Interspecific competition between *Diadegma semiclausum* Hellen and *Diadegma mollipla* (Holmgren), parasitoids of the diamondback moth, *Plutella xylostella* (L), feeding on a new host plant

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Abstract

Interspecific competition between an introduced parasitoid species aimed at controlling a herbivorous pest species and a native parasitoid parasitising the same host may influence the success of classical biological control programmes. In Kenya, interspecific competition between an introduced and a local parasitoid on two diamondback moth populations (DBM, *Plutella xylostella*) was investigated on two different host plants. We tested simultaneous and delayed competition of the local parasitoid *Diadegma mollipla* Holmgren and its exotic congenus *D. semiclausum* Hellen on a newly aquired DBM host plant (snowpea) in the laboratory. Under simultaneous competition, *D. mollipla* produced more progeny than *D. semiclausum* on snowpea. A head start of *D. Mollipla*, of four and eight hours before its congenus was introduced, resulted in a similar number of progeny of both species. In delayed competition (time intervals of 24 h, 48 h and 72 h), progeny production was similar for both parasitoids when the time interval was 24 h, irrespective of which species parasitized first. More progeny was produced by the species which attacked first, when the time interval was greater than 24 h, although it was only significant at 72 h. Competitive abilites of both parasitoids on the new host plant differed largely between laboratory and semi-field conditions. The influence of two host plants (snowpea and cabbage) on competition was studied in the greenhouse with different host and parasitoid densities. Parasitism levels of *D. semiclausum* were significantly higher than those of *D. mollipla*, regardless of host plant, host and parasitoid densities, but progeny production of *D. mollipla* on snowpea was still slightly higher than on cabbage. As compared to the confinement of parasitoids and larvae to small containers, *D. mollipla* parasitized very few larvae in the cages. Competitive ability of the two parasitoid species tested was influenced both by the density of the searching females and by parameters related to either the host plant and/or the herbivorous hosts.

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Introduction

Interspecific competition among insect parasitoids is a common phenomenon in natural plant-herbivore-parasitoid systems and can influence the population dynamics of insect communities (Bográn *et al*., 2002; DeMoraes & Mescher, 2005). This effect has been substantiated in several biological control programmes, where introduced parasitoids frequently proved to be superior competitors, displacing other parasitoid species (reviewed in Reitz & Trumble, 2002).

In most cases, quarantine regulations require preliminary studies on interspecific competition between exotic and local parasitoids in the laboratory. It is sometimes difficult to quantify the relative importance of factors that play a role in competition in the field, derived from results with laboratory cultures containing two species in a simple and artificial environment with individuals in close proximity to each other. However, a literature review, relating laboratory evaluations of natural enemy efficacy with field evaluations, performed by Mottern *et al*. (2004), concluded that more than 75% of the studies demonstrated that laboratory tests served as good predictors of field efficiency.

In some laboratory studies, differential larval competition and the ability of host discrimination were found to affect direct competitiveness between two parasitoid species (McBrien & Mackauer, 1990; Pijls *et al*., 1995; Bokonon-Ganta *et al*., 1996; Infante *et al*., 2001; Agboka *et al*., 2002; Wang & Messing, 2003). Individual searching efficiency may also be influenced in case two parasitoid species compete for the same host (Chua *et al*., 1990). Few studies have been aimed at investigating the effect of host plants *per se* on interspecific competition between parasitoids (Iwao *et al*., 2001). Host plants may indirectly influence the impact of natural enemies on their herbivore host (Cortesero *et al*., 2000). Levels of attack rates can differ on different host plants because plants frequently mediate host location and, therefore, influence the effectiveness of parasitoids (Benrey *et al*., 1997; Billquist & Ekbom, 2001; Liu & Jiang, 2003). Due to differential host location abilities, competitiveness of two parasitoids on different host plants might be different.

In 2002, the specialist parasitoid *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae) was introduced to Kenya in order to suppress diamondback moth (DBM), *Plutella xylostella* L. (Lepidoptera: Plutellidae), populations in cabbage production areas in the Kenyan highlands. The most important local parasitoid reported so far was *Diadegma mollipla* (Holmgren) (Hymenopera: Ichneumonidae), a generalist parasitoid that, together with other local parasitoid species, never exceeded parasitism levels higher than 15% (Oduor *et al*., 1996). Both *Diadegma* species prefer to parasitize the same larval stages of DBM, have similar temperature requirements but differ in their host specificity (Talekar & Yang, 1991; Rossbach *et al*., 2005; Sithole, 2005). The potato tuber moth *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) is one other host species known for the indigenous *D. mollipla*, but additional hosts are suspected to be in the host range of this species because the

potato tuber moth is also not indigenous to this region. On the other hand, the host range of *Diadegma semiclausum* is restricted to DBM (Abbas, 1988) and has been the most widely used and successfully introduced parasitoid for biocontrol of DBM in several countries (Talekar & Shelton, 1993).

