Predation of green peach aphids by generalist predators in the presence of alternative, Colorado potato beetle egg prey

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Abstract

In Washington State two insect herbivores commonly co-occur on potato (Solanum tuberosum L.), the green peach aphid (“GPA,” Myzus persicae Sulzer) and the Colorado potato beetle (“CPB,” Leptinotarsa decemlineata Say). Locally, generalist predators dominate the community of natural enemies in potato fields. The presence of multiple prey species might distract generalists from feeding on any single target pest. In the laboratory, we examined whether consumption rates of several predator species on focal (GPA) prey was reduced in the presence of alternative (CPB egg) prey. In initial measurements of predation rates we found that two predator species, Nabis spp. and Geocoris spp. bugs, had the highest consumption rates on aphids, potato beetle eggs and small potato beetle larvae. So, we focused on Nabis spp. and Geocoris spp. in later experiments. In Petri dish arenas Nabis ate significantly more GPA per capita than did Geocoris; both predators exhibited weakly suppressed aphid consumption rates when CPB eggs were also present. However, in experiments in larger greenhouse microcosms including potato plants, this weak disruptive effect of CPB eggs disappeared. Geocoris ate nearly identical numbers of aphids across a 4-fold range of CPB egg density. Nabis, in contrast, ate significantly more aphids when 40 CPB eggs were included in microcosms, compared to microcosms with no alternative prey present. Thus, we would not expect any strong disruption of M. persicae control by Nabis spp. or Geocoris spp. when L. decemlineata eggs are also present in the field.

Keywords: Geocoris; Nabis; Polyphagy; Alternative prey; Apparent competition

1. Introduction

Omnivory has long been seen as a factor limiting the ability of generalist predators to contribute to biological control (Walsh and Riley, 1868). However, some authors have proposed that omnivory allows a predator to switch among different prey species as each becomes abundant (Riechert and Lockley, 1984; Symondson et al., 2002). By utilizing alternative prey generalists can increase their densities early, before pests arrive, and later switch to feeding on pests (e.g., Settle et al., 1996). Also, alternative prey allow generalists to correct nutritional imbalances, improving predator survival and fecundity (Bernays and Minkenberg, 1997; Greenstone, 1979; Toft and Wise, 1999). However, alternative prey also can disrupt biological control if predators prefer to feed on non-target alternative prey in preference to target pests (Abrams and Matsuda, 1996).

In potatoes (Solanum tuberosum L.), generalists have had mixed success in biocontrol programs. Predatory pentatomids have been extensively studied as inundative control agents (e.g., Biever and Chauvin, 1992; Hough-Goldstein and McPherson, 1996). While effective if released at a sufficiently high rate, releases of sufficient magnitude to control pests can be prohibitively expensive (Tipping et al., 1999). Conservation of endemic predators may be a more cost-effective strategy. For example, Ferro and co-workers have demonstrated that the coccinellid beetle Coleomegilla maculata can contribute to the biological control of potato pests if the beetles can be drawn into fields from surrounding crops (Haz- zard and Ferro, 1991). Similarly, applying straw mulch
to potato crops can attract predatory ground beetles, improving biological control (Stoner et al., 1996; Zehnder and Hough-Goldstein, 1990). However, there is evidence that alternative prey can disrupt biocontrol of potato pests by generalists. For example, in a series of laboratory experiments, Hazzard and Ferro (1991) found that the presence of green peach aphid (Myzus persicae Sulzer) reduced the number of eggs of the Colorado potato beetle (Leptinotarsa decemlineata Say) consumed by the predatory coccinellid Coleomegilla maculata, apparently because C. maculata prefers to feed on the aphids.

