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Ovarian dynamics and oosorption in two species of predatory lady beetles (Coleoptera: Coccinellidae)

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Abstract. Ovarian development and oviposition dynamics of two species of lady beetle, *Coccinella septempunctata* L. and *C. transversoguttata richardsoni* Brown, are examined in laboratory experiments in which pea aphids (*Acyrthosiphon pisum* Harris) are provided *ad libitum* and then removed. Both species respond to prey removal by stabilizing at lower body weights, and by laying progressively fewer and smaller eggs of reduced viability, until oviposition ceases altogether after several days of starvation. Dissections of females after prey removal reveal similar patterns of oosorption in both species. However, *C. septempunctata* reduces oviposition more rapidly after prey removal than does *C. transversoguttata*. When prey are again provided, *C. septempunctata* soon lay as many eggs as previously but *C. transversoguttata* lay fewer. Females, especially of *C. septempunctata*, that stop producing and resorb eggs in the absence of prey lay more eggs subsequently than do females that feed continually on prey provided *ad libitum* and lay eggs throughout the experiment. Thus, although both species are responsive to a rapid change in prey availability, *C. septempunctata* appears to be especially responsive. Rapid responses to changes in prey availability may contribute to the greater abundance and reproductive success of this introduced species relative to the native *C. transversoguttata* in western North American alfalfa fields that exhibit widely varying pea aphid densities. However, both species engage in oosorption as a means of reserving resources under poor prey conditions and enhancing future reproductive effort when prey conditions improve.

Key words. *Coccinella transversoguttata*, *Coccinella septempunctata*, oosorption, ovarian dynamics, predatory lady beetles, reproduction, reproductive response.

Introduction

The need to allocate limited resources among growth, maintenance and reproduction creates the potential for trade-offs between current and future reproduction (Williams, 1966; Pianka, 1981; Zera & Harshman, 2001). Invertebrate predators in general must balance such trade-offs within the context of prey populations that vary greatly in size over space and time (O'Neil & Wiedenmann, 1987; Bilde & Toft, 1998; Wise, 2006). Thus, females may greatly reduce reproductive effort and favour self-maintenance when prey are scarce (Wiedenmann & O'Neil, 1990; Legaspi & O'Neil, 1994; Eliopoulos *et al.*, 2003) and increase reproductive effort rapidly with increasing prey availability (Coll & Ridgway, 1995; Nakashima & Hirose, 1999). In addition, when food becomes limiting, females may promote their own survival and future reproduction by breaking down and redirecting internally the nutrients from anhydropic oocytes (Bell & Bohm, 1975; Papaj, 2000). Such oosorption can be a key element in the trade-offs between current and future reproduction (Ohgushi & Sawada, 1985; Ohgushi, 1996; Rosenheim *et al.*, 2000).

Aphidophagous lady beetle adults (Coleoptera, Coccinellidae) consume aphids for both self-maintenance and reproduction (Hodek & Honěk, 1996). Females adjust oviposition to current aphid availability (Ives, 1981; Dixon, 2000; Evans *et al.*, 2004) but it is unclear whether and how they respond by oosorption to fluctuation in prey availability. Osawa (2005) reports the occurrence of oosorption in *Harmonia axyridis*. In the present

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study, the ovarian dynamics and quantification of oosorption of *Coccinella septempunctata* L. and *Coccinella transversoguttata richardsoni* Brown are presented from two laboratory experiments in which aphid prey are provided initially *ad libitum* and then are removed from females. *Coccinella septempunctata* is an introduced species that has displaced the native species *C. transversoguttata* from alfalfa fields of western North America in which aphid numbers can vary greatly, often over short spans of time (Evans, 2004; Kajita, 2008). With this species displacement in mind, the responses of these two species (potentially including oosorption) to fluctuations in prey conditions are compared.

Materials and methods

Adult lady beetles used in experiments were collected from alfalfa fields near Logan, Utah, in early spring (late April to early May). These adults had recently arrived in the alfalfa fields from overwintering sites and were not yet fully reproductive (Kajita, 2008). Pea aphids (*Acyrthosiphon pisum* Harris), provided as prey for lady beetles, were reared in the greenhouse on faba bean *Vicia faba*.

In the first experiment (conducted in 2006), the adults initially were held in single-sex groups for 2–3 weeks at 18 °C under an LD 16 : 8 h photoperiod with sugar water (15% sucrose solution) as their sole food. Thereafter, for the experiment, they were maintained as mating pairs at 22 °C under an LD 16 : 8 h photoperiod. Pairs were provided with pea aphids *ad libitum* daily for 15 days, until most females had become reproductively active, and were laying eggs at maximal rates. Prey were removed at the start of day 16, at 09.00 h, and pairs were held without prey for the next 6 days (they were provided instead with a small cotton ball soaked with 15% sucrose solution). Females from ten pairs of each species were sacrificed at the end of day 16 (i.e. at 09.00 h on day 17, 24 h after aphids were removed) and dissected to assess reproductive condition (*sensu* Kurihara, 1975; Phoofolo *et al.*, 1998; and as explained below). Similarly, as many as ten females of each species were sacrificed and dissected at the end of each subsequent day (on days 17–21; fewer than ten pairs were dissected beginning on day 18, as dictated by mortality in the absence of prey, with a minimum of three females dissected for *C. transversoguttata* at the end of day 21). Data from females that died during the experiment, or that laid few or no eggs when provided with excess prey, were excluded.

