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ORIGINAL PAPER

Alfalfa fields promote high reproductive rate of an invasive predatory lady beetle

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Abstract Invasive insect species often may attain high fecundity in agricultural habitats, thereby contributing to their establishment in new geographic regions and their displacement of similar native species. Such may be true for predatory lady beetles (Coleoptera: Coccinellidae) that have been introduced to North America in recent decades, raising concerns of adverse impact on native lady beetles. In northern Utah, *Coccinella septempunctata* L. first appeared in 1991, and is now predominant among lady beetles especially in alfalfa fields. We assessed the suitability of alfalfa fields as breeding habitat for females of *C. septempunctata* and the native, similarly sized *Coccinella transversoguttata richardsoni* Brown. The timing and amount of egg production differed significantly between *C. septempunctata* and *C. transversoguttata* as populations of aphids increased through spring and early summer. Reproduction by both species conformed to the egg window hypothesis, with populations of the predators producing most eggs before aphid numbers peaked. But consistently among fields and years, females of *C. septempunctata* produced more eggs, and did so earlier in the spring, than *C. transversoguttata* females even at low prey density. Furthermore, *C. septempunctata* females were more successful than females of *C. transversoguttata* in approaching their maximum body weights and reproductive output as measured in the laboratory under ideal conditions. The strong reproductive success of *C. septempunctata* may contribute to its displacement of *C. transversoguttata* in irrigated alfalfa in the generally arid Intermountain West of North America and to its establishment as an abundant species in this region of North America.

Keywords Invasive species · Reproduction · Native species · Predatory lady beetles · *Coccinella septempunctata*

Introduction

Agricultural fields are often highly suitable habitats for invasive insect species. These fields can provide invaders with favorable physical conditions (e.g., as provided by irrigation) and abundant food resources, including both host plants for herbivores and pest insects for natural enemies (e.g., Evans and Lanham 1960; Duelli et al. 1990; McKone et al. 2001; Rand and Louda 2006; Rand et al. 2006). Insects introduced for biological control may spread from such

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habitats to become well-established in natural habitats as well (e.g., Henneman and Memmott 2001; Holt and Hochberg 2001; Sheppard et al. 2004).

We address here the suitability of agricultural habitat in promoting the establishment of an invasive lady beetle *Coccinella septempunctata* L., and its displacement of a native congener *Coccinella transversoguttata richardsoni* Brown in the Intermountain West of North America (Evans 1991, 2004). Recent, high-profile invasions of North America by species of predatory lady beetles (Coleoptera, Coccinellidae) have raised widespread concern regarding potentially adverse effects on native North American lady beetles (Howarth 1991; Simberloff and Stiling 1996; Elliott et al. 1996; Obrycki et al. 1998a; Louda et al. 2003). In the generally arid landscape of the Intermountain West, irrigated alfalfa often supports high populations of the pea aphid (*Acyrthosiphon pisum*, Hemiptera: Aphididae) and provides a favorable, mesic environment for aphidophagous lady beetles. Since its arrival and initial establishment in the early 1990s, *C. septempunctata* has consistently maintained large populations in alfalfa fields while at the same time the densities of the formerly abundant *C. transversoguttata* and other native lady beetles have declined (Evans 2004; Elliott et al. 1996; Turnock et al. 2003). *C. septempunctata* occurs as well in many other (both native and disturbed) habitats, although most often in lower numbers (*personal observations*; see also Evans 2000; Hesler and Kieckhefer 2008). The high abundance of *C. septempunctata* in alfalfa reflects its use of this same habitat with pea aphids in its native (Palearctic) range (e.g., Honěk 1982, 1985). Alfalfa in the Intermountain West, as the most widely planted crop in the region, may serve as an important habitat promoting regionally high numbers of *C. septempunctata*.

