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I thank the organizers for inviting me to give the Jan de Wilde memorial lecture. It is a great pleasure and honor for me to come here today, and a particular pleasure to be publicly remembering a person who gave so much to insect biology, to insect biologists, and to organizations involved with the study of insects around the world. I am lucky to be one of those who also remember the man; and so to be able to tell you that for me he was one of those who also had the highest standards, the broadest interests, the warmest personality and the greatest sense of humor. My topic for the seminar is tangential to his interests yet I believe if he were with us today he would be as involved and interested as anyone could be.

Introduction

For many years entomologists, and ecologists generally, have been fascinated by the patterns of host range exhibited by plant-feeding insects. The vast majority of species feed on a very limited range of plants, yet others succeed as extreme generalists, with their food coming from many different plant families. There is clearly an advantage in having the flexibility to feed on many different plants, so that one must look for reasons to be a specialist[1]. Several authors have suggested that there is a relationship between the enormous diversity of insect herbivores and the diversity of plants they feed upon[2]. However, what provided the selection pressure for herbivores to so divide up the resources has been the subject of much discussion. Another point of interest is that a relatively large number of crop pests are generalists; understanding the evolutionary pressures favoring different diet breadths might help us to manage the populations of these pests.

Until relatively recently, detailed investigations of the factors favoring a diversity of different narrow diets in insects has focussed on potential physiological advantages of becoming specialized to deal with host plant chemistry[3]. There may also be morphological specializations that improve the handling of specific vegetation types[4]. There may be an element of chance; some chemicals deter feeding and reduce the number of food plants, even though a diverse array of them could support growth and development if they were accepted[5,6]. Or, being faced with large patches of a particular plant may effectively force a population of insects to feed or starve to death and over time lead to insects that favor the common plant type. In the last ten years there has been a greater appreciation of the role of higher trophic level organisms in shaping herbivore feeding patterns. Predation and parasitism may select for insects that have defenses against these natural enemies, including an ability to use a particular plant for protection[7].

Clearly, there is not just variety in possible selection mechanisms leading to, or maintaining, narrow diets, but interactions among them. In this lecture I want to focus on the importance of neural constraints and some of the interactions with other factors favoring specialization. I think of these neural constraints specifically as the difficulty of attentiveness or vigilance[8,9]. This is a major problem faced by all animals, and one which influences the roles of plant chemistry, predation and other ecological variables in shaping host use patterns.

Natural enemies

To begin with I want to give predators a lot of credit for how herbivores behave. Predators and parasitoids commonly regulate herbivore populations[10]. Also, we have found, in over 1000 hours of field observations that it is up to 100 times more dangerous for caterpillars to feed than not to feed[11]. Furthermore, we have shown that when numbers and sizes of caterpillars are similar, the generalists are more vulnerable than specialists to predation by several different types of predators[12]. There are different ways that herbivores use the host plant to reduce vulnerability to these natural enemies, and in all of them, the strategies can be more successful if the herbivore limits its use of hosts to a few similar plant species.

First, insects may become extraordinarily cryptic on their host plants and the effect can be greatest if the insect uses only one type of host background. We have all seen amazing examples in nature films or in National Geographic magazine. Among visually cryptic species there is some evidence also of chemical crypsis; caterpillars of *Manduca sexta* feeding on different foods have different cuticular wax chemistry[13] and observations of vespid wasps have indicated that the larvae are often walked over without being detected. Like visual crypsis, this strategy can be most effective if a caterpillar retains fidelity to one plant species, so that genetically restricted diets may be made even more restricted by experience[14]. Even among generalists, there appears to be some benefit in an individual staying with one host species especially if it contains unusual or repellent odors[15].

A different approach is for herbivores to sequester host chemicals and become highly distasteful or toxic themselves to potential predators. In general, high levels of one or a few similar compounds will be more effective than a multiplicity of different ones. The monarch butterfly sequestering cardiac glycosides is a classic example, but there are many others. We recently uncovered a novel one with a caterpillar species using quinolizidine alkaloids from its host broom plants[16].

Plants are used as shelters in many ways, there being leaf miners, stem borers, galls for example. A large proportion of smaller caterpillars make houses out of rolled or cut leaves and several authors have demonstrated that the choice of leaf is based more on its value for construction than its value as food[17]; clearly, it matters to have the best materials, and for a given species this will differ according to the shape, size and morphology of the individual caterpillar.

