

Effect of Wild Flowers on Oviposition of *Hippodamia variegata* (Coleoptera: Coccinellidae) in the Laboratory

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ABSTRACT Marginal vegetation in crops is very important for natural enemies and their pest control capacity. The effects of *Brassica nigra* L. (Brassicaceae), *Daucus carota* L. (Apiaceae), and *Sonchus oleraceus* L. (Asteraceae) flowers as supplemental food on the number of eggs laid during 7 d and on the preoviposition time in *Hippodamia variegata* (Goeze, 1777) were studied in the laboratory under conditions of several densities of *Acyrtosiphon pisum* (Harris, 1776). The results show the presence of flowers of *Brassica* and *Sonchus* increased egg production 1.44× and doubled the preoviposition period (2.13×). This suggests that the availability of flowers of *Brassica* and *Sonchus* as supplemental foods (pollen and nectar) in the marginal vegetation of crops can serve to improve reproductive performance of *H. variegata*, specifically under conditions of prey limitation. Thus, the increase in fitness of this predator allows a better response to changes in pest density.

KEY WORDS Coccinellidae, *Hippodamia variegata*, supplemental food, marginal vegetation

Marginal vegetation in crop fields is important for natural enemies, because it provides shelter, prey, and other supplemental food sources, such as nectar and pollen (see Altieri 1992, Lagerlöf and Wallin 1993, Koricheva et al. 2000). Also, some volatile substances they emit may attract natural enemies (Sabelis et al. 1999, Nentwig et al. 2002). Thus, the presence of floral resource plants in landscapes enhances the abundance of natural enemies (Rebek et al. 2005). Because the impact of a predator on its prey may depend on the presence of other species in the community, the biological pest control would benefit from improved understanding of wild plant effects on natural populations.

One of the most important biological characteristics of natural enemies is their numerical response to changes in prey abundance, because it affects control of prey populations. Also, the natural enemy mortality, prey spatial distribution, supplemental food sources, and physical or chemical barriers, can affect the numerical response of natural enemies (Emehute and Egwuatu 1993, de Clercq et al. 2000, Ninkovic et al. 2001, Ruzicka 2001).

Most coccinellids are important natural enemies of aphid species, and they are of important in the natural and biological control of several pest populations (Hodek 1973, Hodek and Honek 1996, Dixon 2000). Similar to many predatory insects, they are facultatively

phytophagous. Surrounding vegetation seems to have a direct effect on the density of some coccinellids by modifying their immigration and emigration patterns (Grez and Prado 2000) and predation rate (Harmon et al. 2000). Also, this enables them to survive periods of low prey densities or to obtain extra nutrients necessary for egg production or overwintering (Hodek and Honek 1996).

The main objective of this work was to analyze, under laboratory conditions, the degree of influence that common wild plants in legume fields in the province of León, Spain, exert on two reproductive characteristics of *Hippodamia variegata* (Goeze, 1777): fecundity and preoviposition period. This coccinellid is the main natural enemy of legume aphid pest *Acyrtosiphon pisum* (Harris, 1776) in this area.

Materials and Methods

The *H. variegata* used in the experiments were reared from 60 to 70 adults collected from the field on *Medicago sativa* L. and marginal weeds. The adults collected were kept together in plastic receptacles with a covering of muselin until they formed mating pairs. The mating pairs were isolated in similar conditions, and every day the eggs laid were transferred to a petri dish with a filter paper on the bottom. The coccinellids were fed ad libitum with aphids from a laboratory culture or from legume crops. The offspring were isolated into groups of five to six individuals and fed ad libitum with aphids until they formed pupae. Every day, the pupae were checked for emerged adults. The newly emerged adults were kept in groups of 15–20 individuals and fed ad libitum with *A. pisum*, an essential prey of *H. variegata* that allow

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the reproduction of the adults and the development of the larvae in the wild (Obrycki and Orr 1990, Majerus 1994). In the next 24 h, the adults who formed mating pairs, each pair was isolated in a 9-cm-diameter petri dish with a corrugated filter paper (5 × 10 cm) on the bottom and were used in experiments. Egg clusters, typically laid on inner surfaces of the petri dishes, were collected daily by transferring the beetles to new dishes, or by simply switching the filter paper. All instars were reared in a laboratory under controlled conditions at mean conditions of 23 ± 2°C temperature, 41 ± 10% RH, and a photoperiod of 16:8 (L:D) h.

