begin ingestion or to lay an egg, and the time spent in pauses during a meal. In addition, the degree of fidelity to the most suitable host in the presence of less suitable host species and genotypes or the ability to choose superior hosts in the presence of a choice of mixed-quality hosts is shown to be greater in specialists than in relative generalists.

No studies are available that compare specialists and generalists within a taxon in their degree of vigilance against natural enemies or their ability to escape attack. A comparative study with caterpillars under attack from vespid wasps clearly demonstrated that specialists had a major advantage (5), but the relative importance of vigilance and other factors such as different kinds of defense was not documented. That grasshoppers switched from their rearing cages to novel cages increased the time taken to make feeding decisions (11) does suggest that attentiveness to nonfood factors (i.e. potential risk) had some impact, especially since this was greater for the individuals reared as generalists than for individuals reared as specialists.

MECHANISMS FOR EFFICIENCY IN SPECIALISTS

Insects searching for an acceptable host plant must first locate and identify an appropriate plant species. Accurate selection of host taxa and proper assessment of individual plant quality should also be achieved with minimum time under most ecological conditions. If speed, taxonomic accuracy, and quality of choices are all to be maximized by very small animals in a very complex sensory world, the adoption of high-contrast signals would be expected, as well as other processes that improve the efficiency of neural processing (29). Certainly it has been known for a long time that unambiguous signals are required for efficient release of receiver behavior (71). Such are the widely occurring species-specific "sign stimuli" first described in detail for intraspecific interactions among stickleback fish (130). These specific signals enable animals to use simple rules of behavior, ensuring rapid recognition and discrimination and quick, appropriate responses. Among phytophagous insects, in which chemicals are of paramount importance, it has been known for some time that plant secondary metabolites can provide insects with such signals (63).

The majority of insect herbivores are relative specialists, using a very restricted number of hosts that typically share characteristic phytochemicals, some volatile and some nonvolatile. A subset of these compounds seems to be of great importance for identification of the host (for reviews, see 19, 112, 122).

Among specialists that have been studied so far, most seem to be specifically and highly sensitive to particular host odor components (1, 67, 127) or to characteristic mixtures of volatile compounds (110, 133). Such sensitivity of olfactory systems is normally seen as an adaptation to host finding, especially when it can be demonstrated that the herbivore is attracted (usually by odor-conditioned anemotaxis) over long distances. For example, the cabbage seed weevil *Ceutorhynchus assimilis* is attracted from >20 m by isothiocyanates in its host plant (57). There are additional functions for such sensitivity, however; the attentiveness or arousal achieved from perception of these chemicals may be important in odor-conditioned visual stimulation that may be the mechanism of synergism among chemical and visual cues used in host discrimination (68). Just as in vertebrates, a mechanism for increasing attentiveness to particular cue types could increase detectability of related ones (8). I argue here that specific host odors have an important role to play in efficient (rapid and accurate) detection and decision making. In other words, the specific odor forms a high-contrast signal that rapidly releases the appropriate behavior.

Sensitivity may be achieved through having relatively large numbers of olfactory receptors (37). For the aphid species *U. ambrosiae*, the specialists had significantly larger numbers and sizes of secondary rhinaria than the generalists (23). There may be a high proportion of the olfactory receptors specifically tuned to particular host odors. This has been demonstrated in the cabbage seed weevil, for example, in which 30% of the olfactory neurons on the antennae respond to the isothiocyanates of its host (32). Finally, for insects in which vision is of paramount importance, such as many butterflies (106), visual cues may be more important than odors, and a specialist could home in on a particular shape especially if its host plant has a leaf shape that is characteristic in the specific location.

