



A General Model for Host Plant Selection in Phytophagous Insects

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We develop a general theoretical framework for exploring the host plant selection behaviour of herbivorous insects. This model can be used to address a number of questions, including the evolution of specialists, generalists, preference hierarchies, and learning. We use our model to: (i) demonstrate the consequences of the extent to which the reproductive success of a foraging female is limited by the rate at which they find host plants (host limitation) or the number of eggs they carry (egg limitation); (ii) emphasize the different consequences of variation in behaviour before and after landing on (locating) a host (termed pre- and post-alighting, respectively); (iii) show that, in contrast to previous predictions, learning can be favoured in post-alighting behaviour—in particular, individuals can be selected to concentrate oviposition on an abundant low-quality host, whilst ignoring a rare higher-quality host; (iv) emphasize the importance of interactions between mechanisms in favouring specialization or learning.

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Introduction

The host plant selection behaviour of phytophagous insects provides a variety of related questions at a number of levels (Futuyma, 1983; Courtney *et al.*, 1989; Renwick, 1989; Thompson & Pellmyr, 1991; Bernays & Chapman, 1994; Mayhew 1997). Why are some species specialists, laying eggs (ovipositing) on only one species, whereas others are generalists, who lay eggs on a number of different species where their larvae can develop (termed polyphagy)? In generalist species, why do females exhibit preference hierarchies, preferring to lay eggs on some host species rather than others? Given the existence of preference hierarchies, should they change with the experience of individuals (learning)?

A large body of theory has addressed these questions, utilizing a range of different approaches, and based upon general foraging models as well as those specifically constructed for phytophagous insects (Stephens & Krebs, 1986). This work has demonstrated that there are a number of factors or mechanisms that may be involved in the evolution of host plant selection behaviour. For example: (a) specialization can be favoured if trade-offs lead to individuals being able to utilize (find, oviposit on and consume as larvae) a single host species more efficiently than multiple species (Levins & MacArthur, 1969; Futuyma, 1983; Bernays & Weislo, 1994); (b) preference hierarchies may be favoured in generalists if they reflect the quality of the different host species for larval development, with females preferring to oviposit on species where offspring fitness will be higher, due to factors such as

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nutritional value, microhabitat or the abundance of natural enemies (Jaenike, 1978; Wiklund, 1981; Singer, 1983; Ward, 1987; Courtney *et al.*, 1989); (c) changes in preference hierarchies (learning) can be favoured for a variety of reasons such as variation in host quality or abundance (Rausher, 1978, 1980; Papaj, 1986a; Dukas & Ellner, 1993; Dukas & Clark, 1995).

Here, we construct a general model for the host plant selection behaviour of phytophagous insects. In doing so, we build upon previous work in two ways. First, we provide a single framework for examining the range of mechanisms that have previously been proposed to explain specialization, generalists and learning (much previous work represents special cases of our model). This allows the causal factors and relative importance of different mechanisms to be compared, and in particular the role of interactions between mechanisms to be explored. Second, we incorporate several important life history traits that have received little attention in previous theoretical work, but are likely to be important for phytophagous insects. Specifically, we consider: (a) the extent to which the reproductive success of a foraging female is limited by the rate at which they find host plants (host limitation) or the number of eggs they carry (egg limitation); (b) the different consequences of variation in behaviour before and after landing on (locating) a host (termed pre- and post-alighting, respectively); (c) when host plant suitability differs within host plant species as well as between; (d) when larval feeding experience can alter host plant suitability.

Our main motivation for constructing this model was to examine when learning would be favoured in the pre- and/or post-alighting host plant selection behaviour of polyphagous species. Previous theoretical work on preference hierarchies has predicted that the relative ranking of preferences for species is fixed—less-favoured species are only oviposited on when the more preferred species are rare or absent (Courtney *et al.*, 1989). However, experience in ovipositing on a host species can increase the preference for landing (pre-alighting preference; e.g. Traynier, 1984; Papaj, 1986a; Landolt & Molina, 1996; Cunningham *et al.*, 1998, 1999) and ovipositing (post-alighting preference; Prokopy *et al.*, 1982; Cunningham *et al.*, 1998, 1999) on that species

relative to others. Although mechanisms such as increased foraging efficiency could explain changes in pre-alighting preferences (Rausher, 1978, 1980; Wiklund, 1981; Dukas & Ellner, 1993; Dukas & Clark, 1995), the adaptive explanations for changing post-alighting preferences are not clear (Papaj & Rausher, 1983, 1987; Cunningham *et al.*, 1998, 1999). In particular, as relatively abundant host species will be encountered more frequently, learning can lead to an increased preference for the most abundant host species. This could result in the situation where females will preferentially oviposit on an abundant host species, irrespective of their innate preferences, and consequently ignore any rare, but higher-quality host species, even when they land on it. We use our model to explore a number of possible situations under which this seemingly paradoxical behaviour can be favoured.

General Model

In this section we construct a general model for host plant selection in polyphagous insects. The mathematical methods that we use are based upon that have been used previously to predict the oviposition behaviour of parasitoid wasps (Charnov & Stephens, 1988; Hunter & Godfray, 1995; West *et al.*, 1999a; see also Stephens & Krebs, 1986). We allow different host plant species to vary in: (1) the quality of resources that they offer for larval development; (2) the rates at which they occur in nature; (3) the rate at which females locate these hosts (i.e. detect or recognize a host that they encounter), and (4) the rate at which females oviposit on them (acceptance) when they are located.

We consider a polyphagous insect which is able to oviposit on K different host species. Only a single egg is ever laid on a host plant, although our model could be extended to include optimization of clutch size. The fitness of an egg laid on host plant species i ($i \in \{1, 2, \dots, K\}$) is given by what we term *host quality*, F_i . Host quality is defined as the survival rate (to adulthood) of a larva laid on that species multiplied by expected lifetime fertility (Charnov & Stephens, 1988). Host quality (F_i) will differ between host species for a number of reasons such as nutritional status and the abundance of natural enemies. Although

not considered here, our model could be used to consider the consequences of seasonal variation in host quality due to leaf age (Rausher, 1980). The density at which host plants occur is λ , and a proportion P_i of these host species is i ($\sum_{i=1}^k P_i = 1$).