The variable analyzed was the daily number of eggs laid by each female. The eggs were counted visually on the filter paper or plastic, but a stereoscopic microscope (20–40×) was used to count eggs on the removed flowers. In total, 160 females were used, i.e., 10 replicates for every combination of 16 treatments.

Two different food sources were combined: 1) larval instar 2 and 3 of *A. pisum* as main food source (aphid), and 2) flowers of wild plants as supplemental food source (plant). Experiments lasted 7 d. The first 2 d, the male was kept together with the female to ensure fertilization and the amount of aphids was doubled, because it is usually implicitly assumed that nutritional requirements for fertility are similar for male and female. Nevertheless, variation in male fitness may be of little or no consequence to biological control in the field provided females have opportunities to engage in multiple matings (Michaud 2005). After the male was removed, the experiments continued for 5 d, assuming that the reproductive delay is 5 d immediately after this period; the number of eggs started high and then declined gradually (Dixon and Agarwala 2002).

There were four levels for aphid: APHID.5, .10, .20, and .30. For each level of aphid, there were four types of conditions for plant: control (without flowers); *Brassica nigra* L. (Brassicaceae), *Daucus carota* L. (Apiaceae), and *Sonchus oleraceus* L. (Asteraceae). The plant species were selected because none can be used as food by *A. pisum*, *H. variegata* is frequent on these plants (Bertolaccini 2002), and the main aphid food on these plants, i.e., *B. nigra*, *Brevicoryne brassicae* (L., 1758); *D. carota*, *Semiaphis dauci* (F., 1775); and *S. oleraceus*, *Uroleucon sonchi* (L., 1767) and *Hyperomyzus lactucae* (L., 1758), are not pests of legume crops.

The aphids were renewed daily by removing the leftovers and adding fresh aphids from a laboratory culture on *Phaseolus vulgaris* L. We did not use full plants; only a part of the umbel of *Daucus*, three to four open flowers of *Brassica* (cut off the upper part with close flowers), and a flower of *Sonchus* were used. The flowers were removed and replaced daily by newly cut flowers. The new flowers were visually examined to eliminate small insects or eggs, but they were not searched too thoroughly, to keep them intact. Thus, we assumed that the coccinellids fed mainly on pollen and nectar.

In total, 1,120 data points were registered (four aphid × 4 plant × 7 d × 10 females). The effect of food

Table 1. Range and mean ± 1 SE of eggs laid for females during 7-day period for different levels of normal (aphid) and supplemental (plant) feeding (n = 10)

Plant	Aphid.05	Aphid.10	Aphid.20	Aphid.30
Control				
Range	0–3	0–14	0–52	0–87
Mean	0.3 ± 0.30	1.5 ± 1.39	6.7 ± 5.13	22.1 ± 9.94
<i>Brassica</i>				
Range	0–20	0–46	0–60	0–91
Mean	4.9 ± 2.24	17.5 ± 4.59	26.5 ± 7.28	52.1 ± 9.87
<i>Daucus</i>				
Range	0–0	0–38	0–52	0–56
Mean	0 ± 0	5.9 ± 3.88	12.1 ± 6.17	10.5 ± 6.02
<i>Sonchus</i>				
Range	0–14	0–56	0–78	0–81
Mean	3.4 ± 1.82	14.8 ± 5.72	29.8 ± 8.61	39.4 ± 11.31
Suppl				
Range	0–20	0–56	0–78	0–91
Mean	4.15 ± 1.42	16.15 ± 3.58	28.15 ± 5.50	45.75 ± 7.45
NoSuppl				
Range	0–3	0–38	0–52	0–87
Mean	0.15 ± 0.15	3.70 ± 2.07	9.40 ± 3.96	16.30 ± 5.81

source on *H. variegata* reproductive capacity was analyzed using standard statistical models: 1) female fecundity as the total number of eggs laid along the whole experiment by Poisson log-linear model (i.e., generalized linear model for count data by using Poisson distribution and the log link; see Agresti 1996); and 2) preoviposition period as the time needed to begin oviposition from mating pairs by survival analysis by using the Weibull distribution (e.g., Kachman 1999). We used R version 2.3 statistical software (The R Development Core Team 2005) for all the statistical analyses.