Odors may function in behavioral efficiency after contact with the host, increasing arousal, attentiveness, and decisiveness, but for most specialists examined in sufficient detail, gustatory cues that signal the specific host are also important and arguably play similar roles. In some extreme specialists, great sensitivity to one or a few host-specific chemicals appears to result in such chemicals being the dominant factor in host selection (60, 100, 112). That butterflies such as checkerspots utilize plants from multiple families, simply because of the presence of iridoid glycosides in host plants that are otherwise extraordinarily diverse physically and chemically (33), is startling evidence of the impact and dominance of simple chemical signals on insect behavior and host use. Evidence is beginning to suggest that such cases are not unusual. Indeed, in a recent study, the sensitivity of the cabbage root fly to a novel chemical in brassicas was found to be so extreme that the sensitivity of the chemoreceptors is actually in the range normally associated with pheromone detection (108). It is too soon to tell whether such phenomena are widespread, but their very occurrence may suggest a value greater than host identification per se. The remarkable diversity of chemicals found among plant taxa and within individual plants allows potentially clear signals for

every specialist herbivore, whether it specializes at the level of plant species, tribe, or family (9). The convergent evolution of certain chemical products in different plant groups also has allowed certain insect species to use unrelated host plants, as with the Lepidoptera, for example, which use iridoid glycosides (checkerspot butterflies) or glucosinolates (cabbage butterflies) for host identification. That plant taxa heavily endowed with relatively unusual chemicals or suites of chemicals are often hosts for relatively large numbers of specialist-insect species (4) could also suggest that the chemicals are not just plant defenses to be overcome but strong cues that are useful for insects in that they provide signals for making positive choices.

As well as being sensitive to and attracted by host-specific chemicals, specialists tend to be deterred more than generalists by nonhost secondary metabolites (18, 27), and I suggest that specialists benefit from the strong contrasts between positive cues from hosts and negative cues from nonhosts.

THE NONSPECIALIST'S DILEMMA AND SOME SOLUTIONS

Presumably, benefits of polyphagy outweigh disadvantages for those species that use many host plants, but, because efficiency of decision making is likely to be of great significance in an ecological setting (see below), one might expect there to be selection for mechanisms to ameliorate problems of reduced efficiency. One such mechanism may be to maintain a larger and more sophisticated nervous system, as suggested by Levins & MacArthur (83; see below). Many insect species are oligophagous and perhaps gain some of the neural advantages of specificity while retaining some flexibility. However, several neural processes may aid improved contrasts for the insect. Interactions among sensory inputs at the sense organ or beyond can function to reduce ambiguous inputs, increasing the likelihood of a clear negative or positive signal. For example, each sensory system has some kind of lateral inhibition whereby the dominance of a particular sensory input is enhanced by reduction of competing but minor inputs. This is best known in the visual system, but there is evidence of its occurrence in other sensory modalities, including hearing and olfaction (9).

In general it is thought that negative and positive inputs are additive centrally, although the weights of these input types may differ (112). If the contact chemoreceptor cells respond to positive and negative inputs independently, then an additive effect would lead an insect to respond to whatever the balance may be at a particular time. If a positive input such as sugar is held constant, increasing concentrations of a deterrent such as nicotine result in a typical concentration-response effect but one that is shifted to the positive side by the presence of the sucrose. Among phytophagous insects, interactions among chemical stimulants at the level of chemoreceptors commonly occur, with deterrents reducing input from positive neurons and vice versa (112, 114, 134). Simple models illustrate that such interactions between

positive and negative chemicals in the sensillum can sharply alter the shape of dose response functions so that a gradual change without interactions becomes a step function when interactions occur (9). Critical experiments are needed to test the relevance of this observation in practice, but Blaney & Simmonds (31) suggest that such interactions may be more common in insects with broad host ranges. If so, this may be seen as one of the ways in which an insect with less definitive signal detection for high-quality hosts may improve its ability to make a positive or negative decision quickly. An additional factor among caterpillars may be that specialists are more readily deterred by nonhost compounds, thus improving contrast between host and nonhost (21).

