Evolutionary ecology of oviposition strategies

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Abstract

Finding and choosing a good site for oviposition is a challenging task for females of herbivorous insects, and her decision has far-reaching and profound consequences for the life history of her offspring. One of the most prominent features of host plant preference is that the range of host plants accepted for oviposition is often very narrow. The reason for this widespread specialization is a question that has puzzled researchers for many years, and even though interesting progress has been made, it still waits for a completely satisfying answer. The oviposition strategy of an insect is a complex trade-off between many, sometimes contradictory, factors, including host plant range, clutch size, host quality, the difficulty of finding hosts of sufficient quality, the chances of finding even better hosts, predation risks on her and her offspring, larval mobility and host-finding capability, microclimate, etc. Thus, although the female's prime goal may be to choose an oviposition site that maximizes offspring survival and performance the outcome is not necessarily a perfect match between female host plant preference and larval performance.

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7.1. Introduction

Most insect larvae are small and relatively immobile, so the ovipositing female often single-handedly makes the choice of larval food. This sets the stage for an interesting but complex problem. While choosing oviposition site, the female not only has to evaluate the suitability of the host as larval food, she must also take mortality risks into account, due to microhabitat and enemies. In addition, she must choose a strategy that maximizes search efficiency and host encounter rates, and she must decide on how long she should spend searching for the best host before accepting alternatives. Of course, she must also at all times ensure that she herself survives to lay her full complement of eggs. In short, the process of choosing oviposition sites must be a daunting task for a small insect. As there are so many variables involved, and so many insect species, it is understandable that the evolutionary solutions to this task will be manifold. It is the objective of this chapter to outline some of the generalizations that nevertheless can be made, as well as some of the important exceptions.

The subject of the chapter is enormous, and there will be some biases. A small fraction of the amazingly diverse group of insects stands for a lion's share of the available studies. The groups that have received most attention are typically conspicuous and easy to spot and follow or have a large economic impact, e.g. as agricultural pests. As most of these groups are herbivorous, there will be a bias toward plant-feeding insects as well.

7.2. Phylogenetic patterns

Comparative methods offer an increasingly rich set of tools to investigate the large-scale patterns behind insect oviposition strategies. Phylogenetic methods can be used to test for broad correlations between characters, investigate alternative historical scenarios, as well as to test specific hypotheses about historical sequences of events. The main limiting factor has been the poor availability of robust phylogenies with adequate resolution for the involved lineages. However, such phylogenies are slowly emerging, and as a consequence, so are studies using comparative methods to investigate the relationship between insects and hosts. Much of this work has been devoted to the questions of specialization, of conservatism in host associations and the role of host plant chemistry in determining the patterns of host use. The large and interesting issue of host specialization will be treated under its own heading below.

One of the earliest non-cladistic attempts at a broad comparative study of host use was Ehrlich and Raven's (1964) seminal study on the coevolution between butterflies and plants. The main conclusions from this paper were that most butterfly-plant associations are relatively specialized and that there is a general tendency for related butterflies to be associated with related plants. They also proposed a coevolutionary explanation for these patterns based on plant secondary metabolites and escape and radiation of the associated lineages. A more recent re-analysis of the butterfly-plant system using more robust phylogenetic methods confirmed the general patterns of high specialization and conservatism in the group, but concluded that these patterns could not have been caused by the coevolutionary process that Ehrlich and Raven proposed (Janz and Nylin, 1998). Coevolution may still be an important process in insect-plant interactions, but it cannot be the cause of these large-scale patterns.

Even though the influence of host plant chemistry on the patterns of host use is often substantial (Becerra, 1997; Wahlberg, 2001), other factors may also have significant effects, such as habitat choice (Anderson, 1993), plant growth form (Janz and Nylin, 1998; Beccaloni and Symons, 2000) and diapause pattern (Carey, 1994). Predation has also been shown to affect oviposition patterns in many species (Bernays, 1989; Stamp and Bowers, 1993; Eigenbrode et al., 1995) and could potentially affect phylogenetic patterns of host use (but see Keese, 1997).

A complicating factor for comparative studies of host use is to distinguish oviposition patterns from larval feeding patterns, which can often be quite different (see below). Host use in many phytophagous insects is really two characters, only partially correlated. At the same time, this complication offers an opportunity to understand how larval feeding capacities influence the oviposition strategies of the female. Following that reasoning, the complication has been turned into an advantage in a series of interesting studies on the history of host associations of the beetle genus *Ophraella* (Futuyma et al., 1993; Futuyma et al., 1994; Funk et al., 1995; Futuyma et al., 1995; Keese, 1998). By screening the species in the genus for genetic variation in host use traits they have been able to demonstrate a connection between present oviposition patterns and historical host use. Genetic variation for larval feeding and survival was typically found on plants that are used as hosts by close relatives (e.g. Futuyma et al., 1995). Present oviposition patterns and past colonization of novel hosts have thus been constrained by genetic variance for host use, which itself is

influenced by historical host use (e.g. Funk et al., 1995). Using a somewhat similar approach, Janz et al. (2001) showed that this phenomenon is not unique for leaf-feeding beetles. Larval survival on non-hosts in the butterfly tribe Nymphalini was biased towards plants that are used by other members of this group. In fact, almost all members of the tribe had some capacity to feed and survive on stinging nettles, the ancestral host plant of the tribe. Phylogenetic optimizations also showed a remarkably high number of colonizations and losses within the Nymphalini, certainly not conforming to the conservative pattern of host use found at higher levels in this same system. As a limited set of plant families was responsible for a majority of these changes in host use, it was concluded that there is non-independence in these patterns of host associations (Janz et al., 2001). Clearly, there is a historical component in the present patterns of host use, suggesting a complex interaction between "hidden" larval feeding capacities, oviposition preferences and host plant availability and suitability.

Phylogenetic studies on different levels of resolution and studies on preference variation within and between conspecific populations have reinforced this somewhat puzzling paradox regarding the flexibility of oviposition preference hierarchies. The *Papilio machaon* species complex of butterflies is associated with the same general set of plants (mainly Apiaceae, but also Asteraceae and occasionally Rutaceae), but differ in ranking and degree of specialization. Thompson (1998) showed how modest modifications in oviposition preference within a geographic mosaic of populations have resulted in the present pattern of host use among species in this group. Almost all studies that have investigated oviposition preference variation using individually controlled experiments have found significant individual variation within populations (Tabashnik et al., 1981; Rausher, 1983; Singer, 1983; Stanton and Cook, 1983; Thompson, 1988c; Janz et al., 1994; Bossart and Scriber, 1999; Sadeghi and Gilbert, 1999). Detailed studies on variation in oviposition preference in the butterfly *Euphydryas editha* have also revealed evidence for considerable differences in oviposition preference between populations in close geographical proximity (e.g. Singer et al., 1989; Radtkey and Singer, 1995; Singer and Thomas, 1996), painting a picture of oviposition preference as a relatively flexible trait allowing for rapid evolution of host associations. How does this conform to the conservative patterns found at higher levels? Janz and Nylin (2001) offered an explanation for this paradox, suggesting that the conservative pattern on higher levels are caused by the

fact that many changes in host associations tend to go back and forth between the same plants, masking a good deal of the dynamics at lower levels and on an ecological scale. Thus, oviposition preference may be ecologically and evolutionarily flexible and opportunistic, but only within certain constraints, set by the ability to feed and survive on the plants. This also suggests that, with enough knowledge of a system, we should be able to make predictions about future colonizations and host shifts, which could be of high importance for pest management and control.

7.3. Oviposition site selection

The process whereby an ovipositing insect approaches a potential host plant and decides whether to lay an egg on it or not involves several behavioural phases, and engages to varying degrees all insect senses. These phases include the choice of habitat, the approaching of a plant from a distance, the decision to land on the potential host or not, the decision to oviposit or not, and, when applicable, the size of the egg batch (e.g. Jones, 1991; Bernays and Chapman, 1994; Schoonhoven et al., 1998). It is important to emphasize at an early stage that the relative importance of the various host-finding stages and the senses used in each stage will vary considerably between species. Perhaps the most important behavioural distinction lies between pre- and post-alighting decisions, i.e. the decisions leading the female to approach and land on a plant and the decisions to oviposit on the plant after encountering it. These terms refer to fundamentally different behavioural processes; the first involves searching for a potential host, the other involves assessment of host quality leading to acceptance or rejection of the host.

Potential hosts will usually vary in quality and preference is generally expressed as a hierarchical ranking of acceptable hosts. Wiklund (1975; 1981) first drew attention to the hierarchical nature of host plant ranges. Female *Papilio machaon* butterflies were more likely to oviposit on some plants, but will accept lower ranked plants to a lesser degree, especially if the higher-ranked plants are not available. The degree to which an ovipositing insect discriminates against plants lower down in the hierarchy is referred to as its specificity or degree of specialization. Wiklund (1981) proposed a dual function for the preference hierarchy: to ensure that most eggs are oviposited on the optimal host plant as long as it is present, and to make possible the deposition of eggs on sub-optimal plants when the optimal host plant is not present. The hierarchical nature of host preference has

been a fundamental key to understanding the evolutionary ecology of oviposition strategies (Singer, 1982; Singer, 1983; Courtney et al., 1989; Singer et al., 1992; Thompson, 1993; Singer, 2001).

7.3.1. Searching, finding and accepting

The first task facing a female insect about to oviposit is to find a suitable patch in which to search for hosts, i.e. where suitable hosts are relatively abundant. It is clear that ovipositing insects do have an ability to aggregate in patches with high local host availability (Wiklund and Åhrberg, 1978; Stanton, 1982; Thomas and Singer, 1987). Sometimes habitat choice can even overshadow the choice of actual host species (Kibota and Courtney, 1991). Both olfactory and visual cues can be important at this stage, as in the next: the location of a potential host from a distance (Bernays and Chapman, 1994; Schoonhoven et al., 1998). However, the extent that insects actually search for its hosts differs among species. While some species use visual search images of shape, size or spectral quality to identify host plants from a distance (Prokopy and Owens, 1983), others use olfactory cues to direct movement towards the source of the odour (Willis and Arbas, 1991; Meiners et al., 2000). Quite often the visual and olfactory stimuli must interact to cause arousal and directed movement in the insect (Schoonhoven et al., 1998). However, some herbivorous insects, that use small, inconspicuous, or otherwise "unapparent" plants as hosts, can show a more or less random flight behaviour within a patch of high host abundance, landing on hosts and non-hosts roughly according to their abundance (Wiklund, 1977; Stanton, 1982; Parmesan et al., 1995).

