

Negative dietary effects of Colorado potato beetle eggs for the larvae of native and introduced ladybird beetles

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Abstract

Aphidophagous ladybird beetles (Coleoptera: Coccinellidae) are attracted to and feed heavily on aphids, but many species will also feed opportunistically on other prey that they encounter. In potatoes (*Solanum tuberosum* L.) in Washington State, USA, coccinellids feed on both green peach aphids (“GPA,” *Myzus persicae* Sulzer) and eggs of the Colorado potato beetle (“CPB,” *Leptinotarsa decemlineata* Say). The guild of aphidophagous ladybirds includes two native species, *Hippodamia convergens* Guérin-Ménéville and *Coccinella transversoguttata* Brown. Recently, an introduced species, *Coccinella septempunctata* L., has invaded and apparently displaced its native congener. A second exotic, *Harmonia axyridis* Pallas, has colonized the area and is becoming more abundant. We compared larval development of each species on a monotypic diet of GPA, a monotypic diet of CPB eggs, or a mixed diet of both GPA and CPB eggs. Our goal was to answer two questions: (1) do larvae of the four ladybird species benefit from including CPB eggs in their diet and (2) do the four ladybird species differ in their ability to utilize CPB eggs as prey? No larva of any species completed development on a pure diet of CPB eggs, and survivorship was highest for all species when they fed on a pure diet of GPA. One native species, *H. convergens*, and one exotic species, *H. axyridis*, exhibited significantly lower survivorship on a mixed diet of both CPB eggs and GPA, compared to a pure GPA diet; *H. axyridis* also took longer to develop from egg to adult when both prey were provided. Survivorship of the two *Coccinella* spp. was not altered by the inclusion of CPB eggs with GPA, although CPB eggs lengthened the development time of *C. transversoguttata*. Adult size was not consistently affected by diet for any of the coccinellids. Overall, no ladybird species benefited from the inclusion of potato beetle eggs in its diet. The two *Coccinella* species responded similarly to the inclusion of CPB eggs, and so we would not expect any difference in the success of coccinellid larval development in potato fields following the replacement of *C. transversoguttata* by *C. septempunctata*. *Hippodamia convergens* and *H. axyridis*, the two species whose survivorship was depressed by combining CPB egg and aphid prey, were also the two species that consumed the greatest number of CPB eggs during successful larval development. A comparison of total egg consumption by each species cohort suggested that displacement of the other species by *H. axyridis* would not alter CPB biological control, because the higher per capita feeding rate by *H. axyridis* larvae compensated for individuals’ greater mortality risk on a diet including CPB eggs.

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1. Introduction

The usefulness of generalist predators as biological control agents has long been questioned (Hagen and van den Bosch, 1968; Van den Bosch, 1971; Wardle and Buckle, 1923). Generalists’ long generation times, ten-

dency to feed on other predators rather than pests, and inability to achieve a tight dynamical linkage with any single pest species run counter to the traits thought to be required in an effective biocontrol agent (Debach and Rosen, 1991; Rosenheim et al., 1995). However, some authors have suggested that catholic feeding habits could actually improve the ability of generalists to contribute to biological control (Riechert and Lockley, 1984; Symondson et al., 2002), for example allowing generalist predators to maintain their populations on other

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prey when pests are not present (Settle et al., 1996). Also, being a generalist allows predators to achieve balanced nutrition through the inclusion of multiple, nutritionally complementary foods in their diet (Bernays and Minkenberg, 1997; Denno and Fagan, 2003). For several species of generalist predator, mixed prey diets have been shown to be nutritionally superior to monotypic diets of a single prey species (Evans et al., 1999; Greenstone, 1979; Toft and Wise, 1999a,b).

