
Host selection in phytophagous insects: a new explanation for learning in adults

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Insect learning can change the preferences an egg laying female displays towards different host plant species. Current hypotheses propose that learning may be advantageous in adult host selection behaviour through improved recognition, accuracy or selectivity in foraging. In this paper, we present a hypothesis for when learning can be advantageous without such improvements in adult host foraging. Specifically, that learning can be an advantageous strategy for egg laying females when larvae must feed on more than one plant in order to complete development, if the fitness of larvae is reduced when they switch to a different host species. Here, larvae benefit from developing on the most abundant host species, which is the most likely choice of host for an adult insect which increases its preference for a host species through learning. The hypothesis is formalised with a mathematical model and we provide evidence from studies on the behavioural ecology of a number of insect species which demonstrate that the assumptions of this hypothesis may frequently be fulfilled in nature. We discuss how multiple mechanisms may convey advantages in insect learning and that benefits to larval development, which have so far been overlooked, should be considered in explanations for the widespread occurrence of learning.

When phytophagous insects lay their eggs on many host species (polyphagy), adult females do not select all hosts equally. Instead, preferences in both pre-alighting (host finding) and post-alighting (host acceptance) foraging behaviour are often shown towards particular host species. Host preferences show a strong heritable component and are thought to represent the suitability of hosts for larval survival (Singer 1983, Courtney et al. 1989, Singer et al. 1989, Thompson 1998). Suitability can depend upon a number of factors such as nutritional quality, host plant defence chemicals, prevalence of natural enemies or microenvironment (Thompson and Pellmyr 1991).

Such preferences are not always fixed. Ovipositing insects have been shown to change their preferences for

different host species during their lifespan. Specifically, experimental work has demonstrated that insect learning can significantly change the host selection behaviour of ovipositing insects; previous experience of a host plant can lead to an increased preference for that host species (e.g. Prokopy et al. 1982, Papaj 1986, Landolt and Molina 1996, Cunningham et al. 1998).

When experience of a host species results in a change in preference, innate host selection preferences may not be displayed (e.g. Landolt and Molina 1996). As a result of learning, the most abundant host species may instead become favoured by the insect. Courtney and Kibota (1990) use existing theories of learning behaviour to show how insect learning and the environment may interact to change an insect's host selection behaviour to favour one species. In their review they explain how the selection of a particular host species by an insect is probabilistic. Factors such as inbuilt (innate) preferences, changes in preference (learning) and environmental abundance of each host species all interact to determine which host an insect is most likely to alight on. When the abundance of one host species is high, this will favour the probability that the insect lands on this species. This experience then increases the probability of landing on this host species subsequently. If the insect lands on a host species that is relatively rare, the insect may still be more likely to land on a different host species subsequently, if this host plant is abundant, even with the increased preference which occurs with experience. Since learning is a gradual process (classically known as a "learning curve"), and is reversible on encountering other host species, the insect is most likely to end up favouring the most abundant host species. Such changes in preference conflict with

foraging theories which assume that relative preferences for different host species remain fixed and suggest that females lay on less favourable host species *only* when more suitable species are rare or absent (see Courtney et al. 1989).

Why then should insects prefer to lay on a host species which they have previously encountered? Explanations for the advantages of learning in oviposition are currently based around the idea that by concentrating on a particular host species, the rate at which adults find and utilise hosts will be increased (Papaj and Prokopy 1989, Schoonhoven et al. 1998, West and Cunningham unpubl.). The fitness of an ovipositing female will be proportional to the number of hosts that she oviposits on multiplied by the quality of offspring produced (survival to adulthood multiplied by expected fecundity). Adult learning may increase the number of eggs a female lays on host plants within her lifespan. Offspring quality will be determined by the suitability of the host species on which it develops.

