Predation by Adult and Larval Lady Beetles (Coleoptera: Coccinellidae) on Initial Contact with Lady Beetle Eggs

TED E. COTTRELL[1]

USDA–ARS, Southeastern Fruit and Tree Nut Research Laboratory, 21 Dunbar Rd., Byron, GA 31008

Environ. Entomol. 36(2): 390–401 (2007)

ABSTRACT Naïve adults and larvae of the native lady beetles *Coleomegilla maculata* (DeGeer), *Cycloneda munda* (Say), *Hippodamia convergens* Guérin-Méneville, *Olla v-nigrum* (Mulsant), and the exotic lady beetle *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) were tested for their initial response to eggs of these five lady beetle species and for egg consumption on first contact and after 3 h. Additionally, field-collected *O. v-nigrum* and *H. axyridis* adults were tested. *C. maculata, H. axyridis,* and *O. v-nigrum* adults responded similarly to all egg species on first contact. Higher numbers of *C. munda* adults did not eat *C. maculata, H. convergens,* and *O. v-nigrum* eggs on first contact compared with numbers that did eat *C. munda* and *H. axyridis* eggs. *H. convergens* adults always ate *C. munda* eggs but hardly ate *H. axyridis* eggs on first contact. Results showed that over the 3-h interval, egg predation by those predators feeding on first contact was always higher, except for adults and larvae of *C. maculata*, than for those that did not feed on first contact. Thus, acceptance of eggs on initial contact does impact egg survival. It is likely that eggs of all native species tested (i.e., *C. maculata, C. munda, H. convergens,* and *O. v-nigrum*), but not exotic *H. axyridis* eggs, are suitable food for *C. maculata, H. convergens,* and *O. v-nigrum*, whereas only *C. munda* eggs serve as suitable food for *C. munda*. In direct contrast, all egg species tested would likely serve as suitable food for the exotic *H. axyridis*.

KEY WORDS intraguild predation, *Coleomegilla maculata*, *Cycloneda munda*, *Harmonia axyridis*, *Hippodamia convergens*, *Olla v-nigrum*

Predation of lady beetle (Coleoptera: Coccinellidae) eggs is widely reported (Mills 1982, Osawa 1992, Hodek 1996, Cottrell and Yeargan 1998a, b). Most reports concern egg predation by larvae, especially sibling egg cannibalism by neonates (Banks 1956, Pienkowski 1965), although later instars may cannibalize eggs they encounter (Kaddou 1960, Mills 1982, Cottrell and Yeargan 1998a, b). In fact, direct observations have shown that most predation on coccinellid eggs is done by coccinellids with fewer direct observations of noncoccinellid species eating coccinellid eggs. In plantings of sweet corn (*Zea mays* L.), *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae) and a recently established exotic lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) (Tedders and Schaefer 1994), were the first- and second-most frequently observed predators, respectively, of *C. maculata* eggs (Cottrell and Yeargan 1998a, b).

Coccinellidae, including the egg stage, are chemically defended. This may explain why egg predation, especially egg cannibalism, by coccinellid species, rather than noncoccinellid species, is more common (Ayer and Browne 1977, Ceryngier and Hodek 1996, Hemptinne et al. 2000). In addition, the different defensive alkaloids produced by Coccinellidae typically vary between species (Ayer and Browne 1977), and the relative tolerance of these defensive compounds by predating coccinellids may explain why the breadth of interspecific egg predation among Coccinellidae is variable. In fact, studies show that interspecific egg predation between two species may not be complementary (Hemptinne et al. 2000, Burgio et al. 2002, Cottrell 2004, 2005). Field observations (Cottrell and Yeargan 1998a, b) and laboratory studies (Cottrell and Yeargan 1998c, Cottrell 2004, 2005) showed that *H. axyridis* fed and completed development on eggs of certain native species. However, those same native species fed on a lower percentage of available *H. axyridis* eggs and could not complete development on those eggs. Thus, the possible impact of an introduced species, such as *H. axyridis,* on populations of native Coccinellidae is of interest.

The polyphagous predator *H. axyridis* quickly dispersed over much of North America (Coderre et al. 1995, Lamana and Miller 1996) and has become established in many habitats with the potential to interact with many native species of Coccinellidae (Ted-

---

[1] Corresponding author, e-mail: tcottrell@saa.ars.usda.gov.

ders and Schaefer 1994, LaMana and Miller 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Wells and McPherson 1999, Koch 2003, Snyder et al. 2004). Laboratory studies on egg predation indicated that *H. axyridis* could negatively impact species of native Coccinellidae (Cottrell and Yeargan 1998c, Sato and Dixon 2004, Burgio et al. 2005). Field studies (Musser and Shelton 2003, Lundgren et al. 2004) have indicated that the spatial and temporal overlap of *H. axyridis* with the native *C. maculata* on corn was limited, with *C. maculata* resorting to a predominantly pollinivorous habit during anthesis but with *H. axyridis* remaining predaceous (Lundgren et al. 2004). Nonetheless, the widespread distribution of *H. axyridis* provides many opportunities for contact with *C. maculata* and other native Coccinellidae. Without testing, however, it is unlikely that outcomes of those interactions will be known.

It has been shown that eggs of the native coccinellids *Olla v-nigrum* (Mulsant) and *C. maculata* readily serve as suitable prey for development of *H. axyridis* larvae but not vice versa (Cottrell 2004). From this we might expect *H. axyridis* to negatively impact those native species in natural settings. However, this type of data does not account for the initial reaction of the predator to the prey. Typical predator foraging behavior (Banks 1956, Kaddou 1960, Rowlands and Chapin 1978, Carter and Dixon 1982) on initial rejection of an egg cluster as prey should increase the probability of survival for that egg cluster. For example, Carter and Dixon (1982) reported that the duration of area-restricted searching behavior increased after prey consumption. Thus, an initial encounter with an egg cluster that does not lead to egg predation would be unlikely to identify that egg cluster as prey and, in the absence of local prey (i.e., aphids), would thus induce the predator to leave that area quicker. When a rejected egg cluster and aphids occur nearby, the predator's chance of subsequent encounters with the egg cluster are increased. Nevertheless, abundant food can make it less likely for encountered coccinellid eggs to be eaten (Cottrell 2005). In addition, different foraging strategies, related to patch emigration, by species of Coccinellidae will affect egg survival (Sato et al. 2003). As an intraguild predator, larval *H. axyridis* have been found to be superior against other species of Coccinellidae, typically escaping attack but successfully attacking heterospecific competitors (Yasuda et al. 2001, Snyder et al. 2004). Thus, knowing the propensity to feed on eggs during the initial contact with an egg cluster would further elucidate potential intraguild relations among coccinellid species in natural settings, especially when those species overlap spatially and temporally.

The objective of this study was to examine the response of four native species (*C. maculata*, *O. v-nigrum*, *Cycloneda munda* Say, and *Hippodamia convergens* Guérin-Méneville) and one exotic species (*H. axyridis*) of Coccinellidae to their initial contact with a coccinellid egg cluster. This was done using laboratory-reared adults (except for *H. convergens*) and larvae of each species exposed to eggs of each coccinellid species using no-choice assays. In addition, the same tests were conducted using field-collected adults of the native *O. v-nigrum* and exotic *H. axyridis*, which were locally abundant in numbers sufficient for testing.

Materials and Methods

Insects. Laboratory colonies of *O. v-nigrum* and *H. axyridis* originated from adult beetles collected from pecan orchards at the USDA–ARS, Southeastern Fruit and Tree Nut Research Laboratory (Byron, GA). The *C. maculata* colony originated from overwintering adult beetles collected near Lexington, KY. The *C. munda* colony originated from adults collected near Bonnieville, KY. The *H. convergens* adults used in the study were purchased from Gardens Alive! (Lawrenceburg, IN). Field-collected adults of each species, except for *H. convergens*, from the USDA laboratory at Byron, GA, were added intermittently to the colonies. Voucher specimens were placed in the insect collection at the USDA–ARS, Southeastern Fruit and Tree Nut Research Laboratory (Byron, GA). Each species was housed in 9-cm-diameter petri dishes in an environmental chamber at 25 ± 1°C and a photoperiod of 14:10 (L:D) h. All lady beetle species were reared on frozen *Ephestia kuehniella* Keller (Lepidoptera: Pyralidae) eggs, supplemented with a beef-based diet (Beneficial Insectary, Redding CA), and water was provided with a moistened cotton dental wick (Cottrell 2005). This same diet was provided to *H. convergens* adults. Florist's paper (green) was used to line lids of petri dishes containing adult female coccinellids (Cottrell and Yeargan 1998a). The paper provided an ovipositional substrate for the lady beetles that could be easily removed and replaced. Egg clusters were from mated, laboratory-reared beetles, except for *H. convergens* adults, which were purchased and handled similarly. Egg clusters from all species were collected daily and stored at 10 ± 1°C. Egg clusters used in assays were $\leq$24 h old.

