

Feeding status of the parasitoid *Diadegma semiclausum* affects biological control of *Plutella xylostella*: a simulation study

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Life history characteristics of the diamondback moth (DBM), *Plutella xylostella*, a worldwide pest on cruciferous crops, and its important natural enemy, the parasitoid *Diadegma semiclausum* have intensely been studied. In addition, the searching behaviour of the parasitoid and the role of foraging experiences have been studied. Recently, fed and unfed individuals of the parasitoid *D. semiclausum*, that forage for hosts in field cages have been shown to differ considerably in their patch leaving tendencies from plant patches with different host densities. Moreover, flight patterns in the field differ between fed and unfed parasitoids. Separately, all these data do not necessarily amount to knowledge on what happens at the field scale.

In this paper, results from behavioural studies are integrated with studies on longevity of parasitoids and host development to assess the field-wide impact of nutritional state on biological control efficacy. To achieve this, an individual based, spatially explicit, simulation model is developed to study how differences in behaviour and longevity between fed and unfed parasitoids affect the percentage parasitism and thereby the biological pest control of DBM in the field. The results are discussed in the light of improving biological control of DBM in broccoli fields if nectar sources are supplied in borders of the crop fields.

Keywords: diamondback moth, conservation biological control, feeding status, spatial model

One of the most destructive pests of brassica crop species around the world is the diamondback moth (DBM), *Plutella xylostella* (L.) (Waterhouse & Norris 1987). Because this pest has developed resistance to almost all major classes of insecticides (Talekar & Shelton 1993), maximising the role of natural control measures has been emphasised as one of the ways to reduce reliance on insecticides. Larval parasitoids are most commonly used as biological control agents of DBM. *Diadegma semiclausum* (Hellén) a solitary specialist parasitoid on DBM has established in Australia.

For a farmer it is important to maximise the percentage of parasitism in a crop field. This percentage is the outcome of the foraging behaviour of a population of parasitoids exploiting the host population in the crop at the same time. In studies of foraging and patch exploitation by parasitoids, the decision of when to leave a patch is considered to be of major importance (e.g. Charnov 1976, Hemerik *et al.* 1993, Vos *et al.* 1998, Driessen & Bernstein 1999). Charnov (1976) already concluded that the expected travel time between patches determines the patch residence time in a habitat, thereby suggesting that the interplay between patch leaving decisions and travel times is what really matters for the exploitation of a host population (Vos & Hemerik 2003). Recent experiments on *D. semiclausum* have shown pronounced differences in patch leaving decisions and the choice of the next plant to visit between fed and unfed individuals (Thompson 2002). Moreover, in the laboratory the longevity of unfed individuals of this parasitoid species is as much as ten times lower than that of fed individuals (Yang *et al.* 1993, Winkler *et al.* 2005). Therefore, the availability of feeding resources such as suitable flowers in and around crops might influence levels of parasitoid activity in the crop (Fitton & Walker 1992, Idrus & Grafius 1995, Winkler *et al.* 2006).

Here, the aim is to assess the variation in parasitism of *P. xylostella* larvae by *D. semiclausum*, *i.e.* fed versus unfed females. These differ in longevity and in foraging behaviour due to their different nutritional states. The output of the simulation model is the percentage of second to fourth instar host larvae (L2-L4) that is parasitised after an interaction between hosts and parasitoids of approximately 15 weeks just before autumn starts in the Australian plains. This percentage is computed for both a population of fed and one of unfed parasitoids in a monoculture of broccoli with rows of differently aged plants for a particular difference in longevity between fed and unfed parasitoids. How parasitism level is affected by the longevity of the fed parasitoids is investigated by varying this longevity (4 additional simulations). The effect of the density of parasitoids is checked with one additional simulation run.

MATERIALS AND METHODS

A simulation model was used to study how nutritional state, fed vs. unfed affected the parasitism levels by *D. semiclausum* and thus biological pest control of *P. xylostella* on the Australian plains in autumn. Below, the tri-trophic system is defined. Thereafter, the structure of the model is clarified. Third, the experimental and literature data used for parameter values in the model are described and fourth, the simulated scenarios are briefly presented.

