

Influence of Alternate Prey on Predation of Monarch Butterfly (Lepidoptera: Nymphalidae) Larvae by the Multicolored Asian Lady Beetle (Coleoptera: Coccinellidae)

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ABSTRACT An invasive, exotic coccinellid, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), was recently identified as a potential hazard to immature monarch butterflies, *Danaus plexippus* L. (Lepidoptera: Nymphalidae). To further evaluate the risk of *H. axyridis* impacting *D. plexippus*, we evaluated the influence of an alternate prey, *Aphis nerii* Boyer de Fonscolombe (Homoptera: Aphididae), on the predation rate of *H. axyridis* on *D. plexippus* larvae. When first-instar *D. plexippus* were placed in petri dish arenas with third-instar *H. axyridis* and varying densities of *A. nerii*, *D. plexippus* survival after 24 h increased significantly from 0% with 0 *A. nerii* present to 73% with 30 *A. nerii* present. In predation studies conducted in field cages, survival of *D. plexippus* larvae decreased with increasing densities of *H. axyridis* larvae and tended to increase with increasing *A. nerii* densities. These studies indicate that *H. axyridis* will feed on *D. plexippus* larvae in the presence of *A. nerii*, but that the presence of *A. nerii* lessens the severity of predation on *D. plexippus*.

KEY WORDS *Harmonia axyridis*, *Danaus plexippus*, *Aphis nerii*, nontarget effects, risk assessment

THE SUMMER RANGE OF the monarch butterfly, *Danaus plexippus* L., extends northward into the Midwestern United States and southern Canada (Brower and Malcom 1991), where the primary host for larvae is common milkweed, *Asclepias syriaca* L. (Wassenaar and Hobson 1998), which is ubiquitous in agricultural systems (Hartzler and Buhler 2000). In agricultural habitats, *D. plexippus* must contend with a suite of hazards that may ultimately reduce the size of the spring and summer generations. Examples of such potential hazards include insecticide use (Stanley-Horn et al. 2001) and pollen from transgenic corn expressing toxins originally derived from the soil bacterium, *Bacillus thuringiensis* (Berliner) (e.g., Losey et al. 1999, Hansen Jesse and Obrycki 2000, Sears et al. 2001, Zangerl et al. 2001, Koch et al. 2003a). However, recent risk assessments indicated that, under field conditions, there is a low risk of *D. plexippus* being negatively impacted by commonly grown varieties of insecticidal transgenic corn (Sears et al. 2001, Wolt et al. 2003).

While monitoring the survival of *D. plexippus* on *A. syriaca* near *Bt* corn, Zangerl et al. (2001) noted that predators, particularly coccinellids, may have substantial impacts on the survival of early instars. Koch et al. (2003b) documented that larvae and adults of an exotic coccinellid, *Harmonia axyridis* (Pallas), will prey on immature *D. plexippus* in the absence of alternate prey (e.g., aphids). *H. axyridis* was first documented in North America in 1988 (Chapin and Brou 1991). After

its rapid range expansion and rise to dominance in many systems, nontarget impacts of *H. axyridis* have been noticed throughout much of the continental United States and southern Canada (reviewed by Koch 2003).

Under typical field conditions, eggs and larvae of *D. plexippus* are rarely the sole prey available on *A. syriaca*. *A. syriaca* is host to at least seven aphid species, including the oleander aphid, *Aphis nerii* Boyer de Fonscolombe, which may act as alternate prey for generalist predators (e.g., Leonard 1971, 1973, 1975). The presence of alternate prey has been shown to increase, decrease, or have no effect on target predation (Holt 1977, Abrams and Matsuda 1996, Harmon 2003). Placed within the context of an ecological risk assessment for an exotic predator, the presence of alternate prey may affect the likelihood of a nontarget organism being preyed on. The objectives of these studies were to further quantify the predation of *D. plexippus* by *H. axyridis* and to evaluate the influence of an alternate prey species, *A. nerii*, on this predation rate. The results of this study will contribute to an ecological risk assessment of the effects of *H. axyridis* on *D. plexippus*.

