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# How host plant variability influences the advantages to learning: A theoretical model for oviposition behaviour in Lepidoptera

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## Abstract

Learning can allow individuals to increase their fitness in particular environments. The advantage to learning depends on the predictability of the environment and the extent to which animals can adjust their behaviour. Earlier general models have investigated when environmental predictability might favour the evolution of learning in foraging animals. Here, we construct a theoretical model that predicts the advantages to learning using a specific biological example: oviposition in the Lepidoptera. Our model includes environmental and behavioural complexities relevant to host selection in these insects and tests whether the predictions of the general models still hold. Our results demonstrate how the advantage of learning is maximised when within-generation variability is minimised (the local environment consists mainly of a single host plant species) and between-generation variability is maximised (different host plant species are the most common in different generations). We discuss how our results: (a) can be applied to recent empirical work in different lepidopteran species and (b) predict an important role of learning in lepidopteran agricultural pests.
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## 1. Introduction

It is generally accepted that in variable environments, learning can confer advantages in foraging behaviour (Dukas, 1998; Odling-Smee and Braithwaite, 2003; Shettleworth, 1999; Stephens, 1991; Stephens and Krebs, 1986). However, it is also true that if the environment is too variable, learning will not be advantageous—in the extreme, this trait having no advantage if the environment is completely unpredictable. Consequently, it is necessary to determine how the advantage of learning changes with the extent of environmental variability, and with variability on different time scales. Stephens (1993) has examined this problem from a general perspective and argued that learning is favoured when the environment is predictable within the lifespan of individuals, but unpredictable between one generation and the next.

In this paper, we investigate whether the predictions of Stephens' general model hold when a more specific theoretical model is constructed, which includes biological complexities relevant to the host selection behaviour of particular insects—the Lepidoptera. Our model investigates the advantages to learning in Lepidoptera that oviposit (and develop) on many different host plant species (polyphagy). This group includes many of the world's most important insect pest species. Polyphagous insects have been shown to preferentially select certain host plant species for oviposition (reviewed by Mayhew, 1997; Renwick and Chew, 1994). The proximate basis for relative preferences for different host species are thought to result from the balance between visual, olfactory and tactile cues that act as attractants and deterrents for oviposition (Papaj and Rausher, 1987b; Renwick and Chew, 1994). Early theoretical work argued that these preferences formed a fixed hierarchy that reflected the quality of the different host plant species for larval development, with females preferring to oviposit on plants where their

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offspring will do better (Courtney et al., 1989; Jaenike, 1978; Ward, 1987; Wiklund, 1981).

However, there is increasing evidence that host selection behaviour in many polyphagous lepidopteran species (and other insects) can change with experience (reviewed by Cunningham et al., 2002; Papaj and Prokopy, 1989; Papaj and Lewis, 1993). In particular, learning has been shown to lead to an increase in preference for host plant species upon which females have had previous experience ovipositing (host learning). This can be advantageous if it increases the foraging efficiency of females (Papaj, 1986b; Prokopy et al., 1982; West and Cunningham, 2002), for example, by the formation of a "search image" towards specific hosts (Rausher, 1978), or if females are selected to lay on an abundant host because their larvae need to move between plants of the same species during development (Cunningham et al., 2002, West and Cunningham, 2002). The aim of this paper is to determine how variation in host plant abundance influences the fitness consequences of host-learning behaviour in Lepidoptera, and relate our findings to insects that exploit agricultural environments. Our model looks at learning in Lepidoptera, but also applies more generally to other phytophagous insects where ovipositing females search for patches of varying quality.

## 2. Model

In this section we develop a theoretical model to predict when learning in host plant selection is most advantageous. We are concerned with when experience ovipositing on a host plant species increases the preference for that species relative to others. This form of learning in oviposition behaviour may be more prevalent than previously considered, having been demonstrated in several lepidopteran species (Cunningham et al., 1999, 1998b; Landolt, 2001; Landolt and Molina, 1996; Monks and Kelly, 2003; Papaj, 1986b; Skiri et al., 2005; Stanton, 1984; Traynier, 1984). When experience increases preference for a host plant, host plant abundance will influence host selection behaviour; more abundant host species will be encountered more frequently, increasing the insect's preference for these hosts.