The system

The moth *P. xylostella* lays its eggs on leaves of cruciferous host plants (Talekar & Shelton 1993). Adult female moths start laying eggs at the day of emergence (Harcourt 1957) or soon after copulation (Moller 1988). The eggs of DBM are

generally laid singly or in groups of two to four along the mid-ribs or principal veins on the lower side of leaves (Bhalla & Dubey 1986). Clutches of up to eight eggs are deposited mainly on the upper surface of the leaves (Waterhouse & Norris 1987). Before pupating, DBM has to go through 4 different larval stages (L₁-L₄). The egg to adult development is 283 degree days with a threshold of 7.3°C (Harcourt 1957). Recently, Liu *et al.* (2002) reported details on temperature dependent development of DBM. DBM can survive over a large range of temperatures (Shirai 2000), and its optimum temperature range is reported to be 17-25°C (Atwal 1955). *D. semiclausum* is a pro-ovigenic, specialist parasitoid of *P. xylostella* (Wang 2001). In Australia, *D. semiclausum* is widely established and abundant (Waterhouse & Norris 1987). *D. semiclausum* seems to parasitise more effectively when temperatures are relatively low (15-25°C). From field studies it is known that host plant species affects parasitism of *P. xylostella* by *D. semiclausum* (Yang *et al.* 1993).

Structure of the model

A realistic spatial environment is modelled consisting of broccoli plants with growing number of leaves and a dynamic host larvae population per plant. The foraging behaviour of parasitoids travelling between plants takes place within this environment, a field with at most 24 rows of 25 plants. Simulation time is set to 104 days (February 1 up to May 15) for broccoli (*Brassica oleracea* var. *italica*) grown on the Australian plains in autumn. After this period heavy rains exterminate the DBM larvae.

Plants

A cohort of young broccoli plants (4 rows) is planted every fortnight. The development of the broccoli plants is purely deterministic. The number of leaves that a plant has is used for determining the initial giving up times (GUT) on the patch, *i.e.* the plant. This GUT on empty (uninfested) plants (GUT_{empty}) is assumed to follow an exponential distribution with a mean that linearly increases with the number of leaves. The GUT's reported by Wang (2001) and Thompson (2002) are measured on broccoli plants with 7 leaves. The state of each plant is summarised in a vector containing the numbers of hosts in each larval stage that are unparasitised, once parasitised or superparasitised (parasitised subsequently by two or more conspecifics). Each plant's position in the field is known, and the vector of its neighbouring plants (at most 8) is updated when broccoli is planted. Broccoli plants are harvested at 12 weeks after planting. At the start of the simulation 100 broccoli plants were planted in 4 rows of 25 plants each.

Hosts and parasitoids

Immigration of parasitoids and hosts starts directly after planting of the broccoli plants. During the full simulation, hosts and parasitoids were introduced into the field daily at a density of 5 respectively 0.2 m⁻². Each host entering the sys-

tem is randomly placed on a plant as an early first instar larva. The state of each host is updated when it is encountered by a parasitoid. Hosts entering the pupal stage are removed from the host population, and at harvest all hosts from harvested broccoli plants leave the system.

In the simulations, only female parasitoids are considered. Fifty percent of the parasitoids on harvested plants are relocated in the field while the others are removed. The parasitoids arrive in the broccoli field on a randomly chosen plant. Their expected foraging time depends on their state, fed or unfed. In the model the parasitoids do not interfere with each other. In the course of one day, foraging parasitoids are simulated subsequently: first one parasitoid is exploiting the field for one day and thereafter the next one until every parasitoid alive has completed its foraging day. When parasitoids enter the field they have their complete egg load. Parasitoids that leave a plant are attracted differently to neighbouring plants with different host densities. The relative weights of plants with different host densities (Wang 2001) are given in Table 1. The longevity of parasitoids arriving in the broccoli field depends on their state (fed or unfed).

The parasitoids make patch arrival and leaving decisions at the spatial scale of plants. The behaviour of the parasitoids is stochastic, and is influenced by certain covariates (see below). In total 50 periods of 104 days were simulated for each scenario.

