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## Intraguild predation and successful invasion by introduced ladybird beetles

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**Abstract** Introductions of two ladybird beetle (Coleoptera: Coccinellidae) species, *Coccinella septempunctata* and *Harmonia axyridis*, into North America for aphid biocontrol have been followed by declines in native species. We examined intraguild predation (IGP) between larvae of these two exotic species and larvae of the two most abundant native coccinellids in eastern Washington State, *C. transversoguttata* and *Hippodamia convergens*. In pairings between the two native species in laboratory microcosms containing pea (*Pisum sativum*) plants, neither native had a clear advantage over the other in IGP. When the natives were paired with either *Harmonia axyridis* or *C. septempunctata*, the natives were more frequently the victims than perpetrators of IGP. In contrast, in pairings between the exotic species, neither had an IGP advantage, although overall rates of IGP between these two species were very high. Adding alternative prey (aphids) to microcosms did not alter the frequency and patterns of relative IGP among the coccinellid species. In observations of encounters between larvae, the introduced *H. axyridis* frequently survived multiple encounters with the native *C. transversoguttata*, whereas the native rarely survived a single encounter with *H. axyridis*. Our results suggest that larvae of the native species face increased IGP following invasion by *C. septempunctata* and *H. axyridis*, which may be contributing to the speed with which these exotic ladybird beetles displace the natives following invasion.

**Keywords** Generalist predators · Invasive species · Aphids · Classical biological control

### Introduction

Invasive exotic species often do significant ecological and economic damage (Williamson 1996). A number of factors contribute to an exotic species being a successful invader, including release from natural enemies and parasites (Torchin et al. 2003) and ecological disturbance by humans that opens colonization sites (Mack et al. 2000). However, most introduced species fail to invade successfully (Mack et al. 2000), and ecologists remain limited in their ability to identify likely successful invaders before the fact. Intentional introductions of exotic natural enemies to improve pest control (“classical biological control”) provide the opportunity to study invasiveness rigorously, because these introductions are planned and so can be followed from the beginning (Maron and Vilà 2001). Some biocontrol introductions are spectacular successes, but most fail (Waage and Mills 1992); understanding the underlying basis for failure versus success of classical biological control might yield general insight into biological invasions.

Ladybird beetles (Coleoptera: Coccinellidae) have regularly been introduced into North America from other continents in an attempt to improve biocontrol of aphids and other homopteran pests (DeBach and Rosen 1991). While early introductions tended to be of fairly specialized ladybirds (DeBach and Rosen 1991), recently two coccinellids with more catholic feeding habits—*Coccinella septempunctata* L. and *Harmonia axyridis* Pallas—have been introduced for aphid biocontrol and have become established throughout much of North America (Day et al. 1994; Tedders and Schaeffer 1994; Wheeler and Stoops 1996; Elliot et al. 1996; Brown and Miller 1998). Both beetles feed not only on aphids, but also on a wide range of non-aphid prey including other predators (Evans 1991; Osawa 1993; Hodek and Honek 1996; LaMana and Miller 1996; Obrycki et al. 1998; Cottrell and Yeargan 1999;

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Kajita et al. 2000). Because both ladybird species frequently engage in intraguild predation (IGP), the risk of undesirable non-target impacts is likely heightened. Indeed, their invasion has been followed by sudden and dramatic declines in the density of several native ladybirds (Day et al. 1994; Tedders and Schaeffer 1994; Elliot et al. 1996; Wheeler and Stoops 1996; LaMana and Miller 1996; Brown and Miller 1998); several authors have suggested that IGP of natives by exotics is likely contributing to these declines (Evans 1991; Obrycki et al. 1998; Cottrell and Yeargan 1999; Kajita et al. 2000; Michaud 2002).