It has also been shown in generalist grasshoppers that the firing of one contact chemoreceptor cell can inhibit the firing of another with different specificity in the same sensillum—an interactive effect occurring after the production of the generator potential (134). This finding has parallels in lateral inhibitory mechanisms described for a variety of other sensory systems that are known to sharpen resultant images. Such processes may also be important in producing the particular and synchronous firing of a suite of taste cells, which appears to occur in some beetles only when the requisite mixture of plant chemicals is present (121). With respect to the olfactory system, there is also clear evidence of lateral inhibition at the level of the olfactory lobes and at other steps beyond the peripheral interactions (43).

Highly synergistic behavioral effects of multiple host compounds have been described (120, 123) that may depend on the many additional processes occurring more centrally in the nervous system and the necessary filtering of the most appropriate information at any particular time (see 9 for additional references). Similarly, behavioral studies indicate that insects, like other animals, respond differently to the same level of inputs depending on current behavior. A butterfly laying an egg, for example, is relatively insensitive to disturbance (97), and anyone who has spent time observing insect behavior has probably been struck by the fact that individuals are less readily disturbed during many activities than when they are apparently resting. Central filtering or modulation of circuitry ensures that one behavior is given priority at any one time.

Plasticity of behavior is undoubtedly critical among species whose choices of hosts vary in availability unpredictably. In such cases, fine-tuning of the nervous system through experience may provide many of the benefits enjoyed by specialists. Many species narrow their preferences as a result of experience (75), although the underlying mechanisms are not known (30), but in some cases the change was shown to result from increased or decreased sensitivity of their chemoreceptors to certain metabolites (107). Thus, currently relevant cues may be enhanced by increasing sensitivity to them, while alternative cues may become deterrents. Fine-tuning may also occur centrally, narrowing the range of positive and negative cues that are attended to (97). There is no reason to assume that there is a correlated change in normally measured performance characteristics, because the phenomenon is even found in male tephritid flies that are not feeding and are

separated from females. In this case, experience with fruit of one type predisposes the flies to land on the same fruit type again and also makes it less likely that they will land on an alternative fruit type (102).

Associative learning may serve to increase efficiency of decision making as well as having other possible fitness benefits (46, 50, 73). It is generally expected to have greatest value among generalists for reasons related to choosing highest-quality hosts or most abundant suitable hosts. In the context of the argument presented here, it should also have value in improving rapidity of decision making.

Associative learning has been given most attention in flower visitors, especially honey bees and bumble bees and, as generalists, the findings are also relevant to generalist herbivores. Improved efficiency of foraging has been the major focus, in particular choosing a flower type (shape, color, and odor) with high or consistent levels of nectar and choosing a flower type for which the mechanics of handling have been learned (optimized) (e.g. see 88). What has had less study is the possibility that the attentiveness aspect of the learning process may be important in itself. By focusing on specific cues (even successive ones, each for a short time), a bee can be more effective in decision making at each point of its foraging activity. This case has been further argued elsewhere (13). There is a study, however, demonstrating specifically that bees can selectively attend to minor cues in an environment. Individuals were unable to learn two camouflaged shapes for a food reward, but, after training to the two shapes without camouflage, they were able to attend to them when camouflaged (136).

In addition to adaptive aspects of learning in bees and other flower visitors, memory constraints have typically been put forward as a mechanism underlying floral constancy; that is, because it may be difficult to learn and keep in memory a variety of floral types requiring different types of manipulation, bees should show fidelity to one floral type for extended periods. However, it is difficult to weigh the relative importance of limitations on memory and limitations on information handling when there are several behavioral options at any particular time (42)—perhaps, with limitations on processing, single-minded attentiveness to a few cues has as much of a role to play as limitations on the capacity for short- or long-term memory. It is interesting that, even in the absence of nectar rewards, individual bees consistently go to artificial flowers of particular colors, with different bees focusing on different colors and each switching only after a period of fidelity (70). This suggests that there is an innate pattern of remaining constant to one cue for a period, irrespective of memory factors or rewards.