Response of Laboratory-Reared Adults to Eggs. Laboratory-reared lady beetles, except the purchased *H. convergens*, were known to be naïve regarding interspecific exposure to lady beetle eggs before assays. Intraspecific exposure to eggs could have occurred as sibling egg cannibalism at egg hatch but was only known to occur on a limited basis if a female oviposited in her petri dish before assays. Laboratory-reared beetles were assayed within 3 wk of adult eclosion, and *H. convergens* adults were used within 4 wk of receipt. Each adult species, starved for 24 h before the assay, was tested separately against an egg cluster of each species (i.e., a no-choice test) in a 9-cm-diameter petri dish. Egg clusters of each species were tested using 10 adults of each species (except for *C. maculata* [$n = 8$] against *H. convergens* eggs, *O. v-nigrum* [$n = 6$] against *C. munda* eggs, and *H. convergens* [$n = 15$] against *H. convergens* eggs) using one egg cluster and one beetle at a time. For each adult × egg combination, a single beetle was added to a petri dish to acclimate for 1–2 min, and an egg cluster, on $\approx$1 cm^2 of florist's paper (green), was placed in the center of the petri dish. It was not logistically possible to keep the number of eggs per cluster consistent between species, and no attempt was made to artificially manipulate egg numbers per cluster. The mean number of eggs per cluster ± SEM for *C. maculata, C. munda, H. axyridis, H. convergens,* and *O. v-nigrum* was 17.3 ± 1.0, 11.2 ± 0.8, 26.2 ± 0.8, 15.3 ± 1.5, and 25.3 ± 2.1, respectively. The actions of the adult beetle were observed for 3 h, and data were recorded for occurrence of egg feeding on first contact with the egg cluster, time (min) spent feeding during first contact, number of subsequent egg cluster contacts, and the number of eggs consumed for each contact.

Response of Laboratory-Reared Larvae to Eggs. Larvae of the five coccinellid species were reared to the fourth instar, as determined by recording molts, on *E. kuehniella* eggs, and the meat-based diet. Except for possible sibling egg cannibalism by a few neonates, these individuals were naïve to eggs of all species assayed. Larvae of all species, starved for 4 h, were assayed against eggs of the five coccinellid species (no-choice test) in 9-cm-diameter petri dishes similarly as described for adult beetles. Each egg species was tested using 10 larvae of each species putting one egg cluster and 1 larva together at a time. The mean number of eggs per cluster ± SEM for *C. maculata, C. munda, H. axyridis, H. convergens,* and *O. v-nigrum* was 22.0 ± 0.8, 16.4 ± 0.5, 31.9 ± 1.6, 24.8 ± 0.9, and 28.3 ± 1.1, respectively. Larval actions were observed for 3 h, and data were recorded similarly as for laboratory-reared adults.

Response of Field-Collected Adults to Eggs. Adult *H. axyridis* and *O. v-nigrum* were collected at the USDA–ARS, Southeastern Fruit and Tree Nut Research Laboratory (Byron, GA) in October 2004 when lady beetles are still commonly active and foraging. Adult *H. axyridis* were collected from pecan [*Carya illinoinensis* (Wangenh.) K. Koch] foliage, and adult *O. v-nigrum* were collected from sorghum (*Sorghum bicolor* L. Moench). These adults were taken to the laboratory, and assays were initiated within 30 min of collection such that the hunger status of these beetles would be representative of beetles in the field. The no-choice assays were done in 9-cm-diameter petri dishes using 10 adults each of *H. axyridis* and *O. v-nigrum* against eggs from *C. maculata, C. munda, H. axyridis, H. convergens,* and *O. v-nigrum* as previously described for the laboratory-reared adults. The mean number of eggs per cluster ± SEM for *C. maculata, C. munda, H. axyridis, H. convergens,* and *O. v-nigrum* was 18.7 ± 0.4, 16.1 ± 0.6, 27.8 ± 0.5, 17.9 ± 1.0, and 25.7 ± 0.7, respectively. The actions of the field-collected adult beetles were observed for 3 h, and data were recorded for occurrence of egg feeding on first contact with the egg cluster, time (min) spent feeding during first contact, and the number of eggs consumed.

Statistical Analyses. Fisher exact test for a 2 by 5 table (PROC FREQ; SAS Institute 2002) was used to test the null hypothesis of no association between rows (i.e., the number of individuals that fed on eggs during the initial contact and the number that did not feed on eggs during the initial contact) and columns (i.e., the five species of eggs tested) for each adult and larval species tested. Any individual that did not contact the egg cluster during the 3-h assay was excluded from analysis. The alternative hypothesis of an association between rows and columns was accepted when $P \leq 0.05$. A column (i.e., egg species) that contributed to the significant effect ($P \leq 0.05$) was identified using Fisher exact test with subdivided data. For each predator species, the percentage of each species' eggs consumed on initial contact and the cumulative percentage of each species' eggs consumed after the 3-h interval were arcsine transformed (Zar 1999), separately analyzed using one-way analysis of variance (ANOVA), and mean separation was done using Tukey's honestly significant difference (HSD) when $P < 0.05$ (JMP 2002). Percentage eggs per cluster consumed is presented as back-transformed means (±SE). Additionally, for each predator species, percentage of all species' eggs consumed after 3 h was arcsine transformed, and one-way ANOVA was used to compare egg consumption for those that fed on first contact with those that did not feed on first contact with egg clusters. Percentage eggs per cluster consumed is presented as back-transformed means (±SE). The mean number of contacts during the observation interval for each egg species by each predator species was analyzed using one-way ANOVA and mean separation by Student's *t*-test when $P < 0.05$ (JMP 2002). Last, time (min) spent feeding during the first contact by each predator species with each egg species was analyzed using one-way ANOVA and mean separation by Student's *t*-test when $P < 0.05$ (JMP 2002).

Results

Response of Laboratory-Reared Adults to Eggs. The initial response of adult *C. maculata, H. axyridis,* and *O. v-nigrum* to eggs of all species was not significantly different regarding the numbers that did and did not eat eggs on first contact ($P = 0.7276$ [Fisher exact test], $n = 38$; $P = 0.8096$ [Fisher exact test], $n = 44$, and $P = 0.1726$ [Fisher exact test], $n = 36$, respectively; Fig. 1A, C, and E). The percentage of initial contacts with all egg species that led to egg consumption by adult *C. maculata, H. axyridis,* and *O. v-nigrum* was 45, 57, and 63%, respectively. The response by *C. munda* adults to egg species on first contact was significant ($P = 0.0463$ [Fisher exact test], $n = 31$; Fig. 1B). However, the difference was not significant when the data were subdivided to exclude *C. munda* eggs ($P = 0.1080$ [Fisher exact test], $n = 24$), where four of seven initial contacts resulted in egg consumption, or *H. axyridis* eggs ($P = 0.0648$ [Fisher exact test], $n = 25$), where three of six initial contacts resulted in egg consumption. Although *C. munda* adults contacted eggs of *H. convergens* and *O. v-nigrum,* none fed on those eggs on initial contact (Fig. 1B). When *C. munda* and *H. axyridis* eggs were not considered, *C. munda* adults fed on 5.6% of egg clusters on initial contact. The response of adult *H. convergens* to the different egg species on first contact was significant ($P = 0.0041$

