Plasticity and the Problem of Choice in Food Selection

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ABSTRACT The interaction of plasticity, choice, and diet breadth is discussed, and the problems faced by generalists highlighted. The case is made that insects with very broad diets, and hence an ability to choose among foods at some time in their life history, have a problem making decisions that are efficient in terms of speed and quality. Reinterpretations of data from some insect groups, such as flower visitors, are presented in the light of such a neural problem, and explicit tests of the concept that there are neural constraints are reviewed. Possible mechanisms underlying changes in diet breadth are discussed.

KEY WORDS host plant choice, diet breadth, specialist, generalist, selective attention, neural constraints

I AM PLEASED to provide this article for a commemorative volume that honors Carl Schaefer's contribution to entomology. In particular, his dedication to the production of the *Annals of the Entomological Society of America* for over 25 yr has been a work of major proportions. I look back at the topic of behavioral plasticity that has grown into a new area of work over the last 25 yr, perhaps mostly in just the last 5 yr, and I hope it brings new challenges to the study of entomology.

Fifty years ago insects were generally thought to be hardwired in their behavioral repertoire, with the peculiar exception of honey bees, whose learning ability had been so thoroughly demonstrated to the world by Karl von Frisch. In 1963, Vincent Dethier accurately represented the time and presaged the future in a lecture at a meeting of American Association for the Advancement of Science (1964). He quoted many contemporaries who viewed insects and other so-called lower animals as relatively simple machines, with behavior depending largely on reflexes. He wondered “perhaps these insects are little machines in a deep sleep, but looking at their rigidly armored bodies, their staring eyes, and their mute performance, one cannot help at times wondering if there is anyone inside.” He indicated that they did show motivated behavior, but fell short of suggesting they would be very plastic, or that any besides bees might learn much from experience, let alone have problems in making decisions.

In the years since then, we have learned that all insects studied modify their behavior as a result of physiological state and previous experience; that individuals vary one from another; that the nervous system changes with experience, with external and internal conditions, from day to day, and throughout life. Phytophagous insects have provided model systems for many of these studies and have given us examples for every type of plasticity, and much of it would appear to have adaptive value. It allows compensatory feeding to supply sufficient nutrients, selection of diverse foods to obtain a suitable nutrient balance, avoidance of bad experiences, improved foraging efficiency, and maximization of numbers of eggs laid (e.g., Papaj and Lewis 1993, Bernays 1995, Simpson et al. 1995, Chambers et al. 1996). There is evidence of general fine-tuning of all behavioral repertoires with experience (Papaj 1993). Now, there is a growing interest in the bases of the plasticity; how it occurs, when it is deployed, and what might be involved in making alternative choices. No longer is there just a simple machine. Synapses change in relative strength, new connections can be made, neuromodulators alter the balance of neural circuits and competing pathways must find resolution; decisions must be made in relation to sensory inputs, memory, and physiological state (e.g., Harris-Warwick et al. 1992).

The Generalist’s Dilemma

The downside to all this plasticity is that choosing may be difficult. Making the decision may take time when there are competing inputs, and the organism waits to collect additional information before making a decision. Even after a choice has been made, the detection of a possibly better alternative may distract attention and reduce the effectiveness of current behavior.

Patterns of neuronal activity that are mutually exclusive, such as those involved in feeding and escape, are known (e.g., Bellman and Krasne 1983); but I will argue that the difficulties entailed in having diverse
inputs competing for attention in relation to a specific behavior, provide the greatest challenge for generalist insects as well as other animals that have a choice of foods in nature. The challenge may not be immediately obvious because solutions may have at least partially been found in the course of evolution. The costs may also be deceptively subtle or difficult to measure. This article makes the case for the potential importance of choice as a problem.

