The relationship between predator density, community composition, and field predation of Colorado potato beetle eggs

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Abstract

Conservation biological control programs seek to increase natural enemy densities through the adoption of more benign farming practices, under the assumption that higher predator densities will lead to more effective pest suppression. However, predator–predator interference may lead to diminishing returns in improved pest control as predator densities increase. We examined the relationship between predator density and predation rates on Colorado potato beetle eggs in production potato fields. These potato fields naturally spanned a 10-fold range in predator density, due to differences in management practices. Periodically through the growing season we simultaneously measured predator densities and subjected sentinel eggs masses to predation, allowing us to correlate predator density and egg predation for each field on each sample date. Egg predation rates were significantly positively correlated with total predator densities, a correlation that was not improved when predator densities were scaled to reflect differences in feeding rates on potato beetle eggs of the constituent predator taxa. There was no correlation between per-capita egg predation rates and predator density, and so no evidence that predator interference increased with increasing predator density. We divided predators into six dominant taxa—dwarf spiders, crab spiders, minute pirate bugs, big-eyed bugs, damsel bugs, and Lygus bugs (together constituting 93% of all predators collected), and a seventh group, “other predators” that included all other, less common, taxa—and examined correlations between all predator combinations and egg predation rates. The highest correlation was between combined densities of the six most common predator taxa, excluding only the “other predators” grouping. This suggests that predators may be largely equivalent in their impact on Colorado potato beetle eggs, and that field scouts might be able to ignore uncommon predator taxa when sampling for natural enemies.

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1. Introduction

Generalist predators of insects are often expected to be important for controlling pests in agricultural systems (Altieri, 1995). The intuitive prediction is that increasing the density of generalist predators in a crop should subsequently increase predation on pests (Chang and Kareiva, 1999; Walsh and Riley, 1868). On the other hand, increases in the abundance of certain predators can actually decrease predation on a target pest due to negative predator–predator interactions such as intraguild predation (Rosenheim et al., 1993). Despite the possibility of intraguild predation, generalist predators contribute to the biological control of pests in crops such as rice (Settle et al., 1996), soybeans (Carter and Rypstra, 1995), grains (Lang, 2003), alfalfa (Snyder and Ives, 2003), and vegetable gardens (Snyder and Wise, 2001).

The Colorado potato beetle (“CPB,” Leptinotarsa decemlineata Say) damages potato (Solanum tuberosum L.) crops by defoliating plants (Walsh, 1866), substantially reducing potato yields if beetle populations are not kept in check (Hare, 1980). Historically, biological control has played a limited role in CPB management...
Scientists have identified many species of natural enemies of the CPB (Casagrande, 1987; Hare, 1990). Scientists have identified many species of natural enemies of the CPB (Casagrande, 1987; Hough-Goldstein et al., 1993; Shimer, 1869), but by themselves indigenous natural enemies are generally not capable of suppressing potato beetles below damaging densities (Hare, 1990; Hilbeck et al., 1997; Tamaki, 1981). However, the ability of the CPB to evolve resistance to numerous insecticides (Miyo et al., 1999; Noro, 2001) is one reason why research on alternative control methods is a continuing priority. Combining biological control with other compatible control methods may be a useful tactic (Hare, 1990; Hilbeck et al., 1998).

In Washington State potato crops, CPB have historically been controlled using applications of broad-spectrum insecticides (Ruffie and Miller, 2002). However, in response to changing federal regulations (Epstein et al., 2000) and a growing appreciation of the value of natural enemy conservation (Koss, 2003), local potato growers have begun to adopt the use of selective insecticides (Koss, 2003). For example, some potato farmers have been applying a variety of relatively new pest control compounds such as pymetrozine and spinosad (Koss, 2003) that are less toxic to beneficial organisms than are many broad-spectrum insecticides (Sechser et al., 2005; Williams et al., 2006). In addition, organic potato production is growing in the state (Koss, 2003). The CPB eggs used in our laboratory and field predation assays were the progeny of female beetles collected from production potato fields in the vicinity of Othello, WA, USA, during the summer of 2003. Adult beetles were reared in a greenhouse at 22°C and 16:8 L:D, and fed live potato foliage. Eggs were harvested daily and placed in a refrigerator (4°C) to retard egg development. Clutch size was standardized (at 20 eggs for laboratory feeding trials, or at 10–20 eggs for field predation measures, see below) by carefully cutting away excess eggs using dissecting scissors.

