No nutritional benefits of egg cannibalism for *Coleomegilla maculata* (Coleoptera: Coccinellidae) on a high-quality diet

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Abstract

Egg cannibalism serves various functions in the Coccinellidae. Here we examined the fitness consequences of egg cannibalism by neonates, fourth instar larvae, and prereproductive adults of *Coleomegilla maculata* DeGeer, with beetles fed a diet of *Ephestia kuehniella* Zeller eggs. Cannibalism of two eggs by neonates had no effect on development, and cannibalism of five eggs by fourth instars did not benefit any aspect of reproduction, but delayed pupation slightly. Cannibalism of eggs by prereproductive adults had no effect on reproductive success in any combination of reciprocal crosses of cannibals and non-cannibals. Females did not recognize, nor avoid consuming, their own clutches, and cannibalism propensity did not change following mating and onset of oviposition in either sex. These results contrast with those for more strictly aphidophagous species in which larvae gain developmental benefits, and females may recognize and avoid filial egg clusters while using cannibalism to interfere with conspecific females, whereas males reduce egg cannibalism after mating because they cannot recognize filial clusters. Egg cannibalism may confer developmental benefits to *C. maculata* when diet is suboptimal, as previously shown, but no such benefits were evident on the high-quality *E. kuehniella* egg diet. Female *C. maculata* do not require aphids to reproduce and distribute their eggs broadly in the environment, given that larvae can develop on pollen and non-aphid prey. Thus, *C. maculata* is not subject to the intraspecific competition that selects for cannibalism in more aphidophagous species, and also lacks many secondary adaptations associated with the behaviour.

Keywords: development, ecology, fecundity, fertility, filial cannibalism, reproduction

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Introduction

Cannibalism, the killing and eating of conspecifics, is now widely recognized as a behaviour that can enhance individual fitness under a variety of conditions. In general terms,

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cannibals often gain nutritional benefits over non-cannibals, advantages in intraspecific competition, or both (Fox, 1975; Polis, 1981). The nutritional benefits of cannibalism can range from subtle changes in developmental rate, to dramatic alterations in life history, to the difference between life and death when faced with starvation (Richardson *et al.*, 2010). However, the indirect benefits of cannibalism conferred via reduced intraspecific competition can be more obscure and may be specific to a particular life stage, gender, or ecological context (Alabi *et al.*, 2008; Bayoumy & Michaud, 2015). A number of potential costs must be balanced against these benefits,

including the risk of injury, disease (Rudolf & Antonovics, 2007), or loss of inclusive fitness if a close relative is cannibalized (Joseph *et al.*, 1999).

Eggs are a life stage often targeted by cannibals (e.g., Richardson *et al.*, 2010), as they are relatively defenceless and represent a store of conspecific protein and other nutrients in an undifferentiated and easily digestible form. In the extreme, infertile 'trophic' eggs are produced by some ant species as a way to store nutrients (Crespi, 1992). In other species, egg-clustering is a way that females can increase the probability of sibling egg cannibalism among their progeny when such behaviour improves net female fitness (Michaud & Grant, 2004; Barros-Bellanda & Zucoloto, 2005; Collie *et al.*, 2013). Many species of Coccinellidae, in particular, lay clustered eggs and derive various benefits from egg-cannibalism, whether they are predaceous (Osawa, 1992), or herbivorous (Nakamura & Ohgushi, 1981; Nakamura *et al.*, 2004). Potential benefits include faster development, increased adult size, and fitness gained by reducing conspecific competition for progeny (Bayoumy & Michaud, 2015). Potential costs include the possibility of inadvertent filial cannibalism (Agarwala & Dixon, 1993).

Recently, Bayoumy & Michaud (2015) assessed the life history consequences of egg cannibalism in three life stages of *Hippodamia convergens* Guerin-Meneville. Cannibalism by neonate larvae reduced their developmental time and resulted in heavier male adults. Cannibalism in the fourth instar accelerated pupation and the resulting adults laid eggs that hatched faster than those of non-cannibals, and had higher fertility if they were laid by cannibal mothers. Virgin male and female adults initially expressed similar cannibalism propensities, but egg cannibalism by females increased after mating, whereas it decreased in males. Female adults were able to distinguish and avoid cannibalizing clusters of their own eggs laid 24 h earlier. Because females did not gain any reproductive benefits from adult egg cannibalism, the function of increased egg cannibalism by mated females was inferred to be interference with the reproductive success of conspecific females. These patterns of cannibalism appeared to be consistent with the overall ecology of the species in its High Plains habitat, where adults scramble to reproduce quickly on ephemeral aphid outbreaks and may spend many months in reproductive diapause between generations (Michaud & Qureshi, 2006).