In a similar, second experiment (conducted in 2007), adults collected from alfalfa fields were paired immediately upon collection, placed at 22 °C under an LD 16 : 8 h photoperiod, and offered pea aphids *ad libitum* daily for 15 days. Beginning on day 16, prey were withheld for 6 days from pairs of *C. septempunctata* and *C. transversoguttata* (15% sucrose solution was provided). Females from 10–12 such pairs of each species were sacrificed on each of these 6 days and dissected as in the first experiment. Pairs without prey for 6 days that were not sacrificed (26 pairs of each species) were provided prey again *ad libitum* daily, beginning on day 22 and ending on day 31. An additional ten pairs of *C. septempunctata* and 12 pairs of *C. transversoguttata* were provided with prey *ad libitum* continuously throughout the entire 31 days of the experimental period.

For both experiments, pairs were held individually in Petri dishes (diameter = 5.7 cm, height = 1.5 cm). Each pair was transferred daily to a new Petri dish provisioned with an excess amount of pea aphids. One drop of water was also added on the lid of the Petri dish. A strip of folded filter paper was put in each Petri dish, both to create oviposition sites for females and to minimize egg cannibalism by males and their disturbance of ovipositing females. Males that died during experiments were replaced, such that females remained paired with a male throughout the experiment.

The fresh weights of females were measured every fifth day during days when adults were provided with prey *ad libitum*, and every day during the period without prey. The number of eggs produced in 24 h by each female was recorded when pairs were transferred to new Petri dishes. During the period without prey, eggs were removed and counted even more frequently to minimize cannibalism (which occurred in only approximately three instances but, on these occasions, the residues of the one or two eggs eaten could be identified, and the cannibalized eggs were added into counts of daily egg production). The length and width of five randomly selected eggs per female were measured on days 15–21 during both experiments for those females that laid eggs. Egg volume (mm^3) was calculated from these measurements (*sensu* Phoofolo *et al.*, 1998; Richards & Evans, 1998), and a mean egg volume was then calculated for each female. Egg viability was also measured on days 15–21 during both experiments. For one egg batch from each female, the emergence of hatchlings (held at 22 °C under an LD 16 : 8 h photoperiod) was checked every 4–6 h to estimate the percentage of eggs that were viable. To prevent sibling egg cannibalism, hatchlings were removed immediately.

Females were sacrificed for dissection each morning after egg production and fresh weight was measured. Upon dissection, the three most developed egg follicles in ovarioles from each ovary were measured for length and width (for a total of six follicles per females). The number of mature oocytes in lateral oviducts, recognized by their fully developed shape, was also counted.

Statistical analysis

The initial fresh weights of females were compared with the averages of fresh weights on days 10 and 15 by paired *t*-tests for each species. The fresh weights of females on days 15–21 were analysed by repeated measures analysis of variance (ANOVA). For the second experiment, an additional repeated measures ANOVA was conducted for fresh weights on days 22–31, when prey were provided again *ad libitum*. Data were square root-transformed for analyses.

As a measure of maximal reproductive rate, the mean daily egg production of females over days 13–15 was compared between species by one-way ANOVA. Egg production over days 15–18 was analysed by repeated measures ANOVA, as was daily egg production during days 24–31 of the second experiment. Two-way ANOVA was used to compare egg production by the two species in the second experiment during days 13–15 and days 29–31; separate analyses were conducted for females with or without the aphid removal treatment. Two-way ANOVA was conducted also to compare relative rates of egg production after versus before the period of prey removal (i.e. egg production during days 29–31/days 13–15) for females of the two species with or without the aphid removal treatment. Data were square root-transformed for analyses.

The volume and viability of eggs produced on days 15–19 and days 15–18, respectively, were analysed by two-way repeated measures ANOVA (experiment × species, with days as repeated measures). The total number of mature oocytes found in lateral oviducts and the mean size of the three most developed follicles in the ovarioles were analysed by three-way ANOVA (experiment × species × day).

Results from ovarian dissections were combined with the numbers of eggs laid daily to compare between species the dynamics of egg production over the next 6 days after prey removal on day 16. For these comparisons, three means for individual females were considered, namely the number of mature oocytes found by dissection in a female's lateral oviducts: (i) at the end of a given day (e.g. day 16) and (ii) at the end of the next day (e.g. day 17), and (iii) the number of eggs laid in the interim (e.g. during day 17). Positive net egg production occurred when the sum of (ii) + (iii) was greater than (i), and negative net egg production occurred when this sum of (ii) + (iii) was less than (i). Three-way ANOVAS (species × experiment × day) were used for analyses of days 16 and 17, and of days 17 and 18 with log transformation. One-way ANOVAS were used also to compare the number of mature oocytes in oviducts at the end of a given day with either the number of eggs laid during the next day or the number of mature oocytes present at the end of the next day.

To assess the overall tendency of oosorption after prey removal, an index was calculated for each of the females sacrificed on day 21 (i.e. 6 days after prey removal). The total numbers of eggs laid by these females during the final 5 days without food (days 17–21) was divided by the sum of the mean number of mature oocytes for each day during days 16–21. The values of this index were analysed by combining the results from the two experiments for each species (one-way ANOVA) as well as by distinguishing between the results obtained from the two experiments (two-way ANOVA with experiment × species).

