Host shift to peas in the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) and response of its parasitoid *Diadegma mollipla* (Hymenoptera: Ichneumonidae)

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Abstract

Host shifts in herbivorous insects are thought to sometimes provide enemy-free space on the novel host plant. A population of the diamondback moth *Plutella xylostella* (Linnaeus), an oligophagous pest on crucifers, recently shifted to sugar snap- and snowpeas (*Pisum sativum*) in Kenya, resulting in heavy damage to these crops. The impact of this host shift on the interaction with *Diadegma mollipla* (Holmgren), one of the most frequent parasitoid species attacking *P. xylostella* in this area, was investigated. Parasitism rates and development of two strains of *D. mollipla*, one reared from a cabbage-feeding strain of *P. xylostella* and the second from the new pea-feeding strain, changed based on the host-plant that *P. xylostella* fed upon, with both parasitoid strains more effective on the novel host plant. Parasitism by the cabbage-*D. mollipla* strain on *P. xylostella* infesting peas was four times higher than on *P. xylostella* infesting cabbage when a single plant species was present. However, when both crops were offered together, the level of parasitism dropped to the level seen when cabbage was offered alone. *Diadegma mollipla* developed on both hosts, but cabbage-*D. mollipla* had a longer total development time. Pupae of cabbage-feeding *P. xylostella* were significantly heavier than pupae of pea-feeding *P. xylostella* and parasitism had no influence on these differences. *Diadegma mollipla* preferred to parasitize the pea-feeding *P. xylostella*. Thus, the host shift by *P. xylostella* to a novel host plant did not necessarily provide enemy-free space, with the parasitoid species tested. The implications of these findings for the host–parasitoid relationship are discussed.

Keywords: *Plutella xylostella*, diamondback moth, crucifers, host shift, *Diadegma mollipla*, *Pisum sativum*, Kenya

Introduction

Although most herbivorous insect species are specialized feeders on just one plant family (Bernays & Chapman, 1994), a few abrupt host shifts to new plant families have been reported (Strong, 1979; Bush, 1994). Specialization by herbivores on specific plant species has been discussed in relation to the sequestration of the potentially deleterious

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chemistry of the host plants (Ehrlich & Raven, 1964). Another paradigm, however, relates the restricted diet breadth of herbivores to the action of natural enemies (Jeffries & Lawton, 1984). Plants strongly influence the evolutionary and behavioural ecology of host–parasitoid associations. Plant chemistry and structure influence the risk and level of parasitism (Price *et al.*, 1980; Godfray, 1994). Stimuli emanating from the plant or the plant–herbivore interaction are used for host location by natural enemies (Vinson, 1976; Vet & Dicke, 1992; De Moraes *et al.*, 1998). Feeding on a novel plant species could be advantageous for the herbivorous insect when specialized natural enemies (e.g. parasitoids) can not find or are unsuccessful in attacking herbivores on novel host plants.

The diamondback moth *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) is one of the most destructive pests on crucifers worldwide. It is considered stenophagous and limited to crucifers (Talekar & Shelton, 1993), although records of sporadic occurrences on other crops exist (Löhr, 2001). Recently, a diamondback moth population in central Kenya, in the area of Lake Naivasha, shifted to pea, causing heavy damage to this plant (Löhr, 2001). We hypothesize that this novel host-plant association will influence the interactions between the herbivore and its natural enemies.

One of the most frequent parasitoids of *P. xylostella* in Kenya is an internal larval parasitoid, *Diadegma mollipla* (Holmgren) (Hymenoptera: Ichneumonidae), according to a recently published revision of the *Diadegma* species complex attacking diamondback moth (Azidah *et al.*, 2000). This species is also known as a parasitoid of the potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) and is reported to be indigenous to eastern and southern Africa. However, the original native host is unknown (Broodryk, 1971; Gupta, 1974; Azidah *et al.*, 2000). In the east African highlands *D. mollipla* is frequently found attacking *P. xylostella* on brassica crops, but parasitism rates are not particularly high. Overall field parasitism was reported to be less than 20% with *D. mollipla* being the most abundant species (Odour *et al.*, 1996). Very little is known about the biology of this parasitoid species in association with *P. xylostella*. In the present study parasitism and development of *D. mollipla* was investigated to determine the effect of the host shift to peas by the diamondback moth.

