Bulletin of Entomological Research

cambridge.org/ber

Research Paper

Cite this article: Batista MC, Heimpel GE, Bulgarella M, Venzon M (2022). Diet breadth of the aphid predator *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae). *Bulletin of Entomological Research* **112**, 528–535. https://doi.org/10.1017/S0007485321001061

Received: 16 March 2021
Revised: 21 October 2021
Accepted: 22 November 2021
First published online: 8 March 2022

Keywords:
Biological control; generalist predator; phylogeny; prey range

Author for correspondence:
Michela C. Batista,
Email: michelabatista@professor.uema.br

Diet breadth of the aphid predator *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae)

Michela C. Batista[1,2], George E. Heimpel[3], Mariana Bulgarella[4] and Madelaine Venzon[5]

[1]Programa de Pós-Graduação em Agricultura e Ambiente, Universidade Estadual do Maranhão, Balsas, Brazil; [2]Departamento de Entomologia, Universidade Federal de Viçosa, Viçosa, Brazil; [3]Department of Entomology, University of Minnesota, St Paul, USA; [4]School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand and [5]Empresa de Pesquisa Agropecuária de Minas Gerais – EPAMIG, Viçosa, Brazil

Abstract

The performance (development and reproduction) of generalist predators can vary greatly among the prey species that they use, and these differences can influence the ability of predatory insects to suppress pest populations. The aim of this study was to compare the performance of larvae of the green lacewing *Chrysoperla rufilabris* (Burmeister, 1839) by offering 16 species of aphids and by assessing the effects of each species on the survival, larval development time, prey consumption, pupal mass and egg load of adult *Chr. rufilabris* females taking aphid phylogeny into account. *Chrysoperla rufilabris* larvae preyed on individuals from all 16 aphid species, but complete development, adult emergence and egg load production were achieved only in seven species. As a general pattern, the best levels of performance were achieved for an aphid clade that includes the soybean aphid, *Aphis glycines* (Matsumara, 1917), and for a milkweed-feeding species, *Myzocallis asclepiadis* (Monell, 1879). We found significant phylogenetic clustering for most of the performance traits indicating the aspects of specialization in the diet breadth of *Chr. rufilabris* despite the fact that this species is considered a generalist aphid predator. These findings can help us to understand the interactions of this species in agroecological food webs, where it is commonly found, and provide insights into why natural, conservation biological control or augmentative releases may succeed or fail.

Introduction

While arthropod generalist predators can be important biological control agents (Symondson *et al.*, 2002; Tscharntke *et al.*, 2007; Heimpel and Mills, 2017; Michalko *et al.*, 2019), the extent to which the consumption of different prey species impacts their performance (development and reproduction) can influence their ability to establish in cropping areas and suppress pest populations (Bilde and Toft, 2001; van Driesche *et al.*, 2008). Different prey species can vary in nutritional value, with the consumption of suboptimal prey species leading to impaired development and/or reduced reproduction of predatory individuals. Additionally, some prey species can exhibit behavioural or chemical defences, which may impair predator performance as well as limiting consumption (Rana *et al.*, 2002; Toft, 2005).

Specializing on a prey species (or on a prey type more generally) can be advantageous if the specialist predator is able to better utilize a prey species than a generalist predator would. This is a reflection of the classical trade-off between diet breadth and the efficiency of prey use (Asplen *et al.*, 2012) in which generalist predators need to balance the benefits of having a broad host range with potentially inferior per-prey suitability (Futuyma and Moreno, 1988; Rana *et al.*, 2002; Straub *et al.*, 2011; Forister *et al.*, 2012; Gordon and Weirauch, 2016). The term 'specialist' need not to apply only to monophagous predators (or parasitoids), however, and prey (or host) species that are more closely related to one another may have more similar suitable traits for a given predator species than prey species that are more distantly related, leading to oligophagy (or 'stenophagy') (Agrawal and Kotanen, 2003; Desneux *et al.*, 2012; Eklof and Stouffer, 2016; Brousseau *et al.*, 2018; Monticelli *et al.*, 2019; Heimpel *et al.*, 2021). Thus, the phylogeny of prey species may provide information on various aspects of predator–prey relationships, including predictions of possible food web interactions that may drive species distribution and ecological processes (Cavender-Bares *et al.*, 2009; Brousseau *et al.*, 2018).