[Fisher exact test], $n = 47$; Fig. 1D). The difference was not significant when the data were subdivided to exclude *C. munda* eggs ($P = 0.0784$ [Fisher exact test], $n = 39$), where eight of eight initial contacts resulted in egg consumption, or *H. axyridis* eggs ($P = 0.0609$ [Fisher exact test], $n = 39$), where one of eight initial contacts resulted in egg consumption. Without those two egg species, 58% of *H. convergens* adults fed on egg clusters on initial contact. The percentage of eggs per cluster consumed by adult *C. maculata* or *H. axyridis* was not significant for different egg species after initial contact ($F = 0.54$; df = 4,33; $P = 0.7071$ and $F = 0.11$; df = 4,39; $P = 0.9778$, respectively; Fig. 2A) or after the 3-h interval ($F = 1.73$; df = 4,33; $P = 0.1664$ and $F = 0.17$; df = 4,39; $P = 0.9495$, respectively; Fig. 2B). However, this difference was significant for adult *C. munda, H. convergens,* and *O. v-nigrum* after initial contact ($F = 4.11$; df = 4,26; $P = 0.0103$, $F = 5.11$; df = 4,42; $P = 0.0019$, and $F = 10.89$; df = 4,30; $P < 0.0001$, respectively; Fig. 2A) and after the 3-h interval ($F = 8.63$; df = 4,26; $P = 0.0001$, $F = 3.66$; df = 4,42; $P = 0.0121$, and $F = 14.25$; df = 4,30; $P < 0.0001$, respectively; Fig. 2B). For adults of *C. munda, H. axyridis, H. convergens,* and *O. v-nigrum* that contacted egg clusters during the 3-h observation period, those that fed during the initial contact fed on a significantly higher percentage of eggs per cluster than those that did not feed on initial contact ($F = 29.83$; df = 1,29; $P < 0.0001$, $F = 48.28$; df = 1,42; $P < 0.0001$, $F = 37.72$; df = 1,45; $P < 0.0001$, and $F = 27.13$; df = 1,33; $P < 0.0001$, respectively; Fig. 3A). Native species (*C. maculata, C. munda, H. convergens,* and *O. v-nigrum*) ate 6% of *H. axyridis* eggs per cluster when feeding on first contact, whereas *H. axyridis* adults ate 74% of native species' eggs per cluster on first contact. Native species ate 59% of native species' eggs per cluster on first contact, whereas *H. axyridis* ate 89% of *H. axyridis* eggs per cluster on first contact. After 3 h, when considering only those adults that fed on first contact, native species consumed 20% of *H. axyridis* eggs per cluster and adult *H. axyridis* consumed 79% of native eggs per cluster. The difference in mean number of egg cluster contacts by predators over the 3-h interval was significant for laboratory-reared *C. maculata* and *O. v-nigrum* adults ($F = 3.43$; df = 4,33; $P = 0.0190$ and $F = 4.15$; df = 4,30; $P = 0.0086$, respectively; Table 1) but not for *C. munda, H. axyridis,* or *H. convergens* adults ($F = 0.49$; df = 4,26; $P = 0.7423$, $F = 1.02$; df = 4,39; $P = 0.4076$, or $F = 2.24$; df = 4,42; $P = 0.0806$, respectively; Table 1). Time spent feeding on the different egg species during the initial contact was significantly different for adult *H. convergens* ($F = 4.26$; df = 4,42; $P = 0.0055$) but not for adults of *C. maculata* ($F = 0.76$;

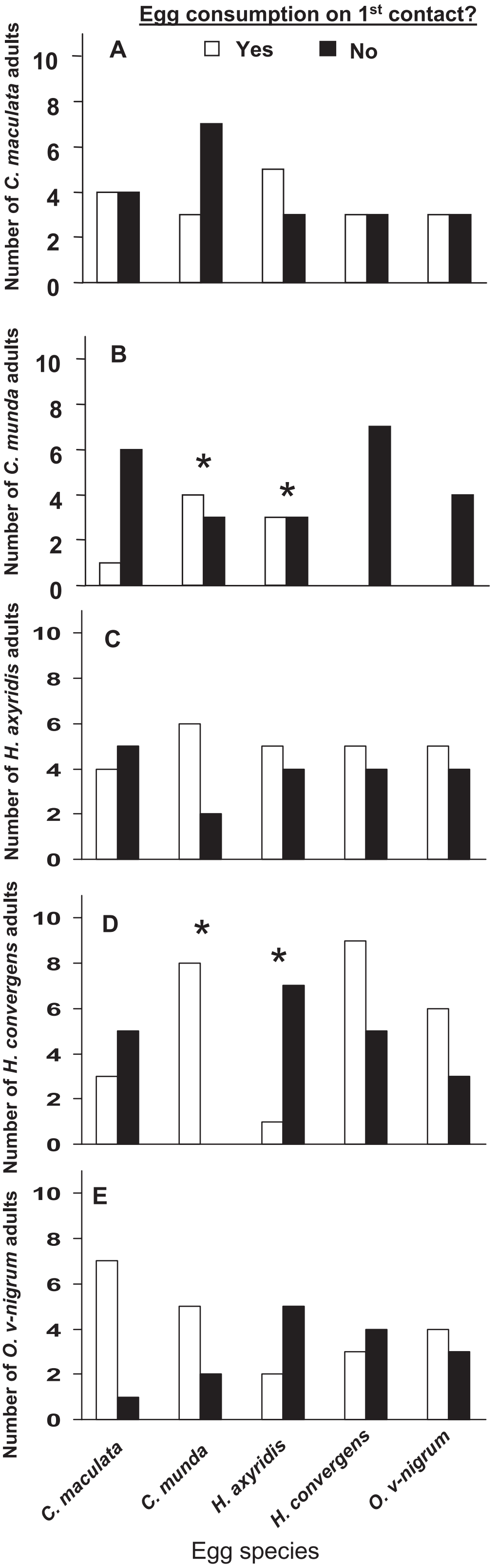

Fig. 1. Egg acceptance and rejection on first contact by adults of (A) *C. maculata*, (B) *C. munda*, (C) *H. axyridis*, (D) *H. convergens*, and (E) *O. v-nigrum*. *Number of adults accepting and rejecting that species' eggs on the initial encounter was significantly different ($P < 0.05$, Fisher exact test) from the number of adults accepting and rejecting eggs of other species on the initial encounter.

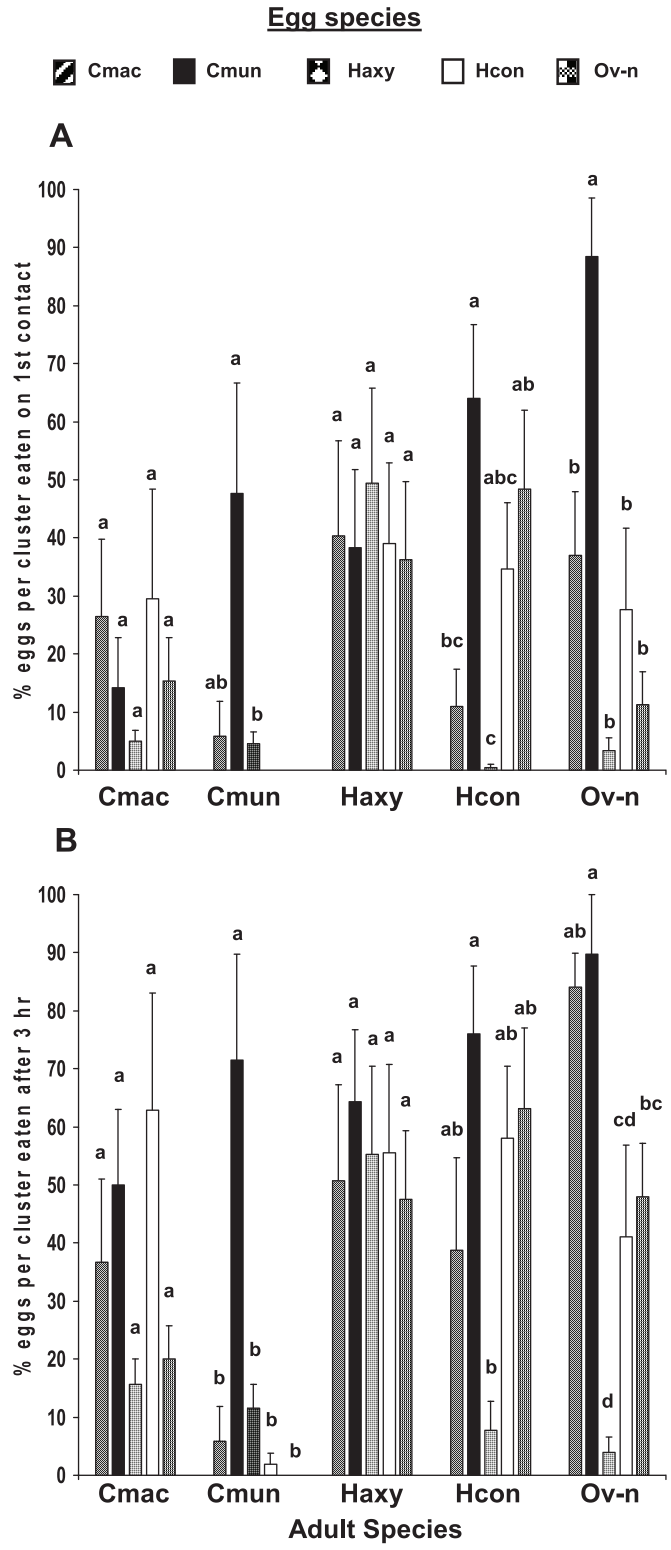

Fig. 2. Percentage of eggs per cluster consumed by laboratory-reared adult coccinellids on (A) initial contact and (B) after a 3-h interval. Significant difference ($P < 0.05$) in percentage consumption of the different egg species by each predator species is denoted by unlike letters above columns. Cmac, *C. maculata*; Cmun, *C. munda*; Haxy, *H. axyridis*; Hcon, *H. convergens*; Ov-n, *O. v-nigrum*.