Materials and methods

Insect cultures of P. xylostella *and* D. mollipla

Cabbage strain of P. xylostella *(c-DBM)*

Diamondback moth larvae were collected in cabbage fields in Limuru, Kiambu District, Kenya and reared in the laboratory at ambient temperature ($23 \pm 2°C$) on potted cabbage plants (*Brassica oleracea* L. var. *capitata* (Copenhagen Market)). Pupae were removed from the plants and after emergence, adults were transferred to a perspex cage ($43 \times 23 \times 22$ cm). Aluminium foil strips, coated with cabbage leaf extract, were affixed to the top of the cage as a stimulus for oviposition. The foil was slightly crumpled in order to produce an irregular surface as a tactile stimulus for the female moths to trigger egg deposition (see also Shelton *et al.*, 1991). Cotton wool soaked with a 10% sugar solution, placed in a small plastic tube affixed to the cage wall, was provided as an adult food source; water was provided in the same way.

Pea strain of P. xylostella *(p-DBM)*

Larvae of *P. xylostella* were collected in a sugar snap pea field (*Pisum sativum* var. Oregon sugar pod) near Naivasha, Nakuru District south of Lake Naivasha, Kenya. They were subsequently maintained on potted plants of the same pea variety in the laboratory at ambient temperature ($23 \pm 2°C$). Food and water were provided for adult moths as described above. Pea leaf extract on aluminium foil proved not to be a sufficient stimulus for oviposition, as female moths preferred to lay eggs on the cage walls instead. Therefore, a transparent crumpled plastic bag containing a cabbage leaf was suspended from the top of a perpex cage. This approach successfully triggered oviposition and ensured that deposited eggs did not come into contact with the leaf, such that hatching larvae could easily be transferred from the bag to pea plants.

Cabbage strain of D. mollipla *(c-*D. mollipla*)*

Twenty parasitized pupae were collected from cabbage fields in Kabsabet, Nandi District of western Kenya and Limuru, Kiambu District, central Kenya, and used to establish a parasitoid culture. Parasitoids were reared on second and third instar c-DBM larvae, on cabbage, in perspex cages. Parasitized c-DBM larvae were maintained separately. Pupae were collected into a small container and newly emerged parasitoid adults were then kept in perspex cages for at least one day, to ensure mating, before exposure to hosts. *Plutella xylostella* larvae were renewed every two to three days until the parasitoids died. Honey solution (20%) and water were supplied on cotton wool as a food source for adult parasitoids.

Pea strain of D. mollipla *(p-*D. mollipla*)*

The culture was established starting with a single parasitoid pair found in *P. xylostella* larvae collected from pea fields in Naivasha, and maintained on a p-DBM culture. Otherwise, the maintenance of this culture followed the same procedure as for c-*D. mollipla*.

Effect of host larvae on parasitism

The acceptance and parasitism rate of the two parasitoid strains was compared on the common c-DBM and on the new p-DBM larvae.

All experiments were conducted under laboratory conditions at ambient temperature ($23 \pm 2°C$). Single mated two- to three-day-old female *D. mollipla* were tested; preliminary tests with *D. mollipla* showed peak searching activity after this period. Naive and experienced c-*D. mollipla* and p-*D. mollipla* parasitoids were tested. Naive females did not have contact with any *P. xylostella* larvae before the experiment. To gain experience, females were allowed to parasitize larvae of the *P. xylostella* strain they emerged from 24 h before the trial. A single cabbage leaf was infested with 25 four-day-old second instar *P. xylostella* larvae and was kept in a small plastic container ($5 \times 8 \times 17$ cm). After 2 h a female parasitoid was released into the container and left for 24 h to parasitize hosts. Respectively, a pea leaflet of the same size as the cabbage leaf was infested with p-DBM larvae and treated as described above. Fully expanded leaves from four- to six-week-old plants of both plant species were used. The following combinations were