In 2000, the normally crucifer-specific DBM extended its host range to snowpeas in a horticulture production area in Naivasha in the Rift Valley of Kenya. Research on the parasitism efficiency of *D. mollipla* on DBM on the new host plant proved that the parasitoid species did better on DBM on snowpeas as compared to cabbage (Rossbach *et al*., 2006a). Host location studies revealed that *D. mollipla* was able to find its host equally well on cabbage and on peas, whereas *D. semiclausum* used crucifer-typical volatiles as host-finding cues and prefered cabbage over DBM-infested snowpea (Rossbach *et al*., 2005). Therefore, we assumed that on the new host plant *D. mollipla* should have a competitive advantage over its introduced congenus and should be able to establish a niche on peas when displaced on cabbage. In the laboratory Sithole (2005) demonstrated a clear advantage in competition of *D. semiclausum* over *D. mollipla* on DBM when feeding on cabbage. Observations in the field confirmed that the exotic species out-competed and even displaced most of the generalist indigenous species on DBM on cabbage, including *D. mollipla* (Momanyi *et al*., 2006; Löhr *et al*., 2007). Coinciding with this study, natural total parasitism of DBM in kale and in snowpea fields was investigated, and results indicated potential differences between laboratory and field competition (Rossbach *et al*., 2006b).

The first objective of this study was to examine the influence of a new host plant of a herbivore host on an introduced and on a locally competing parasitoid species. The second objective aimed at comparing laboratory results with field observations in order to evaluate predictions for the field situation from competition studies in the laboratory. We determined progeny production under simultaneous and delayed interspecific competition in the laboratory. Moreover, we studied the influence of host plants on competition and the effect of different host and parasitoid densities in greenhouse experiments.

Material and methods

Host plants and larvae

The cabbage strain of the diamondback moth (DBM) originated from cabbage fields at Wundanyi, Taita Taveta District, Kenya (Altitude: 1650 m, 03°26′11′′S, 038°20′37′′E) and was reared in an insectary (T = 23 ± 2°C) on potted cabbage plants (*Brassica oleracea* L. var. *capitata* (Copenhagen Market)). The pea strain of the diamondback moth was collected from a sugar snap pea field (*Pisum sativum*, var. Oregon sugar pod) near Naivasha in Nakuru District, Kenya (Altitude: 1500 m, 00°44′98′′S, 036°26′2′′E). Since 2000, the

colony has been maintained on potted snowpeas (*Pisum sativum*, var. Oregon sugar pod) in the laboratory. For a detailed description of rearing methods of both DBM strains, see Löhr & Gathu (2002).

Parasitoids

A culture of *D. mollipla* was started with DBM larvae collected in Naro Moru, Nyeri District, Kenya. Parasitoids were multiplied for three generations in the laboratory before they were used for the experiments. A colony of *D. semiclausum* was started in October 2001 with pupae imported from the Asian Vegetable Research and Development Center (AVRDC) in Taiwan. This culture had been maintained in the laboratory for three years when experiments were conducted. Both parasitoid species were reared separately on second and third instar DBM larvae on cabbage leaves in perspex cages serving as parasitism chambers ($20 \times 20 \times 25$ cm). Parasitized larvae were transfered to plastic boxes covered with nylon mesh for ventilation and fed with cabbage leaves until pupation. Pupae were then removed and kept in separate containers. Emerging parasitoids were released into parasitism chambers. Honey was provided as a food source for adults. Age of females used for the experiments varied between two and five days. Both species had no oviposition experience before the experiments started.

Simultaneous intra- and interspecific competition

Three plastic oviposition chambers ($15 \times 15 \times 15$ cm) were prepared, and each was provided with 50 second instar DBM larvae on a pea leaf. Larvae were given two hours to settle on the leaf. Thereafter, two mated parasitoid females were introduced into these chambers, belonging to either *D. mollipla* or *D. semiclausum*. Additionally, one female from each of the two parasitoid species was introduced to the third chamber. After 24 h, all parasitoid adults were removed, and the DBM larvae were reared to adults. The number of parasitoid pupae and progeny for each species emerging at the end of the experiment was recorded. Dead larvae were dissected in order to check for parasitoid eggs or larvae. Parasitoid larvae were counted and included into total parasitism. Larvae of the two *Diadegma* species cannot be differentiated, and parasitoid larvae could, therefore, not be assigned to a particular species. The experiment was conducted at $23 \pm 2°$C and replicated 15 times.