In potatoes, augmentative releases of generalist predators can effectively control some pests (Biever and Chauvin, 1992; Hough-Goldstein et al., 1993; Hough-Goldstein and McPherson, 1996). However, predator augmentation can be prohibitively expensive on a large scale (Tipping et al., 1999), and so conservation of endemic predators may be a more cost effective strategy (Brust, 1994; Hilbeck and Kennedy, 1996; Hilbeck et al., 1997; Nault and Kennedy, 2000; Tamaki and Weeks, 1972). The effectiveness of predator guilds in controlling potato pests was suggested over 130 years ago (Walsh and Riley, 1868), but more recently the use of broad-spectrum insecticides has limited the utility of biological control (Ruffle and Miller, 2002). However, the availability of newer insecticides with selective modes of action, and the growing organic sector, has revitalized interest in biological control in potatoes (Hilbeck and Kennedy, 1996; Koss, 2003; Ruffle and Miller, 2002). In Washington two insect pests, the green peach aphid (“GPA,” *Myzus persicae* Sulzer) and the Colorado potato beetle (“CPB,” *Leptinotarsa decemlineata* Say), consistently exert significant economic damage to potato crops (Koss, 2003). The GPA reduces yields by vectoring viral diseases of potatoes, while CPB damage plants through defoliation (Koss et al., 2004).

Locally, the community of natural enemies in potato fields is dominated by a diverse guild of generalist predators (Koss, 2003; Tamaki and Weeks, 1972). Several species of predacious bug are numerically dominant, but coccinellids (Coleoptera: Coccinellidae) can also be abundant when robust populations of the GPA are present (Tamaki and Weeks, 1972). While coccinellids are probably drawn to fields by the presence of aphids, once there ladybird beetles also feed on CPB eggs, behavior similar to that observed for the ladybird species *Coleomegilla maculata* DeGeer in eastern North America (Hazzard et al., 1991; Hilbeck and Kennedy, 1996; Munyaneza and Obrycki, 1997a,b, 1998a,b; Nault and Kennedy, 2000). Work with *C. maculata* has shown that these ladybirds readily feed on CPB eggs, but inclusion of CPB eggs in the coccinellid’s diet retards development even when combined with high quality aphid prey (Hazzard et al., 1991; Munyaneza and Obrycki, 1997a,b, 1998a,b).

Two native species, *Hippodamia convergens* Guérin-Méneville and *Coccinella transversoguttata* Brown, have historically dominated the community of aphidophagous

coccinellids in eastern Washington (Elberson, 1992; Tamaki and Weeks, 1972). *Coccinella septempunctata*, a species native to Europe and Asia that was released into North America in an attempt to improve aphid biological control, reached our region by the early 1990’s (Elberson, 1992). By the end of the decade, *C. septempunctata* was common in agricultural fields while the native *C. transversoguttata* was rare (White and Eigenbrode, 2000; Youssef, 2000). Similar displacement of natives by *C. septempunctata* has been reported throughout North America (Brown and Miller, 1998; Day et al., 1994; Elliot et al., 1996; Evans, 2000; Wheeler and Stoops, 1996). Recently, a second exotic native to Asia, *Harmonia axyridis* Pallas, has increased in abundance locally (Snyder et al., 2004). First reported in 2000, *H. axyridis* is now becoming more common in irrigated agricultural fields in eastern Washington (Snyder et al., 2004), including potato fields (W.E. Snyder, personal observation). Like *C. septempunctata*, throughout North America invasion by *H. axyridis* has been followed by declines in native ladybird species (Brown and Miller, 1998; LaMana and Miller, 1996; Michaud, 2002; Tedders and Schaeffer, 1994; but see Nault and Kennedy, 2003).

Locally, CPB are present in most fields throughout the growing season while GPA colonize fields from south to north throughout the summer (Koss, 2003), so that most fields housing GPA populations also contain CPB. Thus, the successful development of coccinellid larvae within potato fields will in part depend on the species’ ability to utilize both prey as food. We performed a series of laboratory experiments to determine if the four locally common coccinellid species suffer a developmental cost from including CPB eggs in their diets, and whether the native and introduced coccinellid species differ in their ability to utilize CPB eggs as prey. If species differ in their ability to make use of CPB prey, rates of successful coccinellid larval development within potato fields may change as regional coccinellid species composition changes.