Materials and Methods

Insects. *Harmonia axyridis* and *D. plexippus* used in these studies were obtained and maintained as in Koch et al. (2003b). *A. nerii* were initially obtained from a

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greenhouse colony maintained on *Hoya* sp. by the Minnesota Department of Agriculture, St. Paul, MN.

Laboratory Study. A completely randomized design with four *A. nerii* density treatments and 10 replications per treatment was used for this experiment. The experimental arenas were 10 by 1.5-cm petri dishes lined with moistened filter paper. Three first-instar *D. plexippus* were transferred, using a small soft-tipped brush, from *A. syriaca* to the arenas. Before being transferred, all *D. plexippus* larvae were allowed to feed on potted *A. syriaca* (pot volume: 3.8 liters) for 6–18 h after egg hatch. Again, using a small soft-tipped brush, 0, 3, 9, or 30 late-instar nymphs and apterous adults of *A. nerii* were transferred from *A. syriaca* to the arenas. *A. syriaca* infested with *A. nerii* came from the source cages used in the cage studies described below. A single third-instar *H. axyridis*, starved for 24 h, was placed into each arena. The arenas were held at 25°C with a photoperiod of 16:8 (L:D) h. After 6, 12, and 24 h, the number of *D. plexippus* and *A. nerii* remaining were recorded. Nymphs produced by *A. nerii* during the course of the study were removed at each inspection time. *H. axyridis* were monitored for molting for 24 h after completion of the experiment to ensure that a premolt period had not altered our results.

Counts of *D. plexippus* remaining at each sample time were $\log x + 1$ transformed to stabilize variances. The transformed *D. plexippus* counts were analyzed using repeated measures analysis of variance (ANOVA) with a first order autoregressive covariance structure (PROC MIXED; SAS Institute 2000). The ANOVA model included main effects for time and *A. nerii* density (0, 3, 9, and 30 *A. nerii* per dish) and the interaction of time and *A. nerii* density. Differences in *D. plexippus* survival among levels of *A. nerii* density were tested for using Bonferroni-adjusted contrasts of the least squares means for each pairwise combination of levels of the main effect.

To assess whether *H. axyridis* larvae showed any preference for *D. plexippus* or *A. nerii*, the proportion of *D. plexippus* in the overall mass of prey consumed between observation periods was regressed against the proportion of *D. plexippus* in the overall mass of initial prey at the beginning of each observation period. To determine the mass of individual *A. nerii*, four groups of five aphids were weighed, resulting in an average mass of 0.41 mg/aphid. The mass of first-instar *D. plexippus* was assumed to be 0.9 mg/larva based on measurements of \approx 24-h-old larvae by Stanley-Horn et al. (2001). A linear regression was fit to the data (PROC REG; SAS Institute 2000) and compared with a hypothesized model of random predation (i.e., no preference shown among prey) that would have an intercept of 0 and a slope of 1. A one-sample *t*-test was used to compare the intercepts and slopes of the predicted and fitted lines.

Field Study. Three trials of a caged field predation experiment were conducted at the Rosemount Research and Outreach Center, University of Minnesota, Rosemount, MN, in 2002 and 2003. *A. syriaca* seeds from Prairie Moon Nursery (Winona, MN) were