We assume that females do not necessarily recognize every individual plant that they encounter, and that individual plants of host species i are located at a rate O_i . This term includes the time taken to decide on whether or not to oviposit on a plant of that species, which may involve pre- and post-alighting behaviour. An egg is laid on an individual plant of species i at a rate A_i (termed the post-alighting acceptance rate of species i). The rate at which eggs are laid on individuals of host plant species i is therefore given by $\lambda P_i O_i A_i$.

We consider a proovigenic species in which females emerge with all their eggs mature and ready to lay. In Appendix A we show that similar results are obtained with a model for a synovigenic species in which females mature eggs throughout their lives. We assume that each female has x eggs, and that the mortality rate per unit time of a female is μ . For mathematical simplicity we assume that the time taken to oviposit is negligible (as it is for the species on which we carry out empirical research, *Helicoverpa armigera*, but possibly not others), although oviposition time could be added easily into the model, and allowed to differ between host plant species [see Rosenheim (1999a, b) for a recent discussion of how oviposition time can be incorporated into more complex models and how it can be important in some parasitoid species]. The maximum reproductive lifespan of a female, τ (i.e. time before she runs out of eggs), is given by

$$\tau = \frac{x}{\lambda \sum_{i=1}^K P_i O_i A_i}, \quad (1)$$

her initial egg load divided by her rate of oviposition.

The fitness of a female (W) is therefore given by the equation

$$W = \left(\int_0^\tau e^{-\mu t} dt \right) \left(\lambda \sum_{i=1}^K P_i O_i A_i F_i \right), \quad (2)$$

where the first term in brackets is her expected lifespan, and the second term in brackets her rate of gain fitness per unit time.

An important feature of eqn (2) is that it allows a female's reproductive success to be limited by the number of eggs she carries (egg limited) or the number of host plants that she can locate (host or time limited). Previous theoretical models have frequently assumed that females are only limited by the number of hosts that she can locate (i.e. that the upper limit to the integral in eqn (2) is infinite). However, the possibility of egg limitation should be incorporated because empirical data suggest that it occurs (see discussion), and because it will determine the advantages of factors that can result from learning, such as increased foraging efficiency (e.g. locating extra hosts may provide little benefit to females who are egg limited). The importance of egg or host limitation is captured in our model by the single dimensionless combination, $\phi = \mu x / \lambda$. In the case of pure egg limitation, ϕ approaches zero; while for pure host limitation, ϕ approaches infinity. Host limitation is greatest when the risk of mortality is high, initial egg load is high, and host encounter rate is low. Following West *et al.* (1999a) we construct an index of host limitation $\Phi = \phi / (1 + \phi)$ that maps the egg/host limitation continuum onto the unit interval, with zero being pure egg limitation, and one being pure host limitation. Our general model allows any number of host plant species. In the following sections, where we provide specific solutions, we assume that there are two host plant species ($k = 2$). This keeps the mathematics simple, and facilitates explanation. The same general qualitative predictions apply when there are more host plant species.

Our aim is to determine the optimal oviposition strategy (evolutionary stable strategy, ESS), in terms of acceptance rates of the different host plant species (A_i), under a number of different scenarios. Previous work has focused on the situation when the relative ranking of preferences for different host plant species are fixed (reviewed by Courtney *et al.*, 1989). In model I we show that this type of scenario arises as a special case of our general model. Then, in models II–IV, we consider a series of more complex scenarios, where the relative rankings of preferences for different

host plant species may change. Although these models can be used to examine the advantage of specialization, our aim is to consider when learning, should be favoured (learning can be thought of as providing a means for facultative specialization). In particular, we show when females should preferentially oviposit on an abundant host species, regardless of their innate preferences, and consequently ignore any rare, but higher-quality host species, even when they land on them. An important point here is that our model does not contain or assume an explicit mechanism of the learning process—instead we aim to show how variation in the relative abundance of host plant species can select for females to preferentially oviposit on different host plants, a behaviour that has been observed to result from learning (Cunningham *et al.*, 1998).

Model I: Host Limitation and Host Plant Selection

A number of theoretical models developed for insects with phytophagous and other feeding habits (e.g. Jaenike, 1978; Rausher, 1985; Charnov & Stephens, 1988; Courtney *et al.*, 1989) predict that when more favourable hosts (higher host quality, F_i) are rare or absent, females are selected to broaden the range of species on which they will oviposit, such that they also lay eggs on less favourable hosts (lower F_i). In this section, we show that this prediction arises as a special case of our general model. In particular, we show that as females become more host-limited they are selected to oviposit on less favourable hosts, whilst still ovipositing on more favourable hosts.

Assume that all host plant species are found at the same rate, and so $O_i = 1$ for all i . For simplicity and ease we consider the case when there are two host plant species ($i = \{1, 2\}$), one of which ($i = 1$) is higher quality for offspring development than the other ($i = 2$). Specifically, $F_1 = 1$ and $F_2 < 1$. The better quality host species will always be accepted for oviposition ($A_1 = 1$) and so our aim is to determine the optimal rate at which the lower quality host species will be accepted (i.e. the value of A_2).

In order to find the optimal (ESS) acceptance of plant species two we assume a rare mutant that adopts the strategy A'_2 (with resultant fitness

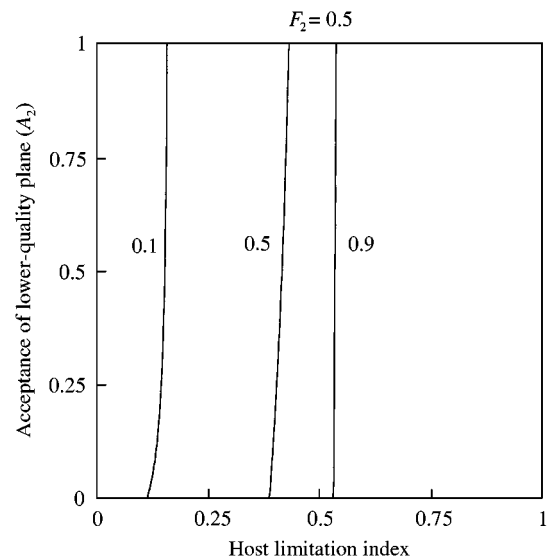


FIG. 1. The acceptance of the lower-quality host species (A_2) against the extent of host limitation (Φ) in model I. The different lines show when the higher-quality species makes up a different proportion of the plants encountered (P_1). Acceptance of the lower-quality host species is increased by: (1) a greater extent of host limitation (higher Ω), (2) a lower proportion of plants being the higher-quality host species (lower P_1).

