

CHAPTER 1. THEORETICAL PERSPECTIVE ON
BUTTERFLY-HOST PLANT INTERACTIONS

1.1 Introduction

During the past century hundreds of articles have been published on insect-host plant interactions. These have primarily dealt with natural history, but many are theoretical as well (for bibliography, see Brues 1946 and Gilbert 1976). The following discussion selects some of the highlights of this literature which are particularly relevant to the butterfly-host plant interaction. This discussion shares one strong bias with currently popular theories about the interaction of butterflies and their host plants: the emphasis on host plant "secondary products" biochemistry. Until recently, this bias has been justified, because host plant biochemistry tends to set the interaction apart from general ecological theory. Due to a high degree of host specificity, most butterflies appear to select host plants on the basis of secondary products chemistry rather than on the basis of general ecological considerations (see discussion below). Other groups of insects are less host-specific, and with these insects ecological theories have progressed (Gilbert 1976). However, with regard to herbivores such as butterflies, purely ecological data and theory apart from natural history observation is quite scarce (Gilbert and Singer 1975).

1.2 Early Contributions

The foundations for the study of insect-host plant relationships were clearly delineated by Charles T. Brues in the 1920's (Brues 1920; 1924). Brues used three categories of phytophagous insects which are still widely used. Insects which feed on a single species of host plant, Brues called monophagous, while insects which feed on a definite few host plant species and those which feed upon a wide variety of host plant species are called oligophagous and polyphagous, respectively. These terms actually represent points along a continuum of specialization. They range from specializing on a single type of plant tissue of a particularly sized and situated subset of a plant species, to generalized feeding on plants in many families (Gilbert and Smiley 1978). Most insects are monophagous or oligophagous.

Brues also recognized the relationship between larval and adult feeding preferences. In most insects the adult female is the agent for host plant selection and larvae are obliged to grow and develop where eggs were placed by the adult female. Thus, as Brues pointed out, oviposition preference on the part of the adult female insect must be compatible with larval ability to feed upon a given host plant. However, Brues made the important point that "any change in the instincts of oviposition compatible with larval tastes might quickly become a definite characteristic of the species." In other words, the adult females can readily evolve to

use any subset of the host plants that are palatable to the larvae.

Brues also realized the importance of host plant chemistry to insect oviposition choice. However, he seemed to regard host plant chemicals as serving more as behavioral cues to host plant selection than as possible toxic feeding deterrents. Brues concluded that instinct rather than physiological adaptation is the determining cause of food plant selection. He is not clear, however, as to what factors in an insect's environment will influence the evolution of these instincts.

Brues showed an awareness of the possibility of insect-host plant evolutionary interactions. He referred to the published lists of food plant records for North American butterflies, and observed a striking pattern in which butterfly taxa (including genera, subfamilies and even families) are restricted in feeding to single host plant families or groups of related plant families. This he referred to as "parallel evolution" and Brues stated that it "must be restricted to a development of undesirable attributes on the part of the plants and adaptations on the part of the insects to overcome such barriers to feeding." Based on his examination of several insect-host plant relationships, Brues concluded that this "parallel evolution" is more likely between higher taxa than between single species.

1.3 Chemical Basis of Behavior

Between the 1920's and the present, the behavioral mechanism

by which host plants are found by ovipositing insects was investigated in great detail. This is best exemplified in the writings of Dethier (1947, 1954). It was found that insects have highly developed chemical sensitivities by which they can detect and respond appropriately to very low concentrations of certain specific chemicals. Further, these chemicals were shown to function in nature as behavioral attractants or repellants. The anatomy and physiology of the sensory cells was investigated, resulting in a remarkably well-defined system of structure and function. For example, it was established that the foretarsal "drumming" behavior exhibited by cabbage butterflies during oviposition searching functions to bring certain foretarsal chemosensory hairs into contact with plant leaves; when mustard oil glucosides are present, oviposition is stimulated. Because these chemicals are characteristic of the host plants used by the butterfly, this causes the butterfly to oviposit on the correct type of host plants (Ma and Schoonhoven 1973). It was also found in cabbage butterflies that specific chemicals can induce larval feeding on otherwise unacceptable food plants; the chemicals act on chemosensory cells in the mouthparts of the larva. Thus, larval feeding behavior was shown to be controlled in some cases by the presence or absence of specific host plant chemicals (David and Gardner 1966).

Since the 1950's, work on the sensory physiology of host plant selection has broadened considerably. It now appears that the simple "chemical attractant" syndrome described above is the

exception rather than the rule, and that chemical/behavioral choices are made on the basis of the relative strengths of a great many chemical (or other) sensory stimuli rather than the presence or absence of a specific chemical (Dethier 1976). Thus, a cabbage butterfly can select a group of plants that are generally suitable by the presence of mustard oil compounds, but can choose among these "potential" host plants on the basis of many other cues (Jones 1977). This is important because it explains why many insects show a remarkable "botanical instinct" and are able to identify related plant taxa even when no single chemical or other characteristic is known to be held in common by all the plants (Brues 1920, Dethier 1976).