2. Materials and methods

The community of natural enemies in Washington potato fields is numerically dominated by a diverse group of generalist predators (Koss and Snyder, in review; Tamaki and Weeks, 1972). In potato foliage, the most abundant predators are predatory bugs (Hemiptera) in the genera Nabis, Geocoris, and Orius, spiders (Araneae) in the families Linyphiidae and Thomisidae, and coccinellid beetles (Coleoptera: Coccinellidae) (Koss, 2003; Tamaki and Weeks, 1972). While not typically considered predators, Lygus spp. (Hemiptera: Lygaeidae) bugs are abundant in local potato fields and will opportunistically feed on soft-bodied potato herbivores (Koss, 2003). Other predators more rarely collected in the foliage include members of several beetle families (Coleoptera: Anthicidae, Carabidae), lacewings (Neuroptera: Chrysopidae, Hemerobiidae), mantids (Mantodea: Mantidae), predaceous flies (Diptera: Syrphidae, Dolichopodidae), and less-common predaceous bugs (Hemiptera: Reduviidae) (Koss, 2003).

2.1. Predator feeding rates in the laboratory

To compare the appetites of different predators, we measured the number of CPB eggs consumed by predators in simple laboratory microcosms consisting of 9-cm diameter Petri dishes provisioned with a moistened cotton wick. In each bioassay, we placed an individual predator in a Petri dish with 20 CPB eggs attached to a small (ca. 1 cm²) piece of potato leaf. We checked each dish for the number of intact CPB eggs every 24 h until the final check at 72 h. Our trials also included Petri dishes containing 20 CPB eggs but no predator, which served as controls. We conducted the feeding bioassays in an environmental control chamber (“Intellus,” Percival Scientific, Perry, Iowa) at 22°C and 16:8 L:D. We tested field-collected individuals of the most abundant predator taxa as revealed in our field sampling; predators were held at 22°C and 16:8 L:D in the laboratory for 16 h (overnight) before being used in the laboratory assays, provided with water but not food.

2.2. Field measurements of predator densities and egg predation rates

We conducted our fieldwork in seven potato fields on commercial farms managed by cooperating growers. Fields were between 24 and 48 ha, irrigated, located in...
the Columbia Basin in the vicinity of the city of Othello, WA, and were either managed conventionally or certified organic (Table 1). Fields 1–6 were managed by one grower, while field 7 was managed by a second grower.

Vacuum samples were collected using a D-Vac suction sampler (Model B&S, D-Vac, Ventura, CA). On each sampling date, we took D-vac samples from groups of 10 plants in five different locations within each field (total N = 50 plants sampled per field per sample date). The D-vac collecting tube was held over each plant, and vigorously shaken, for 15 s. We sampled all seven fields between June 17–25 (grouped together into sampling period 1) and July 9–14 (grouped into sampling period 2). On August 1 (sampling period 3), our sampling was limited to only five fields, because we were unable to access fields 3 and 5 on that date. D-vac samples were placed in a cooler (5°C) and returned to the laboratory, where they were held in a freezer (−20°C) until sorting. All predatory insects and spiders were sorted and counted from these samples.