planted into 3.8-liter pots in a greenhouse at 28°C with a photoperiod of 16:8 (L:D) h. When the plants reached a height of 10–20 cm, they were moved outside and placed into one of two source cages (1.82 by 1.82 by 2.74 m, 32 by 32 cm Lumite screen; BioQuip, Gardena, CA). In one source cage, all plants were infested with *A. nerii* by placing *A. nerii*-infested *Hoya* sp. florets onto the uppermost leaves of the potted plants. As the *Hoya* sp. florets desiccated, *A. nerii* moved to the *A. syriaca*. These aphids were the source for the laboratory study described above as well as for the experiment described below. Plants in the other source cage remained aphid free. In a fallow field, cages (as previously described) were established with four potted *A. syriaca* in each cage. In each cage, two plants were from the source cage with *A. nerii*, and the other two plants were from the source cage without *A. nerii*. These plants were designated as having high and low aphid densities, respectively. A small soft-tipped brush was used to place four 12- to 24-h-old first-instar *D. plexippus* onto the second pair of open leaves from the top of each plant. Four larvae per plant represented a high-end density estimate for *D. plexippus* on *A. syriaca* in agricultural systems (R.L.K., unpublished data). Each cage was randomly assigned to receive 0, 1, or 4 third-instar *H. axyridis* per plant (0, 4, or 16 *H. axyridis* per cage). These densities of *H. axyridis* were used previously by Koch et al. (2003b) and cover the range of observed densities on *A. syriaca* in agricultural systems (R.L.K., unpublished data). Using a small soft-tipped brush, *H. axyridis*, previously starved for 24 h, were placed onto the fourth pair of leaves from the top of the plants. Three trials of this experiment were conducted beginning 29 June and 12 August 2002 and 12 July 2003 (trials 1, 2, and 3, respectively). Trial 1 had four replications, and trials 2 and 3 had three replications each. At initiation of the trials, plants exhibited normal latex production (e.g., Zalucki et al. 2002) and were 15–25 cm tall. Before the pots were placed into the cages, each plant and pot was thoroughly inspected, and all unwanted arthropods were removed. For trials 1 and 2, plants were inspected after 1, 3, and 7 d. For trial 3, plants were inspected after 1, 2, 3, 4, 5, 6, and 9 d. On each inspection date, the numbers of *D. plexippus*, *A. nerii*, and *H. axyridis* remaining on the plants were recorded. On each inspection date, *A. nerii* found on plants that were supposed to be at the low aphid density were removed.

Counts of *D. plexippus* larvae remaining on each sample date were $\log x + 1$ transformed to stabilize variances. The transformed *D. plexippus* counts were analyzed separately for each trial using repeated measures ANOVA with a first order autoregressive covariance structure (PROC MIXED; SAS Institute 2000). The ANOVA model included main effects for days since predator release, *H. axyridis* density (0, 1, or 4 larvae per plant), *A. nerii* density (low versus high), and two- and three-way interactions of the main effects. If the main effects for *H. axyridis* or *A. nerii* density were significant ($P > 0.05$), differences among levels were tested using Bonferroni-adjusted contrasts

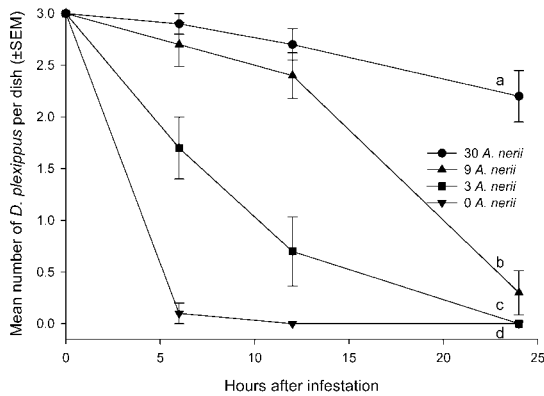


Fig. 1. Effect of *A. nerii* densities on the survival of *D. plexippus* larvae in laboratory studies with *H. axyridis* as predator. Lines with different letters preceding the final point differ significantly ($P < 0.05$), repeated measures ANOVA and Bonferroni-adjusted contrasts.

of the least squares means for each pairwise combination of levels within each main effect.

Modeling. Multiple linear regression was used to further evaluate the effects of *H. axyridis* and *A. nerii* densities on *D. plexippus* survival in the field cage studies (PROC REG; SAS Institute 2000). Survival of *D. plexippus* over the first day of the experiment was chosen to reflect the worst-case scenario in a risk assessment (i.e., the highest densities of recently starved predators) and to minimize the potential confounding effect of *D. plexippus* larval movement away from apparently suitable host plants (Koch et al. 2003a). For each trial, the 1-d survival of *D. plexippus* on plants with high and low aphid densities from each cage were standardized as the proportion of *D. plexippus* surviving relative to the survival in cages with zero *H. axyridis* per plant. Independent variables for the multiple regression model were *H. axyridis* density, *A. nerii* density, and the interaction between these two densities. *H. axyridis* densities were scored as the median density of *H. axyridis* on the plants between days 0 and 1. *A. nerii* density was included in the model as a categorical predictor (i.e., 0 = low aphid density, and 1 = high aphid density).