Learning in oviposition behaviour is therefore predicted to be advantageous when increases in foraging efficiency on a particular, more abundant host species outweigh the disadvantages of ignoring higher quality, but less abundant host species. Increased foraging efficiency through learning has not yet been shown in insect oviposition behaviour, but may occur through improved recognition, accuracy or selectivity of host selection when an insect concentrates on a single host species (see Bernays 1996, Janz and Nylin 1997).

Here, we consider a situation where learning in the host selection behaviour of ovipositing insects can be advantageous without direct improvements in adult foraging efficiency. When larvae move between, and feed on, a number of plants during development, they can suffer fitness costs when they switch to feed on a different host species. Costs caused by switching hosts will be minimised in larvae which develop on a more abundant species. Consequently, the fitness return from laying an egg on a particular host species will increase with its relative abundance. In these insects, learning would allow ovipositing adults to concentrate on the more abundant (and thus more suitable) host plant species. Our specific aims are to: (1) present this hypothesis, and (2) review empirical evidence which suggests that this advantage to learning may occur in many insect species, particularly in the Lepidoptera.

In presenting this hypothesis, we re-examine a crucial assumption from which theories of host selection and juvenile survival have been developed: that differences in suitability between host species are fixed. Clearly, the suitability of a host plant for larval development may vary through differences in genotypic, temporal, seasonal, or induced variability in host plant physiology (Damman and Feeny 1988, Schoonhoven et al. 1998). Here, we propose that relative suitability of different host plant species for juvenile development and survival

can vary with the local abundance of each individual host species, through the effects of previous larval experience.

Hypothesis

In polyphagous insects, the suitability of a host species for larval development and survival differs between host plant species. Relative host suitability within a species is often considered as being fixed: particular host species are more suitable for larval survival than others. However, we propose that host suitability can vary with previous larval feeding history. Our hypothesis concerns insect species which exhibit two basic traits: (1) larvae feed on more than one plant in order to complete their development, and (2) the fitness of larvae is reduced if they must switch host species during development. Where these assumptions are fulfilled, when a larva's environment consists of a number of different host species each with varying abundance, the chances of having to develop on multiple host species will be lowest when it begins its development on the most abundant host species. If the fitness reduction, either when developing on multiple host species or of finding the same host species is high, we predict that an oviposition strategy which favours the most abundant host species will be most advantageous. Learning is such a strategy.

Models

We formalise our hypothesis using two models. In both models we assume that: (1) there are two host species, A and B; (2) the relative abundance of species A and B are d and $(1 - d)$ respectively (if $d > 0.5$ then A is the most abundant species, and if $d < 0.5$ then B is the most abundant species); (3) individual larvae feed on two host plants during their development; (4) the fitness of larvae developing entirely on species A or B (i.e. both host plants required for development are from the same species) are 1.0 and f , respectively; (5) f is between 0 and 1.0 ($0 < f < 1$), so that the fitness of a larva developing on species B can be equal or less than that of a larva developing on species A.

The two models differ in how we assume larvae move between host plants. In model I we assume that no host preferences are expressed by foraging larvae; after finishing on their first host plant, larvae move at random to another host plant. Our model shows how the fitness of larvae from eggs laid on each host species varies with relative host abundance. In Model II we extend Model I to include preferences in larval foraging. Here, we assume that larvae continue to search until they find the same host plant species on which

they had previously developed. This model therefore considers the fitness of larvae from eggs laid on each host when the foraging costs and benefits of selecting the same host species are considered.

By showing that the optimal strategy varies with host abundance we show that learning is an advantageous trait in adult host selection behaviour; adult insects that select the most abundant host are choosing the most suitable host for their offspring.