Here, we present an examination of IGP among larvae of a community of ladybird beetles found in eastern Washington State. We examine interactions between two native species (*Coccinella transversoguttata* Brown and *Hippodamia convergens* Guérin-Méneville), a well-established exotic species (*C. septempunctata*), and a second exotic that has just begun invading the region (*Harmonia axyridis*). Larvae of the three species already common in the state overlap both temporally and spatially throughout the growing season in a variety of regional crops (Youssef 2000), and so interactions among these species are common in the field. Because *H. axyridis* is still rare locally, we have less information on the frequency of encounters between this species and the others, although in other parts of the state we have observed *H. axyridis* larvae foraging with larvae of the other species (W.E. Snyder, personal observation), and larvae of *H. axyridis* and *C. septempunctata* commonly prey upon one another in the field in their native ranges (Hironori and Katsuhiko 1997). Our work expands on earlier studies of IGP between larvae of native and exotic coccinellids by including plants in the experimental arenas, examining the influence of alternative prey (aphids) on IGP rates, and examining interactions among multiple native and exotic coccinellid species. Previous studies have included some of these elements and some of the species that we examined (e.g., Evans 1991; Obrycki et al. 1998; Cottrell and Yeargan 1999; Kajita et al. 2000; Yasuda et al. 2001; Michaud 2002), but never all of these elements together and never for pairings among the four coccinellid species that we report on here.

## Materials and methods

### The ladybird beetle community

Prior to the early 1990s, two species of native coccinellids dominated agricultural fields in eastern Washington and northern Idaho: *H. convergens*, and *C. transversoguttata* (Elberson 1992), with individuals of *H. convergens* making up 80% of the community and *C. transversoguttata* making up most of the other 20%.

*Coccinella septempunctata* and *H. axyridis* have similar introduction histories. Numerous attempts were made to introduce both beetles into North America (Day et al. 1994; Tedders and Schaeffer 1994; Wheeler and Stoops 1996), although these intentional releases may have failed to establish the beetles. Self-sustaining populations were first located near port cities rather than near release points (Day et al. 1994; Wheeler and Stoops 1996). *Coccinella septempunctata*

reached eastern Washington and northern Idaho in the early 1990s (Elberson 1992), and by 1998 *C. septempunctata* had almost completely replaced the native *Coccinella* species, with *C. septempunctata* representing 20–34% of the coccinellid community and *C. transversoguttata* less than 1% (Youssef 2000; White and Eigenbrode 2000; Rutledge et al. 2003). However, the native *H. convergens* appeared to be more tolerant of *C. septempunctata*, and still represented 65–80% of the coccinellid community following invasion by *C. septempunctata* (Youssef 2000; White and Eigenbrode 2000). Locally, *H. axyridis* was first collected in Pullman, Wash., USA in 2000 and has not yet become abundant, although this species is now dominant throughout much of the rest of Washington State (W. Snyder, personal observation).

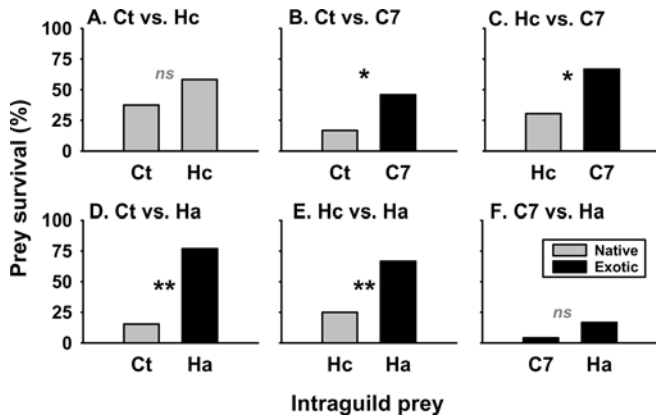
All four coccinellid species feed both on aphids and the larvae of other coccinellids (Hodek and Honek 1996, W.E. Snyder, personal observation). Of the four species we examined, based on pronotum widths, in the third instar their relative sizes are *H. convergens* < *C. transversoguttata* = *C. septempunctata* < *H. axyridis*; in the fourth instar their relative sizes are *H. convergens* < *H. axyridis* = *C. transversoguttata* < *C. septempunctata* (W.E. Snyder and G. Clevenger, unpublished data).