The behavioural cycle of a single foraging parasitoid is summarised in a flowchart (Fig. 1): When a parasitoid arrives at a plant (#) it draws its initial GUT from an exponential distribution with the mean depending on the number of leaves and whether the plant contains host larvae or not. An empty plant is left after this drawn GUT; after drawing a travel time and choosing one of the neighbouring plants to start searching on the behavioural cycle starts again from (#). If the plant contains some hosts an encounter time is drawn from the appropriate exponential distribution. In case (A) the GUT is less than the encounter time and thus the parasitoid leaves the plant after the drawn GUT. After travelling and choosing one of the neighbouring plants for foraging the behavioural cycle is resumed at (#). In case (B) the GUT is greater than the encounter time and a host is encountered. A handling time is drawn from the appropriate exponential distribution, and then the stage of the larva can be assessed. First and fourth stage larvae are not parasitised, whereas second and third larval stages are accepted with a probability P_{accept} (see below). If a larva is rejected then a GUT adjusted for changed covariate values is drawn as in the proportional hazards model given below and an encounter time is drawn from the same distribution as before. Thereafter, case (A) or case (B) applies. Eventually case (A) applies, the current plant is left and another plant can be visited.

At the end of a simulation the percentage parasitism is computed as 100 times the number of L2-L4 larvae that have been parasitised divided by the total number of L2-L4 larvae present, because larvae are only at risk for parasitism if they have reached L2.

Parameter values

Table 1 gives an overview of the parameters used, their description and values.

Plants

Broccoli plants have three leaves when planted. One, two, three, five and eight weeks after planting broccoli plants have a total of four, five, six, seven and eight leaves. After this week the number of leaves is constant until harvesting takes place after 12 weeks.

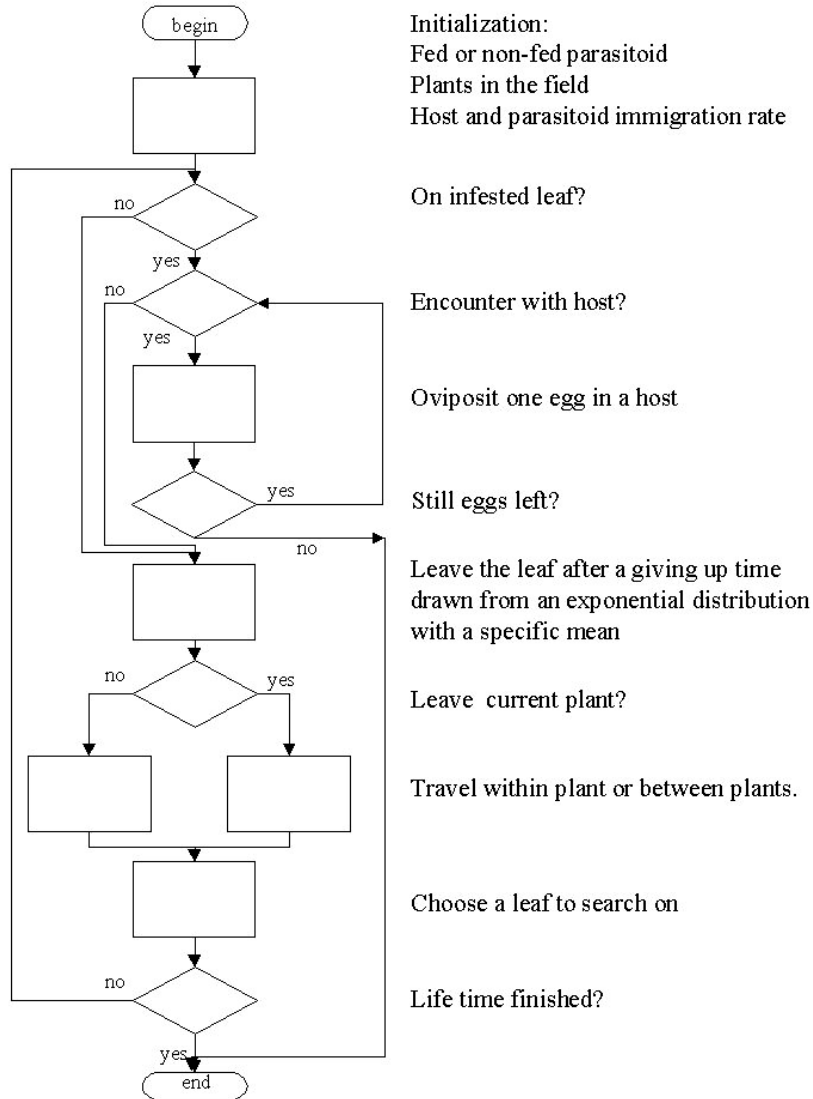


Figure 1. Flowchart of the foraging behaviour of a *D. semiclausum* parasitoid in a broccoli field. This is part of the total program explained in the text.