We used a sentinel egg method (e.g., Hilbeck and Kennedy, 1996) to measure the predation rate in each potato field. On each sample date, we attached 10 groups of 10–20 CPB eggs each, with egg clutches on a ca. 1-cm² piece of potato foliage where they had been deposited by the female beetle, to potato leaves using a small drop of Elmer’s glue (Borden, Columbus Ohio, USA). The glue was entirely covered by the potato foliage and does not alter predator behavior (Koss et al., 2004). Concurrently we also stapled five groups of 10–20 CPB eggs that were enclosed within a cloth sleeve (52 × 52 mesh lumite screening; Bioquip, Gardena, CA, USA) so that predators could not reach them; these eggs served as controls for mortality not due to predation. We left the eggs for 2 days, then recovered them and recorded the number of eggs that were still viable by returning eggs to the laboratory and allowing them to complete development to hatching in a growth chamber (22°C and 16:8 L:D). We did this because feeding by some predators, for example those with piercing-sucking mouthparts, does not always leave obvious signs that predation has occurred (Koss, 2003). For each field we then calculated the predation rate by subtracting the average proportion of viable sentinel eggs from the proportion of viable control eggs, in that field on that sample date.

2.3. Observations of predation events in the field

We opportunistically recorded predation events that we saw while setting and recollecting the CPB eggs used to measure predation rates. We also inspected naturally occurring CPB egg masses on four dates in August to determine what, if any, predators were consuming them. On August 7, 63 CPB egg masses were monitored. Each was inspected for associated predators three times (once every 2 h) from 18:00 to 01:00 h. On August 12 between 13:00 and 15:00 h, 29 egg masses were located and examined once for predators. On August 14, 17 egg masses were located and checked for predators once beginning at 11:00 h, and a second time beginning at 13:00 h. On August 15, 14 egg masses were inspected for predators three times (every 2 h) beginning at 08:00 h.

2.4. Statistics

All analyses were conducted using SYSTAT statistical software (SPSS, Chicago, Illinois, USA). For the laboratory predation rate measurements, we compared CPB egg consumption rates among the different predator species using ANOVA followed by Tukey's HSD post hoc test. The field estimates of predation rate were correlated to the total abundance of predators in the corresponding vacuum sample, in that field and on that date. To attempt to identify predator taxa that correlated particularly strongly with CPB predation, we performed correlations between field estimates of predation rate and subsets of the predator assemblage. With these correlations, we sought only to determine whether predators could be found that would indicate high predation on CPB and thus be useful to field scouts, and not necessarily which predators were causing the most CPB mortality. All possible combinations of the seven

<table>
<thead>
<tr>
<th>Field, location</th>
<th>Management</th>
<th>Preparation</th>
<th>Insecticides used before and during our sampling period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, central Adams Co.</td>
<td>Conventional</td>
<td>Fumigated</td>
<td>Pymetrozine and indoxacarb (June 9), pymetrozine (July 28)</td>
</tr>
<tr>
<td>2, southern Adams Co.</td>
<td>Conventional</td>
<td>Fumigated</td>
<td>Carbaryl (July 14)</td>
</tr>
<tr>
<td>3, central Adams Co.</td>
<td>Conventional</td>
<td>Cover cropped</td>
<td>Methamidophos and esfenvalerate (June 9)</td>
</tr>
<tr>
<td>4, southern Adams Co.</td>
<td>Conventional</td>
<td>Cover cropped</td>
<td>Carbazil (July 14)</td>
</tr>
<tr>
<td>5, southern Adams Co.</td>
<td>Organic</td>
<td>Cover cropped</td>
<td>Garlic extract (July 3, July 16), cottonseed oil, clove oil, and garlic extract (July 24)</td>
</tr>
<tr>
<td>6, southern Adams Co.</td>
<td>Organic</td>
<td>Cover cropped</td>
<td>Garlic extract (July 3, July 16), cottonseed oil, clove oil, and garlic extract (July 24)</td>
</tr>
<tr>
<td>7, northern Franklin Co.</td>
<td>Organic</td>
<td>Cover cropped</td>
<td>None</td>
</tr>
</tbody>
</table>