### Experiments

Founders of our ladybird beetle colonies were collected in eastern Washington State. Beetles were 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. Larvae were separated at hatching and reared individually on the same diet and under the same environmental conditions as adults.

Our experiments consisted of two sets of pairings, one with one species as a fourth instar larva (“predator”) and the other species as a third instar larva (“prey”); and a second set with these predator–prey roles reversed. We chose to pair fourth and third instar larvae because: (1) coccinellid larvae spend >75% of developmental time, and consume >75% of total prey eaten as larvae, while in these two instars (Hodek and Honek 1996), making them the most likely instars to interact in the field; and (2) preliminary experiments revealed that larvae in the same instar rarely preyed upon one another, while IGP almost always resulted when stages were very different in size (e.g., larvae with eggs, fourth instar larvae with first instar larvae; S. Yang, W. Snyder and G. Clevenger, unpublished data). Each experiment also included eight to ten larvae of each prey species individually caged without a predator and serving as no-IGP controls; these larvae were always recovered alive at the end of the trial.

Our microcosms were 8 cm-wide × 20 cm-tall plastic cylinders (tubes), covered on the top with organdy mesh. The tubes were placed over ca. 10 cm-tall pea (*Pisum sativum* L.) plants. The bottom of the tube was twisted into the soil, preventing larvae from escaping. In this first set of pairings, the prey larva was added to the tube first, and allowed to acclimate to the tube for 12 h (overnight). At 0900 hours the next morning we added the predator larva to the tube, allowed the predator and prey larvae to interact for 8 h, and then carefully searched each tube and recorded whether either larva had been eaten. We measured the pronotum width of each larva before adding it to the microcosm, to enable us to calculate the size advantage of the predator larva in each pairing. Pronotum width is a reliable means to compare size among larvae, whereas for the soft bodied larvae other measures such as total body length and weight fluctuate with food and water consumption (Preziosi et al. 1999). We established 24 replicates of each predator-prey pairing, for each of the 12 possible combinations of each species as predator and prey. Microcosms were housed in a greenhouse at conditions identical to those under which the colonies were maintained (see above). Predation rates were compared statistically by Chi-square, and the relative magnitude of size advantage in the two pairings was compared using a *t*-test. We examined the relationship between size



**Fig. 1a–f** Intraguild predation among (a) *C. transversoguttata* (Ct) and *H. convergens* (Hc), (b) *C. transversoguttata* and *C. septempunctata* (C7), (c) *H. convergens* and *C. septempunctata*, (d) *C. transversoguttata* and *H. axyridis* (Ha), (e) *H. convergens* and *H. axyridis* and (f) *C. septempunctata* and *H. axyridis*. Within each pairing, third instars (“Intraguild Prey”) were paired with fourth instars (“Intraguild Predator”) of the other species, and vice versa. Black bars represent pairings in which exotic species were prey, while grey bars represent those in which native species were prey; histograms give the percent of replicates in which prey survived, and asterisks indicate a significant difference (Chi-square; \* $0.01 \leq P < 0.05$ , \*\* $P < 0.01$ )

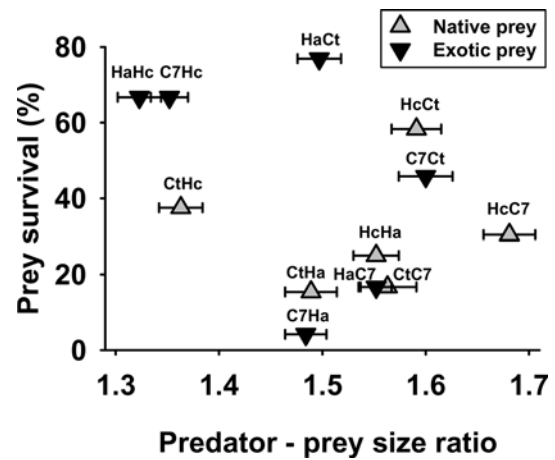
advantage and IGP using linear regression. These and all subsequent statistical analyses were performed using SYSTAT (SPSS, Chicago, Ill., USA).

