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REVIEW ARTICLE

Learning in *Helicoverpa armigera* (Lepidoptera: Noctuidae): a new look at the behaviour and control of a polyphagous pest

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Abstract

Recent experimental evidence has shown that learning occurs in the host selection behaviour of *Helicoverpa armigera* (Hübner), one of the world's most important agricultural pests. This paper discusses how the occurrence of learning changes our understanding of the host selection behaviour of this polyphagous moth. Host preferences determined from previous laboratory studies may be vastly different from preferences exhibited by moths in the field, where the abundance of particular hosts may be more likely to determine host preference. In support of this prediction, a number of field studies have shown that the 'attractiveness' of different hosts for *H. armigera* oviposition may depend on the relative abundance of these host species. Insect learning may play a fundamental role in the design and application of present and future integrated pest management strategies such as the use of host volatiles, trap crops and resistant crop varieties for monitoring and controlling this important pest species.

Introduction

Helicoverpa (Heliothis) armigera (Hübner) (Lepidoptera: Noctuidae) is a highly polyphagous agricultural pest. Host species for *H. armigera* come from a broad spectrum of families and include important agricultural crops such as cotton, maize, chickpea, pigeonpea, sorghum, sunflower, soyabean and groundnuts (Fitt, 1989). Females lay eggs on the flowering and fruiting structures of these crops, where voracious larval feeding leads to substantial economic loss (Reed & Pawar, 1982). The ability of ovipositing females to locate and utilize a wide range of hosts from a number of families is one of the major factors contributing to the pest status of this moth (Zalucki *et al.*, 1986; Fitt, 1989). Modern pest management strategies for control of *H. armigera* rely upon an understanding of the oviposition behaviour of this insect. However, despite its importance, the host selection behaviour of this moth is still poorly understood (Zalucki *et al.*, 1986; Fitt & Boyan, 1991).

Learning, defined as a change in behaviour with experience (Papaj & Prokopy, 1989) has been demonstrated in a number of insect species (Papaj & Lewis, 1993). This is particularly true in the Lepidoptera, where learning has been well documented in both feeding and oviposition of several butterflies (Swihart & Swihart, 1970; Stanton, 1984; Traynier, 1984, 1986; Lewis, 1986, 1993; Papaj, 1986a,b; Papaj & Rausher, 1987; Goulson & Cory, 1993; Goulson *et al.*, 1997). However, it is only recently that the existence of learning has been studied in adult moths (Firempong & Zalucki, 1991;

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Hartlieb, 1995, 1996; Kelber, 1996; Landolt & Molina, 1996; Fan *et al*., 1997; Kelber & Pfaff, 1997; Cunningham *et al*., 1998a,b). In *H. armigera,* learning has been demonstrated in the oviposition (Cunningham *et al*., 1998a) and feeding (Hartlieb, 1995; Cunningham *et al*., 1998b) behaviour of adult moths.

Learning is advantageous because it allows individuals to respond to certain variable environments (see Stephens, 1993). If different hosts vary unpredictably in their abundance (either spatially and/or temporally) then learning may improve an insect's foraging. Many of the hosts of *H. armigera* are agricultural crops and occur in large patches of a single (but variable) host species. Similarly, many of the native hosts of *H. armigera* grow in dense patches (Zalucki *et al*., 1994). In such environments, an oviposition strategy which favours the most abundant host may be one with the greatest reproductive benefits.

This paper reviews the evidence for learning in *H. armigera* and discusses how this affects the interpretation of laboratory studies on host selection and our understanding of the ecology of this moth. The effect that learning may have on host selection in the field is discussed, and evidence from field studies indicating that learning may be influencing host selection is presented. A general review on the possible application of learning to pest management was presented by Prokopy & Lewis (1993). In this paper, we look specifically at our current knowledge of the host selection behaviour of a single important pest species in which learning has been shown to occur. We show how our knowledge of learning could be essential in the application and design of pest management strategies to control this pest, such as the use of host volatiles, trap crops and resistant crop varieties.

Experimental evidence for learning in *H. armigera*

Learning in the oviposition behaviour of *H. armigera* was first considered by Firempong & Zalucki (1991). The first detailed evidence for learning in the oviposition behaviour of this species was provided by Cunningham *et al*. (1998a). In this study, experience with a particular host species significantly increased the probability of selection of that species for subsequent oviposition. This was demonstrated in both a laboratory flight cage and a large glasshouse. The glasshouse used in the study contained both host and non-host species for *H. armigera* in an attempt to simulate a field situation. In addition, ovipositing moths demonstrated learning in post-alighting behaviour ('host acceptance'). Using a technique for tethering moths (see Jallow & Zalucki, 1995) prior experience with a particular host species was shown to increase acceptance of that host compared with other hosts.