tested: exposure of c-DBM and p-DBM to naive and experienced c-*D. mollipla*, p-DBM to naive p-*D. mollipla* and c-DBM to experienced p-*D. mollipla*. The *P. xylostella* larvae were exposed only on their respective food plant (i.e. c-DBM on a cabbage leaf and p-DBM on a pea leaf). Each combination was replicated 20 times, except for the pea strain of the parasitoid, where only seven c-DBM replicates were available for the naive females and five p-DBM replicates for the experienced females. Unfortunately, the p-*D. mollipla* culture collapsed during experimentation and this parasitoid strain could not be renewed because it was not found again in the field.

After removing the parasitoid, the *P. xylostella* larvae were fed on their respective food plants until reaching the adult stage. The number of parasitoid pupae in each container was recorded. *Plutella xylostella* larvae that died were dissected in order to search for the parasitoid egg or larva to obtain the total number of parasitized larvae. The single egg deposited by *D. mollipla* was very easy to detect in dissected larvae.

Effect of host plants on parasitism

After having found successful parasitism of *D. mollipla* on the new p-DBM strain in the small containers, a larger cage setup was installed in order to determine the influence of the host plant on the parasitism rate. Tests were conducted with whole potted plants, housed in a screened metal-framed cage measuring $60 \times 45 \times 45$ cm. The experiment was conducted with either four cabbage plants or four pea plants offered as the single host plants, or in a mixed host plant situation with two plants from each crop. Only the experienced c-*D. mollipla* strain was used because naive parasitoids tended to show no searching behaviour. p-*D. mollipla* was not available due to the above mentioned collapse of the culture. To reduce the influence of variability of performance for individual females, three parasitoids were released in the cage. All treatments were replicated three times.

Four plants (4–6 weeks after transplanting; 6–8 leaves) were placed in the cage approximately 20 cm apart. Each plant was infested a day before exposure with ten second instar *P. xylostella* larvae, using larvae reared on that respective host plant. Larvae were then exposed for 48 h to three- to four-day-old parasitoids. The larvae were subsequently kept in plastic containers on leaves of their host plant, with larvae of the same plant kept together. The number of parasitized pupae was recorded.

Host/parasitoid development

In order to detect the development success of the two *D. mollipla* strains on c-DBM and p-DBM, pupal weight of hosts and duration of development of parasitoids were compared. In small containers ($5 \times 8 \times 17$ cm), 20 to 30 *P. xylostella* larvae were exposed for 24 h to three to four females of *D. mollipla*. Age of larvae (four days old), the size of food plant leaves provided, and parasitoid–DBM combinations did not differ from the experimental setup for the effect of host larvae on parasitism. The number of females was usually sufficient to parasitize most of the *P. xylostella* larvae due to the small size of the container. After exposure, larvae were kept individually in vials, fed either whole leaves or leaf discs of their respective food plants, and

checked daily for pupation. In order to compare the development time of parasitized with unparasitized *P. xylostella*, development duration was counted from day 4 (the day of exposure). Spinning of the cocoon by the *P. xylostella* distinguished between the larval and pupal period of the parasitoid. Pupae were weighed on a Mettler analytical balance to the nearest 0.01 mg.

Statistical analysis

Multiple comparisons of mean development times and pupal weights of parasitoids were performed using an ANOVA (Student Newman Keuls (SNK) test). For the comparison of mean development time and weight of unparasitized larvae of the two *P. xylostella* strains, the T-test was used. Comparisons of mean parasitism rates between parasitoid–host combinations were conducted with the Student Newman Keuls test. Parasitism rates on different host plants were compared using the Tukey test. Differences were considered statistically significant at the $P = 0.05$ level, for all comparisons made. The Chi-square adaptation test was used in order to determine if the sex ratio deviates from an expected 1 : 1 ratio. For the comparison of differences in sex ratios between parasitoid–diamondback moth combinations, the Chi-square 2×2 was applied.