Results

Effect on Oviposition Rate. The response variable is the total number of eggs laid by each of the 160 females during the 7-d experimental period. Table 1 shows the range and mean of the response outcome grouped by aphid levels and plant species. Table 2 shows the analysis of deviance table and the estimated coeffi-

Table 2. Analysis of deviance and the estimated coefficients for saturated model using Plant.Control and APHID.05 as baselines

	Residual			
	df	Deviance	df	Deviance
Null			159	5286.4
Plant	3	720.7	156	4565.6
Aphid	3	1326.6	153	3239.1
Plant × aphid	9	142.6	144	3096.4
Coefficients	Estimate	SE	z value	Pr(>z)
<i>Brassica</i>	2.793	0.595	4.696	<0.001
<i>Sonchus</i>	2.428	0.602	4.031	<0.001
APHID.10	1.609	0.633	2.545	0.011
APHID.20	3.106	0.590	5.263	<0.001
APHID.30	4.300	0.581	7.397	<0.001
<i>Brassica</i> :APHID.20	-1.418	0.610	-2.324	0.020
<i>Brassica</i> :APHID.30	-1.936	0.600	-3.225	0.001
<i>Sonchus</i> :APHID.30	-1.850	0.608	-3.041	0.002

Only coefficients significantly different from zero (P < 0.05) are shown.

Table 3. Distribution of the number of females in the first day of oviposition for all aphid \times plant treatments ($n = 10$)

	Plant	First day of oviposition							
		d.1	d.2	d.3	d.4	d.5	d.6	d.7	+0.7
APHID.05	Control	1	9
	<i>Brassica</i>	.	.	3	1	.	.	.	6
	<i>Daucus</i>	10
	<i>Sonchus</i>	.	.	.	1	1	1	.	7
APHID.10	Control	.	.	.	1	1	.	.	8
	<i>Brassica</i>	1	2	3	2	.	.	.	2
	<i>Daucus</i>	.	.	1	1	.	.	1	7
	<i>Sonchus</i>	.	.	3	1	1	2	.	3
APHID.20	Control	.	.	.	1	.	1	1	7
	<i>Brassica</i>	.	1	2	2	1	1	.	3
	<i>Daucus</i>	.	.	3	.	.	1	.	6
	<i>Sonchus</i>	.	2	4	.	1	.	.	3
APHID.30	Control	1	.	.	2	.	1	1	5
	<i>Brassica</i>	.	1	8	1
	<i>Daucus</i>	.	1	.	1	.	.	2	6
	<i>Sonchus</i>	.	2	1	4	.	.	.	3

Column +0.7 includes the females that did not begin oviposition during the first 7 d of trial.

cients for the saturated Poisson log-linear model. An important percentage of null deviance (58.6%) is explained by individual differences between the females, but the food sources also contribute to the total number of eggs laid by females, because together they explained 41.4% of total deviance of the model.

The Poisson log-linear analysis shows a significant interaction between normal and supplemental food sources. There are significant differences in the coefficients of APHID.20 \times *Brassica*, APHID.30 \times *Brassica*, and APHID.30 \times *Sonchus* interactions. The negative coefficients could indicate the lack of a log-linear response at high feeding levels when supplemental food is available. This slow down in the response indicates an upper limit in oviposition rate.

The increase in the amount of prey favors higher rates of oviposition. Therefore, the number of eggs laid under medium and high feeding levels (APHID.10 to APHID.30; mean = 19.91) is significantly higher than those laid under low feeding levels (APHID.05; mean = 2.15).

Daucus as supplemental feeding did not increase oviposition in comparison with control ($z = 0.054$, $P = 0.957$), whereas *Sonchus* and *Brassica* enhance oviposition, showing no significant difference between them. Because of this, two levels of plant were left for the next analysis: NoSuppl (=control and *Daucus*) and Suppl (= *Brassica* and *Sonchus*). The Poisson log-linear analysis of wild plant flower presence with two plant levels shows a positive effect on egg laying (deviance = 710.17, $df = 1$, $P < 0.001$), so that their supply multiplies 2.17–4.47 times ($\alpha = 0.05$, mean = 3.32) the total number of eggs laid per female, compared with the lack of supplemental feeding.