After alighting on a potential host, the female must decide whether to oviposit or not. While previous decisions may involve search images, learning and other methods to maximize host encounter rates, the post alighting decisions are probably more focused on evaluating the quality of this particular host in relation to other potential hosts (Papaj and Rausher, 1987). Furthermore, while the pre-alighting phases mainly involve visual and/or olfactory cues, the post-alighting phase is probably more based on contact chemoreception, although olfaction and vision may still play a role (Bernays and Chapman, 1994). Some species, such as parasitoids and fruit- or seed feeders, oviposit into hosts or host structures that can only support a very limited number of larvae. These species may also use cues that do not originate from the host to discriminate against already occupied hosts, such as the presence

of conspecific larval frass (e.g. Hilker, 1985; Hilker and Klein, 1989) or deterrent pheromone markings from another females (see chapter 3). As the insect at least in part evaluates different types of cues during the different phases, preference trials could potentially produce divergent results, depending on what behavioural phase or phases the trial is designed to investigate. Most oviposition trials are based on one of two methods: either they use simultaneous choice trials try to pick up a combined effect of the pre- and post-alighting phases (e.g. Wiklund, 1974; Wiklund, 1975; Thompson, 1993; Janz and Nylin, 1997), or they use sequential trails to measure only the post-alighting decisions (e.g. Singer, 1982; Singer, 1986; Singer and Lee, 2000). Both these methods have their strengths and weaknesses, but it is troublesome that so few attempts have been made to compare their outcomes (c.f. Janz, 1999; Janz and Thompson, 2001).

7.3.2. Maternal care

7.3.2.1. Quality vs. quantity

Ovipositing herbivorous (and parasitic) insects typically leave the eggs on their own after oviposition, and these systems do not appear as the typical place to look for maternal care. The tremendous variation in egg size among insects indicates that there the resource invested per individual offspring is quite variable (Fox and Czesak, 2000). Indeed, some herbivorous insects actually do tend their eggs after laying them (e.g. Mappes and Kaitala, 1994). Moreover, there are ways that the ovipositing female can care for her offspring, without actually tending them. The fitness of an ovipositing female is determined by the product of her realized fecundity and the mean fitness of her offspring. Wiklund and Persson (1983) pointed out that the time spent by a female searching for good sites for oviposition can be seen as a form of maternal care that counterbalances the lower oviposition rate. By spending more time searching for a good oviposition site, she assures a higher fitness for her offspring. The female may increase her oviposition rate by including lower-ranked hosts in her repertoire, but the eggs laid on these plants will have a lower chance of surviving and reproducing. Thus, host plant specificity can be seen as a form of maternal care in itself. At the other endpoint we have species where the choice of host plant has been almost completely displaced from the female to the larvae. In these cases, the first instar larvae have developed adaptations, such as ballooning, that allow them to search and find host plants by themselves (e.g. Marques et al., 1994; Tammaru et al., 1995).

This opens for a potential conflict between the mother and her offspring: they may not agree on what is a suitable host plant or oviposition site (Roitberg and Mangel, 1993; Weisser et al., 1994; Nylin et al., 1996; Scheirs et al., 2000). The trade-off will be most pronounced in situations where the best larval host plant is rare. In such cases females may search for a poorer plant that is more abundant, as long as this increases her oviposition rate more than the loss in larval fitness (c.f. Bernays and Chapman, 1994). Thus, even when the ranking of hosts by ovipositing females and larvae is in close agreement, there could be a potential trans-generational conflict in the degree of specialization on the "best" hosts (Nylin and Janz, 1996).

7.3.2.2. Egg protection

In addition to spending time searching for a good oviposition site, the female can also invest in various types of egg protection. This topic is extensively covered in other chapters in this book, so I will only briefly mention some of the various types of egg protection, and comment on some evolutionary aspects. The type of protection the female provides can vary substantially, from purely behavioural to physical or chemical protection. Perhaps the most common (and presumably the least costly) form of egg protection is camouflage. Most eggs have some degree of crypsis on the normal oviposition sites. Many species also oviposit on structures of the host where the egg is more difficult for a predator to see, such as the leaf edges. In some species the eggs (or scales covering the eggs) are instead brightly coloured. This is typically interpreted as aposematic signalling of unpalatability in the form of chemical or physical protection (Rothschild, 1992; Floater, 1998). Physical protection can take the form of tough eggshells and other structures that make the eggs more difficult to handle for predators (e.g. Floater, 1998; Gerson et al., 1998). The diversity off chemical protection of eggs is enormous, and is comprehensively treated in chapter 10 of this volume. In some species the protective chemicals is transferred to the ovipositing female via the spermatophore as a nuptial gift at mating (Dussourd et al., 1991; Conner et al., 2000), which adds another layer of evolutionary complexity to the issue (compare chapter 11).

Some species defend their eggs by guarding them against predators (e.g. Mappes and Kaitala, 1994). The golden egg bug, *Phyllomorpha laciniata*, has an even more refined strategy: the females protect their eggs by ovipositing on the backs of conspecific males

and other females, where the eggs gain protection from their bearers (Kaitala and Axen, 2000; Kaitala et al., 2000; Miettinen and Kaitala, 2000). Another type of behavioural protection (probably coupled with both chemical and physical protection) is the covering of the egg masses with faeces (Arakaki, 1988; Damman and Cappuccino, 1991).

Egg protection can be seen another form of maternal care, whereby the ovipositing female increases the chances of survival for her offspring by providing some kind of defence for the eggs, which would otherwise be more exposed to enemies. In most cases, egg protection probably carries a substantial cost, whether the protection is chemical, physical or behavioural. Thus, a female that invests heavily in egg defence will not be able to lay as many eggs as a female that does not protect her eggs. Hence, the investment in egg defence is very similar to the trade-off between quality and quantity of offspring discussed in the previous section. Egg protection should thus be correlated with degree of specialization, especially in cases where the protective function is more or less tied to a specific host.

7.3.3. The pros and cons of laying egg clutches

One of the most striking aspects of insect oviposition strategies is the variation in clutch size. While females of some species always lay their eggs singly, other species lay several hundred eggs per batch. Parasitoid systems are especially well suited for these questions, because the resource to be exploited is particularly well defined, but many of the problems apply to herbivorous insects as well. Much effort has gone into trying to understand the causes of this variation, but the answer is elusive. There are about as many theories as there are researchers. Many researchers have found a positive correlation between clutch size and the size or local density of the food resource (Pilson and Rausher, 1988; Vasconcellosneto and Monteiro, 1993; Lemasurier, 1994; Fox et al., 1996; Zaviezo and Mills, 2000). Another advantage of egg clustering for a time-constrained ovipositing female is that it can reduce search time (Courtney, 1984). Under some circumstances it can also decrease the egg desiccation risk (Clark and Faeth, 1998). For species that lay the eggs openly on the host (like many herbivorous insects), it has been suggested that the production of toxic or otherwise protected eggs and larvae (who often feed communally on the host) will favour the evolution of egg clustering (Stamp, 1980). Communal feeding can in itself increase larval survival, either by allowing them to more efficiently utilize the food resource (Crowe, 1995), or by predator deterrence (Gamberale and Tullberg, 1996; Gamberale and

Tullberg, 1998). Finally, competition over limited resources has been suggested to reduce clutch size (Vasconcellosneto and Monteiro, 1993; Visser, 1996; Visser and Rosenheim, 1998).

Part of the reason why clutch size variation has proven so hard to explain is probably because clutch size is part of a tightly co-evolved trait complex, where causal relationships can be complicated to tease apart. The relationship between unpalatability of eggs and larvae, clutch size, and aposematic coloration can serve as an example of this, and of how a combination of experimental, phylogenetic and theoretical studies can be used to disentangle even closely intertwined characters like this. As mentioned above, toxic or otherwise unpalatable eggs and larvae have been suggested to favour the evolution of egg clustering. Or is it egg clustering that favours the evolution of unpalatable eggs and larvae? Unpalatability is often coupled with aposematic signalling, adding yet another layer of complexity to the picture. Using phylogenetic techniques, Sillén-Tullberg (1988) showed that aposematic coloration typically preceded group living in butterfly larvae, rejecting the hypothesis aposematism must evolve by kin selection (Harvey, 1983). Instead, aposematism seemed to favour the evolution of egg clustering (and larval gregariousness). Experimental and theoretical studies have confirmed this by demonstrating that aposematic (and distasteful) larvae often survive predator attacks (Wiklund and Järvi, 1982; Tullberg et al., 2000), and that larval aggregations will increase the effect of the aversive signal (Gamberale and Tullberg, 1996; Gamberale and Tullberg, 1998).

7.3.4. Genetics, plasticity and learning

Our knowledge of the factors determining oviposition preference are still relatively poorly known, and this is an interesting field that deserves much more attention in the future. A number of studies have demonstrated a high heritability of oviposition preference, indicating a strong genetic component in host choice (e.g. Tabashnik et al., 1981; Singer et al., 1988; Carriere and Roitberg, 1995; Barker and Starmer, 1999). Several studies have also reported a large effect of major genes host plant use (Guldemond, 1990; Sheck and Gould, 1993; de Jong et al., 2000; Craig et al., 2001). Furthermore, there is evidence for sex linkage of oviposition preference, especially among the Lepidoptera where a substantial part of the species- and population differentiating variation appears to be concentrated to the paternally inherited X chromosome (Thompson, 1988b; Scriber et al., 1991; Scriber,

1994; Janz, 1998; 2001). These observations indicate that oviposition preference can sometimes be part of large co-adapted gene complexes, which may play an important role in population and species differentiation (Charlesworth et al., 1987; Hagen and Scriber, 1989; Scriber, 1994; Sperling, 1994; Hagen and Scriber, 1995).

