Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae

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Abstract

Predation upon lady beetle (Coleoptera: Coccinellidae) eggs in the field is most often instances of egg cannibalism by larvae or adults while the majority of the remaining predation events upon coccinellid eggs is done by other species of Coccinellidae. Thus the recent introduction and establishment of *Harmonia axyridis* in the US could negatively affect native species of Coccinellidae via egg predation. However, little is known regarding the suitability of interspecific coccinellid eggs as a food source for larval development. In this study, it was found that native first or third instar *Coleomegilla maculata* and *Olla v-nigrum* larvae were incapable of surviving to the adult stage when provided solely exotic *H. axyridis* eggs. In stark contrast, *H. axyridis* larvae survived equally well when cannibalizing eggs or eating eggs of either native species. When *C. maculata* and *O. v-nigrum* were grouped as 'native' and compared with the exotic *H. axyridis*, more native eggs were attacked than exotic eggs and a higher percentage of eggs was attacked by *H. axyridis* larvae. Native and exotic larvae attacked a similar percentage of native eggs but native larvae attacked significantly fewer exotic eggs than did exotic larvae. These data suggest that *H. axyridis* may prey upon the eggs of these native species, when encountered in the field, compared with the likelihood of the native species preying upon *H. axyridis* eggs. Therefore, eggs of the native species *C. maculata* and *O. v-nigrum* will continue to be subjected to cannibalism and also to possible predation by other native species and the exotic *H. axyridis*.
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1. Introduction

Introduction of the multicolored Asian lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), into the US was first documented in 1916. Subsequent releases at various locations in the US continued through the 1980's and accidental introductions at seaports are another probable source (Gordon, 1985; Tedders and Schaefer, 1994). This new species quickly spread across much of North America (Chapin and Brou, 1991; Colunga-Garcia and Gage, 1998; Cottrell and Yeargan,

1998c; Dreistadt et al., 1995; Hesler et al., 2001; Krafsur et al., 1997; LaMana and Miller, 1996; Michaud, 2002; Tedders and Schaefer, 1994; Coderre et al., 1995). Harmonia axyridis now thrives in North American habitats such as forests, orchards, and row crops (Colunga-Garcia and Gage, 1998; Tedders and Schaefer, 1994; Wallace and Hain, 2000). In fact, *H. axyridis* is one of the predominant coccinellid species in pecan orchards, *Carya illinoinensis* (Wangenh.) C. Koch (TEC, unpublished data), apple orchards, *Malus pumila* Mill. (Brown and Miller, 1998), citrus groves (*Citrus* spp.) (Michaud, 2002), tobacco fields (*Nicotiana tabacum* L.) (Wells and McPherson, 1999), and sweet corn plantings (*Zea mays* L.) (Cottrell and Yeargan, 1998c). A literature review for *H. axyridis* is provided by Koch (2003).

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A combination of traits most likely contributed to successful and rapid establishment of *H. axyridis* in North America. These traits include high fecundity (Michaud, 2002), aggressive behavior (Kajita et al., 2000; Michaud, 2002; Yasuda and Ohnuma, 1999), high mobility (With et al., 2002), large body size (Michaud, 2002), low susceptibility to a parasitoid (Hoogendoorn and Heimpel, 2002), low susceptibility to pathogens adapted to native Coccinellidae (Cottrell and Shapiro-Ilan, 2003), and a polyphagous diet (Hodek and Honék, 1996). This polyphagous diet, that includes various insect pest species, also has been reported to include non-pest species such as *Danaus plexippus* (Lepidoptera: Nymphalidae) larvae (Koch et al., 2003) and natural enemies as observed through instances of intraguild predation on eggs and larvae of the native *C. maculata* in the field (Cottrell and Yeargan, 1998a,b,c).

Harmonia axyridis has invaded habitats already colonized by species of native Coccinellidae, thus increasing the likelihood of intraguild predation between the native and exotic species. Elliot et al. (1996) suggested that invasion of the US by the exotic *Coccinella septempunctata* (Coleoptera: Coccinellidae) may have reduced populations of certain native species. In fact, *H. axyridis* is commonly reported as an intraguild predator when studies involve *C. septempunctata* and *H. axyridis* (Kajita et al., 2000; Takahashi, 1989; Yasuda and Ohnuma, 1999; Yasuda et al., 2001). Laboratory studies by Cottrell and Yeargan (1998c) revealed that *H. axyridis* could complete development on a diet of only *C. maculata* eggs and that the outcome of intraguild interactions between larvae of these two species, when no food source was provided, typically favored *H. axyridis*.

Thus, the objective of this study was to examine inter- and intraspecific egg predation among exotic (i.e., *H. axyridis*) and native species (i.e., *O. v-nigrum* and *C. maculata*) to determine the suitability of the eggs of different species for larval development. Data were collected on survival, days required by larvae to complete development, and fresh adult weights when larvae were reared solely on eggs of each species or control diets. In addition, data were collected on consumption of the eggs of each species by larvae of each species.