Since the 1940's, the number and diversity of secondary plant compounds known from plant leaf tissues increased exponentially. This knowledge helped to stimulate the search for behavioral attractants and repellents discussed above. It also resulted in a slightly different idea, that these compounds were toxic to the majority of herbivorous animals and may have evolved as an evolutionary response to herbivore pressure (Frankel 1959). For centuries it has been known that some secondary plant compounds are toxic, but the realization during the 1950's was that the majority of plant leaves appear to have these compounds. Thus the hypothesis was advanced that host plant choice by insects is determined by host plant chemistry, not only proximally in terms of behavior, but ultimately, in terms of selection for avoidance of dangerous plant

toxins (Whittaker and Feeny 1971). Today, this hypothesis remains largely untested. One difficulty has been that it is difficult to distinguish between a behaviorally negative response (to plant chemicals) and a case of actual poisoning by the toxin; both may result in reduced feeding and growth by the insect.

1.4 Coevolution of Plants and Insects

During the 1950's, experiments on the genetics of plant resistance and herbivore parasite virulence led to a model of "gene-for-gene" coevolution. The model consists of resistance alleles in the plant and counter-resistance (virulence) alleles in the parasite. These coexist in a stable steady-state equilibrium (Mode 1959). The idea of a coevolutionary balance between host plant resistance and herbivore "virulence" was used by Ehrlich and Raven (1964) to explain the observed pattern of butterfly/host plant taxonomic relationships. This pattern, which was outlined forty years earlier by Brues, is that certain groups of related butterflies feed only on certain groups of related plants (see above). Brues asserts that "parallel" (or co-) evolution is possible between groups of butterflies and host plants; what Ehrlich and Raven postulate is that not only do the groups "coevolve," but that the pattern owes its origin to the simultaneous coevolutionary radiation of host plant groups and their associated butterfly groups from ancestral butterfly/host plant pairs of species. Ehrlich and Raven

go on to postulate that host plant secondary compounds have evolved in response to these, and perhaps other herbivores, and that the great diversity in butterflies and higher plants derives from the tendency for host plants to diverge in secondary chemistry in order to avoid coevolved herbivores. This theory has been difficult to verify experimentally. One problem is that "coevolution" is often defined to mean the concurrent evolution of single host and herbivore species. However, as Brues stated, most cases of parallel evolution between insects and their host plants seem to be at the level of higher taxa such as genera and families, while at the species level specificity may not be great enough to permit sufficiently long coevolutionary relationships. Thus, the gene-for-gene model of coevolution may be inadequate to account for the kind of patterns discussed by Ehrlich and Raven.

Recent work insect/host plant coevolution has concentrated on single species relationships. Morphological structures on plants which are specifically anti-herbivore are now well-documented for some species (Benson et al. 1976; Gilbert 1975). It has proven difficult to demonstrate that any particular chemical is directed against a specific herbivore. Seemingly, most toxic anti-herbivore chemicals are effective against most plant pathogens and herbivores, and since plant species invariably have more than one herbivore it is difficult to prove that a chemical is specifically directed against a single herbivorous species.

1.5 Strategies of Plant Chemical Defense

In the early 1970's it became apparent that there were certain trends in the distributions of secondary plant compounds (Cates and Orians 1975; Otte 1975; Futuyma 1976). Feeny (1976) has proposed that there are two strategies a plant can take to avoid herbivory. One is toxicity, as exemplified by nicotine alkaloids or mustard oil glucosides, while the other is to store large amounts of tannins. Tannins are not in themselves toxic, but they act to make proteins indigestible to herbivores. The "toxicity strategy," Feeny argues, should be much cheaper for the plant to produce than tannins, by virtue of the low concentrations necessary for toxicity to be effective. Feeny proposes that the "toxin strategy" is sufficient if the plant is so ephemeral or rare that host-specific herbivores cannot build up dense populations on the plant and defoliate it. This follows from the supposition that because specialized detoxification mechanisms are necessary, only specialist herbivores can eat large amounts of a toxic plant and survive. He then proposes that this strategy is insufficient if the plant is common and readily available to herbivores. In this case specialist herbivores can build up high enough population densities to seriously damage the plant. The second strategy of storing tannins will reduce the nutritive value of the host plant to all herbivores, including specialists. This defense probably cannot be easily avoided. It has not yet been conclusively demonstrated that tannins cannot be counteracted, since the organisms investigated

have not been "tannin-specific" herbivores. Nevertheless, Feeny (1976) and others (Rhoades and Cates 1977) support the general hypothesis by demonstrating that many ephemeral plants or plant tissues lack tannins, while late-successional plants often store large quantities of tannins. Feeny also proposes that plants with tannins would be as edible to generalist herbivores as to specialists, and that therefore the tannin-producing plants should possess more generalist herbivores, while toxin-producing plants would have more host-specific herbivores. This hypothesis remains untested.