Effect on Preoviposition Time. The response variable is the number of females by first day of oviposition. Table 3 presents the distribution of preoviposition days for all aphid \times plant treatments. The generalized analysis shows that time needed to begin oviposition depends both on the kind of flower as

Table 4. Coefficients and standard error for the survival model by using Weibull distribution

Coefficient	Estimate	SE	z value	Pr(>z)
Intercept	3.151	0.253	12.445	<0.001
<i>Brassica</i>	-0.864	0.188	-4.602	<0.001
<i>Daucus</i>	-0.008	0.213	-0.039	0.969
<i>Sonchus</i>	-0.631	0.188	-3.352	<0.001
APHID.10	-0.679	0.216	-3.146	0.002
APHID.20	-0.663	0.215	-3.081	0.002
APHID.30	-0.892	0.214	-4.171	<0.001

supplemental feeding (deviance = 33.11, $df = 3$, $P < 0.001$), and the amount of aphids supplied as normal feeding (deviance = 25.10, $df = 3$, $P < 0.01$), with no interaction being detected (deviance = 5.98; $df = 9$; $P < 0.74$). Table 4 shows the estimated coefficients from the plant + aphid model, with no interaction (null deviance = 493.8, $df = 158$).

The medium and high levels of aphid abundance (APHID.10 to APHID.30) show significant differences, compared with low level (APHID.05). In spite of this, there is no significant difference between them. These results suggest that aphid scarcity delays the beginning of the oviposition, with the preoviposition period doubling (2.13 times) at lower feeding levels. However, above the APHID.10 level there is no significant reduction, even if aphids are very abundant. Then, APHID levels were regrouped into two levels: reduced (APHID.05) and normal (APHID.10 to APHID.30).

The response to *Daucus* flowers does not show any difference compared with the control, suggesting that the supply of this kind of plant does not reduce the response time. However, both *Sonchus* and *Brassica* show clear differences, compared with the control, increasing the probability of oviposition onset (Fig. 1).

From these results the data were further analyzed, considering two normal feeding levels (aphid: reduced and normal) and two levels of supplemental feeding (plant: Suppl and NoSuppl), to estimate an average value for the time needed by half the females to begin oviposition (Fig. 2). The results showed a median value of 19.56 d for the reduced + NoSuppl combination, whereas normal decreased this time (47.05%), similarly to Suppl (47.62%). Therefore, the joint action of both factors allowed 50% of the females to begin oviposition before 4.38 d, i.e., both sources of food reduce the median value in 77.6%.

Discussion

In *H. variegata*, egg production is highly related to the amount of available prey like in other coccinellid species (Wright and Laing 1980, Frazer et al. 1981, Ferran et al. 1984, Ghanim et al. 1984). This response slows down when high amounts of food are reached, indicating the level of maximum response (Dixon and Agarwala 2002).

In this experiment, egg production also responds significantly to supplemental feeding, producing an average increase of 1.44 times the number of eggs per

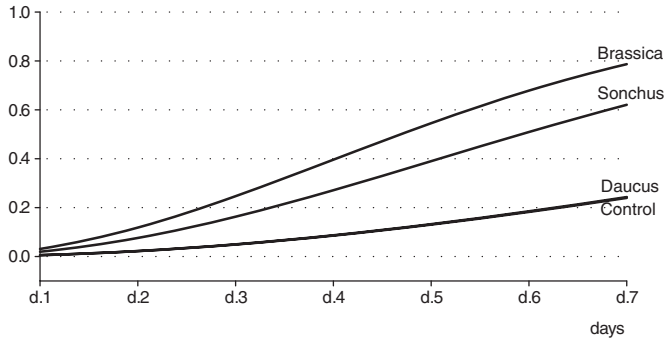


Fig. 1. Probability distribution at the beginning of the oviposition for each treatment with supplemental feeding (PLANT) and an average normal feeding (APHID) value. The curves of *Daucus* and Control are in the same position.

female, even at low prey densities. There was no significant difference ($\chi^2 = 44.9, P = 0.807$) between the treatment with many aphids and without supplemental food (APHID.30 + PLANT.NoSuppl), and the treatment with few aphids and with supplemental food (APHID.05 + PLANT.Suppl). This suggests that the plant flowers could serve as an alternative food at low densities of the aphid preys. In such conditions of prey shortage, the addition of nutrients supplied by wild plant flowers may allow ovogenesis in *H. variegata*.

