Host confusion and the evolution of insect diet breadths

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It is observed that many herbivorous insects develop well, or even better, on hosts which they will not use than on hosts they regularly use. We present a verbal model which explains this often imperfect correlation between host use and host suitability. Our model focuses on limitations in an insect's ability to perceive and integrate host-associated stimuli. We argue that confusion of "good" hosts with "poor" hosts results from an imperfect identification process and will result in selection for either a change in the behavioral response of an insect to host associated stimuli, or a change in the insect's ability to perceive and integrate these stimuli. Specifically, we argue that there are four evolutionary solutions for dealing with the confusion of "good" and "poor" hosts. (1) Insects may continue to use both hosts, despite selection against use of "poor" hosts. (2) Insects may evolve the machinery to distinguish "good" from "poor" hosts. (3) Insects may evolve physiological, morphological, or other characters which increase their fitness on the "poor" hosts. (4) Insects may delete the hosts which are difficult to distinguish from the diet, either by restricting oviposition to other plants currently utilized, or by shifting to a new host (or suite of hosts) which has a characteristic signature and is therefore distinguishable from poor quality hosts. This final option will result in insects avoiding oviposition on plants that are suitable for larval development.

It is often observed that many herbivores develop very well, or even better, on plants that they will not oviposit or feed upon than on plants they regularly use (Dethier 1954, Waldbauer 1962, Wiklund 1974, 1975, 1982, Hsiao 1982, Thompson 1988). Hypotheses proposed which may partially explain this imperfect relationship between host use and host suitability variously implicate predators and parasitoids (Lawton and McNeill 1979, Bernays and Graham 1988, Fox and Eisenbach 1992), plant apparency (Feeny 1976, Rhoades and Cates 1976, Wiklund 1984, Courtney 1986, Chew and Courtney 1991), phenology (Tahvanainen 1983, Straw 1989), abundance (Wiklund 1982), or reliability (predictability) (Futuyma 1976, Cates 1981, Wiklund 1982, Chew and Courtney 1991, Lalonde and Roitberg 1992),

and the interaction between plant chemistry and the neuro-physiological capabilities of insects (Ehrlich and Raven 1964, Smiley 1978, Jermy 1984). However, it is likely no single hypothesis is sufficient to account for apparent maladaptive host use patterns (Bernays 1991a).

One assumption which is frequently implicit, yet unstated, in models of host choice and diet selection is that the organism is able to discriminate perfectly between food types (Stephens and Krebs 1986), and bases its decision on this knowledge. This may be a safe assumption for the vertebrates which are the frequent focus of diet choice studies (but see Getty 1985, Nonacs 1985). However, for most arthropods, perfect information may be a tenuous assumption which can lead to erroneous conclusions. Here, we assume that insects cannot discriminate perfectly among all food types (Fine-Levy et al. 1989). The ability of feeding preferences of herbivorous insects to be induced among some pairs of hosts, yet not others, supports this assumption (e.g. de Boer and Hanson 1984). We propose that this inability to discriminate may produce patterns of host use that are qualitatively in agreement with observed patterns of host use by herbivorous insects.