Delayed simultaneous interspecific competition

We used the same oviposition chambers mentioned above to set up an experiment on time related competitive interactions. Fifty second instar larvae on a pea leaf were exposed to a single female of *D. semiclausum*. Additionally, a single female of *D. mollipla* was introduced into these chambers with a time lag of 4 h and 8 h, respectively, without removing the *D. semiclausum* female. Total oviposition time for all parasitoid females was 24 h. The experiment was repeated in reverse order of parasitoids and was replicated ten times for each time sequence and species order.

Delayed interspecific competition

Fifty second instar larvae on a pea leaf were exposed for 24 h to oviposition by a single *D. semiclausum* female in an oviposition chamber as mentioned above. Larvae were transferred to a fresh pea leaf and then exposed to subsequent 24 h parasitism by *D. mollipla* at different time intervals, i.e. immediately, 24 h and 48 h after exposure to *D. semiclausum*. Each time interval was replicated ten times. The number of parasitoid pupae and progeny for each species emerging at the end of the experiment was recorded. Dead larvae were dissected in order to check for parasitoid eggs or larvae. In the second run of this experiment, DBM larvae were first exposed to *D. mollipla* and then to *D. semiclausum*.

Effect of host plants on interspecific competition

We conducted an experiment in cages placed in a plastic sheet-covered greenhouse to test the influence of the host plant on parasitoid interspecific competition. The cages had plastic frames ($110 \times 90 \times 75$ cm) covered with a fine mesh on all sides and the top. A wooden board (80×100 cm) with four openings (Ø 15 cm) was placed on the bottom of the cages. The board was covered with a layer of soil (1 cm) and was elevated from the ground in order to insert potted plants into the openings. The plants were placed in a 60–40 cm grid, with a diagonal distance of 75 cm. This set-up was chosen in order to simulate field conditions as closely as possible.

DBM larvae were offered either on one host plant species or on two host plants species in three different experimental set-ups. First four potted cabbage plants were introduced into the cage. A day before parasitoid exposure, each plant was infested with 20 second instar DBM larvae reared on cabbage. Twenty-four hours later, two females of each parasitoid species were released into the cage for eight hours (exposure time 8.30 am to 4.30 pm). Larvae were collected immediately after the end of exposure time and reared in separate cages until emergence. Number of parasitoid pupae and species and sex of emerged adults was recorded. The experiment was repeated with DBM reared on peas with four pea plants infested. In the third set-up of this experiment, we used two infested pea plants and two infested cabbage plants offered at the same time. Each host plant exposure experiment was replicated six times (three cages at a time).

Effect of larval density on competition

This experiment was conducted with two host plants (two pea and two cabbage plants) in the cages described above. In the first part, the cabbage plants were infested with 20 larvae and the pea plants with ten larvae. Afterwards, the density of larvae on the two host plant species was reversed. Exposure time of DBM larvae was eight hours, and two females of each parasitoid species were introduced into the cages.

Effect of parasitoid density on competition

Two snowpea and two cabbage plants infested with 20 DBM larvae each were introduced into the cage. The experiment was conducted with three different *D. mollipla* densities. The number of *D. mollipla* females was two, four

and, in the last set-up, six. The number of *D. semiclausum* females was kept constant at two females. Exposure time was eight hours.

Statistical analyses

All data were analyzed using the SAS loglinear modeling GENMOD procedure (SAS Institute, 1999–2000). The model is particularly suitable for count data under the assumption of a Poisson distribution. In cases where the criteria for 'goodness of fit' deviated too far from 0 (value > 1.5), the Poisson regression was replaced by a negative binomial regression with the same SAS procedure.

Results

Simultaneous competition

Simultaneous parasitism of two *D. mollipla* females and of one female of each parasitoid species resulted in a similar number of parasitized larvae and production of a higher number of progeny as compared to two competing *D. semiclausum* females (df = 2, $\chi^2 = 7.14$, $p < 0.05$) (fig. 1a). The number of female progeny was very variable within all parasitoid combinations and, therefore, not significantly different from each other (df = 2, $\chi^2 = 4.13$, $p = 0.12$).

Although *D. mollipla* produced on average twice as many adults as *D. semiclausum*, the difference was not significant due to the high standard deviation (df = 1, $\chi^2 = 3.04$, $p = 0.08$) (fig. 1b). The number of females produced by *D. mollipla* was significantly higher as compared to *D. semiclausum* (df = 1, $\chi^2 = 11.1$, $p < 0.01$).