of W'), and solve $\partial W'/\partial A'_2|_{A_2=A_2} = 0$. This gives the equality

$$\left(F_2 (e^{\phi/(A_2(P_1-1)-P_1)} - 1) + \frac{\phi(A_2F_2 - P_1(A_2F_2 - 1)e^{\phi/(A_2(P_1-1)-P_1)})}{(A_2 + P_1 - A_2P_1)^2} \right) = 0. \quad (3)$$

This must be solved numerically and some examples are given in Fig. 1. These results agree with previous work in that: (a) as females become more host limited they are selected to also oviposit on less favourable hosts; (b) the switch to ovipositing on less favourable hosts shows a threshold (i.e. $0 < A_2 < 1$ occurs over a very small area of parameter space).

Model II: Concentrating on a Plant Species Increases the Efficiency of Host Location/Utilization

HYPOTHESIS AND MODEL

We now consider the possibility that there is a trade-off in the efficiency with which females

can locate different host species. This could occur for a number of reasons. One possibility is that concentrating on a particular species enables information about the environment to be processed more efficiently, and the rate of host plant location/utilization to be increased (Rausher, 1978, 1980; Wiklund, 1981; Stanton, 1984; Lewis, 1986; Fox & Lalonde, 1993; Bernays, 1998; Cunningham *et al.*, 1998; Dukas & Ellner, 1993; Papaj & Lewis, 1993; Dukas & Clark, 1995; Dall & Cuthill, 1997; Bernays & Funk, 1999), especially if different plant species are found in different places or at different times. In order to model this we assume that the time taken to find hosts of that species and decide whether to oviposit (O_i) depends upon the extent to which oviposition behaviour concentrates upon that species (i.e. A_i)—this assumes changes in both pre- and post-alighting behaviour. Specifically,

$$O_i = \left(\frac{A_i}{\sum_{g=1}^K A_i} \right)^l \tag{4}$$

The location/utilization rate of a plant species therefore increases as the acceptance rate of that plant species increases relative to other plant species. The form of this relationship is determined by the parameter l . The relationship is linear with $l = 1$, has an accelerating slope with $l > 1$, and a decelerating slope with $l < 1$ (Fig. 2). Note that when $l = 0$, this reduces to model I. An alternate possibility considered previously (e.g. Dukas & Ellner, 1993; Dukas & Clark, 1995) would have been to assume only changes in pre-alighting behaviour, with the location rate of different host plant species being negatively correlated (i.e. O_1 negatively correlated to O_2).

Assuming only two host plant species as above ($F_1 = 1, F_2 < 1$), and by substituting eqn (4) into eqn (2) we find that

$$W \propto (1 - e^{\phi/(A_2(P_1 - 1))(A_2/(A_1 + A_2))^l - A_1 P_1 (A_1/(A_1 + A_2))^l}) \times \left(A_1 P_1 \left(\frac{A_1}{A_1 + A_2} \right)^l + A_2 F_2 (1 - P_1) \times \left(\frac{A_2}{A_1 + A_2} \right)^l \right) \tag{5}$$

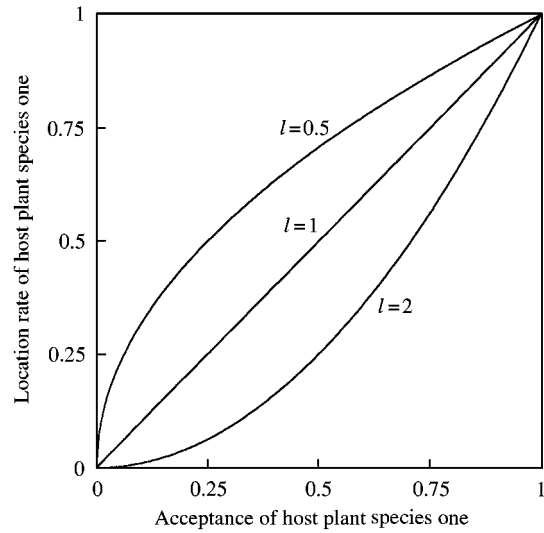


FIG. 2. The location rate of host species one (O_i) as a function of the acceptance rate of that species (A_i), for different values of the shape parameter l (model II). Two host species are assumed, and the acceptance rate of species two is assumed to be one minus the acceptance of species one ($A_2 = 1 - A_1$). Note that the location rate of host species one increases as foraging is concentrated on that species (i.e. higher acceptance of species one).

PREDICTIONS

The predictions that emerge depend critically upon the parameter l , with the critical point being $l \approx 1$ (exactly, $l = 1$ for $\Phi = 0$ or 1). If $l \geq 1$ then the optimum strategy is generally to either accept only host species one ($A_1 = 1, A_2 = 0$), or only host species two ($A_1 = 0, A_2 = 1$). For a certain extent of host limitation (ϕ or Φ) and quality of host species two (F_2), which of these two strategies is optimal depends upon the relative abundance of the two host species: increasing abundance favours oviposition on that species. However, if $l < 1$ then there is also a range of intermediate abundance in which the optimal strategy is to oviposit on both host plant species ($A_1 = 1, A_2 = 1$).

Put into biological terms, the higher the value of l , the greater the advantage from concentrating foraging on a single host species (through specialization or learning). Consequently, if $l \geq 1$ then the optimal strategy is to always concentrate foraging on one host species. The optimal strategy changes from ovipositing on the higher-quality host (species one) to the lower-quality host (species two) at a critical point when the abundance of these species are low and high enough,

respectively. At this point the increased ability to find the (more common) lower-quality host species exactly balances the lower fitness returns from offspring laid. In contrast, if $l < 1$, then there is an intermediate area where the optimal strategy is to oviposit on both host species. In this area the abundance of neither of the two host species is high enough to warrant concentrating oviposition on that species only.