Model I

Here, we assume that if a larva develops upon both host species its fitness is m , where m is also between 1.0 and 0. A principal assumption of our hypothesis is that developing upon two host plants leads to reduced fitness. Therefore we assume that m will generally be less than f . Empirical evidence has shown that the fitness cost of switching host plant species during larval development can vary from slower growth and development to deformed pupae and increased larval and adult mortality (see Scriber 1979, 1982, Szentesi and Jermy 1990). The value of m will therefore vary considerably depending on insect species and host plants consumed. The fitness of a larva developing from an egg laid on A (W_a) is given by $W_a = d + (1 - d)m$. The first term represents the probability that the second plant it feeds upon is A multiplied by its fitness in this case (1.0). The second term represents the probability that the second plant it feeds upon is B ($1 - d$) multiplied by its fitness in this case (m). Similarly, the fitness of a larva developing from an egg laid on B (W_b) is given by $W_b = (1 - d)f + dm$.

Examples of how these two functions change with relative host abundance are given in Fig. 1a and b. As A becomes more common (increasing d) the fitness of an individual commencing development on A (W_a) increases because the likelihood that the second plant encountered is A increases. Similarly, as B becomes more common (decreasing d) the fitness of an individual commencing development on B (W_b) increases because the likelihood that the second plant encountered is B increases. The fitness of individuals commencing development on either A or B is equal at the point where the lines cross ($d = (f - m)/(1 + f - 2m)$). This model therefore demonstrates how varying host abundance can affect larval fitness on hosts, and thus host suitability. Consequently, a greater relative abundance of a host species favours oviposition on that plant.

The point at which the two lines, W_a and W_b , cross represents the host abundance at which the optimal strategy switches between ovipositing on A and B. This point is crucial in determining the advantage that can be gained by selecting the most abundant host. For example, assuming equal abundance of both hosts, if the lines cross when abundance of A is particularly low

(i.e. when d is close to 0) then the advantage of learning will be less since the optimal strategy for most of the parameter space will be to always oviposit on A (see also Stephens 1991). The advantage of learning will be greatest when the host abundance at which the optimal strategy switches between ovipositing on A and B is closer to equal abundance ($d = 0.5$). This occurs when the fitness differences of developing entirely on A or B are minimised ($f \rightarrow 1$), and/or the fitness cost of developing on both A and B is maximised ($m \ll f$).

Model II

In this model we extend Model I to include preferences in larval foraging. Here, we assume that when larvae move to their second host plant they continue to search until they find the same host plant upon which they had previously been feeding.

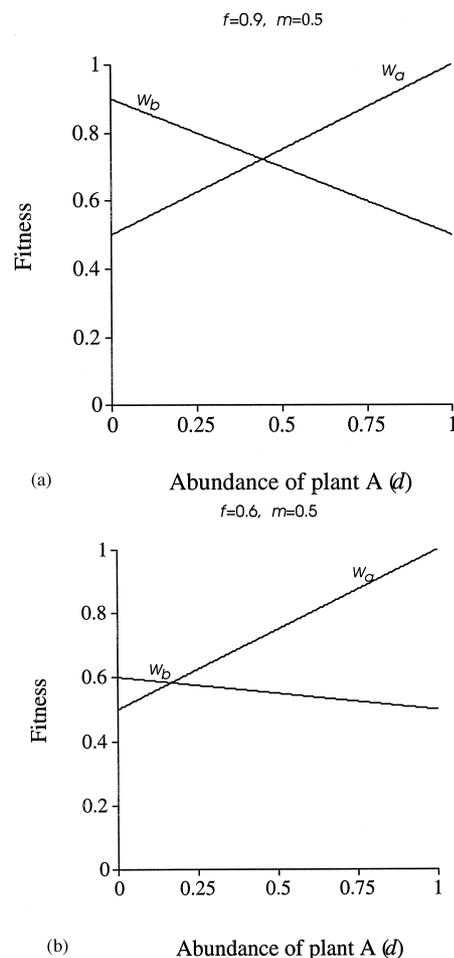


Fig. 1. The fitness return in model I from laying an egg on plant species A (W_a) or plant species B (W_b) against abundance of plant A (d). In a, the fitness for developing entirely on species B ($f = 0.9$) is greater than in b ($f = 0.6$).