Delayed simultaneous competition

Parasitism and progeny production of *D. mollipla* and *D. semiclausum* after total oviposition time of 24 h with a head start of 4 h and 8 h for one species, respectively, are presented in table 1. The combined number of parasitized larvae was similar for each exposure sequence. Individual ovipositing females performed very variably. When *D. semiclausum* was given a head start, the total number of progeny of both species combined was significantly lower as compared to *D. mollipla* starting to attack earlier (df = 3, $\chi^2 = 6.74$, $p < 0.01$). When *D. mollipla* attacked earlier, the number of progeny of each species was similar after 24 h of oviposition. When this species was introduced later, it produced significantly less progeny as compared to *D. semiclausum* (df = 1, $\chi^2 = 5.35$, $p < 0.05$ after 4 h; df = 1, $\chi^2 = 9.33$, $p < 0.01$ after 8 h). The number of female progeny was very low for both species.

Delayed competition

The number of parasitized larvae was similar for all exposure sequences (table 2). The time interval of exposure influenced total and individual progeny production. Significantly fewer adults emerged at time intervals of 48 h and 72 h, regardless which parasitoid species attacked larvae first (df = 5, $\chi^2 = 41.5$, $p < 0.01$). The number of progeny of each species was very variable, and the time interval had no significant effect on the total number of progeny of both species, except for *D. mollipla* at 72 h (df = 5, $\chi^2 = 36.64$, $p < 0.01$). At time intervals of 48 h and 72 h, the species,
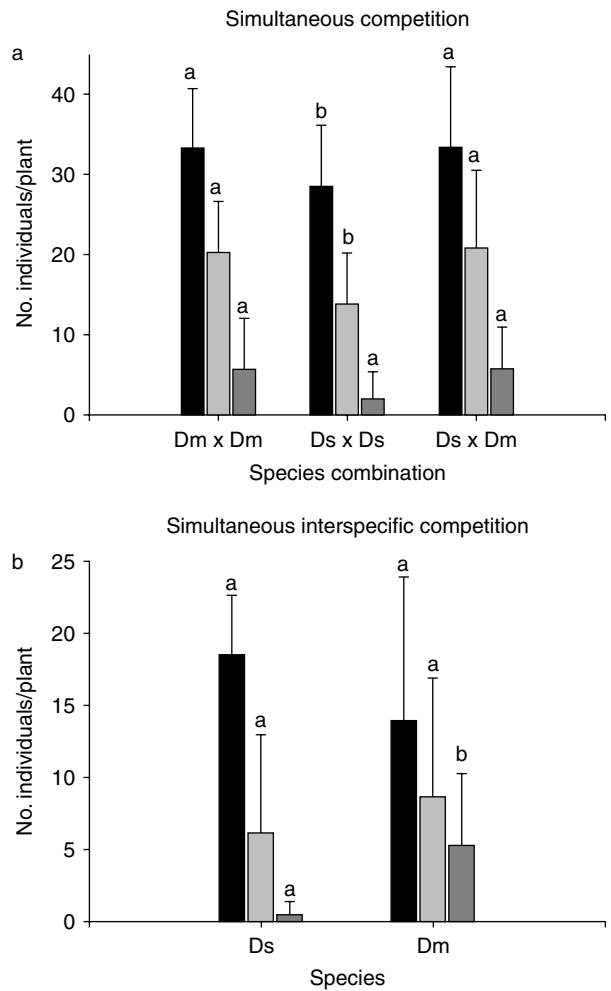

Fig. 1. Simultaneous intra- and interspecific competition between *Diadegma mollipla* (Dm) and *Diadegma semiclausum* (Ds) on *Plutella xylostella* on snowpea. (a) (■, Parasitized; ▢, emerged; ▨, females.) Number of parasitized larvae, total progeny production and emerged females. (b) (■, total emerged; ▢, males; ▨, females.) Progeny production of both species in interspecific competition experiments.

which attacked first, produced more progeny; but this was only significant at 72 h (df = 1, $\chi^2 = 4.39$, $p < 0.05$ for Dm-Ds and df = 1, $\chi^2 = 36.28$, $p < 0.01$ for Ds-Dm). Exposure sequence and time interval had no influence on female progeny. The number of emerged females was very low and varied considerably between individual ovipositing females.