The 1st problem is that decisions need to be made quickly, and having a choice, as most of us know from our own experience, mitigates against speed. Speed of decision may be of direct significance. For example, if the food is a prey item that moves fast, speed is of the essence. There are well known problems for predators of choosing among individuals in a group, a problem made use of by species that gather in flocks or schools or other aggregations and all look alike. Among insects that are gregarious yet palatable, the same phenomenon has been described; predators have greater difficulty capturing an individual in a group of locusts than they do capturing an individual alone (Gillett et al. 1979). Speed of decision may also be directly important where there are time constraints as in butterflies in cool climates. Here, it is not uncommon for females to die without laying eggs at all (Kingsolver 1983), and an inability to choose quickly may result in poor decisions in terms of quality, or simply too few decisions. The bee should not overly its rewarding flower for want of decisiveness, and the grazing herbivore should not spend time wandering aimlessly between potential foods.

Taking time for decision-making is also indirectly costly. While focusing on the choice between alternative foods, attention to danger is reduced. The attention required by one activity takes away from the attention required by the other. This was elegantly demonstrated by Milinski (1990) for fish, and by Lima and Dill (1990) for birds, but there is every reason to assume that it is universal. Also Dukas and Clark (1985) showed that vigilance is difficult to maintain during periods of time anyway, and the problem of having to make additional choices while maintaining vigilance may be much greater than we commonly appreciate. Among insects the problem is possibly exacerbated by the fact that natural enemies come in such very diverse forms and give such different types of cues that a generalized vigilance seems to be a daunting task.

Finally, the importance of attentiveness is critical during the continued performance of a behavior. For example, when feeding on 1 plant or laying eggs on 1 host, it would be highly inefficient and dangerous for an insect to be distracted by alternatives, even when they are potentially superior. Thus, attention must be directed toward the completion of specific activities in relation to their current importance, and the term "selective attention" is used for the presumed neural processes required. An operational definition of selective attention is given by Bernays and Wcislo (1994) although for most humans the need is intuitively obvious. In any case, selective attention is needed for efficient decision-making, must be continued to the end of a sequence of behavior.

The Case of Bees and Other Flower Foragers

A solitary bee with a single host can be hardwired with the floral cues having fixed and high levels of apparency. Selective attention to a subset of cues is not an issue; there should be few competing sensory inputs, no choices to be made. The situation stands in marked contrast to the case of the generalist honey bee or bumble bee which has a big choice, and must make many decisions. Individuals learn to associate visual and chemical cues with reward, and they learn how to effectively manipulate the flower structure to obtain the rewards quickly (e.g., Menzel and Mercer 1987). As the balance of rewards in different flowers changes the insects switch to, and remain with, new and better floral types. Constraint on memory has usually provided the functional explanation of floral constancy; that is, learning a new floral type causes interference with memory of the previous one, with concomitant reduction in handling speed (e.g., Dukas and Real 1993a). In any case, the succession of periods of floral constancy can increase foraging efficiency, provided the pollinators switch to new and better resources when rewards on the current flower type fall.

Floral constancy can be viewed from another perspective, because the learning involves not just an association between cues and rewards. It involves selective attention to the cues that have recently been learned, and such selective attention enables the bee to notice the cues and respond fast. It can result in gathering of nectar or pollen with a minimum of distraction. Here I argue that decision-making is a particular problem for generalists. I further argue that the much-studied learning of honey bees and bumble bees is not just a means of efficient handling—but that the selective attention used as a part of the process of learning may be even more important for effective decision-making per se.

Suggestive data exist that bear on this question. For example, Strickler (1979) noted that among bees with different host ranges, the specialist had the shortest between-flower intervals, whereas Wilson and Stine (1996) made the case that "perceptual conditioning" might be more important than handling efficiency. There is good evidence that among honey bees certain odors and colors are learned more readily than others (e.g., Menzel 1985) and it would be interesting to know if these provide more apparent inputs to short-term memory, allowing them to be more readily noticed. Dukas and Real (1993b), in discussing attentiveness in bees, emphasized the need to process information effectively and showed that individuals learned more slowly when rewarding flowers were of several different types than when only 1 rewarding type was available. They suggested that when the bees' attention was divided, their general ability to detect rewarding types of flowers was greatly reduced. Per-
haps the bees had difficulty in making the decision among the available choices.