Two main insect pests, the green peach aphid ("GPA") and the Colorado potato beetle ("CPB"), commonly infest potatoes in Washington State (Biever and Chauvin, 1992; Mowry, 2001). Both insects are attacked by a variety of specialist and generalist natural enemies (Hough-Goldstein et al., 1993; Tamaki and Weeks, 1972a,b; Walsh and Riley, 1868). We have been examining the role of alternative prey in mediating the biocontrol effectiveness of generalist predators in potatoes. In an earlier series of field and laboratory experiments, we found that predation on CPB by a generalist predator guild decreased in the presence of GPA alternative prey (Koss, 2003). Here we investigate whether the reverse is also true, that GPA predation is reduced when CPB densities increase. We had two goals: (1) to measure predation rates of the most common predators on GPA, CPB eggs and early-instar CPB larvae and (2) to determine whether predation rates on GPA focal prey are reduced with increasing background densities of CPB eggs as alternative prey.

2. Materials and methods

2.1. Study organisms

Green peach aphid female nymphs hatch from eggs that have overwintered on the primary host, often fruit trees in the family Prunaceae (Biever, 1995). After several asexual generations on the primary host, winged morphs develop and disperse to a herbaceous host, such as the cultivated potato, Solanum tuberosum (Biever, 1995). Migrating GPA vector over 100 plant viruses (Blackman and Eastop, 2000), including the potato leafroll virus (PLRV). PLRV causes upward curling of the leaves, stunted plant growth, and necrotic spotting inside the tuber prior to or after harvest (Mowry, 2001). Transmission of viruses may cause severe damage and reduce crop yields even when aphid densities are low (Blackman, 1976), and so in Washington these aphids have typically been controlled by calendar sprays of organophosphate and carbamate insecticides (Mowry, 2001). However, novel selective aphicides have broadened growers’ control options. Also, a growing organic sector in the state relies on fresh processing of potatoes to avoid PLRV-induced degradation of tuber quality in storage, so that tight control of GPA is not necessary (A. McErlich, personal communication).

The Colorado potato beetle is a notorious pest of S. tuberosum throughout North America and Europe (Felt, 1938; Walsh, 1865). CPB damage plants by consuming the foliage, and may reduce tuber yields by as much as 50% (Ferro et al., 1983; Hare, 1980). CPB overwinter as reproductively diapausing adults in the soil of potato fields or areas bordering potato fields, emerge in the spring, and immediately start feeding on potato foliage (Weber and Ferro, 1993). Each adult female beetle is capable of laying more than 300 eggs during her lifetime (Voss and Ferro, 1992). In most parts of the world CPB is resistant to a wide variety of pesticides (Weber et al., 1994), including some of the new, more selective pesticides (Zhao et al., 2000).

In plant foliage, the predator guild in Washington State potato fields is dominated numerically by predaceous Hemiptera, primarily two species of big-eyed bug, Geocoris bullatus Stål and G. pallens Say, and two species of damsel bug, Nabis americoferus Carayon and N. alternatus Parshley (Koss, 2003; Tamaki and Weeks, 1972a,b). Geocoris spp. and Nabis spp. are omnivorous, actively foraging generalist predators that feed on a broad spectrum of prey species, including soft-bodied insects, insect eggs, seeds, pollen, and plant fluids (Cohen, 1990). With live specimens, the two Geocoris species, and also the two Nabis species, cannot be reliably assigned to species (Tamaki and Weeks, 1972b). We used field-collected predators for our field and laboratory experiments, and so both our Geocoris and Nabis were a mixture of the two common species in each genus.

Carabid beetles and linyphiid spiders numerically dominate the ground predator guild of Washington State potato fields (Koss, 2003). Carabids are able to climb the foliage of the potato plant and consume large numbers of CPB eggs and first instar larvae (Brust, 1994), and have been found to significantly reduce CPB populations (Cappaert et al., 1991). The most common carabid species in local potato fields are a complex of two morphologically nearly identical Bembidion spp., Bembidion ripicola Kirby, and Bembidion obscurllum Motschulsky (Koss, 2003); we did not attempt to distinguish between these two species in our laboratory experiments. Linyphiids will opportunistically consume aphids that fall into their webs, although they do not actively search for prey (Sunderland et al., 1986, 1987). Common linyphiids in local potato fields include Erigone dentosa,Walckenaeria subspiralis, Halorates ksenius, Mioneta sp., and Lepthyphantes tenuis (Koss, 2003); these spiders cannot be reliably assigned to species using live specimens (R. Crawford, personal communication) and so a mixture of species was used in our feeding trials.
2.2. Experiments