In contrast, the reproduction of *Coleomegilla maculata* De Geer, a North American species sympatric with *H. convergens*, is not so constrained by aphid availability. A highly polyphagous and facultatively omnivorous species (Hodek, 1996), it can develop on an exclusive diet of pollen (Michaud & Grant, 2005) and even produce a few viable eggs without animal prey (Lundgren & Weidenmann, 2004). Egg cannibalism by both larvae and adults of *C. maculata* has been well documented in field studies (Cottrell & Yeargan, 1998*a*, *b*; Schellhorn & Andow, 1999*a*, *b*), but less is known about its fitness consequences for specific life stages. In the present work, we replicated with *C. maculata* the series of experiments conducted with *H. convergens* by Bayoumy & Michaud (2015). We hypothesized that differences in ecology between the two species was reflected in different patterns of cannibalism behaviour. For example, the ability of *H. convergens* females to recognize their own egg clusters suggests that they have a high probability of re-encountering them in nature. This is consistent with ovipositional activity that is normally quite compressed in both time and space, dependent as they are on ephemeral and localized blooms of aphids. In contrast,

C. maculata produce smaller clutches of eggs more continuously over a longer period (see Vargas *et al.*, 2013 for a direct comparison), presumably distributing them far more widely across different habitats. Therefore, although we hypothesized that *C. maculata* would gain developmental benefits from neonate egg cannibalism similar to *H. convergens*, and possibly some reproductive benefits of cannibalizing in the fourth instar, we hypothesized that there would be little or no advantage for adult females to recognize filial versus non-filial egg clusters. Similarly, we hypothesized that there would be no change in cannibalism behaviour following a change in mating status for either male or female adults, as males would have low probability of encountering egg clusters they have sired, and females would gain little, if any, advantage from interfering with the reproductive success of conspecifics.

Materials and methods

Insect colony

A stock colony of *C. maculata* was established from ca. 160 adults collected from a corn field in Hays, KS, USA in May 2016. Adults were held in a 1 l glass mason jar filled with strips of wax paper to serve as harbourage and provisioned daily with eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) with water provided on a cotton wick. Jars were kept in a growth chamber set to 18 ± 1 °C, 55–65% RH and a 16:8 L:D photoperiod. Previous work has shown these conditions to be ideal for maintaining beetles in reproductive diapause for extended periods prior to breeding.

To produce beetles for experiments, 50 adult *C. maculata* females were isolated in plastic Petri dishes (5.5 cm diameter) and fed *E. kuehniella* eggs with water provided on a small piece of sponge, both refreshed daily. Females in reproductive diapause quickly mature eggs and begin oviposition upon isolation. Egg clusters were collected daily by transferring beetles to fresh dishes and the eggs were held in a climate-controlled growth chamber set to 26 ± 1.0 °C, 55–65% RH, and a 16:8 L:D daylength until eclosion. Neonate larvae were transferred to plastic Petri dishes (5.5 cm diam), five per dish, labelled according to their maternal lineage, and provisioned with frozen eggs of *E. kuehniella* plus water on a small cube of sponge, both refreshed every 2 days until larvae pupated. From experience, we knew that larvae of this species rarely cannibalize each other when good quality food is provided ad libitum. Upon emergence, adults were sexed, isolated in Petri dishes, and numbered according to their maternal lineage in order to prevent the pairing of siblings.

