

# Learning in the nectar foraging behaviour of *Helicoverpa armigera*

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**Abstract.** 1. Learning may enable insects to obtain nectar from flowers more efficiently. Learning in nectar foraging has been shown primarily in studies of bees and butterflies. Here, learning is demonstrated in the nectar foraging behaviour of a noctuid moth, *Helicoverpa armigera*.

2. The present studies show that: (1) previous experience with a flowering host species increases the probability of that species being selected for nectar foraging, and (2) previous experience of a particular flower type (food source at bottom or top of the corolla tube) increases the likelihood of the food source being found when that flower type is being searched.

3. The implications of these findings for understanding the pattern of oviposition observed in wild populations of this important pest species are discussed.

**Key words.** Bollworm, feeding, foraging, learning, nectar.

## Introduction

In many insect species, the primary food source for adults is nectar obtained from flowers. Nectar foraging may involve the exploitation of flowers of a number of species that are morphologically distinct. In this case, the locations of nectaries may vary considerably among flower species, and so require different manipulation of the flower by a forager. Learning, defined here as the modification of behaviour through experience, may enable insects to select and/or handle particular types of flowers more efficiently, and could therefore be one mechanism by which individuals increase their nectar foraging ability (Lewis, 1986; Papaj & Prokopy, 1989).

Despite its possible importance, the prevalence and influence of learning in nectar foraging behaviour across the various insect orders is not clear (Gould & Marler, 1984). The majority of research on learning in nectar foraging has been carried out in the Hymenoptera. In particular, detailed studies on the honey bee *Apis mellifera* have demonstrated its ability to learn the odour, colour, and shape of host flowers (Gould, 1984, 1993; Heinrich, 1984; Hammer, 1993; Menzel *et al.*, 1993). Perhaps the next best studied order is the Lepidoptera, where the learning of host stimuli in nectar foraging has been demonstrated in several butterfly species (Swihart & Swihart, 1970; Lewis,

1986, 1989, 1993; Goulson & Cory, 1993). However, at present there is limited evidence for learning in the nectar foraging behaviour of adult moths (Hartlieb, 1995, 1996; Kelber, 1996; Fan *et al.*, 1997).

*Helicoverpa armigera* (Lepidoptera: Noctuidae) is a widespread polyphagous pest species of world-wide economic importance on many agricultural and horticultural crops (Zalucki *et al.*, 1986; Fitt, 1989). In a previous paper it was demonstrated that adult females show learning in the choice of hosts for oviposition (Cunningham *et al.*, 1998). The aim of this paper was to examine whether male and female adults of *H. armigera* exhibit learning in nectar foraging behaviour. Specifically, whether previous experience influences: (1) the selection of hosts for nectar foraging, and (2) the success rate of food discovery within a flower. The possible importance of learning in nectar foraging for both the feeding and oviposition behaviour of *H. armigera* in the field is discussed.

## Materials and methods

*Helicoverpa armigera* larvae were reared in a controlled environment (25 °C, 70% r.h., and a LD 14:10 h regime) on a standard artificial diet for *Helicoverpa* species (Teakle, 1991). The use of an artificial diet removed the possibility of alterations in adult behaviour due to host plant experience in the larval stage. Larvae were separated 2–3 days after hatching (second or third instar) to prevent cannibalism, and transferred to individual 30-ml pots (containing 15 ml of artificial diet) until

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pupation. Pupae were removed from the pots, sterilized in 0.2% (w/v) sodium hypochlorite, sexed, and placed in holding cages (0.45 × 0.45 × 0.45 m) until eclosion. An Indian strain of *H. armigera* (eggs provided by the Natural Resources Institute, Chatham, U.K.) was used in experiment 1 and an Australian strain of *H. armigera* (supplied by the Department of Primary Industries, Toowoomba, Australia) in experiment 2.