Perhaps more surprising is the common observation, across several taxonomic groups, that oviposition preference and larval performance are under different genetic control. This was suggested in early studies on butterflies and weevils (Wiklund, 1974; Wasserman and Futuyma, 1981), and has later been confirmed in as diverse organisms as papilionid butterflies (Thompson, 1988b; Thompson et al., 1990), nymphalid butterflies (Janz, 1998; Janz, 2001), chrysomelid beetles (Keese, 1996), and aphids (Guldemond, 1990).

As it must be very important for the female to oviposit on plants that the larvae can feed most efficiently on, why is not a good correlation assured by linkage or pleiotropy? Part of the answer may lie in the asymmetrical relationship between the traits. While ovipositions on plants that the larvae cannot survive on are very costly for the female, there is not necessarily a high cost associated with the capacity to feed on a wider range of plants than the female normally oviposits on. On the contrary, this would probably be adaptive, as females sometimes make oviposition mistakes (see below) and the original food plant can be depleted. Different genetic determination of preference and performance also permits a larger flexibility in host plant selection, allowing the female to base her choice on other criteria than larval performance.

Such flexibility in host choice can be achieved by phenotypic plasticity in preference, including learning. Plasticity in oviposition preference appears to be very common. For example, many studies have shown changes in preference caused by the insect's motivational state, as defined by egg load or time since last oviposition (Singer et al., 1992; Prokopy et al., 1994b; Ueno, 1999; Agnew and Singer, 2000). Adjustment of preference based on physiological state allows the female to oviposit on the best hosts when they are readily available, but to accept poorer hosts after prolonged times without oviposition. Learning has been demonstrated from a number of taxa of ovipositing insects and appears to be an important means of preference modification in many species (Papaj and Prokopy, 1989; Papaj and Lewis, 1992). While motivational changes typically affect post-alighting decisions, i.e. the acceptance of a host after finding it (e.g. Prokopy et al., 1994b), most

examples of learning by ovipositing females involve the host searching stage (Rausher, 1978; Prokopy et al., 1994a; Allard and Papaj, 1996). The most common objective of learning in insect oviposition is to avoid wasting time on preferred hosts that are rare. Thus, although the underlying mechanisms may be different, both these types of plastic adjustment of preference allows the female to maintain a rigid, genetically determined rank order of hosts, with retained flexibility in the face of uncertainty. The role of adult learning in oviposition preference is well established as a fairly common phenomenon (Papaj and Lewis, 1992).

From time to time, it has been suggested that oviposition preference can also be affected by exposure of immature stages to different hosts. According to this hypothesis, host plant exposure (feeding) results in a "imprinting" on the larva that remains through metamorphosis. The imprinting then results in an elevated preference in the ovipositing female for the larval host plant. This idea originated in the first part of the last century (Hopkins, 1917; Craighead, 1921) and has come to be known as the "Hopkins' host selection principle" or pre-adult experience. The hypothesis requires a mechanism for transferring information of larval experience through metamorphosis to the adult female. Corbet (1985) proposed that chemical cues originating from the larval food could persist within the pupa to affect the emerging adult insect (the "chemical legacy hypothesis"). The transfer of memory information through metamorphosis appears possible in principle (Elamrani et al., 1991; Tully et al., 1994), but its relevance for host preference has yet to be convincingly demonstrated (Veltman and Corbet, 1991; Barron and Corbet, 1999). Several studies have tried to experimentally test the Hopkins host selection principle. The overwhelming majority of these studies have failed to find empirical support for it (Wiklund, 1974; Tabashnik et al., 1981; Williams, 1983; van Emden et al., 1996; Rojas and Wyatt, 1999; Solarz and Newan, 2001). Moreover, early adult learning in species that pupate on or in its host (e.g. Cortesero and Monge, 1994) can easily be confused with pre-adult learning. Nevertheless, a few studies have indicated that information on larval feeding experience might indeed have passed to the ovipositing female and affected host choice (e.g. Anderson et al., 1995; Bossart and Scriber, 1999). Thus, it cannot be entirely ruled out that this process might play a role under certain circumstances, and it may be worth investigating what those circumstances are.

From the scattered studies made thus far, we can conclude that a vast majority of the observed preference variance in nature has a genetic background, often modified by plasticity and adult learning. However, the relative importance of these factors across insect taxa remains to be sorted out. The same can be said about the contribution of sex chromosomes vs. autosomes and of major genes vs. genes with quantitative effects to the observed preference variation within and among individuals and populations, and across species.

7.4. Specialization

Host plant range is a prominent and much debated feature of the interaction between herbivorous insects and plants. In most insects, the ovipositing female determines the feeding site for her offspring. Thus, the behavioural processes of egg deposition probably play a large role in host range evolution.

A vast majority of insects are relative specialists, i.e. they oviposit on (or in) and feed on a very restricted number of host species (Janzen, 1988; Futuyma, 1991; Bernays and Chapman, 1994; Thompson, 1994; Schoonhoven et al., 1998). Considering the obvious advantages of being able to use a wider set of resources, this bias towards specialization is puzzling and calls for a general explanation (e.g. Futuyma and Moreno, 1988). Although present across most insect taxa, the pattern is not universally true; a few groups contain mostly generalists, such as Orthoptera (Bernays and Minkenberg, 1997), and the groups that are dominated by specialists typically include polyphagous exceptions (Janz and Nylin, 1998; Janz et al., 2001). If there is such a strong push towards specialization, why is the trend not universal? There is a need to explain not only the rule of high specialization, but also the exceptions of polyphagy (Janz, 1999).

Scriber (1973) demonstrated a latitudinal trend among papilionid butterflies in degree of specialization: Papilionidae species tend to have wider host ranges in temperate areas then in tropical. In a more recent study, comparing Papilionidea (excluding Hesperiidae) in South-East Asia and the western Palearctic, Fiedler (1998) found no corresponding increase in host plant range in the temperate regions. In fact, the pattern was reversed for one group of lycaenid butterflies. Thus, if there is a relationship between host range and latitude, it is not likely to be a simplistic increase or decrease. Moreover, as Fiedler (1998) pointed out, taxonomic idiosyncrasies can render it difficult to draw generalized conclusions. However,

the relationship between latitude and host plant range need not be static and uniform. There are more subtle indications of a connection between parts of the temperate regions and increased host plant ranges. Nylin (1988), and Scriber and Lederhouse (1992) hypothesized that specialization in many temperate species will depend on voltinism patterns (see also Hodkinson, 1997). The number of generations a species can fit into the period with favourable temperatures will depend on latitude. The length of the season will force the females to use different oviposition strategies. In regions where there is just about possible to have a partial second generation, there will be strong selection to use plants that can sustain fast larval development. On the other hand, in some regions there will never be enough time for a second generation and selection to focus on the "fastest" host plants will be relaxed, allowing for other plants to be incorporated into the repertoire.

A long-standing issue is whether host specialization is a directional process leading to an evolutionary dead end (see Thompson, 1994). While it seems clear that host specificity is not irreversible, recent phylogenetic studies have shown that there can exist a trend toward increasing specialization, at least within certain lineages (Wiegmann et al., 1993; Kelley and Farrell, 1998). Yet, other studies have shown that the trend is not universal (Thompson, 1998); some groups even show a reversed trend (Janz et al., 2001; Termonia et al., 2001). The most important conclusion from these studies is probably that host range evolution is very dynamic, with repeated host range expansions followed by re-specialization. The trend for any particular group depends on the evolutionary phase the group happens to be in at the time-slice under investigation (Janz et al., 2001).

7.4.1. Internal vs. external factors

The factors influencing insect diet width are often divided into chemical and ecological aspects. However, just as most chemical factors act through ecological interactions, many of the ecological interactions involve chemical stimuli (Feeny, 1992). Chemistry and ecology are thus closely intertwined. A more accurate terminology would perhaps be to distinguish between internal and external factors, where internal factors refer to features intrinsic to the insect-plant system, such as plant chemistry, herbivore behaviour and physiology, and plant and herbivore genetics. External effects then include all extrinsic factors acting on the insect-plant interaction, such as ecological interactions with other organisms (Table 7.1).

Table 7.1. Factors influencing evolution oviposition behaviour of herbivorous insects

(A) INTERNAL FACTORS OF PLANT-HERBIVORE INTERACTIONS

Plant factors	Herbivore factors
Plant genome and phenotype	Female:
Plant physiology	Genome and phenotype
Chemical cues	Physiology (e.g. age, egg load)
Physical cues; plant architecture	Search time; fitness
Plant density	Offspring (eggs, larvae, pupae):
Plant distribution	Performance of offspring on host chosen by the female (phenotype, plasticity and selection)

(B) EXTERNAL FACTORS Of PLANT-HERBIVRORE INTERACTIONS

Abiotic conditions (soil, temperature, etc.)

Enemies of herbivores:

    Of female

    Of offspring (egg, larvae, pupae)

Competitors:

    Of herbivores

    Of plants

There is little doubt that the chemical constitution of the plants is of importance for their suitability as hosts for herbivorous insects (see chapter 2). It has long been known that the insects use chemical cues when identifying plants for oviposition (Dethier, 1941; Fraenkel, 1959; Feeny, 1992). Similarly, it is obvious that growth and survival of larvae are affected

by plant chemistry (e.g. Thorsteinson, 1960; Scriber, 1988; Zangerl and Berenbaum, 1993). Early models of coevolution and host tracking had a strong emphasis on plant chemistry (e.g. Ehrlich and Raven, 1964; Feeny, 1975; Berenbaum, 1983; Jermy, 1984) and a recent phylogenetic study on melitaeine butterflies and their hosts also showed that at least these species do track certain aspects of host plant chemistry (Wahlberg, 2001).

