

Oviposition of diamondback moth in the presence and absence of a novel host plant

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Abstract

The diamondback moth (DBM, *Plutella xylostella* L. (Lepidoptera: Plutellidae)) consumes a wide variety of brassicaceous host plants and is a common pest of crucifer crops worldwide. A highly unusual infestation of a sugar pea crop was recorded in Kenya in 1999, which persisted for two consecutive years. A strain (DBM-P) from this population was established in the laboratory and is the only one of several strains tested that can complete larval development on sugar peas. The oviposition acceptance and preference of the DBM-P strain was assessed in the presence of cabbage plants, sugar pea plants or both, in comparison to another strain (DBM-Cj) that was collected from cabbage and is unable to grow on pea plants. As expected, DBM-Cj females preferred to oviposit on cabbage plants. Surprisingly, DBM-P females also laid most eggs on cabbage and very few on peas. However, they laid significantly more eggs on the cabbage plant when pea plants were present. Our findings suggest that DBM-P manifested the initial stages of an evolutionary host range expansion, which is incomplete due to lack of oviposition fidelity on pea plants.

Keywords: *Plutella xylostella*, Lepidoptera, specialist, herbivore, host shift, host plant preference, crucifer

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Introduction

We are surrounded by a plethora of herbivorous insects feeding on many different kinds of host plants. This high ecological diversity results from a dynamic process in which insect populations may change their ecological niches throughout evolution (Funk *et al.*, 2002; Janz & Nylin, 2008). When an insect species adds a new host plant to its diet, host range expansion has occurred. When it has lost the ability to feed on the original host plant as well, this is considered a host shift (Tabashnik, 1983; Bernays & Chapman, 1994). Research on host range expansions and shifts in herbivorous insects has been focused mostly on the

crucial role that adaptation to the host plant plays in the early stages of speciation as a starting point for diversification (Bush, 1969; Via, 1999; Schwarz *et al.*, 2005; Janz *et al.*, 2006; Mercader & Scriber, 2007) or understanding the coevolutionary processes between herbivorous insects and their plant hosts (Ehrlich & Raven, 1964; Wheat *et al.*, 2007; Stenberg *et al.*, 2008). Only recently, the evolutionary dynamics of the process have received increasing attention (Janz *et al.*, 2001, 2006). Does the acquisition of novel food sources proceed via sudden shifts or rather via gradual expansions of the host range? How does the subsequent loss of the ability to feed on the original food source occur? In most species these changes have taken place in the evolutionary past, so that the sequence of events leading to the current state of ecological differentiation cannot be studied easily.

Successful range expansion to a new host plant requires both physiological and behavioural adaptations (Wasserman

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& Futuyma, 1981): (i) larvae must be able to recognize, digest and fully develop on the newly acquired host plant; and (ii) adult females have to be able to find and accept the new plant as an oviposition site (Rausher, 1982; Thomas *et al.*, 1987; Bowers *et al.*, 1992). In many cases, the newly acquired host plants are chemically similar to the original host (Ehrlich & Raven, 1964; Becerra & Venable, 1999; Murphy & Feeny, 2006). For example, populations of the apple maggot fly, *Rhagoletis pomonella* (Diptera: Tephritidae), shifted from native hawthorn trees to introduced apple trees during the mid-19th century (Bush, 1969; Feder *et al.*, 1994; Forbes *et al.*, 2005) so that there are now two host races. Both host trees belong to the Rosaceae. Another example is the host plant range expansion by the legume feeding butterfly *Colias eriphyle* (Lepidoptera: Pieridae) to the forage crop alfalfa (*Medicago sativa*) about 100 years ago (Tabashnik, 1983), with the new host plant also belonging to the Fabaceae. It is rare to find the acceptance of a novel host plant species that belongs to a chemically and evolutionarily unrelated group of plants, which has not been previously utilized as a host within the evolutionary lineage of the herbivore (Strong, 1979; Bush, 1994).