The numerical dominance of *C. septempunctata* over native lady beetles in alfalfa suggests that this habitat is especially suitable for this invasive lady beetle in comparison with native competitors. We test this hypothesis here by comparing the ability of overwintering females of *C. septempunctata* and the similarly sized *C. transversoguttata* to reproduce in this habitat. Superior reproductive success of the invasive species in this habitat might account in part for its displacement of its native congener. We compare the seasonal reproductive patterns of both lady beetle species with the temporal dynamics of aphid populations in alfalfa. Such comparison is made in part with reference to the egg window hypothesis (Hemptinne et al. 1992; Kindlmann and Dixon 1993; Dixon 1997, 2000) and its key prediction that aphidophagous lady beetles lay most eggs prior to the attainment of peak numbers in local populations of their aphid prey. In addition, the comparison is made in light of the oft-stated hypothesis that high fecundity can be a key life-history trait promoting the success of invasive species (e.g., Baker 1974; Crawley 1986; Hogmire et al. 1992; Rejmanek and Richardson 1996; Boivin et al. 2008; Hodek and Michaud 2008; Kajita 2008).

Materials and methods

Lady beetle and aphid sampling

Lady beetles and pea aphids were sampled each week in alfalfa fields of northern Utah, near Logan in Cache County, from mid April through early July in 2004 and 2005 (lady beetles engaged in little reproduction from mid summer on; Kajita 2008). Two fields were sampled in each year. In 2004, these fields were located at the Utah State University (USU) Animal Science and Caine Dairy Farms. In 2005, fields were located at the USU Cache Junction and Wellsville Farms. The alfalfa in these fields was first cut for hay on June 2, 2004, and June 24, 2005. A strip (15 × 50–60 m) of alfalfa was left uncut in each field. This strip was sampled thereafter for the next 2–3 weeks until the cut alfalfa had re-grown to 30 cm height and could once again be sampled for both lady beetles and pea aphids.

Densities of pea aphids were determined weekly by sampling 20 alfalfa stems at each of 5 randomly selected locations at each census in each field in 2004, and 10 alfalfa stems at each of 25 random locations in each field in 2005. Stems were shaken within a white bucket (30 cm in diameter × 35 cm in height) and the dislodged pea aphids were counted (previous use of this technique was shown to dislodge more than 97% of the aphids from the stems; Evans, personal observations).

To concentrate lady beetle adults in alfalfa fields for collection of large numbers, 10 m^2 plots within each field were sprayed with a sugar solution (15% sucrose) each week during the growing season (e.g., Evans and England 1996). Sugar acts as an arrestant (but not an attractant) for lady beetles (Evans and Swallow 1993 and references therein). Consumption of the sugar does not result in egg production (and oviposition) in *C. septempunctata* and *C. transversoguttata*, which instead is stimulated by aphid consumption (Richards and Evans 1998). Lady beetles were collected from plots during the next 2–5 days following sugar spraying, and brought to the lab immediately. The females' wet weights were measured, and then each female was placed individually in a Petri dish (5.5 cm in diameter, 1.5 cm in height) with one drop of sugar water (15% sucrose) on the lid. Dishes were kept in an incubator (22°C, 16L:8D) for 48 h. Eggs laid in the dishes were counted at 24 and 48 h. In those relatively few instances in which females cannibalized some of their own eggs, the residue (or presence of eggshell) from each cannibalized egg (a spot where the egg had been attached to the substrate) was noted and included in counts of eggs produced (Hironori and Katsuhiro 1997). Maintaining females in this fashion provided a non-lethal method to estimate the number of mature or nearly mature eggs that a female had at the time of collection. Females held without prey will proceed to lay such eggs (rather than resorb them) over a 48-h period upon removal from prey (Richards and Evans 1998; Honěk et al. 2008; Kajita and Evans 2009). Sample sizes for different periods of the season, as defined below in *Data Analyses*, are presented in the Results.

Sweep-net sampling (10 sweeps × 10 samples) was conducted in 2004 to examine the number of lady beetle larvae occurring in the alfalfa fields after the first cut (i.e., when larvae became abundant enough to sample) from June 11 to July 14. Sampling was initiated near the center of the fields, with successive samples taken along a transect towards the edge of the field. Thereafter, visual censuses (of 60 person-minutes) were conducted for pupae along the edge of each field (where pupae could be found most readily). All collected larvae and pupae were placed in a vial, and immediately brought back to the lab to distinguish species. To confirm species identity, each larva or pupa was kept individually in a Petri dish with prey (pea aphids) until it molted into an adult.

In 2005, visual censuses were conducted weekly to examine the population dynamics of adult predatory lady beetles in fields. These censuses were conducted in areas other than in the sucrose plots. As with sweep sampling in 2004, each census (of 60 person-minutes) began in the center of the field and continued along a straight transect toward the edge of the field. Adult lady beetles were collected from the alfalfa foliage, placed in a vial, and identified to species thereafter in the lab.