Learning has also been experimentally demonstrated in the nectar foraging behaviour of *H. armigera* (Cunningham *et al*., 1998b). Unmated male and female moths showed a preference for locating host species with which they had previous experience of nectar feeding. Furthermore, learning was shown to decrease the 'handling time' after alighting on a flower: previous experience with a particular flower type increased the likelihood that moths found the food source when that flower type was being searched.

The underlying mechanism involved in learning behaviour in *H. armigera* in feeding has been investigated by Hartlieb (1996). Classical conditioning experiments showed that individual moths learned to associate a feeding stimulus (antennal stimulation with sugar) with an olfactory stimulus. The olfactory stimulus in this experiment consisted of volatile components from flowering cotton. The mechanism and stimuli involved in learning in oviposition in *H. armigera* have not been investigated. However, classical conditioning has been demonstrated in the oviposition behaviour of other lepidopterous species, the butterflies *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae) (Traynier, 1984) and *Battus philenor* Linnaeus (Lepidoptera: Papilionidae) (Papaj, 1986a). These insects associated a chemical oviposition stimulus with a visual stimulus from the oviposition substrate (colour in *P. rapae*, leaf shape in *B. philenor*).

Implications of learning in *H. armigera*

Laboratory study and host selection behaviour

Adult *H. armigera* oviposit on a large number of hosts from a number of families. In the laboratory, the relative preferences of host-seeking females for different host species and genotypes have been investigated by counting eggs laid by moths kept in cages with mixed hosts (Firempong & Zalucki, 1990b; Butter & Singh, 1996) and by using tethered moths to assess post-alighting responses to hosts (Jallow & Zalucki, 1996). Through such studies, using adult moths with no experience of host species, it was concluded that ovipositing females show a graded discrimination among potential host species which has been termed a 'hierarchy of preference'. This relative preference for different hosts is thought to arise from the balance between attractants and deterrents to which the insect responds (Renwick & Chew, 1994). The adaptive significance of such a hierarchy has been hypothesized to relate to differential levels of juvenile survival (Rausher, 1983; Thompson, 1988; Janz *et al.,* 1994).

Host preference hierarchies in *H. armigera* have a strong genetic component and do not differ significantly between different moth populations regardless of differences in the host availability between geographic localities (Firempong & Zalucki, 1990a; Jallow & Zalucki, 1996). Thompson (1993) suggested that such 'evolutionary conservative' differences in preference between hosts allow polyphagous species to utilize a more favourable host if or when it becomes available.

However, experimental evidence for learning in *H. armigera* has demonstrated that previous experience with a host species increases the relative attractiveness of that host (Cunningham *et al*., 1998a). Therefore, as a result of learning, preferences for different hosts displayed by adult moths which have encountered a host species may be vastly different from the preferences of moths without any host experience. Consequently, the hierarchies of preference displayed in the laboratory may not correspond to preferences shown by either individuals or populations in the field. In the field, the most abundant host species is likely to be encountered most frequently. As a result of this, learning may result in ovipositing *H. armigera* discriminating preferentially towards the most locally abundant host species. Such changes in host selection preference as a result of changing host abundance have already been clearly demonstrated in a number of detailed studies on learning in the butterfly *B. philenor* (Papaj, 1986a,b,c; Papaj & Rausher, 1987).

Learning may help us to understand how *H. armigera* can so successfully utilize low ranking hosts such as cotton, towards which they show a low preference in the laboratory. In areas where cotton is grown abundantly, oviposition and subsequent larval damage by *H. armigera* can be severe (Singh & Sidhu, 1990). However, laboratory experiments on host preferences of populations of *H. armigera* have shown that populations from areas where cotton is grown abundantly do not differ in host preferences from populations where cotton cultivation is less common (Firempong & Zalucki, 1990a; Jallow & Zalucki, 1996). Learning may increase host selection for cotton in areas where it is a predominant crop, ensuring that ovipositing moths recognize and utilize the most abundant (albeit less preferred) host.