A common result from foraging theory is that a given host plant species generally should be either ignored or accepted totally (i.e. $A_i = 0$ or 1), usually referred to as the zero-one rule (Stephens & Krebs, 1986; Charnov & Stephens, 1988). In all cases that we considered the areas where an intermediate acceptance proportion is favoured ($0 < A_i < 1$) were extremely small (e.g. Fig. 1). This allows us to ignore these areas for explanation purposes in this and later sections.

We now consider the boundary regions at which the optimum strategy switches between the three strategies that can be optimal: ovipositing on only one of the two host plant species or both. These switching points can be found by considering the point at which the fitness of the different strategies are equal (e.g. the fitness of ovipositing on only host plant species one ($A_1 = 1, A_2 = 0$) is equal to that of ovipositing on only host plant species two ($A_1 = 0, A_2 = 1$) when

$$F_2 = P_1(1 - e^{-\phi/P_1})/(P_1 - 1)(e^{\phi/(P_1 - 1)} - 1),$$

and some examples are shown in Fig. 3.

Oviposition on the lower-quality host (species two) is made more likely with: (1) a higher relative abundance of host species two (lower P_1); (2) higher quality of host species two (larger F_2), and (3) a greater extent of host limitation (higher ϕ). In cases where there is an intermediate area, in which oviposition on both host plant species is favoured ($l < 1$), the range of abundance (P_1) over which this is the favoured strategy is increased with: (1) higher quality of host species two (higher F_2); (2) a greater extent of host limitation (higher ϕ), and (3) a lower value of l . The extent of host limitation is important because it alters the advantage that a female gains by the increased location efficiency that results from concentrating foraging on a single host species.

This model (and those that follow) predicts situations in which the optimal strategy is for females to preferentially oviposit on an abundant low-quality host plant species, while ignoring a rare, but higher-quality host plant species. This is the pattern which learning in oviposition behaviour can lead to (Cunningham *et al.*, 1998), and which we are attempting to explain.

Model III: Concentrating on a Plant Species Increases the Ability to Discriminate Intraspecific Variation in Plant Quality

HYPOTHESIS AND MODEL

We now consider the possibility that there is a trade-off between the number of host species that a female is foraging for, and the ability to detect differences in plant quality within species. This could occur for a number of reasons, such as: (a) females can concentrate their foraging in areas where individuals of a certain host species tend to be above-average quality, or (b) concentrating on a particular host species enables females to process more information about that species, and so detect variation in the quality of individual plants more efficiently [see Janz & Nylin (1997) for an example of such an advantage with specialization]. A conceptually similar possibility that would also lead to an increase in offspring fitness by concentrating oviposition on a single host, and would be covered by the same model, is that females produce eggs of a size appropriate for the host species which they are encountering (Fox *et al.* 1997).

In order to model this scenario we assume that the quality of a host species (F_i) increases as individuals concentrate on foraging and oviposition on that host (i.e. higher A_i and lower $A_{\neq i}$). Specifically,

$$F_i = f_i \left(\frac{A_i}{\sum_{i=1}^K A_i} \right)^m, \quad (6)$$

where f_i is the average quality of host species i . The quality of a host species therefore increases as oviposition is concentrated on that host species relative to other host species. Note that: (i) as in model II we are assuming that this occurs due to changes in both pre- and post-alighting