Learning in oviposition behaviour may be advantageous for several reasons. First, by concentrating foraging on a particular species it can allow information about the environment to be processed more efficiently, increasing the rate of host plant location or utilisation (Bernays, 1998; Bernays and Funk, 1999; Dukas and Ellner, 1993; Dukas and Clark, 1995; Janz et al., 2005; Lewis, 1986; Papaj, 1986a; Rausher, 1978, 1980; Stanton, 1984; West and Cunningham, 2002). Second, it could allow females to increase their foraging efficiency by allowing them to find plants of higher quality (Janz and Nylin, 1997; West and Cunningham, 2002) or regulate the production of eggs (Fox et al., 1997). Third, if larvae move between host plants of the same species during development, then ovipositing on an abundant host plant species could make it easier for larvae to find other plants (Cunningham et al., 2002; West and Cunningham, 2002).

### 2.1. Basic model

We extend the general model constructed by West and Cunningham (2002) to allow examination of the consequences of environmental variation. Our model allows different host plant species to vary in: (1) the quality of resources that they offer for larval development; (2) the relative frequency at which they occur in nature (relative abundance); (3) the proportion of individual plants of that species which are located by females (location or recognition) and (4) the proportion of located plants on which females oviposit (acceptance or discrimination).

The model considers a polyphagous insect that is able to oviposit on $K$ different host plant species, with a single egg being laid on each host plant. The fitness of an egg laid on host plant species $i$ ($i \in \{1, 2, \ldots, K\}$) is given by host quality, $F_i$, which is defined as the survival rate (to adulthood) of a larvae laid on that species multiplied by expected lifetime fertility. The density at which host plants occur is $\lambda$, and a proportion $P_i$ of these is host species $i$ ($\sum_{i=1}^{K} P_i = 1$). A proportion $O_i$ of the individual plants of host species $I$ are located by the foraging female ($0 \leqslant O_i \leqslant 1$). An egg is laid on a proportion $A_i$ of individual plants of species $i$ (acceptance or oviposition; $0 \leqslant A_i \leqslant 1$). The rate at which eggs are laid on individuals of host plant species $i$ is therefore given by $\lambda P_i O_i A_i$.

Each female has $x$ eggs, and the mortality rate per unit time of a female is $\mu$. Consequently, the maximum reproductive lifespan of a female, $\tau$ (i.e. how long before she runs out of eggs), is given by

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

her initial egg load divided by her rate of oviposition. The fitness of a female ($W$) is therefore given by the equation

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

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

As discussed above, advantages to learning can arise for a number of reasons. The predictions when using any of these mechanisms are very similar (West and Cunningham, 2002), and so here we only consider the case where concentrating on an abundant host plant species allows females to increase their foraging efficiency by finding hosts more efficiently (forming a "search image", Rausher, 1978). In order to do this we assume that the proportion of individual plants that a female finds ($O_i$) is correlated with the extent to which individuals focus oviposition behaviour on that species ($A_i$; i.e. $O_i \propto A_i$). This therefore assumes correlated changes in both pre-alighting and

post-alighting behaviour, as has been observed (Cunningham et al., 1998b), but similar predictions arise in more complex cases where they are disentangled, such as if location rates of different species are negatively correlated (see Dukas and Ellner, 1993; Dukas and Clark, 1995; West and Cunningham, 2002). Specifically:

$$O_i = \left( \frac{A_i}{\sum_{g=1}^{K} A_i} \right)^l. \tag{3}$$

The location rate of a plant species ($\lambda O_i$) therefore increases as foraging and oviposition is focused on that 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 $l < 1$ (West and Cunningham, 2002).

Our general model allows any number of host plant species. However, 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. Plant species one is assumed to be higher quality than plant species 2 ($F_1 = 1, F_2 < 1$).

### 2.2. Environmental variation

We split variation in host plant abundance into between- and within-generation components. This facilitates comparison with Stephen's (1991, 1993) models and allows us to show their applicability to agricultural systems. In order to model variation between generations we assumed that in each generation, the probability that host plant species one is more common (i.e. $A_1 > 0.5$) is given by $d_a$. A measure of the between-generation persistence, $\beta$, is given by $\beta = \sqrt{1 - 4d_a(1 - d_a)}$, which is: greatest when one of the two host plant species is consistently the most common in each generation ($d_a \to 0$, or $d_a \to 1$: $\beta = 1$), and least when both host plant species are equally likely to be most common ($d_a \to 0.5$: $\beta = 0$).