The host plant species, tomato (*Lycopersicon esculentum* L.) and tobacco (*Nicotiana tabacum* L.), were reared in a tropical greenhouse where temperatures fluctuated between 19 and 30 °C. Flowering terminals used in treatment cages in experiment 1 (at 25 °C) were cut ≈ 30 min prior to commencing the experiment, and placed in water to help prevent wilting.

#### *Experiment 1: previous experience and host selection for nectar foraging*

The aim of this experiment was to test whether moths given prior experience on tomato or tobacco exhibit differences in the species they select for nectar foraging. The moths were maintained under a reverse phase day/night pattern (hereafter, 'day/night' refers to the moths' pattern). On the first night of the experiment, newly eclosed moths were sexed and transferred to holding cages (0.45 × 0.45 × 0.45 m). On the second night, equal numbers of each sex of *H. armigera* were transferred to three treatment cages (0.45 × 0.45 × 0.45 m), each with a different feeding site. The feeding sites in the three cages were: (1) flowering tobacco terminals, (2) flowering tomato terminals, and (3) artificial sites – cotton wool balls wrapped in nappy liner and tied to a wooden splint 20 cm above the floor of the cage. Tobacco flowers are borne in terminal paniced racemes, forming a distinct flowerhead at the apex of the flower, whereas flowering tomato terminals grow from the internodes. A similar host area and number of flowering structures were created by placing several tomato terminals, which included both flowers and foliage, in the treatment cages. Additional feeding sites were provided on the hosts by placing droplets of honey (≈ 20 µl) on the surface of the flowers or on the artificial sites. Flowers (or cotton wool balls) were replaced with fresh material in each treatment cage 60 min after nightfall. Typical moth feeding behaviours were observed in all treatments: adults hovered around flowers or artificial sites, and exhibited proboscis and antennal movements characteristic of foraging behaviour upon landing (Brantjes, 1976; Pivnick & McNeil, 1985).

On the third night, the moths were tested for host preferences when selecting foraging sites in a laboratory flight cage (3.0 × 3.2 × 2.3 m). The flight cage contained two discrete patches of fully intact host plants, one patch containing two tobacco plants, and the other three tomato plants to create a similar host area. Any possible problems due to different heights of the flowers (Firempong & Zalucki, 1990) were minimized by raising the tomato plants to the same height as the tobacco plants.

After dusk, equal numbers of moths (male and female) were released from each of the three treatment groups (exposed to tobacco, tomato, or artificial sites) in three sequential 40-

min periods, allowing 5 min between each period to collect remaining inactive moths. Preference for a host was assigned when a moth carried out a controlled flight approaching a patch and remained within 5–10 cm of the host for more than 5 s. After such behaviour, the insect was captured. The number, sex, and preference of all captured insects were recorded at the end of the experiment. The experiment was repeated over ten consecutive nights, using different moths each night and randomizing the order of release of each treatment group. The moths used on the different nights were always tested at the same age, on the fourth night following their eclosion. The total numbers used on each night ranged from thirty-six (twelve in each treatment) to seventy-two (twenty-four in each treatment). The position of the patches was swapped daily to control for possible position effects.

#### *Experiment 2: previous experience and food discovery*

The aim of this experiment was to examine whether the experience of foraging on flowers that varied in the locality of a food source (honey solution) altered subsequent food discovery. All treatments and subsequent testing were carried out with tobacco flowers in a glasshouse, allowing ambient daylight and a decline in light intensity at dusk.

Tobacco flowers of the same age (the first day that the corolla tube was fully open) were taken, cut at the pedicel, and any nectar that had accumulated in the corolla tube was removed with a pipette. These flowers were divided into two treatments. In the first treatment, the corolla tube was plugged at the top end (furthest from the calyx) using absorbent cotton wool, allowing the anthers to protrude past the plug. Moths feeding on these flowers would gain experience feeding at the top lip of the corolla, and were prevented access to the corolla tube. In the second treatment, a cotton wool plug was inserted into the base of the corolla tube using forceps, flattening the stamens against the corolla, but leaving them intact. Moths feeding on these flowers would gain experience feeding at the base of the corolla. For both treatments, 150 µl of honey solution (30% v/v) were placed on the cotton wool plugs. Artificial feeding sites were constructed by inserting eight flowers from the same treatment into holes in a rectangular sheet of card arranged in two rows of four. These artificial feeding sites were clamped at a height of 20 cm (from the base of the card to the floor of the cage) in each of the two treatment cages.