We conducted laboratory experiments in arenas of two types: small Petri dish microcosms and larger microcosms in a greenhouse that included sprigs of potato foliage. In small Petri dish microcosms we first conducted no-choice tests, pairing Geocoris spp., Nabis spp., Bembidion spp., and linyphiid spiders with either GPA or CPB prey. In additional Petri dish and larger microcosm experiments we focused on two predator taxa, Geocoris spp. and Nabis spp., that are among the most abundant and voracious predators in Washington State potato fields (Koss, 2003). Predators were field collected from commercial potato fields in the vicinity of Othello, WA, USA, and used in feeding trials within 24-h of being collected. All predators were starved for 12-h (overnight) before being used in trials. Adult predators were used in all experiments.

GPA came from a long-term laboratory colony originally collected from potato fields in the vicinity of Prosser, WA, USA. Aphids were maintained in a greenhouse at ambient day length and 22–25°C. Adult CPB collected in eastern Washington potato fields produced the eggs and larvae used in our feeding trials. Eggs were harvested daily and placed in a refrigerator (4°C) to retard egg development. Beetles in the colony were fed live potato foliage and were housed in the same greenhouse as the aphid colony.

2.3. Predator no-choice experiments using GPA and CPB prey

We conducted a series of three Petri dish experiments to measure predation rates by Geocoris spp., Nabis spp., Bembidion spp., and linyphiid spiders on GPA, CPB eggs, and CPB second instar larvae. One predator was added to each dish, along with 10 prey, with 8–10 replicates of each predator–prey pairing. Water was provided using a moistened cotton dental wick. The number of prey remaining was recorded after 72 h. Each experiment included 10 control dishes where prey were housed without a predator. Rarely, predators died before 72 h; these replicates were excluded.

2.4. Geocoris and Nabis choice experiments in small arenas

These experiments were conducted to determine if the presence of CPB eggs will reduce predator consumption of GPA, and if the presence of GPA affects predator consumption of CPB eggs. Our arenas were 100-mm x 15-mm plastic Petri dishes, containing a moist cotton wick but otherwise empty. In these arenas we established the following treatments: 20 aphids and one Geocoris (Geo A); 20 aphids and one Nabis (Nab A); 5 CPB eggs and one Geocoris (Geo E); 5 CPB eggs and one Nabis (Nab E); 20 aphids, 5 eggs, and one Geocoris (Geo A+E); 20 aphids, 5 eggs, and one Nabis (Nab A + E); and a control with 20 aphids, 5 eggs, and no predator (No predator). We established 10 replicates of each of the 7 treatments (total N = 70). Eggs and aphids were added to the dishes on a small square (≤1 cm²) of potato foliage. The potato foliage was creased so that predators had access to both sides of the leaf. The total number of prey (eggs and aphids) remaining was recorded at 24, 48, and 72 h.

2.5. Geocoris and Nabis choice in larger microcosms including plant foliage

In larger microcosms including potato foliage, we again examined whether the presence of CPB eggs disrupts biocontrol of GPA. Our microcosms were 8-cm wide × 20-cm tall plastic cylinders, covered on the top with organdy mesh. Two round windows, approximately 3.5 cm in diameter, were cut into the sides of the tubes and covered with mesh to provide airflow. Each tube contained a single, ca. 15-cm long potato stem cutting submerged in a 33.3-mL (9-dram) vial of water capped with a piece of Parafilm (American National Can, Chicago, IL, USA). Vials containing plant stems were buried in watered soil in 10-cm diameter pots. Burying the vials in the soil kept the stems turgid and allowed arthropods to easily climb the plants. The bottom of each plastic tube was twisted into the soil to form a seal with the edge of the pot, preventing arthropod escape.