Here, we suggest that apparent sub-optimal host choice decisions by herbivorous insects may be one result of natural selection favoring avoidance of poor quality plants. We argue that many herbivorous insects may be doing the best they can while operating under limitations in their ability to perceive and integrate host stimuli. We present a simple verbal and graphical model describing host choice when insects have access to limited and often confusing information. In addition to formalizing our hypothesis, our model indicates some areas in insect and plant biology for which we still lack the basic information necessary to understand insect feeding and oviposition decisions.
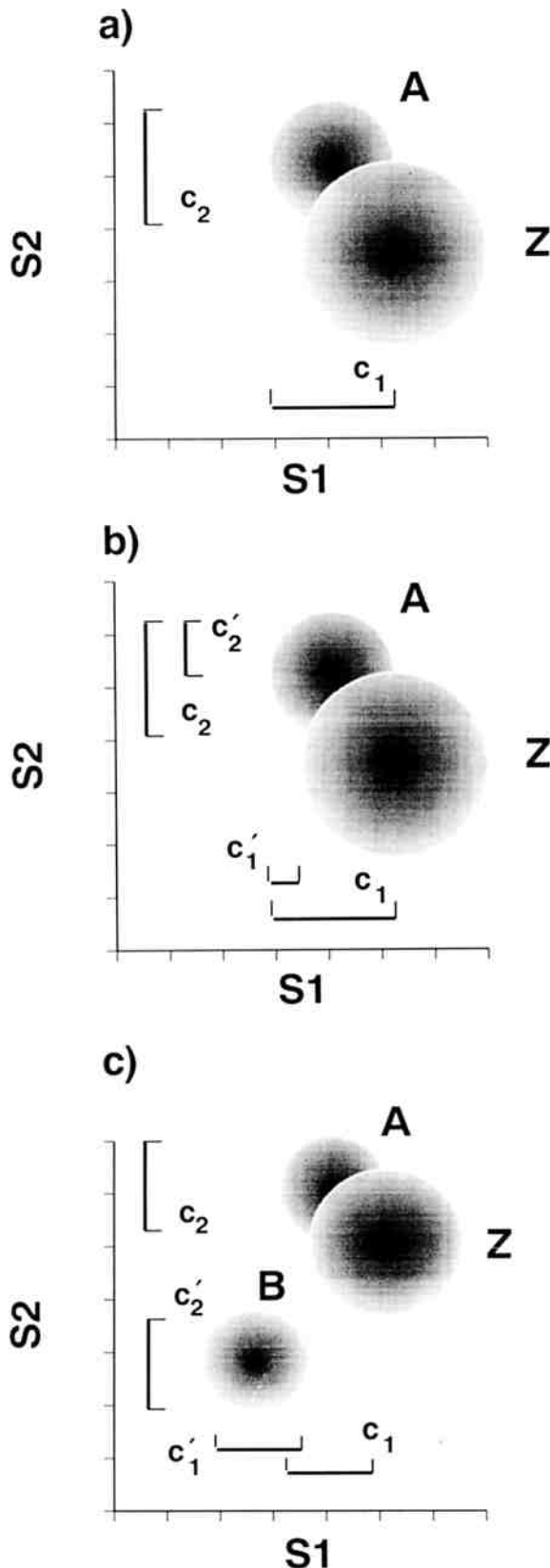
A basic model incorporating information processing limitations

In our model, when the insect encounters a potential host, either from a distance or by direct contact, it is exposed to a complex array of host-associated stimuli (chemical, visual, or tactile), rather than a single host-associated stimulus (Dethier 1976, Fine-Levy et al. 1988). Following Getz and Page (1991), we refer to these complex mixtures of stimuli as *signatures* because they provide information on the identity and physiological state of the potential host. The signature, or set of stimuli an insect encounters, can be thought of as points in n-dimensional space, where n is the number of all stimuli present in an environment, with the axes representing the relative concentration or intensity of the *i*th stimulus (Fig. 1a).

The signature that a plant expresses can vary both spatially (e.g., among parts of a plant or with distance from a plant) and temporally (e.g., due to quantitative and qualitative fluctuations in chemical composition of plant volatiles as a function of temperature, plant age, or plant physiological state). Following Getz and Page (1991), a signature has a space and time-varying representation $S(z,t) = [s_1(z,t),...,s_n(z,t)]$ in a signature space where $s_i(z,t)$ represents the absolute concentrations of the *i*th compound (or the intensity of the *i*th wavelength, etc.) at location z and time t (Fig. 1). Thus, we can define the signature as perceived by a receiver as the average value of a signature $S(z,t)$ perceived over a sampling interval T: S_{zt}. We will assume that all useful information is contained in S_{zt}.

Once an insect has encountered a signature, it must determine whether these stimuli represent a suitable host for feeding or oviposition (i.e., it must correctly identify the host). The insect is faced with the problem, however, that some plants which differ dramatically in their suitability as hosts may have similar signatures. Assume first that when an insect encounters a potential host, it encounters the perceived signature S_{zt}, which it identifies as the signature corresponding to plant U_i

Fig. 1. Signatures of hypothetical plants A, B and Z in two-dimensional space, where the axes represent the concentration or intensity of each stimulus. Each signature has a space- and time-varying representation $S(z,t) = [s_1(z,t),...,s_n(z,t)]$ in a signature space, where $s_i(z,t)$ represents the absolute concentrations of the *i*th compound at location z and time t. Variation in s(z,t) is represented in the figure by the variation about the median stimulus intensity. c_1 and c_2 represent the ranges of stimulus intensities (concentrations) which illicit a receptor cell response in our hypothetical insect. (a) Signatures of A and Z are not reliably distinguishable based on the responses of c_1 and c_2 because of the overlap of signatures. To reliably distinguish these signatures, a shift in the sensitivity of c_1 or c_2 is required, such as the shift to c_1' or c_2' (b). If another "good" host is available, such as plant B (c), a shift in either c_1 or c_2 may result in rejection of both plant A and Z, and acceptance of B.