2. Materials and methods

2.1. Insect colonies

Laboratory colonies of *O. v-nigrum* and *H. axyridis* originated from adults collected from pecan orchards at the USDA, Agricultural Research Service, Southeastern Fruit and Tree Nut Research Laboratory at Byron, GA. The *C. maculata* colony originated from overwintering adults collected near Lexington, KY, USA with intermittent addition of field-collected adults from the USDA

laboratory at Byron, GA, USA. Each species was housed in 9-cm petri dishes in an environmental chamber at $25 \pm 1\,°C$ and a photoperiod of 14:10 (L:D) h. *O. v-nigrum* and *H. axyridis* were fed live blackmargined aphids (*Monellia caryella* [Homoptera: Aphididae]), yellow pecan aphids (*Monelliopsis pecanis* [Homoptera: Aphididae]), frozen *Helicoverpa zea* [Lepidoptera: Noctuidae] eggs, frozen *Ephestia kuhniella* [Lepidoptera: Pyralidae] eggs, supplemented with a ground beef-beef liver diet (Cohen, 1985), and water provided with a moistened cotton dental wick. The polyphagous *C. maculata* was fed the ground beef-beef liver diet and supplemented with lepidopteran eggs (Cottrell and Yeargan, 1998a). Aphids fed to coccinellids were reared on foliage of greenhouse-grown seedling pecans (Cottrell et al., 2002). Green florist paper was used to line lids of petri dishes containing adult female coccinellids (Cottrell and Yeargan, 1998a). The paper provided coccinellids an ovipositional substrate that could be easily removed and replaced. Egg clusters used in all rearing or feeding assays were from mated, laboratory-reared coccinellids. These egg clusters were collected daily and stored at $10 \pm 1\,°C$. The quantity of egg clusters needed for rearing or feeding assays usually required collection of eggs over several days; eggs used in studies were $\leqslant 7$ days old.

2.2. First instar feeding assays

First instars were obtained by collecting eggs from each of the coccinellid species, in colony, over several days and holding those eggs in an environmental chamber at $25 \pm 1\,°C$ and a photoperiod of 14:10 (L:D) h. Only larvae hatching on the same day were used for this experiment. In each of two separate trials, individual first instars were placed in petri dishes and provisioned with a moistened cotton dental wick and randomly assigned to receive *H. axyridis*, *C. maculata* or *O. v-nigrum* eggs ad libitum daily; the second trial included a control diet provided ad libitum daily (i.e., pecan aphids for *H. axyridis* and *O. v-nigrum* or the meat-based diet for *C. maculata*). Both trials used three randomized complete blocks. For each block in trial 1, 10 first instars of each species each received eggs from one of the three coccinellid species; whereas in trial 2, three first instars were used for eggs of each species and the control diet in two of the three blocks but four first instars were used in the third block. Numbers of larvae per treatment were dictated by availability of concurrent hatching eggs across species. In trial 1, nine treatment combinations (i.e., 3 predator species by 3 diets) were used and in trial 2, 12 treatment combinations (i.e., 3 predator species by 4 diets) were used. In trial 1, each of the three blocks consisted of nine stacks of petri dishes (10 petri dishes/ stack) with each stack representing a different predator species × diet combination. Treatment combinations were randomly arranged within blocks. Trial 2 used 12

stacks of petri dishes (3 or 4 dishes/stack) with treatment combinations randomly arranged within blocks. Larvae were provided their assigned diet ad libitum each day until pupation or death. In both trials, larvae were monitored daily to record the number of days to develop (e.g., duration of each instar and pupal stage and the date of adult emergence) or date of death if appropriate. Larval death was determined by failure to respond with movement when gently probed. Pupal death was determined by gently stroking the pupa with a camel hair brush. If a pupa did not respond to this slight irritation, by making itself erect after numerous gentle strokes, death was recorded. Upon pupation, remaining diet (i.e., eggs, aphids or meat-based diet) and the moistened cotton wick were removed from the petri dish such that newly emerging adults would have no source of food or water. About 24 h after adult emergence (to provide time for the cuticle to harden), individuals were weighed using a Mettler AE260 DeltaRange scale (Mettler Instrument, Hightstown, NJ).

2.3. Third instar feeding assay

Larvae from each of the coccinellid species were reared on a diet of frozen *E. kuhniella* eggs through the second instar in an environmental chamber at $25 \pm 1\,°C$ and a photoperiod of 14:10 (L:D) h. Only larvae of each species that reached the third instar on the same day were used for this experiment. The experimental design was similar to the previously described first instar feeding assays. Third instars were provisioned, ad libitum, daily with eggs from one of the three coccinellid species or a control diet of *E. kuhniella* eggs and a moistened cotton dental wick such that in each of three randomized complete blocks, five third instars of each species each received eggs of *H. axyridis*, *C. maculata*, *O. v-nigrum* or *E. kuhniella*. This resulted in 12 combinations (i.e., 3 predator species and 4 egg diets). Each of the three blocks consisted of 12 stacks of petri dishes (5 petri dishes/stack) with each stack representing a different predator species × diet combination. Treatments were randomly arranged within blocks. Larvae were monitored daily to record days to develop (i.e., duration of third and fourth instar, pupal stage, and date of adult emergence) and date of death when appropriate. About 24 h after an adult emerged, adult fresh weights were taken.

2.4. Rates of egg consumption by third instars

In a separate experiment, *H. axyridis*, *O. v-nigrum*, and *C. maculata* were reared through the second instar on a pecan aphid diet or the meat-based diet only for the latter species. Only larvae of each species that reached the third instar on the same day were selected for this experiment. Individual larvae of each species were randomly assigned to petri dishes containing a single cluster of *H. axyridis*, *O. v-nigrum* or *C. maculata* eggs and a moistened cotton dental wick. Numbers of eggs per cluster were counted before the assays began and only clusters with similar numbers of eggs (within and between species) were used. In each of four blocks of a RCB, each predator species × egg species combination was replicated using four larvae, each in an individual petri dish. The experiment was done in an environmental chamber at $25 \pm 1\,°C$ and a photoperiod of 14:10 (L:D) h. Numbers of eggs attacked (i.e., partially consumed + entirely consumed) were determined with the aid of a dissecting microscope at 3, 6, 12, 24, and 48 h after the assay began and the percentage attacked calculated.