Effect of host plants on interspecific competition

The total number of parasitized DBM larvae per plant was similar, irrespective of plant species and host plant combination. *Diadegma mollipla* produced significantly less progeny than *D. semiclausum* on both host plants (df = 1, $\chi^2 = 44.7$, $p < 0.01$; df = 1, $\chi^2 = 50.3$, $p < 0.01$: table 3). When DBM infested pea plants were offered alone or simultaneously with infested cabbage plants, *D. mollipla* produced

Table 1. Delayed simultaneous interspecific competition between *Diadegma mollipla* (Dm) and *Diadegma semiclausum* (Ds) on *Plutella xylostella* on snowpea. The second parasitoid was introduced after 4 h and 8 h, respectively. Total parasitism duration was 24 h.

Exposure sequence [h]	No. parasit. DBM	No. emerged parasitoids	*D. mollipla*		*D. semiclausum*	
			total	females	total	females
Dm–Ds [4]	32.4 ± 8.2a	24.8 ± 9.7a	10.5 ± 10.1a	4.2 ± 7.4a	14.3 ± 12.1a	1.6 ± 3.7a
Dm–Ds [8]	26.6 ± 6.7a	21.4 ± 5.1a	7.5 ± 9.8a	1.2 ± 3.1a	13.9 ± 9.1a	2.7 ± 2.1a
Ds–Dm [4]	28.9 ± 4.7a	10.8 ± 7.9b	2.8 ± 2.7b*	0.6 ± 0.8a	8.0 ± 6.9a*	1.0 ± 2.1a
Ds–Dm [8]	29.0 ± 13.4a	18.9 ± 14.9ab	1.0 ± 1.9b*	0.1 ± 0.3a*	17.9 ± 14.3a*	5.5 ± 6.6a*

Figures represent mean ± SD. Different letters indicate significant differences within a column, and an asterisk denotes significant differences between the species ($p < 0.05$).

Table 2. Delayed interspecific competition of *Diadegma mollipla* (Dm) and *Diadegma semiclausum* (Ds) on *Plutella xylostella* on snowpea. Time intervals of exposure were 24 h, 48 h and 72 h between parasitoids.

Exposure sequence [h]	No. parasit. DBM	No. emerged parasitoids	*D. mollipla*		*D. semiclausum*	
			total	females	total	females
Dm–Ds [24]	37.3 ± 5.8a	25.1 ± 3.7a	12.1 ± 9.6a	2.0 ± 4.0a	13.0 ± 9.7a	3.3 ± 5.8a
Dm–Ds [48]	36.7 ± 6.1a	19.4 ± 4.7b	12.6 ± 7.4a	3.3 ± 3.8a	6.8 ± 5.8a	0.9 ± 2.5a
Dm–Ds [72]	33.8 ± 9.6a	17.1 ± 7.3b	11.4 ± 6.9a*	1.1 ± 2.3a	5.7 ± 3.6a*	1.4 ± 2.0a
Ds–Dm [24]	33.8 ± 7.4a	26.4 ± 8.2a	12.2 ± 8.2a	6.5 ± 7.1a*	14.2 ± 13.4a	1.0 ± 1.7a*
Ds–Dm [48]	28.4 ± 14.5a	17.4 ± 9.5b	5.9 ± 6.6a	2.1 ± 3.0a	11.5 ± 10.4a	0.9 ± 2.2a
Ds–Dm [72]	30.3 ± 5.6a	16.6 ± 7.9b	0.3 ± 0.5b*	0.0 ± 0.0a*	16.3 ± 7.9a*	2.7 ± 3.5a*

Figures represent mean ± SD. Different letters indicate significant difference within columns and an asterisk indicates significant differences between the species ($p < 0.05$).

Table 3. Effect of host plants on interspecific competition of *Diadegma mollipla* (Dm) and *Diadegma semiclausum* (Ds) on *Plutella xylostella*. Figures represent mean ± SD. Different letters indicate significant differences within columns, and the asterix indicate significant differences between the species ($p < 0.05$).

Host plant	No. parasit. DBM	No. emerged parasitoids	*D. mollipla*		*D. semiclausum*	
			total	females	total	females
cabbage	9.6 ± 3.0a	8.1 ± 2.6a	0a*	–	8.1 ± 2.6a*	0.9 ± 1.3a
pea	10.5 ± 3.4a	8.0 ± 3.6a	0.8 ± 1.3b*	–	7.3 ± 3.4a*	0.5 ± 0.8a
cabbage/pea	8.3 ± 4.4a	7.2 ± 3.9a	0.5 ± 0.7b*	–	6.8 ± 3.7a*	0.3 ± 0.6a

an average of less than one larva per plant, whereas *D. semiclausum* produced an average of seven offspring. When cabbage was offered alone, all progeny was produced by *D. semiclausum*. In the mixed host plant exposure, the number of offspring of *D. mollipla* was similar on both host plants (0.3 on cabbage, 0.6 on pea) (df = 1, $\chi^2 = 0.83$, $p = 0.36$). *Diadegma semiclausum* also produced similar numbers (6.9 on cabbage, 6.6 on pea) (df = 1, $\chi^2 = 0.10$, $p = 0.75$).