A minority of insect herbivore species are extreme individual generalists, apparently adapted to situations in which food plant quality or abundance is variable or unpredictable or the food plants are all very rich in potentially noxious secondary metabolites (119). Such herbivores engage in food mixing, eating a variety of plants and frequently making choices about what to eat and what to ignore. Such food mixers often appear to be stimulated by novel chemicals, potentially reducing the inefficiency and complexity of decision making (15, 17, 119). In addition, in the grasshopper *Taeniopoda eques*, runs of fidelity to one plant species occurred

even during series of encounters with diverse plant species, suggesting that, like
bees, they focused sequentially on particular food items (29).

Diet quality alters relative acceptability of alternatives depending on nutri-
ent need—a flexibility that is dependent on variation in the strength of inputs
from different nutrient chemoreceptors (116). Such physiological feedback may
improve the speed or accuracy of decision making although, among herbivores,
it has been clearly demonstrated so far only in grasshoppers and in generalist
caterpillars.

FITNESS BENEFITS OF BEHAVIORAL EFFICIENCY IN HOST CHOICE AND FEEDING

I argue that behavioral efficiency is considerably more than simply an ability
to choose a reasonable host (26, 74). Speed of host finding and host choice has
several potential benefits, and these are compounded with the need for choosing an
appropriate plant taxon and individual plant or plant part of relatively high quality.
Clearly, choosing the best of available alternatives is very important and may be
optimized in species that are egg limited.

Speed is particularly important for ovipositing insects that are time limited
for any reason, such as those that have limited suitable flight periods (44, 77). In
a more general sense speed has been considered important in optimal foraging
models and in apostatic food selection, in which time is at a premium because
of resource limitation and/or competition (113, 125). Speed of decision making
may be much more critical for survival in phytophagous insects, however. I argue
that, for animals as small as insects, the ecological risks are sufficiently severe
that attentiveness to them is always important and that time takes on an additional
significance in decision-making processes themselves. In particular, time mat-
ters in that fast decisions reduce opportunity for predation during foraging. The
limits on simultaneous processing of diverse sensory inputs may impose a need
for selective attention to different tasks in succession. Focusing attention on find-
ing and choosing host plants reduces attentiveness to other risks and necessitates
haste in the choice of host and execution of host-related behaviors. Alternatively,
divided attention between foraging and escape from predators means that the sim-
plest possible cues about resources would be an advantage. Although not studied
specifically in insects, it is well known in birds and fish and mammals that foraging
and predator avoidance compete for attention, with outcomes that usually involve
a reduced ability to obtain suitable food (79, 85, 90, 91, 135) if not greater levels
of predation (52a, 79). The neural limitations that require selective attention and
lead to divided attention under predation risk have measurable costs. The problem
is further compounded by the fact that vigilance cannot be maintained for long
periods without rest (51).

Predation risk is one that is difficult to quantify and thus to evaluate as a selective
factor in herbivore-plant interactions, but there are indications that this has often

TABLE 1 Results of observations on numbers of active predators and numbers of insect herbivores in ten 0.25-m^3 spaces in a Costa Rican rainforest during a period of 15 min

	No. of invertebrate predators	No. of visible insect herbivores	Ratio of predators: insect herbivores
Mean	6	3	2:1
Range	2–11	0–9	2:0–2:1.5

been greatly underestimated. It is not that predation (as well as parasitism) isn't recognized as one of the major risks of insect herbivores; extraordinary levels and types of predation have been documented in numerous systems (see 124). Rather, the minute-by-minute implications with respect to behavioral choices have not been thoroughly considered. One indication of the instantaneous importance of predators for insect herbivore behavior was obtained from observations on relative numerical abundance of insect herbivores and predaceous invertebrates over a period of time in tropical vegetation. From ten 15-min continuous observations of forest edge plots (1 m high × 1 m wide × 0.25 m deep) in the Costa Rican rainforest, the average numbers of active invertebrate predators and parasitoids (including jumping spiders, reduviid bugs, ants, and wasps) exceeded those of visible herbivores (caterpillars, plant-sucking Hemiptera, grasshoppers, and leaf beetles) by nearly 2 to 1 (Table 1). The relatively large numbers of natural enemies of herbivores is a reflection of their mobility and provides direct evidence of the persistent problem of this kind of ecological risk, requiring constant attention.