df = 4,33; $P = 0.5589$), *C. munda* ($F = 0.68$; df = 4,26; $P = 0.6149$), *H. axyridis* ($F = 0.67$; df = 4,39; $P = 0.6180$), or *O. v-nigrum* ($F = 0.68$; df = 4,29; $P = 0.6111$; Table 1).

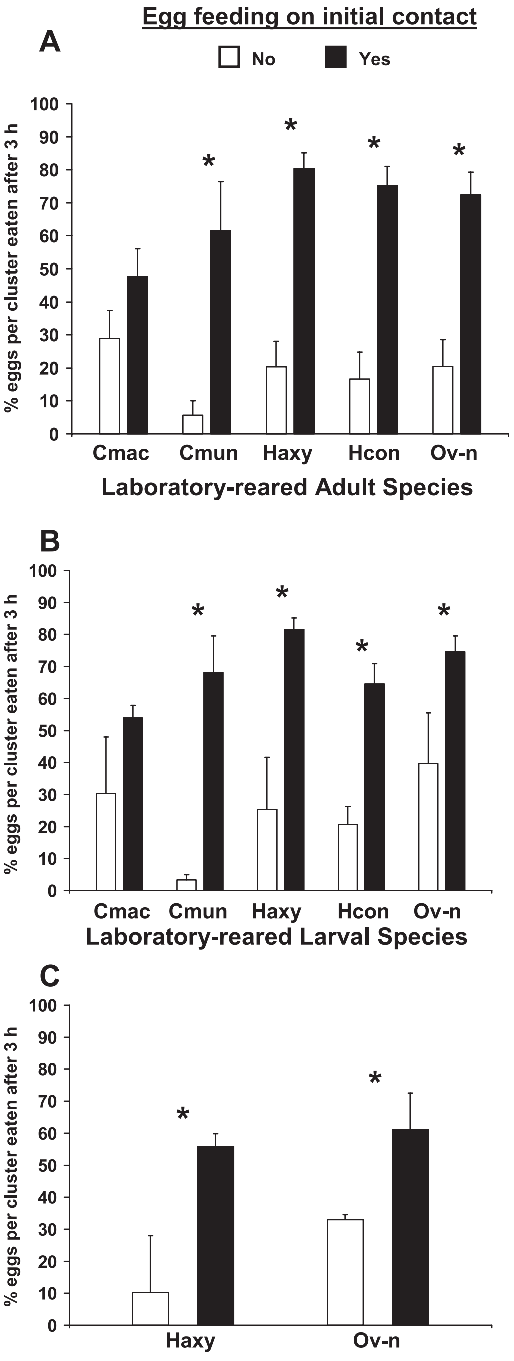

Fig. 3. Percentage of eggs per cluster, combined egg species (*C. maculata, C. munda, H. axyridis, H. convergens,* and *O. v-nigrum*), consumed after 3 h by (A) laboratory-reared adults, (B) laboratory-reared larvae, and (C) field-collected adults of *H. axyridis* and *O. v-nigrum* comparing egg consumption for those that did and did not feed on initial contact with egg clusters. Significant difference ($P < 0.05$) in percentage consumption is denoted by an asterisk above paired columns. Cmac, *C. maculata*; Cmun, *C. munda*; Haxy, *H. axyridis*; Hcon, *H. convergens*; Ov-n, *O. v-nigrum.*

Response of Laboratory-Reared Larvae to Eggs. The response of *C. maculata* larvae to different egg species on first contact was not significant ($P = 0.0814$ [Fisher exact test], $n = 46$). Eighty-nine percent of *C. maculata* larvae ate eggs on first contact (Fig. 4A). The response of *C. munda* larvae to different egg species on first contact was significant ($P = 0.0180$ [Fisher exact test], $n = 24$; Fig. 4B). Although *C. munda* larvae contacted eggs of *H. axyridis, H. convergens,* and *O. v-nigrum,* none ate those eggs on initial contact (Fig. 4B). The effect was not significant when the data were subdivided to exclude *C. munda* eggs ($P = 0.3158$ [Fisher exact test], $n = 19$), where three of five initial contacts resulted in egg consumption. The response of *H. axyridis* larvae to egg species on first contact was significant ($P = 0.0471$ [Fisher exact test], $n = 39$; Fig. 4C). However, the response was not significant when data were subdivided to exclude *C. maculata* eggs ($P = 0.0627$ [Fisher exact test], $n = 31$), where five of eight initial contacts resulted in egg consumption, or *O. v-nigrum* eggs ($P = 0.0670$ [Fisher exact test], $n = 34$), where three of five initial contacts resulted in egg consumption. Without these two egg species, 96% of *H. axyridis* larvae fed on egg clusters on initial contact. *H. convergens* larvae responded significantly different to egg species on first contact ($P = 0.0106$ [Fisher exact test], $n = 41$; Fig. 4D). The effect was not significant when the data were subdivided to exclude eggs of both *H. axyridis,* where 2 of 10 initial contacts led to consumption, and *O. v-nigrum,* where 2 of 9 initial contacts led to consumption of *O. v-nigrum* eggs ($P = 1.000$ [Fisher exact test], $n = 22$). Without these two egg species, 77% of *H. convergens* larvae fed on egg clusters on initial contact. The response by *O. v-nigrum* larvae to the different egg species on first contact was significant ($P = 0.0296$ [Fisher exact test], $n = 45$; Fig. 4E). However, there was no significant effect when data were subdivided to exclude *H. axyridis* eggs, where four of nine initial contacts resulted in egg consumption ($P = 0.8866$ [Fisher Exact test], $n = 36$). Without *H. axyridis* eggs, 92% of *O. v-nigrum* larvae fed on egg clusters on initial contact. The percentage of eggs per cluster consumed by larval *C. maculata, C. munda, H. axyridis, H. convergens,* and *O. v-nigrum* was significant for different egg species after initial contact ($F = 6.42$; df = 4,41; $P = 0.0004$, $F = 3.73$; df = 4,19; $P = 0.0210$, $F = 3.30$; df = 4,33; $P = 0.0222$, $F = 5.93$; df = 4,36; $P = 0.0009$, and $F = 15.22$; df = 4,40; $P = 0.0001$, respectively; Fig. 5A) and also after the 3-h interval ($F = 7.65$; df = 4,41; $P = 0.0001$, $F = 4.63$; df = 4,19; $P = 0.0089$, $F = 3.68$; df = 4,33; $P = 0.0138$, $F = 4.88$; df = 4,36; $P = 0.0030$, $F = 28.42$; df = 4,40; $P = 0.0001$, respectively; Fig. 5B). For *C. munda, H. axyridis, H. convergens,* and *O. v-nigrum* larvae that contacted egg clusters during the 3-h observation period, those that fed during the initial contact fed on a significantly higher percentage of eggs per cluster than those that did not feed on initial contact ($F = 68.99$; df = 1,22; $P < 0.0001$, $F = 29.76$; df = 1,36; $P < 0.0001$, $F = 28.44$; df = 1,39; $P < 0.0001$, and $F = 7.68$; df = 1,43; $P = 0.0082$, respectively; Fig. 3B). Native larvae (*C. maculata, C. munda, H. convergens,* and *O. v-nigrum*) ate 11% of *H. axyridis* eggs per cluster when feeding on first contact, whereas *H. axyridis* larvae ate 82% of native eggs per cluster on first contact. Native larvae, however, ate 68% of native eggs per cluster on first contact, and *H. axyridis* ate 56% of *H. axyridis* eggs per cluster on first contact. After 3 h, when considering only those larvae that fed on first contact, native larvae (excluding *C. munda* that did not eat *H. axyridis* eggs on first contact) consumed 20% of *H. axyridis* eggs per cluster, and larval *H. axyridis* consumed 85% of native eggs per cluster. The mean number of egg cluster contacts by larvae over the 3-h interval was significantly different for laboratory-reared *C. munda* and *H. convergens* ($F = 4.08$; df = 4,45; $P = 0.0066$ and $F = 3.64$; df = 4,45; $P = 0.0118$, respectively; Table 1) but not for *C. maculata, H. axyridis,* or *O. v-nigrum* larvae ($F = 2.30$; df = 4,45; $P = 0.0730$, $F = 2.31$; df = 4,39; $P = 0.0722$, or $F = 1.79$; df = 4,45; $P = 0.1470$, respectively; Table 1). Time spent feeding on the different egg species during the initial contact was significantly different for *C. munda* larvae ($F = 3.16$; df = 4,19; $P = 0.0376$) but not for larvae of *C. maculata* ($F = 1.11$; df = 4,41; $P = 0.3661$), *H. axyridis* ($F = 1.05$; df = 4,33; $P = 0.3988$), *H. convergens* ($F = 1.75$; df = 4,36; $P = 0.1597$), or *O. v-nigrum* ($F = 0.28$; df = 4,40; $P = 0.8870$; Table 1).