2.5. Statistical analyses

Percentage mortality of first and third instars fed the different diets was transformed using the arcsine transformation (Zar, 1999) and analyzed using one-way ANOVA by larval species for the first and third instar feeding assays. Percentage mortality is presented as back-transformed means (±SE). Additionally, one-way ANOVA was used to analyze effect of diet on mean days to complete development and mean adult fresh weight, by species. In cases where a specific predator species × diet treatment had no larvae to complete development to the adult stage, that treatment was not considered for developmental or weight data analysis. When appropriate (i.e., $P < 0.05$), mean separation was done using Tukey's HSD (JMP, 2002). The cumulative percentage of eggs attacked by third instars at 48 h was arcsine transformed and analyzed using a two-way ANOVA. Linear contrasts were made using *C. maculata* and *O. v-nigrum* grouped as 'native' versus *H. axyridis* as the 'exotic' species. Contrasts between native and exotic were used to compare: (1) percentage of native eggs versus exotic eggs attacked, (2) percentage of all eggs attacked by native versus exotic species, (3) percentage of native eggs attacked by native versus exotic species, and (4) percentage of exotic eggs attacked by native versus exotic species (JMP, 2002). As relates to orthogonality, these contrasts were not mutually orthogonal, however, Keuhl (1994) states that selection of contrasts must not be dictated by orthogonality but rather to answer specific research questions. A comparisonwise Type I error rate of $\alpha = 0.013$ was used to assure an experimentwise Type I error rate of $\alpha = 0.05$ (Keuhl, 1994). Back-transformed means (±SE) are presented.

3. Results

3.1. First instar feeding assays

Percentage mortality of larval *C. maculata*, starting from the first instar, was significantly higher when fed

solely exotic *H. axyridis* eggs compared with other diets, in both Trial 1 ($F=94.14$; $df=2, 4$; $P<0.0004$) and Trial 2 ($F=10.44$; $df=3, 6$; $P=0.0085$) (Trial 1, Fig. 1A and Trial 2, Fig. 1B). No significant difference in mortality was detected among any of the other diets fed *C. maculata*. Similarly, percentage mortality of *O. v-nigrum*, starting from the first instar, was significantly higher

when fed solely exotic *H. axyridis* eggs compared with other diets, in Trial 1 ($F=33.59$; $df=2, 4$; $P=0.0032$) and in Trial 2 ($F=60.25$; $df=3, 6$; $P<0.0001$) (Fig. 1). Other diets had no significant effect upon mortality of *O. v-nigrum*. No diet had any significant effect upon percentage mortality of *H. axyridis* in either Trial 1 or 2 ($F=2.78$; $df=2, 4$; $P=0.1753$ and $F=3.51$; $df=3, 6$;
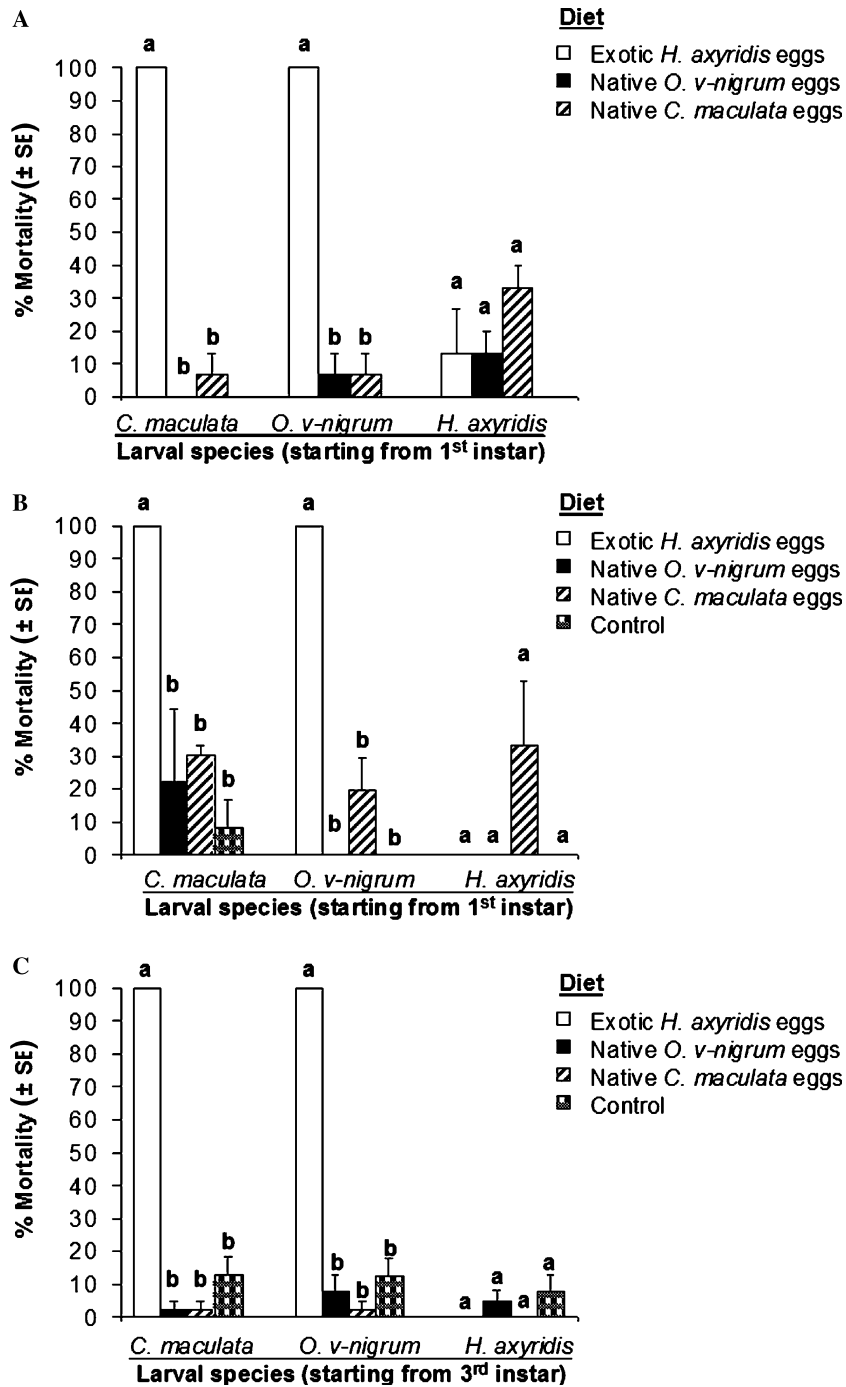