Results

Laboratory Study. In petri dish arenas, survival of *D. plexippus* larvae increased with increasing density of *A. nerii* (Fig. 1). Survival of *D. plexippus* over time differed significantly among all levels of *A. nerii* density (Fig. 1; Table 1). By 24 h, the mean (\pm SEM) number of *D. plexippus* larvae remaining per dish decreased to 0, 0, 0.3 ± 0.21 , and 2.2 ± 0.25 for dishes with 0, 3, 9, and 30 *A. nerii*, respectively (Fig. 1).

The regressions of the proportion of *D. plexippus* in the mass of prey consumed versus the proportion of *D. plexippus* in the mass of initial prey resulted in lines with slopes that did not differ significantly from one for all observation periods (6 h: $t = 0.076$, $df = 28$, $P =$

Table 1. Repeated measures ANOVA table for survival of *D. plexippus* larvae in laboratory and field predation studies with *H. axyridis* and *A. nerii*

Source	df	F	P
Laboratory			
Time	3,144	142.83	<0.0001
<i>A. nerii</i>	3,144	120.91	<0.0001
Time \times <i>A. nerii</i>	9,144	24.06	<0.0001
Field: trial 1			
Time	3,168	19.53	<0.0001
<i>H. axyridis</i>	2,168	13.56	<0.0001
<i>A. nerii</i>	1,168	0.61	0.4375
Time \times <i>H. axyridis</i>	6,168	2.76	0.0140
Time \times <i>A. nerii</i>	3,168	0.71	0.5462
<i>H. axyridis</i> \times <i>A. nerii</i>	2,168	1.72	0.1823
Time \times <i>H. axyridis</i> \times <i>A. nerii</i>	6,168	0.75	0.6106
Field: trial 2			
Time	3,120	19.54	<0.0001
<i>H. axyridis</i>	2,120	24.56	<0.0001
<i>A. nerii</i>	1,120	7.11	0.0087
Time \times <i>H. axyridis</i>	6,120	3.10	0.0074
Time \times <i>A. nerii</i>	3,120	0.96	0.4141
<i>H. axyridis</i> \times <i>A. nerii</i>	2,120	0.07	0.9286
Time \times <i>H. axyridis</i> \times <i>A. nerii</i>	6,120	0.72	0.6353
Field: trial 3			
Time	7,240	52.57	<0.0001
<i>H. axyridis</i>	2,240	25.32	<0.0001
<i>A. nerii</i>	1,240	62.24	<0.0001
Time \times <i>H. axyridis</i>	14,240	1.29	0.2140
Time \times <i>A. nerii</i>	7,240	1.65	0.1232
<i>H. axyridis</i> \times <i>A. nerii</i>	2,240	3.62	0.0282
Time \times <i>H. axyridis</i> \times <i>A. nerii</i>	14,240	0.89	0.5719

The laboratory study was conducted with one *H. axyridis* per dish and four levels of *A. nerii* density (0, 3, 9, or 30 *A. nerii* per dish). The field study was conducted with three levels of *H. axyridis* density (0, 1, or 4 *H. axyridis* per plant) and two levels of *A. nerii* density (low vs high).

0.94; 12 h: $t = -1.12$, $df = 25$, $P = 0.27$; 24 h: $t = 1.45$, $df = 18$, $P = 0.16$; Fig. 2). The intercept of the fitted line for the observation at 6 h (-0.23 ± 0.096) was significantly less than zero ($t = -2.38$, $df = 28$, $P = 0.024$; Fig. 2). However, the intercepts did not differ significantly from zero for the observations at 12 ($t = -0.48$, $df = 25$, $P = 0.64$) and 24 h ($t = -1.89$, $df = 18$, $P = 0.074$; Fig. 2).