Data analyses

In both 2004 and 2005, overwintered lady beetles were especially active in producing and laying eggs in alfalfa for a period of about 1 month during spring through early summer. For analyses, the data were divided therefore into 3 periods of the season: an early period (when most lady beetles were still inactive reproductively), a peak period (the mid, 4-week period during which most lady beetle reproduction occurred), and a late period (occurring after the first cut of alfalfa and when surviving females from the overwintering generation were joined by newly molted adults from the new summer generation). For further discrimination, the peak period (with high reproductive activity) was divided into 3 parts: early peak (1 week), mid peak (2 weeks), and late peak (1 week) (Table 1).

Differences in weather conditions between years resulted in different seasonal timing of lady beetle reproductive activity between 2004 and 2005. In particular, the spring of 2005 was cooler and wetter than the spring of 2004, and correspondingly lady beetle reproductive activity occurred later in 2005 (Table 1).

To compare between years, the first week ("week 1") for the field studies in each year was considered to be the third week of April (beginning April 19 and 18 in 2004 and 2005, respectively). This is the week that sampling of alfalfa fields began in 2004, whereas the first week of sampling in the cooler spring of 2005 was week 4 (May 9). As indicated in Table 1, data were pooled from individual females (collected in the field and evaluated in the lab) according to weeks of collection that correspond to the seasonal periods (and sub-periods) of reproductive activity as described above.

The reproductive activity of females of *C. septempuctata* and *C. transversoguttata* was compared during the different periods of the season by conducting three sets of analyses. All analyses were performed by using SAS 9.1 (SAS Institute 2002).

First, a comparison was made of the percentages of field collected females that were gravid when collected and produced eggs when held subsequently

Table 1 Periods during which adult lady beetles and aphids were sampled in alfalfa fields in 2004 and 2005, with periods identified both by numbered sampling weeks and by dates

Reproductive period	2004	2005
Early (pre-peak)	1–4 (April 19–May 16)	4–6 (May 9–May 30)
Peak		
Early peak	5 (May 17–24)	7 (May 31–June 6)
Mid peak	6–7 (May 25–June 7)	8–9 (June 7–20)
Late peak	8 (June 8–14)	10 (June 21–27)
Late (post-peak)	9–13 (June 15–July 19)	11–14 (June 28–July 25)

for 48 h in the laboratory. This comparison was made for females of the two species collected during the early and late periods (as defined above), and during each of the 3 peak reproductive sub-periods (early, mid, and late). Because seasonal reproductive patterns (including seasonal percentages of females that were gravid) were very similar overall between the two fields sampled in a given year, these patterns were compared for *C. septempunctata* and *C. transversoguttata* by pooling data from the two fields. To account for small sample sizes (particularly of *C. transversoguttata* females) in comparisons, an exact test (Monte Carlo Estimate, $n = 10{,}000$) was used for the analyses (sample sizes are presented below with the results of the statistical tests).

Second, the reproductive activity of *C. septempunctata* and *C. transversoguttata* was also compared for the number of eggs laid during 48 h after collection. For this comparison, only those females that laid eggs (one or more) were included. A two-way analysis of variance (ANOVA) was used to compare between the two species and the two years, the number of eggs (transformed by square root) laid. The analysis was focused on the mid peak time period each year (weeks 6 and 7 in 2004, and weeks 8 and 9 in 2005), when reproductive activity overall was at its height (patterns between species and years during mid peak were apparent also at lower overall rates of reproduction both earlier and later in the year; Kajita 2008).

Third, rates of egg production of gravid females of *C. septempunctata* and *C. transversoguttata* collected from the field at mid peak were compared to the potential rates that females could achieve under ideal conditions. Thus, the rates of field collected gravid females were estimated as the number of eggs laid in the 48 h following collection divided by the mean number of eggs laid in 48 h by a reproductively active, overwintered female when maintained in the laboratory and provided with excess pea aphids (estimated as 162.9 for *C. septempunctata*, and 116.3 for *C. transversoguttata*; Kajita 2008). Data were transformed by square root, and then analyzed by two-way ANOVA (species, year, species × year).

