

## IDEA

## Reducing ambiguity in describing plant–insect interactions: “preference”, “acceptability” and “electivity”

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### Abstract

Ecologists and evolutionary biologists have a common interest in plant–insect interactions. Ecologists develop terminology describing patterns of association between plants and insects, while evolutionary biologists use the same words to denote potentially heritable traits of individuals. Use of the same terms to describe both traits of the interaction and traits of the organisms hinders communication. An example is “preference”, often used by ecologists to denote properties of the plant–insect interaction and by behavioural or evolutionary biologists to denote insect traits. The existing term “electivity” could be incorporated into the lexicon of plant–insect interactions to supplant the ecological use of “preference”. The term “preference” would then denote a behavioural trait of the insect. The mirror-image trait of the plant would be “acceptability”. This could be a step towards a common terminology that would be usable by both ecologists and evolutionists.

### Keywords

Acceptability, electivity, insect, plant, preference.

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### INTRODUCTION

Patterns of association among plants and insects can be described entomocentrically as diets of particular insects (Thompson 1993; Futuyma *et al.* 1995) or phytocentrically as herbivore guild structure on particular plants (Root 1973; Simms & Rausher 1989). No matter how they are described, they are principally traits of the plant–insect interaction, not of the interacting organisms (Singer & Parmesan 1993). As such, they should be described in terms that make it clear that they are not traits of individuals. However, described they must be, since they often comprise the most ecologically relevant measures of patterns in the field. We also need to describe traits of plants and insects that influence the generation of these ecological patterns, since such traits are required for evolutionary models. Below, I argue that the current usage of “preference” and “acceptability” is inconsistent, and that “preference” is used as a trait both of the insect and of the interaction.

### PREFERENCE DEFINED AS A TRAIT OF THE INSECT

The term “preference” implies behaviour. If “preference” were used as a behavioural trait of an insect, the

insect could be regarded as preferring plant A over plant B if an encounter with A were more likely to result in feeding or oviposition than an encounter with B. If two insects in the same motivational state differ in their likelihoods of accepting the same plants, then they differ in their preference for those plants. This is a qualitative definition. It can be rendered quantitative by defining an insect’s preference for a particular set of plants as its set of likelihoods of accepting those plants, measured either across all motivation states or at a specified level of motivation (Singer 1986; Singer *et al.* 1992). When defined in this manner, preference is a behavioural trait that can be measured experimentally and compared among individual insects. Although it has no meaning outside the context of a specified set of plants it is not directly sensitive to changes of the density or dispersion of those plants.

### ACCEPTABILITY DEFINED AS A PLANT TRAIT

If “acceptability” were used as a plant trait, it could be the set of likelihoods that a plant will be accepted for feeding or oviposition by a specified insect or set of insects that encounter it. This would be a mirror-image of the definition of “preference”.

## CURRENT USAGE OF "PREFERENCE" AND "ACCEPTABILITY"

Although most biologists would, if asked, state that "preference" is a trait of insects and "acceptability" is a trait of plants, current usage is inconsistent in this respect. I am not accusing writers of failing to understand their own work, but of describing it in ways that could confuse readers, especially those in different disciplines. Here are some quotes from recent papers, each with a comment showing how the phenomenon would be described using the terminology developed here.

**1** Karban & Myers (1989), in their review of plant induced responses, defined such responses as "changes in plants that affect insect preference or performance". This usage has been generally adopted and is explicit in recent publications on induced defense. Agrawal (1998) writes: "induced plant responses reduce the performance or preference of herbivores". However, it is the plant that changes, not the insect. If an induced response deters insect feeding, then the insect prefers plants that are not so induced, and there is no implication in Karban & Myers' definition that this preference might change. Therefore, using the terminology developed here, induced responses would be described as changes in plant acceptability for insect feeding or changes in plant suitability for insect development.

**2** "Nutritional stress due to prolonged ingestion of the inferior food, mesquite, did not increase the acceptability of mulberry" (Bernays *et al.* 1997). In this example the insect suffered the nutritional stress, and any changes occurred in the insect, not in the plant. They would be described as changes of preference and/or motivation, motivation being the general level of willingness to feed or oviposit, without reference to specific resources (Singer *et al.* 1992).

**3** "Adult (insect) experience can alter the relative acceptability of host plants to ovipositing *H. armigera*" (Cunningham *et al.* 1998). Here, again, the change is in the insect, not the plant. Motivation was controlled in these experiments, so this is a change in preference.

**4** "Plant resistance to insect herbivores may derive from traits influencing herbivore preference, traits influencing the suitability of the plant as a host, or both" (Horner & Abrahamson 1992). This quote describes preference explicitly as an insect trait but uses it as a plant trait, and places it in the same category as host suitability.

