Invasion of the Florida Citrus Ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and Asymmetric Competition with a Native Species, *Cycloneda sanguinea*

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ABSTRACT Field data collected from the major citrus-producing regions of Florida over the past 5 yr indicate that the introduction of the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas), has increased in abundance while the formerly dominant *Cycloneda sanguinea* (L.) has declined. What is known of the diet breadth, habitat preferences, and thermal thresholds for development of these two species indicates considerable niche overlap. The larger *H. axyridis* has many intrinsic advantages over *C. sanguinea,* including higher fecundity and fertility, and a lower rate of larval cannibalism. In laboratory tests, adults and larvae of *H. axyridis* consumed eggs of *C. sanguinea* more readily than vice versa. All *H. axyridis* adults provided with either a conspecific or a heterospecific second-instar larva killed and ate it, whereas only 15% of *C. sanguinea* adults consumed a second-instar larva of *H. axyridis* over a 24-h period. Larvae of *H. axyridis* were more aggressive against larvae of *C. sanguinea* in laboratory tests than vice versa; even when *H. axyridis* larvae were paired with a *C. sanguinea* larva 2 d older and two to three times as large, they won 67% of contests. In choice tests, larvae of both species preferred to feed on dead *C. sanguinea* larvae than on dead *H. axyridis* larvae. Larvae of *H. axyridis* were capable of completing development exclusively as intraguild predators on *C. sanguinea* larvae, whereas the reverse was not true. The data suggest that *H. axyridis* is a highly evolved interspecific competitor, whereas *C. sanguinea* is adapted more to intraspecific competition and has few defenses against *H. axyridis.* Competitive displacement of *C. sanguinea* by *H. axyridis* appears to be in progress in the citrus ecosystem in Florida.

KEY WORDS multicolored Asian lady beetle, *Harmonia axyridis,* biodiversity, biological control, competition, intraguild predation

THE MULTICOLORED ASIAN LADY BEETLE, *Harmonia axyridis* (Pallas), was intentionally introduced to North America at least six times in the last century (Gordon 1985) to control a range of arboreal homopteran pests. Most recently it was released in North Carolina in 1983 to control the red pine bast scale, *Matsucoccus resinosae* (McClure 1987). It was not confirmed as established in the United States until years later in Louisiana and Georgia (Chapin and Brou 1991), hundreds of kilometers from the nearest release site. It is therefore suspected that establishment resulted from accidental introductions rather than from the intentional releases (Day et al. 1994). Subsequently, *H. axyridis* invaded coccinellid communities in arboreal habitats throughout continental United States from Florida and Georgia in the south, to Michigan, Ontario, Quebec, New Brunswick, and Nova Scotia in the north, and Texas, California, Oregon, and Washington in the west (Coderre et al. 1995, Dreisdadt et al. 1995, Hoebeke and Wheeler 1996, Nalepa et al. 1996). It is now an important biological control agent of aphids in pecan (LaRock and Ellington 1996), apple (Brown and Miller 1998), sweet corn (Cottrell and Yeargan 1998), and citrus (Michaud 2000a), among other crops.

Evidence is now accumulating to suggest that the abundance of some other coccinellid species, including *Coccinella novemnotata* (Wheeler and Hoebeke 1995), *Brachiacantha ursina, Chilocorus stigma,* and *Cycloneda munda* (Colunga-Garcia and Gage 1998), is declining concurrently with the advent of *H. axyridis* and another introduced species, *Coccinella septempunctata.* For example, LaMana and Miller (1996) reported that *H. axyridis* comprised 70% of total coccinellids they collected from arboreal habitats in western Oregon in 1993 and 1994. Similarly, Brown and Miller (1998) documented the dramatic rise in dominance of *H. axyridis* in apple orchards in West Virginia from 1994 to 1995. However, direct evidence of the potential mechanisms of competitive displacement of native species by *H. axyridis* has been lacking. The purpose of this paper was to present field data that indicate *H. axyridis* is in the process of replacing the

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native ladybeetle *Cycloneda sanguinea* L. as the dominant aphidophagous coccinellid in the citrus ecosystem in Florida, and the results of a series of laboratory studies that elucidate the asymmetric nature of competitive interactions between these two species.

In terms of geographic range, *C. sanguinea* is subtropical in distribution throughout the Americas, whereas *H. axyridis* thrives in both temperate and subtropical regions worldwide. The apparent lack of a true diapause in *C. sanguinea* may be responsible for limiting its northern range below an isotherm corresponding approximately to 33° north latitude (Gordon 1985). However, *H. axyridis* shows both facultative aestivation and true diapause (Coderre et al. 1995) and is very resistant to winter conditions, reportedly surviving temperatures as low as –30°C for short periods (Iablokoff-Khnzorian 1982). The upper thermal thresholds for completion of development in these species have not been compared directly and are therefore one subject of investigation in the current study.