An index was calculated for the total number of eggs laid each week by the populations of *C. septempunctata* and *C. transversoguttata* females during 2005 (when visual censuses were conducted to determine seasonal patterns of adult abundance). The number of eggs per female (for all females combined, including those that did not lay eggs) was multiplied times relative abundance (i.e., the number of adults counted per 60 person-minutes of visual censusing).

Three-way ANOVA (species × year × period) was used to compare changes in wet weight of all females of *C. septempunctata* and *C. transversoguttata* collected in alfalfa fields between early and peak periods. Wet weights of females collected in alfalfa fields in 2004 and 2005 during the peak period were also compared by two-way ANOVA after dividing them by the mean wet weight of a fully fed female (estimated as 63.0 mg for *C. septempunctata* and 55.4 mg for *C. transversoguttata*; Kajita 2008).

Results

The density of pea aphids in alfalfa fields increased from late April through the spring and early summer, with a delay in the cool spring of 2005 (Fig. 1). After the alfalfa was cut for the first harvest (in early June in 2004, and in late June in 2005), aphid populations declined greatly in uncut and cut sections. Declines in uncut sections reflected increasing daytime temperatures and likely also increasing damage from alfalfa weevil larvae (*Hypera postica* [Gyllenhal]). Aphid populations remained very low thereafter as high daytime temperatures prevailed in late June and July.

In 2004, adults of *C. septempunctata* were observed to be the most abundant lady beetles present in the alfalfa fields, and they were collected in greatest numbers from sugar plots throughout the season. In 2005, weekly visual censusing of adults revealed that *C. septempunctata* was again the most common species present throughout the spring. At the two fields, 72.7% of adults in early weeks and 55.5% in peak weeks were *C. septempunctata*, while 7.3 and 10.7% were *C. transversoguttata*. Almost 100% of adults at both fields in late weeks were *C. septempunctata*.

The wet weights of field-collected females of *C. septempunctata* were greater than those of *C. transversoguttata* throughout the experimental period (Kajita 2008). Comparison of weights in early and peak periods by three-way ANOVA yielded significant effects, including a significant three-way interaction of species × year × period (Table 2). Females of both species gained weight from the early to peak period, but the absolute gain in weight (mg of weight gain) was larger for *C. septempunctata* females (Fig. 2). This was especially true in 2005, when cold weather during the early period was associated with low aphid populations and lower mean weights of females of both species than was the case in early 2004.

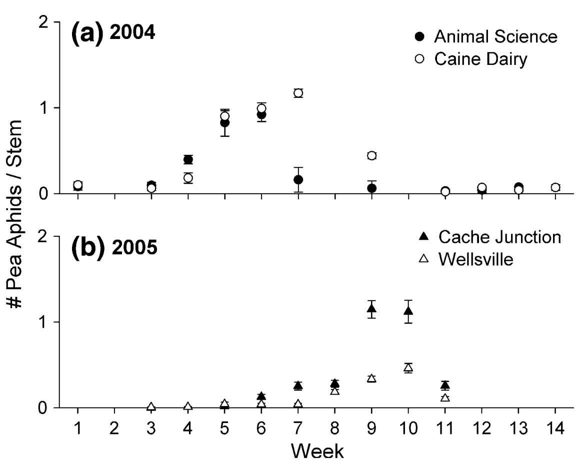

Fig. 1 The mean number of pea aphids per stem (±SE) that occurred in alfalfa fields sampled in **a** 2004 and **b** 2005. Data are plotted by numbered week of collection (Table 1; e.g., week 1 began April 18–19, week 5 began May 16–17, and week 10 began June 20–21)

Field collected females of both species during the peak period in 2004 and 2005 weighed less than females provided with excess aphids in the lab (Kajita 2008). Mean weights of field collected females of *C. septempunctata* were 79 ± 1% of maximum potential weight in both 2004 and 2005, compared with relatively lower mean weights of females of *C. transversoguttata* (73 ± 2 and 75 ± 1% of maximum weight in 2004 and 2005, respectively; two-way ANOVA: effect of species $F_{1,620} = 13.38$, $P = 0.0003$; effect of year $F_{1,620} = 0.29$, $P = 0.59$; interaction of species × year $F_{1,620} = 0.49$, $P = 0.49$).

