

WILEY

Online Proofing System

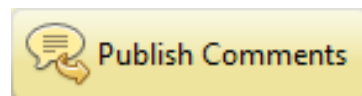
Enabling the Adobe PDF Viewer

In order to proof your article Adobe Reader or Adobe Acrobat needs to be your browser's default PDF viewer. See how to set this up for Internet Explorer, Firefox, and Safari at <https://helpx.adobe.com/acrobat/using/display-pdf-in-browser.html>

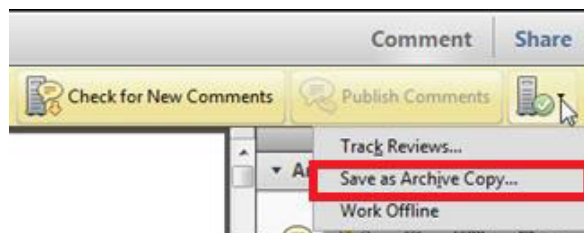
Google Chrome and Microsoft Edge do not support Adobe Reader or Adobe Acrobat as a PDF Viewer. We recommend using Internet Explorer, Firefox, or Safari.

1. Mark your corrections, changes, and query responses using the Annotation Tools outlined on the next 2 pages.

2. Save your proof corrections by clicking the “Publish Comments” button in the yellow banner above. Corrections don’t have to be marked in one sitting. You can publish comments and log back in at a later time to add and publish more comments before you click the “Complete Proof Review” button.



3. When your proof review is complete we recommend you download a copy of your annotated proof for reference in any future correspondence concerning the article before publication. You can do this by clicking on the icon to the right of the ‘Publish Comments’ button and selecting ‘Save as Archive Copy...’.



IMPORTANT: Did you reply to all queries listed on the Author Query Form appearing before your proof?

IMPORTANT: Did you click the “Publish Comments” button to save all your corrections? Any unpublished comments will be lost.

IMPORTANT: Once you click “Complete Proof Review” you will not be able to add or publish additional corrections.

4. When your proof review is complete and all corrections have been published to the server by clicking the “Publish Comments” button, please click the “Complete Proof Review” button appearing above the proof in your web browser window.

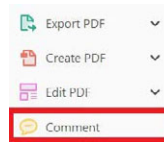
Finalize / Complete Proof Review

USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION


Required software to e-annotate PDFs: **Adobe Acrobat Professional** or **Adobe Reader** (version 11 or above). (Note that this document uses screenshots from **Adobe Reader DC**.)
 The latest version of Acrobat Reader can be downloaded for free at: <http://get.adobe.com/reader/>

Once you have Acrobat Reader open on your computer, click on the **Comment** tab (right-hand panel or under the Tools menu).


This will open up a ribbon panel at the top of the document. Using a tool will place a comment in the right-hand panel. The tools you will use for annotating your proof are shown below:




1. Replace (Ins) Tool – for replacing text.

 Strikes a line through text and opens up a text box where replacement text can be entered.


How to use it:

- Highlight a word or sentence.
- Click on .
- Type the replacement text into the blue box that appears.


*...nitored in populations of relatively homogeneous single n of **Saccharomyces**, and is initiated after carbon source [1]. Sp are referred to as mei n of meiosis-specific g revisiae depends on th inducer of meiosis) [2 T functions as a repre pression, the genes (pression) and RGR1 at ase II mediator subur osome density [8]. SIM irectly or indirectly re*



2. Strikethrough (Del) Tool – for deleting text.

 Strikes a red line through text that is to be deleted.



How to use it:

- Highlight a word or sentence.
- Click on .
- The text will be struck out in red.



...experimental data if available. For ORFs to be had to meet all of the following criteria:


1. Small size (35–250 amino acids).
2. Absence of similarity to known proteins.
3. Absence of functional data which could n the real overlapping gene.
4. Greater than 25% overlap at the N-termin terminus with another coding feature; ovr both ends; or ORF containing a tRNA.


3. Commenting Tool – for highlighting a section to be changed to bold or italic or for general comments.

  Use these 2 tools to highlight the text where a comment is then made.

How to use it:


- Click on .
- Click and drag over the text you need to highlight for the comment you will add.
- Click on .
- Click close to the text you just highlighted.
- Type any instructions regarding the text to be altered into the box that appears.

...nformal invariance:  r
 A: Math. Gen., Vol. 12 N
 This needs to be bold





...lified theory for a matrix
 'ol. 8, 1984, pp. 305–323
 d manuscript, 1984.
 ching fractions for $D0 \rightarrow K+K$
 relation in $D0$ decays' Phys

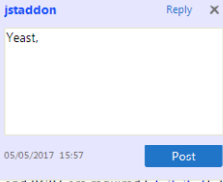
4. Insert Tool – for inserting missing text at specific points in the text.

 Marks an insertion point in the text and opens up a text box where comments can be entered.

How to use it:

- Click on .
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the box that appears.

Meiosis has a central role in the sexual reproduction of nearly all eukaryotes.  *Saccharomyces cerevisiae*, analysis of meiosis, esp by a simple change of n conveniently monitored cells. Sporulation of α cell, the α/α cell, and is of a fermentable carbon sporulation and are refe [2b]. Transcription of meiosis, in *S. cerevisiae* activator, *IME1* (inducer of the gene *RME1* funct Rme1p to exert repressi of *GAL1* gene expression) and *HIG1* are required [1, 2, 3, 4]. These ge



AUTHOR QUERY FORM

Dear Author,

During the preparation of your manuscript for publication, the questions listed below have arisen. Please attend to these matters and return this form with your proof.

Many thanks for your assistance.

Query References	Query	Remarks
Q1	Please confirm that given names (blue) and surnames/family names (vermilion) have been identified and spelled correctly	
Q2	We have processed Figure(s) 1 in colour. If these figures are to be published in colour, please fill out CWA form if not yet done.	
Q3	au:in the earlier text, you mention ' time required to obtain 10 clutches of eggs' - -is this meant to be the same measure? They can be read to mean different things, if co.	

Beyond killing: intra- and interspecific nonconsumptive effects among aphidophagous competitors

MOHAMED H. BAYOUMY,¹ HAGAR S. AWADALLA,²
 DINA MANDOUHFATHY¹ and TAMSIN M. O. MAJERUS³ ¹Economic

Entomology Department, Faculty of Agriculture, Mansoura University, Mansoura, Egypt ²Economic Entomology Department, Faculty of Agriculture, Damitta University, Damitta, Egypt and ³School of Life Sciences, University Park, University of Nottingham, Nottingham, U.K.

Abstract. 1. Beyond killing, predators have nonlethal effects on their potential prey. Because aphids are highly aggregated, their predators aggregate as well, creating conditions optimal for nonconsumptive effects (NCEs) among competing larvae. Although intraguild predator (IGP) density can alter the balance between conflicting forces, little is known about its effect on competing prey.

2. A partitioned Petri-dish that permitted the passage of signals was used to examine the NCEs between competing stages of similar- or different-sized, conspecific or heterospecific, individuals, on development, survival and reproduction of competing prey.

3. *Coccinella undecimpunctata* L. larvae suffered developmental and reproductive costs resulting from the presence of conspecific and heterospecific larvae, but showed no impact on their survival. In contrast, larvae of *Chrysoperla carnea* Stephens and *Hippodamia variegata* (Goeze) gained developmental benefits, without reproductive costs. Faster development can be construed as adaptive, as it reduces immature mortality.

4. Interestingly, threat-sensitive prey responses appear to be species-specific, regardless of predator density. In a *C. carnea* larva–*H. variegata* adult competing system, larvae responded to the threat posed by heterospecific adults, with accelerated development, but suffered reproductive costs. In a *C. carnea* larva–*C. undecimpunctata* adult system, no overall development costs in response to heterospecific adults were evident. The only cost was on survival at higher IGP density. Thus, the phenotype induced under *H. variegata* stress was adaptive for development in aphid colonies, whereas that under *C. undecimpunctata* stress was not.

5. NCEs are not simple vertical forces affecting prey, but can affect guilds on the same trophic level. Co-release of more than one species and density of these species may adversely increase the aphid populations.

Key words. *Chrysoperla carnea*, *Coccinella undecimpunctata*, conspecific and heterospecific interactions, *Hippodamia variegata*, nonlethal effects.