The most commonly used explanation for host plant specificity is the difficulty for the feeding larvae to cope with the diverse chemistry of angiosperm plants (e.g. Schultz, 1988; Feeny, 1990; Feeny, 1992; Zangerl and Berenbaum, 1993; Dobler et al., 1996; Becerra, 1997). The reasoning is that the specific adaptations needed to handle the specific chemicals in one plant (or set of plants) will interfere with the capacity to efficiently utilize other plants, with a different set of secondary compounds. Much effort has gone into demonstrating such a trade-off in feeding efficiency across plant species and results are mixed. Most studies have presented disappointing results (e.g. Scriber and Feeny, 1979; Futuyma and Wasserman, 1981; Futuyma et al., 1993; Carriere and Roitberg, 1994; Fox and Caldwell, 1994; Futuyma et al., 1994; Thompson, 1996; Camara, 1997; Keese, 1998), but a few studies have found evidence for it (Via, 1991; Mackenzie, 1996; Traxler and Joern, 1999). The difficulties with demonstrating such trade-offs have led many authors to shift focus towards other explanations for the widespread host specificity.

Bernays and Graham (1988) argued that the role of plant chemistry in insect-plant interactions has been overemphasized and that generalist predators instead play a dominating role in the evolution of host range. This ignited an intense discussion on the role of plant chemistry as opposed to external factors such as enemies (see Strong, 1988). However, there is no need to polarize, there is too much evidence on the importance of both internal and external factors for any of them to be ignored. Indeed, plant chemistry and predation on the herbivorous insects (as well as other factors such as plant abundance) probably often interact as causes of specialization. When an insect feeds on a plant with a chemical composition it handles poorly, the most direct consequence is that it grows slower. Slower growth means that the insect is exposed to enemies for a longer time and it is therefore more likely to die from predation (Courtney, 1988; Bernays, 2001).

7.4.2. The cost of information

At least a couple of circumstances suggest that explanations for host specificity should be sought for primarily in female oviposition behaviour, rather than in larval growth and survival. First, in most plant-feeding insects, the choice of feeding location for the larvae is more or less exclusively made by the ovipositing female. In any case, the female choice is preceding any additional larval choices. Furthermore, females are often more restricted than larvae in their acceptance of host species (Wiklund, 1975; Smiley, 1978; Roininen and Tahvanainen, 1989; Penz and Araújo, 1990), which indicates that it may be fruitful to search for the primary restrictions on host specificity in the host searching strategies of egg-laying females. One such theory that has recently gained renewed attention focuses on the role of neural limitations in host range evolution (e.g. Bernays and Wcislo, 1994; Bernays, 2001). Levins and MacArthur (1969) first drew attention to the fact that evaluating host plant quality will be increasingly difficult with increasing host range. Although some researchers returned to this idea during the following decades (Courtney, 1983; Futuyma, 1983), the idea did not really catch on until a few years ago with several both theoretical (e.g. Fox and Lalonde, 1993; Larsson and Ekbom, 1995; Bernays, 1996; Dall and Cuthill, 1997; Holmgren and Getz, 2000; Shelton, 2000) and empirical studies (e.g. Nylin and Janz, 1993; Janz and Nylin, 1997; Bernays and Funk, 1999; Nylin et al., 2000; Bernays and Bright, 2001).

Discriminating and evaluating several host species can be very challenging (Fox and Lalonde, 1993; Nylin and Janz, 1993; Larsson and Ekbom, 1995; Nylin et al., 2000). The outcome will largely depend on the cost of acquiring the relevant information to tell the host apart from non-hosts. Kotler and Mitchell (1995). Insects searching for oviposition sites must locate and identify an appropriate host species, host individual, and often a suitable part of the host, against a very complex background of competing stimuli, both visual and olfactory. Oviposition on a host that cannot support larval growth and survival, and failure to oviposit on a host that can, will be very costly. In a complex sensory world, adoption of high-contrast signals would be expected to ensure rapid and appropriate responses (Bernays and Wcislo, 1994). However, each host in an insect's repertoire will carry its own identification problems. They will contain different chemicals, different concentrations and mixtures of similar chemicals, as well as specific mortality risks not only by toxic effects, but also by e.g. desiccation and predation. It is quite possible that the

same chemical cue will have different implications for different hosts. Individual variation between conspecific plant individuals will further complicate the problem (Shelton, 2000; Singer and Lee, 2000). Thus, with increasing host range, it will be increasingly difficult to find the unambiguous noise-free signals that are necessary to make correct decisions fast. An insect that incorporates several host types into its repertoire will need to allocate more of its neural capacities towards discriminating and evaluating alternative host plants and will have to pay by a reduced efficiency of neural processing. The costs associated with this need to identify and assess several host plant species can be of two types: either the insect will have to pay with a longer decision time, or a higher error rate (Bernays, 1998). This hypothesis might go a long way towards a general explanation for the predominance of specialized oviposition strategies, especially since empirical support comes from such different insect groups as butterflies, grasshoppers and aphids (with indirect support from even more groups (Bernays, 2001)).

Relating the neural constraint hypothesis to the discussion of internal and external factors, Bernays (2001) argues that the main problem that plant chemical diversity causes for ovipositing insects is not to detoxify or metabolize these compounds, but to evolve ways to detect distinctive signals that allows fast and accurate identification of each particular plant chemotype. Failure to do so will result in higher error rates or in prolonged decision times, which will both have serious fitness consequences. Prolonged decision times will reduce vigilance against predators, by forcing the insect to direct more attention towards host identification and evaluation. With this view, it is largely the interaction between internal and external factors, mediated by insect physiology and behaviour, which makes it difficult to evolve and maintain wide host ranges (Bernays, 2001).

To summarize, host range evolution, the range of plants actually used by females for oviposition, can be visualized as a balance between various fitness correlates (Figure 7.1). If we picture a "balance of specialization", fitness advantages such as increased fecundity, risk spreading and diet mixing (when applicable) will be in the generalist scale. In the specialist scale we find increased efficiency in host use, including metabolic efficiency as well as efficiency in host finding and identification. Specialization will also allow a better fit of the insect's life cycle to that of its host, and increased enemy protection in the form of host-specific defence features. A number of ecological factors will then determine how much weight should be put in each of these scales, and the balance will tip over towards

increased or decreased specialization. A highly specialized species, with a life cycle that is tightly co-adapted to its host, will not easily become a generalist. Still, if local conditions were to change, the road of generalization will always be open.
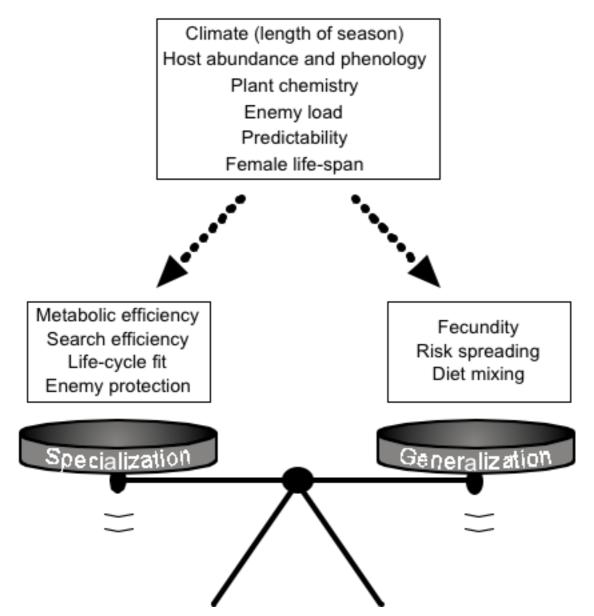

Fig. 1. "The balance of specialization": a visualization of host range evolution, showing the major fitness advantages of specialized and generalized oviposition strategies. The relative weight of these fitness advantages will depend on the state and importance of the ecological factors listed above.

7.5. Preference-performance correlations

In most ovipositing insects, the site chosen by the female at oviposition determines to a high degree where the emerging larva will live and feed. It is therefore a reasonable

assumption that there should be a close match between the hosts that females prefer to oviposit on (or in) and the hosts where larval fitness will be highest. This presumed correlation between female oviposition preference and offspring performance has been the focus of much research for several decades (Thompson, 1988a).

Many studies have demonstrated a good correspondence between preference and performance (e.g. Via, 1986; Singer et al., 1988; Craig et al., 1989; Siemens et al., 1991; Hanks et al., 1993; Nylin and Janz, 1993; Barker and Maczka, 1996). However, it appears to be an equally large number of studies where a correlation could not be found (e.g. Rausher, 1979; Penz and Araújo, 1990; Valladares and Lawton, 1991; Fox and Eisenbach, 1992; Burstein and Wool, 1993; Fox, 1993; Underwood, 1994; Larsson et al., 1995).

7.5.1. Why is the correlation not always perfect?

It may appear peculiar that so many studies have reported a poor correlation between preference and performance, but there are several possible explanations for a weak relationship, thoroughly reviewed by Thompson (1988a) and Thompson and Pellmyr (1991). Generally, these explanations fall in one of two main groups, summarized in Table 7.2. (1) Optimality hypotheses: the females are indeed making the correct choices to maximize offspring success, but they base their choices on one or several parameters that have not been measured, or (2) constraint hypotheses: the females are not optimal in their prediction of offspring performance, due to rapid changes in the environment or to physiological or phylogenetic constraints. Some of these explanations have been touched upon above, while some will be dealt with more comprehensively below.

Table 7.2. Categorization of hypotheses to explain poor correlations between oviposition preference and offspring performance.

Type of hypothesis	Description
Optimality-based	External factors, such as predation, are more important than the direct effects of the host.
	The study failed to identify the relevant performance measure.
	Adult survival (and/or performance in adult feeders) are more important than offspring performance
Constraint-based	Identification problems: Confusion of host and non-host.
	There has not been enough time to adjust preference and performance on a newly colonized host.