Response of Field-Collected Adults to Eggs. No significant difference was detected in the number of *H. axyridis* adults that did, or did not, eat the different egg species on first contact ($P = 0.1576$ [Fisher exact test], $n = 45$; Fig. 6A). Only 20% of field-collected adult *H. axyridis* fed on egg clusters on initial contact. No field-collected *H. axyridis* adult ate *O. v-nigrum* eggs on first contact. A significant difference was detected in the response of field-collected *O. v-nigrum* adults to the different egg species on first contact ($P = 0.0025$ [Fisher exact test], $n = 42$; Fig. 6B). The difference was not significant when the data were subdivided to exclude *O. v-nigrum* eggs ($P = 0.8692$ [Fisher exact test], $n = 34$), where eight of eight initial contacts resulted in egg cannibalism. Without *O. v-nigrum* eggs included, 26% of field-collected *O. v-nigrum* adults fed on egg clusters on initial contact. The difference in the percentage of eggs per cluster consumed by field-collected adults of *H. axyridis* was not significant for the different egg species

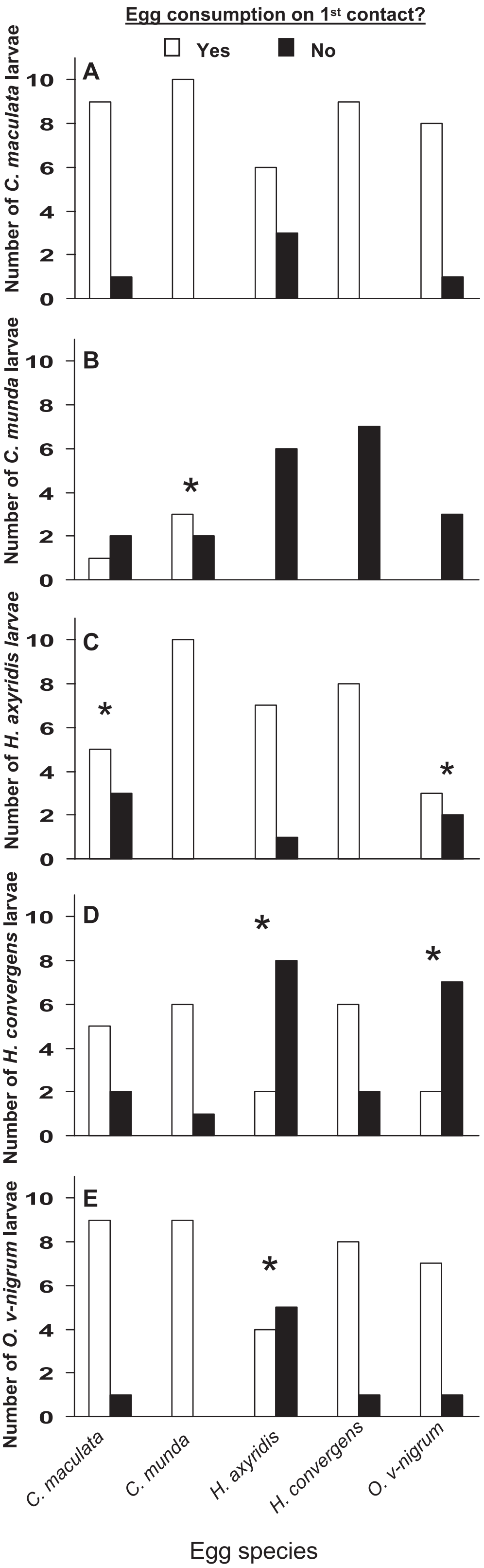

Fig. 4. Egg acceptance and rejection on first contact by larvae of (A) *C. maculata*, (B) *C. munda*, (C) *H. axyridis*, (D) *H. convergens*, and (E) *O. v-nigrum*. *Number of larvae accepting and rejecting that species' eggs on the initial encounter was significantly different ($P < 0.05$, Fisher exact test) from the number of larvae accepting and rejecting eggs of other species on the initial encounter.

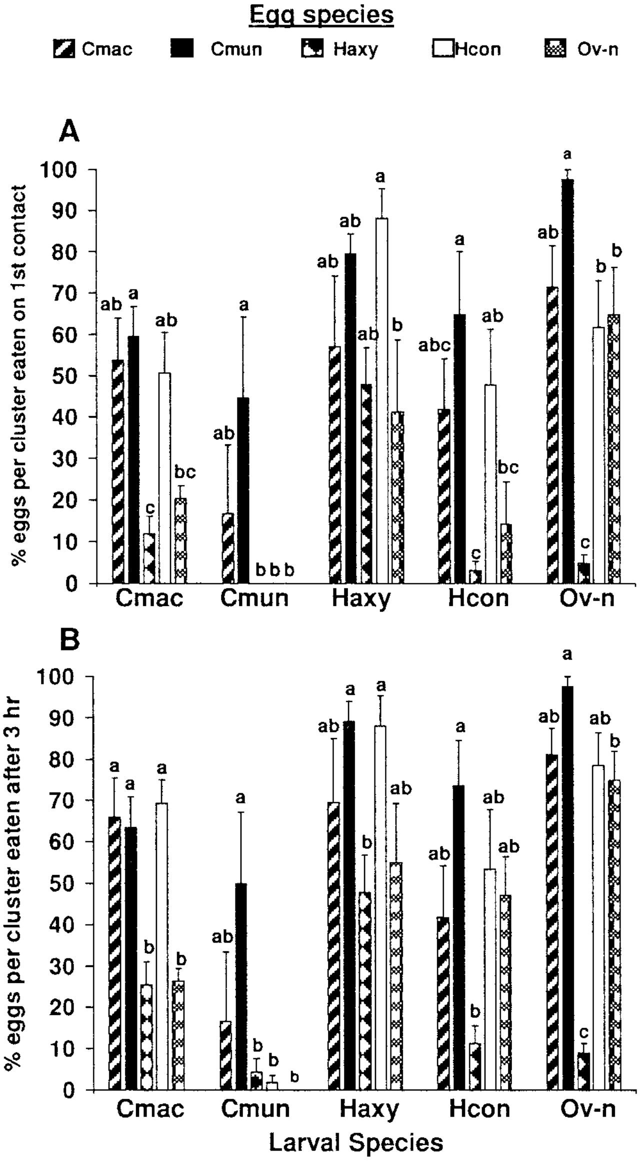

Fig. 5. Percentage of eggs per cluster consumed by laboratory-reared larval coccinellids on (A) initial contact and (B) after a 3-h interval. Significant difference ($P < 0.05$) in percentage consumption of the different egg species by each predator species is denoted by unlike letters above columns. Cmac, *C. maculata*; Cmun, *C. munda*; Haxy, *H. axyridis*; Hcon, *H. convergens*; Ov-n, *O. v-nigrum*.