Introduction

Cascading effects of predators are widely thought to arise by two types of interactions (Preisser *et al.*, 2005): consumptive interactions, in which predators kill and consume prey; and nonconsumptive interactions, inducing phenotypic defence responses

Correspondence: Mohamed H. Bayoumy, Economic Entomology Department, Faculty of Agriculture, Mansoura University, Mansoura, Egypt. E-mail: mh Mohamed@mans.edu.eg

such as reduced mobility, induction of defensive morphologies and changes in life-history traits. These two mechanisms are often treated as dichotomous alternatives (Creel & Christianson, 2008). The ecology of fear – the nonconsumptive effects (NCEs) of predators on their prey – has received increased attention over the past decade, not only for its implications on prey behaviour and development, but also for its higher order impacts for ecosystem dynamics (Ohgushi *et al.*, 2012; Michaud *et al.*, 2016). These impacts can be equivalent to or higher than

that of direct predation, and can sometimes change community composition more than direct interactions (Preisser *et al.*, 2005). The ability of prey to perceive a given predator species through direct and/or indirect cues is a prerequisite for effective, threat-sensitive, anti-predation responses. The volatile cues received from highly aggregated competitors in the same arena of search might have various nonlethal impacts on prey foraging behaviour (Lima & Dill, 1990), development (McCauley *et al.*, 2011), and prey population dynamics (Nakaoka, 2000). These nonlethal impacts are often the outcome of trait alterations by prey under predation risk and are termed ‘trait mediated’ interaction (TMI) (Nakaoka, 2000). Prey that overreact in response to each predator encounter, regardless of the risk posed by the predator, exhibit lower rates of fitness, because investing in anti-predation behaviour is commonly *traded off* against reproduction and/or foraging (Creel & Christianson, 2008). Underestimation of the risk posed by a predator might have dramatic outcomes for prey survival or lead to a decline in reproductive performance. Therefore, prey need to be able to estimate the magnitude of predator threat and modify their behaviour accordingly (Sih, 1986). By evaluating the costs and benefits of the options available to an animal and monitoring its response, it is possible to determine whether an apparent *trade-off* is adaptive or not (Stearns, 1989).

If predatory larvae are themselves potential prey for other predators, they may be sensitive also to NCEs imposed by their heterospecific competitors, or even by conspecific competitors when they are cannibalistic. The idea that predation is not a simple ‘top-down’ process, but also can exist within trophic levels (Polis *et al.*, 1989; Arim & Marquet, 2004), is a substantial ecological concept that has reached prominence during the last decade (Hodek *et al.*, 2012). Both conspecific predation [i.e. cannibalism (CN)] and heterospecific [i.e. intraguild (IG)] predation (IGP) may enhance survival, but also can impose significant intimidation to natural enemies and hinder their role in pest biocontrol (Meisner *et al.*, 2011). Factors that mediate IGP include the presence of alternative prey, life-history stage, size-structure distribution within a population, habitat characteristics and density of interacting species (Mylius *et al.*, 2001; Borer *et al.*, 2003; Janssen *et al.*, 2007). As with many other animals, IGP among aphidophagous species is mutual but asymmetric for size (Polis *et al.*, 1989). Small/younger juveniles are often consumed by larger/older stages. In this context, threats to smaller individuals might have indirect fitness consequences (Sato *et al.*, 2003). The larval stage is the smallest mobile stage and most at risk from IGP (Bayoumy & Michaud, 2015). IGP risk could be reduced by larval anti-predation behaviours, whereas it should be increased in high densities of IG predator (Schausberger, 2003). Here, we focused on the latter. Understanding strategies that allow smaller competitors to develop in the presence of higher densities of bigger competitors is critical in determining whether they have the ability to accelerate their development and to reduce their mortality risks, or not. Anderson & Semlitsch (2014) stated that the IG predator density affected both size and survival of its IG prey, whereas it altered its own growth rate and size but not its survival. High density of IG predators can increase predator–predator mutual interference/competition, diminishing their efficiency in

consuming IG prey (Sih *et al.*, 1998; Bayoumy & Michaud, 2012; Papanikolaou *et al.*, 2016). Several studies have addressed the impact of extraguild prey (e.g. Polis *et al.*, 1989; Lucas *et al.*, 1998; Nóia *et al.*, 2008; Lucas & Rosenheim, 2011) and intraguild prey (Polis *et al.*, 1989) densities on the intensity of IGP and CN, respectively, however, few studies have examined the more subtle NCEs that might be induced by different densities of intraguild predator.

Ecological communities often are characterized by competition among consumers that use the same food resources, particularly those that are patchy and short-lived (Dixon, 1997; Obrycki *et al.*, 1998). For example, several aphidophagous species synchronize in exploiting dense aphid populations, maintain aphid populations at lower densities and commonly compete, at least consumptively, in nature (Frazer *et al.*, 1981; Abd El-Aty, 2016). Aphid populations show ‘boom and bust’ dynamics, often recognized by long intervening periods of aphid scarcity, such that aphidophagous species have life histories specialized for exploiting highly aggregated, but ephemeral, resources (Borges *et al.*, 2011). Because aphids exhibit highly aggregated distributions, their natural enemies tend to aggregate also (Rahman *et al.*, 2010), creating conditions conducive to both conspecific and heterospecific indirect interactions. Interactions between aphidophagous species often have been the subject of CN and IGP trials in both laboratory (Moser & Obrycki, 2009) and field cage studies (Chacon & Heimpel, 2010). Aphidophagous species which engage in CN and IGP are, therefore, excellent model systems for testing ideas about NCEs (Obrycki *et al.*, 1998). Hence, three aphidophagous species that share a wide range of similar prey, often co-occur spatially and temporally in the field, and engage in CN and IGP (Phoofolo & Obrycki, 1998; Michaud & Grant, 2003; Bayoumy & Michaud, 2015; Bayoumy *et al.*, 2016) were selected for this study. These species are the green lacewing (GL), *Chrysoperla carnea* Stephens (Chrysopidae: Neuroptera), the variegata ladybeetle (VL), *Hippodamia variegata* (Goeze) and the 11-spotted ladybeetle (ESL), *Coccinella undecimpunctata* L. (Coccinellidae: Coleoptera). All prey upon the cowpea aphid, *Aphis craccivora* Koch in the field (Abd El-Aty, 2016). Understanding how NCEs affect aphidophagous biocontrol species is vital to maximize the beneficial impact of these organisms. Furthermore, understanding how NCEs between different species in the same environment mutually impact on elements of fitness, may provide useful insight into factors such as rearing conditions, timing of release, benefits (or otherwise) of co-release of more than one biocontrol agent and density of biocontrol insects.

A partitioned Petri-dish was used to examine the NCEs between conspecific or heterospecific larval pairs (Michaud *et al.*, 2016). The configuration of this dish was modified to permit investigation of the NCEs between multiple heterospecific larvae, preventing them from physical contact, while allowing contact with volatile cues from each other. This study hypothesized that (i) the threatened larvae in the presence of similar-sized conspecifics or heterospecifics would exhibit accelerated development and improved reproduction compared to solitary controls, in order to reduce their mortality risk; (ii) the predator species, which often develop on a wider range of food, including non-aphid prey, few of which are likely to be

associated with the same risks of cannibalism or IGP, would exhibit a phenotype with reduced measures of growth, survival or reproduction, compared to solitary controls, under stress of conspecific or heterospecific competitors; and (iii) the presence of larger heterospecifics may be perceived as posing a greater risk of IGP and, hence, the fitness measures of smaller larvae would decline more in the presence of larger heterospecifics, as an adaptive tactic, than in their absence. Furthermore, this effect would increase with increasing the density of larger heterospecific in the same experimental arena.

Materials and methods

All experiments took place in incubators set to 25.0 ± 1.0 °C, $60 \pm 10\%$ relative humidity, and a 16:8 (light: dark) photoperiod. Coccinellid and green lacewing eggs, larvae and adults were isolated in Petri-dishes appropriate to their rearing or experimental stage. Diet and conditions were modified to prevent or encourage reproduction as appropriate (Michaud & Qureshi, 2006; Bayoumy *et al.*, 2016). During rearing stages, individuals were separated to avoid sibling mating and cannibalism. Appendix S1, Supplementary information contains further details of insect-rearing conditions, maintenance and experimental diets.