Continuous watching of caterpillars for 10 h each day in the field in California demonstrated considerable predation by invertebrate predators, even on an aposematic species. Furthermore, the predation was ≤100-fold more likely during feeding than during resting (10), thus illustrating a fitness benefit of rapid feeding rates. Even floral visitors such as bees may benefit greatly from learned efficiency in this context, such as may develop in the course of floral constancy, because predation and parasitism risk at flowers can be very high (93). In addition, I argue that intermittent, hesitant, or picky feeding behaviors and any kind of dithering are dangerous not only because an insect is conspicuous but because an animal attentive to food-related activities is unlikely to be attentive to simultaneous environmental risks (49).

Nutrient quality interacts with the problems of risk and attentiveness. Because protein is often at low concentrations in leaves (especially older leaves) and the nitrogen requirements of insects tend to be relatively high, herbivores often compensate by eating large amounts. Not only is high-quality food better for growth, but the risk of mortality via predation is reduced on nutritious hosts because less time must be spent feeding and thus being vulnerable to predators. Indeed, perhaps the fitness advantage associated with predator avoidance exceeds that of increased growth rate. Safety and growth are important together, of course, in a

larger time scale—feeding on high-quality foliage may also reduce development time, reducing the lifetime risk.

Leaves present very diverse physical challenges, and highly diverse solutions have been found by insects through adaptations of mouthpart morphology. The frequency with which certain mandible types have evolved in separate insect lineages with similar types of food indicates the adaptive value of these structures (8, 25). Furthermore, evolution of mouthparts can be very rapid (35). In view of the ever-present risk of predation, structures that determine handling time may be under great selection pressure. Indeed, the preponderance of herbivores that feed on young, easily handled leaves is probably a matter of safety as much as nutrition.

In summary, the fitness advantage of behavioral efficiency measured as speed of finding and deciding on a host and of executing behaviors is largely a function of escape from natural enemies, at least for insect herbivores.

A completely different but additional potential fitness advantage of specialists is the predicted simplification of their nervous systems. Specialist grasshoppers have smaller numbers of gustatory sensilla than do generalists (37), and studies clearly indicate that, as diet breadth has decreased in various taxa, the numbers of receptors have diminished, with the few extreme specialists having fewest contact chemoreceptors (38). Even rearing individuals in an environment with reduced sensory input can cause the development of fewer olfactory and gustatory sensilla (20, 40, 109). However, in the aphid, *U. ambrosiae*, larger numbers of antennal sensilla were found in populations that had narrower diets than in those with broad diets (23). Nothing is known about the investment in other parts of the neural machinery, although there are indications that the sizes of various parts of the integrative center of insect brains are correlated with behavioral complexity (see 29 for additional references). It is also true that, in the Orthoptera, in which generalists predominate, brain size overall is much greater than in similarly sized hemipteroid or holometabolous species, in which specialists predominate. Further work is needed to establish whether there are adaptive patterns with respect to diet breadth.

DIVERSITY OF INSECTS AND PHYTOCHEMICALS AND ASSOCIATION OF INSECT AND PLANT CLADES

It has become clear from both fossil studies (80) and molecular phylogenies (58, 59) that, among all of the herbivorous insect groups studied, great diversification is historically associated at some level with the expansion and increased diversity of angiosperms. Furthermore, among sister clades of insects with different feeding habits, it is the phytophagous ones that have diversified to a remarkable degree. In the face of extraordinary diversity of plant secondary metabolites, chemistry appears to provide the link between insect diversity and angiosperms, with the best known scenario entailing coevolutionary arms races between insects and plants.