The appearance of *H. axyridis* in Florida dates back to the early 1990s (M. Thomas, personal communication). Before 1996, *H. axyridis* was relatively rare in Florida citrus, possibly due in part to its inability to produce eggs on a diet of the spirea aphid, *Aphis spiraecola* Patch, the dominant aphid prey in citrus before the invasion of the brown citrus aphid, *Toxoptera citricida* (Kirkaldy) (Michaud 2000b). The full diet breadth of *H. axyridis* is probably not known, but it is highly polyphagous (Tedders and Schaefer 1994) and has been reared in the laboratory on diets as diverse as chicken livers and sugar (Hong and Park 1996), pulverized honey bee brood (Okada et al. 1972), and eggs of a brine shrimp (Hongo and Obayashi 1997). Although primarily a predator of aphids, field observations of *H. axyridis* have recorded prey as diverse as mites (Lucas et al. 1997a, 1997b) and weevil eggs (Kalaskar and Evans 2001). In Florida it has been observed to feed on soft scales, mealybugs, psyllids, whitefly larvae, and the eggs of Coleoptera and Lepidoptera (unpublished data). Both *H. axyridis* and *C. sanguinea* prefer arboreal habitats and have similar patterns of seasonal abundance in citrus (Michaud 2000a). All life stages of both species can be observed together on the same colonies of aphids (Michaud 2000b) and psyllids (Michaud 2000c). Because there is such a large degree of niche overlap between these two species in the citrus ecosystem, many opportunities exist for competitive interactions between them. My own field observations in citrus include various records of intraguild predation events; predation by *H. axyridis* larvae on *C. sanguinea* larvae and prepupae, as well as predation on coccinellid eggs by adults and larvae of both species (unpublished data).

Whitcomb (1994) reported that *C. sanguinea,* along with *Coleomegilla maculata* and *Hippodamia convergens,* was one of the most abundant coccinellids in various Florida agroecosystems, being especially dominant in southern portions of the state. Hall and Bennett (1994) reported that *C. sanguinea,* along with *Diomus terminatus,* was one of the most abundant and important predators of the yellow sugarcane aphid, *Sipha flava.* Jackson and Davies (1999) mentioned *C. sanguinea* as one of the most important predators of aphids in citrus. The relative abundance of *C. sanguinea* and *H. axyridis* in Florida citrus from 1997 to 1999 (corresponding to the period of invasion by *T. citricida*) was reported by Michaud (2000b) and indicates that *C. sanguinea* was still the dominant species during this period by a margin of almost 2 to 1 over *H. axyridis.* Observations made in central Florida during the fall of 2000 (unpublished data) suggested that *C. sanguinea* was no longer dominant in citrus and surveys were undertaken in spring of 2001 to collect information on relative abundance of these two species from different citrus-growing regions of the state so that comparisons could be made to the historical data. A series of laboratory experiments was then conducted to assess (1) comparative reproductive potential, (2) upper thermal thresholds for development, (3) comparative rates of larval cannibalism, and (4) outcomes of heterospecific (intraguild) interactions between different life stages.

Materials and Methods

Relative Abundance. During fall 2000 and spring 2001, counts of adult coccinellids were made at a series of locations representing the three major citrus-growing regions in Florida: Southwest Florida (Collier and Hendry Counties), Indian River District (St. Lucie County), and the Central Ridge District (Highlands, and Polk Counties). Visual counts of adult coccinellids were made on flushing and flowering citrus trees where many species come to feed on pollen and nectar and search the newly expanding leaves for suitable prey. Flushed terminals were examined for coccinellids on a mean ± SEM of 50 ± 5.2 trees at each site. Citrus groves were sampled during the daytime, between 0930 and 1530 hours, and each sampling visit lasted 1.5–2.5 h. These data were then compared with data that had been collected in the same manner from these regions in 1997 and 1998 during surveys of the brown citrus aphid, *T. citricida.* The exact sampling dates were as follows. Collier County: 19 May (1997), 15 March (2001). Hendry County: 14 February, 14 May (1998), and 16 March (2001). St. Lucie County: 21 April, 9 July (1997), 15 February, 13 May (1998) and 14 March (2001). Highlands County: 25 July (1997), 21 March (1998) and 21 March (2001). Polk County: 18 March, 18 May, 27 October (1998), 8 March, 21 March and 27 March (2001). The numbers of *C. sanguinea* and *H. axyridis* are each expressed as a proportion of all other coccinellids for each county and compared across dates using an 'n × r' contingency table analysis and the chi-square test (SAS Institute 1998).

Insect Rearing. Stock colonies of beetles were established from adult beetles collected from citrus trees in Polk County, FL, in November 2000. Adult beetles were maintained in 1 liter, wide-mouth glass mason jars filled with shredded wax paper and covered with a fine nylon mesh. Water was provided in jars on a cotton wick. The diet used for stock colonies, and all experiments, consisted of frozen eggs of *Ephestia kuhniella* Zeller (Lepidoptera: Pyralidae) and bee pollen, hereafter referred to as 'food'. Ovipositing females were removed from jars, and isolated in plastic petri dishes (5.5 by 1.0 cm). Eggs were harvested daily and maintained in a Plexiglas incubator on a laboratory bench until hatching, usually 3–4 d later. All stock colonies and laboratory experiments were maintained at an ambient temperature of 24 ± 2°C under cool-white fluorescent lights set to a photoperiod of 16:8 (L:D) h unless otherwise specified. All experiments were conducted on a laboratory bench in plastic petri dishes (5.5 by 1 cm), hereafter referred to as 'dishes.' Water encapsulated in polymer beads (Entomos LLC, Gainesville, FL) was made continuously available to insects in dishes in all experiments. Voucher specimens of both species are deposited at the Florida State Collection of Arthropods, Gainesville, FL.