Effect of host density on interspecific competition

The level of parasitism and progeny production was not influenced by a different number of larvae on host plants (table 4). On the same plant percentage, parasitized larvae, adults and progeny contribution of parasitoid species were similar for the two host densities (10 and 20 larvae per plant) on each host plant (df = 1, $\chi^2 = 2.28$, $p = 0.13$; df = 1, $\chi^2 = 1.89$, $p = 0.16$). The contribution of *D. mollipla* to the total progeny production was significantly lower on both plants, as compared to *D. semiclausum*. The number of offspring of *D. mollipla* was significantly higher on pea than on cabbage (df = 1, $\chi^2 = 10.26$, $p < 0.01$). *Diadegma semiclausum* produced more progeny on cabbage than on pea (df = 1, $\chi^2 = 4.0$,

$p < 0.05$). The latter species also produced significantly more females on cabbage with 20 host larvae than in other density/plant combinations (df = 3, $\chi^2 = 188.4$, $p < 0.01$).

Effect of parasitoid density on interspecific competition

An increasing number of ovipositing females of *D. mollipla* resulted in a decrease of progeny of *D. semiclausum* on the pea plants (df = 2, $\chi^2 = 17.9$, $p < 0.01$) (fig. 2). It did not have an effect on the number of progeny of *D. mollipla* (df = 2, $\chi^2 = 0.10$, $p = 0.95$). The number of *D. mollipla* offspring was consistently low and remained below one larva per plant on both host plants. On cabbage plants, the total number of parasitized larvae, production of progeny and contribution of parasitoid species to total progeny was similar for all parasitoid densities (df = 2, $\chi^2 = 1.18$, $p = 0.55$; df = 2, $\chi^2 = 0.47$, $p = 0.79$) (fig. 2a). The number of progeny produced by *D. semiclausum* on cabbage was significantly higher than the progeny numbers of *D. mollipla* and did not change with an increasing number of ovipositing *D. mollipla* females. On pea plants, higher number of ovipositing *D. mollipla* females resulted in a significant reduction in the number of parasitized larvae

Table 4. Effect of host density and host plants on interspecific competition of *Diadegma mollipla* (Dm) and *Diadegma semiclausum* (Ds) on *Plutella xylostella*. Host densities: ten and 20 larvae on both plants (c-10 and c-20 on cabbage, p-10 and p-20 on pea). Different letters indicate significant differences within columns.

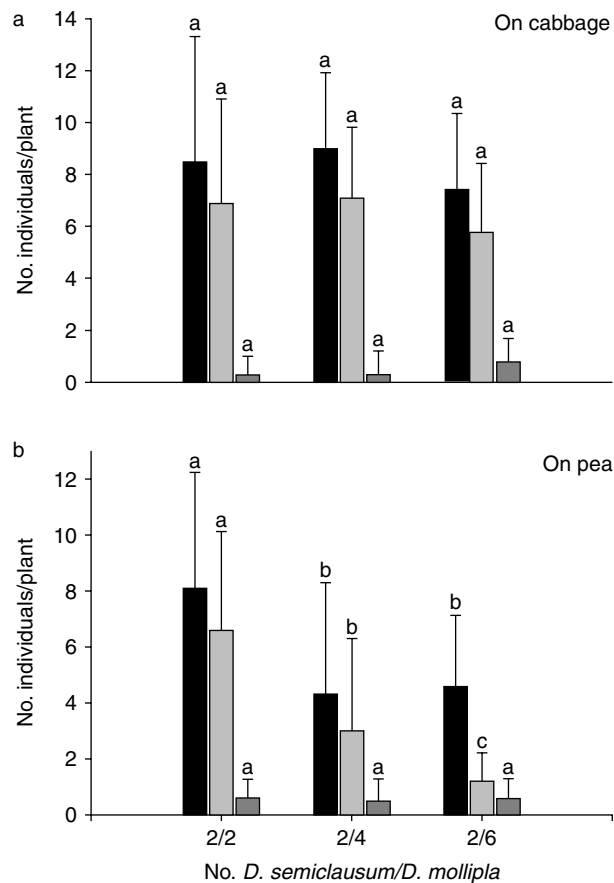| Host density	plant	% parasit. DBM/plant	% emerged/ plant	% D. mollipla		% D. semiclausum	
				total	females	total	females
c-20/p-10	cabbage	63.9a	50.0a	0a	–	100a	44.2a
c-10/p-20	cabbage	59.4a	46.1a	0.9a	–	99.1a	23.5b
c-20/p-10	pea	41.6a	35.8a	12.2b	–	87.7b	20.0b
c-10/p-20	pea	53.2a	40.9a	9.4b	–	90.6b	17.7b