For small herbivores the world is almost two dimensional and the nature of the leaf surface is critical for their ability to hold on and to escape from imminent danger of natural enemies. Recently, it has been demonstrated that the feet of insects are important, and more or less suited to leaves that are shiny, hairy, spiny, rough in different ways, or covered with waxes with very different physical qualities[4]. Indeed, it is now clear that some cases of plant resistance to insect herbivores are based on the ability of various predaceous species to negotiate the leaf surface better than the herbivore[18].

There are some examples of herbivores associating with plants on which ants habitually reside. These herbivores provide secretions for the ants which in turn become bodyguards for the herbivore species concerned, protecting it from other natural enemies[19].

Perhaps more important than all of these is the limited ability of the nervous system and the need for an insect to have clear-cut host cues or signals. Insects, like other animals, must be always vigilant and attentive to danger, but at the same time they must make decisions about other issues, such as when to feed and what to feed on. Brains of animals can process only a limited amount of information at any one time[20], leading to an increased danger during decision-making times, or during activities like feeding or mating. Among vertebrates, it is well-known that trying to attend to more than one behavioral need at a time reduces the ability to perform either behavior efficiently, and this is sometimes termed "information overload"[21]. I will argue the case that decision-making, attentiveness, vigilance and various other terms that describe the problem, pertain also to insects and are relevant and important in the feeding strategies of herbivorous insects. I will make the case that insect herbivores can make use of specific plants to focus their attention; that they can do this more effectively by being specialists; that the benefit of specialization is again related to escaping predation.

Neural constraints in insect herbivores

Rapid, accurate decisions are relatively easy when choices are strictly limited, but difficulties increase sharply as the perceived choices increase. One of the essential functions of the nervous system is to select among incoming signals and canalize information so that accuracy of decisions and actions are possible[22].

Animals have different ways of ensuring that perception, processing of information, and responding in an adaptive manner can occur with maximum accuracy and efficiency. Often there is a genetically enhanced production of, and sensitivity to, particularly important signals. Such are the widely occurring species specific "sign stimuli" first described in detail for intraspecific interactions among stickleback fish[23]. These specific signals enable animals to use simple rules of behavior, ensuring quick, appropriate responses. Different degrees of plasticity have been demonstrated in these studies, with an innate response that may develop automatically, or be modified as a result of experience.

There have been fewer studies on how efficiency of resource use in the face of multiple choices may be achieved, although it is clear that in most animal groups studied, experience reduces the breadth of food items selected[24]. Among insects, experience also may fine tune diet choice[25], while some highly specific chemical signals of food substrates have been demonstrated in a number of food specialists[26].

Levins and MacArthur[27] first proposed that generalist insect herbivores might find it difficult to choose among alternative possible hosts, and that processing the information required to make a suitable choice would require a certain (although unknown) neural capacity. On the other hand, a specialist would need a relatively less complex neural machinery because inputs influencing choices could be simpler. Specific reference to neural limitations in relation to diet breadth have been made by several authors since[8,9,28].

If information processing does constitute a problem for generalists, two types of cost are possible (Fig.1). First, the accuracy or appropriateness of the decision made may be compromised, especially if there is a time constraint. Second, the time taken to make the decision may be lengthened; the selective attention involved in this relatively long decision-making process, and the consequent lack of vigilance, could constitute a significant predation risk. Fig. 1 illustrates a situation in which both accuracy (A) and efficiency (time taken, E) is better for a specialist.

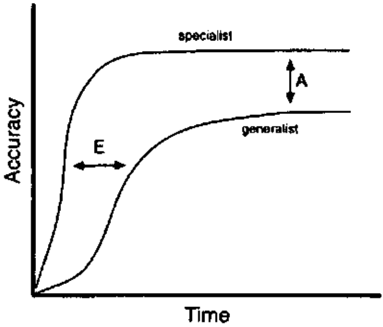

Fig.1. Model to illustrate the potential costs to food generalists in relation to foraging/feeding decisions. A represents a difference in level of accuracy due to constraints on ability to process complex information. E represents a difference in the efficiency (time taken to make a decision) due to constraints on ability to process complex information.