On the first night of the experiment, eclosing moths were sexed and transferred to holding cages. On the following day, equal numbers of each sex were transferred to each treatment cage. These moths were exposed to flowers in the treatment cages on the second and third night, placing fresh feeding sites in the cages 30 min before dusk on each night.

To test the ability of moths to find food, moths were placed in a new holding cage on their fourth night. This holding cage contained flowers that had feeding sites (honey solution) at the base of the corolla tube. Activity was monitored with two Cohu 4710 monochrome CCD video cameras, each linked to a

Panasonic AG-7350 S-VHS video recorder and a FOR-A VTG 22 time generator (FOR-A Company, Japan).

One camera viewed the cage from above and tracked the activity of all moths in the cage. The second camera focused exclusively on the feeding site, such that any moth activity around the site could be recorded in greater detail. As both cameras were linked to timers, which were synchronized, the feeding behaviours of each moth within the cage could be documented. The activity and behaviour of moths around the flowers was monitored for 3 h, starting 1 h before dusk. These experiments were repeated over eight consecutive nights, using different moths each night, and testing the different treatments on alternate nights. All moths were tested at the same age, on the fourth night following eclosion.

For each moth approaching the feeding site, feeding behaviour was monitored using the video equipment. For each individual observed, the first three visits to flowers were monitored, recording: (1) whether the honey solution was discovered, (2) the discovery time of moths that located the honey solution (the time between initial proboscis extension upon alighting on a flower and commencement of feeding), and (3) departure times in moths that did not discover the honey solution. Moths interacting at the same feeding site or exhibiting oviposition behaviour on the flowers were eliminated from the analysis.

Behaviour at the feeding site that involved antennal, proboscis, and head movements equated with nectar foraging was inferred to be pre-discovery searching behaviour (Brantjes, 1976; Cunningham, 1996). Cessation of these behaviours, the insect remaining stationary on the flower with its proboscis extended, was documented as with feeding behaviour (Pivnick & McNeil, 1985; Cunningham, 1996). Insects entering the corolla tube and remaining stationary were also inferred to be feeding.

### *Experiment 3: additional experience and food discovery*

The aim of this experiment was to investigate whether additional experience continued to affect the food discovery ability of moths. These tests were carried out on the moths from experiment 2 that were initially experienced feeding at the top (lip) of the corolla tube. After examining the ability of the moths to find food on day four of experiment 2, these insects were returned to holding cages and exposed to flowers with feeding sites at the base of the corolla tube on nights 5 and 6. On night 7, moths were returned to the test cage and their ability to discover food from flowers with feeding sites at the base of the corolla tube was examined. Ideally, to account for possible age effects, these data should be compared with moths of the same age having undergone only one experience treatment. However, lack of equipment prevented this, as only one test could be performed each night. The behaviour of moths in this experiment was therefore compared with that of the moths from both experience treatments in experiment 2, which included the same moths when they were younger.

### *Statistical analysis*

Proportion data such as the proportion of females selecting a particular host species or the proportion of successful visits to a food source often have non-normal distributions and unequal sample sizes. To avoid these problems, data were analysed using generalized linear modelling techniques (McCullagh & Nelder, 1989) in the GLIM statistical package (Crawley, 1993). Binomially distributed error variances were assumed, and a logit link function employed. Hypothesis testing was carried out using the  $\chi^2$  test on differences in deviance. Experiment 1 used the number of moths selecting tobacco as the response variable, and the total number of moths selecting any host as the binomial denominator. To avoid any possible pseudoreplication (Hurlbert, 1984), moths from each experience treatment, on each night, were summed into a single data point.