Field Study. Soon after initiation of the field experiments, we observed *H. axyridis* larvae capturing and consuming *D. plexippus* larvae and *A. nerii* on the potted *A. syriaca*. In all trials, *D. plexippus* survival decreased significantly with increasing densities of *H. axyridis* (Fig. 3; Table 1). In trials 1 and 2, survival of *D. plexippus* across time did not differ significantly between cages with zero and one *H. axyridis* per plant (Fig. 3A and C; Table 1). However, survival of *D. plexippus* did differ significantly between cages with zero and four *H. axyridis* per plant and one and four *H. axyridis* per plant (Fig. 3A and C; Table 1). In trial 3, survival of *D. plexippus* across time differed significantly among all densities of *H. axyridis* (Fig. 3E; Table 1).

A trend existed for greater *D. plexippus* survival on plants with high compared with low densities of *A. nerii* in all trials (Fig. 3; Table 1). The trend for greater survival on plants with more *A. nerii* was significant in

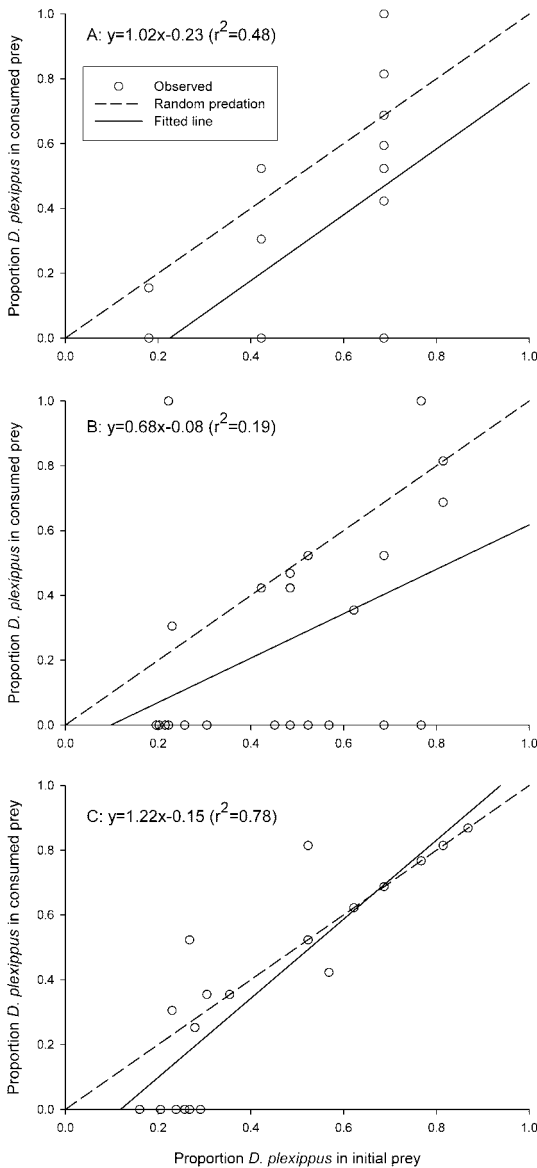


Fig. 2. Linear regression of the proportion of *D. plexippus* in the mass of prey consumed during observation periods ending at 6 (A), 12 (B), and 24 h (C) after initiation of the experiment against the proportion of *D. plexippus* in the mass of initial prey at the onset of each observation period. The hypothesized model for random predation has an intercept of 0 and a slope of 1.

trials 2 and 3 (Fig. 3D and F; Table 1). However, in trial 1, the effect of *A. nerii* density was not significant (Fig. 3B; Table 1).

Throughout the duration of each trial, *A. nerii* densities per plant ranged from 0 to 7.59 ± 1.20 and 75.86 ± 1.20 to $1,348.96 \pm 11.75$ on low and high aphid density plants, respectively. In all trials, densities of *H. axyridis* in cages decreased through time. In trial 1, the density of *H. axyridis* larvae per plant decreased to 0.06 ± 0.06

and 0 in cages with initial predator densities of four and one *H. axyridis* larvae per plant, respectively, by day 7. In trial 2, the mean density of *H. axyridis* larvae per plant decreased to 1.17 ± 0.47 and 0.17 ± 0.11 in cages with initial predator densities of four and one *H. axyridis* larvae per plant, respectively, by day 7. In trial 3, the density of *H. axyridis* larvae per plant decreased to 0 in all cages by day 9.