We repeated a subset of the pairings in microcosms like those described above, but including ten aphids (pea aphids, *Acyrtosiphon pisum*) in half of the 24 replicates of each predator–prey pairing. This density of pea aphids is common in the field (White and Eigenbrode 2000; Snyder and Ives 2003; Rutledge et al. 2003). We included alternative prey because they will sometimes lower rates of IGP (e.g., Lucas et al. 1998). This second series included all pairings of the native species with one another and with each of the two exotic species. We did not again pair *C. septempunctata* and *H. axyridis*; the impact of alternative prey on IGP between these species has been reported elsewhere (Hironori and Katsuhiko 1997). We added the aphids 12 h (overnight) before the addition of coccinellid larvae to the microcosms, to allow the aphids a chance to settle into feeding positions on the plants. We then added both the prey and predator beetle larvae simultaneously at 0900 hours, so that an early-added larva did not deplete aphids. Necessarily, this meant that the prey larvae did not have time to become acclimated to the microcosms. The larvae were allowed to interact for 8 h before the tubes were searched and predation events recorded. For each prey coccinellid, we compared mortality rates in the paired tubes with and without aphids using Chi-square.

We conducted a third set of pairings in our microcosms, this time also including conspecifics as predators. We focused on pairings between the two native species, *H. convergens* and *C. transversoguttata*, and the beetle that proved to be the more aggressive intraguild predator of the two exotic species, *H. axyridis*. We conducted three sets of experimental pairings, again using our plastic tube microcosms, separately examining each of the three species (*C. transversoguttata*, *H. convergens*, and *H. axyridis*) as the prey. In all three sets of pairings *C. transversoguttata*, *H. convergens*, and *H. axyridis* were the fourth instar predators.

#### Behavioral observations

We paired third and fourth instar *C. transversoguttata* and *H. axyridis* larvae, with predator–prey roles reversed in half of the replicates, and observed their interaction for 1 h. Here, we used



**Fig. 2** Relationship between size differential (Predator pronotum width/Prey pronotum width  $\pm 1$  SE) and the percent of replicates where the prey survived, for each pairing presented in Fig. 1. Each pairing is presented as Prey/Predator. For example, *HaHc* represents the pairing where *H. axyridis* was the intraguild prey, and *H. convergens* the intraguild predator. Black symbols represent pairings in which exotic species were prey; grey symbols represent those in which native species were prey

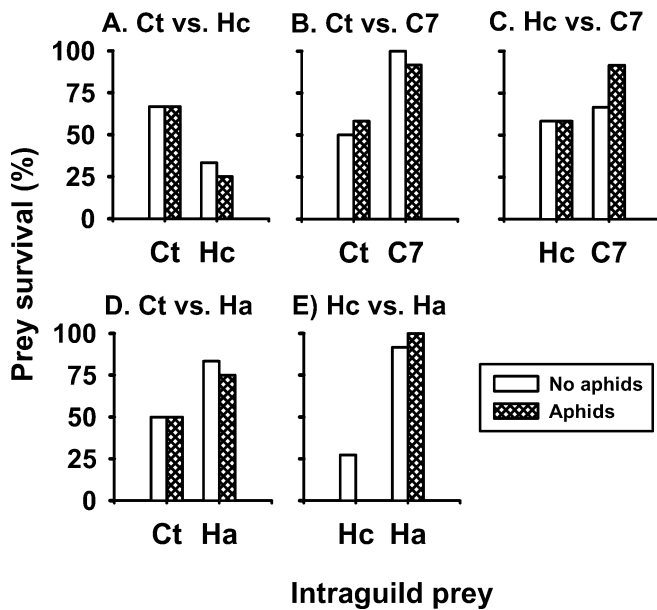
simple arenas, 100-mm  $\times$  15 mm plastic petri dishes, empty but for the two larvae. Our goal was to observe as many direct interactions as possible rather than to mimic precisely the conditions in the microcosms with plants. For each of the 20 replicates of each pairing, we recorded the time to first encounter (an encounter was scored anytime that the two animals touched one another), the number of encounters survived, and whether a pairing resulted in IGP.