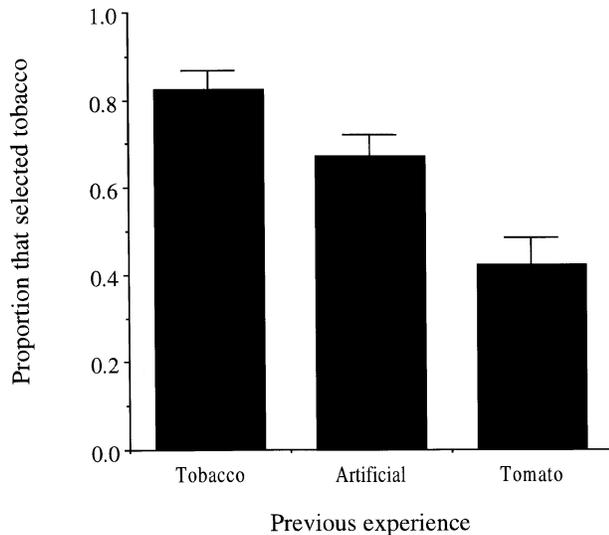
Data from experiment 2 were analysed in two ways. Firstly, the number of successful visits (discovery of the honey solution) out of the first three flower visits made by each moth (see Laverty, 1980) was compared for moths from each treatment. This allowed the inclusion of a number of visits from each individual in the analysis, and was analysed assuming binomial errors. The number of successful visits made in the first three flower visits by a moth was used as the response variable, and the binomial denominator was set at three. However, any visit to a test flower is effectively an *experience*, so a second more conservative analysis was carried out, considering only the first visit for each individual. In this analysis, the response variable was treated as a binary response variable (success or failure) with a binomial denominator of one (Bernoulli distribution). Finally, the time spent searching on the flower by individual moths was analysed using ANOVA, assuming normal errors.

## **Results**

### *Experiment 1: previous experience and host selection for nectar foraging*

A total of 468 moths were placed in the flight cage over the ten nights of testing, and 209 (ninety-six males and 113 females) of these exhibited host selection behaviour for nectar foraging. Considering moths of both sexes, host experience had a significant effect on host selected in the flight cage ( $\chi^2_{(2)} = 24.47, P < 0.001, n = 30$ ), and there was no significant effect due to night of testing ( $\chi^2_{(9)} = 8.81, P = \text{NS}$ ). Experience on a host increased significantly the proportion of moths selecting that host, compared with moths experienced on the alternative host or artificial sites (Fig. 1). Specifically, individuals experienced on tobacco selected tobacco significantly more often than those experienced on tomato ( $\chi^2_{(1)} = 24.14, P < 0.001$ ) or those experienced on artificial sites ( $\chi^2_{(1)} = 4.66, P < 0.05$ ), and individuals experienced on tomato selected tobacco significantly less often (and therefore tomato significantly more often) than those experienced on artificial sites ( $\chi^2_{(1)} = 8.81, P < 0.01$ ).

Very similar results were obtained when males and females



**Fig. 1.** The proportion of moths that selected tobacco flowers for nectar foraging ( $\pm$  SE) from individuals that had previously been experienced on tobacco flowers, artificial sites, or tomato flowers.