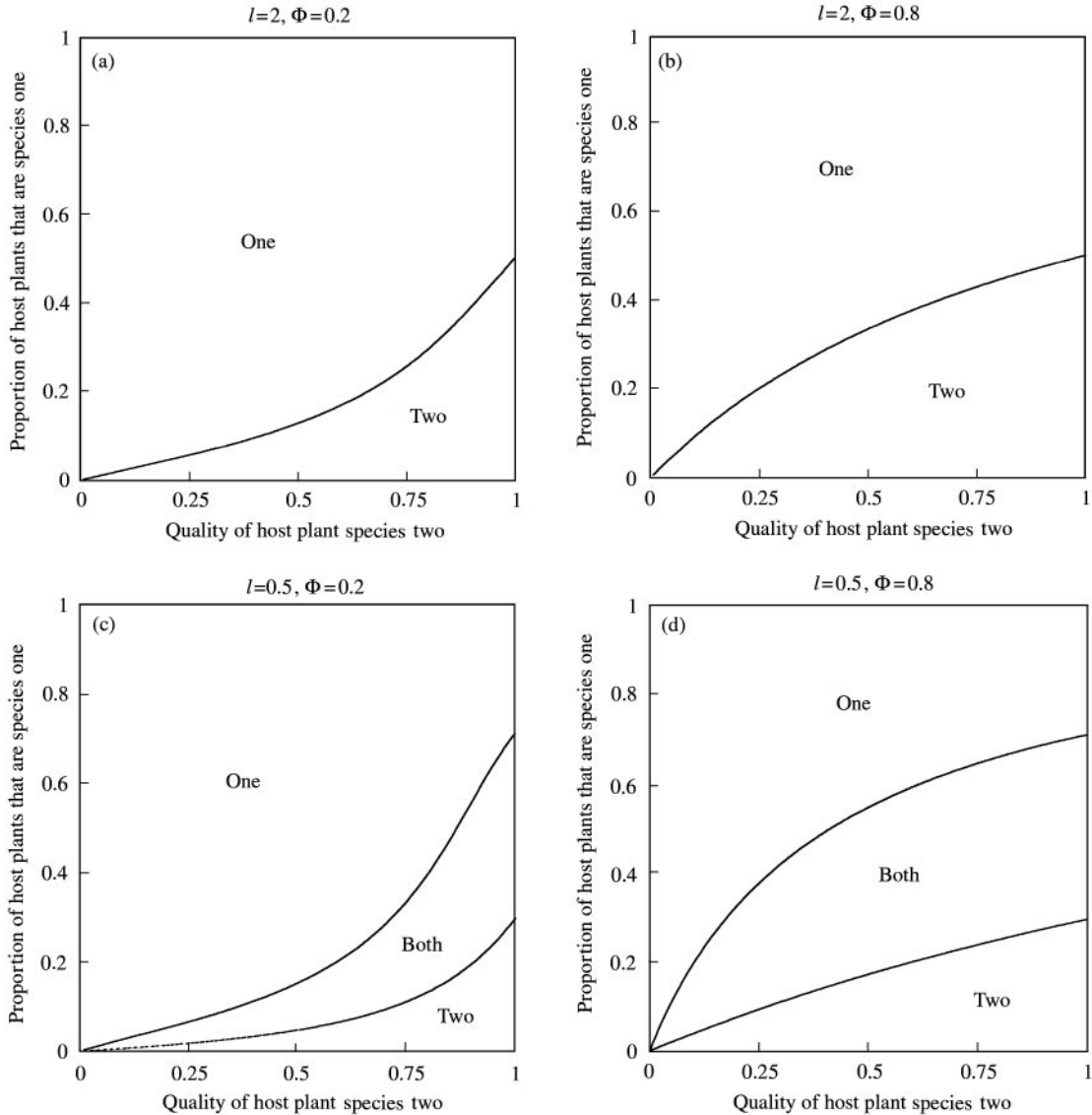


FIG. 3. The area of parameter space for which the different oviposition strategies are favoured with model II. The figures show the areas in which the optimal strategy is to oviposit on only host species one (one), only host species two (two) and both host species (both). The proportion of host plants that are species one (P_1) is given on the Y-axis, and the quality of host species two (F_2) on the X-axis.

behaviour—an alternate possibility would have been to assume only changes in pre-alighting behaviour, with the quality of host species i (F_i) a function of the location rates (e.g. $F_i = f_i(O_i/\sum_{i=1}^K O_i)^m$); (ii) if the increase in average quality comes through rejection of lower-quality plants then a negative correlation between host quality F_i and the pre- and/or post-alighting selection behaviour (O_i or A_i) could be introduced.

The form of the relationship in eqn (6) is determined by the parameter m , as was the case with l in eqn (4) (see Fig. 2). For mathematical simpli-

city and illustrative purposes we assume that all host species are found at the same rate ($O_i = 1$ for all i). Assuming only two host species as above ($f_1 = 1, f_2 < 1$), and by substituting eqn (6) into eqn (2) we find that

$$W \propto (1 - e^{\phi/(A_2(P_1 - 1) - A_1 P_1)}) \left(A_1 P_1 \left(\frac{A_1}{A_1 + A_2} \right)^m + A_2 f_2 (1 - P_1) \left(\frac{A_2}{(A_1 + A_2)} \right)^m \right). \quad (7)$$

PREDICTIONS

The basic predictions of this model are quite similar to those in model II above. If $m \geq 1$ then the optimum strategy is either to accept only host species one ($A_1 = 1, A_2 = 0$), or only host species two ($A_1 = 0, A_2 = 1$). Similar to model II, for a certain extent of host limitation (ϕ or Φ) and average quality of host species two (f_2), which of these two strategies is optimal depends upon the relative abundance of the two host species: increasing abundance favours oviposition on that species. However, in contrast to model II, if $m < 1$ then only in some cases there is a range of intermediate abundance in which the optimal strategy is to oviposit on both host species ($A_1 = 1, A_2 = 1$). This is only the case when the extent of host limitation (ϕ or Φ) is sufficiently high.

As before, the exact point at which the optimum strategy switches between the three strategies (ovipositing on only one of the two host species or both) can be determined. Similar examples to those given in Fig. 3 could be plotted. As in model II, oviposition on the lower-quality host (species two) is made more likely with: (1) a higher relative abundance of host species two (lower P_1) and (2) higher quality of host species two (larger F_2). Similarly, the range of abundance (P_1) in which oviposition on both host plant species is the favoured strategy is increased with: (1) greater quality of host species two (higher F_2), and (2) a lower value of m .

In contrast to model II, model III predicts that: (1) oviposition on the lower-quality host plant species (species two) is made more likely with a lower extent of host limitation (lower ϕ) and, (2) the range of abundance (P_1) in which oviposition on both host plant species is the favoured strategy is increased to a greater amount by a higher extent of host limitation (larger ϕ). This difference arises between models II and III because of how they provide an advantage to concentrating (specializing) oviposition on a single host species. In model II, by concentrating foraging on a single species, females increase the rate at which they locate host plants, which will be more important to females who are host limited. In model III, by concentrating foraging on a single species, females increase the quality of plants which they locate, which is most important to females who

are severely egg limited. These factors could occur simultaneously, providing an advantage across the egg/host limitation continuum, and we consider this possibility in Appendix C.

Model IV: Larvae Use More Than One Host Plant During their Development

HYPOTHESIS AND MODEL

We now consider a situation in which the fitness of offspring laid on a host plant species varies with the density of that species. Specifically, we consider when: (1) larvae feed on more than one plant in order to complete their development, and (2) either (a) larvae prefer plant species they have previously encountered (termed induction of preference), or (b) larvae show no preferences for plant species that they have previously encountered, but receive a fitness cost when feeding on multiple plant species (Cunningham *et al.*, in press).

These assumptions are likely to be satisfied across a wide range of species. First, feeding by larvae on multiple plants is common (Bernays & Chapman, 1994). Possible reasons for this include: (a) having totally consumed a plant; (b) avoidance of mobilized plant chemical defences, and (c) avoidance of natural enemies which are attracted by frass or plant damage (Cunningham *et al.*, in press). Second, there are a large number of studies showing that larvae learn to select and feed upon plant species that they have previously encountered (reviewed by Szentesi & Jermy, 1990; Bernays & Chapman, 1994). In the extreme, larvae of some species will ignore all new food types, and starve to death rather than feed on a new host plant species (termed "starving to death at a Lucullian banquet"; Jermy, 1987). However, the reasons for this induction of preference are unclear (Bernays & Chapman, 1994). One possibility is that it can increase the efficiency with which larvae find or recognize other individual host plants. Experience of a host plant species can also improve a larva's ability to detoxify or digest the tissue of that species (i.e. there is a fitness cost to feeding on multiple plant species Karowe, 1989; Lindroth, 1991; Hung *et al.*, 1997). Widespread evidence for such a metabolic cost when feeding on multiple host plant species is lacking, possibly due to the

difficulties of experimentally separating the consequences of not feeding (resulting from induced preferences) and reduced digestion ability (Bernays & Chapman, 1994).