Neonate egg cannibalism

To assess the developmental consequences of neonate egg cannibalism in *C. maculata*, two groups of neonate larvae ($n = 24$ per treatment) were isolated in plastic Petri dishes (5.5 cm diam) within 24 h of eclosion. Larvae of the treatment group were each provided two conspecific eggs (24–48 h old) on their first day of life, while larvae of the control group were provided only *E. kuehniella* eggs with water on a small cube of sponge. Two eggs represent roughly twice the body weight of a neonate larvae, and previous work has shown that cannibalism of a single egg at this stage can be enough to alter larval life history (Osawa, 2002). Once all treatment larvae consumed their conspecific eggs (<6 h), they were provided ad libitum *E. kuehniella* eggs and water, both refreshed daily, and all

larvae were reared until pupation on this diet without opportunity for any further egg cannibalism. All larvae were examined daily so that all developmental transitions could be tallied to the nearest day. Within 24 h of emergence, all adults were sexed and weighed on an analytical balance (Metler Toledo, model AG285, Columbus, Ohio).

Fourth instar egg cannibalism

To determine whether egg cannibalism later in larval development might benefit reproductive performance, a series of neonate larvae ($n = 200$) were obtained from the egg clusters of 15 unrelated females and isolated in plastic Petri dishes (5.5 cm diam). Larvae were labelled according to their maternal lineage and reared out on a diet of *E. kuehniella* eggs and water. Once larvae reached the fourth instar, they were divided into two groups with each maternal lineage equally represented in each. Larvae in the treatment group were each provided with five conspecific eggs (24–48 h old), in the presence of moth eggs and water, so that egg cannibalism was not driven by a lack of food in this experiment. Observations indicated that all conspecific eggs were consumed within 24 h. Both treatment ($n = 100$) and control larvae ($n = 100$) were then reared out on *E. kuehniella* eggs with water provided on a small cube of sponge, both refreshed daily. The duration of the fourth instar and pupal periods were recorded and, once larvae emerged as adults, they were separated by gender, isolated in clean Petri dishes, and provided *E. kuehniella* eggs and water. When beetles were 10–11 days old, non-sibling beetles were assigned to one of four mating treatments ($n = 20$ per treatment): $♀_{CAN} × ♂_{CAN}$, $♀_{CAN} × ♂_{NON}$, $♀_{NON} × ♂_{CAN}$ and $♀_{NON} × ♂_{NON}$, where CAN and NON indicate cannibals and non-cannibals, respectively. Following termination of mating, females were isolated in Petri dishes (as above) and provided with *E. kuehniella* eggs and water, refreshed daily. Males were then isolated in separate Petri dishes (to prevent any egg cannibalism or disturbance of oviposition by females). The same pairs were reunited for a period of 4–5 h every other day to permit remating in the interest of maintaining female fertility. All eggs were collected daily by switching each female to a clean dish. Egg clusters were held until eclosion under the same conditions as the beetles, and the fecundity, fertility, and egg eclosion time of each female was recorded for 14 days after first oviposition.

Adult egg cannibalism

A series of 200 neonate larvae were obtained from the egg clusters of 15 unrelated females and isolated in plastic Petri dishes (as above) within 24 h of eclosion. Larvae were labelled according to their maternal lineage and reared out on a diet of *E. kuehniella* eggs and water. As adults emerged, a series were selected for the experiment that all emerged on the same day ($n = 88$). These were sorted by gender, isolated in Petri dishes, and divided into two groups of 44, each containing 22 males and 22 females. All adults were provisioned with moth eggs plus water, refreshed daily and, on their second day of adult life, both males and females in the treatment group were each provided with ten conspecific eggs (24–48 h old, all consumed within 24 h), which beetles in the control group did not receive. When beetles were 10–11 day-old (post-emergence), pairs of non-sibling beetles ($n = 22$ pairs per treatment) were established in Petri dishes in four different mating treatments (as in fourth instar egg cannibalism): $♀_{CAN} × ♂_{CAN}$,

$♀_{CAN} × ♂_{NON}$, $♀_{NON} × ♂_{CAN}$ and $♀_{NON} × ♂_{NON}$, where CAN and NON refer to cannibals and non-cannibals, respectively. Following termination of mating, females were again isolated in Petri dishes and supplied with eggs of *E. kuehniella* and water, refreshed daily. Females were each reunited with their male for 4–5 h every other day to maintain fertility. Fecundity and egg fertility data were collected for 14 days after first oviposition for each female.