on first contact with egg clusters ($F = 0.93$; df = 4,42; $P = 0.4535$) or after the 3-h interval ($F = 1.60$; df = 4,42; $P = 0.1913$; Fig. 7A and B). In contrast, the difference was significant for field-collected *O. v-nigrum* after their initial contact ($F = 13.23$; df = 4,37; $P < 0.0001$) and after the 3-h interval ($F = 5.21$; df = 4,37; $P = 0.0020$; Fig. 7A and B). For *H. axyridis* and *O. v-nigrum* adults that contacted egg clusters during the 3-h observation period, those that fed during the initial contact fed on a significantly higher percentage of eggs per cluster than those that did not feed on initial contact ($F = 15.08$; df = 1,44; $P = 0.0003$ and $F = 5.45$; df = 1,40; $P = 0.0247$, respectively; Fig. 3C). Field-collected *O. v-nigrum* adults ate 8% of *H. axyridis* eggs per cluster when they did feed on first contact, whereas *H. axyridis* adults ate 72% of native eggs per cluster on first contact. *Olla v-nigrum* field-collected adults ate 58% of native eggs per cluster on first contact, and *H. axyridis* ate 54% of *H. axyridis* eggs per cluster on first contact. After 3 h, when considering only those field-collected adults that fed on first contact, *O. v-nigrum* ate 54 and 12% of native and *H. axyridis* eggs per cluster, respectively. However, *H. axyridis* adults ate 95% (excluding *O. v-nigrum* eggs for which none were eaten by *H. axyridis*) of native eggs and 54% of *H. axyridis* eggs. The mean number of egg cluster contacts by predators over the 3-h interval was not significantly different for

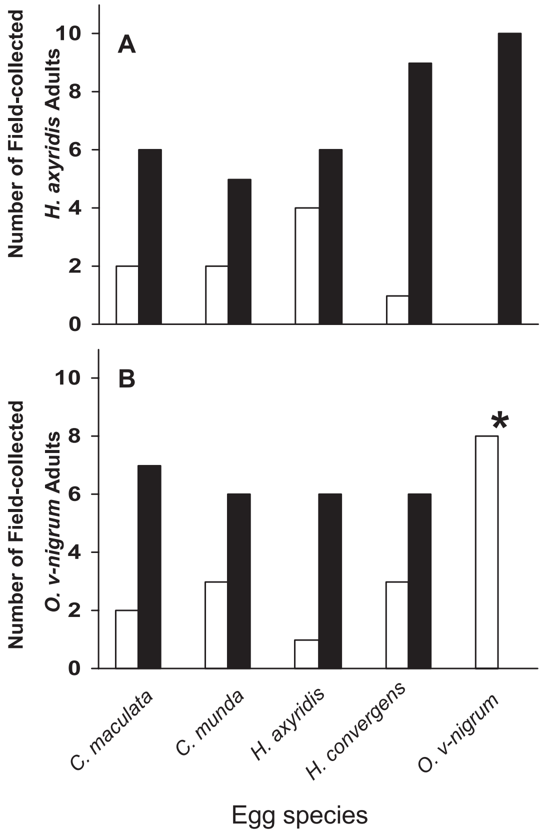

Fig. 6. Egg acceptance and rejection on first contact by field-collected adults of (A) *H. axyridis* and (B) *O. v-nigrum*. *Number of field-collected adults accepting and rejecting that species' eggs on the initial encounter was significantly different ($P < 0.05$, Fisher exact test) from the number of field-collected adults accepting and rejecting eggs of other species on the initial encounter.

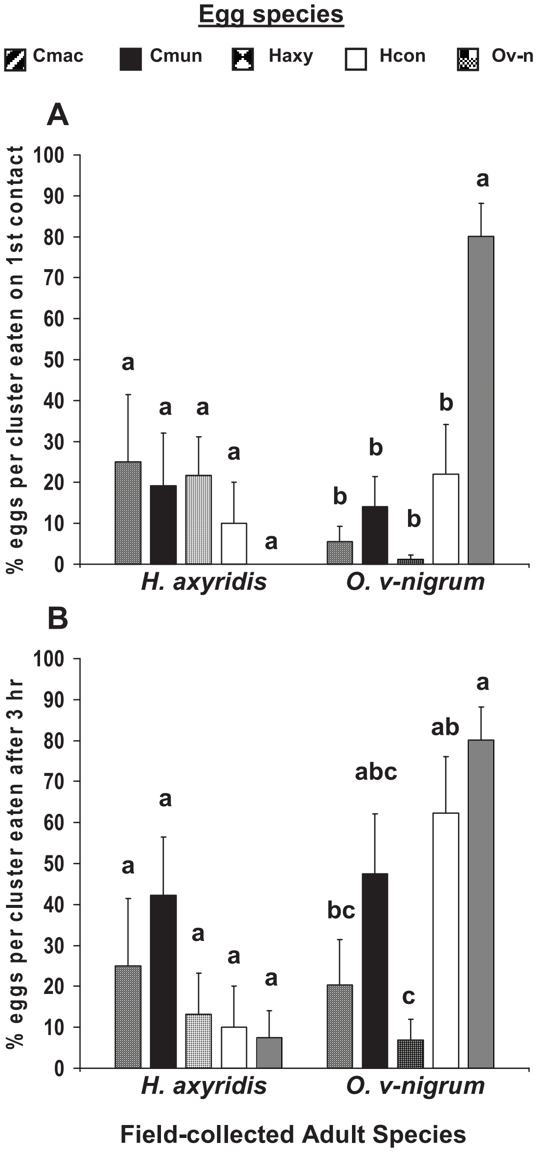

Fig. 7. Percentage of eggs per cluster consumed by field-collected *H. axyridis* and *O. v-nigrum* adults on (A) initial contact and (B) after a 3-h interval. Significant difference ($P < 0.05$) in percentage consumption of the different egg species by each predator species is denoted by unlike letters above columns. Cmac, *C. maculata*; Cmun, *C. munda*; Haxy, *H. axyridis*; Hcon, *H. convergens*; Ov-n, *O. v-nigrum*.

field-collected *H. axyridis* ($F = 2.37$; df = 4,45; $P = 0.0670$) but was significant for *O. v-nigrum* ($F = 2.63$; df = 4,45; $P = 0.0465$; Table 1). Time spent feeding on the different egg species during the initial contact was significant for both *H. axyridis* ($F = 3.83$; df = 4,41; $P = 0.0098$) and *O. v-nigrum* ($F = 3.36$; df = 4,37; $P = 0.0192$ (Table 1).

Discussion

Egg predation on initial contact by a predator can play an important role in egg survival. Typical coccinellid foraging behavior (Banks 1956, Kaddou 1960, Marks 1977, Rowlands and Chapin 1978, Carter and Dixon 1982) suggests that initial contact with a coccinellid egg cluster, when no egg feeding occurs, should not alter the precontact foraging strategy of the predator. Therefore, in the absence of prey, a predator would be likely to leave an area sooner and thus decrease the probability of subsequent contacts with an egg cluster. In fact, Marks (1977) showed that *C. septempunctata* larvae spent less time on plants they previously had searched. In this laboratory study, egg predation by those predators feeding on first contact was always higher, except for adults and larvae of *C. maculata*, than for those that did not feed during the initial contact. The majority of egg consumption by all predator species during the 3-h interval occurred as a result of predation on initial egg contact. Thus, acceptance of eggs for consumption on initial contact does impact egg survival.