Fig. 1. Percentage mortality ($\pm$ SE) starting from the first instar in Trials 1 (A) and 2 (B) or from the third instar (C) when reared only on eggs of *C. maculata*, *O. v-nigrum* or *H. axyridis*. Trial 2 (B) included a control diet of pecan aphids for *O. v-nigrum* and *H. axyridis* or a meat-based diet for *C. maculata*, whereas *E. kuhniella* eggs were used as a control diet when starting from the third instar (C). Mean separation was done using Tukey's HSD test and significant differences ($P<0.05$) within groups of bars are indicated by different letters above individual bars.

$P = 0.0893$) (Figs. 1A and B). In Trials 1 and 2, 93.3 and 100%, respectively, of *C. maculata* died as first instars when fed only *H. axyridis* eggs. In Trial 2, the remaining 6.7% of *C. maculata* first instars molted and died during the second instar. All *O. v-nigrum* larvae, in both trials, died as first instars when fed only *H. axyridis* eggs. Percentage mortality of first instar *H. axyridis* in Trials 1 and 2 was highest (26.7 and 10%, respectively) when fed only *C. maculata* eggs.

The number of days to reach the adult stage was significantly different for *C. maculata* larvae that completed development on *C. maculata* eggs compared with *O. v-nigrum* eggs in Trial 1 ($F = 27.47$; $df = 1, 2$; $P = 0.0345$), whereas no difference in mean days to develop was found in Trial 2 for any diet although statistical significance was approached ($F = 6.79$; $df = 2, 4$; $P = 0.0518$) (Trial 1, Fig. 2A and Trial 2, Fig. 2B). No significant difference in mean number of days to complete develop-
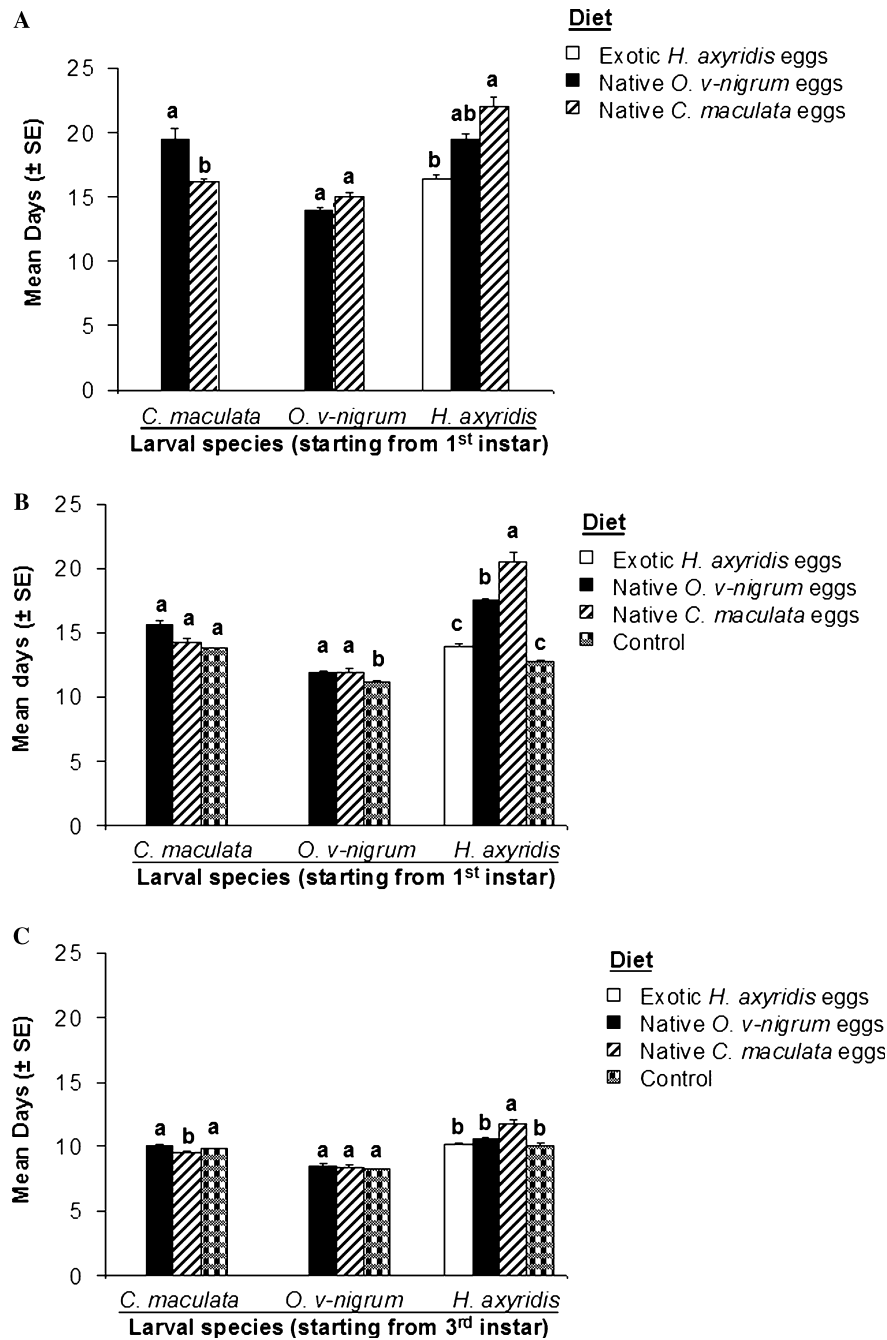