Field preparation for conventional potatoes may include either fumigation or growing mustard during the preceding winter to manage soil-borne pests (McGuire, 2003; Riga et al., 2004). Fumigation is not an option for organic land, so three types of potato fields are found in central Washington: (1) conventional-fumigated, (2) conventional-mustard, and (3) organic.
most abundant predator groups were correlated with predation rate. Thus, in addition to the original correlation between all predators and predation rate, 126 additional correlations were calculated (7 subsets of 1 taxon, 21 subsets of 2 taxa, 35 subsets of 3 taxa, 35 subsets of 4 taxa, 21 subsets of 5 taxa, and 7 subsets of 6 taxa). However, conducting so many correlations using the same dataset inflates the probability of finding a statistically significant correlation by chance alone; therefore, we applied the Bonferroni approximation to adjust for multiple comparisons (Jones, 1984). We also attempted to account for the different appetites of various predators by calculating a correlation between predation rate and the field density of particular predator taxa weighted by the number of CPB eggs that each consumed in the laboratory bioassay. Finally, we calculated per capita predation rates dividing predation rate by predator density, and then calculated the correlation between predator density and per capita predation. We arcsine transformed all predation rate data before analysis. We considered measurements of predation rate from the same field but during different sampling periods as independent in this analysis because events such as insecticide sprays that occurred between samples caused substantial changes in the abundance of natural enemies (see below).

3. Results

3.1. Predator feeding rates in the laboratory

Eight taxa’s predation rates on CPB eggs were quantified in the laboratory bioassay. Assassin bugs (Sinea sp.) had the highest predation rate, followed by ladybird beetles (Hippodamia convergens), damsel bugs, Lygus, big-eyed bugs, ground beetles (Bembidion spp.), dwarf spiders, and minute pirate bugs (Fig. 1).

3.2. Correlations between predator densities and egg predation rates in the field

The most abundant predators in our field samples were dwarf spiders, minute pirate bugs, big-eyed bugs, damsel bugs, and crab spiders (Fig. 2). Bugs in the genus Lygus were abundant. While Lygus are typically herbivorous, some were observed feeding on CPB eggs in the field (see below). Relatively rare predators such as ground beetles, lady beetles, green lacewings, brown lacewings, rove beetles, and assassin bugs were also...
found in the samples. We refer to the collective group of relatively rare predators as “others.” The total densities of predators in a field varied nearly 100-fold, from 1.8 per 10 plants sampled on July 12 in field 3, to 175.4 per 10 plants sampled in field 7 on July 30 (Fig. 2). Although several of the predators’ densities were highly correlated with each other (Table 2), the relative abundances of various predator taxa differed among fields and changed during the summer (Fig. 2). For example, the percentage of predators that were dwarf spiders from one field at one date ranged from 23.2% (in field 6, sampling period 1) to 83.8% (in field 2, sampling period 3).

The average survival of caged CPB eggs was 93%. The range of predation rates on sentinel CPB eggs (mortality in excess of that observed on caged CPB eggs) was 0–26%, with an average of 7%. The predation rate in a field was significantly positively correlated with the total density of predators in D-vac samples taken from that field (correlation coefficient = 0.633, \( P = 0.008 \); Fig. 3). All possible correlations between predation rate and various subsets of the predators were calculated (Fig. 4). Predation rate was more strongly correlated with certain combinations of predators than with total predators. The highest correlation coefficient between predation rate and a set of predators was 0.668, which occurred with three groups: 1. total predators excluding “others,” 2. total predators excluding “others” and big-eyed bugs, and 3. total predators excluding big-eyed bugs and minute pirate bugs. Several other predator combinations had correlations with predation rate that were nearly as high as 0.668. However, only combinations that included at least six of the seven predator taxa were statistically significantly correlated with predation rate when the Bonferroni correction was applied to adjust for multiple comparisons (Fig. 4).