were considered separately. In both cases, host experience had a significant effect on host selected in the flight cage (females:  $\chi^2_{(2)} = 15.36$ ,  $P < 0.001$ ,  $n = 28$ ; males:  $\chi^2_{(1)} = 10.14$ ,  $P < 0.01$ ,  $n = 30$ ), and there was no significant effect due to night of testing (females:  $\chi^2_{(9)} = 9.88$ ,  $P = \text{NS}$ ; males:  $\chi^2_{(9)} = 7.21$ ,  $P = \text{NS}$ ). The reduced sample size when considering females only is due to 2 nights when none of the females from one of the treatment groups exhibited foraging behaviour (females experienced on artificial sites on one occasion, and females experienced on tomato on the other). Considering only females, individuals experienced on tobacco selected tobacco significantly more often than those experienced on tomato ( $\chi^2_{(1)} = 15.24$ ,  $P < 0.001$ ) or artificial sites ( $\chi^2_{(1)} = 4.86$ ,  $P < 0.05$ ). Although females experienced on tomato selected tobacco less often (and therefore tomato more often) than those experienced on artificial sites, this difference was only close to significance ( $\chi^2_{(1)} = 3.51$ ,  $0.1 > P > 0.05$ ). Considering only males, individuals experienced on tobacco selected tobacco significantly more often than those experienced on tomato ( $\chi^2_{(1)} = 8.64$ ,  $P < 0.01$ ), but not significantly more often than those experienced on artificial sites ( $\chi^2_{(1)} = 0.61$ ,  $P = \text{NS}$ ). Males experienced on tomato selected tobacco significantly less often (and therefore tomato significantly more often) than those experienced on artificial sites ( $\chi^2_{(1)} = 5.77$ ,  $P < 0.05$ ).

#### Experiment 2: previous experience and food discovery

**Moth activity.** General activity and behaviour around feeding sites commenced at dusk and continued for approximately 40 min, after which little feeding was witnessed. Foraging bouts were short and interspersed with additional behaviours, predominantly *dispersal* behaviours, with moths flying against the top of the cage (Ramaswamy, 1988). Over eight nights, thirty-three out of a total of 117 moths visited flowers [ $n = 19$

and  $n = 14$  for moths experienced in feeding at the base and top (lip) of the corolla, respectively]. Approximately equal numbers of moths were active on each night and there was no effect of experience treatment on the proportion of moths visiting flowers ( $\chi^2_{(1)} = 0.94$ ,  $P = \text{NS}$ ). Few moths died during the course of the experiment.

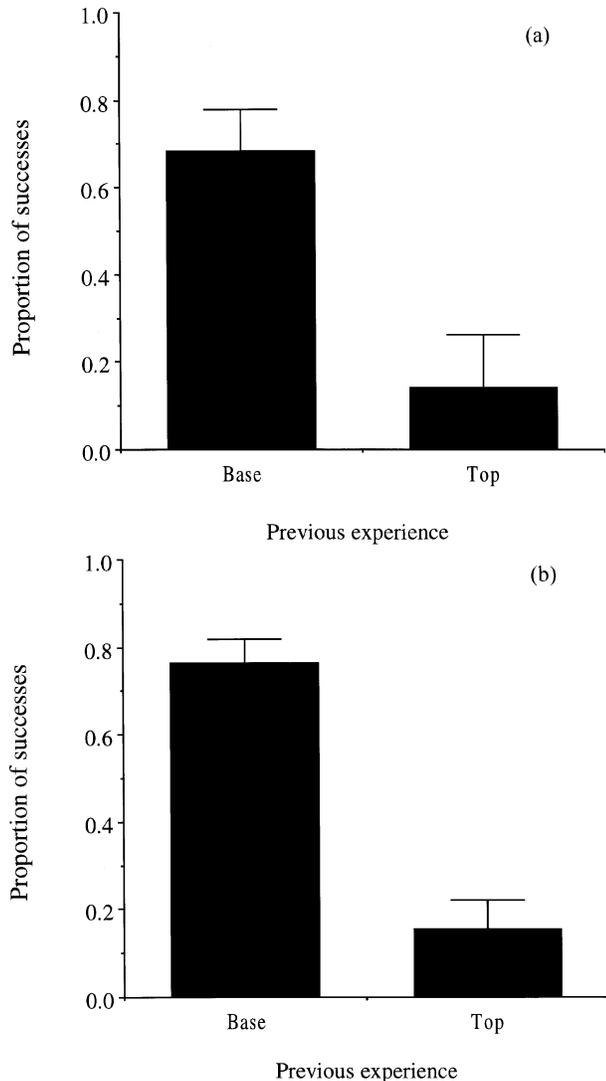
**Food discovery and feeding.** All flowers contained feeding sites (honey solution) at the base of the corolla tube. Feeding behaviour, characterized by proboscis extension and a cessation in activity (Cunningham, 1996), was not displayed unless moths entered the corolla tube partially or fully. No moths were observed feeding while standing on the lip of the flowers. Moths entering the tube frequently folded their wings and crawled forward over the stamens into the tube. This behaviour was noticeably different from the characteristic search behaviour that moths exhibited on alighting on the flower (proboscis searching, head movements, and vigorous antennal movements).