The highly specialized crucifer-feeding diamondback moth (DBM) *Plutella xylostella* L. (Lepidoptera: Plutellidae) provides a unique opportunity to study a contemporary event of adaptation to a chemically and evolutionarily unrelated novel host and the underlying behavioural changes in the herbivore. The natural host range of DBM encompasses wild crucifers (Brassicaceae), and it is a significant worldwide pest of cultivated crucifers, a plant family characterized by the glucosinolate-myrosinase defence system against herbivore attack. DBM has the ability to deactivate this defence system using a highly active glucosinolate-sulfatase and, thus, is specifically adapted to brassicaceous plants (Ratzka *et al.*, 2002). Thus, it was very surprising to find DBM feeding on sugar snap peas, *Pisum sativum* L. var. *macrocarpon*, cultivar Oregon Sugar Pod (Fabaceae) in the field in the area south of Lake Naivasha in the Rift Valley, Kenya, in 1999 (Löhr, 2001). That year, DBM densities on the original cabbage hosts were extremely high, and a neighbouring pea field became infested. Because of its well-known status as a crucifer specialist, the identity of the pest as DBM was doubted until confirmed by an entomologist. In 2000, this local population even expanded to an adjacent field of mangetout peas (*Pisum sativum* L. var. *macrocarpon*, cultivar Snow Green). Because the population persisted as an uncontrollable pest on the pea crop in the following two years, the farmer stopped growing peas, so that this population either became extinct in the field or rejoined the populations feeding on the neighbouring cabbage (B. Löhr, personal communication). Larvae were collected from the pea crop in 2000 and 2002, and have been reared on Oregon Sugar Pod peas in the laboratory since then (Löhr, 2001). While the other populations of diamondback moth that we (Janssen *et al.*, 2008) and others (Zhang *et al.*, 2007) have tested cannot survive on pea plants, this population can complete development on a pea host alone and is now referred to as DBM-P (Löhr & Gathu, 2002), the pea-adapted strain of the diamondback moth. Thus, this DBM population represents a unique and very recent switch or expansion from the original plant family (Brassicaceae) to a new and dissimilar host plant family (Fabaceae) in the field.

To determine whether DBM-P was just in the initial phases of a host range expansion, or has gone further

towards a complete host shift, the process of adaptation in larvae and adults must be examined. Evidence for possible pre-adaptation to peas as a novel host was obtained by Gupta & Thorsteinson (1960a), who showed that out of 62 species of plants from 37 different families (excluding crucifers) offered as leaf disks to DBM larvae only nine species were eaten, six of them from the Fabaceae. If confined to prevent escape, DBM larvae fed on whole plants of three legumes in the laboratory, and 5% overall developed to pupae on *P. sativum*. How well and by what means have DBM-P larvae adapted to the new host compared with the original crucifers? In feeding assays Löhr & Gathu (2002) compared the DBM-P strain to a strain from neighbouring cabbage fields (DBM-C). They showed that DBM-C survived very poorly on peas (88% survival on kale and 2% on peas), but DBM-P did equally well on both host plants (85% survival on kale and 83% on peas). Despite this similar overall survival rate on pea plants, developmental time of DBM-P larvae was still significantly longer on the new host plant peas than on the original kale host plant; and pupal weight was significantly lower for DBM-P reared on pea than on kale. When Löhr & Gathu (2002) started a new laboratory culture from the few DBM-C survivors from pea, and reared these on pea plants, larval survivorship increased gradually from 2% in the first generation to 50% in the fourth generation, suggesting that selection acted to increase the frequency of pea-adapted alleles over time. We have subsequently shown that the ability of DBM-P larvae to complete development on pea has a polygenic genetic basis, which does not diminish the ability to complete development on kale (Henniges-Janssen *et al.*, in prep.). This indicates that DBM-P larvae have expanded their host range to include pea, by means of genetic changes in response to selection, but have not undergone a host shift by losing the ability to perform on the original host.