7.5.1.1. Optimality hypotheses

The most obvious reason for a poor correlation between preference and performance is that the study failed to identify and include factors that influence offspring success. Factors that are external to the insect-plant relationship in a narrow sense, such as local environmental conditions, intra- or interspecific competition, and predation or parasitism, are typically difficult to study under laboratory conditions, and hence are often not included in experimental studies of preference and performance. There are many indications that such external factors can have a strong influence on oviposition preference (Rausher, 1979; Bernays and Graham, 1988; Bernays, 1989; Fox and Eisenbach, 1992; Ryoo and Chun, 1993; Bernays, 1997; Bigger and Fox, 1997; Björkman et al., 1997; Camara, 1997). Are laboratory-based preference-performance studies of no use then? Not necessarily: the

problem of not including factors in the experiments that could potentially be of high importance can be turned into an advantage. By being able to experimentally separate these "internal" and "external" factors, it is sometimes possible to evaluate their relative importance in a particular system, provided that the researcher has been able to include the relevant "internal" performance measurements for the system. Unfortunately, this is not as straightforward as it may seem.

As mentioned, larval performance is a composite term for a variety of measurable fitness components, such as development time, growth rate, pupal weight and survival. For practical reasons, most studies investigating the relationship between oviposition preference and offspring performance only measure one of these components. In an ideal world, one should take all parts of the insect's life cycle into account when trying to understand the host plant choices of the females. A good host plant for the larva is not necessarily good for the egg, the pupa or the emerging adult butterfly (Reavey and Lawton, 1991). Moreover, the different performance components affecting e.g. the larval stage need not be correlated among themselves (Thompson, 1988a; Nylin et al., 1996). In reality, of course, we should expect female host plant preference to be correlated with total fitness and not with just any performance measurement. Total fitness of the ovipositing female also includes factors that act on the female herself, such as predator pressure and the cost of searching for a suitable host (Courtney, 1983; Futuyma, 1983; Stanton, 1984; Underwood, 1994; Janz and Nylin, 1997; Nylin et al., 2000; Bernays, 2001), as well as adult performance in insects that feed on host plants as adults (Scheirs et al., 2000).

A series of studies involving the polyphagous butterfly *Polygonia c-album* and two commonly used host plants, *Urtica dioica* and *Salix caprea*, can serve as an example of how complex the relationship between female preference and offspring fitness can be, even without "external factors". Larvae of *P. c-album* reached a larger size on *Salix* than on *Urtica*, and the larger size was realized in a higher fecundity. On the other hand, larvae grew faster and had higher survival on *Urtica* (Janz et al., 1994). Larval host plant also had a significant effect on the choice of developmental pathway. Larvae reared on *Urtica* were more likely to opt for direct development (Wedell et al., 1997), which could potentially have profound fitness consequences (c.f. Hunter and McNeil, 1997). Moreover, males reared on *Urtica* allocated more protein to their abdomen and reached higher protein contents in their spermatophores (Wedell, N., Janz, N. and Nylin, S., unpubl.). Radioactive

labelling showed that the nitrogen in spermatophores is used to produce eggs, so that females mated with males reared on *Urtica* can spend less of their own resources to produce eggs and they also lived longer (Wedell, 1996). Host plant preference is thus a complex trade-off between a large numbers of factors and the outcome of the trade-off is likely to vary on a spatial as well as a temporal scale. Even if practical constraints will not allow more than one or a few performance measurements to be included in a study, it is important to "know your system" enough to make the most relevant choice of performance components to investigate (Nylin et al., 1996).

7.5.1.2. Constraint hypotheses

Various constraints acting on the ovipositing female may interfere with her ability to choose the best possible site for the development of her offspring. Some cases, where the female deposits her eggs on plants that are lethal for the larvae, are hard to explain in other ways. Such oviposition mistakes have been documented in several species (e.g. Chew, 1977; Feldman and Haber, 1998), and will be more common when the preferred host is easily confused with a non-host that provides the ovipositing female with similar cues. Larsson and Ekbom (1995) suggested that these mistakes could often be the first step towards the colonization of a new host. As mentioned above, oviposition error rate can be expected to increase with increasing host range (Janz and Nylin, 1997) and with increasing similarity between hosts (Fox and Lalonde, 1993; Nylin et al., 2000), suggesting a an interesting link between polyphagy and host shifts.

Another, but related, reason for poor preference-performance correlations is that the host is so newly colonized that the insect has not had time to adjust oviposition preference after offspring performance (Camara, 1997).

7.6. Concluding remarks

It should be clear by now that the behavioural processes involved in host finding and choice of oviposition sites, as well as their causes and consequences, can be exceedingly complex. Several decades of research has advanced our understanding of these processes tremendously, to the extent that some broad generalizations can be made. Examples include the general patterns of specialization and host range evolution, the sequence of behavioural processes involved in host finding and acceptance, and the types of cues involved in this process. Nevertheless, many challenges remain. Much of our knowledge is still based on a

relative small sample of insect species, with a heavy bias toward those that are easy to study and work with in the laboratory and field. In a strict sense, generalizations are always wrong, and we need better knowledge of taxon-specific idiosyncrasies to be able to make better generalizations as well as to sharpen our specific hypotheses. The various features of insect oviposition, such as specificity, clutch size, preference-performance correlations, search efficiency, defence systems, etc., are probably parts of tightly coadapted complexes, and disentangling the causal relationships between them has proven to be very challenging. It has become increasingly clear that an understanding of these relationships calls for a multidisciplinary approach. Much insight has been gathered in the fields of behavioural ecology, chemical ecology, population ecology, physiology and systematics, but the communication between the fields has not always been perfect. I believe that future progress in this field will call for more cooperation and synergy between these fields.

7.7. References

Agnew K, Singer MC. 2000. Does fecundity drive the evolution of insect diet? Oikos 88:533-538

Allard RA, Papaj DR. 1996. Learning of leaf shape by pipevine swallowtail butterflies: A test using artificial leaf models. J. Insect Behav. 9:961-967

Anderson P, Hilker M, Löfqvist J. 1995. Larval diet influence on oviposition behaviour in *Spodoptera littoralis*. Entomol. Exp. Appl. 74:71-82

Anderson RS. 1993. Weevils and plants - phylogenetic versus ecological mediation of evolution of host plant associations in Curculioninae (Coleoptera, Curculionidae). Mem. Ent. Soc. Can. 165:197-232

Arakaki N. 1988. Egg protection with feces in the Ladybeetle, *Pseudoscymnus kurohime* (Miyatake) (Coleoptera, Coccinellidae). Appl. Entomol. Zoolog. 23:495-497

Barker AM, Maczka CJM. 1996. The relationships between host selection and subsequent larval performance in three free-living graminivorous sawflies. Ecol. Entomol. 21:317-327

Barker JSF, Starmer WT. 1999. Environmental effects and the genetics of oviposition site preference for natural yeast substrates in *Drosophila buzzatii*. Hereditas 130:145-175

Barron AB, Corbet SA. 1999. Preimaginal conditioning in Drosophila revisited. Anim. Behav. 58:621-628

Beccaloni GW, Symons FB. 2000. Variation of butterfly diet breadth in relation to host-plant predictability: results from two faunas. Oikos 90:50-66

Becerra JX. 1997. Insects on plants: Macroevolutionary chemical trends in host use. Science 276:253-256

Berenbaum MR. 1983. Coumarins and caterpillars: a case for coevolution. Evolution 37:163-179

Bernays EA. 1989. Host range in phytophagous insects: the potential role of generalist predators. Evol. Ecol. 3:299-311

Bernays EA. 1996. Selective attention and host-plant specialization. Entomol. Exp. Appl. 80:125-131

Bernays EA. 1997. Feeding by lepidopteran larvae is dangerous. Ecol. Entomol. 22:121-123

Bernays EA. 1998. The value of being a resource specialist: behavioral support for a neural hypothesis. Am. Nat. 151:451-464

Bernays EA. 2001. Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. Annu. Rev. Entomol. 46:703-727

Bernays EA, Bright KL. 2001. Food choice causes interrupted feeding in the generalist grasshopper *Schistocerca americana*: further evidence for inefficient decision-making. J. Insect Physiol. 47:63-71

Bernays EA, Chapman RF 1994. Host-plant selection by phytophagous insects. Chapman & Hall, London

Bernays EA, Funk DJ. 1999. Specialists make faster decisions than generalists: experiments with aphids. Proc. R. Soc. Lond. B. 266:151-156

Bernays EA, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69:886-892

Bernays EA, Minkenberg OPJM. 1997. Insect herbivores: Different reasons for being a generalist. Ecology 78:1157-1169

Bernays EA, Wcislo WT. 1994. Sensory capabilities, information processing, and resource specialization. Quart. Rev. Biol. 69:187-204

Bigger DS, Fox LR. 1997. High-density populations of diamondback moth have broader host-plant diets. Oecologia 112:179-186

Björkman C, Larsson S, Bommarco R. 1997. Oviposition preferences in pine sawflies: A trade-off between larval growth and defence against natural enemies. Oikos 79:45-52

Bossart JL, Scriber JM. 1999. Preference variation in the polyphagous tiger swallowtail butterfly (Lepidoptera: Papilionidae). Environ. Entomol. 28:628-637

Burstein M, Wool D. 1993. Gall aphids do not select optimal galling sites (*Smynthurodes betae*, Pemphigidae). Ecol. Entomol. 18:155-164

Camara MD. 1997. A recent host range expansion in *Junonia coenia* Hubner (Nymphalidae): Oviposition preference, survival, growth, and chemical defense. Evolution 51:873-884

Carey DB. 1994. Diapause and the host plant affiliations of Lycaenid butterflies. Oikos 69:259-266

Carriere Y, Roitberg BD. 1994. Trade-offs in responses to host plants within a population of a generalist herbivore, *Choristoneura rosaceana*. Entomol. Exp. Appl. 72:173-180

Carriere Y, Roitberg BD. 1995. Evolution of host-selection behaviour in insect herbivores: Genetic variation and covariation in host acceptance within and between populations of *Choristoneura rosaceana* (Family: Tortricidae), the obliquebanded leafroller. Heredity 74:357-368