Table 1. Mean contacts with egg clusters by predators over 3 h and mean time predators fed during initial contact with egg clusters

		Laboratory-reared adults		Laboratory-reared larvae		Field-collected adults[a]	
Predator species	Egg species	Contacts with egg clusters in 3 h (mean ± SE)[b]	Time (min) at egg cluster during first contact (mean ± SE)[b]	Contacts with egg clusters in 3 h (mean ± SE)[b]	Time (min) at egg cluster during first contact (mean ± SE)[b]	Contacts with egg clusters in 3 h (mean ± SE)[b]	Time (min) at egg cluster during first contact (mean ± SE)[b]
Cmac	Cmac	2.1 ± 0.5b	6.1 ± 3.8a	1.4 ± 0.2b	56.2 ± 15.4a	—	—
	Cmun	6.2 ± 0.9a	3.7 ± 2.4a	1.2 ± 0.2b	54.2 ± 14.8a	—	—
	Haxy	4.0 ± 1.2ab	20.9 ± 12.7a	2.6 ± 0.6a	27.8 ± 14.4a	—	—
	Hcon	1.8 ± 0.7b	13.4 ± 12.6a	1.6 ± 0.3b	31.6 ± 7.5a	—	—
	Ov-n	4.8 ± 1.6ab	11.2 ± 7.1a	1.3 ± 0.2b	58.9 ± 14.3a	—	—
Cmun	Cmac	7.4 ± 3.4a	25.1 ± 25.1a	0.3 ± 0.2c	34.2 ± 34.2ab	—	—
	Cmun	5.9 ± 3.1a	14.8 ± 8.13a	0.9 ± 0.5bc	51.9 ± 22.7a	—	—
	Haxy	3.2 ± 1.0a	4.2 ± 2.5a	4.0 ± 1.5a	0.0 ± 0b	—	—
	Hcon	3.9 ± 1.7a	0.0 ± 0a	2.8 ± 0.9ab	0.0 ± 0b	—	—
	Ov-n	3.8 ± 2.1a	0.0 ± 0a	1.0 ± 0.0c	0.0 ± 0b	—	—
Haxy	Cmac	3.0 ± 1.1a	44.7 ± 19.7a	1.0 ± 0.3a	70.2 ± 21.4a	7.2 ± 2.3a	5.4 ± 3.6b
	Cmun	3.6 ± 1.0a	28.9 ± 14.0a	1.6 ± 0.3a	97.0 ± 16.9a	2.2 ± 0.6a	15.3 ± 10.1b
	Haxy	1.7 ± 0.3a	46.2 ± 21.7a	0.8 ± 0.2a	123.0 ± 21.7a	2.9 ± 0.9a	58.5 ± 25.1a
	Hcon	2.2 ± 0.9a	29.1 ± 15.2a	0.8 ± 0.1a	80.2 ± 12.0a	6.6 ± 1.5a	1.5 ± 1.5b
	Ov-n	1.8 ± 0.6a	68.9 ± 25.9a	0.7 ± 0.3a	77.1 ± 33.2a	6.3 ± 1.6a	0.01 ± 0b
Hcon	Cmac	4.1 ± 0.5a	2.0 ± 1.6b	0.8 ± 0.2a	57.3 ± 25.1a	—	—
	Cmun	1.6 ± 0.3a	23.3 ± 9.3a	1.0 ± 0.3a	69.6 ± 23.7a	—	—
	Haxy	2.0 ± 0.4a	0.16 ± 0.15b	4.1 ± 1.6a	11.6 ± 8.2a	—	—
	Hcon	3.2 ± 0.7a	8.0 ± 2.7b	1.8 ± 0.4a	72.9 ± 25.3a	—	—
	Ov-n	2.4 ± 0.7a	6.1 ± 2.2b	4.7 ± 1.2a	31.7 ± 21.3a	—	
Ov-n	Cmac	3.3 ± 0.5bc	33.2 ± 13.3a	1.3 ± 0.2a	64.6 ± 17.5a	2.3 ± 0.6a	13.2 ± 12.9b
	Cmun	1.0 ± 0.0c	29.2 ± 13.5a	0.9 ± 0.1a	55.1 ± 17.1a	1.3 ± 0.3abc	7.4 ± 4.5b
	Haxy	2.3 ± 0.5bc	19.0 ± 13.9a	1.8 ± 0.3a	45.1 ± 19.4a	1.1 ± 0.3bc	0.5 ± 0.4b
	Hcon	3.4 ± 0.6ab	14.4 ± 11.3a	0.9 ± 0.2a	44.8 ± 13.6a	1.9 ± 0.4ab	7.3 ± 4.7b
	Ov-n	5.4 ± 1.4a	9.7 ± 7.4a	1.1 ± 0.1a	62.1 ± 19.4a	0.8 ± 0.1c	42.4 ± 12.2a

[a] Adults of *H. axyridis* and *O. v-nigrum* were the only field-collected species tested.
[b] Unlike letters following means indicate significant difference ($P < 0.05$) between egg species within each predator species.
Cmac, *C. maculata;* Cmun, *C. munda;* Haxy, *H. axyridis;* Hcon, *H. convergens;* Ov-n, *O. v-nigrum.*

Over the course of the experiment, the number of predator contacts with egg clusters and the time predators spent feeding during the first contact was not necessarily indicative of the amount of consumption. For instance, laboratory-reared *C. munda* and *H. axyridis* adults made similar numbers of contacts with all species' egg clusters. However, *C. munda* mostly cannibalized eggs both on first contact and after 3 h, whereas *H. axyridis* consumed a similar percentage eggs per cluster for each species both on first contact and after 3 h. Also, *O. v-nigrum* adults spent a similar amount of time feeding on eggs of each species during the first contact but ultimately consumed a significantly higher percentage of *O. v-nigrum* than *H. axyridis* eggs per cluster during this initial contact. It has been noted that consumption activity of larvae feeding on the eggs of some species (i.e., *C. maculata* larvae feeding on *H. axyridis* eggs) is slower than when larvae cannibalize eggs (T.E.C., unpublished data).

Cottrell and Yeargan (1998a, b) showed that cannibalism of *C. maculata* eggs was high in plantings of sweet corn, but acceptance of *C. maculata* eggs on initial contact was not determined. In this study, acceptance/rejection of any species' eggs by *C. maculata* on initial contact was not significantly different for laboratory-reared adults or larvae. Similar numbers of these adults accepted/rejected eggs of all species on initial contact, whereas similarly high numbers of *C. maculata* larvae accepted eggs of all species. It is noteworthy that *C. maculata* larvae often accepted *H. axyridis* eggs on first contact given that *H. axyridis* eggs are not suitable for development of first- or third-instar *C. maculata* (Cottrell 2004). This apparent anomaly may speak more for the omnivorous nature of *C. maculata* and the observation by Hodek (1996) that some alternative foods may be highly toxic. Egg species had no effect on percentage egg consumption for *C. maculata* adults whether on the initial contact or after 3 h. In fact, there was no difference in egg predation (all egg species combined) over time by adults or larvae whether feeding occurred during the initial contact or not.

Cycloneda munda was not a robust interspecific egg predator. Except for *C. munda* and *H. axyridis* eggs fed on by adults and *C. munda* eggs fed on by larvae, eggs were mostly rejected on first contact. Overall, egg cannibalism by both adults and larvae was higher than egg predation against all egg species except *C. maculata.* Eggs of *H. convergens* and *O. v-nigrum* were never accepted by adult and larval *C. munda* on first contact, and larvae never accepted *H. axyridis* eggs on first contact. At no point did *C. munda* ever eat *O. v-nigrum* eggs, although contact with eggs was made. *C. munda* was the smallest species used in the study, but its habits were not perceptibly different than other adults or larvae. Unlike *C. maculata, C. munda* ate a higher percentage of eggs per cluster (all egg species combined) over time when they fed on first contact compared with those not feeding on first contact. *C. munda* seems most susceptible to egg predation and the least likely to participate in interspecific egg predation for the species tested.

Adults and larvae of *H. axyridis* followed an acceptance/rejection pattern similar to *C. maculata. H. axyridis* adults (laboratory and field) consumed a similar percentage of each species' eggs on first contact and after 3 h. Larval egg predation on first contact was different only between eggs of *H. convergens* and *O. v-nigrum.* After the 3-h interval, *H. axyridis* egg cannibalism was lower than predation on *C. munda* and *H. convergens* eggs. Nonetheless, the percentage of eggs consumed over time (all egg species combined) by *H. axyridis* adults (laboratory and field) and larvae was higher when they fed on first contact compared with not feeding on first contact. Overall, *H. axyridis* was the most consistent interspecific egg predator tested and also the species least likely to have high interspecific predation against its eggs. In fact, neither *C. maculata* nor *O. v-nigrum* larvae can complete development on a diet of *H. axyridis* eggs. In direct contrast, *H. axyridis* larvae can complete development on a diet of either *C. maculata* or *O. v-nigrum* eggs (Cottrell 2004).

Hippodamia convergens was the only species with different numbers of both adults and larvae accepting/rejecting *H. axyridis* eggs on first contact compared with other egg species. Percentage egg predation by *H. convergens* on *H. axyridis* eggs tended to be lowest for *H. axyridis* eggs. This trend was significant compared with adult predation on *C. munda* and *O. v-nigrum* eggs and larval predation on *C. munda* and *H. convergens* eggs. After 3 h, the difference in percentage predation by *H. convergens* adults and larvae was only significant between *H. axyridis* and *C. munda* eggs. When egg species were combined, *H. convergens* adults and larvae that fed on initial contact with egg clusters consumed a higher percentage of eggs over time than those that did not feed on first contact.