Adaptation of DBM-P adults, in contrast to larvae, has received less attention. The question of whether adult adaptation (i.e. oviposition preference) is a trait independent of larval adaptation has already been addressed (Thompson, 1988), and for several butterfly species it has been found that these traits were indeed controlled by different genes (Wiklund, 1975; Thompson, 1988; Forister, 2005). Adult adaptation, thus, could evolve independently from larval adaptation. Gupta & Thorsteinson (1960b) found low acceptance of *P. sativum* by DBM females in no-choice experiments, with more eggs being laid on the pot or vial than the plant, but considered the plant to contain only weak inhibitors of oviposition if any. The central question we addressed in this study is how readily do DBM-P females accept peas for oviposition; do they still utilize the ancestral plant or do they prefer pea? To address these questions, we performed two types of tests with females of DBM-P as well as with another Kenyan cabbage strain (DBM-Cj) for comparison. To assess oviposition acceptance, no-choice experiments were conducted, in which females were confined with either a cabbage or a pea plant. To assess oviposition preference, females were offered both plant species at the same time. We predicted that DBM-P females would either oviposit similarly well on cabbage and pea plants, or prefer their new host pea for oviposition. We found instead that DBM-P oviposition was increased overall in the presence of pea plants but not specifically targeted to pea plants, suggesting a very early stage in adaptation to the new host.

Materials and methods

Insects

Two strains of *P. xylostella* were used in the oviposition experiments: the cabbage feeding strain (DBM-Cj) and the pea adapted strain (DBM-P). Both strains originate from Kenya and were kindly provided by Bernhard Löhrl from the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya. DBM-P was originally collected from the infested pea field in Naivasha in 2000, and was repeatedly replenished with additional field-collected material from the same site for the next two years (Löhrl & Gathu, 2002). It has been maintained as a laboratory culture since then at ICIPE in Kenya. DBM-Cj derived from a field population from the semi-arid areas about 40 km southeast of Nairobi. Both strains were sent to the Max Planck Institute for Chemical Ecology (Jena, Germany) in May 2005, where they have been reared for more than 50 generations since then. Population sizes of the strains maintained in Kenya are unknown to us, but averaged about 400 adults per generation in Jena. Insect cultures of both strains were reared from egg to adult stage on intact plants (for rearing procedure of plants see below) in mesh cages (60 × 60 × 60 cm) at 21°C, 50% RH and 16:8 L:D photoperiod, with DBM-Cj reared on cabbage and DBM-P reared on pea. For mating and oviposition, adult moths were collected with an aspirator (BioQuip Products, Rancho Dominguez, CA, USA) and transferred from cages to mating boxes (15 × 15 × 5 cm). Each box contained at least 30 individuals, and per generation 12 to 15 boxes were set up. The bottom of the boxes was covered with tissue paper on which leaves of the respective host plants (cabbage or pea) were placed as oviposition sites. Adult moths were fed with 5% honey solution. After eggs were deposited on leaves and the tissue paper, these were transferred to cages and fresh leaves were added to the plastic box.

Plants

Seeds of pea, *Pisum sativum* L. var. *macrocarpon*, cultivar Oregon Sugar Pod, were obtained from Agri-Saaten GmbH (Bad Essen, Germany). Cabbage seeds, *Brassica oleracea* var. *capitata*, cultivar Gloria, were obtained from B and T World Seeds (Aigue-Vives, France). Plants used for rearing of insects were grown in trays (58 × 32 × 11.5 cm) in a peat-based substrate (Klasmann Kultursubstrat TS1, Geeste-Groß Hesepe, Germany) under greenhouse conditions at 21–23°C, 50–60% RH and 14:10 L:D photoperiod. Each tray contained approximately 60 plants. These trays were put into rearing cages. Plants for oviposition experiments developed under the same conditions, except that only seedlings were grown in flat trays. After two weeks, seedlings were separated and grown individually in single pots (7 × 7 × 8 cm). For oviposition experiments, five-week-old single potted pea and cabbage plants of similar size were used. At this stage, both plant species had a leaf area of similar size of approximately 200 cm².