2. Materials and methods

The coccinellid larvae used in our experiments were the progeny of adults collected in agricultural fields in eastern Washington State, USA, during the summer of 2002. Adults were returned to the laboratory and maintained in 100-mm × 15-mm plastic petri dishes on a mixed diet of pea aphid, *Acyrtosiphon pisum* Harris, Russian wheat aphid, *Diuraphis noxia* Mordvilko, and English grain aphid, *Sitobion avenae* F., at 22–25 °C and 16:8 L:D. Water was provided using a moistened dental wick.

Green peach aphids were from a long-term laboratory colony originally collected from potato fields in eastern Washington, maintained in the greenhouse on potato

plants at 22–25°C and 16:8 L:D. Colorado potato beetle eggs were the progeny of adults field collected from local potato fields in the summer of 2002, maintained on potato plants in a greenhouse, under the same conditions as the aphids. CPB eggs were collected daily, and stored in a refrigerator (5°C) until being fed to coccinellids.

2.1. Experiments

In our first series of experiments, we individually examined the development of each coccinellid species on a monotypic diet of GPA, a monotypic diet of CPB eggs, or a mixed diet of GPA and CPB eggs. Larvae were collected within 24 h of hatching, moved individually to a petri dish, and randomly assigned to treatment. Larvae were reared under the same environmental conditions as adults, but at a constant temperature of 25°C. To minimize confounding genetic effects, we evenly distributed larvae from any single clutch across treatments, and never used more than four larvae from the same clutch in any treatment. In all experiments, both GPA and CPB eggs were provided to each coccinellid larva *ad libitum*. Dishes were checked daily, and GPA or CPB eggs were added as necessary so that neither prey was ever absent. Larvae were moved to clean arenas as dishes became soiled, and cotton wicks were moistened as necessary to provide ample drinking water. We established 20 replicates of each diet treatment (total $N = 60$ for each trial with each species). We recorded survivorship to adulthood, development time from first instar larva to adult, and adult size (by measuring pronotum width, see Preziosi et al., 1999).

Because each species was examined separately in the first series of experiments, we could not be certain that any differences in developmental effects of diet were purely attributable to species differences, rather than random variation between experiments. Thus, we conducted an additional experiment where we simultaneously reared larvae of all four coccinellid species. For each species, we reared 20 larvae on a pure diet of GPA, and 20 larvae on a mixed diet of both GPA and CPB (total N per species = 40, total N for the experiment = 160). We excluded the pure CPB egg diet, because no larva of any species completed development on this diet in the earlier experiments. We again recorded survivorship to adulthood, developmental time from first instar larva to adult, and adult size. However, in this final experiment we also counted the number of CPB eggs eaten by each larva each day in the mixed diet treatment, to see if any developmental differences between species corresponded to differences in CPB egg consumption rates.

2.2. Statistics

All analyses were conducted using SYSTAT statistical software (SPSS, Chicago, IL, USA).

Our first series of experiments separately examined diet effects on each species. We found that no larva of any species could complete development on a monotypic diet of Colorado potato beetle eggs, and so this treatment was not included in statistical analyses; instead, we compared larval performance on the monotypic green peach aphid diet to that on the mixed diet. We compared survivorship using χ^2 and development time using a t test. When at least two individuals of each sex completed development on both diets we compared adult size using two-way ANOVA with sex and diet as the two crossed factors; when the fully crossed design was not available, we compared treatments using one-way ANOVA.

In the final experiment we simultaneously compared development of all species. We first analyzed data using two-way ANOVA, with species and diet as the two main factors. Sex was not included as a third factor in analysis of the size data, because one species (*H. convergens*) did not have any males survive on the mixed aphid and potato beetle egg diet. Where we found a significant species by diet interaction, we then compared performance on the two diets separately for each of the species, using the Bonferroni correction so that multiple comparisons did not inflate the Type I error rate (Rice, 1989). Egg consumption rate data were analyzed using one-way ANOVA followed by Tukey's post hoc test.

3. Results

3.1. Diet effects examined individually for each species

First, we individually examined survivorship, development time, and adult size of larvae of each coccinellid species reared on green peach aphids only ("GPA"), Colorado potato beetle eggs only ("CPB"), or a mix of both prey ("Both"). No larva of any of the four coccinellid species completed development on a pure diet of CPB eggs (Figs. 1A–D), and so this treatment was not examined further. Rather, we conducted statistical comparisons of the two treatments with survivors, GPA and Both.