Fig. 2. Mean days to complete development (± SE) starting from the first instar in Trials 1 (A) and 2 (B) or from the third instar (C) when reared only on eggs of *C. maculata*, *O. v-nigrum* or *H. axyridis*. Trial 2 (B) included a control diet of pecan aphids for *O. v-nigrum* and *H. axyridis* or a meat-based diet for *C. maculata*, whereas *E. kuhniella* eggs were used as a control diet when starting from the third instar (C). Mean separation was done using Tukey's HSD test and significant differences ($P < 0.05$) within groups of bars are indicated by different letters above individual bars.

ment, based upon diet, were found for *O. v-nigrum* in Trial 1 ($F = 3.82$; $df = 1, 2$; $P = 0.1897$) but in Trial 2, time to develop was significantly decreased by the control diet ($F = 7.22$; $df = 2, 4$; $P = 0.0470$) (Figs. 2A and B). Development of *H. axyridis* on the diets was significantly different in Trial 1 ($F = 10.49$; $df = 2, 4$; $P = 0.0256$) and Trial 2 ($F = 91.46$; $df = 3, 6$; $P < 0.0001$) (Figs. 2A and B) with the *C. maculata* egg diet always slowing development compared with egg cannibalism and *O. v-nigrum* eggs also slowing development in Trial 2.

Fresh adult weight of *C. maculata* was significantly higher when eggs were cannibalized than when predation upon *O. v-nigrum* eggs occurred ($F = 157.63$; $df = 1, 2$; $P = 0.0063$) in Trial 1 (Trial 1, Fig. 3A). In Trial 2 no difference in fresh adult weight was seen when *C. maculata* fed upon eggs of *C. maculata*, *O. v-nigrum* or the meat diet (Trial 2, Fig. 3B). Fresh adult weights of *O. v-nigrum* when fed only *C. maculata* eggs or *O. v-nigrum* eggs were similar ($P > 0.05$) in Trial 1, whereas in Trial 2 fresh adult weights were significantly
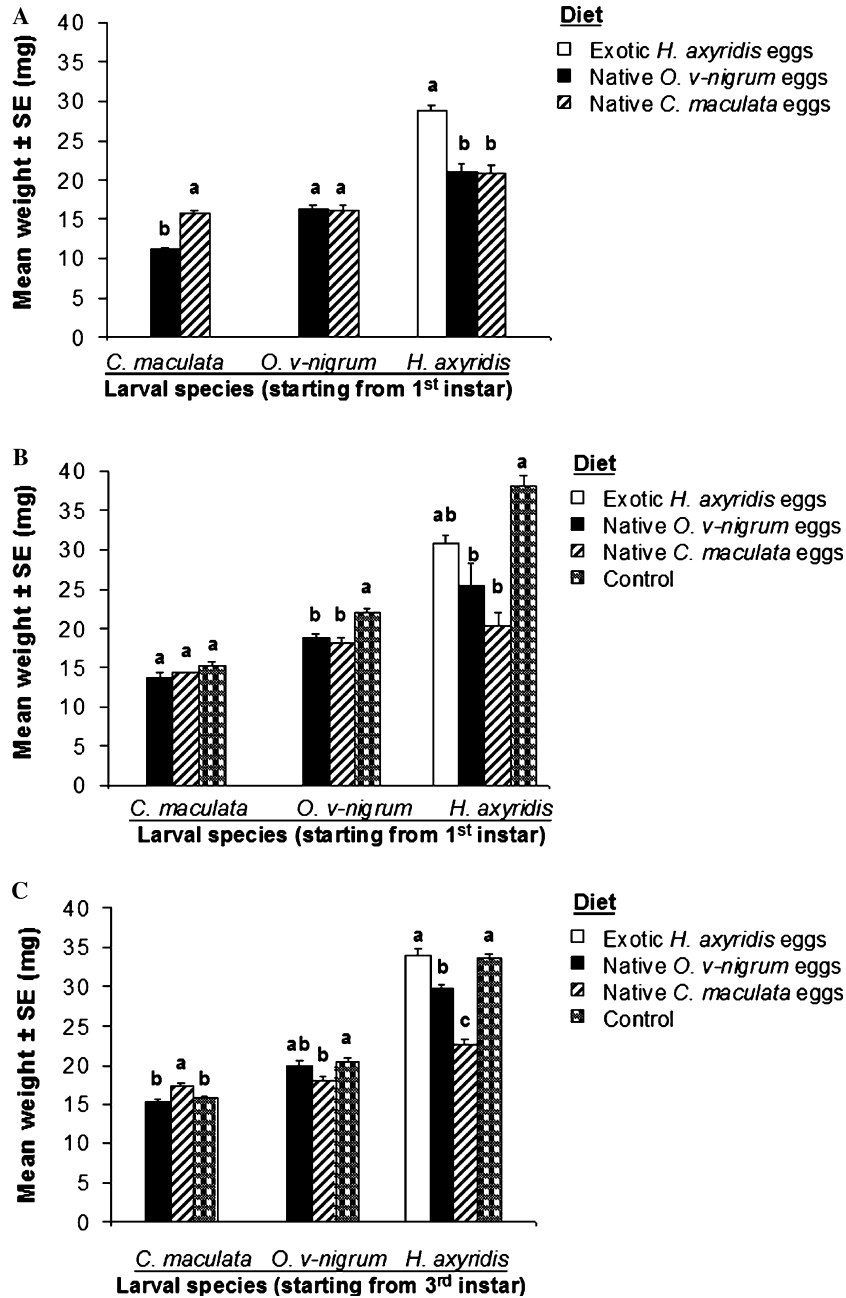