Modeling. The 1-d survival of *D. plexippus* larvae decreased linearly with increasing *H. axyridis* density, with a greater rate of decrease on plants with low compared with high *A. nerii* densities (Fig. 4). Because the effect of *A. nerii* density was not statistically significant ($P = 0.86$), this predictor was removed from the multiple linear regression model. The form of the final model was $D. plexippus$ survival = $0.97 [\pm 0.025] + (H. axyridis \times -0.20 [\pm 0.016]) + (H. axyridis \times A. nerii \times 0.11 [\pm 0.017])$, $r^2 = 0.91$ (Fig. 4). The intercept did not differ significantly from 1 ($t = -1.07$, $df = 15$, $P = 0.30$). A sensitivity analysis was conducted for the model parameters by fixing *H. axyridis* density at 1 and *A. nerii* density at the high density category. Adjustment of the intercept parameter to the limits of its 95% confidence interval (i.e., 0.93, 1.02) resulted in absolute changes in *D. plexippus* survival of 4.9%. Increasing or decreasing the parameter estimate for *H. axyridis* density to the limits of its 95% confidence interval (i.e., -0.22 , -0.17) resulted in absolute changes in *D. plexippus* survival of 2.8%. Adjustment of the parameter estimate for the interaction of *H. axyridis* and *A. nerii* densities to the limits of its 95% confidence interval (i.e., 0.08, 0.14) resulted in absolute changes in *D. plexippus* survival of 3.3 and 3.5%, respectively.

Discussion

Koch et al. (2003b) identified *H. axyridis* as a potential hazard to immature *D. plexippus*. However, the authors cautioned that additional work was needed to further quantify the likelihood of *H. axyridis* preying on *D. plexippus*, particularly in the presence of alternate prey. In this study, *H. axyridis* preyed on *D. plexippus* larvae in the presence of an alternate prey, *A. nerii*. However, the severity of predation on *D. plexippus* decreased with increasing densities of *A. nerii*, suggesting a case of “apparent mutualism” (e.g., Abrams and Matsuda 1996). The presence of aphids as alternate prey has decreased predation on focal prey in other systems as well (Hazzard and Ferro 1991). Apparent mutualism is a reduction in the per capita predation of a prey species when an alternate prey species is present (Holt 1977). With the relatively short time periods over which our experiments were conducted, the observed apparent mutualism may have been caused by *H. axyridis* exhibiting switching or a strongly saturating functional response (Abrams and Matsuda 1996).

The functional response of *H. axyridis* has been examined for various prey species (reviewed in Koch 2003), and in most cases, a saturating functional response was found. For example, *H. axyridis* exhibited a type II functional response when feeding on *Aphis*