The reaction of adult (laboratory) and larval *O. v-nigrum* to eggs on first contact was similar to that of both *C. maculata* and *H. axyridis* adults and larvae. Field-collected adults always cannibalized eggs on first contact but mostly rejected eggs of other species. Predation of *H. axyridis* eggs on first contact and after 3 h was significantly low for both adults (laboratory and field) and larvae. Again, when egg species were combined, predation by *O. v-nigrum* adults (laboratory and field) and larvae was higher for those that did feed on first contact than for those that did not.

It is likely that eggs of all native species tested (i.e., *C. maculata, C. munda, H. convergens,* and *O. v-nigrum*), but not exotic *H. axyridis* eggs, are essential food (i.e., ensure larval development and oviposition as defined by Hodek 1996) for *C. maculata, H. convergens,* and *O. v-nigrum,* whereas only *C. munda* eggs serve as essential food for *C. munda.* In direct contrast, all egg species tested would likely serve as essential food for the exotic *H. axyridis.*

Even though larvae, not adults, represent the larger predation threat to eggs of Coccinellidae (Cottrell and Yeargan 1998a, b), adult Coccinellidae can feed on eggs of Coccinellidae (Cottrell 2005). It was not possible to obtain adequate numbers of all field-collected adult species, or any larval species, given the imposed time constraint to assay field-collected adults under representative hunger conditions as existed in the field. Nonetheless, factors other than starvation likely contributed to overall differences of the initial response of laboratory-reared (including *H. convergens* adults) and field-collected adults to eggs of Coccinellidae. Factors affecting the propensity to eat eggs on first contact in this study could have included diet, hunger level, and acclimation to the laboratory. The laboratory-reared adults were known to be without food for 24 h, whereas the field-collected adults were collected from host plants that contained prey, thus accentuating starvation of laboratory-reared adults. It is also possible that the laboratory diet predisposed laboratory-reared adults to feed on first contact more readily than adults collected from the field. The likely predominant diet of aphids for field-collected adults, along with an unknown level of hunger, could have prompted them to continue searching for aphids, thus bypassing encountered coccinellid eggs during the test. In addition, the nutritional demands of laboratory-reared adults may not have been entirely met, thus encouraging those adults to be more receptive of alternative food. It is likely that, under forced starvation conditions, the number of field-collected adults eating coccinellid eggs on initial contact would increase. Thus, when conditions exist that favor egg predation, e.g., low aphid availability (Osawa 1992), results from this study strongly suggest that native eggs will be attacked by both the native and exotic species, whereas the larger threat to exotic eggs will be cannibalism.

Acknowledgments

Technical support for this research was provided by A. Amis, K. Dixon, and T. Ellis (USDA–ARS, SEFTNRL, Byron, GA). An earlier draft of this manuscript was reviewed by K. V. Yeargan (University of Kentucky, Lexington, KY), A. A. Amis (USDA–ARS, SEFTNRL), and two anonymous reviewers.

References Cited

Ayer, W. A., and L. M. Browne. 1977. The ladybug alkaloids including synthesis and biosynthesis. Heterocycles 7: 685–707.

Banks, C. J. 1956. Observations on the behaviour and mortality in Coccinellidae before dispersal from the egg shells. Proc. R. Entomol. Soc. Lond. 31: 56–61.

Brown, M. W., and S. S. Miller. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis.* Entomol. News. 109: 143–151.

Burgio, G., F. Santi, and S. Maini. 2002. On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Biol. Control 24: 110–116.

Burgio, G., F. Santi, and S. Maini. 2005. Intra-guild predation and cannibalism between *Harmonia axyridis* and *Adalia bipunctata* adults and larvae: laboratory experiments. Bull. Insect. 58: 135–140.

Carter, M. C., and A.F.G. Dixon. 1982. Habitat quality and the foraging behaviour of coccinellid larvae. J. Anim. Ecol. 51: 865–878.

Ceryngier, P., and I. Hodek. 1996. Enemies of Coccinellidae, pp. 319–350. *In* I. Hodek and A. Honěk (eds.), Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Coderre, D., E. Lucas, and I. Gagne. 1995. The occurrence of *Harmonia axyridis* (Coleoptera: Coccinellidae) in Canada. Can. Entomol. 127: 609–611.

Colunga-Garcia, M., and S. H. Gage. 1998. Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coeloptera: Coccinellidae) in a Michigan landscape. Environ. Entomol. 27: 1574–1580.

Cottrell, T. E. 2004. Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. Biol. Control 31: 362–371.

Cottrell, T. E. 2005. Predation and cannibalism of lady beetle eggs by adult lady beetles. Biol. Control 34: 159–164.

Cottrell, T. E., and K. V. Yeargan. 1998a. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environ. Entomol. 27: 1402–1410.

Cottrell, T. E., and K. V. Yeargan. 1998b. Influence of a native weed, *Acalypha ostryaefolia* (Euphorbiaceae), on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environ. Entomol. 27: 1375–1385.

Cottrell, T. E., and K. V. Yeargan. 1998c. Intraguild predation between an introduced lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). J. Kans. Entomol. Soc. 71: 159–163.

Hemptinne, J. L., G. Lognay, C. Gauthier, and A.F.G. Dixon. 2000. Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera: Coccinellidae). Chemoecology 10: 123–128.

Hodek, I. 1996. Food relationships, pp. 143–238. *In* I. Hodek and A. Honěk (eds.), Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands.

JMP. 2002. JMP statistics and graphics guide. SAS Institute, Cary, NC.

Kaddou, I. K. 1960. The feeding behavior of *Hippodamia quinquesignata* (Kirby) larvae. Univ. Calif. Publ. Entomol. 16: 181–232.

Koch, R. L. 2003. The multicolored Asian lady beetle, *Harmonia axyridis:* a review of its biology, uses in biological control, and non-target impacts. J. Insect. Sci. 3: 1–16.

LaMana, M. L., and J. C. Miller. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Biol. Control 6: 232–237.

Lundgren, J. G., A. A. Razzak, and R. N. Wiedenmann. 2004. Population responses and food consumption by predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. Environ. Entomol. 33: 958–963.

Marks, R. J. 1977. Laboratory studies of plant searching behaviour by *Coccinella septempunctata* L. larvae. Bull. Entomol. Res. 67: 235–241.

Mills, N. J. 1982. Voracity, cannibalism and coccinellid predation. J. Appl. Biol. 101: 144–148.

Musser, F. R., and A. M. Shelton. 2003. Factors affecting the temporal and within-plant distribution of coccinellids in corn and their impact on potential intra-guild predation. Environ. Entomol. 32: 575–583.

Osawa, N. 1992. A life table of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae) in relation to the aphid abundance. Jpn. J. Entomol. 60: 575–579.

Pienkowski, R. L. 1965. The incidence and effect of egg cannibalism in first-instar *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). Ann. Entomol. Soc. Am. 58: 150–153.

Rowlands, M. L., and J. W. Chapin. 1978. Prey searching behavior in adults of *Hippodamia convergens* (Coleoptera: Coccinellidae). J. Georgia Entomol. Soc. 13: 309–315.

SAS Institute. 2002. SAS software: version 9.1. SAS Institute, Cary, NC.

Sato, S., and A.F.G. Dixon. 2004. Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. Agric. For. Entomol. 6: 21–24.

Sato, S., A.F.G. Dixon, and H. Yasuda. 2003. Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. Ecol. Entomol. 28: 628–633.

Snyder, W. E., G. M. Clevenger, and S. D. Eigenbrode. 2004. Intraguild predation and successful invasion by introduced ladybird beetles. Oecologia (Berl.) 140: 559–565.

Tedders, W. L., and P. W. Schaefer. 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. Entomol. News 105: 228–243.

Wells, M. L., and R. M. McPherson. 1999. Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). Environ. Entomol. 28: 768–773.

Yasuda, H., T. Kikuchi, P. Kindlmann, and S. Sato. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. J. Insect Behav. 14: 373–384.

Zar, J. H. 1999. Biostatistical Analysis, fourth ed., Prentice Hall, Upper Saddle River, NJ.

Received for publication 22 February 2006; accepted 5 December 2006.