Filial egg cannibalism by females

A series of 100 larvae were isolated in Petri dishes and reared out on *E. kuehniella* eggs and water, as described above. A series of emerging adults ($n = 60$) were then isolated in Petri dishes and fed the same diet. Once they were 10–11 days old post-emergence, these virgin beetles were paired in Petri dishes for about 6 h and directly observed to ensure all pairs successfully copulated. The females were then isolated in Petri dishes and provided with ad libitum *E. kuehniella* eggs and water, refreshed daily. Once females began laying eggs, circles were drawn around egg clusters on tops and bottoms of Petri dishes using different coloured markers to enable recognition of filial and non-filial eggs (colour designations were reversed in half the replicates to prevent any bias in the experiment). When eggs were still <24 h old, filial and non-filial egg clusters of approximately equal size (12–16 eggs) were combined in Petri dish arenas by bringing tops and bottoms together bearing one or the other – half of replicates had filial eggs on the top, the other half, on the bottom. Each female ($n = 27$) was introduced into an arena and, after 24 h, cannibalism of the marked clusters was tallied, along with any freshly laid eggs.

Cannibalism propensity and mating status

To test whether the propensity for adult egg cannibalism was sensitive to mating status, a series of 200 larvae from 15 maternal lineages were reared on eggs of *E. kuehniella* until they emerged as adults. Adults were isolated in 5.5 cm Petri dishes and fed *E. kuehniella* eggs and water. On day 10 post-emergence, adults of the treatment group were paired with a non-sibling of the opposite sex ($n = 43$ pairs), whereas those of the second group remained unmated in isolation ($n = 43$ females and 43 males). All beetles were tested on their 11th day of adult life by transferring them individually to 5.5 cm Petri dishes containing a cluster of conspecific eggs ($n = 10$) that were <48 h old. In replicates with females, these eggs were circled with a marker to distinguish them from any that might be laid during the course of the trial. Trials were conducted in the presence of ad libitum *E. kuehniella* eggs to prevent cannibalism from being driven by hunger alone.

Data analysis

Data sets were first tested for normality (Shapiro–Wilk test) and equality of variance (Levine's test); data sets that passed these tests were analyzed by ANOVA, and those that failed, by Mann–Whitney *U*-test, or Kruskal–Wallis *H* test when more than two groups were compared (SPSS, 1998). Data from the filial egg cannibalism experiment were analysed by means of a paired *t*-test using SPSS (1998). Whenever three or more means were compared by ANOVA, they were separated by the Bonferroni test ($α = 0.05$).

Table 1. Mean (±SE) life history parameters for progeny of *Coleomegilla maculata* females from four mating treatments (CAN, cannibal; NON, control).

Dependent variable	Mating combination (treatment)			
	$\female_{CAN} \times \male_{CAN}$	$\female_{CAN} \times \male_{NON}$	$\female_{NON} \times \male_{CAN}$	$\female_{NON} \times \male_{NON}$
Preoviposition period (day)	19.9 ± 2.27	20.3 ± 2.83	22.1 ± 2.33	21.2 ± 1.37
14-day fecundity (no. eggs)	98.5 ± 13.9	82.4 ± 11.8	112.5 ± 10.3	112.2 ± 14.0
No. reproductive days	6.8 ± 0.73	6.04 ± 0.76	7.73 ± 0.53	7.81 ± 0.69
Egg fertility (% hatching)	67.1 ± 2.98	55.2 ± 5.86	63.6 ± 3.36	57.5 ± 4.66
Eclosion time (day)	3.06 ± 0.04	3.13 ± 0.06	3.07 ± 0.03	3.09 ± 0.06

Cannibals each consumed five conspecific eggs (<24 h old) within 24 h of moulting to the fourth instar. All eggs were collected from each female for 14 days after first oviposition. No values were significantly different among treatments for any dependent variable (Kruskal–Wallis, $\alpha > 0.05$).

Table 2. Mean (±SE) life history parameters for *Coleomegilla maculata* females from four mating treatments (CAN, cannibal; NON, control).