All analyses were performed by using SAS, version 9.1 (SAS Institute, Cary, North Carolina), including repeated measures analyses in Proc Mixed with unstructure model (with degrees of freedom calculated in SAS by the Kenward–Roger method).

Results

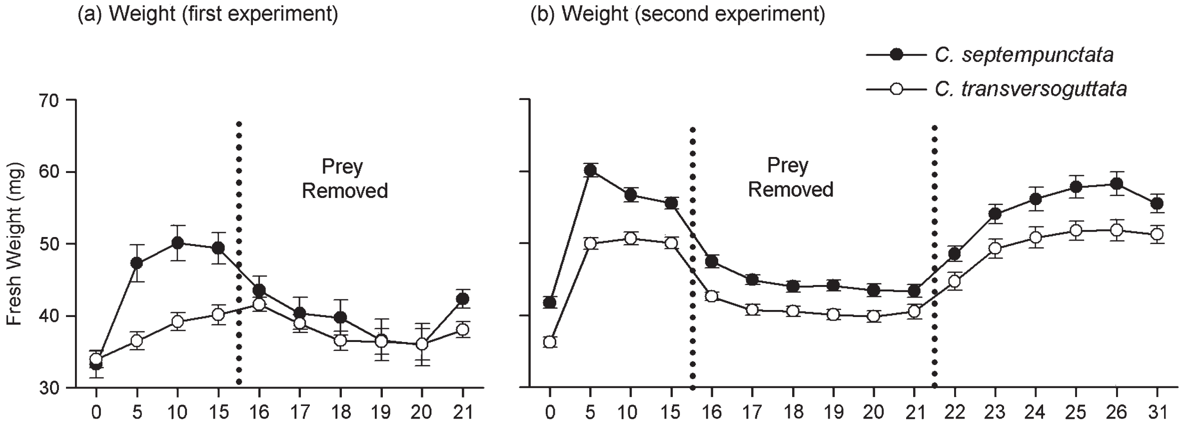
Both species gained weight during the initial 15 days with excess prey in both experiments [paired *t*-test (first and second experiment): *C. septempunctata*: $t_{57} = 19.63, P < 0.0001$; $t_{112} = 18.74$, $P < 0.0001$; *C. transversoguttata*: $t_{62} = 7.81$, $P < 0.0001$; $t_{118} = 23.54$, $P < 0.0001$; Fig. 1a,b]. When prey were removed, females initially lost weight and then stabilized at lower weights [repeated measures ANOVA (first and second experiment): effect of time: $F_{6,2.27} = 9.29$, $P = 0.05$; $F_{6,104} = 131.66$, $P < 0.0001$; effect of species: $F_{1,84.3} = 4.8$, $P = 0.03$; $F_{1,214} = 19.46$, $P < 0.0001$; interaction of time × species: $F_{6,2.77} = 2.34$, $P = 0.27$; $F_{6,104} = 1.87$, $P = 0.09$; Fig. 1a,b].

Fresh weights of females increased when they were provided prey again beginning on day 22 in the second experiment (repeated measures ANOVA, effect of species: $F_{1,91.7} = 11.69$, $P = 0.0009$; effect of time: $F_{6,67.4} = 43.47$, $P < 0.0001$; interaction of species × time: $F_{6,67.4} = 0.84$, $P = 0.54$; Fig. 1b). In general, *C. septempunctata* and *C. transversoguttata* responded similarly in changes in weight, both when aphids were removed and when prey subsequently were provided again.

After sustained feeding on prey *ad libitum*, *C. septempunctata* produced more eggs than did *C. transversoguttata* on days 13–15 [one-way ANOVA (first and second experiment): $F_{1,93} = 67.37$, $P < 0.0001$; $F_{1,215} = 49.19$, $P < 0.0001$; Fig. 1c,d]. Egg production decreased for both species when prey were removed on days 15–18 [repeated measures ANOVA (first and second experiment): $F_{3,93} = 83.14$, $P < 0.0001$; $F_{3,196} = 197.21$, $P < 0.0001$]. However, the pattern of decrease with time differed between the two species (interaction of species × time: $F_{3,93} = 7.96$, $P < 0.0001$; $F_{3,196} = 10.22$, $P < 0.0001$]. In both experiments, *C. septempunctata* laid fewer eggs immediately in response to prey removal on day 16, but *C. transversoguttata* did not do so until one day later on day 17 (Fig. 1c,d). Neither species laid eggs on days 20 and 21.

When pairs were provided prey again beginning on day 22 in the second experiment, both species began producing eggs again soon thereafter (Fig. 1d). *Coccinella septempunctata* came closer to recovering their rates of egg production prior to prey removal than did *C. transversoguttata* [two-way ANOVA, effect of species: $F_{1,89} = 42.48$, $P < 0.0001$; effect of time (days 13–15 versus days 29–31): $F_{1,89} = 1.02$, $P = 0.32$; interaction of species × time: $F_{1,89} = 4.18$, $P = 0.04$; Fig. 2a].