Results

Effect of host larvae on parasitism

The new p-DBM strain was accepted as a host by both *D. mollipla* strains tested. Individual parasitism varied considerably between females of the two parasitoid strains. Figure 1a shows the percentage of *P. xylostella* larvae parasitized by naive parasitoids. Average parasitism per female was lowest for c-*D. mollipla* on c-DBM with 16.9% of larvae parasitized; parasitism by c-*D. mollipla* was higher, 22.9%, on p-DBM. Naive p-*D. mollipla* parasitized 32.2% of exposed p-DBM. Naive females of both parasitoid strains showed a tendency towards higher parasitism on p-DBM, although the differences between the mean percentages of parasitized larvae were not significant (SNK-test df = 2,47; $F = 1.08$; $P = 0.348$), due to the high variation among naive parasitoids. With experienced c-*D. mollipla*, parasitism of p-DBM (47.5%) was significantly higher than parasitism of c-DBM (23.6%) (SNK-test; df = 2,42; $F = 7.27$; $P < 0.05$) (fig. 1b). Experienced p-*D. mollipla* showed with 23.4% a mean parasitism on c-DBM similar to c-*D. mollipla* on c-DBM.

Missing data for naive p-*D. mollipla* parasitizing c-DBM and experienced p-*D. mollipla* parasitizing p-DBM, as well as low number of females tested was due to the already mentioned collapse of this culture.

Effect of host plants on parasitism

The host plant complex had a strong influence on the level of parasitism (fig. 2). Parasitism by c-*D. mollipla* on cabbage plants alone was 6.1% of c-DBM exposed, which was significantly lower than the 26.5% parasitism of p-DBM on pea plants. When both host plants were offered simultaneously, parasitism was comparable to cabbage offered alone (3.5%) (Tukey's test; df = 8,27; $F = 4.54$; $P < 0.05$). In the mixed host plant exposure, however, a higher proportion of larvae were parasitized on peas (2.6%) than on cabbage
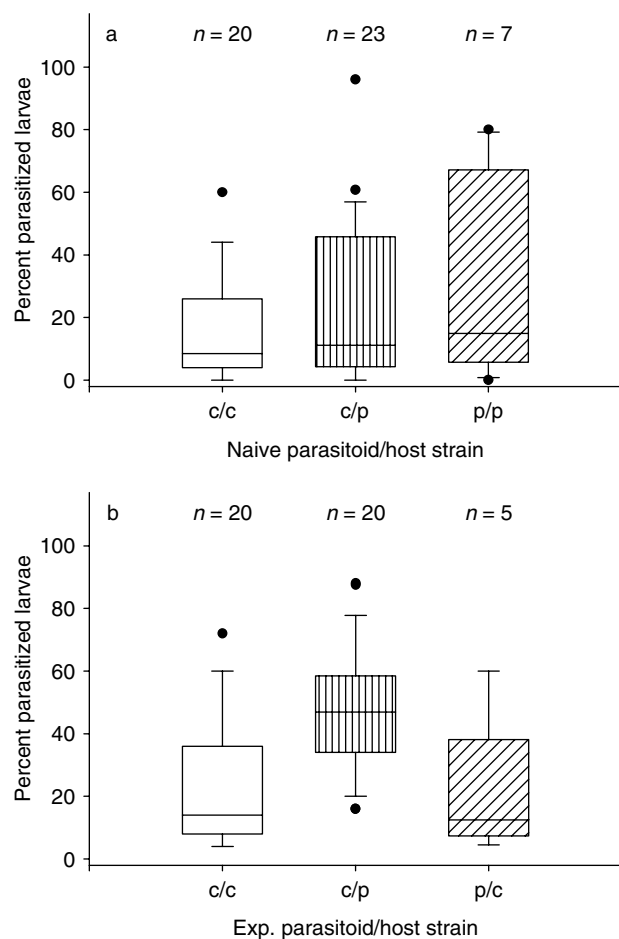
Fig. 1. Variability of parasitism of individual naive (a) and experienced (b) *Diadegma mollipla*: c/c (c-*D. mollipla* on c-DBM), c/p (c-*D. mollipla* on p-DBM), p/p (p-*D. mollipla* on p-DBM), p/c (p-*D. mollipla* on c-DBM).