In general, the seasonal reproductive patterns of *C. septempunctata* and *C. transversoguttata* were similar in both fields for a given year (Fig. 3). Females of both *C. septempunctata* and *C. transversoguttata* produced few eggs during the early period. Egg production rose rapidly during the peak period, only to fall again to low levels in the late period. Throughout the season, *C. septempunctata* females generally produced more eggs during any given week than did *C. transversoguttata* females. This general pattern was reflected in both the percentage of females laying eggs, and the number of eggs laid by gravid females.

In 2004, *C. septempunctata* females on average began to lay eggs earlier during the spring than did females of *C. transversoguttata* (Fig. 4a). More than 20% of *C. septempunctata* females, versus only 6.5% of *C. transversoguttata* females, laid eggs upon collection during the early period (weeks 1–4). Throughout the peak period (weeks 5–8), approximately 80% of *C. septempunctata* females laid eggs. In contrast, the percentage of *C. transversoguttata*

Table 2 Results of three-way ANOVA (species, year and period) for wet weight of females of *Coccinella septempunctata* and *C. transversoguttata* collected from alfalfa fields during early and peak periods in 2004 and 2005

	df	*F*	*P*
Species	1, 2062	270.76	<0.0001
Year	1, 2062	30.62	<0.0001
Species × year	1, 2062	20.81	<0.0001
Period	1, 2062	220.91	<0.0001
Species × period	1, 2062	26.09	<0.0001
Year × period	1, 2062	26.64	<0.0001
Species × year × period	1, 2062	4.92	0.0266

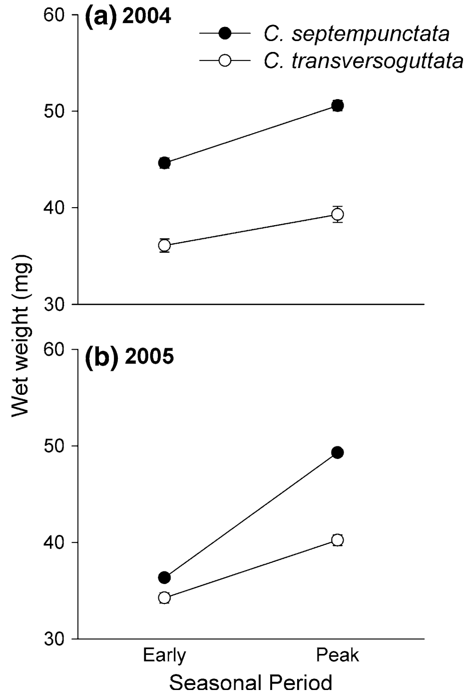

Fig. 2 Changes in mean wet weight (±SE) of females of *Coccinella septempunctata* and *C. transversoguttata* collected in alfalfa fields between early and peak periods in **a** 2004 and **b** 2005