Fecundity and Fertility. It has been shown that larval diet influences not only developmental time and adult weight in these two species, but also the subsequent fecundity and fertility of adult females (Michaud 2000b). Therefore, assessment of female reproductive performance was carried out using field-collected adults that had developed on the natural diets available in citrus groves. The tradeoff was that female age was unknown and fertility and fecundity decline as females approach the end of their reproductive lives. To exclude the oldest females, only data from females laying eggs on at least 7 of the 14 d of the experiment were analyzed. A total of 134 *C. sanguinea* and 78 *H. axyridis* adults was collected in citrus groves in Lake Alfred, Polk County, FL, on 9 March 2001. Females were isolated in individual dishes in a temperature-controlled greenhouse (25 ± 2°C) under natural light and provisioned with food daily. All eggs were harvested and counted daily for a period of 14 d for each female, tallied from the first day of oviposition. The number of total eggs laid per female and the percent of eggs hatching were compared between species by one-way analysis of variance (ANOVA).

Upper Thermal Thresholds for Development. Newly laid egg masses (<24 h old, $n = 10$ per treatment) were held in climate-controlled growth chambers at constant temperatures of 28, 30, or 32°C, 45–65% RH, and a photoperiod of 16:8 (L:D) h. For each high-temperature treatment, an equal number of egg masses were held at 24°C under otherwise identical conditions to serve as controls, because this temperature is close to optimal for incubation of eggs of both species. The number of egg masses hatching in each high-temperature treatment was tallied and compared with those of controls by means of a chi-square goodness-of-fit test.

For each temperature trial, newly eclosed larvae (<24 h old) were divided randomly into two groups ($n = 20$ per group), one held at the treatment temperature, the other held at the control temperature, and provisioned with food daily. Insects were maintained under the same paired sets of environmental conditions described above and larval survival and developmental time (days to formation of a prepupa) were recorded. The number of larvae completing development was compared using a chi-square goodness-of-fit test and developmental time was compared using a one-way ANOVA.

Cannibalism. Comparative rates of cannibalism were measured by confining even-aged larvae (24 ± 8 h old) in groups of four ($n = 24$ replicates for both species). Dishes were checked on a daily basis, fresh food was provided, and all dead larvae were examined for evidence of cannibalism. The number of cannibalism events/replicate and the number of days to each cannibalism event were compared among species by means of one-way ANOVA.

Adult Predation on Larvae. Laboratory-reared adults of each species (3–4 wk old, $n = 40$) were confined individually in dishes with either a single 3-d-old, second-instar conspecific larva ($n = 20$), or a single 3-d-old, second-instar larva of the other species ($n = 20$). Food was provided in each dish and the number of beetles consuming larvae was tallied after 24 h. The numbers of adults consuming conspecific and heterospecific larvae was compared between species using a chi-square goodness-of-fit test.

Adult Predation on Eggs. Egg clusters were harvested from ovipositing females in the stock colonies, eggs were counted, and clusters were used for experiments at <24 h of age. Egg clusters were selected for experiments that ranged in size from 10 to 20 eggs per cluster. Laboratory-reared adults of each species (3–4 wk old) were confined individually in dishes with either an egg cluster of their own species ($n = 20$) or one of the other species ($n = 50$). Food and water beads were provided in each dish and the number of eggs consumed in each replicate was tallied after 24 h. The numbers of conspecific and heterospecific eggs consumed by adults was compared by one-way ANOVA; the numbers of adults consuming conspecific and heterospecific egg clusters was compared using a chi-square goodness-of-fit test.

Larval Predation on Eggs. Egg clusters were harvested from ovipositing females in the stock colonies, eggs were counted, and clusters were used for experiments at <24 h of age. Laboratory-reared, 3-d-old larvae of each species were confined individually in dishes with either a conspecific egg cluster ($n = 20$), or an egg cluster of the other species ($n = 20$). Food and water beads were provided in each dish and the number of eggs consumed by each larva was tallied after 24 h. The data for number of eggs consumed were analyzed by one-way ANOVA; data for numbers of larvae consuming eggs were compared by the chi-square goodness-of-fit test.

Larval Contests. Three series of larval contests were conducted in which a single *H. axyridis* larva was confined individually in a plastic petri dish (as above) with a single *C. sanguinea* larva under the following three conditions: (1) larvae were the same age (24 ± 6 h old), (2) *C. sanguinea* larvae 48 ± 6 h old were paired with *H. axyridis* larvae 24 ± 6 h old, (3) *C. sanguinea* larvae 72 ± 6 h old were paired with *H. axyridis* larvae 24 ± 6 h old. Food and water beads were provided in each dish and fresh food was supplied every third day. Every replicate was examined daily and all dead larvae were examined for any evident causes of mortality. Larvae killed in interaction with the other larva were typically consumed; larvae that died from other causes were not. Larval death resulting from predation was therefore usually easy to distinguish from other causes but in cases of doubt, replicates were excluded from analysis. The time to attack was compared between treatments and species by one-way ANOVA.