Experiments used two forms of partitioned plastic Petri-dishes (9.0 cm diameter \times 2.0 cm height). The first design followed Michaud *et al.* (2016) and used two Petri-dishes to study the interactions between pairs of larvae. Each dish had a cyclic hole (3.0 cm diameter) either in the top or the bottom of the dish. Each hole was covered with a white mesh screen held in place with glue. Both dishes were held together as one unit with a rubber band, creating two chambers with a common window and separated only by the mesh partition. This design allowed each larval species to develop under the stress of conspecific larvae. Larvae were physically isolated in each of the two dishes, preventing physical attack of each other, but allowing contact with volatile cues from each other. In solitary controls, larvae were isolated in the same partitioned Petri-dishes, but one of the dishes was left empty. The second form of partitioned Petri-dish, configured for this study, was used for multiple heterospecific interactions. This form consisted of three chambers created from three Petri-dishes. The upper and lower dishes had single holes (3.0 cm) in the bottom and top, respectively, whereas the middle one had two holes, one each in the top and bottom, each hole covered with a circular panel of white mesh screen as before. All three dishes were held together with a rubber band, creating three chambers separated only by the mesh partitions. Again larval predators were physically isolated in each of the three chambers, but remained in contact with chemical signals from each other (Fig. 1).

Nonconsumptive effects of competing con- and heterospecific larvae were investigated via seven treatments, consisting of all possible combinations of larvae, both conspecific and heterospecific, with control larvae of each species reared in solitude: GL (solitary), VL (solitary), ESL (solitary), GL + GL, VL + VL, ESL + ESL and GL + VL + ESL. Following eclosion of eggs, neonate larvae (< 24 h old) of each species were assigned to

treatments. Each treatment was replicated 30 times. Developmental data, including time to pupation, time to adult emergence, larval and pupal survival, for individuals in conspecific treatments were collected from both partitions. Female adults were allowed to mate and lay eggs. For each female, the total female fecundity, fertility and time required to obtain 10 clutches of eggs were recorded.

Intraguild predator density-dependent, threat-sensitive prey responses were investigated by rearing individual first instar GL larvae in one partition of the Petri-dish under stress of various densities (1:0, 1:1, 1:2 and 1:3) of ESL or VL adults in the other partition. Each group was replicated 60–80 times. Larval and pupal survival and developmental periods were recorded. Female adults that emerged were mated and total female fecundity, fertility and time required to obtain 10 clutches of eggs were recorded.

Statistical analysis

Data for all measurements were tested for assumptions of normality (Shapiro–Wilks test) prior to ANOVA. Development time, female fecundity and fertility, and the time to obtain 10 days of oviposition for all treatments were analyzed by one-way ANOVA and means separated by Bonferroni test ($\alpha = 0.05$). The proportions of progeny surviving to adulthood were compared between treatments using chi-squared (χ^2) goodness-of-fit tests. The *P*-values obtained by these χ^2 tests were adjusted for multiple comparisons using Bonferroni correction (P/n , where *n* is the number of pairs in the multiple comparison). All analyses were performed using SigmaPlot 12 (2011; Systat Software, San Jose, CA, U.S.A.).

Results

Nonconsumptive effects of competing con- and heterospecific larvae

Exposure to cues from competing conspecific and heterospecific predatory larvae, resulted in faster larval development ($F_{2,119} = 8.29$, $P < 0.001$) and shorter total developmental period ($F_{2,211} = 13.39$, $P < 0.001$) for the GL when compared to solitary controls, although egg incubation and pupation periods did not differ between treatments ($F_{2,119} = 0.08$, $P = 0.092$; $F_{2,111} = 2.19$, $P = 0.12$, respectively; Fig. 2). Progeny survival of GL did not vary between treatments ($\chi^2 = 1.08$, $df = 2$; $P = 0.58$; survival percentiles: GL = 96.67%, GL + GL = 91.67%, GL + ESL + VL = 90.00%). Female adults resulting from larvae developed in the presence of either conspecific or heterospecific cues did not differ from solitary control females in 10-day fecundity ($F_{2,30} = 0.55$, $P = 0.58$), egg fertility ($F_{2,30} = 1.13$, $P = 0.34$), or the time required to produce 10 days of oviposition ($F_{2,30} = 1.51$, $P = 0.24$).

There were significant differences between treatments, in larval and total developmental periods ($F_{2,117} = 7.38$, $P < 0.001$; $F_{2,112} = 3.45$, $P = 0.03$, respectively) of ESL, whereas the egg incubation period and pupal duration did not vary between treatments ($F_{2,119} = 0.84$, $P = 0.43$; $F_{2,112} = 0.74$, $P = 0.48$,

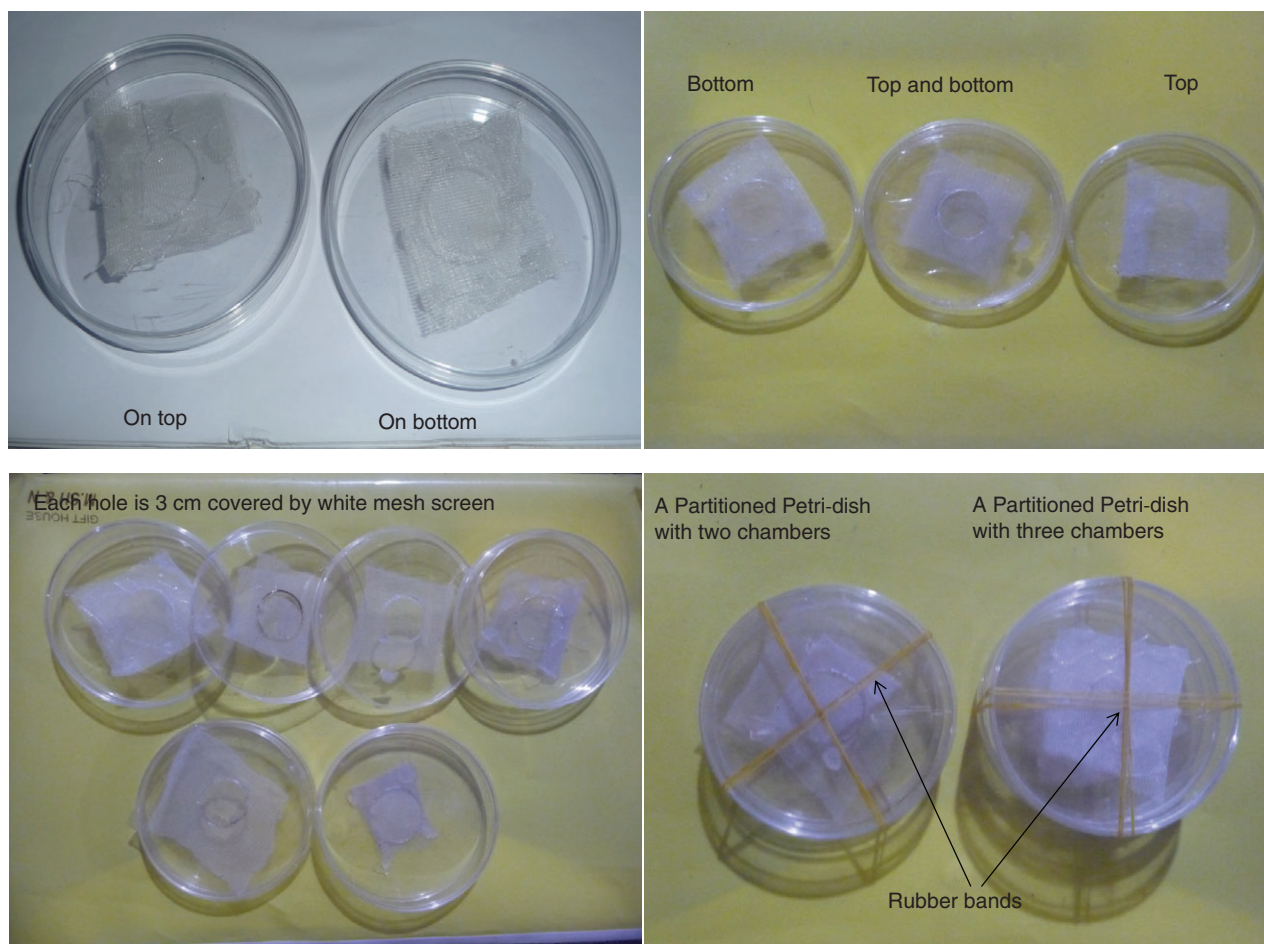


Fig. 1. A photograph of the experimental partitioned Petri-dishes. These consisted of two or three Petri-dishes, all held together with a rubber band, creating two or three chambers, with a common interactive window, separated only by the white mesh partitions. The upper and lower dishes had single holes (3.0 cm) in the bottom and top, respectively, whereas the middle dish (where present) had two holes, one each in the top and bottom each hole covered with a circular panel of white mesh screen. [Colour figure can be viewed at wileyonlinelibrary.com].