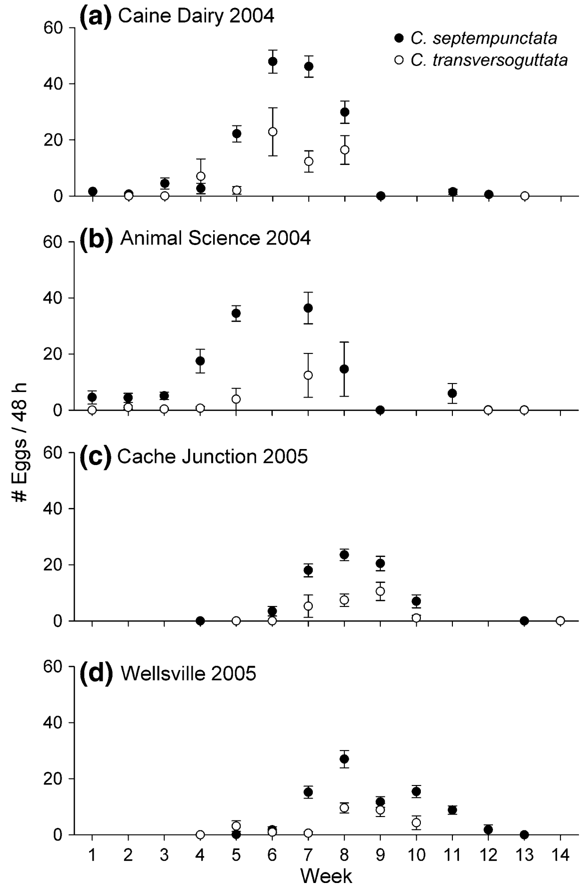

Fig. 3 The mean number of eggs (±SE) laid by females of *Coccinella septempunctata* and *C. transversoguttata* over 48 h after they were collected from alfalfa fields at **a** Caine Dairy and **b** Animal Science Farms in 2004, and **c** Cache Junction and **d** Wellsville Farms in 2005. Data are plotted for all females combined (i.e., including females that laid no eggs), by numbered week of collection (Table 1; e.g., week 1 began April 18–19, week 5 began May 16–17, and week 10 began June 20–21)

that laid eggs increased more gradually, and did not reach its maximum (at less than 60%) until late in the peak period (week 8). Most of the lady beetles collected from mid-June on (weeks 9–14) were new adults (recognized by their soft and brightly colored exoskeletons) that did not lay eggs.

During the cool spring of 2005, very few females (less than 3%) of both *C. septempunctata* and *C. transversoguttata* laid eggs during the early period (weeks 4–6) (Fig. 4b). However, as the temperatures warmed by week 7, once again a much greater percentage of *C. septempunctata* females (50%) than of *C. transversoguttata* females (12%) became reproductively active and laid eggs. A greater percentage of *C. septempunctata* females continued to lay eggs thereafter (including during the late period); however, there were not significant differences between *C. septempunctata* and *C. transversoguttata* during the late peak and late period (week 10, and weeks 11–14, Fig. 4b).

Consistently among fields and between years, gravid *C. septempunctata* females laid more eggs during the mid-peak period than gravid *C. transversoguttata* females (two-way ANOVA: effect of species $F_{1,398} = 34.47$, $P < 0.0001$, interaction of year × species $F_{1,398} = 1.15, P = 0.18$). Thus, gravid *C. septempunctata* versus *C. transversoguttata* females laid 54.6 ± 2.4 (±SE) versus 30.8 ± 4.3 eggs when held for 48 h upon collection from alfalfa fields in 2004, and 31.7 ± 1.3 versus 19.2 ± 1.5 eggs in 2005. Overall, the average egg production of both species was greater in 2004 than in 2005 (effect of year $F_{1,398} = 96.87, P < 0.0001$).

In both years, the ratio of egg production of field-collected females to mean egg production of females

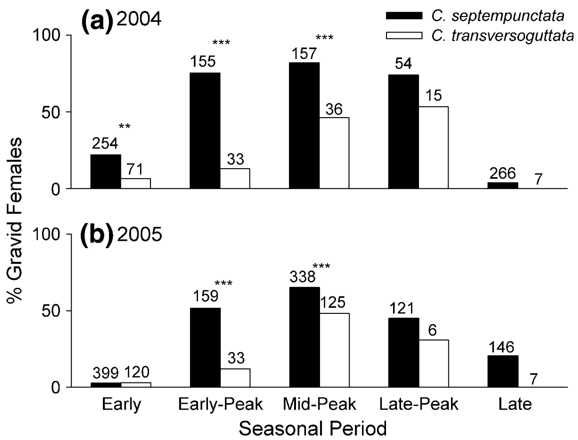

Fig. 4 The percentage of field collected females of *Coccinella septempunctata* and *C. transversoguttata* that were gravid (i.e., that laid eggs over a 48 h holding period) in **a** 2004 and **b** 2005. ** and *** represent $P < 0.001$, and $P < 0.001$ by Monte Carlo Estimate ($n = 10{,}000$) for the exact test ($P > 0.05$ in all other cases). *Numbers above bars* represent sample sizes (numbers of females collected for two fields combined in each year)

maintained on an excess diet of pea aphids in the laboratory was greater for *C. septempunctata* than for *C. transversoguttata* during the mid-peak period (2004: 0.33 ± 0.01 versus 0.26 ± 0.04; 2005: 0.26 ± 0.01 versus 0.16 ± 0.02; two-way ANOVA: effect of species $F_{1,398} = 6.04$, $P = 0.014$, effect of interaction of year × species $F_{1,398} = 1.09$, $P = 0.29$). For both species, the field rate of reproduction more closely matched the maximum potential rate in 2004 than in 2005 (effect of year $F_{1,398} = 35.37$, $P < 0.0001$).