In a study with naive bees in an artificial arena with artificial flowers of different colors, Hill et al. (1997) demonstrated that individual bees showed floral constancy (different bees to different colors), although the artificial flowers had no rewards at all. One interpretation of this would be that bees have a tendency to simply focus on a color, any color, to make decisions quickly. This process was suggested in an experiment with bumble bees foraging on artificial flowers where individuals were shown to have runs on single colors, although all colors were equally rewarding (Keasar et al. 1997).

Butterflies also show floral constancy and, as with bees, the literature tends to put emphasis on learning to handle the different floral types (e.g., Lewis and Lipani 1989), yet the mechanistic basis of the consistent short-term preference for 1 flower type could well be a matter of selective attention. In a recent study with the pipevine swallowtail butterfly, Battus philenor (L.), individuals were trained to respond to different colored cardboard circles with oviposition-stimulating chemicals or a central source of nectar. Some individuals successfully learned 2 colors—going to one color when they were ready to oviposit and the other when they were foraging for nectar. However, others landed on the 2 colors but did not then differentiate which one was appropriate for egg-laying and which was appropriate for nectarating (Weiss and Papaj, unpublished data). An explanation for this might be that these individuals had developed the selective attention to the 2 colors out of all the alternatives but had not learned the relevant associations.

Hover flies also show floral constancy (Goulson and Wright 1998), and here there is no requirement for learning to handle different floral types because the pollen they require is always very apparent and available without manipulating the flowers. In this case, selective attention seems to be an adequate explanation for the phenomenon.

Oviposition by Butterflies

Few species of butterfly are true generalists when it comes to host plants used, but most use >1 plant species, and choices can be modified by experience. Thus, the pipevine swallowtail butterfly can choose one or other of its host-plant species, and learn to land on either a broad-leaved or a narrow-leaved one. Where only 1 host species was interspersed among nonhosts, the butterfly quickly learned to land on the appropriate plant; where >1 species of host plant was present, individuals were less efficient, and they landed less on any host when a choice was available (Papaj 1990). Although this phenomenon was discussed as interference with learning, it could also be thought of as indecision, the result of the indecisiveness being reduced oviposition. The plasticity was useful in learning about the host among nonhosts, but there were costs in having a choice among different hosts available together.

A study on the blue butterfly Glaucopsyche lygdamus (Doubleday) in the Rocky Mountains (Carey 1992) demonstrated an expected effect of experience; landings and egg laying events were more likely on a host that had recently been experienced than on alternative, equally suitable hosts. In addition, variation existed among individuals. On any day, some stayed with one host, while others stayed with a different host. Individuals that moved between hosts, and gave superficial evidence of indecision, were also less likely to lay an egg at all during the limited landing time on any plant. One interpretation is that these indecisive individuals were unable to pay sufficient attention to 1 plant, and that even when they landed, there was insufficient focusing to oviposit in the short landing time available.

Janz and Nylin (1997) reported on butterflies that all include stinging nettle among their hosts although they have different host ranges. Using species pairs and intraspecific population differences in host ranges, they showed that specialists laid eggs preferentially on the high quality nettle, while the more generalized species laid eggs equally on good and bad nettle plants. They interpreted the results in terms of discrimination ability; the specialists, with a narrow focus on host signals, could make better use of additional cues relevant to host quality. Further work is needed however to distinguish between making qualitatively better decisions because of better information gathered or because, being more decisive, the specialists had time to make the evaluation.

Studies on Hemiptera

Although this group has had relatively little attention, it has been demonstrated that some generalist plant-feeding species are poor at selecting the best quality foods when they have a choice of foods readily available (Bernays and Minkenberg 1997). One species, the whitetfly, Bemisia tabaci (Gennadius), was studied in depth. Here, individual adults in well ventilated cages with a choice of healthy growing plants often chose the lowest ranking species in terms of development. Individuals that had a choice of 3 different plant species moved more and settled for shorter periods than individuals with a choice of 3 of the same plant species. Even when settled on the most favored and most suitable host plant, an individual with alternatives in the vicinity was highly likely to show increased restlessness and abbreviated feeding bouts (Bernays 1999). The simplest explanation of this behavior may be that individuals were distracted by the sight or odor of >1 plant type and their level of selective attention to the current host was inadequate to keep them settled.