Table 1. Parameter values used in the simulations, based on experiments with fed and unfed *D. semiclausum* parasitoids. All parameters involving time were simulated as exponential distributions.

Parameter description	value	dimension
Mean giving up time on empty leaves (GUT_{empty}) ^b	10	s
Mean giving up time on infested leaves ($GUT_{infested}$) ^b	100, 1000 ^a	s
Mean interval between ovipositions ^c	15	s
Mean handling time of hosts ^c	245	s
Mean travel times between plants ^d	2	s
Number of hours spent foraging in 24 h ^b	10	h
Weights for plants with 0, 1, 2, 3, ≥ 4 hosts ^c	0.2, 0.8, 1, 1, 1.4	
Number of leaves on which GUT_{empty} was measured ^b	7	
P(stay in same row as current plant) ^b	7/8, 8/11 ^a	
Locally perceived Environment	8	plant
Mean longevity of parasitoids ^d	1, 10 ^a	day
Egg load of parasitoids ^c	30-45	eggs
Distance between rows	50	cm
Distance between plants within a row	35	cm
Duration of hosts L1, L2-L3, L4 stage	4, 8, 4	day
Daily production rate of hosts	5	$m^{-2} day^{-1}$
Host's daily probability to die	0.014	day^{-1}
Daily immigration rate of parasitoids	0.2	$m^{-2} day^{-1}$
Parasitoids daily probability to leave the field	0.1	day^{-1}
Harvest time	84	day
Total simulation time	104	day

^a when two values are given the first is for the unfed and the second for the fed parasitoid; ^b data from L. Thompson (2002); ^c data from X-G Wang (2001); ^d M.A. Keller personal observation

Hosts

In a pest situation in southern Australia the number of host larvae per plant can be 36, but during a large part of the year the number of hosts per plant is less than 6 (N.A. Schellhorn, pers. comm.). Host densities peak at broccoli of 7-9 weeks old. The first and last larval stages (L₁, L₄) are often not attacked, because L₁ is a leaf miner and not easily found, whereas L₄ is highly aggressive and therefore avoided (Wang 2001). The L₂ and L₃ larval stages are readily accepted for parasitisation by *D. semiclausum*. Based on data of their temperature-dependent development (Liu *et al.* 2002; averaged over the range 12-24°C), L₁-L₄ last respectively 3.9, 4.2, 3.3 and 4.2 days. In the model each stages of L₁-L₄ lasts four days

(Table 1). During larval development 80% of the larvae survive until pupation (Wakisaka *et al.* 1992). Based on this value and the total larval development time of 16 days the daily probability to die is computed as $1-(0.8)^{1/16}=0.014 \text{ day}^{-1}$.

Parasitoids

Schellhorn (pers. comm.) marked adult parasitoids of natural populations by spraying with dye and trapped them inside and outside a broccoli field. The recaptured adult numbers were approximately equal, suggesting that the parasitoids move randomly in and out of the field. For the density of parasitoids per m^2 , Schellhorn *et al.* (2004) reported from field data a value between 0.5 and 1 with a standard error of 0.5. No data are available on the proportion of parasitoids that leave the field, but it is assumed to be 0.1 day^{-1} .

The maximum longevity of fed and unfed parasitoids in the laboratory is 3 and 28 days, respectively (Yang *et al.* 1993). Based on the parasitoid's longevity its foraging time is determined. *D. semiclausum* parasitoids are reported to be active during the day from approximately 7.00 AM to 5.00 PM (Thompson 2002). Thus, foraging time is $10/24$ of the total lifetime. These pro-ovigenic parasitoids have according to Wang (2001) an egg load of 30-45 eggs after 1-7 days.