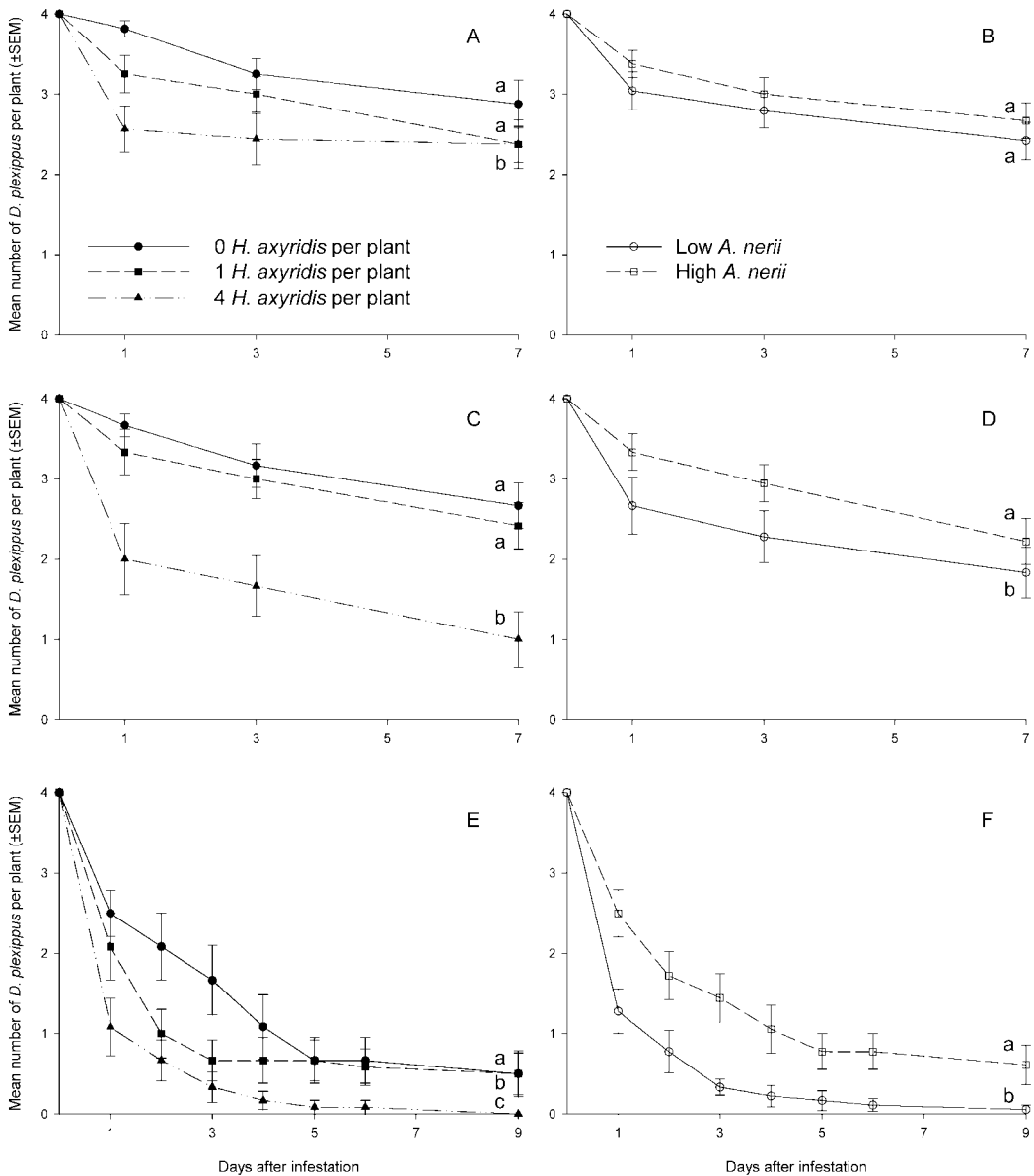


Fig. 3. Effect of *H. axyridis* and *A. nerii* densities on the survival of *D. plexippus* larvae in caged predation studies. A and B, C and D, and E and F are from trials 1, 2, and 3, respectively. A, C, and E show the effect of *H. axyridis* density. B, D, and F show the effect of *A. nerii* density. Lines with different letters preceding the final point differ significantly ($P < 0.05$), repeated measures ANOVA and Bonferroni-adjusted contrasts.

gossypii Glover (Lee and Kang 2004) and immature *D. plexippus* (Koch et al. 2003b). This tendency for a saturating functional response for *H. axyridis* may be the most likely mechanism driving our observed apparent mutualism, but an important question remains of whether or not the saturation point was reached under the experimental conditions.