Among females that fed and reproduced continuously throughout the second experiment, *C. septempunctata* produced more eggs than *C. transversoguttata* but both species produced fewer eggs over time (days 13–15 versus days 29–31, two-way ANOVA, effect of species: $F_{1,28} = 21.84$, $P < 0.0001$; effect of time: $F_{1,28} = 8.08$, $P = 0.008$; interaction of species × time: $F_{1,28} = 0.08$, $P = 0.78$; Fig. 2b). Interestingly, females of both species with the aphid removal treatment had significantly higher reproductive rate than females without the treatment for 6 days (two-way ANOVA: effect of treatment: $F_{1,58} = 5.08$, $P = 0.028$; effect of



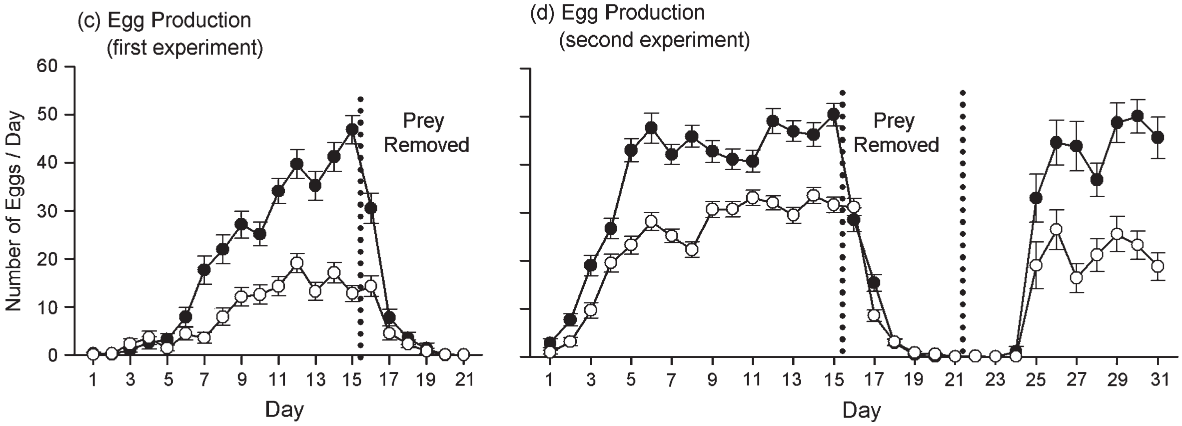


Fig. 1. (a, b) Fresh weight (mean ± SE) and (c, d) egg production (mean ± SE) of *Coccinella septempunctata* and *Coccinella transversoguttata* in the first and second experiment. As indicated by vertical lines, aphids were removed after 15 days (i.e. at the beginning of day 16), and they were provided again beginning on day 22 in the second experiment.

species: $F_{1,58} = 8.19$, $P = 0.006$; interaction of treatment × species: $F_{1,58} = 0.78$, $P = 0.38$; Fig. 2c).

Coccinella transversoguttata laid larger eggs than did *C. septempunctata* (Fig. 3 and Table 1). Both species produced smaller and smaller eggs on successive days in both experiments. The three-way interaction (experiment × species × day) was not significant; however, there were significant interactions of species × day, and experiment × day, reflecting the relatively large eggs that were produced on day 17 in the first experiment by *C. transversoguttata*. The percentages of egg viability did not differ between the two species (Fig. 4 and Table 1). There were significant effects of experiment and day of experiment in response to prey removal: viability was higher on average in the second experiment than in the first but, in both, viability declined on days 15–18 (Fig. 4). The three-way interaction (experiment × species × day) was not significant; however, the interaction of species × day was significant (Table 1), reflecting that differences in viability between the two species were highly variable among days.

The ovaries of females on days 16–21 contained oocytes that differed widely in stage of development. Fewer mature oocytes were found in lateral oviducts over time for both species (Fig. 5a,b and Table 2). There was a marginal effect of species (Table 2). In the first experiment, *C. septempunctata* had more mature oocytes in their oviducts 24 h after prey removal on day 16 than did *C. transversoguttata*; however, the interaction (experiment × species × day) was not significant.

Smaller and smaller egg follicles were found within ovarioles in both species after prey removal (Fig. 5c,d and Table 2). The decrease in follicle size over time happened especially rapidly in the second experiment after prey removal, leading to a significant interaction of experiment × day. In addition, there was a significant three-way interaction (experiment × species × day) (Table 2). This interaction reflected that follicle size tended to decrease more rapidly for *C. septempunctata* than for *C. transversoguttata* in both experiments, but was expressed later and most clearly in the first experiment (day 19 versus day 18) than in the second (day 18 versus day 17) (Fig. 5).

Positive net egg production on day 17 was apparent for *C. septempunctata* in the second (but not the first) experiment and for *C. transversoguttata* in both experiments (Fig. 6 and Table 3). These results indicate that, during the second 24 h