There are some suggestive data on both of these factors in butterflies. With respect to efficiency (E) for example, Papaj[29] 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. Similarly, Carey[30] showed that among individuals of the blue butterfly, *Glauchopsyche lygdamus*, those that specialized on one of the available hosts were more likely to lay an egg in the limited landing time, than those that alternated among hosts. With respect to accuracy (A), Janz and Nylin[31] showed that among species and populations of nymphalid butterflies with different host ranges but one host in common, the specialists made fewer errors in relation to host plant quality than did the relative generalists.

Experimental test of efficiency in grasshoppers

I tested the efficiency (E) of decision-making, in relation to diet breadth. The specific prediction was that individuals of these generalist grasshoppers that had experienced mixtures of good food types over a period of time would require greater processing procedures and therefore longer decision times and greater hesitancy during a meal, than individuals accustomed to only one such food type.

The experiments were conducted on the assumption that the grasshoppers used were plastic enough to change their behavior as a result of their experience during development[32]. That is, individuals would learn that there was only one food available, or they would learn that a choice of foods was available, and in this way become behavioral specialists or behavioral generalists. I used *Schistocerca americana* which feeds readily in the laboratory on artificial diets that support good growth and development. This means that individuals can be reared on defined diets with or without the addition of plant compounds that provide chemical markers. I selected an array of diverse plant chemicals that were readily fed upon, were non-toxic and yet distinguishable, and occurred in typical, acceptable food plants. These provided markers that would enable the insect to identify separate food dishes even though the foods were nutritionally identical.

There were seven treatments; six in which the insects received a group of six food dishes each dish having just one of the six test flavors (singles), and one in which insects received one food dish of each of the six flavors (mix). Individuals were reared from hatching until the stage before adulthood, when they were behaviorally examined to test the hypothesis that experience with single foods during development would lead to more rapid decision-making in relation to feeding than would experience with multiple foods (the situation that these grasshoppers ordinarily encounter in the field).

First, I made observations on all individual insects feeding in their separate cages on new dishes of their assigned foods and using a computer, monitored the ingestion of one complete meal in detail. Individuals ready to feed descended from their roosts near the light, and moved towards the food dishes. Individuals fed immediately after contact or they continued to taste the same or another food before feeding. They fed on one food or on multiple foods before returning at the end of the meal to the resting position at the top of the cage.

Immediately after this Meal 1, I transferred insects to novel arenas each with an array of the six foods. When ready to feed again, insects left the illuminated end where they rest, and moved to the dishes at the other end of the arenas. Once again, during this Meal 2, I monitored on computer, all tasting and feeding events at each dish. I predicted that the insects having the mixed diet would have relatively long decision times and low feeding decisiveness.

In both Meal 1 and Meal 2, decision time, the time between contacting food and the beginning of feeding, was significantly shorter in the single flavor treatments than in the mixed flavor treatment. Similarly, the feeding decisiveness was greater during the meal in single flavor treatments than in the mixed treatment; that is there was much less time spent pausing during the meal. Survivorship and growth were not generally better in the mixed treatment than the single treatments, and the times spent feeding during both Meal 1 and Meal 2 were not significantly different in the two groups. Also, the rest between meals was similar in the two groups, indicating that the levels of hunger were similar.

These data show that individuals conditioned to a monotonous diet had more decisive feeding behavior than individuals conditioned with a choice of foods. In other words the efficiency of the individuals that had a choice was poorer than that of individuals with no choice. The data are consistent with the general idea that a simple clear signal allows faster or better decisions than complex signals, just as sign stimuli improve behavioral efficiencies in other contexts including courtship of birds, aggressive displays in stickleback fish and feeding of young birds, as well as warning colors used by some insects and snakes to defend against predation.

Interaction of efficiency in food choice, with predation and plant chemistry

The fact that food choice reduces decisiveness provides support for the hypothesis that food specialization, including acquired specialization (even if temporary), enables animals to make faster decisions. Since foraging is risky and generally reduces vigilance[21,33], faster decisions could provide a significant benefit and provide one of the bases for the evolution of narrow diets in insects. For insects, such risks are probably widespread[34] and emphasize the need to make rapid decisions, and to ensure that there is attentiveness to the feeding process to reduce handling times. The value of simplifying the neural message and/or the neural processing is apparent, and the value of specializing on a resource (anything) that provides strong cues is evident.