Oviposition experiments

Oviposition experiments were designed to evaluate the oviposition acceptance (no-choice) and preference (choice) of DBM adult females of the newly evolved pea host strain in comparison to the crucifer host strain. Five virgin female and

male moths were collected for each trial from the colony by removing intact pupae (with cocoon) from the rearing cages and isolating them in plastic vials to prevent uncontrolled mating and egg laying. Isolated pupae were stored in a growth chamber at 21°C, 50% RH and 16:8 L:D photoperiod. After emergence, moths were provided with 5% honey solution. Thirty-six to 48 hours after emergence, adult moths were sexed and released into mesh cages (60 × 60 × 60 cm) in groups of five males and five females. Placement of moths in the cages was always done at around 5 pm. Once placed in the cages, moths were allowed to freely mate and oviposit on the offered host plant(s). Cotton balls saturated with 5% honey solution were placed in cages to serve as feeding sites. Plants were watered regularly. Moths were left in cages for three consecutive days (72 h). After three days, plants were removed from the cage and the numbers of eggs laid on each host plant were counted; eggs laid at other sites in the cage were ignored. Eggs laid elsewhere in the cage were omitted from the analysis because of the high chance of missing some of the minute eggs. In addition, individuals from eggs off the plant would have a very low chance of survival in the field, and thus would not substantially promote a host range expansion in nature. In the acceptance (no-choice) test, either a cabbage or a pea plant was placed in the cage. In the preference (choice) test, one plant of each species, cabbage and pea, were positioned in the cage such that the distance between both plants was about 40 cm with no physical contact. This resulted in three experimental set-ups: (i) a pea plant, or (ii) a cabbage plant offered separately, and (iii) a pea and a cabbage plant offered together in one cage. Both acceptance and preference test were repeated six times for each of the strains, i.e. DBM-P and DBM-Cj. All experiments were conducted in a controlled climate chamber at 21°C, 50% RH and 16:8 L:D photoperiod.

To assess variation in developmental time between the two strains, we analyzed the generation times in days of both strains over the past four years in the laboratory, i.e. from September 2006 until January 2010.

Data analysis

A two-way analysis of variance (ANOVA) was conducted to determine differences in the total number of eggs laid on the plants in the different tests. First, combining results from acceptance and preference tests, we tested for overall effects of strain, treatment (choice, no-choice pea plant and no-choice cabbage plant) and the interaction between strain and treatment. Since we found significant differences between the strains, we subsequently assessed differences in the total number of eggs laid on the plants within strains across all three treatments, using one-way ANOVA with a Tukey adjustment for multiple comparisons. To assess whether the generation times significantly differed between the two strains, we conducted a two-tailed Student's *t*-test. All analyses were performed using SAS software version 9.1 (SAS Institute, 2002–2003).

Results

The total number of eggs laid on the plants differed significantly between strains and across the three treatments (no-choice pea plant, no-choice cabbage plant, choice of both) (table 1). Overall, DBM-Cj females laid significantly more eggs than DBM-P females (fig. 1, table 1). There was a

Table 1. Summary of two-way analysis of variance (ANOVA) results on egg numbers deposited on different host plants by *P. xylostella* pea and cabbage strain females. ANOVA on the three different treatments: no-choice cabbage, no-choice pea, choice cabbage and pea.

Source of variation	df	Sum of squares	Mean square	F-value	P	
Strain	1	5852.03	5852.03	6.77	0.0128	*
Treatment	2	18,449.56	9224.78	10.67	0.0002	***
Strain × Treatment	2	4847.56	2423.78	2.80	0.0720	n.s.

NS, not significant; *, $P < 0.05$; ***, $P < 0.001$.