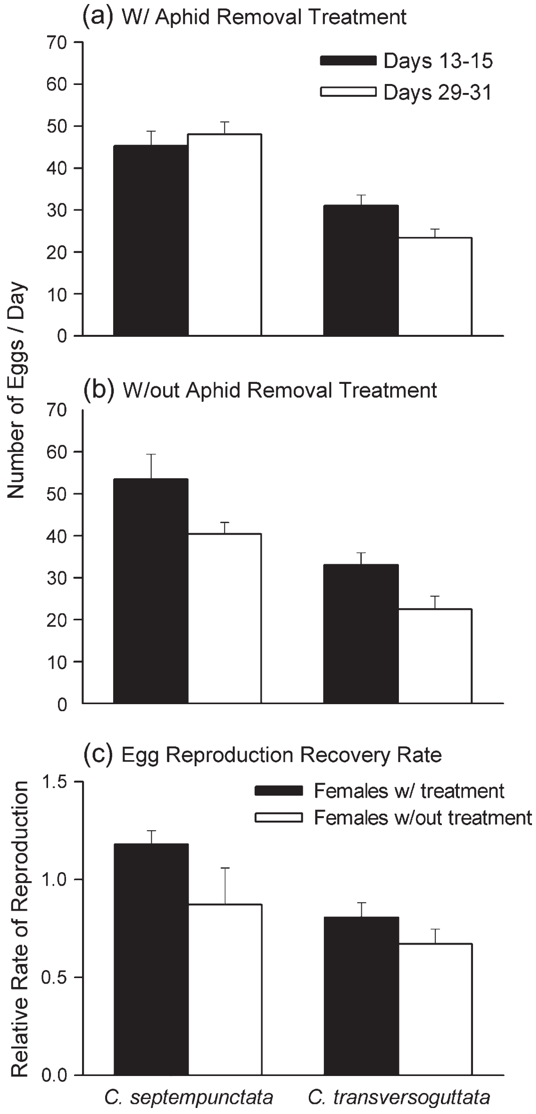


Fig. 2. Mean ± SE daily egg production in the second experiment on days 13–15 and days 29–31 for (a) females with the aphid removal treatment for 6 days (days 16–21) and (b) females without the aphid removal treatment (that were provided with prey *ad libitum* throughout the entire 31-day experimental period); and (c) rate of egg production during days 29–31 relative to days 13–15 for the two groups of females (with or without the aphid removal treatment).

after prey removal (i.e. during day 17), females continued to mature additional eggs in their reproductive tracts. Furthermore, the number of eggs laid during day 17 did not differ significantly from the number of mature oocytes in lateral oviducts at the end of day 16 for *C. septempunctata* in the second experiment, or for *C. transversoguttata* in either experiment (one-way ANOVA, $P > 0.1$ in each case), suggesting that all of the mature oocytes present in the oviduct at the end of day 16 were laid over the next 24 h.

A similar analysis for day 18 reveals that for *C. septempunctata* in the second experiment, and *C. transversoguttata* in both experiments, the pattern switched to negative net egg production (Fig. 6 and Table 3). These results indicate that, during the third 24 h after prey removal (i.e. during day 18), some mature oocytes were reduced in size (partially resorbed) rather than being laid. Approximately 4.8 mature oocytes in *C. septempunctata* in the second experiment, and 4.2 and 1.6 mature oocytes in *C. transversoguttata* in the first and second experiment, respectively, disappeared during the next 24 h (i.e. they could not be accounted for by the number of eggs laid over the next 24 h + the number of mature oocytes present at the end of the day; Fig. 6).

Coccinella septempunctata in the first experiment deviated from this general pattern, in that their net egg production appeared to be positive rather than negative on day 18 (as reflected in a marginally significant interaction of species × experiment × days) (Table 3). They switched to net negative egg production on the next day (day 19), when they also ceased laying eggs (Fig. 6a). In the absence of egg-laying, the numbers of mature oocytes that were present in these females' lateral oviducts decreased during day 19 compared with day 18 (one-way ANOVA, $F_{1,13} = 12.16$, $P = 0.004$). Approximately five mature oocytes per female disappeared during day 19.

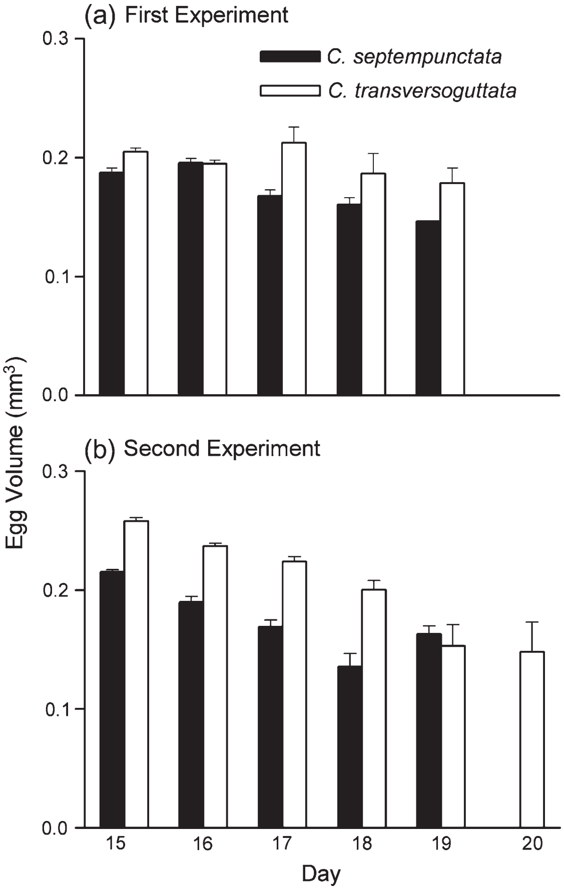


Fig. 3. Mean ± SE egg volume (mm^3) of *Coccinella septempunctata* and *Coccinella transversoguttata* during the (a) first and (b) second experiment.

Table 1. Results of two-way repeated measures analysis of variance of egg volume and viability in the first and second experiments (experiment effect) for both *Coccinella septempunctata* and *Coccinella transversogutatta* (species effect) on days 15–19 and days 15–18 of each experiment (day effect), respectively.