For some predator-prey systems, the apparent mutualism could result from predator switching in response to prey density (e.g., Murdoch 1969, Murdoch and Oaten 1975). However, we are unaware of a

switching response being documented for *H. axyridis* predation. The regression analysis conducted on the laboratory data suggested that *H. axyridis* was consuming fewer *D. plexippus* larvae than would be expected by random predation (i.e., intercept < 0) from 0 to 6 h after initiation of the experiment. Our study was not designed to examine the mechanism behind this phenomenon, but several potential explanations exist. For example, *H. axyridis* may have an innate preference for aphids, or larvae of *D. plexippus* may be more successful than *A. nerii* at fending off or escaping

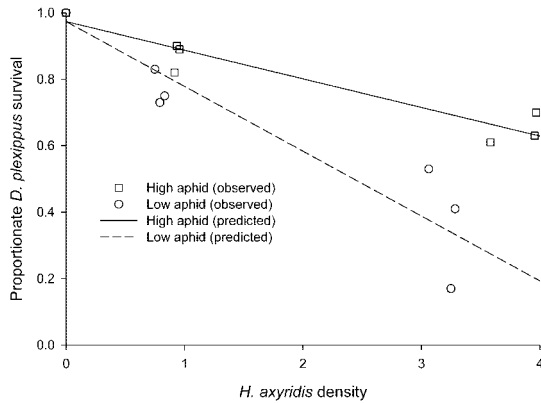


Fig. 4. Multiple linear regression for the proportionate survival of *D. plexippus*, relative to survival at the zero predator density, over the first 24 h in the cage study. Predictors for the model are median predator density between initiation of the experiment and 24 h, and aphid density at 24 h as a categorical predictor (0 = low aphid density; 1 = high aphid density). The resulting model was: $D. plexippus$ survival = $0.97 + (H. axyridis \times -0.20) + (H. axyridis \times A. nerii \times 0.11)$, $r^2 = 0.91$.

from predators. Because the observed and hypothesized lines relating the proportion of *D. plexippus* in the prey consumed to the proportion of *D. plexippus* in the initial prey were parallel at all observation periods, it seems that switching as a function of prey densities did not occur in this experiment.

Because *D. plexippus* densities were not varied in our study, we cannot rule out the possibility that the per capita predation of *D. plexippus* could be reduced by simply increasing densities of *D. plexippus*. However, the starting density of four *D. plexippus* per plant in our study was a reasonable high-end estimate of natural *D. plexippus* densities (R.L.K., unpublished data). We felt that increasing densities of *D. plexippus* to greater than four larvae per plant would have jeopardized the reality of our study. In an examination of the influence of alternate prey on the predation of green peach aphid, *Myzus persicae* Sulzer, by hemipteran predators, Koss et al. (2004) also varied the density of the alternate prey while keeping densities of the target prey constant.

In the context of an ecological risk assessment (EPA 1998), the risk of *H. axyridis* impacting *D. plexippus* is defined as the joint probability of *D. plexippus* co-occurring temporally and spatially with *H. axyridis* (i.e., exposure) and *H. axyridis* preying on *D. plexippus* if they co-occur (i.e., effect). Koch et al. (2004) qualitatively rated the risk of an effect occurring as moderate to high. The predation model developed in this paper could be used to quantitatively estimate the probability of *D. plexippus* mortality under varying conditions of *H. axyridis* and aphid densities for the effect end of the risk equation. The model showed that *D. plexippus* survival decreased linearly with increasing *H. axyridis* density and that increased *A. nerii* densities decreased the rate at which *D. plexippus*

mortality occurred. Despite year-to-year variability under field conditions, the impact of *H. axyridis* and *A. nerii* populations on *D. plexippus* survival was remarkably similar, as evidenced by the relatively high r^2 value (i.e., $r^2 = 0.91$) obtained from the fit of the model. To accommodate other predatory developmental stages of *H. axyridis*, predation parameters could be adjusted to account for the relative differences in predation rates among developmental stages. Otherwise, a suite of parameters could be empirically derived through further study of different developmental stages of *H. axyridis* preying on *D. plexippus*. An argument could be made that the data going into the model does not incorporate effects or interactions of other natural enemies of *D. plexippus*. We contend that the predominance of *H. axyridis* among the predators of *D. plexippus* occurring on *A. syriaca* in agricultural systems (R.L.K., unpublished data) justifies our use of this approach to develop an initial risk assessment of the predation of *H. axyridis* on *D. plexippus*. However, examination of the relative impact and interaction of other natural enemies in this system would help to further refine this model.

Acknowledgments

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