respectively; Fig. 2). There were no significant differences between conspecific, heterospecific and solitary controls in survival of immature stages of ESL ($\chi^2 = 0.15$, $df = 2$, $P = 0.93$; survival percentiles: ESL = 93.33%, ESL + ESL = 95.00%, ESL + GL + VL = 93.33%). Adult females that developed from conspecific and heterospecific treatments showed decreased 10-day fecundity ($F_{2,32} = 4.13$, $P = 0.03$) and egg viability ($F_{2,32} = 4.99$, $P = 0.01$; Fig. 3) compared to solitary controls. However, these females tended to prolong the time required to obtain 10 days of eggs compared to control females ($F_{2,32} = 22.59$, $P < 0.001$; mean \pm SE: control 10.50 ± 0.22 day, conspecific 13.63 ± 0.43 , heterospecific 13.75 ± 0.41).

All predatory larva exposure treatments resulted in faster development for the VL larvae in conspecific and heterospecific interactions ($F_{2,115} = 6.48$, $P = 0.002$) when compared to solitary controls. Shorter total developmental times resulted ($F_{2,107} = 6.80$, $P = 0.002$), although there was no effect on incubation and pupation periods ($F_{2,119} = 0.25$, $P = 0.78$ and

$F_{2,107} = 0.75$, $P = 0.48$; Fig. 2). Immature survival of VL did not differ between competing conspecific and heterospecific larvae and solitary controls ($\chi^2 = 0.56$, $df = 2$, $P = 0.76$; survival percentiles: VL = 93.33%, VL + VL = 88.33%, VL + GL + ESL = 90.00%). Adult females that developed following exposure to chemical cues of conspecific and heterospecific larvae did not differ from those of solitary controls in 10-day fecundity ($F_{2,30} = 1.41$, $P = 0.26$) or egg viability ($F_{2,30} = 0.97$, $P = 0.39$). Further, the time required to collect 10 days of eggs was similar among treatments ($F_{2,30} = 0.15$, $P = 0.86$; mean \pm SE: control 12.27 ± 0.59 d, conspecific 12.20 ± 0.49 , heterospecific 12.60 ± 0.52).

Intraguild predator density-dependent, threat-sensitive prey responses

There was no effect of density-dependent nonconsumptive presence of heterospecific adults of ESL on the incubation

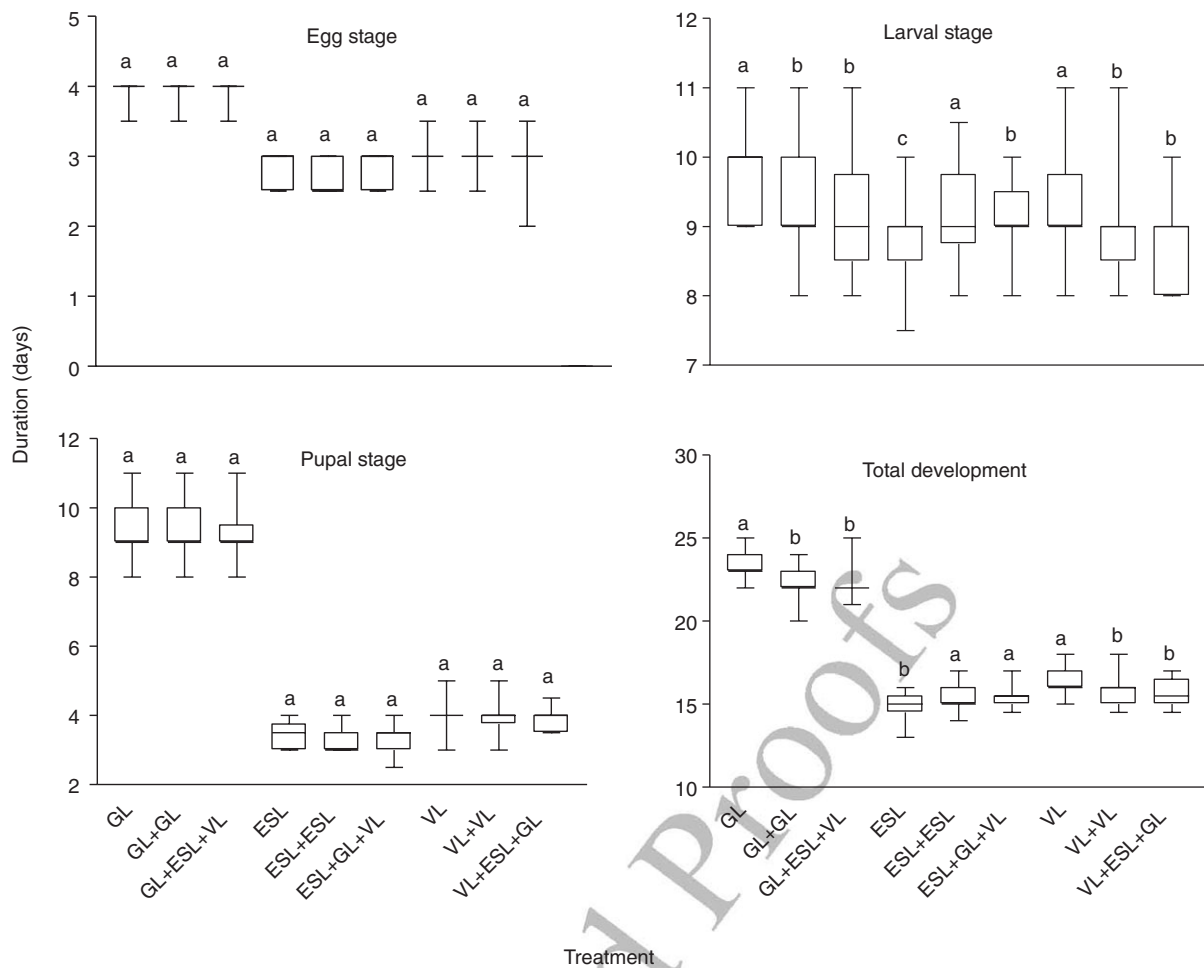


Fig. 2. Box-whisker plots of life-history parameters for green lacewing (GL), 11-spotted ladybeetle (ESL) and variegata ladybeetle (VL) individuals subjected to one of three scenarios, either solitary development, or development in contact with volatile cues from a conspecific or heterospecific larva in a partitioned Petri-dish. Thin black lines in the box = medians. Lower and upper limits of the box represent 25th and 75th percentiles, lower and upper whiskers denote 10th and 90th percentiles, where the lower and upper dots stand for 5th and 95th percentiles. Box-plots bearing the same letters are not significantly different (ANOVA followed by Bonferroni test, $\alpha = 0.05$) for each group of combinations.

period ($F_{3,259} = 0.12$, $P = 0.95$) of GL eggs. When heterospecific adult densities increased, development time of GL larvae increased ($F_{3,252} = 2.88$, $P = 0.04$) and the length of the pupal stage decreased ($F_{3,252} = 3.65$, $P = 0.01$) compared to solitary controls (Table 1). Exposure to cues from ESL did not affect the total developmental times relative to control treatment, as density of beetles increased ($F_{3,241} = 0.25$, $P = 0.86$). However, survival of GL individuals significantly decreased as density of heterospecifics increased ($\chi^2 = 9.55$, $df = 3$, $P = 0.02$). Pairwise comparisons revealed that there were only significant differences in progeny survival between 1 GL_L: 0 ESL_A and 1 GL_L: 3 ESL_A ($\chi^2 = 10.60$, $df = 1$, $P = 0.001$) and 1 GL_L: 1 ESL_A and 1 GL_L: 3 ESL_A ($\chi^2 = 5.79$, $df = 1$, $P = 0.02$; Table 1). The various ratios of GL larva (GL_L) to ESL adult (ESL_A) showed no difference in 10-day fecundity ($F_{3,36} = 1.75$, $P = 0.18$) or egg fertility ($F_{3,36} = 1.69$, $P = 0.19$; Fig. 4) of the adult GL produced (Fig. 4). The time required to obtain 10 clutches also did not differ between treatments ($F_{3,36} = 0.69$, $P = 0.56$; mean \pm SE: 1

GL_L: 0 ESL_A, 13.20 ± 0.95 day; 1 GL_L: 1 ESL_A, 12.67 ± 0.85 ; 1 GL_L: 2 ESL_A, 13.82 ± 0.81 ; 1 GL_L: 3 ESL_A, 14.20 ± 0.49).