## Results

Neither native species had an IGP advantage over the other ( $X^2=2.09$ ,  $df=1$ ,  $P=0.15$ ; Fig. 1a). Both native species were more often victims of IGP when paired with the exotic *C. septempunctata* ( $X^2=4.75$ ,  $df=1$ ,  $P=0.029$  for pairings of *C. transversoguttata* and *C. septempunctata*;  $X^2=6.17$ ,  $df=1$ ,  $P=0.013$  for pairings of *H. convergens* and *C. septempunctata*; Fig. 1b,c). The native species also were more often victims in pairings with the more recent invader, *H. axyridis*, ( $X^2=19.81$ ,  $df=1$ ,  $P<0.001$  for pairings of *C. transversoguttata* and *H. axyridis*;  $X^2=8.39$ ,  $df=1$ ,  $P=0.004$ ; for pairings of *H. convergens* and *H. axyridis*, Fig. 1d,e). When the two exotic species were paired together, neither species had an IGP advantage over the other ( $X^2=2.01$ ,  $df=1$ ,  $P=0.16$ ; Fig. 1f), but IGP was very frequent, occurring in over 80% of both pairings. Overall, there was no relationship between the size advantage of the intraguild predator and its rate of IGP ( $R^2=0.129$ ,  $P=0.252$ ; Fig. 2).

We repeated the pairings of the native species with one another, and with the introduced species, but this time included alternative prey (aphids) in half of the microcosms. The relative IGP advantages were the same as those that occurred in the first group of pairings without prey. In no case did the addition of aphids significantly alter the likelihood of IGP occurring (Chi-squared with





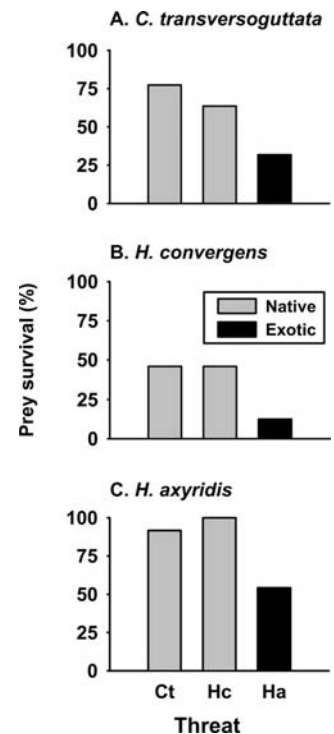
**Fig. 3a–e** Intraguild predation with (shaded bar) and without (open bar) ten pea aphids present as alternative prey, among **a** *C. transversoguttata* and *H. convergens*, **b** *C. transversoguttata* and *C. septempunctata*, **c** *H. convergens* and *C. septempunctata*, **d** *C. transversoguttata* and *H. axyridis*, and **e** *H. convergens* and *H. axyridis*. Prey species are listed on the x-axis, symbols as in Fig. 1

$df=1$ ;  $P>0.10$  for all comparisons of IGP on each intraguild prey species by each intraguild predator species in the presence versus absence of aphids; Fig. 3).