## HOST USE AND ELECTIVITY: PROPERTIES OF THE INTERACTION

1

The term "preference" has been defined (Hassell & Southwood 1978; Crawley 1984) as the proportions of

different food items in the diet relative to the proportions of these same items that are available in the habitat. This ecological definition is identical with that of "electivity" (Ivlev 1961), which could supplant "preference" for this particular use. A related term, "host use", refers to the proportions of items in the diet without reference to their availabilities (Singer 1986). Below are three stylized examples, the first two modified from a previous account (Singer 1986), to show that both use and electivity are sensitive to changes in plant dispersion, plant density and plant quality, but preference is not affected by such changes. For this reason it should be helpful to view host use and electivity as properties of the plant-insect interaction, not as traits of insects. In the examples below, it is assumed for simplicity that neither the plants nor the insects are changing. Plants show no induced responses and the (postlighting) oviposition preferences of insects are fixed. The assumption of fixed plant and insect quality helps us to describe events that occur over very short time periods, but is not crucial to the concepts in any general sense.

*Example 1* If an insect is equally likely to accept two different plants, A and B, upon encountering them, it has no preference between those plants by the behavioural definition of preference. The relative use of plants A and B will then be determined by the relative rates at which A and B are encountered. Encounter rate is influenced by ecological properties of plant populations and communities as well as by those of individuals. For example, one factor that affects encounter rate is dispersion. If the overall densities of two plants are identical, they may still differ in dispersion. When they do, a randomly moving insect will encounter the more clumped plant less often (Hamilton 1971; Mackay & Singer 1982; Stanton 1982). If the insect has no behavioural preference, it will feed more often on the less clumped plant, generating an "apparent preference" for this plant (Mackay & Singer 1982). Any changes in plant dispersion without changes in mean density will change both host use and electivity, even though the plants have not changed in quality and the insects still have exactly the same preference (Singer 1986). Thus, both use and electivity are more sensitive than preference to changes in plant dispersion.

*Example 2* When a preferred host and a lower-ranked host grow in juxtaposition, most insects encounter both of them while deciding on which to feed. They then accumulate on their preferred host. As the spacing of the resources increases, many of the insects encountering the lower-ranked host have not recently experienced their preferred host, and their tendency to remain in patches of the low-ranked host may increase (Kareiva 1982). Thus, as spacing of host patches increases, electivity and host use both change and the distribution of insects between the

two hosts depends less on behavioural preference and more on the population dynamics on the two resources (Singer & Thomas 1996). In the absence of learning, however, behavioural preference remains constant, because of the way in which encounter and motivation are incorporated into its definition.

*Example 3* Even when no learning occurs, host density can affect both host use and electivity (Rausher 1983). Any natural reduction of host density sufficient to reduce the rate of feeding or oviposition will raise the mean motivation of searching insects. If the insects behave like those studied by Pilson & Rausher (1988) or Singer *et al.* (1992), the increase in motivation will render encounters with the less-preferred host more likely to result in feeding/oviposition. Thus, such a reduction of density, even with no change in the relative frequency of different host types, would alter both electivity and use. Using the definition of preference suggested here, preference would not be changed because it is a separate trait from motivation. A detailed advocacy of conceptual separation between preference and motivation, and an example in which these traits were measured separately in the field, is given elsewhere (Singer *et al.* 1992).

The effects of host density and dispersion in these three stylized examples show that electivity and use are closer than preference to being traits of the plant/insect interaction rather than traits of individuals, since they are sensitive to changes of traits other than the quality of individual plants or insects. For these reasons it is useful to classify host use and electivity as traits of the interaction and preference and acceptability as traits of the insects and plants, respectively. A practical demonstration of this was given by Singer & Parmesan (1993), who compared one insect species and two plant species between two sites where electivities were very different. They found that the mechanism producing geographical variation of electivity was twofold: insects showed genetic variation of preference among sites and plants showed genetic variation of acceptability among sites. At one site, a plant species was rarely used by the insect partly because the local insect population tended to prefer a different plant species and partly because local plants were less acceptable (to insects from either site) than plants from the conspecific population that was used by the insects. So the observed variation in electivity was clearly an emergent property of the plant–insect interaction, since it resulted from variation among both insect and plant populations. This study applies an egalitarian treatment to variation among plants and variation among insects. However, the moral from this result is that, even when a study concentrates only on variation among insects, it is appropriate to describe the patterns of plant–insect association observed in the field as electivities, and then

ask to what extent these patterns are generated by variation of insect traits (Kuussaari *et al.* 2000).

The situation in nature is usually more complex than in the stylized examples developed here. Insects may learn, and may change preference in response to encounter rates (Jaenike 1982; Prokopy *et al.* 1982; Hoffman 1985; Cunningham *et al.* 1998). At the same time, plants may change in acceptability due to their individual history of attack by insects (Karban & Myers 1989; Agrawal 1998). It is important to know whether change is occurring in one organism or both. This may not always be possible to ascertain. However, if we lack the terminology to describe these possibilities clearly we are less likely to devise experiments that illuminate them. When preference is modified by learning, it may respond to both the absolute and the relative rates of encounter with different hosts. Insertion of learning into Examples 2 and 3 above would add complexity by generating preference-mediated effects on electivity of both host density and dispersion.

I hope that the approach suggested here will clarify problems that hinder communication among workers in plant–insect interactions. In theory, there is no reason why a common terminology cannot be adopted for behavioural, evolutionary and ecological work. Alas, in practice, our vocabulary may be too depauperate for this to be achieved without coining new jargon. Advice on this question would be welcome!

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