Field evidence for learning

The marked differences in preference which can occur as a result of experience with a host species, emphasizes the need to study host location behaviour in the insects natural habitat. A rigorously controlled laboratory test, although suitable for identifying particular behavioural mechanisms, does little to define the role such mechanisms play in shaping behaviour in the field (Parmesan *et al.*, 1995). Evidently, learning has been shown to significantly change preferences for host species and necessitates that we take a new look at our interpretation of 'host preference hierarchies' when attempting to understand host selection behaviour. However, the role of learning in host selection in the field has yet to be determined for *H. armigera* or any other major polyphagous pest species.

If learning is exhibited by *H. armigera* in the field, it is predicted that more abundant hosts should receive proportionally more eggs than less abundant hosts, irrespective of the relative preference displayed in the laboratory. Moths will be more likely to encounter (and thus 'experience') the more abundant host species whilst foraging, and learning will increase the relative preference for this host species. More eggs will be laid proportionally on the more abundant species as it becomes the preferred host species for ovipositing moths.

Conversely, if learning does not occur, or has little influence in the field compared with innate preferences, it is predicted that more abundant hosts should not receive proportionally more eggs than less abundant hosts. In this scenario, host preferences in the field are expected to be the same as the relative preferences shown in the laboratory. Moths will be more likely to oviposit on the 'preferable' host species. Consequently, more eggs will be laid proportionally on these species regardless of abundance.

Although there are at present no field studies on the influence of learning in *H. armigera*, a number of studies have looked at *H. armigera* oviposition on 'attractive' hosts, placed in small patches of a more abundant, but less attractive, alternative host. Although these field experiments were not designed to test learning *per se*, they provide initial evidence that host abundance may be important in host selection in the field.

In an investigation into the oviposition behaviour of *H. armigera* on cotton, Pyke *et al.* (1987) planted two strips of pigeon pea (200 m by 6 rows each) within a background of cotton (200 m by 84 rows), such that the abundance of the surrounding cotton was around seven times that of the pigeonpea. Flowering pigeonpea and squaring cotton are the stages of growth when these plants are susceptible to *H. armigera* attack. To ensure that flowering pigeonpea was available throughout the squaring stage of cotton, both early and late varieties of pigeonpea were mixed within the strips.

Egg sampling, based on whole plant counts, on both cotton (n = 20 per sample) and pigeonpea (n = 100 per sample) over a three month period revealed that a greater proportion of eggs was laid on pigeonpea than on cotton prior to squaring (on average six times more eggs on pigeonpea over seven sampling dates). However, once the cotton entered the squaring stage, very few eggs were laid on the pigeonpea, which was still flowering (on average six times more eggs on the cotton than on pigeonpea over four sampling dates). This is despite the fact that flowering pigeonpea is regarded as being considerably more attractive to ovipositing *H. armigera* than squaring cotton (Shanower & Romeis, 1999). The results of this experiment suggested that in this field situation, cotton was more attractive than pigeonpea once the (more abundant) cotton crop was squaring.

Further evidence supporting a difference in host preference by *H. armigera* in the field compared with the laboratory has been provided by Dillon & Fitt (unpublished data). They investigated *H. armigera* oviposition on a number of hosts, in patches ranging from 6 × 6 m up to 24 × 24 m set in a background of cotton. The hosts used (sorghum, sunflower, maize, pigeonpea and soyabean) are all more preferable to ovipositing *H. armigera* than cotton (see Firempong & Zalucki, 1990a; Jallow & Zalucki, 1996). In these studies, the patches of more attractive hosts did not receive the numbers of *H. armigera* eggs expected; the proportion of eggs laid on these patches was never more, and often less, than on the surrounding cotton.

From the above evidence it is clear that laboratory defined preferences of *H. armigera* for different hosts may have little bearing on *H. armigera* host selection in the field. Laboratory studies on relative host preferences of *H. armigera* have been carried out on populations of moths from the areas studied in the above experiments (Firempong & Zalucki, 1990a; Jallow & Zalucki, 1996) in which cotton was shown to be a host of low relative preference. The above field evidence demonstrates that when cotton is abundant and other hosts are less common, *H. armigera* oviposition preference for cotton can be greater than for alternative hosts. A greater preference for the more abundant host, regardless of 'innate' relative preferences demonstrated in the laboratory is in agreement with the hypothesis that learning may play an important role in host plant selection in the field.