Egg volume	d.f.	*F*	*P*	Egg viability	d.f.	*F*	*P*
Experiment	1,13.1	0.86	0.3695	Experiment	1,147	8.35	0.0044
Species	1,13.1	34.33	< 0.0001	Species	1,147	0.53	0.4671
Experiment × Species	1,13.1	0.06	0.8099	Experiment × Species	1,147	1.62	0.2049
Day (days 15–19)	4,30.4	14.55	< 0.0001	Day (day 15–day 18)	3,160	24.42	< 0.0001
Experiment × Day	4,30.4	6.28	0.0008	Experiment × Day	3,160	1.29	0.2790
Species × Day	4,30.4	2.91	0.0379	Species × Day	3,160	3.55	0.0158
Experiment × Species × Day	4,30.4	1.62	0.1946	Experiment × Species × Day	3,160	0.06	0.9827

d.f., degrees of freedom.

Females of *C. septempunctata* and *C. transversoguttata* in both experiments laid very few eggs on days 19–21. The small numbers of mature oocytes that were present in lateral oviducts decreased over time, likely reflecting oosorption. For both experiments combined, the mean value of the index of oosorption for *C. septempunctata* and *C. transversoguttata* was 0.43 ± 0.09, and 0.46 ± 0.09, respectively (one-way ANOVA, $F_{1,34} = 0.03$, $P = 0.86$). The mean value of this index for *C. septempunctata* and *C. transversoguttata*, respectively, was 0.27 ± 0.11 and 0.05 ± 0.05 in the first experiment, and 0.53 ± 0.12 and 0.56 ± 0.09 in the second experiment (two-way ANOVA: effect of species: $F_{1,32} = 0.43$, $P = 0.51$; effect of experiment: $F_{1,32} = 6.98$, $P = 0.01$; interaction of species × experiment: $F_{1,32} = 0.70$, $P = 0.41$). Reflecting the better condition of females in general in the second experiment (for which they were provided immediately with excess aphids upon collection), the index values for both species were significantly higher in this than in the first experiment.

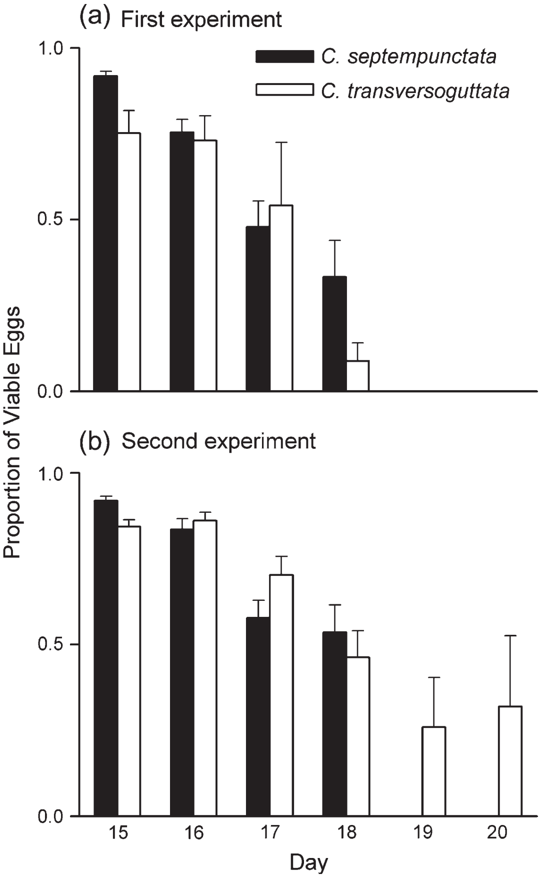


Fig. 4. Mean ± SE egg viability of *Coccinella septempunctata* and *Coccinella transversoguttata* during the (a) first and (b) second experiment.

Discussion

In the present study, *C. septempunctata* females weigh more and produce more eggs (of smaller size) than do *C. transversoguttata* females. Nonetheless, both species respond similarly when prey are provided *ad libitum* for an extended period, and then replaced by an alternative food (i.e. 15% sucrose solution). Their responses are similar for both self-maintenance (as reflected in changes in their weight) and reproduction (as reflected in changes in rates of egg production, egg volume, the number and volume of mature oocytes, and egg viability). After initially dropping in weight with the removal of prey, both species settle into lower, but stable weights as they adjust quickly to refrain from laying any further eggs. These results are consistent with those of previous studies of lady beetles (Ives, 1981) and other insect predators (Wiedenmann & O'Neil, 1990; Nakashima & Hirose, 1999). Egg volume and viability also decrease when prey are withheld from females. Even so, females lay viable eggs after as many as 3–4 days without prey, although the number laid is small. Both species respond rapidly with resumed laying of eggs in large numbers within 2–3 days, after prey are again provided after a 6-day period without prey, as observed in the second experiment.