There was no effect of density-dependent nonconsumptive presence of heterospecific adults of VL on the incubation period of GL eggs in all predator exposure treatments ($F_{3,239} = 0.69$, $P = 0.55$). All predator exposure treatments resulted in faster larval development of GL larvae when compared to solitary controls ($F_{3,230} = 5.43$, $P = 0.001$). Longer total developmental times occurred in solitary controls compared to exposure treatments ($F_{3,219} = 8.12$, $P < 0.001$), although there was no effect on the pupation period ($F_{3,219} = 1.39$, $P = 0.25$; Table 1). Progeny survival of GL was similar among treatments as density of the heterospecific ladybeetle increased ($\chi^2 = 0.57$, $df = 3$, $P = 0.90$). Pairwise comparisons also revealed that there were no differences in survival between any combinations of GL:VL densities (Table 1). When individual GL larvae (GL_L) were reared under the presence of different densities of VL adults (VL_A), no significant differences between treatments in the time

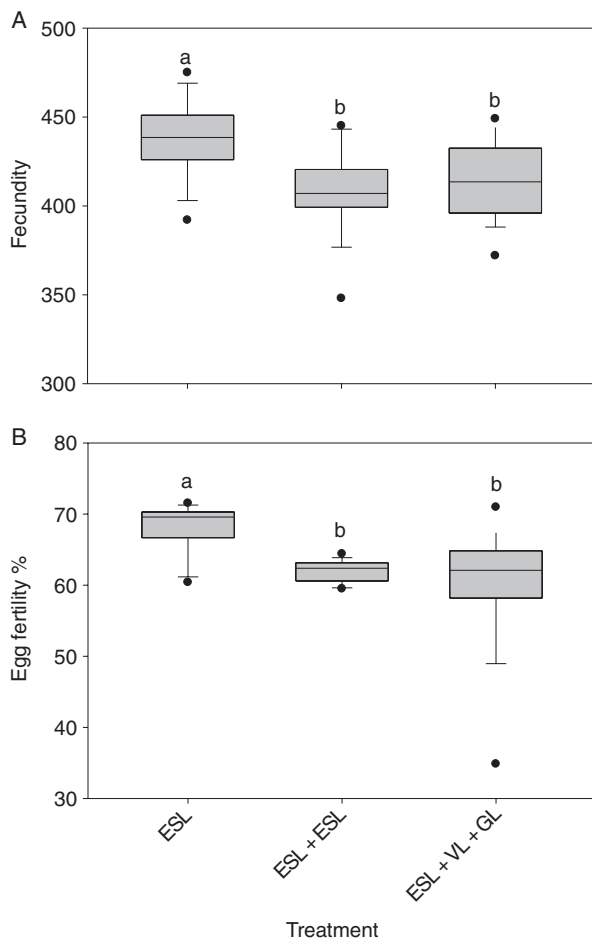


Fig. 3. Box-whisker plots of 10-day egg fecundities (A) and fertilities (B) for females of 11-spotted ladybeetle (ESL) that had developed either in the presence of volatile cues of conspecific (ESL) or heterospecific [green lacewing (GL) + variegata ladybeetle (VL)] larvae, or developed in isolation. Thin black lines in the box = medians. Lower and upper limits of the box represent 25th and 75th percentiles, lower and upper whiskers denote 10th and 90th percentiles, where the lower and upper dots stand for 5th and 95th percentiles. Stars above and below the lower and upper boundaries are outliers. Box-plots bearing the same letters are not significantly different (ANOVA followed by Bonferroni test, $\alpha = 0.05$).

required to obtain 10 clutches of eggs ($F_{3,45} = 1.61$, $P = 0.20$) when compared to solitary controls, were detected (mean \pm SE: 1 GL_L: 0 VL_A, 13.20 \pm 0.95 day; 1 GL_L: 1 VL_A, 12.92 \pm 0.47; 1 GL_L: 2 VL_A, 14.58 \pm 0.95; 1 GL_L: 3 VL_A, 14.64 \pm 0.75). However, there were significant differences between treatments in 10-day egg fecundity ($F_{3,44} = 2.92$, $P = 0.04$) and fertility of GL females ($F_{3,44} = 3.90$, $P = 0.02$; Fig. 5).

Discussion

Empirical data have confirmed the presence of intraspecific variation in age at time of reproductive maturity for individuals facing different predation risks. Theoretically, such variation can

occur by either physiological or behavioural responses (Noonburg & Nisbet, 2005). The accelerated development for the two aphid predators, GL and VL, in the presence of predation risk partially supports our first hypothesis. However, faster development did not increase the risk of immature mortality: thus, there was no *trade-off* in survival rates as a consequence of reduced age at maturity. Our results therefore are inconsistent with the 'physiological stress' of survivor life history (Noonburg & Nisbet, 2005; Hawlena & Schmitz, 2010), in which individuals delay development to mature at a larger size in order to reduce predation risks that are inversely correlated with body size. Although body weight was not measured in this study, it is possible that the shorter time of larval development may decrease the allocation of resources, and hence the size at maturity. Given this faster development, and that females are usually capable of converting all resources received into reproductive output, even a small additional foraging effort, would lead to a significant gain in their fecundity (Berger *et al.*, 2006). The faster development derived under predation stress responses can be explained as adaptive, in the sense of reducing the risk of immature mortality in response to the presence of competitors, but it is not consistent with the 'general stress paradigm' of predator-induced effects on prey phenotypes (Hawlena & Schmitz, 2010), because it did not occur at the expense of fecundity: thus, there was no *trade-off* in female reproductive performance as a consequence of reduced age at metamorphosis (Abrams & Rowe, 1996). Regarding trade-offs faced by an animal, one common hypothesis is that developing faster and being more fecund is often linked with increased risk of predation prior to maturation (Roff, 1992). However, our results are consistent with a 'behavioural response' in which, for a given food density, a higher foraging activity in the presence of competitors led to higher ingestion rate, and hence faster growth rate (Lima & Dill, 1990). Although the cost of predator-induced larval phenotypes may not be evident until after metamorphosis (Benard & Fordyce, 2003), the 10-day fecundities and egg viabilities of GL and VL exposed to NCEs, either from conspecific or heterospecific competitors, were virtually identical to those of solitary larvae. Our results demonstrate asymmetric IGP between GL or VL and other competitors because there was neither an increase in the larval mortality for either predator species in presence of other competing larvae, nor a decrease in reproduction of either predator species, despite a shorter period of development, suggesting that larval confrontations will not adversely affect GL and VL populations. Thus, given no apparent costs of the competitor-induced phenotype, in the absence of the risk for GL and VL, as is normally observed for most induced defences (Harvell, 1990), we infer that these aphid predators can potentially achieve higher reproductive fitness in the presence of predation risk than in its absence, despite faster growth – provided that they survive cannibalism or IGP interactions. However, there may be hidden costs that have not been quantified in this study such as the quality of offspring. In addition, because the experimental set-up prevented larvae from walking on surfaces previously occupied by conspecific or heterospecific potential predators, chemotactile cues were prevented. Several studies (e.g. Binz *et al.*, 2016) suggest that this type of cue can provide arthropods with information on predation risk. In the present

Table 1. Mean (\pm SE) development parameters for progeny of green lacewing (GL), as intraguild prey, under predation risk of various densities of intraguild predator