Five of the abundant taxa in the field (dwarf spiders, big-eyed bugs, damsel bugs, minute pirate bugs, and Lygus) were among the predators whose feeding rates on CPB eggs were quantified in the laboratory. Weighting the field densities of that group of five predators by their laboratory consumption of CPB eggs did not improve correlations with predation rate on sentinel eggs. The correlation coefficient weighted by laboratory consumption for dwarf spiders, big-eyed bugs, damsel bugs, minute pirate bugs, and Lygus was 0.635, which was less than the unweighted correlation coefficient for that group (0.663).

The values for per capita predation rate in the field ranged from 0 to 0.016 eggs removed per predator. Fifteen of the 16 values were between 0 and 0.0043. The highest value was from field 3 during the second sampling period. Per capita predation was not significantly correlated with predator density (correlation coefficient = −0.223, \( P > 0.2 \)). Removal of the point with the highest per capita predation rate changed the sign of the correlation coefficient, but the correlation was still not statistically significant (correlation coefficient = 0.282, \( P > 0.2 \)).

### 3.3. Observations of predation events in the field

Predators seen attacking CPB eggs in the field over the summer were lady beetles (twice), damsel bugs (twice), Lygus (twice), stinkbugs (once), assassin bugs (once), and minute pirate bugs (once). Stinkbugs were also observed attacking CPB larvae (four times), as were assassin bugs (twice). However, some of the larger predators were also observed eating other smaller predators. Assassin bugs were recorded feeding on a brown lacewing and on a dwarf spider, while a damsel bug was seen feeding on a Lygus.

### Table 2

Correlation matrix for predator densities in D-vac samples

<table>
<thead>
<tr>
<th></th>
<th>Dwarf spiders</th>
<th>Minute pirate bugs</th>
<th>Damsel bugs</th>
<th>Big-eyed bugs</th>
<th>Crab spiders</th>
<th>Lygus</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dwarf spiders</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minute pirate bugs</td>
<td>0.410</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Damsel bugs</td>
<td>0.306</td>
<td>0.971</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Big-eyed bugs</td>
<td>0.065</td>
<td>0.073</td>
<td>0.117</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crab spiders</td>
<td>0.278</td>
<td>−0.038</td>
<td>0.008</td>
<td>0.060</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lygus</td>
<td>0.248</td>
<td>0.847</td>
<td>0.866</td>
<td>0.072</td>
<td>−0.042</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Others</td>
<td>0.494</td>
<td>0.730</td>
<td>0.760</td>
<td>0.262</td>
<td>0.282</td>
<td>0.808</td>
<td>1</td>
</tr>
</tbody>
</table>
Fig. 4. Correlations between predation rate and every possible combination of seven predator taxa. Panels display predation rate correlated with (A) individual predator taxa, (B) combinations of two taxa, (C) combinations of three predator taxa, (D) combinations of four predator taxa, (E) combinations of five predator taxa, and (F) combinations of six predator taxa. On each panel, the horizontal line at correlation coefficient = 0.497 indicates the critical value for $P \leq 0.05$ with $n = 16$ (Zar, 1974). In (A) and (F), the horizontal line at correlation coefficient = 0.646 indicates the critical value after applying the Bonferroni correction for seven comparisons. In (B) and (E), the horizontal line at correlation coefficient = 0.705 indicates the critical value after applying the Bonferroni correction for 21 comparisons. In (C) and (D), the horizontal line at correlation coefficient = 0.728 indicates the critical value after applying the Bonferroni correction for 35 comparisons. Abbreviations used: L, Lygus; O, Orius; N, Nabis; D, dwarf spiders; T, “others”; C, crab spiders; and G, Geocoris.
4. Discussion