Here, we consider a scenario where larvae prefer plant species they have previously encountered. In Appendix B we show that similar results are obtained if we assume that after finishing on their first host plant larvae move at random to another host plant, and that there is a fitness cost to feeding on multiple host plant species. We assume that larvae feed upon two hosts plants, the plant upon which they are laid and one other. We assume that when larvae move to their second host plant that they continue to search until they find an individual of the same plant species. We assume that there are two host species that vary in quality ($f_1 = 1$; $f_2 < 1$). Our aim is to determine whether post-alighting host acceptance (A_i) can be expected to change, and so we assume that all host species are located at the same rate ($O_i = 1$ for all i), although similar results can be obtained by setting the post-alighting acceptance rate the same for all species ($A_i = 1$ for all i), and determining how foraging behaviour (O_i) is expected to evolve.

Assume that when larvae move to their second host plant they continue to search until they find the same species upon which they were feeding. Assume that the decrement in fitness of each movement between host plants (i.e. rejection of an individual of the host plant species they did not feed upon, and continuation of searching) is g . The value of g incorporates a number of factors such as predation and reduced growth. If an egg is laid on plant species one then the probability that it takes n moves to find another individual of plant species one multiplied by the fitness consequences of n moves (S_n) is $(1 - P_1)^{n-1} P_1 (1 - g)^n$

$$W \propto \frac{(1 - e^{\phi/(A_2(P_1 - 1) - A_1 P_1)})(A_1 P_1^2(1 + P_1(g - 1)) + A_2(P_1 - 1)^2 f_2(P_1(g - 1) - g))(1 - g)}{(1 + P_1(g - 1))(P_1(g - 1) - g)}. \quad (10)$$

(similar results are found with other fitness functions). The sum of all the possibilities ($\sum_{n=1}^{\infty} S_n$) can be put into the form of a geometric series, in which case the fitness of an egg laid on host plant species one is given by

$$F_1 = P_1(1 - g)/(1 - (1 - P_1)(1 - g)). \quad (8)$$

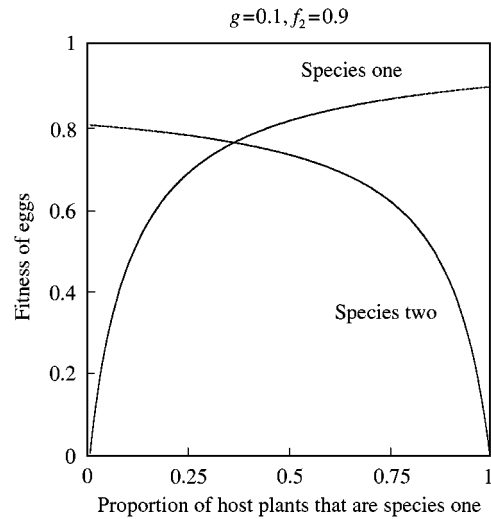


FIG. 4. The fitness return, in model IV, from laying an egg on the different host species against the proportion of host plants that are species one.

Similarly, the fitness of an egg laid on host plant species two is given by

$$F_2 = f_2(1 - P_1)(1 - g)/(1 - P_1(1 - g)). \quad (9)$$

Examples of how the fitness of eggs laid on the two host species varies with abundance are shown in Fig. 4. As host species one becomes more common (increasing P_1) the fitness of an individual laid on this species (F_1) increases because another individual of that species is found more quickly. Similarly, as host species two becomes more common (decreasing P_1) the fitness of an individual laid on this species (F_2) increases because another individual of that species is found more quickly.

Substituting eqns (8) and (9) into eqn (2) we find that

PREDICTIONS

The way in which fitness varies with the acceptance of the two host species is qualitatively similar to that in models II and III, especially when $l < 1$ or $m < 1$. As the abundance of host species one (P_1) moves from low (0.1) to medium

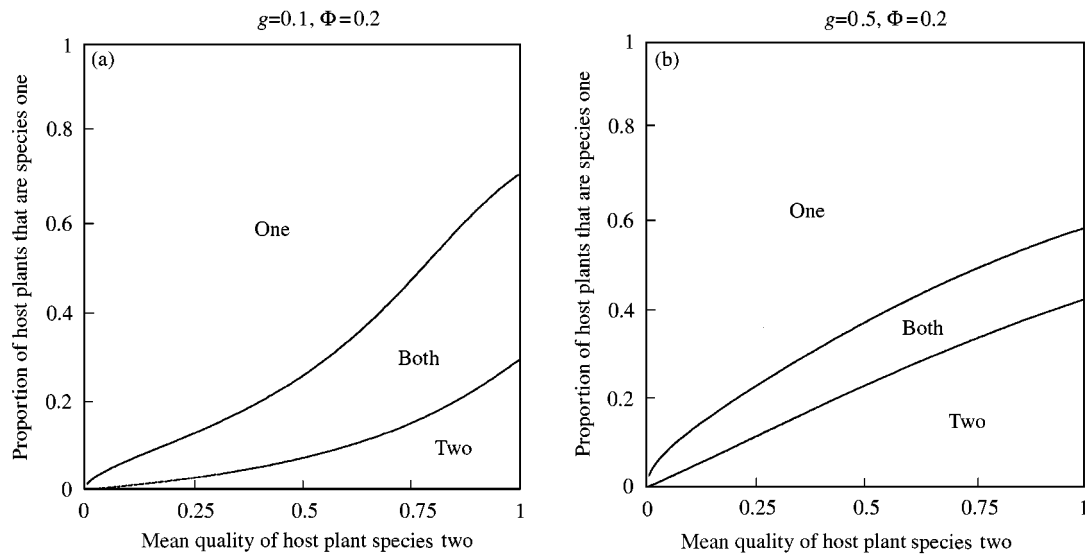


FIG. 5. The area of parameter space for which the different oviposition strategies are favoured with model IV. The figures show the areas in which the optimal strategy is to oviposit on only host species one (one), only host species two (two) and both host species (both). The proportion of host plants that are species one (P_1) is given on the Y-axis, and the mean quality of host species two (f_2) on the X-axis.