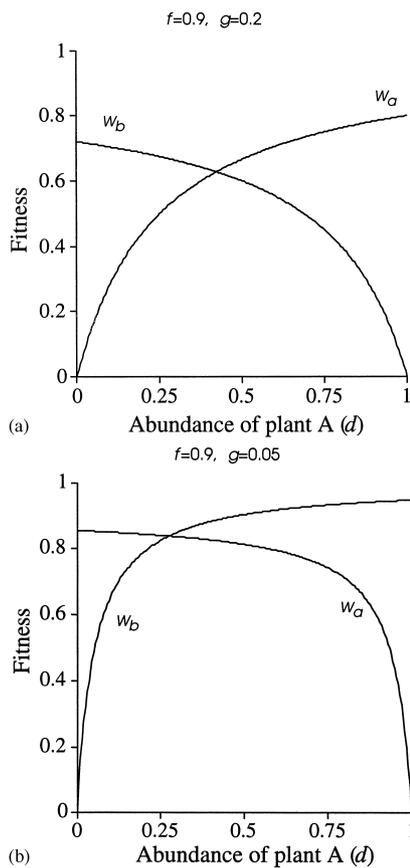


Fig. 2. The fitness return in model II from laying an egg on plant species A (W_a) or plant species B (W_b) against abundance of plant A (d). In a, the cost of moving to a new host plant is greater ($g = 0.2$) than in b ($g = 0.05$).

Movement between host plants (i.e. rejecting a host plant and continuing to search) is given a cost to fitness (g). The value of g represents the costs associated with increased searching time and may incorporate factors such as reduced time spent feeding or exposure to unsuitable environments. Note that g represents searching costs and does not include any fitness benefit from moving from the previous host plant (such as avoiding predators); any such benefit would apply to all individuals and so can be excluded from our model. If an egg is laid on plant A then the probability that it takes n moves to find another individual of plant A multiplied by the fitness consequences of n moves ($P_{a,n}$) is $(1-d)^{n-1}d(1-g)^n$. The sum of all the possibilities ($\sum_{n=1}^{\infty} P_{a,n}$) can be put into the form of a geometric series, and the fitness of an egg laid on plant A will be $W_a = d(1-g)/(1-(1-d)(1-g))$. Similarly, the fitness of an egg laid on plant B will be $W_b = f(1-d)(1-g)/(1-d(1-g))$.

Examples of how these two functions change with relative host abundance are given in Fig. 2. As A becomes more common (increasing d) the fitness of an

individual emerging as a larva on A (W_a) increases because another individual of plant A is found more quickly. Similarly, as B becomes more common (decreasing d) the fitness of an individual emerging from an egg laid on B (W_b) increases because another individual of plant B is found more quickly. The fitness of individuals that lay on A or B is equal at the point where the lines cross ($d = (1-f+2fg - \sqrt{1-2f+f^2+4fg^2})/2(1-f-g+fg)$). As in model I this demonstrates that different strategies are favoured with different relative host abundance of each species. The host abundance at which the optimal strategy switches between ovipositing on A and B is closer to $d=0.5$ when the fitness differences of developing entirely on A or B are minimised ($f \rightarrow 1$), and/or the fitness cost moving between plants is maximised ($g \rightarrow 1$).

Validity of the hypothesis

Our hypothesis is bound by two important assumptions. Firstly, that larvae use more than one host plant during development and, secondly, that switching host species during development reduces juvenile fitness. The advantages of adult learning proposed in this hypothesis are only valid in insect species where both these traits are borne out. In this section we look at evidence which suggests that these particular traits may be widespread throughout the Insecta, and particularly in the Lepidoptera.