In order to model variation within generations we assumed that in each generation, the proportion of plants that are the most common species ($A_i$) is given by $0.5 + z/2$, where $z$ is a binomially distributed random number, with a mean equal to $\omega$, and a binomial denominator $n$ (in all results that follow, $n$ was assumed to be 10). A measure of the within-generation persistence is therefore given by $\omega$, which is greatest when the most common host plant species tends to be all of the plants ($\omega \to 1$), and least when the
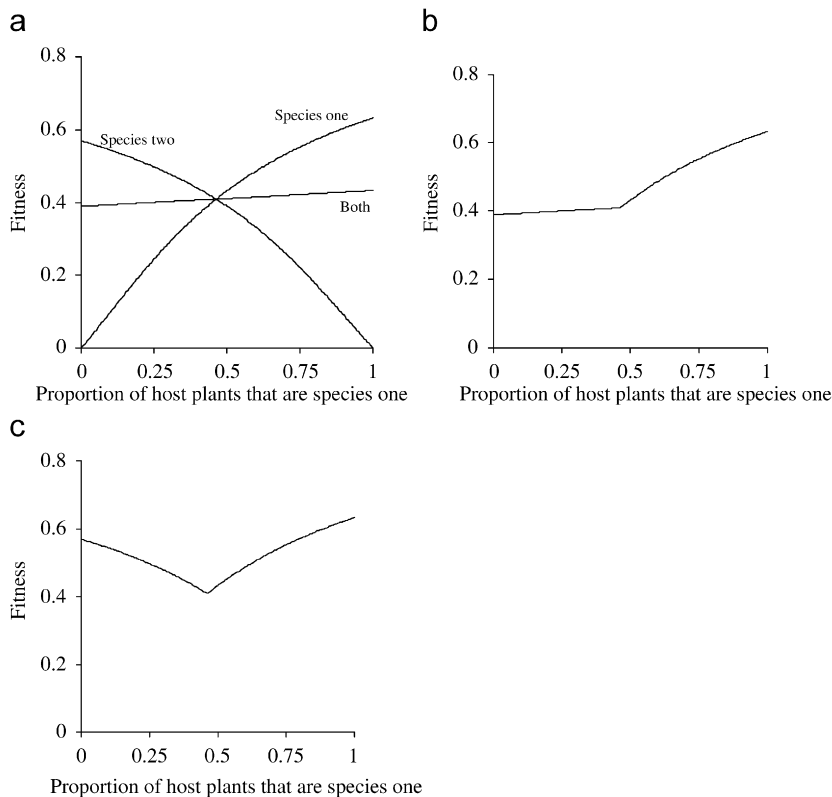


Fig. 1. Fitness (as given by Eq. (2)) plotted against the proportion of host plants that are species one for various foraging strategies. (a) The different lines represent the strategies: forage for and oviposit on species one only; forage for and oviposit on species two only, and forage for and oviposit on both species. (b) The fitness of females who use a fixed preference hierarchy (following Courtney et al., 1989). These females always oviposit on the higher quality host plant species (species one). However, when species one is rare they also oviposit on the lower quality host plant species (species two). (c) The fitness of females who learn and adjust their preference hierarchy in response to the relative abundance of the different host plant species (following West and Cunningham, 2002). These females switch to concentrating oviposition on only the lower quality host plant species when that provides a higher fitness return than ovipositing on both species. In all cases $l = 1.0$, $f_2 = 0.9$ and $\Phi = 0.5$.

most common host plant tends to be only slightly more common ($\omega \to 0$). Our simulation of within- and between-generation variability represents the simplest possible case, and is stimulated by application to the agricultural environment (see Section 4). More complex possibilities could also be constructed, such as correlations between generations.

### 2.3. Oviposition strategies

We tested the advantage of learning by comparing the fitness of individuals who either: (i) learn to adjust their preference hierarchy in response to the relative abundance of different plant species or (ii) follow a fixed preference hierarchy that is not adjusted by learning. We used the fixed preference hierarchy model of Courtney et al. (1989) (see also Mayhew, 1998; Singer, 1983; Wiklund, 1981). In this case, females are assumed to always oviposit on the higher quality host plant species. However, when this species is rare they also oviposit on the lower quality host plant species, as previously analysed in model I of West and Cunningham (2002), and illustrated in Fig. 1b. More complex fixed preference models could be developed, such as allowing for variable benefits of host feeding by adults (Mayhew, 2001; Scheirs et al., 2000), but we see no reason why adding such complications would give qualitatively different results.