(0.5) to high (0.9), the optimal strategy changes from oviposit on species two only ($A_1 = 0$, $A_2 = 1$) to oviposit on both host species ($A_1 = 1$, $A_2 = 1$) to oviposit on host species one only ($A_1 = 1$, $A_2 = 0$).

As before, the exact point at which the optimum strategy switches between the three strategies (ovipositing on only one of the two host species or both) can be determined, and some examples are given in Fig. 5. Switching from oviposition on the higher-quality host species ($i = 1$) to both host species and then the lower-quality host species ($i = 2$) is favoured by: (1) a higher proportion of the host plants being the lower-quality species (lower P_1); (2) a lower extent of host limitation (smaller ϕ); (3) the quality of species two being more similar to that of species one (higher f_2), and (4) a higher fitness cost for moving between individual host plants (higher g).

The area of parameter space in which the optimal strategy is to oviposit on both species ($A_1 = 1$, $A_2 = 1$) is increased by: (1) a lower fitness cost for moving between individual host plants (smaller g); (2) the quality of host species two becoming increasingly higher (larger f_2), and (3) a greater extent of host limitation (higher ϕ) (Fig. 5). If the extent of host limitation is high

enough then the optimal strategy over the entire parameter space can be to oviposit on both host species ($A_1 = 1$, $A_2 = 1$).

Discussion

GENERAL MODEL

We have presented a general model for the host plant selection behaviour of polyphagous insects, that can be used to address a wide range of topics, including the evolution of specialists, generalists, preference hierarchies, and learning. A major advantage of this approach is that it allows the causal factors and relative importance of different mechanisms to be compared. For example, model IV predicts a much larger area of parameter space in which the strategy of ovipositing on both host species ($A_1 = 1$, $A_2 = 1$; reducing the advantages of specialization or learning) is the optimal strategy, compared with models II and III (compare Fig. 3 with Fig. 5). The reason for this is that in models II and III, concentrating foraging and oviposition on a single host increases the rate of finding that host or the average host quality, whereas in model IV the fitness return from laying an egg on the different host species varies with their

abundance, and not with the way in which females forage. This reduces the advantage of concentrating foraging and oviposition (specializing) on a single species.

Our model emphasizes the importance of two factors that have received comparatively little attention in previous theoretical work. First, it emphasizes the different consequences of variation in pre- and post-alighting behaviour, a point that we will return to below, when discussing learning. Second, it allows the role of host and egg limitation to be investigated. In particular, it shows that with some mechanisms, specialization (or generalists learning to concentrate foraging and oviposition on the most abundant host plant species) is differently favoured by the extent of host or egg limitation (models III and IV). This stresses the fact that specialization or learning can be favoured across a wider range of parameter space when multiple mechanisms are at work (see Appendix C for how multiple mechanisms may be combined in a single model).

LEARNING AND FUTURE DIRECTIONS

Can it be adaptive for post-alighting behaviour to change through learning? It has previously been suggested that learning in pre-alighting behaviour can be expected, in response to host abundance (see models II and III), but that learning in post-alighting behaviour should not occur, with post-alighting preference hierarchies fixed to represent host quality (Prokopy *et al.*, 1982; Papaj, 1986b; Papaj & Rausher, 1987). However, learning has been observed in post-alighting behaviour. For example, individuals of the moth *Helicoverpa armigera* are more likely to oviposit on (accept) host plant species on which they have previous experience (Cunningham *et al.*, 1998). Our model demonstrates several mechanisms which would favour individuals who bias their post-alighting preference hierarchies towards more abundant host plant species (which they are more likely to have experienced in the past). First, concentrating both pre- and post-alighting behaviour on a single host plant species can increase the efficiency with which that host is found and utilized (models II and III). Essentially, concentrating on a single species means that less

information needs to be processed by a foraging individual, simplifying the world. Second, in some cases we have argued that host quality (F_i) is not fixed, but increases with abundance (models III and IV), which clearly provides a potential advantage for learning in post-alighting preferences. Furthermore, in many cases, host selection behaviour will be a series of linked behaviours, and foraging insects may not distinguish sensory information from different visual, olfactory and chemotactic cues into distinct pre- and post-alighting phases, suggesting that interactions between these behaviours may be crucial and that it is artificial to divide them into distinct phases (Cunningham *et al.*, 1998).

Our model emphasizes several areas that require empirical work. (1) Experimental or comparative data could be used to test the assumptions of the models and estimate the relevant parameters estimated. For example, does concentrating oviposition on a single host plant species lead to an increase in foraging efficiency or quality of hosts utilized, and if so, what is the shape of the relationship—the parameters l and m (Rausher, 1980; Janz & Nylin, 1997; Bernays, 1998; Benays & Funk, 1999)? (2) Our model provides a single framework with which empirical data could be used to assess the relative importance of different mechanisms that may favour specialization or learning. (3) Fundamental to all mechanisms is an estimate of the extent of host and egg limitation. Although little is known about this in phytophagous insects, it is currently a matter of much debate in the parasitic wasp literature (because of its importance for behaviour and population dynamics), where empirical methodologies for its estimation have been developed, and both theoretical predictions and empirical data support an intermediate position biased towards host limitation (Driessen & Hemerik, 1992; Rosenheim, 1996, 1999a, b; Shea *et al.*, 1996; Ellers *et al.*, 1998, 2000; Sevenster *et al.*, 1998; Casas *et al.*, 2000; Rosenheim *et al.*, 2000; West & Rivero, 2000).

We conclude by noting that although we have constructed a general model that could be applied to many situations, there are several ways in which theory could be developed. For example: (1) our model could be expanded to incorporate factors such as the time taken for pre- and

post-alighting; (2) simulation studies could be used to assess the relative fitness of different strategies (specialist, generalists who do and do not learn) when the abundance of different host plants varies between generations (Stephens, 1991); (3) our models have suggested several reasons why learning in pre- and post-alighting host selection behaviour could be favoured (by examining how preference hierarchies are favoured to change with environmental conditions)—an alternative and complementary approach would be to construct dynamic mechanistic models that predict how females should learn, altering their oviposition behaviour with previous experience and physiological state (see Rausher, 1985; Stephens & Krebs, 1986; Stephens, 1987, 1991; Mangel & Clark, 1988). In addition, although our focus has been on phytophagous insects, our models could easily be applied to species with different life histories (e.g. Jaenike, 1982, 1983; Prokopy *et al.*, 1982; Charnov & Stephen 1988).