Dependent variable	Mating combination (treatment)			
	$\female_{CAN} \times \male_{CAN}$	$\female_{CAN} \times \male_{NON}$	$\female_{NON} \times \male_{CAN}$	$\female_{NON} \times \male_{NON}$
Preoviposition period (day)	8.7 ± 0.67	8.8 ± 1.29	8.1 ± 1.16	11.4 ± 2.12
14-day fecundity (no. eggs)	45.0 ± 14.1	40.8 ± 9.5	50.8 ± 10.1	35.8 ± 9.30
No. reproductive days	3.09 ± 0.71	3.64 ± 0.59	3.95 ± 0.59	3.05 ± 0.68
Egg fertility (% hatching)	73.0 ± 5.2	67.5 ± 5.3	72.1 ± 6.2	50.8 ± 9.00
Eclosion time (day)	3.11 ± 0.08	3.07 ± 0.04	3.14 ± 0.06	3.17 ± 0.09

Cannibals each consumed ten conspecific eggs (<24 h old) 24–48 h after emergence as an adult. All eggs were collected from each female for 14 days after first oviposition. No values were significantly different among treatments for any dependent variable (ANOVA, $\alpha > 0.05$).

Results

Neonate egg cannibalism

Cannibalism of two eggs within 24 h of eclosion did not affect any aspect of *C. maculata* development. Data for total developmental time failed the Shapiro–Wilk test for normality ($W = 0.775$, $P < 0.001$) and were analyzed by Mann–Whitney U-test. Cannibal larvae averaged 17.6 ± 0.15 days in the larval stage, versus 17.8 ± 0.13 days for controls ($U = 235.5$, $P = 0.235$). Pupation time (the time from pupal moult to adult emergence) was almost constant at 4 days (one male in the cannibal treatment required 5 days). Data for adult weight also failed the Shapiro–Wilk test for normality ($W = 0.944$, $P = 0.022$) and were analyzed by Mann–Whitney U-test. Adult weight was also unaffected by cannibalism in both males (control: 12.1 ± 0.27 vs. cannibal: 11.9 ± 0.29 mg, $U = 70.0$, $P = 0.479$) and females (control: 13.2 ± 0.37 vs. cannibal: 14.2 ± 0.42 mg, $U = 36.5$, $P = 0.116$).

Fourth instar egg cannibalism

Cannibalism of five eggs within 24 h of moulting to the fourth instar caused a small increase in the duration of the fourth instar compared to controls (3.8 ± 0.05 vs. 3.5 ± 0.05 d; $W = 0.689$, $P < 0.001$; $U = 3023.0$, $P < 0.001$), but had no effect on pupal duration, which averaged 4.0 ± 0.2 d ($W = 0.208$, $P < 0.001$; $U = 4414.5$, $P = 0.687$). Neither the fresh weight of males ($W = 0.988$, $P = 0.102$; $F_{1,95} = 0.09$, $P = 0.772$) nor females ($W = 1.02$, $P = 0.157$; $F_{1,90} = 0.83$, $P = 0.366$) was significantly affected by egg cannibalism. The reproductive performance of reciprocal crosses did not differ in any respect among treatments (preoviposition period: $W = 0.774$, $P < 0.001$, $H = 2.69$, $P = 0.442$; 14-day fecundity: $W = 0.759$, $P < 0.001$, $H = 3.52$,

$P = 0.318$; number of reproductive days: $W = 0.820$, $P < 0.001$, $H = 3.10$, $P = 0.377$; egg fertility: $W = 0.757$, $P < 0.001$, $H = 1.91$, $P = 0.592$; or time to eclosion: $W = 0.787$, $P < 0.001$, $H = 1.68$, $P = 0.643$; table 1).

Adult egg cannibalism

Cannibalism of ten eggs on the second day of adult life had no effect on the preoviposition period of females ($W = 0.592$, $P < 0.001$, $H = 4.44$, $P = 0.218$), their 14-day fecundity ($W = 0.601$, $P < 0.001$, $H = 3.04$, $P = 0.386$), number of reproductive days ($W = 0.906$, $P < 0.001$, $H = 2.71$, $P = 0.438$), egg fertility ($W = 0.716$, $P < 0.001$, $H = 3.02$, $P = 0.389$), or time to eclosion ($W = 0.796$, $P < 0.001$, $H = 1.68$, $P = 0.642$; table 2).