The number of successful visits to flowers with the feeding site at the base of the corolla was recorded. Moths experienced feeding at this site had a significantly greater proportion of successful visits (food discovery) than moths that had experienced feeding at the top (lip) of the corolla (Fig. 2). This result held whether the proportion of successes in the first three visits ( $\chi^2_{(1)} = 35.63$ ,  $P < 0.001$ ), or only the first visit ( $\chi^2_{(1)} = 10.29$ ,  $P < 0.01$ ) was considered.

Successful visits to flowers by moths experienced in feeding at the top (lip) of the corolla tube were relatively uncommon (five in total), so there was a scarcity of information on handling times in moths that found the reward in this group. This led to low statistical power when comparing between treatments the time taken to locate the food source. Given this caveat, there was no significant difference between the treatments [moths experienced feeding at the base of the corolla and moths experienced feeding at the top (lip) of the corolla] in: (1) time spent on searching behaviours before either entering the tube or departing ( $F_{(1,21)} = 3.41$ ,  $n = 23$ ), (2) the time to find the food source in moths that did locate it ( $F_{(1,24)} = 0.20$ ), and (3) the search time in moths that did not find the food source ( $F_{(1,31)} = 0.05$ ); all  $P = \text{NS}$ .

#### Experiment 3: additional experience and food discovery

Moths from experiment 2 that were initially experienced feeding at the top (lip) of the corolla were subsequently experienced feeding at the base of the corolla tube ( $n = 9$ ). The success rates of food discovery at the base of the corolla tube in these moths were then significantly greater than before this subsequent experience (first three visits:  $\chi^2_{(1)} = 21.28$ ,  $P < 0.001$ ; first visit:  $\chi^2_{(1)} = 9.77$ ,  $P < 0.01$ ), and not significantly different from the moths that had experienced feeding at the base of the corolla tube in experiment 2 (first three visits:  $\chi^2_{(1)} = 0.34$ ,  $P = \text{NS}$ ; first visit:  $\chi^2_{(1)} = 0.27$ ,  $P = \text{NS}$ ).



**Fig. 2.** The proportion of successful visits to flowers with the feeding site at the base of the corolla ( $\pm$  SE) from individuals that had previously been experienced feeding at the base or top (lip) of the corolla; (a) shows only the first visit made by each moth, and (b) the first three visits.

## Discussion

In experiment 1, exposing newly-emerged *H. armigera* adults to flowers of a particular host species influenced subsequent host selection for nectar foraging. Moths that had experienced feeding on a particular host species preferred to forage for nectar on that species (Fig. 1). The influence of previous experience on subsequent host choice in the selection of oviposition sites for *H. armigera* has been demonstrated previously (Cunningham *et al.*, 1998). However, in this study the preference is exhibited by both males and females, and occurs in females that were not ovipositing. Consequently, this preference cannot merely be a result of selection for oviposition

sites. In addition, it shows that learning behaviour occurs in both sexes of *H. armigera*.

In experiment 2, previous experience also significantly affected the ability of moths to find a food source in a flower. Moths experienced in feeding from a food source at the base of a flower's corolla tube subsequently showed a significantly greater proportion of successful visits (discovery of food source) to such flowers than moths that had experienced feeding from a food source at the top (lip) of the corolla tube (Fig. 2). This increased success in moths experienced on a particular type of flower in locating the food source in that flower provides an advantage for the increased selection of that type of flower as a foraging site (Lewis, 1986; Laverty, 1994).