Development on Heterospecific Larvae. For each species, 24 newly eclosed larvae (<24 h old) were divided randomly into two groups of 12 and placed individually into plastic petri dishes. Larvae in the treatment group were provisioned daily with water beads and fresh corpses of the opposite species (killed by freezing), whereas larvae in the control group received the standard food. Mortality was recorded daily and developmental times and adult dry weights were recorded for survivors. Mortality data were compared using the chi-square goodness-of-fit test and data for developmental time and adult dry weight, by one-way ANOVA.

Results

Relative Abundance. Comparisons of proportional abundance did not reveal any significant differences among dates before 1999 in either St. Lucie County or Highlands County; only a single pre-1999 sample date was available for Collier and Hendry Counties. The relative abundance of *C. sanguinea* was significantly higher in Polk county in fall than in the preceding summer (chi-square = 55.642, df = 1, $P < 0.001$). A comparison of data pooled before and after 1999 revealed that the relative abundance of *H. axyridis* increased significantly as a proportion of total coccinellids in three of the five counties, whereas the relative abundance of *C. sanguinea* has decreased significantly in all five (Fig. 1). When data are pooled statewide before and after 1999, the relative abundance of *H. axyridis* as a proportion of total coccinellids has increased significantly (chi-square = 69.264, df = 1, $P < 0.001$), whereas that of *C. sanguinea* has decreased significantly (chi-square = 278.949, df = 1, $P < 0.001$).

Fecundity and Fertility. The sex ratio of field-collected beetles (% female) was 37.3% ($n = 134$) and 79.5 ($n = 78$) for *C. sanguinea* and *H. axyridis*, respectively (test of proportions, $P < 0.001$). Females of *H. axyridis* laid significantly more eggs over the 2-wk period than did females of *C. sanguinea*, and a significantly larger percentage of these eggs hatched (Fig. 2).

Upper Thermal Thresholds for Development. No egg clusters of either species hatched at 32°C ($n = 10$ in both cases), or at 30°C ($n = 10$ in both cases). At 28°C, eight out of 10 *C. sanguinea* egg clusters hatched, compared with nine out of 10 at 24°C (chi-square = 1.11, NS). Nine out of 10 *H. axyridis* egg clusters hatched at 28°C, compared with 10 out of 10 at 24°C (chi-square = 1.11, NS).

Larvae of both species ($n = 20$) experienced 100% mortality at temperatures of 30 and 32°C. Larvae of *C. sanguinea* experienced 35% mortality at 28°C, significantly more than the 7% mortality of larvae held at 24°C (chi-square = 6.94, $P < 0.01$), although the mean larval developmental time of survivors at 28°C (±SEM) was 6.8 ± 0.19 d as opposed to 9.1 ± 0.16 d at 24°C ($F = 83.368$; df = 1, 29; $P < 0.001$). Larvae of *H. axyridis* experienced only 5% mortality at 28°C, not significantly different from larvae held at 24°C that had 100% survival (chi-square = 0.25, NS) and mean larval developmental time (±SEM) was 7.1 ± 0.11 d as opposed to 9.6 ± 0.11 d ($F = 246.547$; df = 1, 37; $P < 0.001$).

Cannibalism. When larvae of each species were reared 4/dish the mean number of cannibalism events per replicate (±SEM) was 1.75 ± 0.14 for *C. sanguinea* versus 1.04 ± 0.14 for *H. axyridis* ($F = 12.907$; df = 1, 49; $P < 0.001$). The mean time (±SEM) to a cannibalism event was 3.50 ± 0.73 d for *C. sanguinea* and 5.24 ± 0.68 d for *H. axyridis* ($F = 7.974$; df = 1, 76; $P = 0.006$).

Adult Predation on Larvae. One hundred percent of *H. axyridis* adults ($n = 20$) consumed the conspecific larva within the 24-h period, compared with 90% of the *C. sanguinea* adults ($n = 20$) (chi-square = 1.00, NS). However, 100% of *H. axyridis* adults ($n = 20$) confined with a *C. sanguinea* larva consumed it, compared with only 15% of *C. sanguinea* adults confined with an *H. axyridis* larva (chi-square = 72.25, $P < 0.001$).

Adult Predation on Eggs. Adults of *H. axyridis* consumed *C. sanguinea* eggs and eggs of conspecific females in equal numbers in no-choice situations over a 24-h period (Means ± SEM = 4.4 ± 0.8 eggs/adult and 4.7 ± 1.7 eggs/adult, respectively; $F = 0.036$; df = 1, 68; $P = 0.850$). Fifty-six percent of adults ate at least one *C. sanguinea* egg, whereas 70% consumed at least one conspecific egg. Adults feeding on *C. sanguinea* eggs consumed a mean ± SEM of 4.40 ± 0.75 eggs (=60.5 ± 5.2% of available eggs) with six adults consuming the entire egg cluster.