Learning and polyphagy

Polyphagy at the species level, as has been demonstrated in *H. armigera*, does not necessarily imply polyphagy at the individual level. Polyphagous populations could be made up of individuals which are predominantly monophagous (Karowe, 1989). At present, the degree of polyphagy expressed by individual *H. armigera* in the field is unknown. Ovipositing females could utilize a number of hosts or restrict laying to a single host. The degree of polyphagy expressed by females could depend on genetic differences (Jallow & Zalucki, 1996), differences in egg load (Jallow & Zalucki, 1998) or time since the last egg deposition (Courtney *et al.*, 1989), or experienced induced changes (Waser, 1986).

The extent to which learning restricts the host selection of *H. armigera* is crucial to our interpretation of polyphagy in this species. Learning can lead to a restriction of host use to a single species regardless of the presence of other hosts, a phenomenon which has been termed host constancy (see Waser, 1986; Wells & Wells, 1986). In the Lepidoptera, host constancy has been demonstrated in nectar foraging behaviour in butterflies (Lewis, 1989; Goulson & Cory, 1993; Goulson *et al*., 1997). Host constancy in oviposition could not only lead to selection predominantly towards the most abundant host, but also rejection of other less abundant hosts regardless of their suitability for oviposition. This could have considerable implications in our understanding and formulation of pest management strategies to control this moth.

Pest management using host plant volatiles

Volatiles from plants are likely to play an important role in host location. Laboratory evidence has demonstrated that *H. armigera* (Rembold *et al*., 1991; Hartlieb & Rembold, 1996) and other moths of the genus *Helicoverpa* (Tingle *et al*., 1990, Mitchell *et al*., 1991; Tingle & Mitchell, 1992), show upwind flight towards certain host volatiles. The use of host volatiles has been proposed as a potential lure for both male and female insects, and as a means of monitoring and forecasting populations (Tingle & Mitchell, 1992; Udayagiri & Mason, 1995).

Olfactory cues have been shown to be an important facet of learning in *H. armigera* (Hartlieb, 1995) and *H. virescens* (Hartlieb, 1996). If the response to particular volatiles is increased through learning, then experience of a host will alter the extent to which *H. armigera* responds towards these chemicals. If future pest management strategies incorporate host volatiles into trapping and monitoring moth populations, the affect of the local abundance of different hosts on trapping effectiveness will have to be considered. For example, lures containing volatile chemicals common to flowering tobacco (a host which has commonly been thought to be 'highly attractive' to *H. armigera* (Jallow & Zalucki, 1996)) may be less successful in a geographical region in which cotton is the principal crop, compared to one in which tobacco predominates. The mix of crops within a region and their relative abundance and distribution will all be factors which could alter the responsiveness of *H. armigera* to volatiles and consequently the effectiveness of volatile traps.

Any use of volatiles for monitoring and forecasting in *H. armigera* control would require calibration to account for the effects of learning and host abundance. Changes in response to different host volatiles may, however, provide an effective way of monitoring changes in *H. armigera* oviposition behaviour in the field. As the abundance of a particular crop species in its most susceptible stage to *H. armigera* attack (predominantly the flowering or fruiting stage) increases, changes in the responsiveness of adults to specific host volatiles may occur through learning, and could be monitored. In this way, volatiles may be used to forecast changes in the level of susceptibility of different crops as they enter these susceptible growth stages. Prokopy & Lewis (1993) have highlighted a number of ways in which learning may influence accurate sampling of insect populations for pest management.

Trap cropping

Trap crops are host plant species grown in small patches to lure insects away from much larger patches of the major crop. The patches of the trap crop species concentrate the pest species in a particular area where they cause less economic damage or can be more easily destroyed (Hokkannen, 1991). The principle of trap cropping relies on the knowledge that pests will prefer certain host species to others. Host species that are particularly attractive to *H. armigera* have therefore often been proposed for use as trap crops (Firempong & Zalucki, 1990a; Jallow & Zalucki, 1995).

Trap cropping systems have been effectively employed in controlling a number of insect pest species. However, these systems have not been successfully used for the control of lepidopterous pests (Hokkanen, 1991; Luther *et al*., 1996). Indeed, trap crops used to control *H. armigera* may receive fewer eggs than the main crop (Pyke *et al.*, 1987). In pest species such as *H. armigera*, learning provides an explanation for the lack of success in the use of trap crops (see also Prokopy & Lewis, 1993). Changes in preference through adult experience may lead to the most abundant host becoming the most preferred host, thereby rendering the trap crop ineffective as a control mechanism. Field studies such as those by Pyke *et al.* (1987) and Dillon & Fitt (unpublished) add weight to such a hypothesis.