1.6 Evolution of Host Specialization

Virtually all of the modern theories about insect-host plant relationships depend on the assumption that host-specific insects have some competitive advantage over generalist species and that this potentially leads to host specificity (Dethier 1954; Whittaker and Feeny 1971; Feeny 1976). The only direct evidence supporting this assumption is the study by Krieger, Feeny, and Wilkinson (1971) which demonstrates that host-specific insects digest their food "more efficiently" using a lower activity of digestive enzymes than generalist species. However, other studies (Slansky 1976) have not supported this "digestive efficiency" hypothesis, in spite of its plausibility.

Dethier (1954) discusses at length how host plant specialization could arise from polyphagy, a process which logically depends on the advantages of specialization. However, even though he states

firmly that specialist types have a competitive advantage over generalists, he does not make use of this assertion in discussing the evolution of monophagy; perhaps this is due to a lack of experimental data. Instead, he argues for a process involving the formation of host races by learning and habituation, which eventually lead to reproductive isolation and speciation. While this pattern of speciation has undoubtedly occurred in some insects (Dethier 1954; Bush 1969, 1974), the role of learning and habituation is questionable, and in any case a great many insects may not fit the assumptions of possessing sympatric host races or selecting host plants on the basis of learning and habituation. Most butterflies (except those in the family Lycaenidae; Gilbert 1976) do not fit Dethier's scheme very well (Gilbert and Singer 1975).

Singer (1971) discusses the evolution of host plant preference in Euphydryas butterflies. He argues that some host plants are intrinsically more suitable than others for a given insect population, and that the insects will evolve to prefer those plants by differential survivorship and fecundity. The quality of the different host plants is determined not by larval feeding ability (which results from host plant chemistry), but by "cryptic" ecological factors correlated to host plant choice. From his and other studies, the idea is gaining prominence that host plant selection may depend on non-chemical components of host plant suitability (Gilbert 1976)

1.7 Prospectus

As stated in the introductory paragraph, there has been in the past a strong bias toward biochemical aspects of the study of butterfly-host plant interactions. Extremely important information and theory has resulted from this approach. However, this bias is no longer justified. At present there are many very interesting and potentially powerful hypotheses derived from the biochemically-oriented investigations, but field studies and ecological theories are lacking to evaluate them. Only very recently have ecological studies of butterfly-host plant interactions been forthcoming (Singer 1971; Chew 1975; Jones 1977), and few of these have addressed the hypotheses directly. Intensive studies are needed of the ecology of local populations with different histories, ecology, and biochemical properties (Gilbert 1976). This type of investigation is necessary to answer such important questions as (1) Why does an insect evolve to use a particular host plant or set of host plants? (2) What are the phenotypic and microevolutionary alternatives open to an insect population in exploiting the food plant resource? (3) What effects do insect herbivores have on host plant demography, i.e. what is the insects' selective potential? (4) What are the phenotypic and microevolutionary alternatives open to host plants in avoiding insect herbivores? and (5) What is the role of other ecological factors such as competition and predation?

This project, described in Chapters 2-5, was designed to

answer some of the above questions, with a combined field and laboratory study of several Heliconius butterfly species and their passifloraceous host plants (Benson et al. 1976). By investigating the distribution and abundances of host plants, the quality of host plants as perceived by the butterflies, and the behavioral responses of the butterflies to the host plants, I hope to develop a general understanding of the host plant ecology of these insects. Heliconius are very suitable for such a study.

The species investigated are very similar in overall behavior and morphology, thus simplifying the techniques required to study them, but they differ widely in their reproductive and oviposition strategies (see Chapter 3.2). It is therefore possible to test hypotheses about the butterfly-host plant interaction on several different species with known differences in behavior and ecology. This facilitates making correlations between insect oviposition behavior and host plant quality, distribution, and abundance. In addition, the taxonomy of these species is well understood, which allows the testing of hypotheses about the coevolutionary process.

The project was organized to provide the broad data base required to answer general questions about the ecology of the butterfly-host plant interaction. This has required sacrificing highly detailed, in-depth studies, but at all times I have tried to maintain a balance between breadth and depth of investigation. For example, some species have received much more detailed studies of their oviposition behavior than others, while other species received

no laboratory investigation at all due to logistical problems in obtaining and maintaining stocks. However, the overall result is more comprehensive and detailed than any previous ecological study of these butterflies.

The project will be presented as follows. Chapter 2 gives a broad overview of the ecology of Heliconius and Passiflora, which are considered independently of each other. Habitat structure is described, and the habitat "preferences" or "affinities" of the species of Heliconius and Passiflora are investigated. Absolute and relative abundances are calculated as well for each species. Even at this level of generalization there are significant patterns relating to niche differentiation and avoidance of competition and predation. In Chapter 3, host plant choice by female Heliconius, is discussed. The results will be interpreted by using the data on abundance and distribution in Chapter 2. This may help answer the question: How is host plant selection affected by host distribution and abundance? In Chapter 4 host plant palatability to the larvae is investigated. With this data it is possible to test hypotheses about the evolution (and possible coevolution) of host plant feeding specialization. Other aspects of host plant quality are explored in Chapter 5; in particular, the role of Heliconius predators and parasitoids is discussed. In Chapter 6 a synthesis of the material is presented. Extensive data and data analysis peripheral to the ideas discussed in the text are in the Appendices.