All microcosms contained the same density of GPA, while densities of CPB eggs varied. We established four treatments: a control of 100 GPA only, no predators (Con); 100 aphids and predators (O); 100 aphids, 10 CPB eggs and predators (10); and 100 aphids, 40 CPB eggs, and predators (40). Each treatment was replicated 10 times (total N = 40). First, clutches of 10 L. decemlineata eggs (either a single clutch or 4 clutches), attached to small (≤1 cm²) pieces of potato foliage where they had been deposited by female CPB, were glued to potato stems (in treatments 10 and 40) using a small drop of Elmer’s glue (Borden, Columbus OH, USA). The glue droplet was entirely covered by the egg mass, and did not alter predator behavior (Snyder and Ives, 2001, 2003). Clutch size was standardized at 10 eggs by carefully cutting away excess eggs using a dissecting scissors. Next, aphids were applied to foliage and then the microcosms were left undisturbed overnight, to provide aphids with time to locate and settle into feeding sites. After this 12-h aphid settlement period, predators were released into the microcosms. The experiment was run once with Geocoris spp. as the focal predator and once with Nabis spp. as the focal predator. Four Geocoris were used in the former while 2 Nabis were used in the latter, because the per capita feeding rate of Nabis is ca. 2 times that of Geocoris (Fig. 1). After 72 h, we terminated the experiment,
destructively sampling each microcosm to determine the number of aphids, eggs, and predators remaining in each.

2.6. Statistics

Predation rates, and final arthropod densities in the greenhouse microcosm experiments, were analyzed using ANOVA followed by Tukey’s post hoc test. For the Petri dish experiment, insect counts were repeated through time in the same dishes, and so those data were analyzed using multivariate repeated-measures ANOVA in SYSTAT (SPSS, Chicago, IL, USA).

3. Results

We conducted three types of laboratory experiments. First, we used Petri dish no choice arenas to compare predator consumption rates of GPA, CPB eggs, and second instar CPB larvae. Second, we conducted predator choice experiments in Petri dishes where both GPA and CPB eggs were present in some arenas. Third, we examined disruption of GPA predation in the presence of CPB egg alternative prey in larger microcosms that included plants.

3.1. Predator consumption rates of GPA and CPB

Predators significantly differed in their predation rates on GPA, CPB eggs, and CPB larvae ($P < 0.001$ for all comparisons). *Nabis* ate more aphids than did any predator other than *Bembidion*; linyphiids ate the fewest aphids (Fig. 1A). For both CPB eggs and larvae, *Nabis* ate the greatest number of CPB, while consumption by *Geocoris* and *Bembidion* was intermediate and the rate of CPB predation by linyphiids did not differ from control mortality (Figs. 1B and C).

3.2. Geocoris and Nabis choice in simple arenas

Differences in *Nabis* and *Geocoris* predation on GPA were consistent through time (Wilks’ $\lambda = 0.99$, $F_{2.32} = 0.008$, $P = 0.99$), as were diet treatment effects (Wilks’ $\lambda = 0.98$, $F_{2.32} = 0.38$, $P = 0.68$) and the interaction between predator and diet (Wilks’ $\lambda = 0.96$, $F_{2.32} = 0.68$, $P = 0.52$). *Nabis* consumed significantly more aphids than did *Geocoris* ($F_{1.33} = 12.61$, $P = 0.001$; Fig. 2A). Aphid consumption was marginally reduced when CPB eggs were present ($F_{1.33} = 4.00$, $P = 0.054$; Fig. 2A); both predators responded to the presence of CPB eggs similarly (predator × food interaction; $F_{1.33} = 1.17$, $P = 0.29$; Fig. 2A).

*Nabis* and *Geocoris* responded differently when presented with CPB eggs only, versus eggs presented together with GPA. *Geocoris* paired only with CPB eggs gradually ate more eggs than did *Geocoris* with a choice of GPA or CPB eggs. In contrast, *Nabis*, after 24 h, ate large numbers of CPB eggs when only eggs were available, but only consumed CPB eggs after 48 h when both prey were available, leading to a statistically significant predator × food × time interaction (Wilks’ $\lambda = 0.77$, $F_{2.31} = 4.60$, $P = 0.018$; Fig. 2B).