Charlesworth B, Coyne JA, Barton NH. 1987. The relative rates of evolution of sex chromosomes and autosomes. Am. Nat. 130:113-146

Chew FS. 1977. Coevolution of pierid butterflies and their cruciferous food plants. II. The distribution of eggs on potential food plants. Evolution 31:568-579

Clark BR, Faeth SH. 1998. The evolution of egg clustering in butterflies: A test of the egg desiccation hypothesis. Evol. Ecol. 12:543-552

Conner WE, Boada R, Schroeder FC, Gonzalez A, Meinwald J, Eisner T. 2000. Chemical defense: Bestowal of a nuptial alkaloidal garment by a male moth on its mate. Proc. Natl. Acad. Sci. USA 97:14406-14411

Corbet SA. 1985. Insect chemosensory responses, a chemical legacy hypothesis. Ecol. Entomol. 10:143-153

Cortesero AM, Monge JP. 1994. Influence of preemergence experience on response to host and host-plant odors in the larval parasitoid *Eupelmus vuilleti*. Entomol. Exp. Appl. 72:281-288

Courtney SP. 1983. Models of host plant location by butterflies: the effect of search images and searching efficiency. Oecologia 59:317-321

Courtney SP. 1984. The evolution of egg clustering by butterflies and other insects. Am. Nat. 123:276-281

Courtney SP. 1988. If it's not coevolution, then it must be predation? Ecology 69:910-911

Courtney SP, Chen GK, Gardner A. 1989. A general model for individual host selection. Oikos 55:55-65

Craig TP, Horner JD, Itami JK. 2001. Genetics, experience, and host-plant preference in Eurosta solidaginis: Implications for host shifts and speciation. Evolution 55:773-782

Craig TP, Itami JK, Price PW. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. Ecology 70:1691-1699

Craighead FC. 1921. Hopkins host-selection principle as related to certain cerambycid beetles. Journal of Agricultural Research 22:189-220

Crowe ML. 1995. The effect of season and group size on survivorship and larval growth in *Plagiodera versicolora*. Ecol Entomol 20:27-32

Dall SRX, Cuthill IC. 1997. The information costs of generalism. Oikos 80:197-202

Damman H, Cappuccino N. 1991. 2 forms of egg defense in a chrysomelid beetle - Egg clumping and excrement cover. Ecol. Entomol. 16:163-167

de Jong PW, Frandsen HO, Rasmussen L, Nielsen JK. 2000. Genetics of resistance against defences of the host plant *Barbarea vulgaris* in a Danish flea beetle population. Proc. R. Soc. Lond. B. 267:1663-1670

Dethier VG. 1941. Chemical factors determining the choice of food plants by *Papilio* larvae. Am. Nat. 75:61-73

Dobler S, Mardulyn P, Pasteels JM, RowellRahier M. 1996. Host-plant switches and the evolution of chemical defense and life history in the leaf beetle genus *Oreina*. Evolution 50:2373-2386

Dussourd DE, Harvis CA, Meinwald J, Eisner T. 1991. Pheromonal advertisement of a nuptial gift by a male moth (*Utetheisa ornatrix*). Proc. Natl. Acad. Sci. USA 88:9224-9227

Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. Evolution 18:586-608

Eigenbrode SD, Moodie S, Castagnola T. 1995. Predators mediate host plant resistance to a phytophagous pest in cabbage with glossy leaf wax. Entomol. Exp. Appl. 77:335-342

Elamrani A, Cadieu N, Cadieu JC. 1991. Influence of preimaginal conditioning with alcohol on choice of food substrate and oviposition behavior of the adult *Drosophila melanogaster*. Behav. Process. 24:153-165

Feeny P. 1975. Biochemical coevolution between plants and their insect herbivores. In: Gilbert LE, Raven PH (eds) *Coevolution of animals and plants*. University of Texas Press, Austin, pp 5-19

Feeny P. 1990. Theories of plant chemical defence. Symp. Biol. Hung. 39:163-175

Feeny P. 1992. The evolution of chemical ecology: contributions from the study of herbivorous insects. In: *Herbivores: their interactions with secondary plant metabolites*, vol 2: Evolutionary and ecological processes. Academic Press, New York

Feldman TS, Haber WA. 1998. Oviposition behavior, host plant use, and diet breadth of *Anthanassa* butterflies (Lepidoptera : Nymphalidae) using plants in the Acanthaceae in a Costa Rican community. Fla. Entomol. 81:396-406

Fiedler K. 1998. Diet breadth and host plant diversity of tropical- vs. temperate-zone herbivores: South-east Asian and west Palaearctic butterflies as a case study. Ecol. Entomol. 23:285-297

Floater GJ. 1998. Tuft scales and egg protection in *Ochrogaster lunifer* Herrich- Schaffer (Lepidoptera : Thaumetopoeidae). Aust. J. Entomol. 37:34-39

Fox CW. 1993. A quantitative genetic analysis of oviposition preference and larval performance on two hosts in the bruchid beetle, *Callosobruchus maculatus*. Evolution 47:166-175

Fox CW, Caldwell RL. 1994. Host-associated fitness trade-offs do not limit the evolution of diet breadth in the small milkweed bug *Lygaeus kalmii* (Hemiptera, Lygaeidae). Oecologia 97:382-389

Fox CW, Czesak ME. 2000. Evolutionary ecology of progeny size in arthropods. Annu. Rev. Entomol. 45:341-369

Fox CW, Lalonde RG. 1993. Host confusion and the evolution of insect diet breadths. Oikos 67:577-581

Fox CW, Martin JD, Thakar MS, Mousseau TA. 1996. Clutch size manipulations in two seed beetles: Consequences for progeny fitness. Oecologia 108:88-94

Fox LR, Eisenbach J. 1992. Contrary choices - possible exploitation of enemy-free space by herbivorous insects in cultivated vs wild crucifers. Oecologia 89:574-579

Fraenkel GS. 1959. The raison d'être of secondary plant substances. Science 129:1466-1470

Funk DJ, Futuyma DJ, Ortí G, Meyer A. 1995. A history of host associations and evolutionary diversification for *Ophraella* (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. Evolution 49:1008-1017

Futuyma DJ. 1983. Selective factors in the evolution of host choice by phytophagous insects. In: Ahmad S (ed) *Herbivorous Insects: Host-seeking Behavior and Mechanisms*. Academic Press, New York, pp 227-244

Futuyma DJ. 1991. Evolution of host specificity in herbivorous insects: genetic, ecological, and phylogenetic aspects. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW (eds) *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley & Sons, New York, pp 431-454

Futuyma DJ, Keese MC, Funk DJ. 1995. Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. Evolution 49:797-809

Futuyma DJ, Keese MC, Scheffer SJ. 1993. Genetic constraints and the phylogeny of insect-plant associations - responses of *Ophraella communa* (Coleoptera, Chrysomelidae) to host plants of its congeners. Evolution 47:888-905

Futuyma DJ, Moreno G. 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Syst. 19:207-233

Futuyma DJ, Walsh JS, Morton T, Funk DJ, Keese MC. 1994. Genetic variation in a phylogenetic context - responses of 2 specialized leaf beetles (Coleoptera, Chrysomelidae) to host plants of their congeners. J. Evol. Biol. 7:127-146

Futuyma DJ, Wasserman SS. 1981. Food plant specialization and feeding efficiency in the tent caterpillars *Malacosoma disstria* (Hübner) and *M. americanum* (Fabricius). Entomol. Exp. Appl. 30:106-110

Gamberale G, Tullberg BS. 1996. Evidence for a more effective signal in aggregated aposematic prey. Anim. Behav. 52:597-601

Gamberale G, Tullberg BS. 1998. Aposematism and gregariousness: the combined effect of group size and coloration on signal repellence. Proc. R. Soc. Lond. B. 265:889-894

Gerson EA, Kelsey RG, McComb WC, Ross DW. 1998. Palatability of *Coloradia pandora* (Lepidoptera : Saturniidae) eggs to a rodent predator: Contributions of physical and chemical characteristics. Environ. Entomol. 27:709-716

Guldemond JA. 1990. Evolutionary genetics of the aphid *Cryptomyzus*, with a preliminary analysis of the inheritance of host plant preference, reproductive performance and host-alteration. Entomol. Exp. Appl. 57:65-76

Hagen RH, Scriber JM. 1989. Sex-linked diapause, color, and allozyme loci in Papilio glaucus : Linkage analysis and significance in a hybrid zone. J. Hered. 80:179-185

Hagen RH, Scriber JM. 1995. Sex chromosomes and speciation in tiger swallowtails. In: Scriber JM, Tsubaki Y, Lederhouse RC (eds) *Swallowtail Butterflies: Their Ecology and Evolutionary Biology.* Scientific Publishers, PO Box 15718, Gainesville, FL 32604, pp 211-227

Hanks LM, Paine TD, Millar JG. 1993. Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata.* Oecologia 95:22-29

Harvey P. 1983. Why some insects look pretty nasty. New Scientist 97:26-27

Hilker M. 1985. Larvenkot als Eiablage-Deterrens bei *Spodoptera littoralis.* Naturwiss. 72:485-486

Hilker M, Klein B. 1989. Investigation of oviposition deterrent in the larval frass of *Spodoptera littoralis* (Boisd.). J. chem. Ecol. 15:929-938

Hodkinson ID. 1997. Progressive restriction of host plant exploitation along a climatic gradient: The willow psyllid *Cacopsylla groenlandica* in Greenland. Ecol. Entomol. 22:47-54

Holmgren NMA, Getz WM. 2000. Evolution of host plant selection in insects under perceptual constraints: A simulation study. Evol. Ecol. Res. 2:81-106

Hopkins AD. 1917. A discussion of C G Hewitt's paper on "Insect behavior". J. Econ. Entomol. 10:92-93

Hunter MD, McNeil JN. 1997. Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. Ecology 78:977-986