Larval development on several host plants

The occurrence and frequency of larval movements between host plants have received little attention in empirical studies to date. Despite this, such movements are probably common to larvae of many insect species (Bernays and Minkenber 1997). Frequent movements between plants have been observed in larvae of several species of butterfly which feed on small host plants. Example of these are the butterflies *Issoria lathonia*, *Argynnis paphia*, *Mesoacidalia aglaja*, *Euphydryas maturna* (post-hibernation) and *Parnassius apollo* (StefanDewenter and Tschardtke 1997, Wahlberg 2000, Wiklund pers. comm.). When larval feeding leads to the depletion of the food resource from its current host, larvae must locate a new host in order to complete development. This has been shown to occur in a number of species (Dethier 1959, Jones 1977). Movement between hosts may be particularly prevalent in species where egg masses are laid on a single host (Floater 1996), or where larval feeding occurs only on specific host tissues (e.g. flowering or fruiting parts) (Zalucki et al. 1986).

However, depleted resources do not explain the frequent movements between hosts displayed by larvae of

many species (Heinrich 1979, Borkin 1982, Hansen et al. 1984, Dethier 1989). Evidently, inter-plant movements common to many insect larvae may also occur through other ecological or environmental factors. Such factors may include the avoidance of predators which are attracted to larvae, frass or damaged host plants (Marston et al. 1978, Montllor and Bernays 1993, Moraes et al. 1998), competition (inter-/intra-specific) (Damman 1993), changes in plant defence chemicals as a result of feeding (Edwards and Wratten 1983, Damman 1993), or because larvae are dislodged from their hosts (Myers and Campbell 1976, Jones 1977).

Our hypothesis is concerned with larvae moving between host plants, where discrimination by larvae between different host species may occur, and where moving can impose a cost. Thus, the advantages to adult learning predicted in our model are more likely in insects feeding from herbaceous host species compared to tree feeding species. In the former, larval movements between hosts and exposure to other host and non-host species whilst foraging will be more likely to occur.

Rejecting a host and continuing to search for an alternative host may involve a cost associated with reduced feeding and possible exposure to unfavourable environments. For simplicity, our models consider only that an insect requires two hosts in order to complete development. Clearly, empirical evidence (see above examples) suggests that many caterpillars utilise several host plants. As the number of hosts used increases, the frequency of movement between plants will become higher. This will increase the fitness cost of having been laid on a less abundant host plant species, leading to a greater advantage for learning in adult foraging behaviour. This can be qualitatively shown with our model by raising the fitness cost of moving between plants (g), as the number of hosts required to complete development increases (see Fig. 2b).

Switching hosts and host suitability

The empirical evidence demonstrating that switching hosts during development can be disadvantageous to larval growth and survival in many insect species (i.e. $m < f$) is seen in studies on larval learning in host selection, commonly referred to as induction of feeding preference. Induced feeding preferences have been shown in lepidopterous larvae, where this trait appears to be widespread, and have also been shown to occur in other insect families (Szentesi and Jermy 1990). The incidence, variation, underlying physiology, and possible role of induced preferences have been studied in detail elsewhere (see reviews by Szentesi and Jermy 1990, Bernays 1995, Bernays and Weiss 1996).

In studies on induced feeding preferences, larvae show an increased preference for a host species on

which they have had previous experience feeding. Furthermore, induced preferences can lead to reduced fitness when larvae develop on more than one host species. This may occur through decreased growth rate, food utilisation, pupal weight, and/or an increased time to pupation when larvae are forced to switch host species (e.g. Scriber 1979, 1982, Karowe 1989).

Both behavioural and physiological processes may be responsible for these changes in fitness. Experience may involve neurological changes in the peripheral sensilla or central nervous system of feeding larvae (Bernays and Weiss 1996) resulting in changes in the host finding or host recognition behaviour of larvae towards different species (Bernays 1995). In addition, experience has been shown to increase the efficiency with which larvae can digest the hosts' tissue; through changes in the uptake of nutrients or detoxification of defence chemicals present in the host tissue (Lindroth 1991, Bernays and Weiss 1996, Hung et al. 1997).

Where previous feeding history affects the foraging behaviour and/or the suitability of the host substrate for growth, larvae may have a higher fitness when they develop on a single host species. Relative host suitability can therefore be variable. Consequently, when larvae are required to forage for additional hosts during development, their fitness will be higher when they have commenced development on the most abundant host.