Treatment (Larva + adult density)	Development times									
	Egg stage		Larval stage		Pupal stage		Total development		Survival %	
	+ESL _A	+VL _A	+ESL _A	+VL _A	+ESL _A	+VL _A	+ESL _A	+VL _A	+ESL _A	+VL _A
1 GL _L + 0	3.93 \pm 0.02 a	3.93 \pm 0.02 a	9.71 \pm 0.10 b	9.75 \pm 0.09 a	9.39 \pm 0.08 a	9.36 \pm 0.07 a	23.04 \pm 0.13 a	23.05 \pm 0.09 a	91.67 a	90.00 a
1 GL _L + 1	3.94 \pm 0.02 a	3.89 \pm 0.03 a	9.79 \pm 0.13 b	9.35 \pm 0.08 b	9.15 \pm 0.08 ab	9.15 \pm 0.07 a	22.92 \pm 0.16 a	22.38 \pm 0.10 b	90.00 a	91.67 a
1 GL _L + 2	3.94 \pm 0.02 a	3.93 \pm 0.02 a	9.87 \pm 0.09 b	9.37 \pm 0.07 b	9.13 \pm 0.08 ab	9.28 \pm 0.06 a	22.96 \pm 0.13 a	22.57 \pm 0.09 b	85.00 a	93.33 a
1 GL _L + 3	3.92 \pm 0.02 a	3.94 \pm 0.02 a	10.17 \pm 0.12 a	9.43 \pm 0.08 b	9.02 \pm 0.08 b	9.35 \pm 0.07 a	23.08 \pm 0.15 a	22.67 \pm 0.09 b	73.33 b	90.00 a

Four treatments of intraguild prey - intraguild predator in which an individual green lacewing larva (GL_L) was separately reared in the presence of different densities of either 11-spotted ladybeetle adults (+ESL_A) or variegata ladybeetle adults (+VL_A) in a partitioned rearing unit.

Development time values bearing the same letters in a column are not-significantly different (ANOVA followed by Bonferroni test, $\alpha = 0.05$). Survival data bearing the same letters are not-significantly different (χ^2 test).

study it can be assumed that results were not influenced by such cues.

The developmental response of ESL to the presence of conspecific or heterospecific competitor cues supports our second hypothesis and appears consistent with the 'behavioral hypothesis' of survivor life history (Ball & Baker, 1996; Noonburg & Nisbet, 2005), but appears inconsistent with the 'physiological hypothesis' of survivor life history. Energy intake and mobility are reduced and individuals develop more slowly, typically emerging with lower fitness. The threat of competitors exerted various fitness costs on developing ESL larvae (slower development and lower reproductive performances) and these life-history changes cannot be construed as adaptive tactics for avoiding the predation stress (Ball & Baker, 1996). Thus, ESL appears more likely to be negatively affected by volatile cues of its competitors than both GL and VL. Generalist predators often develop on a wider range of prey, few of which would present the hazardous environment of an aphid colony (Michaud *et al.*, 2016), and thus we infer that ESL has no history of directional selection for adaptive developmental plasticity in response to the highly competitive environment of an aphid colony. In contrast to GL and VL, NCEs had greater impacts on reproductive performance of ESL females that developed under the predation risks of conspecific or heterospecific competitors, than those of solitary controls. Based on the development and reproductive costs incurred under predation risks, ESL appears to lose fitness in such conditions. An alternative explanation, however, is that the female is able to modify fertilization in response to perceived risk. Trophic egg provision is a recognized strategy adopted by females from a diverse range of species and parental care systems, where eggs (or egg-like structures) are produced for consumption by offspring (Perry & Roitberg, 2005). Here we have demonstrated that there is a significant drop in egg fertility for ESL when developed in the presence of other conspecifics or heterospecifics as compared to those reared in isolation. This could be explained by an adaptive increase in trophic egg production as a response to the perceived competition for resources.

The apparent difference in outcome for the three aphid predator species could be explained behaviourally according to, first, the innate behaviour of both types of predator species. GL and HV are more adapted to be cannibalistic species even at

satiety conditions (Noppe *et al.*, 2012; Aleosfoor *et al.*, 2014), whereas ESL is less cannibalistic and exhibits this behaviour particularly at food depletion situations (Aleosfoor *et al.*, 2014; Bayoumy & Michaud, 2015). Second, the differences in adaptive tactics for the three predator species may result in different outcomes. However, predation risk can have greater impacts on foraging behaviour than on growth or reproduction (Preisser & Bolnick, 2008), and such behavioural effects might not be detectable with food provided *ad libitum* in a confined space.

Density is a significant ecological factor in predator-prey and IGP systems that can diminish and increase a predator's ability to kill its prey (Obrycki *et al.*, 1998; Lucas & Rosenheim, 2011). Following confrontation with cues of other competitors, the density of the ESL adults (IG predator) did not alter overall development or reproduction of its IG prey, but did affect prey survival. In contrast, the density of VL adults affected the development and reproduction of IG prey in GL-VL confrontations, but not the survival of the IG prey. These findings support the idea that resource-poor environments for IG predators (i.e. inducing higher intraspecific competition) may be substantially worse for IG prey. In the systems investigated, the more IG predator adult VL and ESL in the partitioned Petri-dish, the higher the impact on development and survival of their IG prey, respectively. This implies that the cues released by VL, as IG predators, may encourage IG prey (i.e. GL) food consumption, resulting in faster development compared to solitary controls, similar to the higher leaf consumption and weight gain reported in crickets under risk of predation by spiders (Bucher *et al.*, 2014). However, the cues produced at higher density of ESL, as IG predator, perhaps inhibit larval feeding and thus increase their mortality. The inverse relationship of survival with density of IG predator, ESL, was obvious (i.e. thinning effects), whereby the lowest density of ESL and control treatment generated greater survival. The low survival at higher density of IG predator, in the 1 GL_L-3 ESL_A experimental combination, may be because higher concentrations of faecal cues, which have been shown to decrease conspecific feeding, were received from the IG predator, ESL (Grostal & Dicke, 1999). The confrontation between the similar-sized ladybirds and/or lacewing larvae often creates a low intensity of IGP even at low densities of extraguild, EG, prey (Lucas *et al.*, 1998; Obrycki *et al.*, 1998), but this is not the

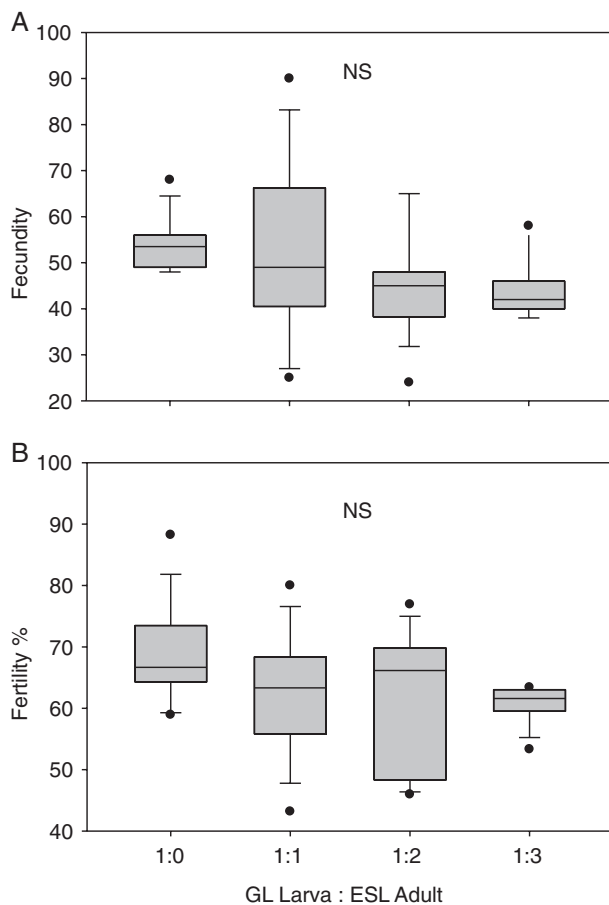


Fig. 4. Box-whisker plots of 10-day egg fecundities (A) and fertilities (B) when 10 clutches were collected from each green lacewing (GL) female that had developed and emerged under predation risk of various intraguild predator densities. Under these conditions, each individual GL larva was reared in the presence of 11-spotted ladybeetle (ESL) adults in a partitioned Petri-dish. Thin black lines in the box = medians. Lower and upper limits of the box represent 25th and 75th percentiles, lower and upper whiskers denote 10th and 90th percentiles, where the lower and upper dots stand for 5th and 95th percentiles. Stars above and below the lower and upper boundaries are outliers. Values were analysed by ANOVA and means separated by Bonferroni Test ($\alpha = 0.05$).

situation with different life stages, as observed. As IG predator, coccinellids usually have sublethal impacts on IG prey (Hoogenboom & Heimpel, 2004). Although both ESL and VL feed on a wide range of prey, the IGP outcomes and consequences may vary depending on the IG prey used and experimental environment (Noppe *et al.*, 2012).