Among the hundreds of thousands of plant phenols, alkaloids, terpenoids, iridoids, flavonoids, steroids, and other secondary chemicals, many appear to have no effects at all on insect herbivores, whereas others stimulate feeding and/or growth. Some are sequestered, either obviously in aposematic species (34) or in the cuticle of species not warningly colored (24), although some insects gain protection from predators as a result of the gut contents alone (126). Many are clearly toxic in general and serve as plant defenses against many herbivores (111). It is not at all clear whether an inability to deal with toxins reflects an ability that has been lost, as suggested for grass-feeding grasshoppers (6, 21), or whether the plants have evolved specific defenses against particular insect herbivores (4). Both seem likely. When there are more or less congruent clades of particular insect taxa and their host plants, arms races and coevolution tend to be invoked as the underlying reasons for both the diversity of insect herbivores and patterns of phylogenesis (59). However, the compilation of studies presented by these authors indicates that, although some degree of congruence in insect and plant phylogenies is common, it is rarely precise.

Theoretically, patterns of parallel phylogenies could also easily arise from herbivore tracking of diverse genotypes in a plant population and subsequent speciation of herbivores on established plant host races or species. Neither fossil nor molecular studies are likely to resolve the issue of precisely when changes occurred in either plant or insect, so that the mechanism underlying patterns of congruence will remain uncertain. Many recent phylogenetic studies show relatively very poor correlation between insect and host plant clades (3, 65, 92), with strong evidence for repeated moves between different established plant lineages. There is often an indication that insects have moved to plants with similar chemical profiles, regardless of whether the plants are related. Further resolution of the alternatives through phylogenetic studies requires, in addition, knowledge of plant chemistry and insect behavior at least. The clearest evidence for tracking chemicals in this way has been demonstrated in one study of a group of beetles and their host plants (3). The question then is, do they track a suite of chemicals that they are able to tolerate (or even benefit from because they obtain protection by using the chemicals as defense) or do they track a chemical or suite of chemicals that provides the signals of their host plants? The latter has sometimes been described as a neural constraint, yet such a constraint carries with it the great advantage of having a clear sign stimulus.

If strong and unambiguous cues assist insect herbivores in making rapid decisions and remaining attentive to a particular host during feeding or oviposition, selection on the sensory system and its central nervous projections would favor those insects that match the fine-tuning of their detection of distinctive signals with particular plant chemotypes. Because the primary value of this ability relates to survival in the presence of predators, selection on the nervous system would thus be acting through mechanisms that could improve vigilance. In any case, as plants changed and diversified chemically, insect herbivores, being so dependent on specific cues, might also have changed and diversified so that discrimination

of signals from hosts could be maintained at maximum levels of detection and contrast in every particular population. Many secondary chemicals in plants have been considered toxic when closer study has demonstrated that they are actually deterrents only (18), the effects on test insects being caused by starvation. The interesting thing about this finding is that it demonstrates how dependent the insects in question have become on particular cues that characterize their normal hosts. It also illustrates the limitations incumbent on specialists that have optimized in the direction of behavioral efficiency on one plant chemotype. Thus the evolution of highly sensitive chemoreceptors for detecting host-specific chemicals, while valuable for behavioral efficiency, may greatly restrict what can be accepted.

Testing this hypothesis requires examining populations of particular insect herbivore species, establishing the level of specificity of relevant receptors for host-specific compounds, and comparing the degree of vigilance with the specificity of the receptor or neural pathway. For example, survivorship in the presence of predators would be correlated with degree of match between receptor specificity and presence of specific compounds in the host(s).

Interestingly, even if tracking of plant chemotypes were to be firmly established as a major process in evolution of host affiliation, coevolutionary processes could still be important. However, rather than invoking arms races and toxins, the currency would be in terms of signal information. For example, a herbivore may use chemical A as a sign stimulus for its host. Populations of the plants may evolve to produce an enzyme altering A to B. If there is rigidity in the chemosensory system of the herbivore that relates to sign stimuli, plants with B may escape herbivory until variation in the herbivore allows a switch to plants containing B as the appropriate signal.