Recent studies with the aphid Uroleucon ambrosiae (Thomas) have shown that populations in the Eastern United States are largely monophagous on Ambrosia trifida L., while those in Arizona feed on other species of Asteraceae in several different tribes (Funk and Bernays, unpublished data). Specific tests addressed the question: are eastern individuals more decisive
than western individuals? In several different experiments, individuals of the more specialized clones found the principal host more readily in windtunnels and large cages, and located the single host in a bouquet of nonhosts sooner than did individuals of the generalist clones. For example, when provided with host and nonhost material at distances of only 10-20 cm, the individuals from all the eastern clones were invariably faster at locating the host than were individuals from the western clones. Furthermore, studies with the electrical penetration graph, which allows identification of within-plant activities of the mouthparts, showed that the specialists sampled the cell sap sooner, and settled into phloem-feeding more quickly than did the more generalized clones (Bernays and Funk 1999). For whatever reason, the answer seems clear, that the clones with a greater stringency for specific characteristic host chemicals (and perhaps sensitivity to nonhost chemicals) made quicker decisions.

Grazing Insects

A considerable amount of work has been done on generalist grasshopper food choice and foraging in the laboratory (e.g., Simpson et al. 1995) and in the field (e.g., Chambers et al. 1996). In the laboratory it is clear that individuals are able to select a nutritionally balanced diet from a mixture of unbalanced ones when they are in simple arenas, and possibly even when they are in the field if choices are limited. Underlying this achievement is an ability to learn positive and negative features of different foods, together with need-dependent changes in relative taste sensitivity for amino acids versus carbohydrates (e.g., Simpson and Raubenheimer 1996). In the field, some species are faced with an extraordinary diversity of acceptable foods, however, and the choice is made greater by high levels of locomotion, such that dozens of different food plant species are encountered per hour (Raubenheimer and Bernays 1993). It is not known whether learning can be employed where prodigious amounts of memory would be required to make learning valuable. One might envisage that such an animal would have difficulty in making the choice of what to feed on and for how long. A similar problem faces caterpillars of some arctic moths that are found actively foraging on as many as twenty different plants during the course of a single day (M. S. Singer, personal communication).

A comparison of data from the complex field situation and data from a simple laboratory situation suggests that the apparent indecisiveness may be greater in the field. For the grasshopper, Tamiopoda eques Burmeister, continuous observation of individuals in nature showed that all acceptable hosts were rejected on occasion, with >60% of all contacts on such foods resulting in rejection or nibbles of a few seconds duration (n = 628), after which the insects continued walking (Raubenheimer and Bernays 1993). Even the most highly ranked hosts were often rejected. By contrast, in the laboratory, where 2 or 3 plants were available in small cages, almost all contacts resulted in a feeding bouts of >30 s (Bernays et al. 1992). Similarly, with the arctic caterpillar Comma canescens (Strecker); >60% of contacts with known food plants in the field resulted in rejection, while observations on 1, 2 or 3 such foods in the laboratory (56 caterpillars, 1,150 food contacts) resulted in 24, 17 and 22% rejection respectively (E.A.B. and M. S. Singer, unpublished data).

An explicit test of the hypothesis that generalization is associated with long decision times was undertaken with the grasshopper Schistocerca americana (Drury). This species is a generalist with well-developed learning abilities, and individuals were reared as generalists or specialists by providing them with single or mixed foods. The foods consisted of dishes of nutritionally identical artificial diet; individuals had access either to 6 dishes that were each flavored with 1 plant secondary metabolite, or to 6 that were each faced with a different flavor. Observations on insects with these different experiences showed that those reared with the mixture took considerably longer to choose which food to feed from after contacting food at the beginning of a meal, than did insects reared with single food types. In addition, the generalist treatment led to differences in patterns of ingestion; generalist insects had prolonged meals frequently interrupted by pauses and switches to new food dishes. Even when insects from the specialist treatment were allowed to choose among the 6 different foods, they made relatively fast decisions. In addition, when insects were placed in novel environments with the same choices available, the generalists were even more indecisive than the specialists: overall meal times were approximately double those of specialists, although total amounts eaten were similar (Bernays 1998a). These data provide direct evidence of indecision in the face of choices, and an inability to show selective attention, to the degree that foods could be selected quickly and meals ingested in the minimum time.