In both alfalfa fields in 2005, many more *C. septempunctata* than *C. transversoguttata* eggs were produced throughout the season (estimated by the index of total number of eggs laid each week by the populations of *C. septempunctata* and *C. transversoguttata* females during 2005; see Methods). Both species produced large numbers of eggs before the aphid populations peaked in size (Fig. 5).

Most larvae (89%) and pupae (98%) that occurred in the Animal Science and Caine Dairy alfalfa fields in 2004 belonged to *C. septempunctata*. A few individuals of other species, *Hippodamia convergens* Guerin, *H. quinquesignata* (Kirby), and *H. sinuata crotchi* (Casey), were collected (see Kajita 2008 for details). Interestingly, no larvae or pupae of *C. transversoguttata* occurred in the samples.

Discussion

The invasive *C. septempunctata* has much greater success in reproducing in the alfalfa habitat than does the native *C. transversoguttata*. While producing greater numbers of eggs throughout the season, females of *C. septempunctata* began producing eggs earlier in the season and also more nearly reached their potential egg production (as measured in the laboratory) than did females of *C. transversoguttata*. Further reflecting that the invasive species was particularly successful in reproducing in this habitat, most of the larvae and pupae recovered from fields were individuals of *C. septempunctata*. These results support the generalization that invasive species are often characterized by unusually high fecundity (e.g., Baker 1974; Crawley 1986; Hogmire et al. 1992; Rejmanek and Richardson 1996; Boivin et al. 2008; Hodek and Michaud 2008).

The much greater reproductive activity of *C. septempunctata* than *C. transversoguttata* in alfalfa was also readily apparent in the analysis of seasonal population patterns as measured in 2005. Interestingly, females of *C. septempunctata* and *C. transversoguttata* collectively (i.e., as populations) produced most eggs before pea aphid numbers

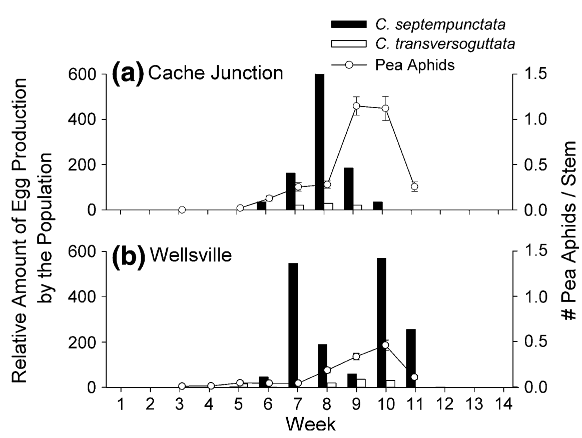

Fig. 5 Estimates of population-level relative egg production for *Coccinella septempunctata* and *C. transversoguttata* (determined as the mean number of eggs laid by a female during a given week [for all females combined] × the abundance of females that week as determined from visual censusing), and weekly mean aphid abundance in alfalfa fields (±SE) at **a** Cache Junction and **b** Wellsville Farms in 2005. Data are plotted by numbered week of collection (Table 1; e.g., week 1 began April 18–19, week 5 began May 16–17, and week 10 began June 20–21)

peaked, as predicted by the egg window hypothesis for aphidophagous lady beetles (Hemptinne et al. 1992; Kindlmann and Dixon 1993; Dixon 1997, 2000). The hypothesis states that the optimal reproductive strategy for a female lady beetle is to lay her eggs early in the development of a local aphid population (i.e., before aphid numbers peak), such that her offspring can complete development before aphid numbers decline severely and immature lady beetles become highly vulnerable to starvation, cannibalism and intraguild predation. Other field studies have also supported the egg window hypothesis (Hemptinne et al. 1992; Dixon 2000; Osawa 2000).

Why is the invasive *C. septempunctata* able to reproduce more successfully in alfalfa fields than the native *C. transversoguttata*? Throughout the spring, females of *C. septempunctata* in alfalfa fields achieved and maintained higher body weights as well as higher rates of egg production (relative to maxima as established in the laboratory) than did females of *C. transversoguttata*. Such success may reflect greater foraging ability by *C. septempunctata* not only for preferred aphids which occurred at low density, but also for a variety of other prey that aphidophagous lady beetles are known to consume (Hagen 1987; Pemberton and Vandenberg 1993; Hodek and Honěk 1996; Davidson 2008). Such prey include larvae of the alfalfa weevil that reach very high densities every spring and that can serve as alternative prey when pea aphid populations are low (Evans 2004; Evans and Toler 2007; Davidson 2008).