Filial egg cannibalism by females

Similar mean numbers of filial and conspecific eggs were offered to each of 27 females in the choice test (4.96 ± 0.36 vs. 4.96 ± 0.30 eggs; $t = 0.00$, $P_{(2\text{-tailed})} = 1.000$), and similar numbers were consumed (2.15 ± 0.45 vs. 2.96 ± 0.39; $t = 1.55$, $P_{(2\text{-tailed})} = 0.133$).

Cannibalism propensity and mating status

Adult males consumed similar numbers of eggs before (mean ± SE = 6.9 ± 0.6) and after (mean ± SE = 7.6 ± 0.5) mating ($W = 0.280$, $P < 0.001$; $U = 845.0$, $P = 0.476$), and so did females (8.1 ± 0.5 vs. 7.3 ± 0.6; $W = 0.293$, $P < 0.001$; $U = 852.5$, $P = 0.473$). Males cannibalized more eggs than females as virgins ($U = 687.5$, $P = 0.028$), but there were no gender differences after mating ($U = 845.0$, $P = 0.457$).

Discussion

Egg cannibalism by neonate larvae did not affect the developmental time of *C. maculata*, nor the duration of any immature life stage, compared with larvae that did not cannibalize. This result falsified our first hypothesis and stands in contrast to previous results for the same species (e.g., Gagne *et al.*, 2002) and those for most other lady beetle species that have been examined in this regard (Osawa, 1992, 2002; Michaud & Grant, 2004; Omkar *et al.*, 2006, 2007; Pervez *et al.*, 2006; Roy *et al.*, 2007; Bayoumy & Michaud, 2015). Whereas most of the latter studies employed aphids as the primary larval diet, the present study employed eggs of *E. kuehniella* and this may account for the absence of effects on developmental time. Apart from being a passive, rather than active prey, that require no energy to subdue, the moth eggs are also a richer source of protein and lipids than are aphids (Specty *et al.*, 2003) and have been shown to be superior to *Schizaphis graminum* (Rondani), a natural prey species, for *C. maculata* larval development (Michaud & Jyoti, 2008). Thus, the present results do not rule out potential developmental benefits of neonate egg cannibalism when the subsequent larval diet is inferior.

Michaud & Grant (2004) studied the life history consequences of neonate egg cannibalism in three aphidophagous coccinellids and obtained similar results across species in some regards (faster development), but species-specific differences in others (larger body size in either male, female or both sexes). An *E. kuehniella* diet was also used in this study, and differences among species responses were attributed to differences among them in the relative suitability of the moth egg diet provided subsequent to cannibalism. Only males achieved larger body size in *Cycloneda sanguinea* (L), the species for which moth eggs were less suitable, whereas both sexes achieved larger body size in *H. axyridis*, for which *E. kuehniella* is close to an optimum diet. These results also conflicted with earlier results of Osawa (2002) who found that male *H. axyridis* neonates benefited more than females from cannibalizing a single egg when the subsequent diet was *Aphis spiraecola* Patch, which happen to be an exceptionally low quality prey for most coccinellids (e.g., Michaud, 2000). Michaud & Grant (2004) inferred that females are more sensitive to diet quality than males, and therefore only achieved the full benefits of neonate egg cannibalism when the subsequent diet quality was sufficiently high. The results for *C. maculata* contrast with these for more strictly aphidophagous species, because aphidophagy is a lifestyle that selects for cannibalism, and hence for physiological adaptations that benefit from it. If *C. maculata* rarely cannibalizes eggs in nature, it would not evolve the associated adaptations, and nutritional benefits of egg cannibalism would be evident only when it compensates for an otherwise low quality diet. Thus, the developmental benefits of neonate egg cannibalism observed by Gagne *et al.* (2002) most likely reflect the fact that *A. pisum* is inferior as a monotypic diet for *C. maculata*, whereas, an *E. kuehniella* diet is closer to optimal.