Increasing the density of VL adults, as IG predator, in the same space of development for GL larva, as IG prey, yielded a phenotype with faster development and higher reproductive performance compared to that generated with ESL adults. This supports our third hypothesis. Benefits of IGP on *Neoseiulus cucumeris* (Oudemans), as IG prey, by the predatory mite *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae), as IG predator, have been demonstrated in terms of faster development and higher oviposition rate (Buitenhuis *et al.*, 2010). Given no

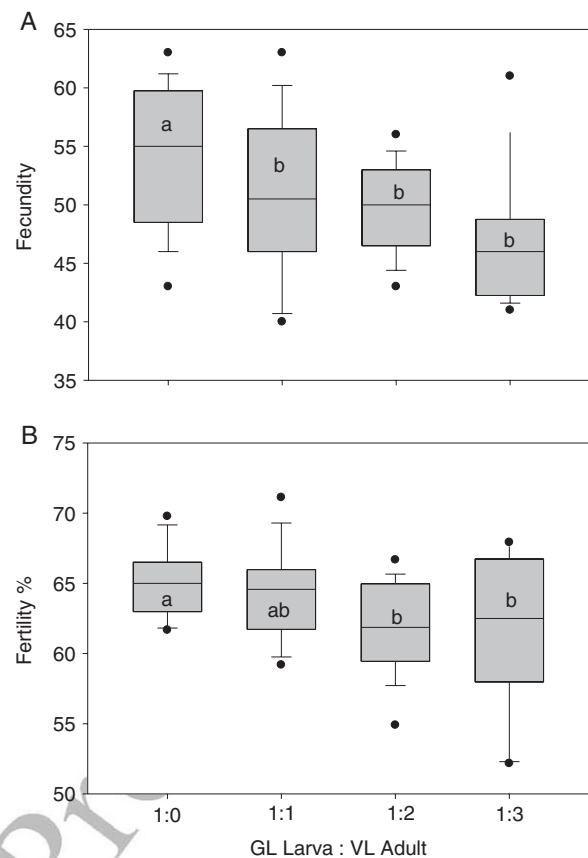


Fig. 5. Box-whisker plots of 10-day egg fecundities (A) and fertilities (B) when 10 clutches were collected from each green lacewing (GL) female that had developed and emerged under predation risk of various intraguild predator densities. Under such conditions, each individual GL larva was reared in the presence of variegated ladybeetle (VL) adults in a partitioned Petri-dish. Thin black lines in the box = medians. Lower and upper limits of the box represent 25th and 75th percentiles, lower and upper whiskers denote 10th and 90th percentiles where the lower and upper dots stand for 5th and 95th percentiles. Stars above and below the lower and upper boundaries are outliers. Box-plots bearing the same letters are not significantly different ANOVA followed by Bonferroni test, $\alpha = 0.05$.

apparent reproductive costs of the competitor-induced phenotype in the presence of risk for GL larvae, this aphid predator larva can potentially achieve higher fitness in the presence of volatile cues released by ESL adults than those of VL adults, particularly as adult density increases. Thus, the lower reproductive performance for female GL that developed in the presence of different densities of heterospecific IG predators, VL, is probably due to the lower allocation of resources, as a result of fear (i.e. 'physiological stress') during development. Soares & Serpa (2007) found that the presence of *H. axyridis* led to a decline in fecundity of ESL, even when the extraguild prey density was high. The IG prey could benefit from a release of IGP pressure if the new IG predator has a negative effect on another IG predator species that is an important predator of the IG prey. This has been proposed for ladybirds: the arrival of a second invasive

IG predator *H. axyridis* in North America may have released some indigenous IG prey (smaller ladybirds) from predation by a previous invader *Coccinella septempunctata* L. (Brown, 2003). There was therefore *trade-off* in reproductive rates of GL females as a consequence of faster development at metamorphosis, and thus this is consistent with the ‘general stress paradigm’ of predator-induced effects on prey phenotypes (Hawlena & Schmitz, 2010). Extending this reasoning to include conspecific and heterospecific larval–larval nonconsumptive interactions, the faster development of GL (IG prey) larvae, obtained under various stress density responses of VL adults, can be explained as adaptive in the sense of reducing the risk of immature mortality in response to the stress of the presence of VL competitors. This is consistent with the ‘physiological stress’ of survivor life history (Noonburg & Nisbet, 2005; Hawlena & Schmitz, 2010). The current study demonstrates that there were no reproductive costs for GL in their confrontations with similar-sized heterospecific larvae, but there were in those with different sizes of heterospecific VL (i.e. larvae/adults), even though there was a shorter development time in the latter case. IGP often is largely asymmetric and feeding events may occur both among (mutual predation) and within (cannibalism) species. This is because trophic level mainly increases with body size (Miller & Rudolf, 2011). It is clear that these interactions are complex and vary not only with the species involved in the interaction, but also with the life stage, available resources and structure of the environment. Further studies to investigate these complex interactions are needed in order to facilitate maximal beneficial impact of these important biocontrol insects.

Acknowledgments

We thank John J. Obrycki (University of Kentucky) for providing helpful comments that greatly improved the manuscript and M. M. Ramadan (Mansoura University) for maintaining the insect cultures.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Insect-rearing procedures, experimental arena design and further treatment details.

References

- Abd El-Aty, H.S. (2016) *Comparative studies of certain natural enemies associated with the cowpea aphid, Aphis craccivora Koch.* PhD thesis, Mansoura University, Egypt, 133 pp.
- Abrams, P.A. & Rowe, L. (1996) The effects of predation on the age and size of maturity of prey. *Evolution*, **50**, 1052–1106.
- Aleosfoor, M., Mortazavi, N. & Poorkashkooli, M. (2014) Comparison cannibalistic behaviour between two ladybirds, *Coccinella septempunctata* L. and *Hippodamia variegata* (Goeze) under laboratory experiments. *Munis Entomology & Zoology*, **9**, 645–650.
- Anderson, T.L. & Semlitsch, R.D. (2014) High intraguild predator density induces thinning effects on and increases temporal overlap with prey populations. *Population Ecology*, **56**, 265–273.