The probability to accept a host upon encounter depends on experience of the parasitoid and the state of the encountered host. The probability to accept (P_{accept}) the host upon encounter depends on (1) whether the encountered host is already parasitised (p : Yes/No= $1/0$), (2) the cumulative number of ovipositions (n) by the parasitoid during the current visit and (3) the time (t in seconds) since the parasitoid started its current visit (Wang 2001). The formula given by Wang (2001) is

$$P_{\text{accept}} = \exp(f(p,n,t)) / (1 + \exp(f(p,n,t))), \text{ with } f(p,n,t) = 3.8 - 4.1p + 0.224n + 0.00093t.$$

The patch leaving tendency of *D. semiclausum* is modelled as a proportional hazards model (Cox 1972) with 5 covariates and a constant baseline leaving tendency (λ), that is when all covariates are 0. The formula is:

$$h(s,r,n,v,d) = \lambda \cdot \exp(\beta_s \cdot s + \beta_r \cdot r + \beta_n \cdot n + \beta_v \cdot v + \beta_d \cdot d).$$

Thus, the GUT on empty plants follow an exponential distribution with mean $1/\lambda$ (see also Table 1). The covariates that influence the parasitoid's leaving tendency (Wang 2001, Wang & Keller 2004) are (1) the state of the latest encountered host s , with value 1 or 0 for superparasitised or not ($\beta_s=1.08$); (2) whether yes or no a rejection r (value 1 or 0) occurred at the latest encounter ($\beta_r=1.79$); (3) the cumulative number n of ovipositions during the current visit ($\beta_n=0.405$); (4) the rate of the last oviposition ($v=1/[\text{observed time from patch}$

entry to first oviposition or between two subsequent ovipositions]; $\beta_v=9.5$); and (5) the density of hosts d , being 0, when the host density on a plant is 0, 1, 2 or 3 hosts, or 1 when 4 or more hosts are present ($\beta_d=-1.5$).

Diadegma semiclausum behaves differently on empty and infested plants. For simulation of the parasitoid's foraging behaviour the mean interval between ovipositions, the handling time of hosts and the mean travel time between plants have to be known. In the field most of the parasitoids leaving the current plant choose one of its direct neighbouring plants to land upon next. Thompson (2002) also discovered that the probability to stay within the same row of plants differed between fed and unfed parasitoids (Table 1).

Simulation scenarios

The longevity of unfed and fed parasitoids is reported from laboratory and semi-field studies as maximal 3 and 28 days. Under field circumstances, longevity is probably shorter. Therefore, the longevities of unfed and fed parasitoids are simulated with exponentially distributed variables with means of respectively 1 and 10 days (scenario 1). In that case only 5% of the unfed and fed parasitoids have a lifetime exceeding 3 and 30 days respectively. For 1 replicate of the simulation the dynamics of the hosts and plants are the same when simulating fed or unfed parasitoids. Thus, a pairwise comparison between fed and unfed parasitoids can be performed.

To determine which difference in longevity between fed and unfed parasitoids still has a considerable effect on the realised percentage parasitism the longevity of the fed parasitoids was varied (scenarios 2-5 with longevities of 8, 4, 2 and 1 days on average, see Table 2), while the unfed parasitoids have a fixed average longevity of 1 day. The effect of the density of parasitoids on the resulting percentage parasitism (scenario 6), is investigated by simulating with a higher (=doubled) parasitoid density only in the case were fed parasitoid lived on average 10 days (Table 2).

RESULTS

In total, 50 replicates for each of the six scenarios were simulated. In each of the simulated scenarios the average total number of hosts per plant was 10.5, whereas the average number of L2-L4 larvae per plant was 7.4. In the scenarios 1-5 with an immigration rate of parasitoids of $0.2 \text{ m}^{-2} \text{ day}^{-1}$ the resulting density of unfed parasitoids always was $0.34 \text{ parasitoid m}^{-2}$. The corresponding values for fed parasitoids with average longevity of 1, 2, 4, 8 and 10 days were respectively 0.34, 0.53, 0.88, 1.53 and 1.82 m^{-2} . The simulation set-up was chosen in such a way that the results obtained with fed and unfed parasitoids could easily be compared. The resulting parasitism percentages of the larger hosts (L2-L4) are given in Table 2. In the scenarios 1-4, the difference between the percentage parasitism realised by fed parasitoids was higher than the corresponding one realised by

Table 2. The percentage parasitism of the larval stages L2 to L4 as resulting from the simulations; the range of outcomes from the simulation study is given between brackets. The longevity of the fed parasitoids was varied, since the longevity of *D. semiclausum* parasitoids were only known from laboratory experiments. The average percentage parasitism was determined by computing the squared sine back-transformation of the average from the arcsine square root transformed fractions.