Adults of *C. sanguinea* consumed more eggs of conspecific females than those of *H. axyridis* in no-choice situations over a 24-h period (Means ± SEM = 8.3 ± 1.1 eggs/adult (61 ± 6.3%) versus 1.3 ± 0.3 eggs/adult (7 ± 2.1%), respectively; $F = 63.170$; df = 1, 68; $P < 0.001$). A majority of adults (72%) did not consume any *H. axyridis* eggs and in no case was an egg cluster completely consumed.

Comparisons between species revealed that twice as many *H. axyridis* adults consumed heterospecific eggs as did *C. sanguinea* adults (28 versus 14; chi-square = 7.00; $P < 0.01$). When the numbers of heterospecific eggs consumed were compared between species, *H. axyridis* adults consumed significantly more *C. sanguinea* eggs than vice versa when all replicates were considered ($F = 14.679$; df = 1, 98; $P < 0.001$), and when only adults consuming eggs were considered ($F = 6.179$; df = 1, 40; $P = 0.017$).

Larval Predation on Eggs. Three-day-old larvae of *H. axyridis* consumed significantly more conspecific eggs than eggs of *C. sanguinea* in no-choice situations

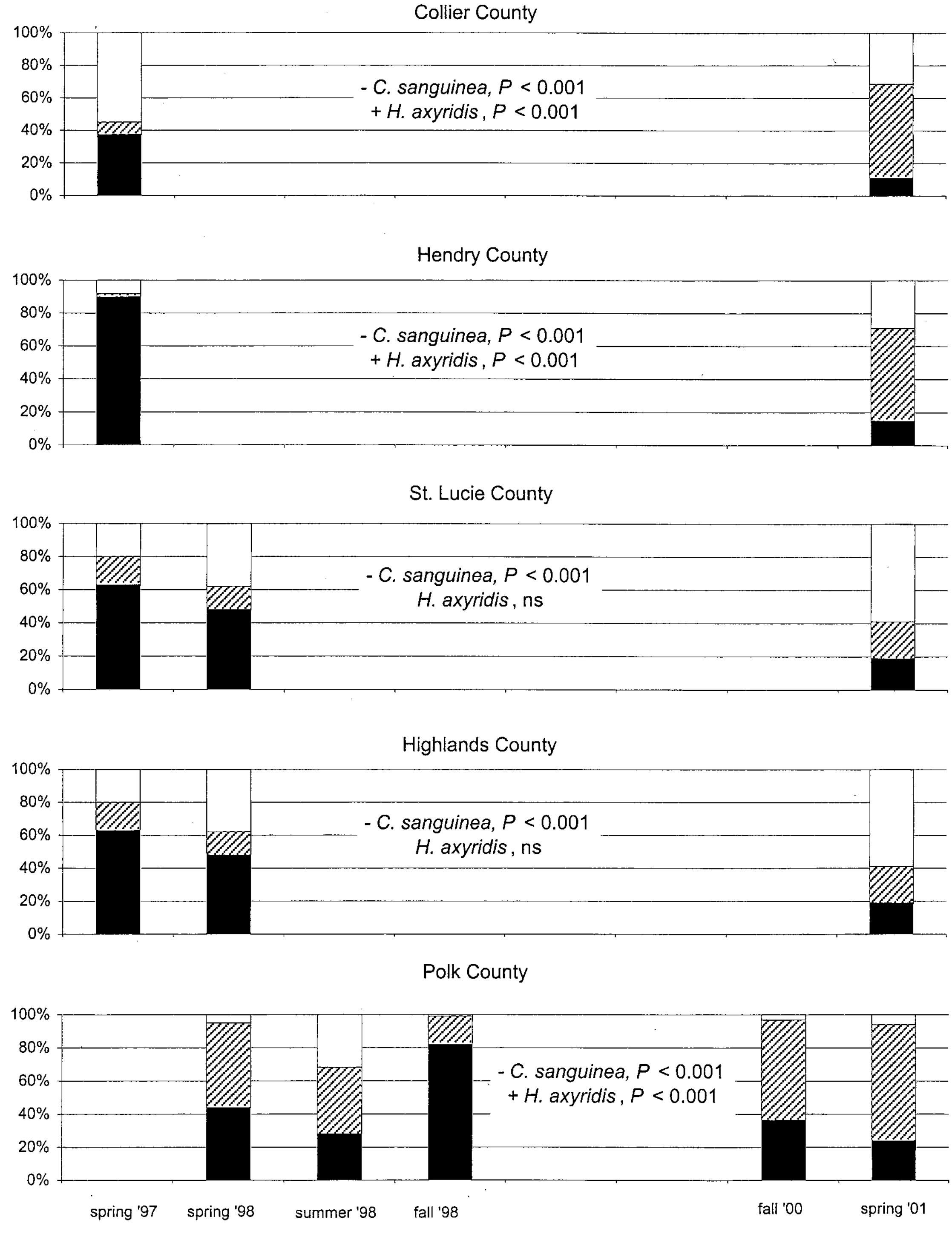

Fig. 1. Abundance of *H. axyridis* (hatched bars) and *C. sanguinea* (solid bars) relative to all other coccinellids (open bars) over various sampling dates in five different Florida counties representing different regions of the state: southwest Florida (Collier and Hendry Counties), east coast (St. Lucie County), and central ridge (Highlands and Polk Counties). Data were compared before and after 1999 using contingency table analysis and the chi-square test; '-' indicates significant decline in relative abundance, '+' indicates significant increase.