The extent to which larval learning influences feeding preferences on different hosts varies considerably between insect species. In some species, strong preferences are retained for particular host plant species regardless of experience, whereas in other species larvae show the strongest preferences for the host species on which they have previously fed regardless of innate preferences and in the extreme may refuse to feed on any but the experienced host species (see examples in Szentesi and Jermy 1990).

Consequently, the benefits of adult learning would be expected to differ between insect species: When larval learning leads to *large* changes in relative host suitability, adult learning (laying on the most abundant host) would be expected to be *more* advantageous to larval survival. We predict this is more likely to occur when (1) the fitness differences between developing on different host plant species are small when each larva feeds on plants from only one species, (2) the costs for a larva feeding on multiple host plant species are high, and (3) the costs of foraging for the same host species are low. Conversely, where larval learning does not substantially change relative host suitability, adult learning may be less advantageous. Empirical work comparing the presence and absence of adult learning in species which do and do not exhibit the above traits may provide evidence for the generality of this theory.

Conclusions

Studies on the advantages of insect learning in adult oviposition behaviour have focused on possible improvements in adult host finding and utilisation. We have proposed an additional benefit based on the idea that host suitability for larval development varies with host species abundance. In many species, individual larvae feed on more than one host plant. Where induced feeding preferences lead to increased survival when these insects move between hosts of the *same* species we predict that the host suitability of a plant species will be positively correlated to its abundance. Since the initial host for most larvae is determined by the oviposition choice of their mothers, finding individuals of the same host plant species becomes easier for larvae the greater the abundance of the host plant species that they are laid on.

This hypothesis leads to an advantage for learning in the oviposition behaviour of adult polyphagous insects which has, as yet, remained unexplored. Foraging adult females are likely to encounter more abundant host plant species more frequently. Where a more abundant host is more suitable for larval development, adult learning could lead to an increase in their preference for this host plant species, increasing the fitness of their offspring.

We suggest that the fitness of larvae developing from eggs laid on more abundant host plant species may increase through the behavioural and physiological changes associated with an induction of larval feeding preference. The possible benefits of induced preferences have received considerable attention (see Szentesi and Jermy 1990, Bernays 1995, Bernays and Weiss 1996), and it is clear that such preferences exist in many species which do not come into contact with multiple host species during development, and thus are not applicable to our model. Induced feeding preferences may thus be an ancestral trait. Bernays (1996) suggests that such a trait may have evolved to override environmental noise and channel appropriate sensory information more efficiently. Our hypothesis implies that an association between learning in larval foraging and learning in adult foraging may exist in certain insect species and suggests that co-evolution between these traits may have occurred.

The assumptions of our hypothesis require that both induction of feeding preference and larval movement between hosts must exist for this advantage to adult learning. Although these traits are common in insects (Szentesi and Jermy 1990, Bernays and Minkenberg 1997) there is a paucity in the literature of insect species in which both these traits have been studied. Larval movement between hosts and induced larval feeding preferences have been shown in *Helicoverpa armigera* (Aboul-Nasr 1981, Zalucki et al. 1986). This is a highly polyphagous insect where adult learning in oviposition

has also been demonstrated (Cunningham et al. 1998). Clearly, more studies identifying the frequency with which these traits occur simultaneously are imperative in order to elucidate whether this particular advantage to adult learning is widespread.

Learning covers a number of different underlying physiological mechanisms (e.g. sensitisation, habituation, or associative learning) which vary the way in which this trait is influenced and expressed (Papaj and Prokopy 1989, Bernays and Weiss 1996). Clearly, different mechanisms may be important in different species. Multiple mechanisms are needed to explain a number of life history traits (e.g. Holborn and Stearns 1982, West et al. 1999) and this may well be the case with insect learning (West and Cunningham unpubl.). Neglecting alternative hypothesis for advantages to learning may prevent us from understanding or appreciating the complexity of this ubiquitous trait.

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