(whether by comparison with a memory template or some other mechanism), where j = 1,...,N (Getz and Page 1991). Thus, $P(S_j)$ is the probability that a randomly selected plant has a perceived signature S_{zt} which results in classification of the plant as U_j (whether correctly or incorrectly). Our first question of interest, then, is: What is the probability that an insect will correctly classify a plant?, or, What is the probability that a randomly selected plant, classified as plant U_j, is actually plant U_j?

Let us define $P(U_j)$ as the probability that a randomly selected plant is plant U_j, and let $P(U_j|S_j)$ be the probability that, given that a perceived signature S_j, the plant is actually U_j. Thus, the probability that a perceived signature S_j is *incorrectly* classified as U_j (i.e. the plant is not U_j), is $1 - P(U_j|S_j)$. By Bayes' formula, we find that:

$$P(U_j|S_j) = \frac{P(S_j|U_j) \times P(U_j)}{P(S_j)} \tag{1}$$

where $P(S_j)$ is the probability that a randomly selected signature S_{zt} will be classified as U_j (correctly or incorrectly), and $P(S_j|U_j)$ is the probability that the encountered host U_j, expresses a signature S_j.

For simplicity, first consider a two plant situation, where plant U_1 is a host, and plant U_2 is not a host. Using our definitions from above, $P(S_1|U_1)$ is the probability that an individual of plant species U_1 produces a signature S_{zt} which is classified as plant U_1. Similarly, $P(S_1|U_2)$ is the probability that an individual of plant species U_2 produces a signature S_{zt} which is classified as plant U_1 (incorrectly). We can now rewrite Bayes' theorem (eq. 1) as:

$$P(U_1|S_1) = \frac{P(S_1|U_1) \times P(U_1)}{P(S_1)} \tag{2}$$

By expanding the denominator we find:

$$P(U_1|S_1) = \frac{P(S_1|U_1) \times P(U_1)}{P(S_1|U_1) \times P(U_1) + P(S_1|U_2) \times P(U_2)} \tag{3}$$

where $P(S_1|U_1) \times P(U_1)$ is the probability of encountering a signature S_1 which is originating from an individual of host U_1 and $P(S_1|U_2) \times P(U_2)$ is the probability of encountering a signature S_1 which is originating from an individual of host U_2. Dividing both the numerator and denominator by $P(S_1|U_1) \times P(U_1)$, we get:

$$P(U_1|S_1) = \frac{1}{1 + \dfrac{P(S_1|U_2) \times P(U_2)}{P(S_1|U_1) \times P(U_1)}} \tag{4}$$

From Bayes' theorem, we have found that the probability that an insect will correctly identify a plant, after

perceiving a signature, is dependent on the ratio of the abundances of the two hosts, and the relative proportions of each host that express a signature which is identified as U_1. Thus, the rarer encounters with U_1 are relative to encounters with U_2, the larger the denominator, and thus the smaller the probability that a plant which is identified as U_1 is actually U_1 (i.e., the larger the probability of mistakenly classifying a plant which is not U_1 as U_1). Similarly, the larger the proportion of U_2 plants that have signatures which are mistaken for U_1 (i.e., $P(S_1|U_2)$ is large), or the smaller the proportion of U_1 plants that have signatures which are classified as U_1 (i.e., $P(S_1|U_1)$ is small), the larger the probability that a plant which is identified as U_2 is *not* U_1.

Because insects will generally encounter more than two plant species in a habitat, we now expand eq. 4 to include N plant species and obtain the multiple host case:

$$P(U_1|S_1) = \frac{1}{1 + \displaystyle\sum_{j=2}^{n} \dfrac{P(S_1|U_j) \times P(U_j)}{P(S_1|U_1) \times P(U_1)}} \tag{5}$$

Note that when only plant U_1 produces a signature which is classified as U_1, such that $P(S_1|U_j) = 0$ for all j not equal to 1, then $P(U_1|S_1) = 1$. If $P(S_1|U_j) = 0$ for all plants the insect may ever encounter, then no confusion of plant identity should result.

Imagine a hypothetical population of potential hosts. Assume that plant species A is a "good" host, and that all other plants are "poor" hosts. We can now create a simple scenario which illustrates our main points. Assume plant A and Z have very similar signatures, and are thus nearly indistinguishable from each other. At time t = 0, plant Z is very rare (or absent) in a particular habitat, such that selection favors individuals that oviposit on plant A. However, plant Z later increases in abundance (or is introduced; e.g., Chew 1977), and the frequency with which the insect mistakes Z for A, and thus deposits eggs on Z, becomes large. These eggs laid on plant Z will have low fitness, and selection will favor females which avoid plant Z. However, because Z is confused with A, females selected to avoid Z are also selected to avoid A.