Although the general patterns are similar for results of the two experiments, there are some differences in the specific results between the first and the second experiments. For example, the most marked difference is the higher daily egg production by *C. transversoguttata* females prior to removal of aphids in the second versus the first experiment. The differences in specific results most likely reflect the differing

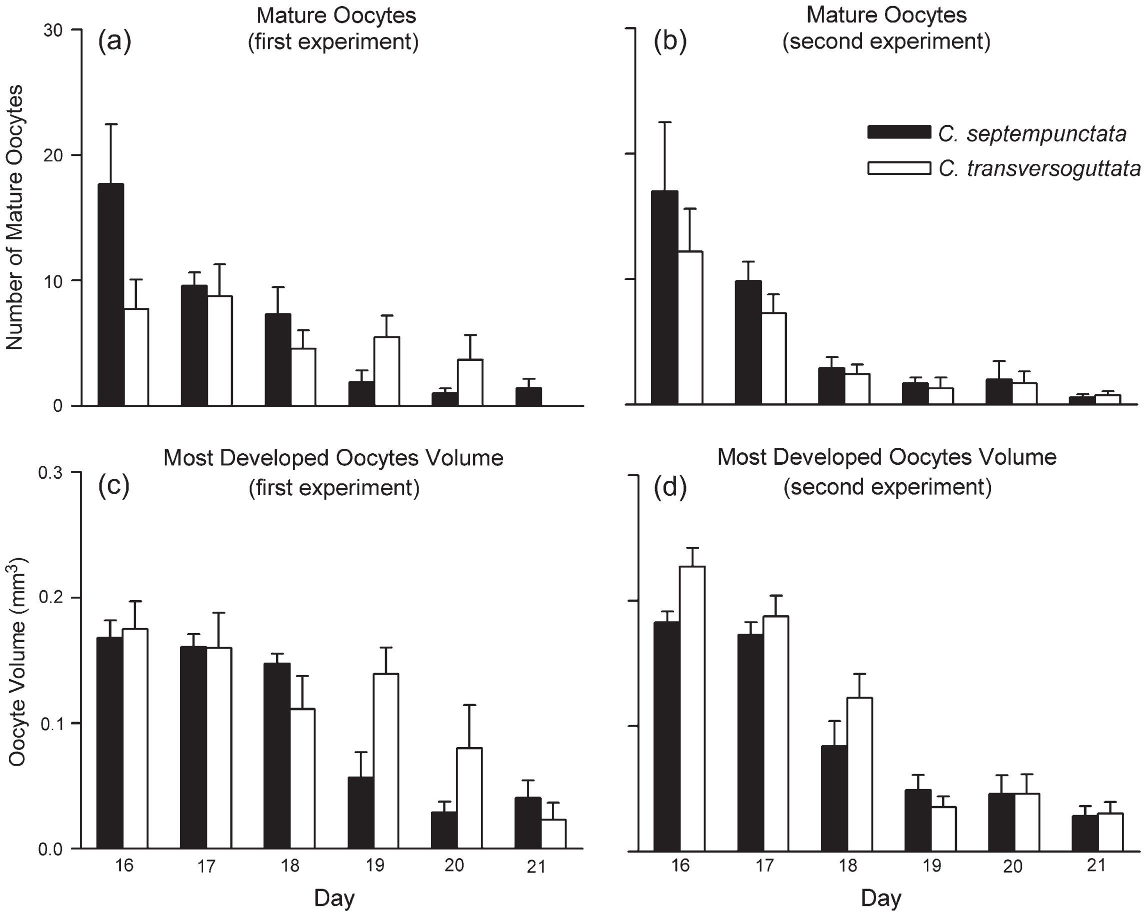


Fig. 5. Mean ± SE number of mature oocytes of *Coccinella septempunctata* and *Coccinella transversoguttata* found in lateral oviducts (left and right combined) in the (a) first and (b) second experiment; and the mean ± SE volume (mm^3) of the six most developed follicles in ovarioles of *C. septempunctata* and *C. transversoguttata* in the (c) first and (d) second experiment, on individual days without prey during the experimental period.

initial treatments of lady beetles (i.e. individuals for the second experiment are provided excess aphids immediately upon collection, whereas those for the first experiment are provided with only 15% sugar solution for the initial 2 weeks after collection from alfalfa fields).

The two species differ in two intriguing ways in their responses to changes in prey availability. *Coccinella septempunctata* females respond more quickly than do *C. transversoguttata* females to prey removal by laying fewer eggs within the next 24 h than previously. Also, upon resumption of oviposition, *C. septempunctata* females lay almost as many eggs daily as before prey are removed, but *C. transversoguttata* still lay fewer eggs at the end of the experiment compared with prior to the removal of prey. Hence, *C. septempunctata* may have a

Table 2. Results of three-way analysis of variance on the number of mature oocytes and the volumes of the most developed follicles in the first and second experiments (experiment effect) for both *Coccinella septempunctata* and *Coccinella transversogutatta* (species effect) on days 16–21 of experiments (day effect).

Number of mature oocytes	d.f.	*F*	*P*	Volumes of follicles	d.f.	*F*	*P*
Experiment	1,212	1.95	0.1643	Experiment	1,210	0.84	0.3606
Species	1,212	3.40	0.0664	Species	1,210	1.28	0.2595
Experiment × Species	1,212	0.17	0.6787	Experiment × Species	1,210	0.08	0.7724
Day (days 16–21)	5,212	29.10	< 0.0001	Day (day 16–day 21)	5,210	48.67	< 0.0001
Experiment × Day	5,212	1.34	0.2485	Experiment × Day	5,210	3.38	0.0058
Species × Day	5,212	2.09	0.0678	Species × Day	5,210	1.06	0.3832
Experiment × Species × Day	5,212	1.93	0.0906	Experiment × Species × Day	5,210	3.95	0.0019

d.f., degrees of freedom.