3.3. Geocoris predator choice microcosm experiments with GPA and CPB egg prey

Determined by destructive sampling after the 72-h visual sample, *Geocoris* did not eat more CPB eggs when 40 were provided, compared to tubes where 10 eggs were provided ($F_{1.18} = 0.56$, $P = 0.46$; Fig. 3A). Final aphid densities significantly differed ($F_{3.36} = 27.70$, $P < 0.001$; Fig. 3C), because Con aphid densities were higher than in any treatment including predators ($P < 0.001$ for all comparisons, Tukey’s post hoc test);
densities in predator treatments (0, 10, and 40) did not differ from one another (P > 0.90 for all comparisons, Tukey’s post hoc test). Final Geocoris densities did not differ between treatments (F_{2,27} = 2.59, P = 0.094; Fig. 3E).

3.4. Nabis choice microcosm experiments with GPA and CPB egg prey

After 72h, Nabis consumed slightly greater numbers of CPB when 40 were provided than when 10 eggs were provided (F_{1,17} = 4.50, P = 0.049; Fig. 3B). Aphid densities significantly differed by treatment (F_{3,36} = 22.97, P < 0.001, Fig. 3D). Aphid densities were highest in Con (P < 0.001 for comparisons with all predator treatments, Tukey’s post hoc test). Among the three predator treatments, aphid densities were highest in 0, intermediate in 10, and lowest in 40 (Fig. 3D; statistics provided in figure). Final Nabis densities were identical among treatments (F_{2,27} = 0.00, P = 1.00; Fig. 3F).

4. Discussion

In our feeding rate trials, Geocoris and Nabis consistently had the highest predation rates on the potato pests, although Bembidion was an equally efficient predator on aphids. These trials likely overestimated the true field impact of two predators, Bembidion spp. and linyphiids, that forage primarily on the ground and so likely contact foliage pests less frequently than do Geocoris and Nabis. Nabis appeared to be increasingly important as prey size increased, and was clearly superior at preying upon second instar CPB larvae (Fig. 1C). Geocoris and Nabis are also numerically dominant in production fields. In an intensive 2-year survey of predator communities in potato fields in eastern Washington, Koss (2003) found that these two predators represented >50% of the community of predators in the foliage. Both their numerical dominance and high feeding rates suggest that Geocoris and Nabis are particularly important for control of both GPA and CPB in the field. Thus, we focused subsequent experiments on Geocoris and Nabis.

In the Petri dish choice arenas, Geocoris appeared to decrease its predation rate on GPA proportionally when CPB eggs were added to the microcosms. However, in the larger greenhouse microcosms including plants, there was no evidence for a disruptive effect of CPB eggs—GPA predation rates were nearly identical when no, 10 or 40 CPB eggs were included in microcosms. In the simple choice arenas, Nabis appeared to exhibit little alteration of GPA predation in the presence versus absence of CPB eggs, consistent with a preference for feeding on aphids reported elsewhere (Koss, 2003). Similarly, there was no evidence for disruption of GPA predation by the provision of CPB alternative prey in the greenhouse microcosms. Oddly, predation of GPA by Nabis actually increased when more CPB eggs were present. Several species of actively foraging insects switch from extensive to intensive search behavior following the capture of a prey item (Curio, 1976; Heimpel and Hough-Goldstein, 1994; Hodek and Honek, 1996). Intensive search behavior includes slower movements and more frequent turns, which can increase encounters when prey are concentrated in a relatively small area. We hypothesize that in the case of Nabis, CPB eggs might trigger a switch to intensive search behavior that leads to increased consumption of GPA.