In the second series of pairings that included conspecific predators, both natives were significantly more likely to be preyed upon by the introduced predator *H. axyridis* than by native conspecifics (*C. transversoguttata*:  $X^2=9.17$ ,  $df=1$ ,  $P=0.002$ ; *H. convergens*:  $X^2=6.45$ ,  $df=1$ ,  $P=0.011$ ; Fig. 4a,b). Overall, IGP rates on both natives were higher when paired with *H. axyridis* than with one another or conspecifics (pooled mortality in the *H. convergens* and *C. transversoguttata* treatments versus that in the *H. axyridis* treatment; *C. transversoguttata*:  $X^2=8.96$ ,  $df=1$ ,  $P=0.003$ ; *H. convergens*:  $X^2=8.79$ ,  $df=1$ ,  $P=0.012$ ; Fig. 4a,b). In contrast, *H. axyridis* was preyed upon more often by conspecifics than by the two native species ( $X^2=18.77$ ,  $df=1$ ,  $P<0.001$ ; Fig. 4c).

In observed pairings, the time to first encounter did not differ between trials in which *H. axyridis* fourth instar larvae (predator) were paired with *C. transversoguttata* third instar larvae (prey) and those in which predator–prey roles for these species were reversed ( $F_{1,37}=2.15$ ,  $P=0.15$ ; Fig. 5a). Prey *C. transversoguttata* were usually preyed upon by *H. axyridis*, while only one *H. axyridis* prey was killed by a *C. transversoguttata* predator ( $X^2=24.86$ ,  $df=1$ ,  $P<0.001$ ; Fig. 5b). *Coccinella transversoguttata* larvae rarely survived more than one encounter with *H. axyridis*, but on average *H. axyridis* survived three encounters with the native ( $F_{1,37}=21.51$ ,  $P<0.001$ ; Fig. 5c).

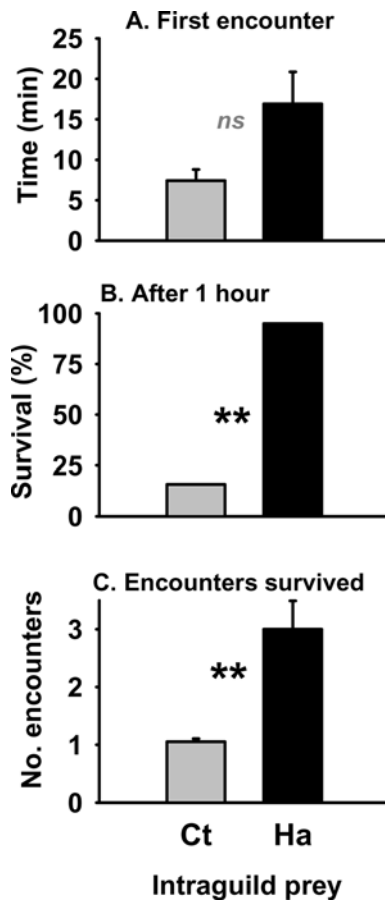
**Fig. 4a–c** Intraguild predation and cannibalism by two native predators, *C. transversoguttata* and *H. convergens*, and the exotic predator, *H. axyridis*, on third instar larvae as prey **a** *C. transversoguttata*, **b** *H. convergens*, and **c** *H. axyridis*



## Discussion

The two native species were equally likely to prey upon one another, but both were more likely to be preyed upon by the exotic species *C. septempunctata* and *H. axyridis* than vice versa. IGP was very frequent between the two exotic species, but neither had an advantage over the other. For the natives, cannibalism was less frequent than IGP by *H. axyridis*, but for *H. axyridis* cannibalism posed a greater threat than IGP by either native. We found that the native *C. transversoguttata* was almost always killed upon its first encounter with a larger *H. axyridis* larva, while prey *H. axyridis* usually survived several encounters with the native *C. transversoguttata*. We have found very similar results in observed pairings of the other native, *H. convergens*, with *H. axyridis* (W. Snyder, G. Clevenger and S. Eigenbrode, unpublished data). If our laboratory studies accurately reproduce field behavior, we suggest that IGP pressure on our native ladybird beetles increased previously with invasion by *C. septempunctata* and will increase further with invasion by *H. axyridis*. The next step will be to reproduce species pairings in larger arenas in the field. These species commonly co-occur both spatially and temporally in both North America (Youssef 2000) and, for *H. axyridis* and *C. septempunctata*, in their native range (Hironori and Katsuhiko 1997). So, IGP in the field is likely, as has been demonstrated between *H. axyridis* and *C. septempunctata* larvae in Asia (Hironori and Katsuhiko 1997).