Fig. 2. Effect of *Diadegma mollipla* density on DBM offered on (a) cabbage and (b) pea as host plants on interspecific competition with *D. semiclausum*. Number of females: 2/2 (two *D. mollipla* females; 2/4 (four *D. mollipla*); 2/6 (six *D. mollipla*); and two *D. semiclausum* (■, parasitized; ▢, Ds; ▨, Dm).

(df = 2, χ^2 = 6.47, $p < 0.05$) and production of progeny (df = 2, χ^2 = 13.31, $p < 0.01$) due to a reduction of *D. semiclausum* progeny from 6.6 (equal number of ovipositing females) to 1.2 (six *D. mollipla* females) (fig. 2b).

Discussion

In simultaneous intra- and interspecific competition experiments in the laboratory, *D. mollipla* was superior to *D. semiclausum* on snowpea. In an identical experimental set-up using cabbage as host plants, *D. semiclausum* clearly out-competed *D. mollipla*, producing 73% of total progeny (Sithole, 2005). Both species are able to discriminate between parasitized and unparasitized larvae and do not super-parasitize (Lloyd, 1940; Ullyet, 1943, 1947; Venkatraman, 1964; Yang *et al.*, 1994). Interspecific host discrimination between *D. semiclausum* and *Cotesia plutellae* resulted in multi-parasitzed larvae (Shi *et al.*, 2004). However, in our study, preliminary dissections of host larvae after simultaneous parasitism contained only one egg. Therefore, we assumed that almost all progeny emerged from singly parasitized larvae and competition took place between adults, depending on which species parasitized more hosts within the given time. Mortality of parasitized hosts was mainly attributed to failure of emergence. Only very few hosts died during their larval stage, and they contained a single parasitoid embryo. Higher mortality of pupae from snowpeas, as compared to cabbage, occurred in both species (Rossbach *et al.*, 2006c; Rossbach, unpublished data). Higher parasitism levels of *Diadegma mollipla* on DBM on snowpea, as compared to DBM on cabbage, have been demonstrated in an earlier study (Rossbach *et al.*, 2006a); whereas, for *D. semiclausum*, the reverse was true (Rossbach *et al.*, 2006c). The ability of a species to produce proportionally more females than its competitor is crucial for its performance (Reitz & Trumble, 2002). We did not specifically investigate this parameter in order to measure performance because of the differential time both species were kept in culture and the concomitant decline in females in laboratory cultures. Furthermore, the number of females was extremely variable for both species in all experiments, thus complicating the interpretation of the results.

In the delayed competition experiments on snowpea, the first attacker was the clear winner when the time interval was greater than 24 h. Presence of hosts parasitized by either species seemed to have negatively affected the ability of the other to locate unparasitized larvae for parasitism. On cabbage, whichever of the two species, *D. semiclausum* or *D. mollipla*, had first access to the host, irrespective of exposure interval, predominated with 85–97% of the emerging progeny (Sithole, 2005). Similar results were reported from delayed competition experiments with other parasitoid species (McBrien & Mackauer, 1990; Shi *et al.*, 2004; DeMoraes & Mescher, 2005; Muli *et al.*, 2005). In our study, the number of parasitized DBM larvae was constant for all exposure sequences and time intervals (except for Ds-Dm (48 h)); but total progeny was significantly reduced at time intervals of 48 h and 72 h, irrespective of which species parasitized first. After these time intervals, host larvae were already in their third to fourth instar. Most likely, higher pupal parasitoid mortality was caused by a shorter

development duration that remained for the second attacker and not because of multiparasitism of hosts.