Janz N. 1998. Sex-linked inheritance of host-plant specialization in a polyphagous butterfly. Proc. R. Soc. Lond. B. 265:1675-1678

Janz N. 1999. Ecology and evolution of butterfly host plant range. Doctoral thesis. Stockholm University, Stockholm

Janz N. 2001. Sex-linkage of host plant use in butterflies. In: Boggs CL, Watt WB, Ehrlich PR (eds) *Ecology and evolution taking flight: butterflies as model study systems*. University of Chicago Press, Chicago, p in press

Janz N, Nylin S. 1997. The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. Proc. R. Soc. Lond. B. 264:701-707

Janz N, Nylin S. 1998. Butterflies and plants: a phylogenetic study. Evolution 52:486-502

Janz N, Nylin S, Nyblom K. 2001. Evolutionary dynamics of host plant specialization: a case study of the tribe Nymphalini. Evolution 55:783–796

Janz N, Nylin S, Wedell N. 1994. Host plant utilization in the comma butterfly: sources of variation and evolutionary implications. Oecologia 99:132-140

Janz N, Thompson JN. 2001. Plant polyploidy and host expansion in an insect herbivore. Oecologia in press

Janzen DH. 1988. Ecological characterization of a Costa Rican dry forest caterpillar fauna. Biotropica 20:120-135

Jermy T. 1984. Evolution of insect/host plant relationships. Am. Nat. 124:609-630

Jones RE. 1991. Host location and oviposition on plants. In: Bailey WJ, Ridsdill-Smith J (eds) *Reproductive behaviour of insects: individuals and populations*. Chapman & Hall, London, pp 108-138

Kaitala A, Axen AH. 2000. Egg load and mating status of the golden egg bug affect predation risk. Ecology 81:876-880

Kaitala A, Espadaler X, Lehtonen R. 2000. Ant predation and the cost of egg carrying in the golden egg bug: experiments in the field. Oikos 89:254-258

Keese MC. 1996. Feeding responses of hybrids and the inheritance of host-use traits in leaf feeding beetles (Coleoptera: Chrysomelidae). Heredity 76:36-42

Keese MC. 1997. Does escape to enemy-free space explain host specialization in two closely related leaf-feeding beetles (Coleoptera: Chrysomelidae)? Oecologia 112:81-86

Keese MC. 1998. Performance of two monophagous leaf feeding beetles (Coleoptera: Chrysomelidae) on each other's host plant: Do intrinsic factors determine host plant specialization. J. Evol. Biol. 11:403-419

Kelley ST, Farrell BD. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). Evolution 52:1731-1743

Kibota TT, Courtney SP. 1991. Jack of one trade, master of none - host choice by *Drosophila magnaquinaria*. Oecologia 86:251-260

Kotler BP, Mitchell WA. 1995. The effect of costly information in diet choice. Evol. Ecol. 9:18-29

Larsson S, Ekbom B. 1995. Oviposition mistakes in herbivorous insects: Confusion or a step towards a new host plant? Oikos 72:155-160

Larsson S, Glynn C, Höglund S. 1995. High oviposition rate of *Dasineura marginemtorquens* on *Salix viminalis* genotypes unsuitable for offspring survival. Entomol. Exp. Appl. 77:263-270

Lemasurier AD. 1994. Costs and benefits of egg clustering in *Pieris brassicae*. J. Anim. Ecol. 63:677-685

Levins R, MacArthur RH. 1969. A hypotheses to explain the incidence of monophagy. Ecology 50:910-911

Mackenzie A. 1996. A trade-off for host plant utilization in the black bean aphid, *Aphis fabae*. Evolution 50:155-162

Mappes J, Kaitala A. 1994. Experiments with *Elasmucha grisea* L (Heteroptera, Acanthosomatidae) - does a female parent bug lay as many eggs as she can defend. Behav. Ecol. 5:314-317

Marques RSA, Marques ESA, Price PW. 1994. Female behavior and oviposition choices by an eruptive herbivore, *Disonycha pluriligata* (Coleoptera: Chrysomelidae). Environ. Entomol. 23:887-892

Meiners T, Westerhaus C, Hilker M. 2000. Specificity of chemical cues used by a specialist egg parasitoid during host location. Entomol. Exp. Appl. 95:151-159

Miettinen M, Kaitala A. 2000. Copulation is not a prerequisite to male reception of eggs in the golden egg bug *Phyllomorpha laciniata* (Coreidae; Heteroptera). J. Insect Behav. 13:731-740

Nylin S. 1988. Host plant specialization and seasonality in a polyphagous butterfly, *Polygonia c-album* (Nymphalidae). Oikos 53:381-386

Nylin S, Bergström A, Janz N. 2000. Butterfly host plant choice in the face of possible confusion. J. Insect Behav. 13:469-482

Nylin S, Janz N. 1993. Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae): the choice between bad and worse. Ecol. Entomol. 18:394-398

Nylin S, Janz N. 1996. Host plant preferences in the comma butterfly (*Polygonia c-album*): Do parents and offspring agree? Ecoscience 3:285-289

Nylin S, Janz N, Wedell N. 1996. Oviposition plant preference and offspring performance in the comma butterfly: Correlations and conflicts. Entomol. Exp. Appl. 80:141-144

Papaj DR, Lewis AC 1992. Insect Learning. Ecological and Evolutionary Perspectives. Chapman & Hall, New York

Papaj DR, Prokopy RJ. 1989. Ecological and evolutionary aspects of learning in phytophagous insects. Annu. Rev. Entomol. 34:315-350

Papaj DR, Rausher MD. 1987. Components of conspecific host discrimination behavior in the butterfly *Battus philenor*. Ecology 68:245-253

Parmesan C, Singer MC, Harris I. 1995. Absence of adaptive learning from the oviposition foraging behaviour of a checkerspot butterfly. Anim. Behav. 50:161-175

Penz CM, Araújo AM. 1990. Interaction between *Papilio hectorides* (Papilionidae) and four host plants (Piperaceae) in a southern Brazilian population. J. Res. Lepid. 29:161-171

Pilson D, Rausher MD. 1988. Clutch size adjustment by a swallowtail butterfly. Nature 333:361-363

Prokopy RJ, Bergweiler C, Galarza L, Schwerin J. 1994a. Prior experience affects the visual ability of *Rhagoletis pomonella* flies (Diptera, Tephritidae) to find host fruit. J. Insect Behav. 7:663-677

Prokopy RJ, Owens ED. 1983. Visual detection of plants by herbivorous insects. Annu. Rev. Entomol. 28:337-364

Prokopy RJ, Roitberg BD, Vargas RI. 1994b. Effects of egg load on finding and acceptance of host fruit in *Ceratis capitata* flies. Physiol. Entomol. 19:124-132

Radtkey RR, Singer MC. 1995. Repeated reversals of host-preference evolution in a specialist insect herbivore. Evolution 49:351-359

Rausher MD. 1978. Search image for leaf shape in a butterfly. Science 200:1071-1073

Rausher MD. 1979. Larval habitat suitability and oviposition preference in three related butterflies. Ecology 60:503-511

Rausher MD. 1983. Conditioning and genetic variation as causes of individual variation in the oviposition behaviour of the tortoise beetle, *Deloyala guttata*. Anim. Behav. 31:743-747

Reavey D, Lawton JH. 1991. Larval contribution to fitness in leaf-eating insects. In: Bailey WJ, Ridsdill-Smith J (eds) *Reproductive behaviour of insects: individuals and populations*. Chapman & Hall, London, pp 293-329

Roininen H, Tahvanainen J. 1989. Host selection and larval performance of two willow-feeding sawflies. Ecology 70:129-136

Roitberg BD, Mangel M. 1993. Parent-offspring conflict and life-history consequences in herbivorous insects. Am. Nat. 142:443-456

Rojas JC, Wyatt TD. 1999. The role of pre- and post-imaginal experience in the host-finding and oviposition behaviour of the cabbage moth. Physiol. Entomol. 24:83-89

Rothschild M. 1992. Egg protection by the Atala hairstreak butterfly (*Eumaeus atala florida*). Phytochemistry 31:1959-1960

Ryoo MI, Chun YS. 1993. Oviposition behavior of *Callosobruchus chinensis* (Coleoptera; Bruchidae) and weevil population growth - effects of larval parasitism and competition. Environ. Entomol. 22:1009-1015

Sadeghi H, Gilbert F. 1999. Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. Oecologia 118:405-411

Scheirs J, De Bruyn L, Verhagen R. 2000. Optimization of adult performance determines host choice in a grass miner. Proc. R. Soc. Lond. B. 267:2065-2069

Schoonhoven LM, Jermy T, van Loon JJA 1998. Insect-plant biology: from physiology to evolution. Chapman & Hall, London

Schultz JC. 1988. Many factors influence the evolution of herbivore diets, but plant chemistry is central. Ecology 69:896-897

Scriber JM. 1973. Latitudinal gradients in larval feeding specialization of the world Papilionidae (Lepidoptera). Psyche 80:355-373

Scriber JM. 1988. Tale of the Tiger: Beringial biogeography, binomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies. In: Spencer KC (ed) *Chemical mediation of coevolution*. Academic Press, Chicago, pp 241-301

Scriber JM. 1994. Climatic legacies and sex chromosomes: latitudinal patterns of voltinism, diapause, body size, and host-plant selection on two species of swallowtail butterflies at their hybrid zone. In: Danks HV (ed) *Insect life-cycle polymorphism: theory, evolution and ecological consequences for seasonality and diapause control*. Kluwer Academic Publishers, Dordrecht, Netherlands

Scriber JM, Feeny P. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their food plants. Ecology 60:829-850

Scriber JM, Giebink BL, Snider D. 1991. Reciprocal latitudinal clines in oviposition behaviour of *Papilio glaucus* and *P. canadensis* across the Great Lakes hybrid zone: Possible sex-linkage of oviposition preferences. Oecologia 87:360-368

Scriber JM, Lederhouse RC. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores. In: Hunter MR, Ohgushi T, Price PW (eds) *Effects of resource distribution on animal-plant interactions*. Academic Press, New York, pp 429-466