CHANGES IN HOST AFFILIATION

An insect herbivore species may show genetically based changes in its specificity (how many plant species it uses) or in the rank order of its preference (which plant species is preferred). Specificity evolves in both directions in some phytophagous groups. Rank order preference changes are the basis of host shifts seen in clades of highly specialized insects. With respect to specificity, in the absence of risk (ecological or physiological), an ability to use many plant species is an advantage. By contrast, using few or one plant species can improve fitness when there are tradeoffs obtained on different plants either for physiological or for ecological reasons. Physiological factors examined usually involve growth and development or correlates of these such as digestion and detoxification ability. Ecological factors have not had the same attention but could involve such things as the differential crypsis (46a) and other morphological traits that influence escape from natural enemies and, as I emphasize here, the ability to find, select, and attend to the specific plant so efficiently that vigilance towards natural enemies can be maintained or

TABLE 2 Possible changes that may occur neurally to effect behavioral changes in relation to plants

Genetic change	Effect
Binding-protein conformation	Determines nonpolar compounds carried to dendrite of chemoreceptor
Change in conformation of protein at receptor site on chemoreceptor	Influences sensitivity of cell to particular compounds
Alter numbers of receptor sites for particular chemicals on chemoreceptor	Alter sensitivity of cell to particular compounds
Alter second messenger or membrane properties of + or − chemoreceptor	Alter sensitivity of + or − cell overall
Alter gene expression pattern of receptor proteins on + and − cells	Switch effect of stimulation from + to − or vice versa
Alter wiring of sense cells or interneurones	Switch effect of stimulation from + to − or vice versa
Alter levels of one or more neuromodulators at one or more synapses	Alter weighting of different + and − inputs
Alter sign of synaptic inputs anywhere in the path to controlling center	Alter weighting of different + and − inputs

enhanced. Variation in rank order of preference within and between populations of an insect species may be the norm (45, 46, 72, 94, 118, 128), in which case one can envisage opportunities for divergence into separate species with different hosts (46a).

If it is true that the basis for limited host use in the majority of phytophagous insects lies with behavior (neural) rather than with postingestive constraints as suggested elsewhere (18), then it is to the nervous system that we must look for variation. Table 2 lists the major types of change that could occur. Some appear to be more likely for changes of specificity, whereas others may be more likely for changes of preference.

Evolutionary change in sensory processes and patterns of host affiliation are probably strongly influenced by the group of insects concerned. At the level of order, it should be noted that orthopterans have large brains and very large numbers of sensilla (38) and probably depend on integrative processes more than on directly labeled lines from chemoreceptors that clearly define sign stimuli. Lepidopteran larvae, by contrast, have very small numbers of chemoreceptors and simple brains. For this reason, a small change in a receptor or synapse may have a large impact on behavior of a caterpillar but little effect on behavior of a grasshopper. Thus it has been argued that nonorthopteroid insects may evolve detection and discrimination systems relatively rapidly (37) and so be able to track plant chemical evolution in a way that is less likely for grasshoppers. If this were

so, it would provide additional evidence for the importance of coevolution of insect receptor systems and plants. In other words, it would provide a mechanistic basis for commonly found congruence in plant and insect clades and for phytophagous insect diversity.

CONCLUSIONS

This review depends on knowing the insect—understanding it as an organism. The details of behavior and physiology, especially neurophysiology, have suggested a theoretical approach to the study of insect-plant interactions, specifically the limitations of the nervous system and the effects of these limitations in ecology and evolution. It is suggested that the combination of neural limitations on processing favors reduced diet breadth and that the selection pressure probably acts through effects on vigilance and, thus, ultimately via natural enemies.

ACKNOWLEDGMENTS

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