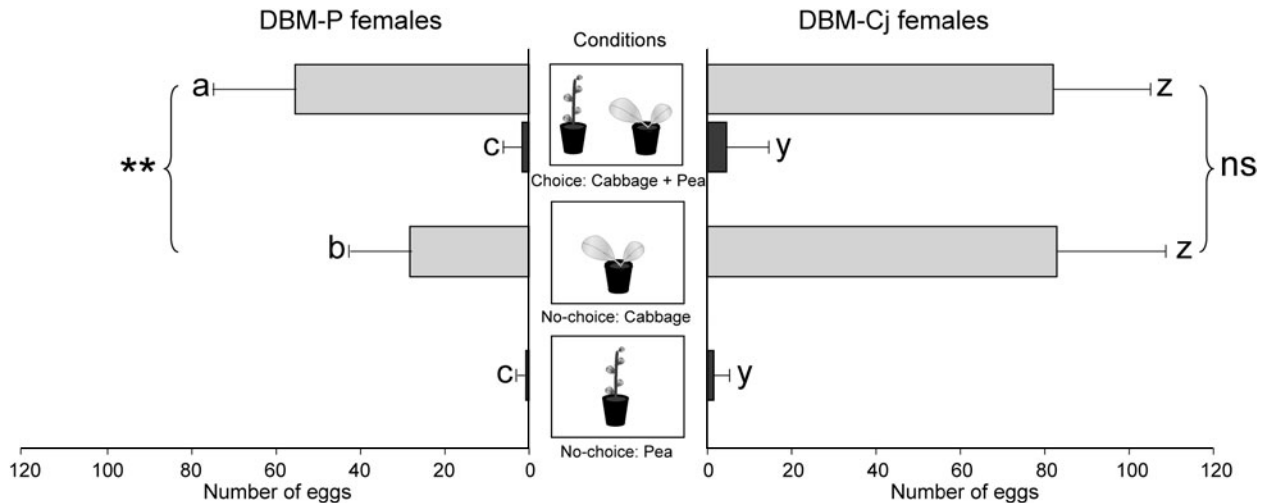


Fig. 1. Number of eggs laid by *P. xylostella* pea (DBM-P) or cabbage strain (DBM-Cj) females on cabbage and pea plants under choice and no-choice conditions, respectively ($n = 6$; mean \pm SD). NS, not significant; **, $P < 0.01$. One-way ANOVA, Tukey's adjustment. Bars marked with same letters are statistically not significant different (\square , number of eggs laid on cabbage plant; \blacksquare , number of eggs laid on pea plant).

suggestive but non-significant strain \times treatment interaction ($P = 0.07$, table 1). Under no-choice conditions, DBM-Cj females deposited on average 82.8 eggs (± 25.9 SD) on cabbage plants and 1.5 eggs (± 3.7 SD) on pea plants (fig. 1). DBM-P females laid on average 28.3 eggs (± 14.4 SD) on cabbage and 0.8 eggs (± 1.6 SD) on pea plants (fig. 1). Thus, under no-choice conditions, both strains oviposited significantly more eggs on cabbage than on pea plants ($P_{\text{adj}} < 0.001$ for DBM-Cj, $P_{\text{adj}} < 0.01$ for DBM-P).

When given a choice between a pea and a cabbage plant, both strains preferred to oviposit on the cabbage plant (fig. 1). DBM-Cj females oviposited on average 82 eggs (± 23 SD) on cabbage and 4.5 eggs (± 10.1 SD) on pea (fig. 1). DBM-P females oviposited on average 55.5 eggs (± 19.6 SD) on cabbage and 1.7 eggs (± 4.0 SD) on pea (fig. 1). Thus, almost all eggs ($> 90\%$) were laid on cabbage plants, irrespective of DBM strain identity. However, DBM-P females laid significantly more eggs on cabbage when given the choice between pea and cabbage plants than when offered a cabbage plant alone (55.5 (± 19.6) versus 28.3 (± 14.4)) ($P_{\text{adj}} < 0.01$; fig. 1). No such difference across treatments was observed for DBM-Cj females (82 eggs ± 23 SD eggs under choice conditions; 82.8 ± 25.9 SD eggs under no-choice conditions; $P_{\text{adj}} = 0.99$).

The generation times between the two strains significantly differed between the two strains ($P < 0.0001$); the

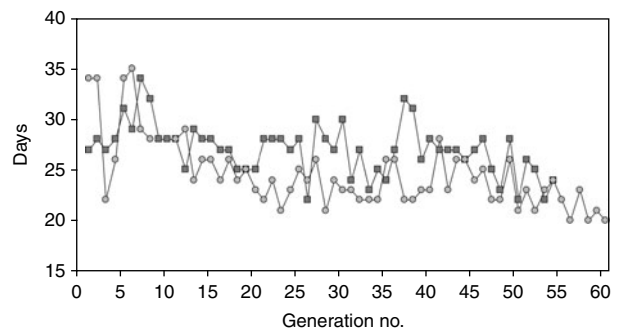


Fig. 2. Generation times in days of the two strains DBM-P on pea and DBM-Cj on kale over a period of four years (from September 2006 until January 2010). The graph starts at 'generation 0', which we set after the strains had stabilized in our rearing at MPICE in Jena. Since DBM-Cj consistently developed faster than DBM-P over the four years, in January 2010 DBM-Cj was in the 60th generation and DBM-P was in the 54th generation (\blacksquare , DBM-P; \circ , DBM-C).

average generation time for DBM-C was 24.5 ± 3.5 days, while the average generation time for DBM-P was 27 ± 2.5 days (fig. 2).