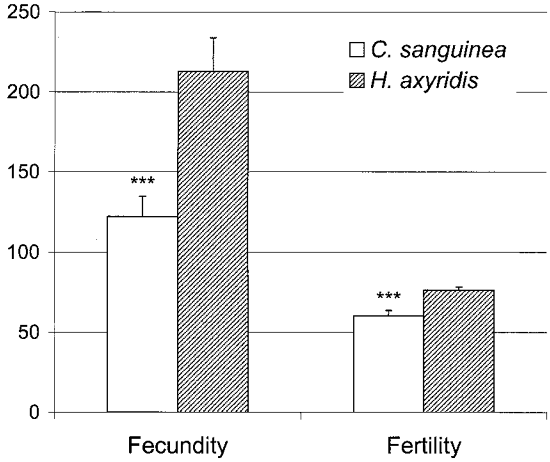

Fig. 2. Mean number of eggs laid per female over 10 d (Fecundity) and percentage of eggs hatching (Fertility) for *Cycloneda sanguinea* and *Harmonia axyridis* fed *Ephestia* eggs. Differences between species were significantly different in analysis of variance (ANOVA), $P < 0.001$ in both cases.

over a 2-d period (means ± SEM = 12.8 ± 1.8 eggs/larva (65 ± 9.1%) versus 4.5 ± 1.30 eggs/larva (27.8 ± 8.0%), respectively; $F = 11.621$; df = 1, 36; $P = 0.002$). Significantly more *H. axyridis* larvae consumed conspecific eggs than consumed heterospecific eggs (16 of 18 versus 10 of 20; chi-square = 17.09, $P < 0.001$).

Three day-old larvae of *C. sanguinea* consumed 7.5 ± 1.1 (mean ± SEM) conspecific eggs each (mean = 66.5% of available eggs) over the 2-d period with eight larvae (40%) consuming all the eggs and only three eating none. No *H. axyridis* eggs were consumed in any replicate ($n = 20$).

Larval Contests. When larvae of both species were the same age (24 ± 8 h old) *H. axyridis* larvae won 100% of larval contests (Fig. 3). The mean time to attack was 3.70 ± 1.10 d. When *C. sanguinea* larvae 48 ± 8 h old were paired with *H. axyridis* larvae 24 ± 8 h old the mean time to attack by an *H. axyridis* larva was 3.89 ± 0.23 d. Although most contests occurred between larvae, the *H. axyridis* larva attacked and fed on the prepupal stage of *C. sanguinea* in two cases (<3% of the contests won by *H. axyridis*). When *C. sanguinea* larvae 72 ± 8 h old were paired with *H. axyridis* larvae 24 ± 8 h old the mean time to attack by an *H. axyridis* larva was 6.17 ± 0.27 d. Again, most contests were won by the *H. axyridis* larvae attacking and killing the *C. sanguinea* larva, although *H. axyridis* attacked the prepupal stage of *C. sanguinea* in 18 cases (14% of the contests won by *H. axyridis*). Attacks by *H. axyridis* larvae occurred significantly later when the *C. sanguinea* larvae had a 2-d developmental advantage, compared with when it had a 1-d developmental advantage ($F = 41.162$; df = 1, 145; $P < 0.001$). There was no difference between these two treatments in time to attack by *C. sanguinea* larvae (2.14 and 2.67 d, respectively; $F = 1.393$; df = 1, 14; NS). The mean number of days to attack was not significantly different between species when *C. sanguinea* were 1 d older (*C. sanguinea* versus *H. axyridis* = 2.20 ± 0.20 versus 3.86 ± 0.23; df = 1, 90; $F = 3.133$; NS) but was significantly later for *H. axyridis* larvae when *C. sanguinea* larvae were 2 d older (*C. sanguinea* versus *H. axyridis* = 2.67 ± 0.33 versus 6.17 ± 0.27; $F = 23.414$; df = 1, 67; $P < 0.001$).