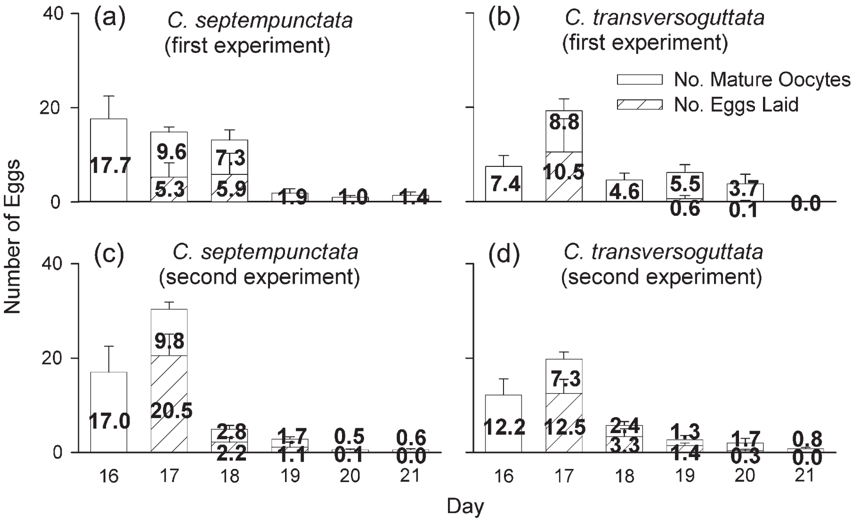


Fig. 6. Number of mature oocytes (mean ± SE) in lateral oviducts (as determined at the end of each day), and the number of eggs (mean ± SE) laid during each day of the starvation period for (a) *Coccinella septempunctata* and (b) *Coccinella transversoguttata* in the two experiments (note that the number of eggs laid on day 16 is not shown).

greater ability than *C. transversoguttata* to adjust its reproductive output to fluctuation in prey availability. This may be an important trait along with others associated with an r-selected lifestyle that has promoted the rapid and highly successful invasion of North America by *C. septempunctata* (Hodek & Honěk, 1996; Evans, 2000; Hodek & Michaud, 2008). In particular, this greater ability to adjust the rate of oviposition could contribute to the greater abundance and reproductive success of *C. septempunctata* relative to *C. transversoguttata* in western North American alfalfa fields that experience great variation in pea aphid densities (Evans, 2004; Kajita, 2008).

Oosorption occurs in both species, without any clear indication from dissections that the two species differ in this capacity. The index of oosorption used in the present study suggests that, for the two experiments combined, as many as 54–57% of mature oocytes may be resorbed during the nonprey period. In parasitoid wasps, starvation (as well as lack of opportunity to oviposit in the absence of hosts) can cause immediate oosorption (Heimpel & Rosenheim, 1995; Heimpel *et al.*, 1997; Rivero-Lynch & Godfray, 1997; Jervis *et al.*, 2000). The data presented in the present study indicate similarly that oosorption begins soon (2–3 days) after lady beetle females stop consuming prey. Another aphidophagous lady beetle *Harmonia axyridis* shows signs of oosorption even more rapidly, within 24 h of prey removal (Osawa, 2005). This recently introduced species has also spread widely throughout North America (and also western Europe; Brown *et al.*, 2008; Koch & Galvan, 2008). As with *C. septempunctata*, its rapid reproductive response to changing food conditions may promote its invasiveness.

It is intriguing that, as demonstrated by the second experiment, females (especially of *C. septempunctata*) that resorb and stop producing eggs in the absence of prey subsequently lay more eggs than do females that continue to feed throughout the experiment on aphids provided in excess. This result may reflect senescence being delayed by the temporary cessation of aphid consumption. It is consistent also with the general hypothesis that oosorption can be a key mechanism

Table 3. Results of three-way analysis of variance for the number of mature oocytes present on 1 day versus net production (eggs laid + mature oocytes present) on the next day, for *C. septempunctata* and *Coccinella transversoguttata* (species effect) in the first and second experiments (experiment effect) on day 16 versus 17, or day 17 versus 18 (day effect).

	Day 16 versus 17			Day 17 versus 18		
	d.f.	*F*	*P*	d.f.	*F*	*P*
Species	1,75	3.53	0.0642	1,70	4.94	0.0295
Experiment	1,75	1.86	0.1764	1,70	1.94	0.1677
Species × Experiment	1,75	0.26	0.6084	1,70	2.11	0.1504
Days	1,75	13.37	0.0005	1,70	8.19	0.0055
Species × Experiment	1,75	1.98	0.1633	1,70	0.82	0.3687
Experiment × Days	1,75	0.04	0.8333	1,70	0.39	0.5365
Species × Experiment × Days	1,75	3.74	0.0568	1,70	3.53	0.0644

d.f., degrees of freedom.

to preserve or enhance lifetime reproduction (Bell & Bohm, 1975; Ohgushi, 1996). Additional studies, including the application of promising molecular tools (Kurihara, 1975; Maeta *et al.*, 1981; Kotaki, 2003; Asplen & Byrne, 2006), are needed to explore further the mechanisms of oosorption and other reproductive traits that enable aphidophagous lady beetles to adapt to the continuously varying availability of their prey.

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