Egg cannibalism by *C. maculata* larvae in the fourth instar caused a small delay in completion of the fourth instar, but there were no effects on pupation time, adult weight, or subsequent reproductive performance. The delay in the onset of pupation probably reflects some displaced consumption of *E. kuehniella* eggs, which represent superior food for *C. maculata* larval development (Michaud & Jyoti, 2008). Once again, these results stand in contrast to those obtained for more

strictly aphidophagous species. In a series of very similar experiments, *H. convergens* larvae that cannibalized a cluster of eggs in the fourth instar had reduced pupation times, and cannibal females had higher egg fertility than non-cannibals, whether they mated with cannibal or non-cannibal males (Bayoumy & Michaud, 2015). Because *H. convergens* females require aphids for egg production (Michaud & Qureshi, 2006), larvae of this species almost invariably develop within aphid colonies where predators will aggregate and opportunities for egg cannibalism by late instar larvae will occur. In contrast, it is probably rare for *C. maculata* larvae to encounter conspecific eggs after they leave their neonate cluster, given that they complete development on a wide range of foods, including pollen, in a variety of habitats (Hodek, 1996; Lundgren & Weidennmann, 2004; Michaud & Grant, 2005).

Egg cannibalism by prereproductive *C. maculata* adults resulted in no apparent costs or benefits to their subsequent reproductive success in any crossing treatment. In contrast, daughters produced by pairs of *H. convergens* cannibals matured to heavier body weights than did those in other treatments, albeit with a small cost in developmental time (Bayoumy & Michaud, 2015). In *Coccinella undecimpunctata* L., fecundity was improved by paternal cannibalism, whereas an improvement in fertility required cannibalism by both parents, and beneficial maternal effects of cannibal mothers were manifest in faster progeny development to larger body size with higher survival relative to non-cannibals (Bayoumy *et al.*, 2016). Although *C. maculata* females cannibalized somewhat more eggs than males when virgin, there were no significant gender differences after mating, and no significant change in cannibalism propensity of either sex as a function of mating status, supporting our hypothesis in this regard. Females were also unable to recognize and avoid cannibalizing their own egg clusters, as hypothesized, and again in contrast to *H. convergens* females (Bayoumy & Michaud, 2015). These results suggest that adult *C. maculata* adults rarely re-encounter their own egg masses in nature, as is more often the case for aphidophagous species that oviposit within aphid infestations that give rise to predator aggregations. Without dependency on aphids for reproduction, *C. maculata* is able to produce smaller egg clusters over a much longer period than *H. convergens* (Vargas *et al.*, 2013) and likely distributes them far more widely in the environment. For example, female *C. maculata* have been shown to express significant oviposition preferences for particular plant species in the absence of any prey (Cottrell & Yeargan, 1998a; Griffin & Yeargan, 2002a, b; Staley & Yeargan, 2005). If *C. maculata* females rarely re-encounter their own egg masses in nature, there would be no need to evolve filial cluster recognition, as do the females of many aphid specialists (e.g., Agarwala & Dixon, 1993). Similarly, with their offspring dispersed widely in the environment, there would be no payoff for females to increase their egg cannibalism following onset of oviposition to reduce local competition for their progeny, nor for males to reduce their egg cannibalism to avoid eating filial clusters. Both of these behavioural changes are observed in *H. convergens* (Bayoumy & Michaud, 2015).

In summary, because of the highly aggregated structure of aphid infestations, strict aphidophagy probably results in high levels of intraspecific competition among both larval and adult coccinellids. These conditions could select for cannibalism even if nutritional benefits of the behaviour are initially weak, because it reduces intraspecific competition. As cannibalism become an increasingly important determinant of

individual fitness, other adaptations will be selected that minimize costs (e.g., filial egg recognition) and maximize benefits (e.g., more effective utilization of the nutrition so obtained in growth and reproduction). This ecological inference is further supported by the high propensities for cannibalism expressed by the larval stages of other primarily aphidophagous predators such as the Chrysopidae (Duelli, 1981; Noppe *et al.*, 2012) and Syrphidae (Branquart *et al.*, 1997; Belliure & Michaud, 2001). We conclude that both larval and adult stages of *C. maculata* readily cannibalize eggs in the presence of suitable food, and probably gain nutritional advantages from doing so under conditions of low prey quality or availability. However, *C. maculata* does not appear to rely on egg cannibalism as an intraspecific interference tactic to the same extent as do more aphidophagous species, and thus displays fewer of the derived adaptations associated with egg cannibalism, whether behavioural or physiological.

Acknowledgements

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