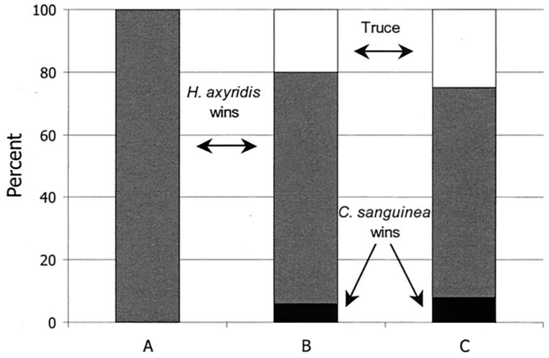

Fig. 3. Percentage of contests won by larvae of *Harmonia axyridis* (hatched bars) or *Cycloneda sanguinea* (solid bars) or that ended in a truce (both larvae pupated successfully = open bars). Larvae were combined in pairs in petri dishes and fed *Ephestia* eggs. Series A, larvae same age; series B, *C. sanguinea* 24 h older than *H. axyridis;* series C, *C. sanguinea* 48 h older than *H. axyridis.*

Development on Heterospecific Larvae. Only four of 12 *C. sanguinea* larvae fed frozen *H. axyridis* larvae reached pupation, compared with 10 of 12 in the control group (chi-square = 30.012, $P = 0.001$). All pupae in the control group yielded viable adults, but none of the treatment pupae did. However, 100% of *H. axyridis* larvae fed frozen *C. sanguinea* larvae survived to eclose as adults and were no different from controls in adult dry weight ($F = 1.941$; df = 1, 23; NS), although their developmental time was significantly extended (12.1 ± 0.23 d versus 9.2 ± 0.21 d; $F = 89.238$; df = 1, 23; $P < 0.001$).

Discussion

It is apparent that *C. sanguinea*, formerly the dominant aphidophagous coccinellid in Florida citrus groves, has declined in abundance throughout Florida while *H. axyridis* has increased during the period of the recent surveys (Fig. 1). The increase in relative abundance of *H. axyridis* was not significant in either St. Lucie or Highlands Counties over the period of these observations as it was in the other three counties, even though the decline of *C. sanguinea* was significant, and there are at least two possible explanations. First, it is apparent that *H. axyridis* was already well established in these two counties when the earlier observations were made. Furthermore, large numbers of *Olla v-nigrum* were present in St. Lucie and Highlands Counties in spring 2001 and comprised 46 and 61% of all coccinellids, respectively, in these two counties. An apparent numerical response of *O. v-nigrum* to infestations of the citrus psyllid *Diaphorina citri* was reported at that time (Michaud 2001a). The relative suitability of *D. citri* as prey for *C. sanguinea, H. axyridis,* and *O. v-nigrum* is currently being assessed in the laboratory.

A comparison of basic biology and life history parameters suggests that *H. axyridis* has many intrinsic advantages over *C. sanguinea.* Adult *H. axyridis* average two to three times the body weight of adult *C. sanguinea* when reared on natural prey such as *Aphis spiraecola* or *T. citricida* (Michaud 2000b). Food consumption was not quantified in these experiments, but the food demand of *H. axyridis* adults and larvae was notably greater than that of *C. sanguinea,* a observation indicative of higher voracity. Field-collected *H. axyridis* females laid significantly more eggs in the laboratory than did females of *C. sanguinea* on the diet of *Ephestia* eggs and bee pollen, and a larger percentage of *H. axyridis* eggs hatched. These results are consistent with the fecundity and fertility of laboratory-reared females of both species observed over many generations (Michaud, unpublished) although it is possible that other diets could produce different results. Although no larvae of either species completed development at 30 or 32°C in these experiments, LaMana and Miller (1998) reported 25% survival of *H. axyridis* at 34°C. Larvae of *H. axyridis* had better survival at 28°C than did those of *C. sanguinea* in these experiments and this might translate into better survival of *H. axyridis* under the high temperature conditions that prevail during Florida summers, even though *C. sanguinea* is more restricted to tropical and subtropical regions (Gordon 1985), and presumably more adapted to high temperatures. However, information is lacking on adult foraging and reproductive behavior of both species under high temperature conditions.

Larval cannibalism occurred earlier and more often in *C. sanguinea* than in *H. axyridis* in experiments where sufficient food was provided for all larvae to complete development. Furthermore, larvae of *C. sanguinea* attack siblings with the same frequency as unrelated larvae (Michaud 2002) and there is no apparent avoidance of sibling-cannibalism as in *H. axyridis* (Joseph et al. 1999). However, *H. axyridis* is the more adapted cannibal and can complete development successfully on a diet of conspecific larvae (Snyder et al. 2000) whereas *C. sanguinea* cannot (Michaud 2002). Thus *H. axyridis* appears to be highly adapted for competing with other coccinellid species, whereas *C. sanguinea* is apparently more aggressive toward conspecific than heterospecific competitors. The cannibalism behavior of *C. sanguinea* may still be adaptive at the level of the individual when intraspecific competition is a strong determinant of fitness, but is probably disadvantagous to the species in competitive interactions with populations of other coccinellids in the field.