Two native species were examined, *H. convergens* and *C. transversoguttata*. *H. convergens* larvae exhibited significantly lower survivorship on a mixed diet of both prey, compared to a pure GPA diet (Fig. 1A, $\chi^2 = 6.47$, $df = 1$, $P = 0.011$). For *H. convergens*, developmental time ($F_{1,20} = 0.93$, $P = 0.35$, Fig. 1E) and adult size ($F_{1,18} = 3.53$, $P = 0.076$; Fig. 1H) did not differ by diet treatment. However, adult males were smaller than females ($F_{1,18} = 6.842$, $P = 0.018$); the treatment by sex interaction term was not statistically significant ($F_{1,18} = 2.069$, $P = 0.17$). For the other native coccinellid, *C. transversoguttata*, survivorship did not differ between GPA and Both diets ($X^2 = 0.25$, $df = 1$, $P = 0.56$; Fig. 1B), although development time was significantly longer on

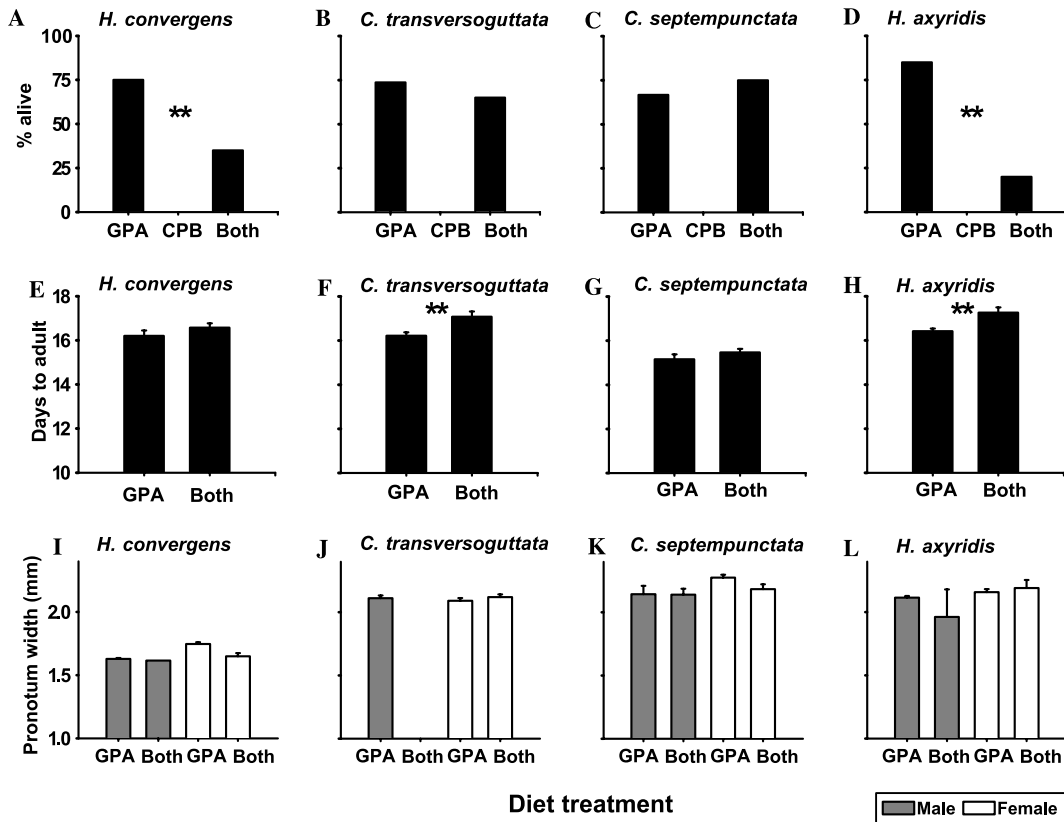


Fig. 1. Percent survivorship from first instar to adult (A–D), development time from first instar to adult (E–H), and adult pronotum width (I–L) for four coccinellid species, *H. convergens*, *C. transversoguttata*, *C. septempunctata*, and *H. axyridis* reared under different diets. Diet treatments were: “GPA,” green peach aphids only; “CPB,” Colorado potato beetle eggs only; and “Both,” a mixed diet of both aphids and eggs. In (I–L), gray bars represent male beetles and white bars represent female beetles. Asterisks indicate significant differences ($P < 0.05$) between GPA and Both treatments. Error bars are ± 1 SE.