Scenario	Longevity of fed parasitoid	Unfed	Fed
1	10	54.8 (52.9-56.7)	65.8 (64.6-66.9)
2	8	54.8 (52.5-56.6)	65.5 (64.3-66.6)
3	4	54.7 (52.6-57.1)	64.0 (62.7-65.0)
4	2	54.7 (53.2-56.8)	60.8 (59.1-62.3)
5	1	54.9 (53.2-56.7)	55.1 (53.6-57.1)
6	10 ^a	77.7 (76.8-78.5)	86.1 (85.6-86.6)

^a here the number of parasitoids introduced daily into the field was set at twice the standard value

unfed parasitoids. In these cases, the realised ranges of parasitism did not overlap. Even if the average longevity of the fed and unfed parasitoids was the same (scenario 5), the behavioural differences between the two states result in a somewhat higher overall percentage parasitism of L2-L4 – all pairwise comparisons show larger percentages for the fed parasitoids, but ranges of parasitism overlap.

In scenario 6 with longevity 10 and $0.4 \text{ m}^{-2} \text{ day}^{-1}$, the values for unfed and fed parasitoids were 0.68 and 3.67 m^{-2} . When the assumed longevities of fed and unfed parasitoid differ by a factor of 10 biological control of the DBM can be improved with about 12% when parasitoids are present at a density of 1.82 m^{-2} . It should however, be noted that 40% of the parasitised hosts was attacked by more than one conspecific female (*i.e.* superparasitised) when unfed individuals were foraging, and this value rose to 47% when parasitoids had an average longevity of 10 days. In accordance with this observation about two third of the unfed parasitoids still alive was egg-limited and for all simulations of fed parasitoids with average longevity greater than 2 days 95% was egg-limited. Doubling the number of parasitoids in the field also increased the realised percentage parasitism, as expected.

DISCUSSION AND CONCLUSION

A lot of characteristics including egg load of the parasitoid were the same for fed and unfed parasitoids. Egg load, for instance, can vary between unfed and fed parasitoids due to egg resorption and egg maturation after eclosion of the adult female parasitoid. Winkler *et al.* (2006) have shown that in semi-field conditions with available nectar sources *D. semiclausum* is not fully pro-ovigenic, because under those circumstances one parasitoid can lay about 490 eggs and thus matures eggs during its adult life. If that is also true for Australian *D. semiclausum* parasitoids, the difference in realised percentage parasitism between the

unfed and fed parasitoids can only be expected to be higher. In such circumstances egg-limitation is expected to occur more often in unfed parasitoids and less often in fed parasitoids.

In the simulation model parasitoids are only searching for hosts and they do not allocate time to search for nectar sources. Because unfed parasitoids are likely to spend more time searching for nectar sources than the fed parasitoids, inclusion of a choice between foraging for hosts or for nectar sources should enlarge the difference in percentages parasitism between fed and unfed parasitoids.

The high percentage superparasitism in the simulation results is due to the fact that the program used the fact that Wang (2001) was not able to show that *D. semiclausum* used the ability to discriminate for refraining from superparasitism. He, however, found a significant effect of an encounter with a superparasitised host on the parasitoid's plant leaving tendency. It cannot be excluded that the parasitoid species is able to discriminate healthy from already superparasitised host, because Legaspi (1986) showed that *D. semiclausum* was able to discriminate.

Under field conditions it is not known what part of the established parasitoid population is unfed. Assuming that the majority of the parasitoids foraging in crop fields have no opportunities to feed on nearby plants, a higher percentage parasitism can be easily obtained, even if fed parasitoids in the field only have a longevity that is on average four times higher than that of unfed parasitoids. One of the first things to investigate is the physiological state of the parasitoids that forage in broccoli fields where plants are infested with DBM larvae.

Modelling studies like this one are highly suitable for bridging the gap between laboratory studies on life history characteristics and behaviour of individuals on the one hand and the reality in the crop field on the other hand. The longevities of parasitoids having either access to wildflowers as nectar sources or not have recently been investigated by Winkler *et al.* (2006). Their results support the conclusion from the simulation that biological control of *P. xylostella* by *D. semiclausum* can be improved when wildflowers bordering the crop fields serve as nectar sources for the parasitoid.

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