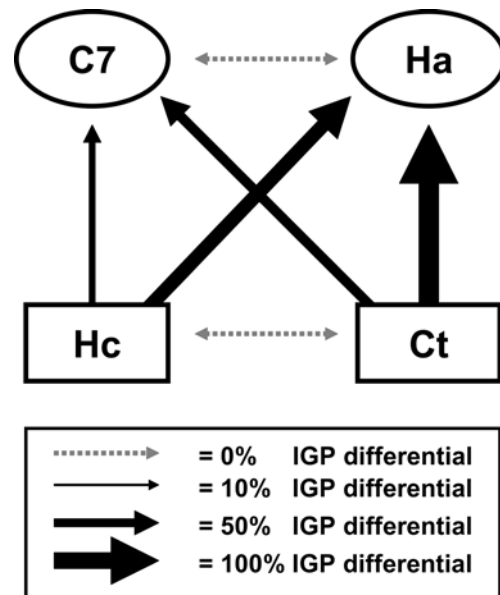
Both *C. septempunctata* and *H. axyridis* are well-documented intraguild predators (Evans 1991; Cottrell and



**Fig. 5a–c** Outcome of 1-h observations between the native beetle *C. transversoguttata* (Ct) and the introduced beetle *H. axyridis* (Ha). **a** Time (min) to first encounter, **b** percent alive after 1 h and **c** number of encounters survived during the observation period (\*\* $P < 0.01$ )

Yeargan 1999; Kajita et al. 2000; Snyder and Ives 2003), and several authors have suggested that IGP might be facilitating invasion by these beetles (Evans 1991; Cottrell and Yeargan 1999; Yasuda and Ohnuma 1999; Michaud 2003). Research on *H. axyridis* in its native range in Asia suggests that this species is a particularly successful intraguild predator there as well, even against *C. septempunctata* with which it is widely sympatric (Hironori and Katsuhiko 1997; Kajita et al. 2000; Yasuda and Ohnuma 1999; Yasuda et al. 2001). Indeed, arrival of *H. axyridis* into several parts of North America has been followed by declines in *C. septempunctata* abundance (Wheeler and Stoops 1996; Brown and Miller 1998). Perhaps as telling, the failure of a species native to North America and Europe, *Adalia bipunctata*, to invade Japan successfully has been linked to this species' vulnerability to IGP by *H. axyridis* (Kajita et al. 2000). We suggest that success at IGP enhances the invasiveness of ladybird beetles by increasing their negative effects on potential competitors (Fig. 6).

It is surprising that the likelihood of IGP was not related to the size differential between predator and prey in our experiments (Fig. 2), because IGP hierarchies often are characterized by larger predators preying on smaller ones



**Fig. 6** Summary of IGP for pairings of the two native species (square box), *C. transversoguttata* (Ct) and *H. convergens* (Hc), and the two exotic species (open oval), *C. septempunctata* (C7) and *H. axyridis* (Ha). Direction of arrow indicates the direction of IGP advantage—that is, they point from IGP victim to IGP predator. Arrow thickness represents the proportion IGP by the more successful intraguild predator minus the proportion IGP by the less successful intraguild predator. Gray arrows indicate pairings where neither species had a statistically significant advantage over the other. This web was calculated from the pairings presented in Fig. 1