Both ($F_{1,25} = 9.44$, $P = 0.005$; Fig. 1F). No male beetle completed development on Both; in a one-way ANOVA of the remaining three sex by treatment classes (male GPA, female GPA, and female Both), there were no significant differences in adult size ($F_{1,23} = 0.65$, $P = 0.43$; Fig. 1J).

Two introduced species were examined, *C. septempunctata* and *H. axyridis*. *C. septempunctata* survivorship ($\chi^2 = 0.32$, $df = 1$, $P = 0.57$; Fig. 1C), development time ($F_{1,26} = 1.32$, $P = 0.26$; Fig. 1G) and adult size ($F_{1,24} = 0.53$, $P = 0.48$; Fig. 1K) did not differ between GPA and Both diets. Male beetles were smaller but not significantly so ($F_{1,24} = 1.80$, $P = 0.192$), and the treatment by sex interaction was not significant ($F_{1,24} = 0.47$, $P = 0.50$). *H. axyridis*, the second exotic coccinellid, had significantly lower survivorship ($\chi^2 = 16.94$, $df = 1$, $P < 0.001$; Fig. 1D) and longer development time ($F_{1,19} = 8.88$, $P = 0.008$; Fig. 1H) on Both than on GPA. Male *H. axyridis* were significantly smaller than females ($F_{1,17} = 7.23$, $P = 0.016$; Fig. 1L). However, adult size was not altered by diet treatment ($F_{1,17} = 1.35$, $P = 0.26$); the diet by sex interaction term was not significant ($F_{1,17} = 3.35$, $P = 0.085$).

3.2. Diet effects compared simultaneously for all four species

We conducted a final experiment where we compared simultaneously the effects of GPA and Both diets on all four species differently, leading to a statistically significant species by diet interaction ($F_{3,150} = 6.74$, $P < 0.001$; Fig. 2A). Separately comparing survivorship of each species on GPA and both, *H. convergens* and *H. axyridis* exhibited significantly higher survivorship on GPA than Both ($\chi^2 = 14.40$, $df = 1$, $P < 0.001$; $\chi^2 = 15.11$, $df = 1$, $P < 0.001$, for *H. convergens* and *H. axyridis*, respectively), whereas survivorship of the two *Coccinella* species was not altered by diet ($P > 0.10$ for both comparisons). Comparing across species within diets, species significantly differed in survivorship on GPA ($\chi^2 = 24.38$, $df = 3$, $P < 0.001$), apparently driven by lower survivorship of *C. transversoguttata* on this diet, and Both ($\chi^2 = 11.12$, $df = 3$, $P = 0.01$), perhaps due to lower survivorship by *H. axyridis* and *H. convergens* with both aphids and potato beetle eggs were provided. Development time was significantly lowered by the