The oviposition strategy of individuals who do learn was based upon the hypothesis that individuals concentrate foraging on the most common species, to maximise foraging efficiency, as analysed in model II of West and Cunningham, (2002) (see also Cunningham et al., 2002; Dukas, 1998; Dukas and Ellner, 1993; Dukas and Clark, 1995; Papaj, 1986a; Papaj and Rausher, 1987a), and illustrated in Fig. 1c. Again, females are assumed to oviposit on only the higher quality host plant when it is common. However, evolution would be expected to select for females that switch to concentrating oviposition on only the lower quality (more abundant) host plant species, when this strategy provides a greater advantage to larval survival, over evolutionary time, than ovipositing on both species (Fig. 1).

The relative fitness of the different strategies was then calculated for the different situations that provide an advantage for learning, for different types of variation in host plant abundance. For given values of $\beta$, we randomly simulated 4000 generations of host plant species abundance, for values of $\omega$ from 0.005 to 0.995 in steps of 0.001. The average (geometric mean) fitness of the different strategies over these 4000 generations were then calculated. Note that with both individuals who do and do not learn, we have assumed perfect behaviour, with individuals behaving exactly as predicted by theory. Whilst this is appropriate as we are interested in the relative fitness of these two strategies, a possible extension for future work would be to consider the effects of behavioural errors (Gardner and West, 2004; Kokko, 2003).

## 3. Results

Sample results are given in Fig. 2, with the fitness of the females who do not learn defined to be 1.0. In all cases, the relative advantage of learning was maximised when: (a) the within-generation persistence is maximised ($\omega \to 1$), with foraging females tending to encounter a single host plant species in each generation and (b) the between-generation persistence is minimised ($\beta \to 0$), with different host plant species tending to be the most common in different generations. If a female is likely to encounter the same host plant species frequently, then it pays for her to learn to focus her foraging efforts on it. If different plants are encountered in different generations then learning provides the best mechanism to do this, because there are no advantages to specialising on a single host plant species.

It should be noted that our predictions show the relative advantage to learning. Although this value is always $\geqslant 1$ (Fig. 1), the evolution of learning will only be favoured when this advantage is greater then any costs of learning. Learning may be costly for a number of reasons, such as time and mistakes while gaining experience, the neurological cost of obtaining and storing memories, or possible constraints to memory (Bernays and Funk, 1999; Chittka et al., 2003; Mayley, 1996; Mery and Kawecki, 2003).

## 4. Discussion

### 4.1. Predictions for learning in Lepidoptera

Our results show that the predictions of Stephens' general model hold in a theoretical model which considers the biological complexities specific to host plant choice in the Lepidoptera. Our model predicts that the relative advantage of learning to concentrate foraging on abundant host plant species is maximised when: (a) within-generation variability is minimised, and a foraging female is likely to encounter only a single host plant species and (b) between-generation
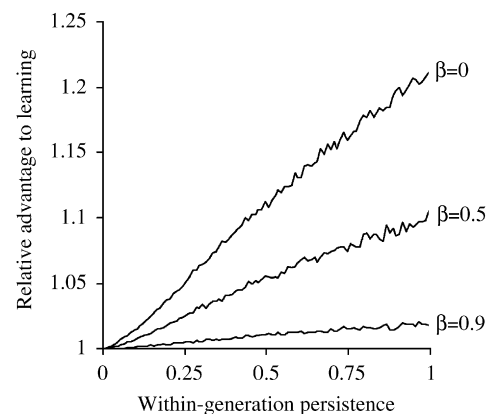


Fig. 2. How the relative advantage to learning changes with variation in within- ($\omega$) and between-generation ($\beta$) persistence of host plants. Plotted is the average fitness of individuals divided by the average fitness of individuals who do not learn. Parameters used: $l = 1.0$, $f_2 = 0.9$ and $\Phi = 0.5$.

variability is maximised, with different host plant species tending to be the most common in different generations. A similar argument could be made for variation in terms of spatial scale, with learning favoured by a lack of variability on the scale at which individuals forage, but extreme variability on a larger scale such that different females encounter different host plant species.