Table 2. Relative percentages of eggs laid by *P. xylostella* Hangzhou cabbage strain females on plants in each of the nine plant × experience treatments of Zhang & Liu (2006) compared to the percentages laid by DBM-Cj and DBM-P females (in bold) under choice and no choice conditions.

Strain		Hangzhou ¹	Hangzhou ¹	Hangzhou ¹	DBM-Cj	DBM-P
Adult pre-exposure to pea		None	After emergence	During and after emergence	None	None
No choice	Cabbage	98.3%	74.3%	83.3%	98.2%	97.3%
No choice	Pea	1.7%	25.7%	16.7%	1.8%	2.7%
Choice ²	Cabbage	98.0%	94.1%	86.1%	94.7%	97.0%
Choice	Pea	2.0%	5.9%	13.9%	5.3%	3.0%

¹ Recalculated from fig. 1 of Zhang & Liu (2006) to eliminate eggs laid on the pot and inner surface of the cage in their experiment, so that the percentages of eggs laid on cabbage and on pea plants sum to 100%. Zhang & Liu (2006) used four females overnight for 12 h, while we used five females for three consecutive days.

² Oviposition on cabbage in the choice experiment of Zhang & Liu (2006) was estimated by subtracting the proportion of eggs laid on pea plants from the total because a separate count of eggs laid on pots and inner cage surface was not provided for this experiment.

Discussion

Since a host range expansion implies the acceptance of the new host as well as the original host plant, and host shift an exclusive preference for the new host, we expected DBM-P either to oviposit similarly on pea plants and on cabbage plants, or to prefer pea plants. However, DBM-P females still preferred cabbage, although unlike DBM-Cj they laid more eggs on the cabbage plant in the presence of pea plants. Three possible explanations for these findings are that: (i) field females had a genetic preference to oviposit on pea, which has been lost in the laboratory because it was not selected for; (ii) field females never had a genetic preference to oviposit on pea, but pea plants generally stimulated oviposition also in the original population; and/or (iii) early-adult experience affects oviposition preference.

Traits promoting larval vs. adult adaptation to pea may have a different genetic basis and may respond differently to selection, both in the field and in laboratory culture. Larval ability to grow and complete development on pea would have been strongly selected for, among offspring of females that had oviposited on peas in the field. That genetic variation for the ability to survive on pea existed at a low level before the first infestation was shown by Löhner & Gathu (2002), who gradually increased the proportion of pea survivors over several generations starting with a population collected from cabbage. This strong selection on initially rare genetic variants is maintained in the laboratory as well, as DBM-P is reared exclusively on pea. If there was also a pre-existing genetic variation for an active oviposition preference on pea, and if initially rare genetic variants with this preference were responsible for the first infestation, this trait would also have been strongly selected for during the first few generations in the field. However, an oviposition preference for pea is not being selected for in our rearing of DBM-P, since eggs deposited on the sides of the rearing containers as well as on the pea plants are used to produce the next generation. Thus, any genetically-determined oviposition preference, if not immediately fixed in the newly established lab population, could have been subsequently lost over many generations of rearing.

Alternatively, the first females to oviposit on pea may not have carried a genetic preference for pea over cabbage, but instead may have been generally stimulated to oviposit on any available surface by volatiles or other cues presented by the proximity of peas. This tendency would have been adaptive in Kenya in the outbreak year of 1999 after most

crucifers had been consumed and were no longer available for oviposition, and it could have also contributed to the continued infestation of the pea crop afterwards. If this tendency had a genetic basis, it would be maintained by selection under our rearing regime; females who lay more eggs in the oviposition containers in the presence of pea do contribute more to the next generation.