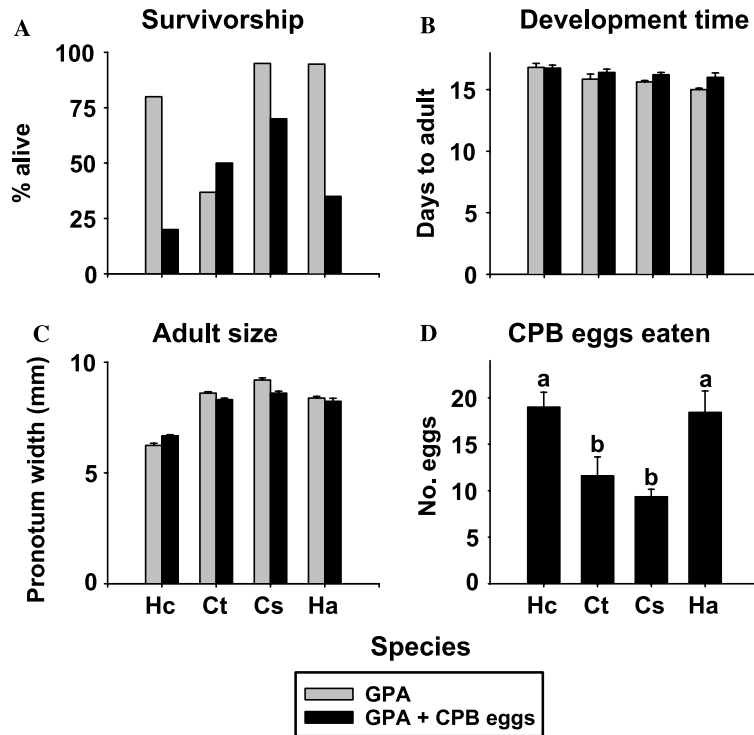


Fig. 2. (A) Percent survivorship from first instar to adult, (B) development time from first instar to adult, (C) adult pronotum width, and (D) cumulative number of Colorado potato beetle eggs eaten during larval development for four coccinellid species, *H. convergens* (Hc), *C. transversoguttata* (Ct), *C. septempunctata* (Cs), and *H. axyridis* (Ha) reared on monotypic versus mixed diets. Gray bars represent larvae reared under a pure diet of green peach aphids (“GPA”), while black bars represent larvae reared under a mixed diet of both green peach aphids and Colorado potato beetle eggs (“GPA + CPB eggs”). Different letters in (D) indicate means that significantly differ using Tukey’s post hoc test ($P < 0.05$). Error bars are ± 1 SE.

inclusion of potato beetle eggs in beetles’ diets ($F_{1,85} = 6.99$, $P = 0.010$; Fig. 2B), and species differed in their development times independent of diet ($F_{3,85} = 6.29$, $P = 0.001$). Development times of the four species responded similarly to diet (species \times diet interaction; $F_{3,85} = 1.04$, $P = 0.38$).

One species (*H. convergens*) had no males survive in the Both treatment, and so we lumped the two sexes for analysis of adult size; exploratory analysis revealed no change in our conclusions by comparing female only beetles. Adult sizes of the four species were not impacted by diet in a consistent manner (species \times diet interaction; $t_{3,85} = 7.39$, $P < 0.001$; Fig. 2C). This significant interaction term appeared to be driven by strongly reduced adult size of *C. septempunctata* in Both compared to GPA ($t_{1,31} = 19.60$, $P < 0.001$) and a weaker response by *C. transversoguttata* ($t_{1,15} = 8.53$, $P = 0.044$); comparisons for the other two species were not significant ($P > 0.10$ for both comparisons).

Species significantly differed in the number of Colorado potato beetle eggs consumed by larvae that completed development ($F_{3,31} = 7.78$, $P = 0.001$; Fig. 2D). *H. convergens* and *H. axyridis* consumed a similar number of eggs, more than were consumed by either *Coccinella* species (Fig. 2D). The two *Coccinella* species did not differ from one another in their consumption of potato beetle eggs (Fig. 2D).

Because the species with the lowest survivorship when CPB eggs were included in their diet, *H. convergens* and *H. axyridis*, also consumed the largest number of CPB eggs when larvae successfully completed development (Fig. 2D), it was difficult to predict how changes in species composition might impact potato beetle control. Thus, we calculated the total number of eggs eaten by each cohort of 20 larvae of each species, including both eggs eaten by larvae that later died and those eaten by larvae that successfully completed development. As a cohort, *C. transversoguttata* larvae ate the most eggs and *H. convergens* the fewest; *H. axyridis* and *C. septempunctata* cohorts consumed nearly identical numbers of eggs (Fig. 3). However, because we did not replicate cohorts, we could not compare species using statistics.