Learning may be of particular advantage to polyphagous lepidopteran species if neurological constraints limit the amount of information that can be processed about host plant suitability. We still know very little about the precise way in which chemical information on host suitability is coded within the insect nervous system (Bruce et al., 2005), but generalists have been shown to sacrifice some information on host suitability as a result of increased hosts range (Janz, 2003; Janz and Nylin, 1997), which may arise through neurological constraints in information processing (that is, the total amount of information on suitability of different oviposition sites that can be processed by the insect nervous system) (Bernays, 1998; Bernays and Funk, 1999). Such constraints may lead to a higher relative advantage of learning with increasing host range, or with hosts that span many plant taxa (e.g. *Helicoverpa armigera*, Zalucki et al., 1994).

However, oligophagous Lepidoptera, such as cruciferous pests, also show learning in their oviposition behaviour (Landolt, 2001; Monks and Kelly, 2003; Traynier, 1984), suggesting that learning is not simply a response to a taxonomically wide host range. Indeed, host plant range should relate to the number of hosts that the insect's sensory system is capable of distinguishing between, not to the number of plant families involved.

Learning has not been observed in all lepidopteran species. To date, the absence of learning has been suggested in the oviposition behaviour of three lepidopteran species; the checkerspot butterfly, *Euphydryas editha* (Parmesan et al., 1995), the eastern black swallowtail *Papilio polyxenes* (Heinz and Feeny, 2005) and Heliconius butterflies, *Heliconius erato* (Kerpel and Moreira, 2005). Further evidence for the absence of learning may be lacking due to difficulties in conclusively proving negative results and in publication biases against negative results (Jennions and Møller, 2002). These experimental studies show that learning is not a ubiquitous trait, but is a trait under selection, the advantage of which varies across species. Natural selection for learning ability in insects is supported by recent experimental studies on *Drosophila melanogaster* (Mery and Kawecki, 2002). In Lepidoptera, there is evidence that learning may only be expressed in behaviours where it is advantageous; In *E. editha*, although learning does not occur in oviposition behaviour, nectar foraging adults show learning in flower choice (McNeely and Singer, 2001). Where learning is utilised in two distinct behaviours, Lepidoptera have been shown to be capable of distinguishing between the two behavioural contexts, as has been shown with feeding and oviposition in *Battus philenor* (Weiss and Papaj, 2003). More generally, the interaction between foraging for plants upon which to nectar feed or lay eggs is an important issue that warrants future theoretical attention (Cunningham et al., 1998a; Janz et al., 2005; Weiss and Papaj, 2003).

### 4.2. Learning in agricultural pests: likelihood and implications

In polyphagous insects that attack crop species, host plant (crop) abundance often varies in a way that would favour learning in oviposition behaviour, as predicted by our model. In the agricultural environment, ovipositing females frequently encounter abundant patches of a single host plant species, as a result of crop monoculture and through environmental factors (e.g. climate or soil quality), which favour the growth of certain crops in particular regions. In general, a particular crop species will be present for longer than the adult lifespan (see for example Nyambo, 1988; Sequeira, 2001; Sequeira et al., 2001; Wardhaugh et al., 1980), whereas between insect generations, ovipositing females will frequently encounter different crop species through crop rotation/seasonal variations in agriculture or long range movement of adult insects (migration).

Our model agrees with the empirical evidence that learning strongly influences host preference in the pest insects *Helicoverpa armigera* (podborer), *Trichoplusia ni* (cabbage looper), *Plutella xylostella* (diamondback moth) and *Pieris brassica* (cabbage white butterfly) (Cunningham et al., 1999, 1998b; Landolt, 2001; Landolt and Molina, 1996; Liu et al., 2005; Monks and Kelly, 2003; Skiri et al., 2005; Traynier, 1984) and also that learning is not a strong determinant of host preference in the lepidopteran species *E. editha*, *P. polyxenes* and *H. erato*, which are not agricultural pest species. Additional empirical studies comparing learning in lepidopteran species that utilise the agricultural environment—for example noctuids (pod-borers, armyworms), tortricids (leaf rollers, stem and fruit borers) and pyralids (stem borers)—with lepidopteran species that are not pest species are, however, required in order to test the hypothesis that learning may have specific advantages to oviposition in the agro-ecosystem.

The applied implications of understanding the influence of learning in the oviposition behaviour of insect pest species are considerable. Many pest management strategies, such as the use of trap crops, host plant volatiles, resistant crop varieties or the use of deterrent applications or sprays (Cunningham et al., 1999; Jallow et al., 2004; Liu et al., 2005) have their roots in a theory of fixed host preferences by insect pests. Such practices may have little effect in controlling or monitoring insect species that change their preferences through learning.

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