Fig. 3. Adult fresh weights (±SE) starting from the first instar in Trials 1 (A) and 2 (B) or from the third instar (C) when reared only on eggs of *C. maculata*, *O. v-nigrum* or *H. axyridis*. Trial 2 (B) included a control diet of pecan aphids for *O. v-nigrum* and *H. axyridis* or a meat-based diet for *C. maculata*, whereas *E. kuhniella* eggs were used as a control diet when starting from the third instar (C). Mean separation was done using Tukey's HSD test and significant differences ($P < 0.05$) within groups of bars are indicated by different letters above individual bars.

higher only when fed pecan aphids ($F = 46.45$; $df = 2$, 4; $P = 0.0017$) (Figs. 3A and B). In both Trial 1 and 2, significant difference in adult fresh weight of *H. axyridis* was detected between diets ($F = 16.27$; $df = 2$, 4; $P = 0.0120$ and $F = 12.78$; $df = 3$, 6; $P = 0.0051$, respectively) (Figs. 3A and B). *H. axyridis* egg cannibalism resulted in greater fresh adult weights compared with predation upon native species' eggs in Trial 1 but not Trial 2. In Trial 2, *H. axyridis* egg cannibalism and the aphid diet resulted in similar fresh adult weights.

3.2. Third instar feeding assay

Percentage mortality was significantly higher for *C. maculata* ($F = 125.02$; $df = 3$, 21; $P < 0.0001$) and *O. v-nigrum* ($F = 109.73$; $df = 3$, 21; $P < 0.0001$), started as third instars, and fed only *H. axyridis* eggs versus eggs of native species or lepidopteran eggs (Fig. 1C). No difference in mortality of *C. maculata* or *O. v-nigrum* was detected among the other diets. Mortality of *H. axyridis*, started as third instars, was not significantly different for any diet ($F = 1.38$; $df = 3$, 21; $P = 0.2759$) (Fig. 1C). All *C. maculata* and *O. v-nigrum* larvae fed only *H. axyridis* eggs died before reaching the pupal stage with most mortality, 62.5 and 95%, respectively, occurring during the fourth instar.

Mean number of days required for *C. maculata* to reach adulthood were significantly lower ($F = 18.06$; $df = 2$, 14; $P = 0.0001$) when eggs were cannibalized than when only *O. v-nigrum* or lepidopteran eggs were provided (Fig. 2C). No significant difference in developmental time was detected for *O. v-nigrum* among the diets ($F = 0.31$; $df = 2$, 14; $P = 0.7382$) (Fig. 2C). However, development of *H. axyridis* was significantly longer when fed only *C. maculata* eggs ($F = 32.81$; $df = 3$, 21; $P < 0.0001$) compared with development on any other diet (Fig. 2C).

Adult fresh weights were significantly higher for *C. maculata* ($F = 12.33$; $df = 2$, 14; $P = 0.0008$) and *H. axyridis* ($F = 93.69$; $df = 3$, 21; $P < 0.0001$) for intraspecific egg predation versus interspecific egg predation (Fig. 3C). *H. axyridis* weight was lowest when provisioned with only *C. maculata* eggs. Adult fresh weight of *O. v-nigrum* was significantly different only when fed *C. maculata* eggs versus the control diet of *E. kuhniella* eggs ($F = 4.65$; $df = 2$, 14; $P = 0.0283$) and not for intraspecific versus interspecific egg predation (Fig. 3C).