However, multiple sensory inputs are the rule, even in the case of apparently very simple behaviors, and the various inputs from the sensory systems are apparently weighted differently in different taxa, depending on whether they are diurnal or nocturnal, specialist or generalist, small or large. Stimuli may be additive, synergistic, or antagonistic, but the final message to be interpreted centrally must be unambiguous if efficient decision-making is to occur.

Each of the different sensory modalities, vision, olfaction, mechanoperception and taste, normally provides part of the overall signal for host or non-host among insect herbivores. In each processing system there are mechanisms for sharpening the sensory message that progresses to the central nervous system. Each involves 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].

Even so, there is a large gap between the amount of information relayed from sense organs and the capacity of the central nervous system to rapidly process it, and selective attention is critically important[20]. Generalists appear to integrate large quantities of sensory neural inputs and to effectively narrow their resource choices by increased attentiveness[8], sometimes for short periods[35], or by learning[36], while specialists are expected to depend more on sign stimuli representing the host, to which they have amplified sensitivity[9]. Among insects, generalist grasshoppers, with large numbers of generalist chemoreceptor cells and relatively large brains[37] contrast strongly with many other insect herbivore groups in which the specialist insect herbivores have fewer receptors predominate. These tend to respond to one or a few key characters that, when presented together or in rapid succession, clearly characterize the host[38]. If the effects of a small group of cues are more than additive (synergistic) at any level, a finely tuned signal from the host may produce a highly characteristic and conspicuous cue. For example, the cabbage butterflies are stimulated to select their hosts by very specific glucosinolates. If the cue used is widespread then the host range will be wide. For example, flower feeders that are generalists can use general floral odors, and those that feed on trees may use phenols such as tannic acid.

Among generalists, choices must be made among a larger group of potential foods and the bases for such decisions may have to be more diverse. In this case, more emphasis may be placed on particular nutrients, the balance of inputs and the whole suite of secondary metabolites. Extreme generalists may simply use the very widespread 6-carbon green leafy volatiles and depend relatively strongly on detecting basic nutrients that they require after they have made contact with the plant.

Since species with narrower host ranges are also most strongly deterred by the many non-host secondary metabolites, sensitivity to novel compounds that repel or deter them provides another avenue for simplification of the message of non-host as opposed to host. It can be argued that speed is ultimately important in a world full of predators and that, indirectly, as well as directly, predation could act as a selective agent in limiting diet breadth.

If speed is maximized in decision-making, or if there is some other reason for a time constraint, there may be a greater potential for making suboptimal decisions with respect to quality. Because it is probably difficult to make good decisions fast, either speed of decision or quality of decision may be compromised. For example, there is often a limited time for eggs to be laid by butterflies due to weather or a limited time to make a decision to lay an egg after landing due to predators on the host plant. In such cases a poor ability, due to neural limitations to integrate multiple sensory inputs is more likely to lead to mistakes, or at least to choices that are relatively poor.

For generalists there is probably a tradeoff between speed (efficiency) and accuracy (choosing the best food); individuals may be best at one or the other (Fig.2). Recent comparative studies have indicated that generalist caterpillars make quick decisions even when there is a choice[39], but they often make poor choices. On the other hand, grasshoppers make good decisions, yet speed is compromised if there is a choice[40].

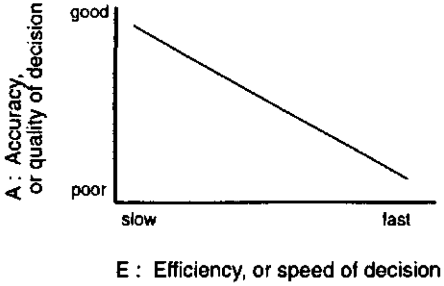

Fig.2. The tradeoff between Efficiency and Accuracy in host plant choice.

Plant chemistry has long been known to have great importance in the choice of plants[26], and is commonly considered largely in terms of plant defenses[41]. Here, I emphasize another element, the importance of specific and clear-cut signals in the efficiency of host selection, so essential to maintain vigilance. Many plant species with highly characteristic chemistry have relatively large proportions of specialist herbivores exploiting them[3], and perhaps this is not so much to do with having to adapt to the chemistry, as making use of it for its signalling value.

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