Relatively Immobile Herbivores

Many species of caterpillars do not actively forage among different host plants, but rather feed where they hatch, and move to another plant only when the 1st is depleted or becomes poor in quality. Similar life styles probably occur with insects in other groups such as beetle larvae and stick insects. However, most behavioral studies have been with caterpillars. Like the heteropterans mentioned above, generalist caterpillars appear to be poor at choosing the best food for their own development when they are faced with a choice (Bernays and Minkenberg 1997). It is possible that individuals feed, by chance, on 1 food plant, and after this experience just stay on it, or even prefer it, although it is not of high quality. Such apparently maladaptive "induction of preference" has been demonstrated in many caterpillar species as well as stick insects (e.g., Jermy 1987), and the question arises as to its functional significance, if any. If there is some adaptive value to the phenomenon, it may be that an individual developing a taste for the food it is already
Fig. 1. Three diet breadths illustrating the decreasing contrast likely for more generalized species. A monophagous insect has a clear yes or no answer to the question of whether this is a host or not. A polyphagous species experiences a gradation from good host species to nonhost, with a long range of intermediate species. Here the choice is more difficult. An oligophagous species is intermediate. Areas of indecision may be reduced by short-term selective attention, imprinting-like processes, or associative learning between sensory cues and good or bad consequences of feeding.

Putting the Studies Together

Taken together, the mixture of miscellaneous data obtained from diverse insect species and experimental protocols points to problems arising from the availability of choice. How attention is focussed on specific behaviors or specific foods for oviposition behavior or feeding is not a trivial issue (Dusenbery 1992) and the problems are greatest for generalists. Yet plasticity has the most potential for generalists, for they may learn one way or another to profit from experience. I argue that the significance of learning may be as much to improve selective attention as to define specific associations.

The generalist herbivore has more potential hosts to choose among, and a bigger gradation of host suitability to make use of if the need arises. It must detect the potential foods, discriminate among them, decide whether to feed on 1 or which to feed upon, and then carry out the motor program. Not only is there a greater range of foods to choose from (Fig. 1), in the gray area of intermediate host acceptability the choices involve weightier decisions. Now there needs to be some decision with respect to relative acceptability in relation to other variables such as motivational state or likelihood of finding better hosts. There can be no clear-cut yes or no answer, and the problem of decision-making is enhanced, perhaps immeasurably. Perhaps the fact that most contacts with edible hosts made by extreme generalists involve rejection (see above) is simply a measure of their indecision.

Empirical support is emerging for the predictions that neural constraints are greatest for generalists and favor specialization (e.g., Levins and MacArthur 1969, Stephens 1987, Bernays and Wcislo 1994, Kotler and Mitchell 1995, Bernays 1996, Dall and Cuthill 1997, Dukas 1998). This plasticity is intimately tied up with how to focus attention on the most relevant or important sensory information in the face of immense numbers of competing neural inputs.

In the few explicit tests of the hypothesis that choice, as experienced by more generalized species or individuals, entails a cost, there appears to be an answer—it is a clear advantage to the relative specialist in terms of efficiency of decisions made. The tests do not include all the difficulties of life in a natural setting such as the presence of natural enemies and other unrelated distractions. If we find significant effects in
the laboratory we will surely find even greater effects in the field.

It seems likely that the critical issue for decisiveness, attentiveness, or whatever terms may be used, is the relative intensity of the contrast between the item to be chosen and all other possible items. The specialist, hardwired to notice only the specific chemical or suite of chemicals in its host plant, may quickly fine tune its behavior in relation to details of foraging or to minutiae of host quality. The generalist has a major task.

Every gradation between extreme generalist and extreme specialist exists, and phylogenetic studies indicate that host range alters in both directions over evolutionary time (e.g., see Bernays 1998b). There are various ecological and biochemical explanations for the different patterns of diet breadth and their possible adaptive bases (e.g., Futuyma and Moreno 1988, Jänicke 1990), yet the role of the nervous system has been studied little. Evidence for neural constraints exists that may even rank as more important than the alternative proposals favoring specialization, and there is a hint of this also from the many studies on search image formation in birds, and from the large body of work on human attentiveness (e.g., LaBerge 1995, Pashler 1998).