Sheck AL, Gould F. 1993. The genetic basis of host range in *Heliothis virescens* - larval survival and growth. Entomol. Exp. Appl. 69:157-172

Shelton AL. 2000. Variable chemical defences in plants and their effects on herbivore behaviour. Evol. Ecol. Res. 2:231-249

Siemens DH, Johnson CD, Woodman RL. 1991. Determinants of host range in bruchid beetles. Ecology 72:1560-1566

Sillén-Tullberg B. 1988. Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. Evolution 42:293-305

Singer MC. 1982. Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. Oecologia 52:224-229

Singer MC. 1983. Determinants of multiple host use by a phytophagous insect population. Evolution 37:389-403

Singer MC. 1986. The definition and measurement of oviposition preference in plant-feeding insects. In: Miller JR, Miller TA (eds) *Insect-plant interactions*. Springer-Verlag, New York, pp 65-94

Singer MC. 2001. Spatial and temporal patterns of checkerspot butterfly-hostplant association: the diverse roles of oviposition preference. In: Boggs CL, Watt WB, Ehrlich PR (eds) *Ecology and evolution taking flight: butterflies as model study systems*. University of Chicago Press, Chicago, p in press

Singer MC, Lee JR. 2000. Discrimination within and between host species by a butterfly: implications for design of preference experiments. Ecology Letters 3:101-105

Singer MC, Ng D, Thomas CD. 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. Evolution 42:977-985

Singer MC, Thomas CD. 1996. Evolutionary responses of a butterfly metapopulation to human- and climate-caused environmental variation. Am. Nat. 148:S9-S39

Singer MC, Thomas CD, Billington HL, Parmesan C. 1989. Variation among conspecific insect populations in the mechanistic basis of diet breadth. Anim. Behav. 37:751-759

Singer MC, Vasco D, Parmesan C, Thomas CD, Ng D. 1992. Distinguishing between 'preference' and 'motivation' in food choice: an example from insect oviposition. Anim. Behav. 44:463-471

Smiley J. 1978. Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. Science 201:745-747

Solarz SL, Newan RM. 2001. Variation in hostplant preference and performance by the milfoil weevil, *Euhrychiopsis lecontei* Dietz, exposed to native and exotic watermilfoils. Oecologia 126:66-67

Sperling FAH. 1994. Sex-linked genes and species differences in Lepidoptera. Can. Entomol. 126:807-818

Stamp NE. 1980. Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly? Am. Nat. 115:367-380

Stamp NE, Bowers MD. 1993. Presence of predatory wasps and stinkbugs alters foraging behavior of cryptic and non-cryptic caterpillars on plantain (Plantago lanceolata). Oecologia 95:376-384

Stanton ML. 1982. Searching in a patchy environment: foodplant selection by *Colias p. eriphyle* butterflies. Ecology 63:839-853

Stanton ML. 1984. Short-term learning and the searching accuracy of egg-laying butterflies. Anim. Behav. 32:33-40

Stanton ML, Cook RE. 1983. Sources of intraspecific variation in the hostplant seeking behavior of *Colias* butterflies. Oecologia 60:365-370

Strong DR. 1988. Insect host range. Ecology 69:885

Tabashnik BE, Wheelock H, Rainbolt JD, Watt WB. 1981. Individual variation in oviposition preference in the butterfly, *Colias eurytheme*. Oecologia 50:225-230

Tammaru T, Kaitaniemi P, Ruohomaki K. 1995. Oviposition choices of *Epirrita autumnata* (Lepidoptera: Geometridae) in relation to its eruptive population dynamics. Oikos 74:296-304

Termonia A, Hsiao TH, Pasteels JM, Milinkovitch MC. 2001. Feeding specialization and host-derived chemical defense in Chrysomeline leaf beetles did not lead to an evolutionary dead end. Proc. Natl. Acad. Sci. USA 98:3909-3914

Thomas CD, Singer MC. 1987. Variation in host preference affects movement patterns within a butterfly population. Ecology 68:1262-1267

Thompson JN. 1988a. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Exp. Appl. 47:3-14

Thompson JN. 1988b. Evolutionary genetics of oviposition preference in swallowtail butterflies. Evolution 42:1223-1234

Thompson JN. 1988c. Variation in preference and specificity in monophagous and oligophagous swallowtail butterflies. Evolution 42:118-128

Thompson JN. 1993. Preference hierarchies and the origin of geographic specialization in host use in swallowtail butterflies. Evolution 47:1585-1594

Thompson JN 1994. The coevolutionary process. University of Chicago Press, Chicago

Thompson JN. 1996. Trade-offs in larval performance on normal and novel hosts. Entomol. Exp. Appl. 80:133-139

Thompson JN. 1998. The evolution of diet breadth: Monophagy and polyphagy in swallowtail butterflies. J. Evol. Biol. 11:563-578

Thompson JN, Pellmyr O. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. Annu. Rev. Entomol. 36:65-89

Thompson JN, Wehling W, Podolsky R. 1990. Evolutionary genetics of host use in swallowtail butterflies. Nature 344:148-150

Thorsteinson AJ. 1960. Host selection in phytophagous insects. Annu. Rev. Entomol. 5:193-218

Traxler MA, Joern A. 1999. Performance tradeoffs for two hosts within and between populations of the oligophagous grasshopper Hesperotettix viridis (Acrididae). Oikos 87:239-250

Tullberg BS, Leimar O, Gamberale-Stille G. 2000. Did aggregation favour the initial evolution of warning coloration? A novel world revisited. Anim. Behav. 59:281-287

Tully T, Cambiazo V, Kruse L. 1994. Memory through metamorphosis in normal and mutant *Drosophila*. J. Neurosci. 14:68-74

Ueno T. 1999. Host-feeding and acceptance by a parasitic wasp (Hymenoptera : Ichneumonidae) as influenced by egg load and experience in a patch. Evol. Ecol. 13:33-44

Underwood DLA. 1994. Intraspecific variability in host plant quality and ovipositional preferences in *Eucheira socialis* (Lepidoptera: Pieridae). Ecol. Entomol. 19:245-256

Valladares G, Lawton JH. 1991. Host-plant selection in the holly leaf-miner: does mother know best? J. Anim. Ecol. 60:227-240

van Emden HF, Sponagl B, Baker T, Ganguly S, Douloumpaka S. 1996. Hopkins 'host selection principle', another nail in its coffin. Physiol. Entomol. 21:325-328

Vasconcellosneto J, Monteiro RF. 1993. Inspection and evaluation of host plant by the butterfly *Mechanitis lysimnia* (Nymph, Ithomiinae) before laying eggs - a mechanism to reduce intraspecific competition. Oecologia 95:431-438

Veltman CJ, Corbet SA. 1991. In search of a model system for exploring the chemical legacy hypothesis - *Drosophila melanogaster* and geraniol. J. chem. Ecol. 17:2459-2468

Via S. 1986. Genetic covariance between oviposition preference an larval performance in an insect herbivore. Evolution 40:778-785

Via S. 1991. The population structure of fitness in a spatial network: demography of pea aphid clones from two crops in a reciprocal transplant. Evolution 45:827-852

Visser ME. 1996. The influence of competition between foragers on clutch size decisions in an insect parasitoid with scramble larval competition. Behav. Ecol. 7:109-114

Visser ME, Rosenheim JA. 1998. The influence of competition between foragers on clutch size decisions in insect parasitoids. Biol. Control 11:169-174

Wahlberg N. 2001. The phylogenetics and biochemistry of host plant specialization in melitaeine butterflies (Lepidoptera: Nymphalidae). Evolution 55:522-537

Wasserman SS, Futuyma DJ. 1981. Evolution of host plant utilization in laboratory populations of the southern cowpea weevil, *Callosobruchus maculatus* Fabricius (Coleoptera: Bruchidae). Evolution 35:605-617

Wedell N. 1996. Mate quality affects reproductive effort in a paternally investing species. Am. Nat. 148:1075-1088

Wedell N, Nylin S, Janz N. 1997. Effects of larval host plant and sex on the propensity to enter diapause in the comma butterfly. Oikos 78:569-575

Weisser WW, Houston AI, Volkl W. 1994. Foraging strategies in solitary parasitoids: the trade-off between female and offspring mortality risks. Evol. Ecol. 8:587-597

Wiegmann BM, Mitter C, Farrell B. 1993. Diversification of Carnivorous Parasitic Insects - Extraordinary Radiation or Specialized Dead-End. Am. Nat. 142:737-754

Wiklund C. 1974. Oviposition preferences in *Papilio machaon* in relation to the host plants of the larvae. Entomol. Exp. Appl. 17:189-198

Wiklund C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. Oecologia 18:185-197

Wiklund C. 1977. Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). Oikos 28:56-68

Wiklund C. 1981. Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. Oikos 36:163-170

Wiklund C, Järvi T. 1982. Survival of distasteful insects after being attacked by naive birds: a reaprisal of the theory of aposematic coloration evolving through individual selection. Evolution 36:998-1002

Wiklund C, Persson A. 1983. Fecundity, and the relation of egg weight to offspring fitness in the speckled wood butterfly *Pararge aegeria*, or why don't butterfly females lay more eggs? Oikos 40:53-63

Wiklund C, Åhrberg C. 1978. Host plants, nectar source plants, and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). Oikos 31:169-183

Williams KS. 1983. The coevolution of *Euphydryas chalcedona* and their larval host plants. III. Oviposition behavior and host plant quality. Oecologia 56:336-340

Willis MA, Arbas EA. 1991. Odor-modulated upwind flight of the sphinx moth, *Manduca sexta* L. J. Comp. Physiol. B. 169:427-440

Zangerl AR, Berenbaum MR. 1993. Plant chemistry, insect adaptations to plant chemistry, and host plant utilization patterns. Ecology 74:47-54

Zaviezo T, Mills N. 2000. Factors influencing the evolution of clutch size in a gregarious insect parasitoid. J. Anim. Ecol. 69:1047-1057