A third explanation for our finding that DBM-P females did not oviposit on pea plants may be the absence of preconditioning in our experiments; individuals were kept from pupation onwards in plastic tubes without exposure to any plant material. Zhang & Liu (2006) compared laboratory oviposition of DBM females collected from cabbage near Hangzhou with or without prior adult exposure to pea plants. Oviposition on pea without pre-exposure was 1–2% in their experiments, similar to our pea-reared DBM-P and cabbage-reared DBM-Cj (table 2). The Hangzhou cabbage strain females pre-exposed to pea plants laid relatively more eggs on them subsequently, although they still preferred to oviposit on cabbage (table 2). Zhang *et al.* (2007) showed that adult exposure to pea odour for three days, even if adults did not emerge in the presence of pea, also increased subsequent oviposition on pea by the Hangzhou cabbage strain. Moreover, Liu *et al.* (2005) and Wang *et al.* (2008) demonstrated that pre-exposure of adult females to odours of the non-host plant *Chrysanthemum morifolium* increased acceptance by ovipositing females.

If larval experience on host plants promoted future adult acceptance, DBM-P adults that fed on pea as larvae would be expected to accept pea more readily than the Hangzhou strain raised on cabbage, but this was not the case (table 2). Zhang & Liu (2006) argued that adult experience, but not larval experience, conditions future adult choices in DBM. The greater importance of adult experience was also seen in earlier bioassays with cabbage strain *P. xylostella*. Whereas larval feeding experience on a neem-based oviposition deterrent did not affect oviposition response in adult females to that deterrent, conditioning after emergence and during the early adult stage altered oviposition preference significantly (Liu & Liu, 2006). These findings are in accordance with the neo-Hopkins principle, that adult behaviour is influenced not by larval but by early adult experience (Jaenike, 1983; Corbet, 1985; Cunningham *et al.*, 1999, 2001).

Thus, DBM-P females might have laid more eggs on pea plants in our experiments if they had emerged from the pupa in the presence of pea and experienced the plant before mating and oviposition. However, lack of pre-oviposition

exposure to cabbage plants did not prevent either strain from ovipositing heavily there. This is probably due to an innate attraction to cabbage, mediated by the presence of glucosinolates (Hopkins *et al.*, 2009). In our experiments, no insects were pre-exposed to either pea or cabbage, so that neither the overall preference for cabbage over pea, nor the increase in cabbage oviposition in the presence of pea by DBM-P but not of DBM-Cj can be explained by a difference in pre-oviposition adult exposure to the plants.

Selection for oviposition on a new host would be strengthened if it offered growth advantages to the larvae, but that situation has not yet been attained by DBM-P. Over 50 generations of rearing on pea, the developmental time of DBM-P was longer than DBM-Cj reared concurrently on cabbage (fig. 2), while DBM-P reared on cabbage developed as fast as DBM-Cj (Löhr & Gathu, 2002; Knolhoff & Heckel, unpublished data). This indicates that, even after 50 generations, pea is not an optimal host plant for DBM-P larvae nor readily accepted by DBM-P females for oviposition, consistent with our hypothesis that this strain represents a very early stage in adaptation to the new host.

Even though we do not think that presence or absence of early-adult experience significantly affected our experimental outcome, it may explain the continuation of infestation in pea fields in Kenya. Since the offspring of the first pioneering females emerged as adults in the presence of the new host (unlike their mothers), their early exposure may have increased their oviposition there and enabled continuation of the infestation, without requiring a genetic oviposition preference for pea. Thus, a type of phenotypic plasticity (Agrawal, 2001; Price *et al.*, 2003) could have facilitated adult adaptation to the new host. A similar effect mediated by early experience has contributed to the well-known host-shift of *Rhagoletis* fruitflies from hawthorn to apple (Bush, 1969), where prior exposure was shown to greatly increase oviposition on apple compared to flies that emerged in the absence of fruit (Prokopy *et al.*, 1982).

In conclusion, our findings suggest that the DBM-P strain represents the early stages of a host range expansion, with genetic adaptations enabling larvae to feed on the new host plant pea, as well as the original host cabbage, while adult females still prefer to oviposit on the original host. Larval adaptation has resulted in comparable survivorship with slightly delayed development on the new host plant, while adult adaptation is incomplete in that there is increased oviposition in the presence of the new host, despite the absence of fidelity to it.

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