Additional experience feeding at the base of the corolla altered the food discovery rate of moths that were initially experienced by feeding at the top (lip) of the corolla. The additional experience increased significantly the number of successful visits to flowers with feeding sites at the base of the flower. Moreover, these moths located the food source at a rate equal to moths that were initially experienced feeding at the base of the corolla. Future work could expand these experiments in a number of ways. In particular, one possible problem with this experiment could be controlled for by comparing the success rate of the additionally experienced moths with singly experienced moths of the same age. Other possibilities would be to examine whether the improved success rate in the second flower type (obtained in the subsequent learning) came at the cost of the success rate in the first flower type, or whether continued experience in a single flower type led to further improvements in the success rate (Lewis, 1986, 1993; Laverty & Plowright, 1988; Laverty, 1994).

In experiment 2, honey solution was more accessible to moths foraging at flowers where the food source was at the top (lip) of the corolla tube. This could affect levels of satiation and so have an effect on feeding behaviour (Cunningham, 1996). For example, moths that had easier access to honey solution could spend less time foraging than moths that were initially unable to find the food source on a flower merely due to differences in individual levels of satiation. However, the results suggest that this is an unlikely explanation of differences in successful discovery of food: neither the number of moths foraging in each treatment nor the time spent searching after alighting on the flower was found to be significantly different in the two treatments.

The phenomenon whereby insects tend to restrict their visits to a single host species that they have experienced is known as flower constancy (Lewis, 1993). Flower constancy may be advantageous if improved handling, gained through experience, outweighs the cost of not visiting other flowers. In bumble bees (*Bombus* sp.), greater constancy occurs when individuals visit more complex flowers, where handling times (and thus the benefits of experience) are greater (Laverty, 1994). It has been suggested that flower constancy may not arise solely from advantages of efficient learning, but also from constraints imposed by learning through limits to memory, or learning other tasks (learning interference; Lewis, 1993). An example of this is that in the butterfly *P. rapae*, flower handling time decreases with experience, but increases with learning another

type of flower (Lewis, 1986). Further studies on *H. armigera* will be required to determine the extent to which it exhibits flower constancy, and the underlying reasons for this.

Learning may help to explain the correlation between high levels of oviposition and host flowering observed in the field; *H. armigera* is a particularly prevalent pest during the flowering stage of crops (Parsons, 1940; Zalucki *et al.*, 1986). Learning occurs in the oviposition behaviour of *H. armigera*, with exposure to a host species increasing the choice of that host for subsequent oviposition (Cunningham *et al.*, 1998). Consequently, the first host species to which an ovipositing female is exposed is crucial in determining future choice of hosts for oviposition. Nectar foraging commences several days before (and throughout) oviposition and so a flowering host species is more likely to be the first host species that females visit when they are ready to oviposit. If learning has also occurred in nectar foraging behaviour, then females will be more likely to use a single flowering host species for both nectar foraging and oviposition.

Utilization of the same host for nectar foraging and oviposition is even more likely if learning in one behaviour influences and constrains other behaviours. Papaj (1986) has suggested that the physiological mechanisms governing oviposition may share elements with those governing feeding behaviour. If this is the case, then learning to select a host for oviposition different from the learned feeding hosts may incur costs. Memory constraints in both feeding and oviposition may therefore limit the ability to learn about more than one or a small number of hosts.

To understand learning in nectar foraging behaviour and its influence on oviposition behaviour, further investigation is required, in particular field studies. Some measure of flower constancy in *H. armigera* needs to be made in order to ascertain the effect of learning on foraging patterns in the field. Lewis (1986) and Laverty (1994) have provided methods for quantifying the extent of flower constancy. Further elucidation of mechanisms involved in learning, particularly which host cues are utilized, would be advantageous both for the understanding of learning in nocturnal insects, and also for possible pest management strategies for *H. armigera* monitoring and control.

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