We now argue that there are at least four potential evolutionary solutions to the problem the insect faces:

(1) Plants A and Z may both be retained in the diet, possibly because the expected fitness when using both A and Z is greater than if the insect shifts to a new suite of hosts or deletes A from its current suite of hosts.

(2) The insect may evolve the machinery to distinguish A from Z. This might occur in two ways. (a) The sensitivities of the insect's peripheral receptors may be refined (Fig. 1b), thus reducing the overlap between signatures of the two plants. However, because stimuli concentrations or intensities vary within plant populations, a reduction in the range of stimuli to which a

receptor is sensitive may carry the cost of reducing the probability that plant A is actually identified as plant A ($P(S_j|U_j)$ decreases). Thus, due to intra-specific variation in signatures, an insect may consistently reject some portion of the individuals in a plant population even though these individuals are suitable hosts (e.g., Karban and Courtney 1987). (b) The number of stimuli an insect centrally processes when comparing plants A and Z may be increased, decreased, or shifted (changing the dimensions of signature space in which the insect is sensitive). This may require a change in receptor structure such that new information is detected by the peripheral nervous system, or a change in neural integration pathways such that information which is already available at the peripheral level is utilized centrally. One possible result of a shift in signature space is that insects may converge on components of plants' signatures which are highly reliable indicators of plant identity – a suite of components for which $P(U_j|S_j)$ is approximately 1, such as salicin in willows (Rank 1992). If the insect converges on components of plant signatures which are highly reliable indicators of identity, this may ultimately result in a reduction in the number of stimuli an insect uses to classify hosts.

(3) The insect may evolve physiological, morphological, or other characters which increase its fitness on plant Z. Although this option may not be uncommon, trade-offs in fitness across hosts, such that insects can not be simultaneously adapted to all hosts (Levins and McArthur 1966), may often prevent insects from attaining high fitness on both hosts simultaneously. These trade-offs may be physiological (Via 1991), morphological (Bernays and Chapman 1986, Moran 1986a, b, Kennedy 1987, Bernays 1991b), or behavioral (Rausher 1985), and they may be expressed as trade-offs in performance (Gould 1979, Fry 1990, Via 1991, Fox 1993), rates of predation (Bernays and Graham 1988, Bernays 1991a), or some other character which influences fitness.

(4) The insect may shift to a new host, plant B, on which it may have lower fitness than on A, but which has a more unique signature and is therefore distinguishable from poor quality hosts (Fig. 1c). Or, if the insect already utilizes B, plant A may be deleted from the diet such that the insect is now utilizing only B. This may be expected to occur when females which oviposit on A (and thus Z) have lower fitness, on average, than females which ignore A (and thus Z) in favor of B. Repeated events of this latter type may result in large reductions in diet breadth, over evolutionary time, and may eventually lead to diet specialization.

Which of the above evolutionary trajectories the insect population will be likely to follow will depend on the amount of genetic variation present for all characters involved, the relative fitness of the various insect genotypes on the plants involved, and the relative abundances of the plants involved.

Other scenarios may involve evolutionary changes in plant chemistry. For example, a poor host, Z, may initially be common but easily distinguishable from the preferred host, A. However, over evolutionary time the signatures of A and Z may converge (whether via selection or drift), such that the probability of confusion increases. A good host (e.g., plant A) may even be selected to mimic a poor host (e.g., plant Z), which is not utilized by the insect. The result is that the insect is faced with the same problem as discussed above.

In the preceding discussion, we have defined plant Z as a "poor" host which is confused with "good" hosts. However, if we restrict our discussion to cues which are used to locate plants from a distance, plant Z could instead be a population of plant species emitting signatures which, when found together, are confused with the signatures of "good" hosts. In this case background sensory noise resulting from sympatric non-host species could produce the problems discussed above.

Thus, our simple conceptual model assumes that pre-existing sensory biases and limitations in either the ability to respond to stimuli, or the ability to centrally integrate these stimuli, limits the evolutionary options an insect has available when responding to selection for avoidance of poor hosts. We thus argue that it is possible that herbivorous insects may drop suitable hosts from their diet when such plants are difficult to discriminate from unsuitable hosts.

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