Simultaneous delayed competition experiments on snowpea suggested that oviposition of *D. mollipla* was influenced by newly parasitized larvae by the *D. semiclausum*. Freshly parasitized larvae by *D. semiclausum* might have disturbed ovipositing *D. mollipla* females. Some parasitoids deposit an external signal after oviposition, allowing host discrimination for conspecifics. The parasitoid *Aphidius smithi*, for example, marks its hosts externally with phero- mones. Mackauer (1990) suggested that these marking pheromones on already parasitized hosts could be detected by antennation and facilitate discrimination. The ecto- parasitoid *Eupelmus vuilleti* (Crw) seems to deposit a chemi- cal compound on the surface of the seeds containing parasitized hosts (Gauthier *et al.*, 1999). At this time, we can only speculate that chemical interference might also play a role in the interaction between *D. mollipla* and *D. semi- clausum*. It is also possible that direct chemical interference between adults occurs in these two parasitoids. An increas- ing number of *D. mollipla* females led to a decrease in progeny of *D. semiclausum* on snowpea. The presence of a higher number of its competitor's females caused *D. semi- clausum* to shun away from the unusual host plant, although the *D. mollipla* females did not parasitize more larvae on any of the host plants. Adults of the parasitoids *Cephalonomia stephanoderis* Betrem and *Prorops nasuta* Water- ston (Hymenoptera: Bethylidae) emit a characteristic smell, presumably to keep away other individuals (Infante *et al.*, 2001). Tamò *et al.* (2006) recently demonstrated that para- sitoid-produced odours can directly affect other members of the third trophic level. In olfactometer tests, females of the parasitoid *Cotesia marginiventris* (Cresson) strongly avoided the smell of its competitor *Cotesia sonorensis* (Cameron).

Findings from the laboratory studies indicated an advantage for *D. mollipla* over *D. semiclausum* on snowpea as compared to cabbage. We, therefore, assumed that the former species could find its niche on snowpea, whereas *D. semiclausum* remained predominant on cabbage. Gradual displacement of *D. mollipla* by the introduced parasitoid on *Brassica* crops in Kenya was predicted by Sithole (2005) in laboratory competition studies. Later, this result was confirmed to occur in the field (Momanyi *et al.*, 2006; Rossbach *et al.*, 2006b; Löhr *et al.*, 2007). However, given more natural conditions in the experimental cages, *D. mollipla* parasitized significantly less larvae than in small containers. As expected, all progeny on cabbage, when offered alone, came from *D. semiclausum*. On pea alone, progeny production of *D. mollipla* did not increase to higher numbers than one individual per plant, whereas *D. semiclausum* produced a constant number of offspring on both plants, whether DBM host strains were offered alone or together. Two different host densities on different host plants did not affect parasitism levels of both parasitoids. *D. mollipla* still produced significantly less progeny than its competitor, but its parasitism rates were higher on its host larvae on snowpea than on cabbage, regardless of the number of larvae available. Wang *et al.* (2004) reported that an increase in host density led to aggregation of *D. semiclausum* adults in the field, but density-dependant increase of parasitism rates was not observed. Higher host density on cabbage resulted in higher production of females by *D. semiclausum*. However, by comparing two densities,

we cannot state if female progeny production is density dependent.

Diadegma semiclausum uses crucifer-typical volatiles to locate its host (Ohara *et al.*, 2003; Bukovinsky *et al.*, 2005). Therefore, it has a better host location ability on cabbage as compared to pea, a plant species outside its normal host plant range. *Diadegma mollipla* has at least one more host, the potato tuber moth. Host location cues of *D. mollipla* are unknown; however, the species seems to use a blend of volatiles existing in a variety of plants (Rossbach *et al.*, 2005). Differential host searching efficiency, due to different host specify of the two parasitoids, might be one expla- nation why *D. mollipla* was significantly less competitive on snowpea in semi-field conditions as compared to the laboratory. While *D. semiclausum* females appeared to be more active and were observed hovering around the plants searching for hosts, *D. mollipla* preferred to rest on the mesh that covered the cage. The relatively small distance between host plants might have facilitated *D. semiclausum* detecting host larvae, even on an unusual host plant. Wang & Keller (2002) observed visual perception of *D. semiclausum* close to host larvae when they compared the host searching efficiency of the DBM specialist, *D. semiclausum*, and the more oligophagous *Cotesia plutellae*. The DBM specialist was more effective, both in the location of DBM and overcoming its host defence.

Results on the competitiveness of *D. mollipla* on snowpea differed largely between laboratory and cage experiments. The latter simulated the field situation more closely except for the parasitism levels of *D. semiclausum* on DBM on snowpea. In the field, the species remained in the original host habitat, probably due to sufficient densities of host larvae on kale plants in neighbouring farms (Rossbach *et al.*, 2006b). *Diadegma mollipla* performed slightly better on snow- pea as compared to cabbage, but remained less competitive than *D. semiclausum* on both host plants. This parasitoid species might still be able to parasitize DBM larvae on snowpeas even in the presence of the overall predominant *D. semiclausum*, especially when the former occurs in higher numbers. However, field observations showed that *D. mollipla* did not establish on DBM in snowpeas after its displacement on kale (Rossbach *et al.*, 2006b). We assumed that the generalist species preferred to withdraw to other natural hosts in native habitats, rather than moving to snowpeas.

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