We found that predation on CPB eggs was higher when fields contained more predators. However, even at the highest observed predator density, 74% of sentinel CPB eggs were intact after 2 days in the field (Fig. 1). Colorado potato beetle eggs can hatch in as few as 4 days (Logan et al., 1985). Thus, even under the observed conditions with the most predators, it seems reasonable to expect that a substantial proportion of eggs would survive to become larvae and begin feeding on plants. Indeed, the organic fields that we monitored were all eventually sprayed with natural insecticides to control CPB (Table 1; field 7 was sprayed with spinosad on August 7, after our final measurements of predation rate). Hilbeck et al. (1997) also concluded that biological control in potatoes grown in North Carolina would not, by itself, adequately suppress CPB. It remains possible that better CPB suppression could be obtained if total predator density in potato fields were to increase, for example via conservation biological control (Barbosa, 1998), because predation on CPB eggs increased through the entire range of observed predator densities and did not appear to reach a plateau at the higher densities.

Despite substantial quantitative work, setting economic injury levels for CPB remains subjective (Nault and Kennedy, 1998). Our results may help growers who are interested in monitoring predator densities and incorporating predation rates in their decisions of whether or not to spray insecticides. Several of the predators that fed on CPB eggs have highly correlated population densities, and so our data do not reveal a single most important predator of CPB eggs. Indeed, correlations of single predator species with field measures of predation on CPB eggs are not as high as the correlation between total predator density and predation. Therefore, when field scouts sample predators to estimate the potential biological control of CPB, several predator species should be counted. However, in our dataset, it is possible to exclude certain groups of predators from the total and obtain a correlation with predation rate that is as high (or higher) as that for all predators. This suggests that in the field, the various predators are functionally similar (Harris, 1995) in terms of predation on CPB eggs. Interestingly, Tamaki (1981) suggested treating the predators attacking the green peach aphid in potatoes as a “predator complex,” wherein different predator species are considered equally important. Factors that could effectively render predators functionally similar for CPB control include intraguild predation and alternative prey. For example, assassin bugs are a relatively rare, generalist predator found only when total predator density was relatively high. Assassin bugs had the highest predation rate on CPB eggs in the laboratory, but also consumed other predators in the field. Thus, higher per capita predation by assassin bugs might be counteracted by their interfering with other, more abundant predators, in an intraguild predation scenario reminiscent of that in cotton found by Rosenheim et al. (1993). However, intraguild predation may not be as strong in potatoes as in cotton, because we did not find a relationship between per capita predation rate and total predator density. Thus, the situation in potatoes may be more similar to systems where assemblages of predators have a net additive effect on prey suppression, despite some predator–predator interference (Lang, 2003; Snyder and Ives, 2003). Similarly, the presence of multiple herbivores and detritivores may influence predation on CPB eggs by generalist predators. The lady beetle H. convergens was another species with a high per capita predation rate on CPB eggs in the laboratory bioassay. However, lady beetles prefer aphids to CPB eggs when offered a choice (Snyder and Clevenger, 2004). Thus, in the short term, alternative prey could dilute the impact of a generalist predator on the population density of a particular focal prey species (Ayres et al., 2001; Snyder et al., 2004). Östman (2004), working on organic farms in Sweden, found that
the predation rate on aphids was positively correlated to both predator density and alternative prey density, suggesting that the positive contribution of alternative prey density to predator density more than offset their dilution of the predators’ functional response.

We found a positive correlation between the total density of an assemblage of generalist predators and predation on sentinel CPB eggs. Because the densities of most of the predators were positively correlated with each other, it is difficult to identify a single, particularly important predator species. Together, six numerically dominant taxa were highly correlated with CPB egg predation, so field scouts might be able to ignore less common predator taxa when sampling to estimate predation on CPB. Because per capita predation does not have a significant relationship to predator density, we suggest that what interference occurs between predators has little effect on their net impact on CPB eggs. Furthermore, the relationship between predator density and predation on CPB eggs is positive over the range of observed predator densities and does not appear to reach a plateau. Therefore, conservation biological control methods that can increase predator densities beyond what we observed may further suppress CPB in potato fields.

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