4. Discussion

None of the four coccinellids we examined was able to complete development on a pure diet of Colorado potato beetle eggs, compared to consistently high survivorship on a pure diet of green peach aphids (Fig. 1). All species could, however, complete development on a mixed diet of both aphids and potato beetle eggs. For both *Coccinella* species, inclusion of CPB eggs in their

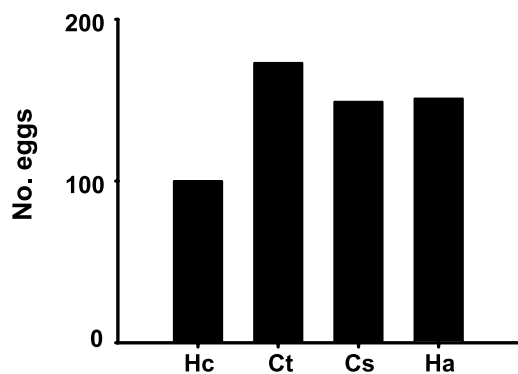


Fig. 3. Total number of CPB eggs consumed by the cohort of 20 larvae of each species, including those that died before reaching the adult stage; data in Fig. 2D are the number of eggs consumed by larvae that successfully completed development only.

diet did not limit the proportion of larvae surviving to adulthood; these two species did, however, eat the fewest CPB eggs as larvae (Fig. 2D). For the other two species, the native *H. convergens* and the exotic *H. axyridis*, inclusion of CPB eggs along with aphids significantly reduced survivorship. This higher mortality correlated with relatively high CPB egg consumption rates; *H. convergens* and *H. axyridis* that completed development ate significantly more CPB eggs as larvae than did either *Coccinella* species. All species showed a trend toward more rapid development on a pure diet of aphids, compared to a mixed GPA and CPB egg diet, and overall developmental rates among the four species were significantly shorter when fed the mixed diet in the experiment where all species were reared simultaneously. In this same experiment both *Coccinella* species exhibited reduced adult size on the mixed prey diet, but this effect was not apparent when the species were examined individually. Overall, across all of the experiments survivorship differences were more consistent than were developmental time and adult size effects. Munyaneza and Obrycki (1998b) found similar results working with the coccinellid *C. maculata*. For this species larval survivorship was as low as 1.7% on a pure beetle egg diet, compared to survivorship as high as 85% on a pure diet of pea aphids (Munyaneza and Obrycki, 1998b).

Omnivory among insects is believed to allow generalists to achieve nutritional balance (Bernays and Minkenberg, 1997; Denno and Fagan, 2003), survive periods when any single food is scarce (Riechert and Lockley, 1984; Symondson et al., 2002), and move from one habitat to another to avoid predators (Schmitz, 1994; Singer and Bernay, 2003). The benefits of food mixing can lead to higher predator densities and improved biological control. For example, many primarily predaceous hemiptera also engage in plant feeding, which complements nutrition from animal prey and allows survival when insect prey are scarce (Cohen, 1990). Eubanks and

Denno (1999, 2000) demonstrated that predaceous big-eyed bugs (*Geocoris punctipes* Say) exhibited higher survivorship when provided with high quality plant food. In field plots where high quality plant food was present, big-eyed bug densities were higher and so pest densities were lower (Eubanks and Denno, 2000). However, in other cases generalist predators actually suffered from including multiple prey in their diets. For example, Toft and Wise (1999a) found that wolf spiders (*Schizocosa ocreata* Hentz) reared on a diet that mixed a low quality prey (the aphid *Aphis nerii* Boyer de Fonscolombe) with higher quality prey exhibited lower survivorship, compared to spiders reared on pure diets of higher quality prey. The spiders would repeatedly feed on low quality prey, apparently unable to form an aversion to them even though the developmental consequences were dire (Toft and Wise, 1999b).