These results support the previous findings that aphidophagous ladybirds can use food of plant origin (pollen, nectaries from flowers, extrafloral nectaries, and conidia and spores of fungi) as supplemental source of nutrition. The occurrence of such type of feeding was demonstrated recently by a very detailed study that combined observations with dissections in *Coccinella septempunctata* L. (Ricci et al. 2005). Some studies even refer to omnivory of some insect predators (Eubanks and Denno 2000, van Rijn et al. 2002, Eubanks and Styrsky 2005). However, food of plant origin cannot be considered a full substitute of aphids for most predatory coccinellid species, although it might be so, e.g., *Tytthaspis* spp. (Ricci 1986) and *Harmonia axyridis* (Pallas) are attracted to an apple (*Malus* spp.) orchard by extrafloral nectar before

aphids arrived (Mathews 2004), which could lead to the ability to respond quickly to aphids once they colonize the crops (Spellman et al. 2006).

The importance of aphids in diet of aphidophagous coccinellids is in accordance with other studies. Although, the rate in treatments with versus without aphid food does not show the same response at low and at high densities of aphids, even *Coleomegilla maculata* (DeGeer), the only species that can develop exclusively with pollen, laid significantly more eggs when females reared on aphids and pollen than only with pollen (Hodek et al. 1978, Lundgren and Wiedemann 2004). The addition of pollen consumption to adult females did not increase fecundity and fertility of *C. maculata*, compared with feeding on only eggs of *Ephestia* (Michaud and Grant 2005).

The analysis of the time response of the beginning of the oviposition shows the existence of additive effects of feeding on flowers. This reduces the preoviposition period. However, the lack of interaction between them, as well as the fact that a high number of aphids (above a minimum value) does not reduce the preoviposition period suggests that food sources complement each other in the female maturation processes. For that, given low prey capture rates the predators having the ability to supplement prey with alternative plant foods such as nectar could have sig-

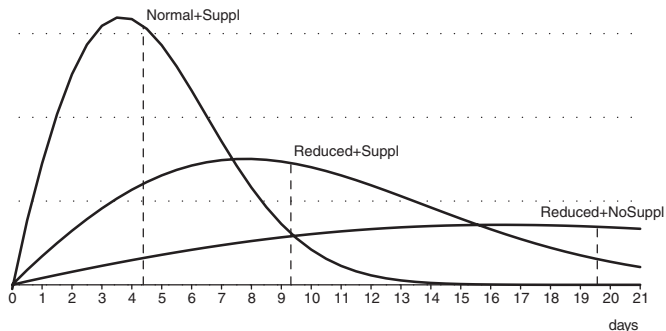


Fig. 2. Weibull probability density function for survival model with two plant levels (Suppl and NoSuppl) and two aphid levels (reduced and normal). Dashed lines show median values.

nificant consequences for an increase the fitness (Yong 2005).

Not all the flowers used in experiments showed a positive effect on reproductive parameters in *H. variegata*. *Brassica* and *Sonchus* flowers significantly increased oviposition rate and reduced the preoviposition period, whereas *Daucus* flowers had no effect. The small size or other unknown factors related to the *Daucus* flowers could explain the negative results.

These laboratory experiments might suggest that the presence of flowers of *Sonchus* and *Brassica*, e.g., as marginal vegetation in crop fields, could increase the egg production and shorten the preoviposition period in *H. variegata*. Thus, the presence of floral resource plants could not only cause local increases in predation on aphids but also could increase the production of coccinellids from one generation to the next (Harmon et al. 2000). Then, it may be possible to enhance populations of coccinellids in agricultural landscapes by manipulating the size and composition of the elements making up the landscape (Elliott et al. 2002). Studies of such general pattern are important because they help to test the generality of observations based on single-species studies and improve our understanding of the importance of plant diversity in the maintenance of invertebrate populations.

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