- Arim, M. & Marquet, P.A. (2004) Intraguild predation: a widespread interaction related to species biology. *Ecological Letter*, **7**, 557–564.
- Ball, S.L. & Baker, R.L. (1996) Predator-induced life history changes: antipredator behavior costs or facultative life history shifts? *Ecology*, **77**, 1116–1124.
- Bayoumy, M.H. & Michaud, J.P. (2012) Parasitism interacts with mutual interference to limit foraging efficiency in larvae of *Nephus includens* (Coleoptera: Coccinellidae). *Biological Control*, **62**, 120–126.
- Bayoumy, M.H. & Michaud, J.P. (2015) Cannibalism in two subtropical lady beetles (Coleoptera: Coccinellidae) as a function of density, life stage, and food supply. *Journal of Insect Behaviour*, **28**, 387–402.
- Bayoumy, M.H., Abou-Elnaga, A.M., Ghanim, A.A. & Mashhoot, G.A. (2016) Egg cannibalism potential benefits for adult reproductive performance and offspring fitness of *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae). *Egyptian Journal of Biological Pest Control*, **26**, 35–42.
- Benard, M.F. & Fordyce, J.A. (2003) Are induced defenses costly? Consequences of predator-induced defenses in western toads, *Bufo boreas*. *Ecology*, **84**, 68–78.
- Berger, D., Walters, R. & Gotthard, K. (2006) What keeps insects small? Size dependent predation on two species of butterfly larvae. *Evolutionary Ecology*, **20**, 575–589.
- Binz, H., Kraft, E.F., Entling, M.H. & Menzel, F. (2016) Behavioral response of a generalist predator to chemotactile cues of two taxonomically distinct prey species. *Chemoecology*, **26**, 153–162.
- Borer, E.T., Briggs, C.J., Murdoch, W.W. & Swarbrick, S.L. (2003) Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity? *Ecological Letter*, **6**, 929–935.
- Borges, I., Soares, A.O., Magro, A. & Hemptinne, J.-L. (2011) Prey availability in time and space is a driving force in life history evolution of predatory insects. *Evolutionary Ecology*, **25**, 1307–1319.
- Brown, M.W. (2003) Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl*, **48**, 141–153.
- Bucher, R., Binz, H., Menzel, F. & Entling, M.H. (2014) Spider cues stimulate feeding, weight gain and survival of crickets. *Ecological Entomology*, **39**, 667–673.
- Buitenhuis, R., Shipp, J.L. & Scott-Dupree, C. (2010) Intra-guild vs extra-guild prey: effect on predator fitness and preference of *Amblyseius swirskii* (Athias-Henriot) and *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae). *Bulletin of Entomological Research*, **100**, 167–173.
- Chacon, J.M. & Heimpel, G.E. (2010) Density-dependent intraguild predation of an aphid parasitoid. *Oecologia*, **164**, 213–220.
- Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194–201.
- Dixon, A.F.G. (1997) Patch quality and fitness in predatory ladybirds. *Ecological Studies*, **130**, 205–223.
- Frazer, B.D., Gilbert, N., Nealis, V. & Raworth, D.A. (1981) Control of aphid density by a complex of predators. *Canadian Entomologist*, **113**, 1035–1041.
- Grostal, P. & Dicke, M. (1999) Direct and indirect cues of predation risk influence behavior and reproduction of prey: a case for acarine interactions. *Behavioural Ecology*, **10**, 422–427.
- Harvell, C.D. (1990) The ecology and evolution of inducible defenses. *The Quarterly Review of Biology*, **65**, 323–324.
- Hawlena, D. & Schmitz, O.J. (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, **176**, 537–556.
- Hodek, I., Van Emden, H.F. & Honèk, A. (2012) *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Blackwell Publishing Ltd, Chichester, U.K.

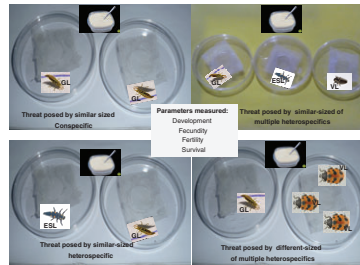
- Hoogendoorn, M. & Heimpel, G.E. (2004) Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomologia Experimentalis et Applicata*, **111**, 19–28.
- Janssen, A., Sabelis, M.W., Magalhães, S., Montserrat, M. & van der Hammen, T. (2007) Habitat structure affects intraguild predation. *Ecology*, **88**, 2713–2719.
- Lima, S. & Dill, L. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Lucas, É. & Rosenheim, J.A. (2011) Influence of extraguild prey density on intraguild predation by heteropteran predators: a review of the evidence and a case study. *Biological Control*, **59**, 61–67.
- Lucas, É., Coderre, D. & Brodeur, J. (1998) Intraguild predation among three aphid predators: characterization and influence of extra-guild prey density. *Ecology*, **79**, 1084–1092.
- McCauley, S.J., Rowe, L. & Fortin, M. (2011) The deadly effects of ‘nonlethal’ predators. *Ecology*, **92**, 2043–2048.
- Meisner, M.H., Harmon, J.P. & Ives, A.R. (2011) Response of coccinellid larvae to conspecific and heterospecific larval tracks: a mechanism that reduces cannibalism and intraguild predation. *Environmental Entomology*, **40**, 103–110.
- Michaud, J.P. & Grant, A.K. (2003) Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera: Coccinellidae) serve a defensive function? *Bulletin of Entomological Research*, **93**, 499–505.
- Michaud, J.P. & Qureshi, J.A. (2006) Reproductive diapause in *Hippodamia convergens* (Coleoptera: Coccinellidae) and its life history consequences. *Biological Control*, **39**, 193–200.
- Michaud, J.P., Barbosa, P.R.R., Bain, C.L. & Torres, J.B. (2016) Extending the “ecology of fear” beyond prey: reciprocal nonconsumptive effects among competing aphid predators. *Environmental Entomology*, **45**, 1398–1403.
- Miller, T.E.X. & Rudolf, V.H.W. (2011) Thinking inside the box: community-level consequences of stage-structured populations. *Trends in Ecology and Evolution*, **26**, 457–466.
- Moser, S.E. & Obyrcki, J.J. (2009) Competition and intraguild predation among three species of coccinellids (Coleoptera: Coccinellidae). *Annals of Entomological Society of America*, **102**, 419–425.
- Mylius, S.D., Klumpers, K., de Roos, A.M. & Persson, L. (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist*, **158**, 259–276.
- Nakaoka, M. (2000) Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology*, **81**, 1031–1045.
- Nóia, M., Borges, I. & Soares, A.O. (2008) Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of intra and extraguild prey densities. *Biological Control*, **46**, 140–146.
- Noonburg, E.G. & Nisbet, R.M. (2005) Behavioural and physiological responses to food availability and predation risk. *Evolutionary Ecology Research*, **7**, 89–104.
- Noppe, C., Michaud, J.P. & DeClerq, P. (2012) Intraguild predation between lady beetles and lacewings: outcomes and consequences vary with focal prey and arena of interaction. *Annals of Entomological Society of America*, **105**, 562–571.
- Obyrcki, J.J., Giles, K.L. & Ormord, A.M. (1998) Experimental assessment of interactions between larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in field cages. *Environmental Entomology*, **27**, 1280–1288.
- Ohgushi, T., Schmitz, O. & Holt, R.D. (2012) *Trait-Mediated Indirect Interactions*. Cambridge University Press, Cambridge, U.K.
- Papanikolaou, N.E., Demiris, N., Milonas, P.G., Preston, S. & Kypraios, T. (2016) Does mutual interference affect the feeding rate of aphidophagous coccinellids? A modeling perspective. *PLoS One*, **11**, e0146168.
- Perry, J.C. & Roitberg, B.D. (2005) Ladybird mothers mitigate offspring starvation risk by laying trophic eggs. *Behavioral Ecology and Sociobiology*, **58**, 578–586.
- Phoofolo, M.W. & Obyrcki, J.J. (1998) Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomologia Experimentalis et Applicata*, **89**, 47–55.
- Polis, G.A., Myers, C.A. & Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *The Annual Review of Ecology, Evolution, and Systematics*, **20**, 297–330.
- Preisser, E.L. & Bolnick, D.I. (2008) The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS One*, **3**, e2465.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.
- Rahman, T., Roff, M.N.M. & Ghani, I.B.A. (2010) Within-field distribution of *Aphis gossypii* and aphidophagous lady beetles in chili, *Capsicum annum*. *Entomologia Experimentalis et Applicata*, **137**, 211–219.
- Roff, D.A. (1992) *The Evolution of Life Histories: Theory and Analysis*. Chapman & Hall, New York, New York.
- Sato, S., Dixon, A.F.G. & Yasuda, H. (2003) Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. *Ecological Entomology*, **28**, 628–633.
- Schausberger, P. (2003) Cannibalism among phytoseiid mites: a review. *Experimental and Applied Acarology*, **29**, 173–191.
- Sih, A. (1986) Antipredator responses and the perception of danger by mosquito larvae. *Ecology*, **67**, 434–441.
- Sih, A., Englund, G. & Wooster, D. (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350–355.
- Soares, A. & Serpa, A. (2007) Interference competition between coccinellid beetle adults (Coleoptera: Coccinellidae): effects on growth and reproductive capacity. *Population Ecology*, **49**, 37–43.
- Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology*, **3**, 259–268.

Accepted 4 July 2018

Associate Editor: Dirk Mikolajewski

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of HTML only. It will not be published as part of main article.



Partitioned Petri-dishes permitting passage of signals were used to examine nonconsumptive effects between competing stages of similar- or different-sized, conspecifics or heterospecifics, on development, survival and reproduction of competing prey.

Coccinella undecimpunctata (ESL) larvae suffered developmental and reproductive costs under the presence of conspecific and heterospecific larvae, but not on their survival. But, *Chrysoperla carnea* (GL) and *Hippodamia variegata* (VL) larvae gained only developmental benefits.

Threat-sensitive prey responses appear to be species-specific. The phenotype of GL larva induced under VL adult stress was adaptive for development in aphid colonies, whereas that by ESL was not.