The various intraguild predation experiments reported here uniformly indicate a greater propensity for adults and larvae of *H. axyridis* to prey on various life stages of *C. sanguinea* than vice versa. Whereas larvae of *C. sanguinea* were able to kill *H. axyridis* larvae when they had a substantial size advantage, they rarely did so (Fig. 2), suggesting that this species exhibits relatively low levels of aggression toward heterospecific larval competitors. However, larvae of *H. axyridis* appeared more aggressive than those of *C. sanguinea* and, when confined with a larger *C. sanguinea* larva, simply delayed their attack until the size difference was effectively nullified before dispatching their more tolerant competitor. Alternatively, earlier attacks by *H. axyridis* larvae when they were still smaller than *C. sanguinea* might have been unsuccessful. It is notable that larvae of *C. sanguinea* possess smooth dorsal surfaces lacking any defensive spines or waxy filaments such as those present in larvae of other coccinellid genera, whereas the dorsal surfaces of larvae of *H. axyridis* are covered with short spines thought to provide some defense against predation (Dixon 2000).

Previous studies have been less successful in demonstrating direct interspecific competition among larvae of other coccinellid species. For example Evans (1991) paired similar-sized larvae of *Hippodamia convergens* with those of *H. tredecimpunctata, H. sinuata crotchi,* and *Coccinella septempunctata* in foraging situations and failed to resolve any differences in the intensity of intra- and interspecific competitive interactions. However, the intensity of interspecific competition is probably specific to particular species combinations. *Harmonia axyridis* may be an extraordinary species in this regard, possessing many intrinsic advantages over other coccinellids that render it a formidable competitor. Yasuda and Shinya (1997) demonstrated the competitive advantages of *H. axyridis* over *C. septempunctata.* Cottrell and Yeargan (1998) successfully reared *H. axyridis* on an exclusive diet of *Coleomegilla maculata* eggs. Phoofolo and Obrycki (1998) showed that *H. axyridis* could develop on an exclusive diet of *Chrysoperla carnea* eggs, whereas *C. septempunctata* could not. Similarly, Yasuda (1999) showed that *H. axyridis* could develop on a diet of larvae of *C. septempunctata,* whereas the reverse was not possible. The results presented here indicate that *H. axyridis* can complete development on a sole diet of *C. sanguinea* larvae with only a slight cost in terms of delayed development, whereas *C. sanguinea* could not develop successfully on *H. axyridis* larvae. When sources of prey are exhausted in the field, the ability of *H. axyridis* to complete development on an exclusive diet of either heterospecific or conspecific larvae (Snyder et al. 2000, Michaud 2002) should translate into a substantial competitive advantage over species such as *C. sanguinea* that lack such capabilities.

Mechanisms of competition are difficult to study in the field because of the inordinate amount of time required to observe predation events, but laboratory tests can lead to artifacts that lack correspondence to 'real world' interactions. The interspecific interactions elicited in these experiments are likely to have little correspondence to the field situation in terms of either the arena of conflict (a petri dish as opposed to a leaf or twig), or their frequency of occurrence (artificially increased by confining insects together). Although it would be tenuous to extrapolate from laboratory tests the real significance of these interactions to populations in the field, there is little reason to expect that the *outcomes* of such interactions would be any different. Nevertheless, it seems unlikely that the mechanisms of competition examined in this study comprise more than a partial explanation of the observed changes in relative abundance of these two species. Dispersal from trees where prey has been exhausted would seem an unlikely recourse for larvae because they would be highly vulnerable to ground-dwelling predators such as ants and would seemingly lack any means of orienting to another tree. Little is known about other sources of coccinellid mortality in citrus, possibly including birds, lizards, and other predacious insects. Comparative studies on the effects of high temperatures on adult foraging behavior and reproduction might reveal some degree of thermally mediated niche partitioning. Populations of both species are still fluctuating and new invasive pests of citrus such as *D. citri* represent major changes in the available food supply that could affect these two species differentially. Further studies are warranted to determine the final outcome of these competitive interactions in the field.

It is clear that the full ecological impacts of *H. axyridis* were never anticipated when decisions were made to introduce it to North America, nor would they be detected by the simple prey specificity studies required by current environmental impact assessments. Nevertheless, *H. axyridis* is highly valued in both agriculture and forestry for biological control of many homopterous pests on a wide range of plant species (Brown and Miller 1998). It also seems probable that *H. axyridis*, with its larger size, greater voracity, and broader diet will prove more effective than *C. sanguinea* as a generalist predator of homopteran pests in citrus. It is also more resistant than *C. sanguinea* to fungicides (Michaud 2001b), acaricides (Michaud 2001c) and insecticides (Michaud 2001d) and more resistant than most native ladybeetles to attacks by the red imported fire ant, *Solenopsis invicta* Buren, (Dutcher et al. 1999), a species that has the potential to disrupt biological control in citrus (Michaud and Browning 1999). However, *H. axyridis* will likely be perceived as undesirable by conservationists given its propensity for aggression against native coccinellids and its potential for reducing species diversity. In urban settings opinion may be more divided; some homeowners may appreciate its potential to control a variety of pests on ornamental trees and shrubs, while those whose houses are invaded by overwintering aggregations (Nalepa et al. 1996) are unlikely to view it so favorably. Conflicts of interest resulting from the importation of biological control agents are well recognized (Howarth 1991) and the invasion of *H. axyridis* can be viewed as either bane or boon, depending on socioeconomic perspectives and the relative value society assigns to biological pest control versus the preservation of indigenous fauna and biodiversity.

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