(0.9%), showing clearly the preference for the pea plant–p-DBM complex.

Development of *P. xylostella* and *D. mollipla*

Plutella xylostella larvae were exactly four days old when exposed to the parasitoids. The development of p-DBM larvae was, at 12.2 days, significantly slower as compared to c-DBM (10.7 days) (T-test; df = 160,137; $F = 1.85$; $P < 0.001$) (table 1). This was a result of the longer pupation period required by the p-DBM (6.5 days) as compared to 5.4 days for the c-DBM strain (t-test; df = 160,137; $F = 5.47$; $P < 0.01$). The duration of the larval stage was similar in both un-parasitized DBM strains (5.3 and 5.7 days) (T-test; df = 160,137; $F = 1.25$; $P = 0.175$).

The parasitoid developed successfully on both host strains. Parasitoids generally showed similar development time, with the exception of the cabbage strain of the parasitoid, which required a longer developmental period on p-DBM (table 1). Parasitized larval duration was extended in both host strains compared to unparasitized larvae (table 1). The larval period ranged between 6.0 days (on c-DBM) and
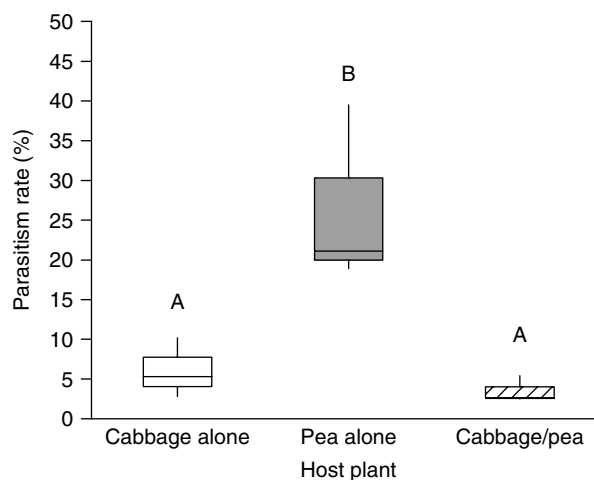

Fig. 2. Influence of host plants on parasitism of c-*Diadegma mollipla*. Means from three replicates. Significant differences are indicated by different capital letters.

6.5 days (on p-DBM) for p-*D. mollipla*, and was similar to c-*D. mollipla* on c-DBM (6.3 days). However, the larval development period was significantly longer for c-*D. mollipla* on p-DBM (8.6 days) (SNK test; df = 3,269; $F = 18.5$; $P < 0.001$). Development of parasitized hosts was considerably longer compared to unparasitized *P. xylostella* because the parasitoid required a longer pupal period (table 1). Pupal duration of c-*D. mollipla* on p-DBM was, at 8.3 days, significantly shorter than in the other host–parasitoid combinations (9.2 and 9.5 days) (SNK test; df = 3,215; $F = 18.4$; $P < 0.001$).

There was no signifcant difference between the weight of parasitized and unparasitized pupae within their respective host plants, but there were significant differences between host plant species (SNK test; df = 5,58; $F = 62.74$; $P < 0.001$) (table 2). Pupal weights of both parasitoid strains reared from p-DBM were significantly lower (4.4 mg and 4.2 mg,) than pupal weights on c-DBM (5.3 mg and 5.7 mg). Correspondingly, pupal weights of unparasitized p-DBM (4.5 mg) was significantly lower than pupal weights of unparasitized c-DBM (5.4 mg).

The sex ratio was similar for all parasitoid–host combinations and did not deviate from an equal distribution between males and females (Chi-Square; df 1, $\chi^2 = 0.10$, $P = 0.91$) (table 2).

Discussion

In the present experiments, overall parasitism was low in all combinations investigated and performance of individual females was highly variable, independent of their hosts. Despite individual variability, preference experiments revealed significantly higher parasitism on p-DBM as compared to c-DBM.