As for other predators, for coccinellids prey mixing sometimes improves, but in other cases actually disrupts, reproduction and development. Evans et al. (1999) compared egg production by two coccinellids, the native *C. transversoguttata* and the introduced *C. septempunctata*, on a mixed diet of weevil larvae (*Hypera postica* Gyllenhal) and limited numbers of pea aphids. They found that both coccinellid species produced more eggs on the mixed diet, compared to pea aphids alone. Similarly, Snyder et al. (2000) found that *H. axyridis* larvae reared on poor quality prey (the aphid *A. nerii*) improved their performance by also cannibalizing smaller conspecifics. Perhaps the best examples of negative effects of dietary mixing by coccinellids come from the well-studied *C. maculata*—aphid—Colorado potato beetle system in eastern North America. *C. maculata* survivorship consistently declined when potato beetle eggs were included in the coccinellid's diet (Hazzard and Ferro, 1991; Munyaneza and Obrycki, 1998a,b). Still, *C. maculata* adults and larvae readily fed on CPB eggs (Hazzard and Ferro, 1991; Hazzard et al., 1991; Munyaneza and Obrycki, 1997a,b, 1998a,b). These results are similar to what we found with the four common species in Washington. All species suffered some cost in reduced survivorship, smaller adult size or delayed development when CPB eggs were included in their diet. Still, all species continued to feed on CPB eggs, even when ad libitum aphids were also provided. However, the two species that ate the fewest CPB eggs as larvae, *C. transversoguttata* and *C. septempunctata*, also had the highest survivorship on a mixed diet of both aphids and potato beetle eggs. It is unclear whether the *Coccinella* species are somewhat repulsed by CPB eggs, or simply relatively more strongly attracted to aphids.

Throughout North America, there is growing evidence that invasion by *C. septempunctata* and *H. axyridis* has been followed by declines in some native coccinellid species (Brown and Miller, 1998; Day et al., 1994; Elliot et al., 1996; Evans, 2000; Michaud, 2002;

Tedders and Schaeffer, 1994; Wheeler and Stoops, 1996). However, there is little information on whether introduction of these species indeed has led to improved aphid biological control (Brown and Miller, 1998). Both of these species are generalists (Hodek and Honek, 1996), feeding on aphids but also other prey including other predators (Evans et al., 1999; Michaud, 2002) and parasitoids (Snyder and Ives, 2003). Indeed, several authors have suggested that predation of native coccinellids by the exotics has sped species replacement (Cottrell and Yeargan, 1999; Evans, 1991; Kajita et al., 2000; Michaud, 2002; Obrycki et al., 1998). The broad prey range of *C. septempunctata* and *H. axyridis* makes it likely that they alter food webs in agroecosystems in complex and unpredictable ways (Snyder et al., 2004).

Coccinellid adults move through the landscape with females laying eggs as they locate aphids (Evans, 2003). Thus, in eastern Washington changes in coccinellid species composition likely reflect the successful development of coccinellid larvae within many crop and non-crop habitats (e.g., Elliot et al., 1996), not just larval performance in potatoes. Rather, landscape level changes in coccinellid species composition affect that in potatoes by altering the available source pool of immigrants (Evans, 2000, 2003; Wissinger, 1997). Then, the abundance of coccinellid larvae in potatoes will, in part, reflect the ability of locally common species to complete development on available prey once coccinellids are in the crop (Munyanza and Obrycki, 1997b). Larvae of the two *Coccinella* species exhibited similar performance on a mixed aphid and potato beetle diet, and so the local replacement of *C. transversoguttata* by *C. septempunctata* might not have altered overall rates of the successful development of coccinellid larvae in potatoes.

In contrast to the exotic *C. septempunctata*, the most recent invader, *H. axyridis*, exhibited significantly reduced larval survivorship on a mixed diet of aphids and potato beetle eggs. However, the per capita consumption rate of CPB eggs by *H. axyridis* was high, and so as a cohort the 20 *H. axyridis* larvae consumed similar numbers of CPB eggs as did the *C. septempunctata* cohort, more than the cohort of *H. convergens* but less than the *C. transversogutta* larvae as a group (Fig. 3); the higher per capita consumption rate by *H. axyridis* somewhat compensated for this species' higher mortality risk on a diet including CPB eggs. This suggests that CPB biological control might be unchanged following *H. axyridis* invasion, provided that the lower rate of successful larval development in potatoes does not alter *H. axyridis* densities landscape-wide. However, several important biological features are missing from this simple comparison across cohorts. Additional data for each coccinellid species such as the relative attractiveness of potatoes as egg-laying sites for females, CPB consumption rates by adults, the impact of CPB consumption on reproductive success, and larva–larva interactions are needed to

formulate a mathematical model of population dynamics that fully addresses how coccinellid species replacements affect biological control.

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