3.3. Rates of egg predation by third instars

Average number of *C. maculata*, *O. v-nigrum*, and *H. axyridis* eggs per cluster (±SE) fed to larvae in this experiment was 18.7 ± 0.3, 21.4 ± 0.8, and 20.2 ± 0.4, respectively. Two-way ANOVA on the arcsine transformed cumulative percentage of eggs attacked after 48 h revealed a significant interaction for predator species × egg species ($F = 31.49$; $df = 4$, 24; $P < 0.0001$). After 48 h, a significantly higher percentage of native eggs ($98.20 \pm 0.83\%$) were attacked (combined attack data for all predator species) compared with the percentage of exotic *H. axyridis* eggs attacked ($65.93 \pm 7.86\%$) ($F = 216.22$; $df = 1$, 24; $P \leqslant 0.0001$). However, *H. axyridis* larvae attacked a higher percentage of all eggs ($99.50 \pm 0.41\%$) compared with the percentage of all eggs attacked by native larvae ($81.41 \pm 5.08\%$) ($F = 72.99$; $df = 1$, 24; $P < 0.0001$). The percentage of native eggs attacked by native larvae versus *H. axyridis* larvae was high (97.67 ± 1.19 and $99.26 \pm 0.61\%$, respectively) but not significantly different ($F = 0.51$; $df = 1$, 24; $P = 0.48$), whereas the percentage of *H. axyridis* eggs attacked by native larvae ($48.89 \pm 4.62\%$) was significantly lower than the percentage attacked by *H. axyridis* larvae (100%) ($F = 190.04$; $df = 1$, 24; $P < 0.0001$). After 48 h, intraspecific egg predation was always 100% with all eggs being entirely consumed (Figs. 4A–C). *C. maculata* and *O. v-nigrum* attacked a high percentage of each other's eggs (92.02 and 98.61%, respectively) with the vast majority of those eggs being entirely consumed (Figs. 4A and B). Similarly, the high percentage of *C. maculata* and *O. v-nigrum* eggs (98.51 and 100%, respectively) attacked by *H. axyridis* were almost all entirely consumed (Fig. 4C). However, 32.9 and 36.5% of *H. axyridis* eggs attacked by *C. maculata* and *O. v-nigrum*, respectively, were only partially consumed after 48 h (Figs. 4A and B).

4. Discussion

The impact of *H. axyridis* upon native natural enemy populations, specifically the Coccinellidae, in North America is not fully known. Data presented in this study suggests that intraguild egg predation could play a role. *Harmonia axyridis* and the native species studied here overlap both spatially and temporally. *H. axyridis* occurs with *C. maculata* on sweet corn (Musser et al., 2004), *O. v-nigrum* in pecan and citrus orchards (Cottrell and Shapiro-Ilan, 2003; Michaud, 2003) and both *C. maculata* and *O. v-nigrum* in peach orchards (T.E. Cottrell, personal observation). Even though two coccinellid species may occupy the same habitat at the same time, species specific oviposition sites within the habitat may differ (e.g., far from, or nearby, aphid aggregations) resulting in decreased potential for intraguild egg predation (Schellhorn and Andow, 1999b). However, predation by *H. axyridis* on *C. maculata* eggs in plantings of sweet corn was reported by Cottrell and Yeargan (1998a,b) and, in fact, *H. axyridis* and *O. v-nigrum* do share oviposition sites on pecan foliage within pecan orchards (TEC, personal observation) and most likely in other arboreal habitats.

Although displacement mechanisms were not studied, Elliot et al. (1996) reported that the introduction and establishment of another exotic coccinellid, *C. septem-*
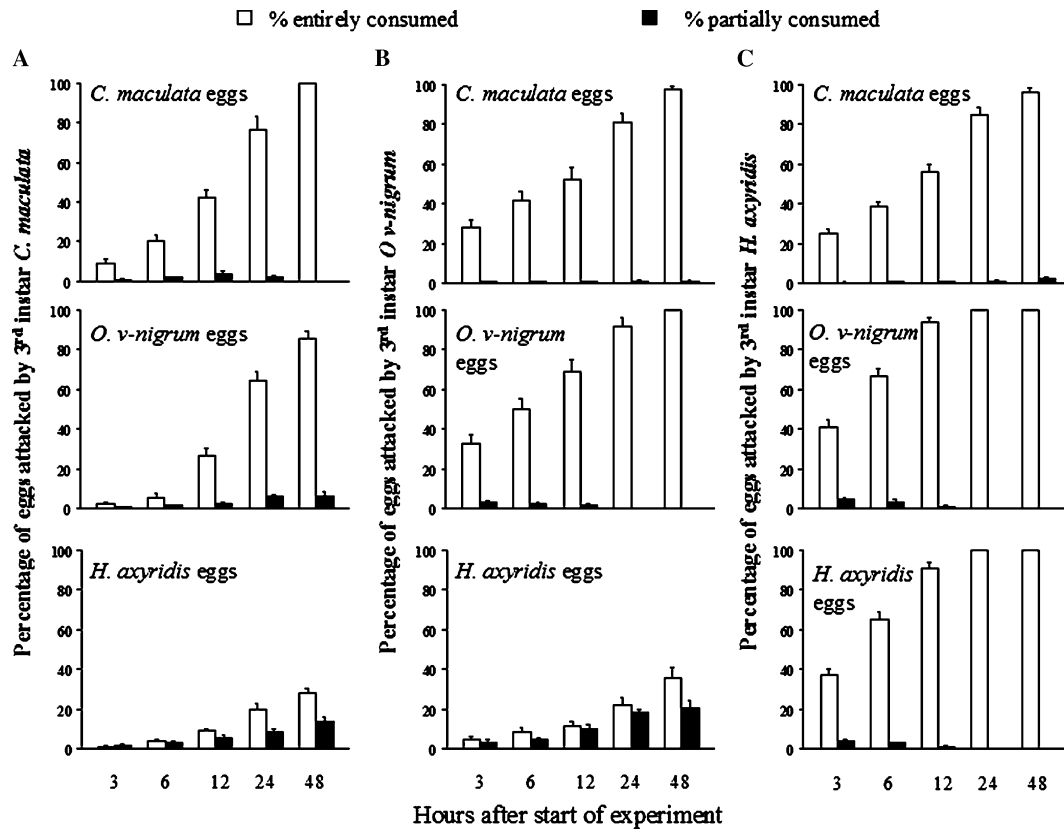
Fig. 4. Cumulative percentage of eggs attacked and entirely consumed or partially consumed by third instars of (A) *C. maculata*, (B) *O. v-nigrum*, and (C) *H. axyridis* at 3, 6, 12, 24, and 48 h.