Two hypotheses may be discussed with regard to these observations: (i) *D. mollipla* has only developed a loose association with *P. xylostella* and its host plant; and (ii) there must be a factor that renders *P. xylostella* on crucifers less attractive than on peas. The first hypothesis is supported by Broodryk (1971) who lists *D. mollipla* as an important

Table 1. Comparison of development time of *Diadegma mollipla* reared on *Plutella xylostella* on cabbage or peas.

Parasitoid strain	Host strain	n	Larval period (days)	Pupal period (days)	Total development time (days)	SNK group
–	Cabbage	138	5.3 ± 0.7	5.4 ± 0.6***	10.7 ± 0.9***	A
–	Pea	161	5.7 ± 0.8	6.5 ± 1.4***	12.2 ± 1.3***	A
Cabbage	Cabbage	86	6.3 ± 0.6	9.5 ± 0.7	15.8 ± 0.7	B
Pea	Cabbage	11	6.0 ± 0.6	9.5 ± 0.5	15.5 ± 0.5	B
Pea	Pea	112	6.5 ± 1.0	9.2 ± 1.1	15.7 ± 0.9	B
Cabbage	Pea	86	8.6 ± 0.9	8.3 ± 1.2	16.9 ± 1.5	C

To distinguish between the larval and pupal periods the spinning of the cocoon by the *P. xylostella* larvae was considered the start of the pupal stage. Larval period and total development time of unparasitized *P. xylostella* larvae were counted from day of exposure to parasitoid (4 days after hatching) (mean $\pm$ STD). Significant differences in means are indicated with capital letters. SNK, Student Newman Keuls test. Differences of means between unparasitized *P. xylostella* are indicated by asterisks ($P < 0.001$, T-test).

Table 2. Comparison of pupal weight and sex ratio of unparasitized *Plutella xylostella* and *Diadegma mollipla*-infested *P. xylostella* reared on cabbage or peas.

Parasitoid strain	Host strain	n	Pupal weight (mg)	SNK group	Sex ratio females
–	Cabbage	138	5.4 ± 0.7	A	–
Cabbage	Cabbage	86	5.3 ± 0.8	A	0.75
Pea	Cabbage	11	5.7 ± 0.8	B	1.60
–	Pea	161	4.5 ± 0.7	C	–
Cabbage	Pea	86	4.4 ± 0.5	C	0.73
Pea	Pea	112	4.2 ± 0.7	C	0.80

Exposure of 4-day-old *P. xylostella* larvae (L2). SNK, Student Newman Keuls test.

parasitoid of the potato tuber moth *Phthorimaea operculella* on potato and tobacco in southern Africa and on potato in Yemen (Kroschel, 1993). However, as *P. operculella* is an introduced species to Africa and *D. mollipla* seems to be indigenous, *P. operculella* cannot be the original host of this species. It is therefore reasonable to assume that *D. mollipla* is a parasitoid with considerable host plasticity. We assume that it might be found to parasitize more free-living or leaf-mining species of Lepidoptera, but we have no evidence to support this assumption. A lack of intrinsic cues to accept the host plant of *P. xylostella* may also explain the generally low parasitism rates of *P. xylostella* observed in the laboratory (Akol *et al.*, 2003) and thus its irrelevance for the control of field populations (Odour *et al.*, 1996; B. Löhr, unpublished survey data).

Factors for the higher attractiveness of peas, as suggested in our second hypothesis, are supported by published papers that report an influence of host plants on parasitism levels of *P. xylostella*. Beck & Cameron (1990) related different levels of parasitism by *Diadegma semiclausum* (Hellén) and *Diadromus collaris* (Gravenhorst) (both Hymenoptera: Ichneumonidae) on three vegetable brassicas to the accessibility of the host larvae to parasitoids. Broccoli, showing the highest parasitism rates, does not form heads like cabbage, thus the leaves provide less shelter for the larvae compared to leaves tightly attached to the head. Idris & Grafius (1996) reported a higher percentage of parasitation of *P. xylostella* by *Diadegma insulare* (Cresson) on cultivated brassicas, compared to wild Brassicaceae. Their findings may be explained by plant quality, as *D. insulare* has been shown to parasitize more *P. xylostella* larvae on N-fertilized than on unfertilized plants (Fox *et al.*, 1990, 1996). However, differences in accessibility of *P. xylostella* do not explain the significant preference of *D. mollipla* females for *P. xylostella* feeding on peas, because *P. xylostella* larvae were freely exposed on leaves during the experiments. At this point we are not able to rule out the possibility of differences in *P. xylostella* suitability as hosts mediated by plant quality. Although fertilizer treatments did not differ between the two host plant species, we do not have data on specific plant compounds rendering the plants more or less attractive to *D. mollipla*.