Thus, for both Geocoris and Nabis predators, we found little evidence for a disruptive effect of CPB alternative prey on predation of GPA focal prey. Working from the perspective of CPB as the focal prey, Hazzard and Ferro (1991) found that the presence of green peach aphids reduced the number of CPB eggs attacked by the coccinellid Coleomegilla maculata. Their laboratory study further found that when both prey were abundant, C. maculata preferred eating GPA to CPB. Something similar may be occurring in our system, with predators exhibiting a preference for feeding on GPA, so that CPB eggs do not distract the predators from attacking aphids.
Previously, in a series of laboratory and field experiments we examined how the presence of GPA alternative prey impacts biocontrol of CPB by the same guild of generalists that we are reporting on here (Koss, 2003). In field cages we found that the generalist guild effectively suppressed CPB when aphid densities were less than 5/plant, as is typical in the early season. However, when aphid densities naturally increased later in the year, the predators no longer were effective CPB control agents. In laboratory microcosms including plants we then demonstrated that both Geocoris and Nabis reduced their rate of attack on CPB eggs as GPA densities increased. However, the disruptive effect of GPA was stronger for Nabis, which appeared to avoid CPB predation even when aphid densities were low. In the Choice Petri dish trials reported here, predators were presented with either GPA only, CPB eggs only, or both prey. Thus, we can again look at how the presence of aphids impacted CPB predation. Geocoris appeared to feed on each prey roughly relative to its abundance. When GPA were present, Geocoris consumption of CPB eggs decreased in equal measure. In contrast, Nabis spp. appeared to have a stronger preference for aphids than did Geocoris. When Nabis had no choice but to feed on CPB eggs, Nabis attacked these prey at a high rate. However, when aphids were present, Nabis fed very little on CPB eggs initially. Later in the experiment, as aphids became depleted, Nabis fed more heavily on CPB eggs. Thus, the behavior of both taxa reported here is quite similar to what we observed in our earlier work (Koss, 2003).

It is important to note that our experiments examined only the short-term impacts of CPB alternative prey. Sometimes short- and long-term impacts of alternative prey can be quite different. For example, Eubanks and Denno (2000a,b) manipulated the quality of lima beans (the alternative prey) in the field and found that when high quality plant food was available, individual predatory bugs (Geocoris punctipes Say) increased their plant

![Fig. 3. Final densities of (A) beetle eggs when paired with Geocoris, (B) beetle eggs when paired with Nabis, (C) aphids when paired with Geocoris, (D) aphids when paired with Nabis, (E) Geocoris predators, and (F) Nabis predators. Treatments: microcosms containing 100 GPA but no CPB eggs or predators (con); predators and aphids but no eggs (0); predators, 100 aphids and 10 CPB eggs (10); and predators, 100 aphids and 40 CPB eggs (40). Letters represent means that are significantly different (P < 0.05) using Tukey’s post hoc test. Error bars are ±1 SE.](pdf)
feeding and reduced their feeding on the target insect pests. However, the numerical response of *G. punctipes* to plots with high quality plants was greater so that the summed predation rate was greater in plots of high quality plants (Eubanks and Denno, 2000b). The increase in predator density compensated for the lower feeding rate of individual predators and led to improved biocontrol. In our system CPB might increase GPA predation rates if predators are attracted to fields that have higher densities of CPB, and then also attack aphids (e.g., Harmon et al., 2000; Östman and Ives, 2003).

Ecologists have envisioned two scenarios: positive and negative prey–prey interactions. Negative prey–prey interactions occur when populations of one (alternative) prey bolster predator densities increasing their impact on a second (focal) prey, an interaction Holt (1977) calls “apparent competition.” Östman and Ives (2003) provide an example of apparent competition. In their alfalfa system, fields with higher pea aphid densities attracted more nabid predators, leading to higher predation rates on potato leafhoppers. Thus, negative prey–prey interactions are to the benefit of biological control (Snyder et al., in press). In contrast, positive prey–prey interactions occur when one (alternative) prey draws predator attacks from a second (focal) prey, shielding the focal species from predation. For example, Halaj and Wise (2002), working in vegetable gardens, found that plots with higher densities of detritivore alternative prey, and thus higher predator densities, did not have lower herbivore densities. Apparently, predators preferred to feed on detritivores, protecting herbivores from increased predation. Thus, negative prey–prey interactions disrupt biological control (Snyder et al., in press). In the case we report here, predators were not strongly attracted to CPB as prey, and so the presence of this alternative prey neither consistently disrupted nor improved biocontrol of the preferred aphids.

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