punctata, in the US resulted in lowered abundance of the native *Coccinella transversoguttata* (Coleoptera: Coccinellidae) and *Adalia bipunctata* (Coleoptera: Coccinellidae) in certain habitats in the Northcentral US. In other studies, the interaction of *H. axyridis* with *C. septempunctata* or *C. maculata* most often resulted in *H. axyridis* having a negative impact upon those two species through intraguild predation (Cottrell and Yeargan, 1998c; Hironori and Katsuhiro, 1997; Yasuda and Ohnuma, 1999). But this is not the case for all interactions among exotic and native Coccinellidae as Hoogendoorn and Heimpel (2004) reported that the presence of *H. axyridis* larvae did not have a significant effect on survival or weight gain in *C. maculata* larvae when caged on corn plants at different prey densities. In addition, Obrycki et al. (1998) reported no significant intra- or interspecific interactions for larvae of the exotic *C. septempunctata* and the native *C. maculata* in field cages. They suggested that habitat complexity may have fostered survival of the smaller *C. maculata*. Other examples exist where exotic species did not have an advantage over native species. In Japan, Kajita et al. (2000) examined the interaction between the native species *C. septempunctata* and *H. axyridis* with the exotic *A. bipunctata* and found that, under conditions of low prey availability, both *C. septempunctata* and *H. axyridis* were intraguild predators of the exotic *A. bipunctata*.

Egg cannibalism by Coccinellidae is common and is considered beneficial when newly hatched larvae eat sibling eggs within the same egg cluster (Banks, 1955; Gagné et al., 2002; Pienkowski, 1965). Interspecific predation of eggs, larvae or pupae, however, generally provides a low quality food for the consumer and most often occurs under starvation conditions when local aphid populations decline (Agarwala and Yasuda, 2001; Schellhorn and Andow, 1999a). Data reported here generally supports the assertion that interspecific coccinellid eggs are of lower quality. *H. axyridis*, although capable of completing development on eggs of native species, typically took longer to develop and had lower adult weights when fed interspecific eggs compared with intraspecific eggs or control diets (i.e., pecan aphids or *E. kuhniella* eggs). For larvae of the native species, *H. axyridis* eggs do not appear to serve even as a low quality food source. When starting with both first and third instars, no native larvae survived when provisioned solely on a diet of *H. axyridis* eggs and native third instars attacked significantly fewer *H. axyridis* eggs. Hemptinne et al. (2000a) suggest it is highly unlikely that coccinellid larvae would encounter sufficient numbers of coccinellid eggs (e.g., for predation and/or cannibalism) in the field to complete development from first instar to adult. Nonetheless, it does matter whether or not coccinellid eggs, when encountered, are either

attacked or passed over. Native third instars attacked fewer *H. axyridis* eggs and many of those eggs were partially consumed. This is in contrast to the high percentage of native eggs attacked by third instars of all species where most eggs attacked were entirely consumed. Agarwala and Dixon (1992) reported reluctance by the coccinellids *A. bipunctata* and *C. septempunctata* to eat eggs of the other species and found that *C. septempunctata* larvae were more likely to die after consuming *A. bipunctata* eggs as opposed to the reverse scenario. However, among the species reported on in the present study, the propensity to feed upon coccinellid eggs favors *H. axyridis*. Both native species attacked a significantly lower percentage of *H. axyridis* eggs and always had 100% mortality. Survival of *H. axyridis* larvae was high and not significantly different for any diet.

Differential survival of larvae when fed only other coccinellid species' eggs could have been mediated by defensive alkaloids, pyrazines and quinolenes. These species specific alkaloids are synthesized de novo by coccinellids and are reported to be found in all developmental stages of Coccinellidae (Agarwala and Yasuda, 2001; Ayer and Browne, 1977; Hemptinne et al., 2000a). Hemptinne et al. (2000b) reported that the presence of heterospecific alkaloids in coccinellid eggs was the reason *A. bipunctata* and *C. septempunctata* preferred egg cannibalism. With regard to days to develop and adult fresh weight, my data on *O. v-nigrum* contradicts Hemptinne et al. (2000b) with similar results whether feeding on its eggs or *C. maculata* eggs (none survived on *H. axyridis* eggs), whereas supporting data were found when significant differences were more likely for *C. maculata* and *H. axyridis* cannibalizing eggs compared with feeding on eggs of other species.

In this laboratory study, the exotic *H. axyridis* has shown potential to negatively affect species of native Coccinellidae. Burgio et al. (2002) found similar levels of *H. axyridis* egg predation against *A. bipunctata* and egg cannibalism by *A. bipunctata*. In addition, egg cannibalism by *H. axyridis* was high. Thus, they suggested it unlikely that *H. axyridis* would negatively impact *A. bipunctata* through intraguild egg predation. In direct comparisons, *H. axyridis* cannibalized eggs but still ate *A. bipunctata* eggs, whereas *A. bipunctata* cannibalized eggs but ate significantly fewer *H. axyridis* eggs. Their results are very similar to those reported here with regard to native versus exotic species, but a different interpretation is suggested here. While intraspecific egg predation is the larger threat, compared with interspecific egg predation, the native species are subjected not only to intraspecific egg predation but also to interspecific egg predation by native and exotic species. Thus, *H. axyridis* is likely to have a negative impact upon native species through intraguild egg predation, especially when aphid populations decline. However, broad generalizations and predictions with regard to which native species will be subject to intraguild egg predation will not suffice. More data are needed, for example, with regard to rates of interspecific egg predation under field conditions, defensive compounds used by the different species of Coccinellidae, e.g., native versus exotic, and whether or not species are able to utilize encountered life stages containing such compounds.

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