The preference of *D. mollipla* for *P. xylostella* feeding on peas may be explained by cues used for host location. It is now well documented that hymenopterous parasitoids use infochemicals to locate their hosts (e.g. reviewed in Vet & Dicke, 1992). These volatiles may originate from the host plant, the herbivore itself or the interaction between plant and herbivore (Drost *et al.*, 1986; Turlings *et al.*, 1991, Agelopoulos & Keller, 1994; Zaki *et al.*, 1998). Evidence that a diamondback moth parasitoid is attracted by kairomones was found in *D. semiclausum* (Davis, 1987; Ohara *et al.*, 2003).

Direct application of these results to the given plant-host–parasitoid system is, however, premature, because cues used can differ even within a genus. Shiojiri *et al.* (2000) demonstrated that *Cotesia plutellae* (Kurdyumov) and *C. glomeratus* (Linnaeus) (Hymenoptera: Braconidae), both parasitoids of *Pieris rapae*, showed different preferences in flight response experiments towards the plant–herbivore complex. Oviposition attempts into feeding holes of both plants tested were observed, even when larvae were absent. Although plant injury-derived volatiles in combination with specific volatiles emitted by the host plant could be an important cue in the searching behaviour of *D. mollipla*, this

still does not explain the preference in c-DBM experienced females of the c-*D. mollipla* strain for p-DBM larvae. Parasitoids associated with crucifer specialist herbivores were shown to be attracted by volatile isothiocyanates (mustard oils) typically released by crucifers when injured (Pivnick, 1993; Murchie *et al.*, 1997). However, crucifer volatiles are unlikely to be used for host location for *D. mollipla*. Recently, Rossbach *et al.*, (2005) were able to demonstrate that *D. mollipla* females are attracted to odours emitted by peas infested with *P. xylostella* but not to odours emitted by cabbage plants infested with *P. xylostella* larvae. This is because *D. mollipla* is either attracted to a non-specific blend of volatiles from a variety of host-infested plants, or it uses other shared cues present in several hosts or host-plant complexes. Therefore we hypothesize that the diamondback moth–crucifer complex is not the preferred host-plant association of *D. mollipla*, although it is widely accepted because of its high abundance and accessibility in Kenya.

Diadegma mollipla was able to develop in either strain of *P. xylostella* without visible problems. Only development time and pupal weight are affected, probably due to growth differences of *P. xylostella* on the two host plants or differing secondary compounds ingested by the host larvae. Growth of both parasitized and unparasitized *P. xylostella* was dependent on the food plant. Pupae of *P. xylostella* were heavier on cabbage than on pea. Either a lower nutritional value or a lack of feeding stimulants of peas could be the reason for these results. Koinobiont parasitoids rely on their host's nutrition and growth potential (Mackauer *et al.*, 1997). When feeding on different food plants, physiology and size of the herbivore can change and this influences the development of the immature parasitoid indirectly (Godfray, 1994). For example, Idris & Grafius (1996) found that developmental time of *D. insulare* on *P. xylostella* on wild crucifers was longer than on cultivated brassica crops. Larval duration of larvae parasitized by *D. mollipla* was longer on both plants as compared to unparasitized larvae. Nutritional demands of the parasitoid often reduce growth and behaviour of their hosts (Strand *et al.*, 1988; Harvey *et al.*, 1999). In contrast Yang *et al.* (1994) found no difference in duration of larval instars between parasitized and healthy *P. xylostella* larvae, but food consumption was reduced in larvae parasitized by *D. semiclausum*.

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