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Appendix A

General Model for Females that Mature Eggs as Adults

Here, we construct a general model for females that mature eggs throughout their life. To construct an exact model would be extremely complicated and require details about the physiological mechanism of egg production that we do not possess at present. However, the biological essence of this type of situation can be captured with a disk equation, as was suggested by Charnov & Stephens (1988), and since used by others (e.g. Hunter & Godfray, 1995; West *et al.*, 1999a). We assume that the maximum number of eggs that can be laid per unit time is y —this corresponds to the maximum rate at which eggs could be matured by adults. If we assume all other assumptions are the same as in our general model in which females are born with a fixed number of eggs, then the general equation for fitness, analogous to eqn (2), is

$$W \propto \frac{\lambda}{1 + (1/y)\lambda(\sum_{i=1}^K \lambda P_i O_i A_i)} \times \left[\sum_{i=1}^K \lambda P_i O_i A_i F_i \right]. \quad (\text{A.1})$$

The first term on the right-hand side represents the rate at which eggs are deposited, and the second term (in square brackets) is the average fitness gain per host. In this model the extent of egg or host limitation is measured by $\phi_2 = y/\lambda$. Again an index of host limitation can be constructed that maps this onto the unit interval, $\Phi_2 = \phi_2/(1 + \phi_2)$, with zero being pure egg limitation, and one being pure host limitation. The assumptions of our different models (I–IV) can be used with eqn (A.1) in exactly the same manner as with eqn (2) to determine the optimal oviposition strategy for a number of scenarios. For example, consider model II, when concentrating on a plant species is assumed to increase the efficiency of host location. If we assume only two host plant species ($F_1 = 1$, $F_2 < 1$), and substitute eqn (4) into eqn (A.1), we find that

$$W \propto \frac{A_1 P_1 \left(\frac{A_1}{(A_1 + A_2)} \right)^i + A_2 F_2 (1 - P_1) \left(\frac{A_2}{(A_1 + A_2)} \right)^i}{A_1 P_1 \left(\frac{A_1}{(A_1 + A_2)} \right)^i + A_2 (1 - P_1) \left(\frac{A_2}{(A_1 + A_2)} \right)^i + \phi_2} \quad (\text{A.2})$$

The predictions of this equation are very similar to those of eqn (5) in model II, and the examples given in Fig. 3.

Appendix B

Extending Model IV to when Larvae do not show Preferences for Particular Host Plant Species

Assume that after feeding on their first host plant larvae move at random to another host plant. If a juvenile feeds upon both host species its fitness is q , where q is also between 1.0 and 0. If feeding upon two host plants leads to reduced fitness then q will be less than $f_1 (= 1)$ or f_2 . This can be accounted for in our model by allowing the fitness return from laying an egg on the different host plant species (F_i) to vary with relative host plant abundance (P_i). Specifically, the fitness of an egg laid on host plant species one is given by

$$F_1 = P_1 + (1 - P_1)q. \quad (\text{B.1})$$

The first term on right-hand side represents the probability that the second plant it feeds upon is

host plant species one (P_1) multiplied by its fitness in this case (1.0). The second term represents the probability that the second plant it feeds upon is host plant species two (P_2) multiplied by its fitness in this case (q). Similarly,

$$F_2 = P_1 q + (1 - P_1) f_2. \quad (\text{B.2})$$

The fitness of ovipositing on a given host plant species increases with its density because the likelihood of the second plant being the same species increases. Substituting eqns (B.1) and (B.2) into eqn (2) we find that

$$W \propto (1 - e^{\phi/(A_2(P_1 - 1) - A_1 P_1)}) (A_2(P_1 - 1) \times ((P_1 - 1)f_2 - P_1 q) + A_1 P_1 (P_1 + q - P_1 q)). \quad (\text{B.3})$$

The pattern of how fitness varies with acceptance of the two host plant species, and overall predictions are qualitatively very similar to those of model IV. Switching from oviposition on the higher-quality host plant species ($i = 1$) to both host plant species and then the lower-quality host plant species ($i = 2$) is favoured by: (1) a higher proportion of the host plants being the lower-quality species (lower P_1); (2) a lower extent of host limitation (smaller ϕ); (3) the quality of species two being more similar to that of species one (higher f_2), and (4) a lower fitness when developing on both host species (lower q). The area of parameter space in which the optimal strategy is to oviposit on both species ($A_1 = 1$, $A_2 = 1$) is reduced by: (1) a lower extent of host limitation (smaller ϕ); (2) the quality of host plant species two being more different to that of host plant species one (lower f_2), and (3) a lower fitness when developing on both host plant species (lower q).

Appendix C

Combining Mechanisms

In this section, we examine the consequences when the different mechanisms from our earlier models operate simultaneously. The possible importance of multiple mechanisms has been emphasized for many areas of life history evolution

(e.g. Hilborn & Stearns, 1982; West *et al.*, 1999b). Consider the possibility that there is a trade-off between: (1) the efficiency with which females can locate different host species (model II), and (2) the number of host plant species that a female is foraging for, and the ability to detect differences in plant quality within species (model III). Combining the mechanisms of models II and III we find that

$$W\alpha \left(1 - e^{\phi/A_2(P_1 - 1)(A_2/(A_1 + A_2))^l - A_1 P_1 (A_1/(A_1 + A_2))^l} \right)$$

$$\times \left(A_1 P_1 \left(\frac{A_1}{A_1 + A_2} \right)^{l+m} - A_2 f_2 (P_1 - 1) \left(\frac{A_2}{A_1 + A_2} \right)^{l+m} \right). \quad (\text{C.1})$$

Combining mechanisms reduces the likelihood and size of an area in which the optimal strategy is to oviposit on both host plant species ($A_1 = 1, A_2 = 1$).