(e.g., Wissinger 1992; Snyder and Hurd 1995; Lucas et al. 1998). Relative IGP advantage among the coccinellids we tested must be determined by behavioral and defensive differences not related to size and influencing (1) ability to capture intraguild prey, and (2) ability to avoid attack by an intraguild predator. *Harmonia axyridis* evidently is using both types of mechanisms to gain an advantage over the native coccinellids. As the intraguild predator, *H. axyridis* was able to capture and kill larvae of the two native species over 70% of the time, whereas as the intraguild prey, it was only captured and killed 25% of the time. *H. axyridis* successfully perpetrated IGP at a higher rate than any species we examined, despite not always being the largest species, and as prey it avoided IGP more successfully than any species we examined. Yasuda et al. (2001) observed encounters between *H. axyridis* and *C. septempunctata* larvae collected from local populations in Japan, where both species are native. They observed that *H. axyridis* larvae attacked *C. septempunctata* more often than *C. septempunctata* attacked *H. axyridis*, and that when attacked *H. axyridis* escaped more often than did *C. septempunctata*. We have begun to investigate the mechanisms that *H. axyridis* uses to gain an advantage against the two native species in our system, and our early results suggest that *H. axyridis* both attacks more successfully and escapes more frequently through a combination of strongly adhesive tarsi and an effective chemical defense (S. Eigenbrode, W. Snyder and G. Clevenger, unpublished data).

While IGP may be contributing to coccinellid species replacement, it is likely that multiple factors act in concert to speed declines in native species. Evans (2004) reported lower densities of both the aphid *A. pisum* and native coccinellids in Utah alfalfa fields following invasion by *C. septempunctata*. Evans (2004) suggested that *C. septempunctata* was depressing aphid densities to levels that were no longer attractive to the adults of native coccinellids, which forage widely across landscapes in search of aphid colonies. Indeed, when aphid densities were experimentally increased in alfalfa plots by excluding *C. septempunctata* and other aphid predators, native coccinellids were attracted to these localized aphid outbreaks at densities similar to those seen before *C. septempunctata* invasion (Evans 2004). However, it was unclear whether sufficient numbers of native coccinellids remained regionally to respond to aphid outbreaks over larger spatial scales (Evans 2004). If it is generally true that *C. septempunctata* is attracted to aphid outbreaks at lower densities than are native coccinellids, and so arrives at aphid colonies sooner, this could exacerbate the IGP advantage over natives that we report here. This is because relatively early arrival at an aphid outbreak should give the progeny of initial *C. septempunctata* colonists a head start on development compared to later-arriving natives, with the resulting size advantage of *C. septempunctata* giving this species an overwhelming advantage in IGP (e.g., Snyder and Hurd 1995). Indeed, early colonization by exotic coccinellids, and thus dramatic differences in the size structure of larvae within a patch, could render irrelevant the relatively subtle advantages between third and fourth instar larvae that we found. Evans (2004) focused on colonization by adult coccinellids; it would be worthwhile to examine how differences in colonization time impact the survivorship of the offspring of these colonists, and to determine whether *H. axyridis* is also attracted to low-density aphid infestations.

Further work is needed to determine how introductions of arthropod generalist predators like ladybird beetles have altered the trophic structure of aphid predator guilds, and whether their introduction has indeed improved biological control. Intraguild predation by generalist predators can disrupt biological control, worsening pest problems (Polis et al. 1989; Rosenheim et al. 1995). There is evidence that some ill-advised biocontrol introductions have had negative impacts on native species (Howarth 1991; Simberloff and Stiling 1996; Louda et al. 1997). Because they are generalists we might expect further alteration of insect communities by *C. septempunctata* and *H. axyridis*. For example, *H. axyridis* has been shown to feed on the pupae of parasitoid wasps, contributing to disruption of biocontrol by the highly effective specialists (Snyder and Ives 2003). These impacts might be widespread because the beetles also commonly occur in non-agricultural habitats (LaMana and Miller 1998). A theoretical explanation for the invasiveness of species, if it can be achieved, will have to be built upon understanding how specific exotic species can overwhelm native competitors. Regardless of their impact on biological control, it is evident that *H. axyridis*

and *C. septempunctata* are altering insect communities by outcompeting native coccinellids. Our study suggests negative interactions among larvae could be one mechanism contributing to these species replacements.

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