How experiential and evolutionary changes might occur and where in the nervous system they occur, is of critical interest. An understanding of the mechanisms may influence thinking about the evolutionary pressures favoring different diet breadths and a focus on what the individual animal perceives, and how it canalizes information promises to be useful. The strength of signals, the degree of contrast between positive and negative inputs, and the ways in which such contrasts may be magnified seem to be fruitful avenues for exploration. Specialists become generalists; the green flag in a sea of red ones becomes a scattering of different shades of green in a background of gray-greens, grays, and reds; and vice versa. Is it possible for such a major behavioral change to occur from a simple physiological change? Carson and Ohta (1981) have, after all, already demonstrated that diet breadth change in a Drosophila species may reside in a single gene influencing female behavior. It has also been shown in a theoretical paper that evolution from generalism to specialization under perceptual constraints could occur relatively rapidly (Holmgren and Getz 1999).

When an insect herbivore takes the pathway to becoming relatively specialized, there are several different levels where neural changes may effect the change in behavior. First, at the sensory level, enhanced sensitivity to 1 or more positive host-specific signals may occur, leading to a stronger contrast between the specific host and other potential hosts. Or, there may be an increase in sensitivity to the repellent or deterrent compounds contained in nonhosts, again increasing contrast between host and nonhost. Alternatively, the way the positive and negative inputs interact in the chemosensitive sensillum may enhance contrast (see Bernays 1996). Such changes may reside in as few as 1 or 2 gene products.

At the level of the subesophageal ganglion where the mouthpart taste receptors make their 1st synapse, there could be changes that increase the gain from either positive or negative inputs, perhaps caused by a change in release rates of 1 of the neurotransmitters, or by release of 1 or more neuromodulators in the region. Small changes then, at either the sensillum level or at the level of the 1st synapse, could have the effect of vastly changing the contrasts between different potential host, good host and poor host, host and nonhost.

So far, data comparing mutants in Bombyx (Asakura, in prep.) and sibling species of Heliothis with different host ranges (Bernays and Chapman, in prep.), indicate that behavioral differences do not necessarily have their origin in the taste receptor system. The generalist Heliothis virescens (F.) and the specialist H. subflexa apparently have identical responses at the level of the taste receptors. In the case of Bombyx, one mutant that is relatively more polyphagous than the wild type has deterrent cells less sensitive to 1 class of deterrent compounds, whereas another polyphagous mutant appears to be the same as the wildtype.

Assuming that, at some level, the contrast between positive and negative inputs can provide the basis for clear-cut decisions, one might imagine that the increasing contrast in favor of positive inputs would enable increased attentiveness and consequently faster decisions. This in turn would allow faster output to motor neurons.

Alternative routes for faster decisions are likely. For example, if certain host-specific stimuli assume greater significance by, for example, heightened sensitivity of positive input sensory cells, these inputs may cause an increase in general level of excitation. Earlier papers noted and discussed a "central excitatory state" in which it was found that contact with a favored host elicited very active food seeking behavior (Bernays and Chapman 1974), and it was later shown that excitation levels at the start of the meal in locusts could determine the subsequent meal size (Simpson et al. 1988). It is therefore feasible that the level of excitation in relation to favored food may itself provide the mechanism for increased specific attentiveness.

Another important factor is that of experience, the memory of which can add weight to the channels that enhance attentiveness. The "search image," whereby an animal may selectively perceive food items or host plants after successful initial encounters (e.g., Dawkins 1971, Rausher 1978) is one such example. It may be the same process as that involved with floral constancy among flower visitors (Dukas and Real 1993b). Longer-term, imprinting effects such as induced food preferences in caterpillars is another.

The balancing act between always having a reasonable availability of resources and maximizing the signal contrast is the balancing act of plasticity; not just for traditional learning paradigms, but for selective attention.
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