Differences in life-cycle phenology also may contribute to the earlier and greater reproductive activity of *C. septempunctata* versus *C. transversoguttata*, as has been suggested in other comparisons of invasive and resident insects (e.g., Boivin et al. 2008). North American populations of *C. septempunctata* have stronger tendency to be univoltine than do populations of *C. transversoguttata* (Obrycki and Tauber 1981; Phoofolo et al. 1998; Kajita 2008; Hodek and Honěk 1996). Among overwintering adults therefore, those of *C. septempunctata* may have more time in the summer and fall to prepare for winter diapause, and consequently may emerge the following spring with relatively high fat reserves with which to initiate reproduction (e.g., Hodek and Honěk 1996; Barron and Wilson 1998; Dixon 2000). In addition, as observed in visual censuses in the present study, overwintered females of *C. septempunctata* tend to arrive in alfalfa fields earlier in the spring than do females of *C. transversoguttata*.

The highly successful invasion of North America in recent decades by *C. septempunctata* and other introduced lady beetles (especially *Harmonia axyridis* Pallas) has led to widespread concern about their effects on native lady beetles (e.g., Louda et al. 2003). In alfalfa fields of the Intermountain West, populations of *C. septempunctata* have increased greatly, while at the same time populations of *C. transversoguttata* and other native lady beetles have declined (Evans 2000, 2004). Similar patterns in various habitats in other parts of North America (e.g., Elliott et al. 1996; Turnock et al. 2003; Hesler and Kieckhefer 2008; Brown and Miller 1998; Brown 2003) have stimulated great interest in potential causes of such species replacement.

Intraguild predation (IGP) has been widely hypothesized as one mechanism for the successful establishment of *C. septempunctata* (e.g., Obrycki et al. 1998a; Kajita et al. 2000, 2006; Snyder et al. 2004; Yasuda et al. 2004). IGP by *C. septempunctata* adults on *C. transversoguttata* eggs or larvae could have contributed to the observed greater reproductive success of *C. septempunctata* in alfalfa fields. This was not addressed in the present study, however, and in general the importance of such IGP in accounting for replacement of native lady beetles by *C. septempunctata* has yet to be demonstrated in the field (e.g., Obrycki et al. 1998b).

Exploitative competition may also be important in accounting for the displacement of native lady beetles by *C. septempunctata* in alfalfa fields studied here. Aphid populations in alfalfa during the present studies were low in comparison to densities recorded prior to the introduction of *C. septempunctata* (Evans 2004). In succeeding well in reproducing and reaching high numbers in alfalfa, *C. septempunctata* may now be limiting the population growth of pea aphids in this habitat. Consequently, native lady beetles may have abandoned alfalfa fields to forage elsewhere. As indicated by the results of the present study, females of the native *C. transversoguttata*, in contrast to females of *C. septempunctata*, achieve relatively little reproductive success while foraging in alfalfa fields with current, low aphid populations.

In summary, irrigated alfalfa is a distinctive habitat in the arid Intermountain West of North

America. Following the introduction of this crop to the region in the mid nineteenth century, alfalfa fields have provided a widespread, very favorable, mesic environment for aphidophagous lady beetles (Evans 2000). The field data presented here indicate that alfalfa is a much more suitable habitat for reproduction by *C. septempunctata* than by the native species *C. transversoguttata*. The large degree of reproductive success achieved by *C. septempunctata* in this habitat may intensify its competitive effect on *C. transversoguttata* and thereby contribute to its displacement of the native congener. Our results further suggest that alfalfa, as an abundant habitat of the western landscape, may often produce large numbers of *C. septempunctata* that can then disperse widely as adults among many other habitats as well (including habitats that can be less favorable for reproduction). Further study, including study of reproductive success of this invasive and other lady beetle species in habitats other than alfalfa, is required to evaluate whether such a process may contribute to adverse effects on numbers of native lady beetles across the landscape (Evans 2004; Hesler and Kieckhefer 2008).

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