Paradoxically, host selection behaviour favouring the most abundant host may mean that patches of more preferable hosts receive fewer eggs. The trap crop itself may therefore diminish in suitability to *H. armigera* attack. The extent to which hosts can be 'hidden' within a background of an alternative host, needs to be quantified. Small patches of high value crops (those which can tolerate little damage, such as tomatoes, or ornamental crops) may evade *H. armigera* attack if hidden within a more abundant host which can tolerate a greater level of *H. armigera* oviposition (e.g. sorghum (Shanower & Romeis, 1999) or a native host such as *Sonchus* (Asteraceae) (Gu & Walter, 1998)).

Host flowering and oviposition

It is well documented that *H. armigera* oviposition is particularly prevalent during the flowering stages of its hosts (Parsons, 1940; Roome, 1975; Broadley, 1978; Wardhaugh *et al.*, 1980; Topper 1987; Nyambo, 1988) and it has been suggested that adult feeding may influence egg distribution in oviposition (Topper, 1987; Cunningham *et al.*, 1998b). Learning may contribute to this correlation.

In *H. armigera*, learning has been shown in feeding behaviour; moths show a preference for foraging for food from the host species on which they have previous experience (Cunningham *et al.*, 1998b). If the host experienced through nectar foraging is also a suitable host for oviposition, learning in feeding behaviour will increase the likelihood that ovipositing moths come into contact with this host. The first host species that an ovipositing female is exposed to is crucial in determining its future choice of hosts since experience increases the oviposition preference for a host species (Cunningham *et al.*, 1998a). Nectar foraging commences several days before (and throughout) oviposition and thus hosts visited for feeding are likely to be visited prior to and at the commencement of oviposition.

Hosts that provide both feeding and oviposition sites are therefore likely to be the first hosts visited by ovipositing moths, and oviposition preference for these hosts will be increased through early adult experience.

In addition, learning in nectar foraging may influence host selection for oviposition if physiological mechanisms governing oviposition behaviour share elements with those governing feeding behaviour (Papaj, 1986c). Behavioural constraints imposed through learning (Waser, 1986; Lewis, 1993) may favour location of a single host for feeding and oviposition. This would increase the attractiveness of hosts which provide both feeding and oviposition sites.

Understanding the relationship between feeding and oviposition in *H. armigera* is important in the development of nectariless plants for resistant crop varieties in *H. armigera* control programmes. As discussed, early adult experience is an important factor in determining the oviposition preference of *H. armigera* and the likelihood of experience with a particular host may be increased through the presence of feeding sites. The success of nectariless varieties in reducing *H. armigera* attack within a region may depend heavily on the prevalence and abundance of host crops containing sources of nectar. For example, if the most abundant crops are cotton varieties containing nectaries, the effectiveness of nectariless cotton varieties may be reduced; learning having increased the oviposition preferences for all cotton varieties through early feeding and oviposition experience on the more abundant nectary bearing cotton varieties. If, however, all cotton crops within a region are nectariless varieties, these crops may incur a reduced *H. armigera* attack by reducing experience which occurs as a result of early adult feeding behaviour. In this instance, the severity of attack on these nectariless varieties would also depend on the prevalence of alternative host species which provide feeding and oviposition sites.

Conclusions

Learning is of fundamental importance in understanding the host selection behaviour of *H. armigera*. Laboratory evidence determining the relative preference of *H. armigera* for different host species does not account for the effect of experience, which can significantly alter host selection behaviour. In a field situation, the preference of *H. armigera* for different host species may be affected by the prevalence and abundance of these hosts. Field evidence from a number of studies supports this hypothesis.

With the increasing resistance that *H. armigera* is exhibiting towards a wide range of pesticides (McCaffery *et al*., 1991) the necessity to design future pest management strategies to control this moth becomes more apparent. Current research into the use of volatiles for monitoring and trapping, the use of trap crops and resistant crop varieties for controlling this moth all require a detailed understanding of host selection behaviour. It is essential that learning behaviour is considered in the design and implementation of these programmes. Furthermore, as learning has been observed in the oviposition behaviour of other polyphagous pest species (Prokopy & Lewis, 1993; Landolt & Molina, 1996) the conclusions of this review may apply to the future control of a wide range of agricultural pests.

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