The green lacewing *Chrysoperla rufilabris* Burmeister (1839) (Neuroptera: Chrysopidae) is a Nearctic predator that can be naturally found in various crops (Brooks, 1994). The larvae of this species prey on several species of soft-bodied pests, including eggs and nymphs/larvae from Hemiptera, Lepidoptera, Coleoptera, Thysanoptera and Acari, while adults feed on nectar, pollen and honeydew (Hydorn and Whitcomb, 1979; Woolfolk *et al.*, 2004). Despite this, *Chr. rufilabris* is known mainly as aphidophagous (Legaspi *et al.*, 1994; Albuquerque, 2009;

Table 1. Aphid species and host plants on which they were cultured, and number of replicates

Aphid species	Subfamily/tribe	Host plant	No. of replicates
Schizaphis graminum Rondani (1852)	Aphidinae/Aphidini	*Hordeum vulgare* L. (1753)	20
Rhopalosiphum padi L. (1758)		*H. vulgare*	20
Rhopalosiphum maidis Fitch (1856)		*H. vulgare*	25
Aphis monardae Oestlund (1887)		*Monarda fistulosa* L. (1753)	32
Aphis oestlundi Gillette (1927)		*Oenothera biennis* L. (1753)	35
Aphis gossypii Glover (1877)		*Gossypium hirsutum* L. (1753)	39
		Asclepias syriaca L. (1753)	30
Aphis glycines Matsumara (1917)		*Glycine max* (L.), Merr. (1917)	27
Aphis asclepiadis Fitch (1851)		*A. syriaca*	44
Aphis nerii Boyer de Fonscolombe (1841)		*Asclepias incarnata* L. (1753)	20
Aphis craccivora Kock (1854)		*Vicia fabae* L. (1753)	25
Aphis fabae Scopoli (1763)		*Rumex altissimus* Wood (1853)	17
Uroleucon obscuricaudatus Olive (1965)	Aphidinae/Macrosiphini	*Heliopsis helianthoides* (L.) Sw.(1827)	12
Uroleucon sonchii L. (1767)		*Sonchus* sp.	40
Sitobion avenae Fabricius (1775)		*H. vulgare*	15
Myzus persicae Sulzer (1776)		*R. altissimus*	17
Myzocallis asclepiadis Monell (1879)	Calaphidinae/Panaphidini	*A. syriaca*	37
Ephestia kuehniella Zeller (1879) eggs (control)	–	–	70

Control replicates included.

Dhandapani *et al.*, 2016), and it is commercialized as a biological control agent of aphids in North America and Europe (Tauber *et al.*, 2000; Pappas *et al.*, 2011; van Lenteren, 2012; Leppla *et al.*, 2018; Perring *et al.*, 2018). Although *Chr. rufilabris* is often described as a generalist aphid feeder, not much is known about the phylogenetic relations among species within its diet breadth, and most studies on *Chr. rufilabris* diet are restricted to a few aphid species (Legaspi *et al.*, 1994; Giles *et al.*, 2000; Chen and Liu, 2001). Usually, the diet breadth of so-called generalist species comprises distantly phylogenetically related prey/host species, while specialists tend to feed on closely related ones, and closely related species are presumed to share characters that can make them suitable for a given consumer (Futuyma and Moreno, 1988; Straub *et al.*, 2011; Desneux *et al.*, 2012, Gordon and Weirauch, 2016; Monticelli *et al.*, 2019; Heimpel *et al.*, 2021).

Our aim was to evaluate the diet breadth of *Chr. rufilabris* over 16 species of aphids and to assess the effects of each aphid species on the developmental time of larvae and the egg load of adult females. We also determined whether these traits are more similar for more closely related aphid species, and thus verified to what extend *Chr. rufilabris* is a generalist aphid predator, or if there is a trend towards oligophagy in this species.

Material and methods

Insect cultures

Chrysoperla rufilabris eggs were acquired from Beneficial Insectary Inc. (Redding, California, USA) in shipments that arrived every 15 days over the course of the study. Eggs were transferred to transparent plastic containers (5 cm height, 11 cm diameter) that contained layers of paper towel and monitored daily until hatch. Newly emerged larvae were kept individually in plastic vials (2.5 cm diameter, 7 cm height), provided with *Ephestia kuehniella* (Zeller, 1879) (Lepidoptera: Pyralidae) eggs, acquired from Beneficial Insectary Inc., *ad libitum* and kept in a growth chamber at 25°C, 60% relative humidity (RH) and 16:8 h light:dark (L:D), until reaching the second instar. Eggs of *E. kuehniella* are known to be an optimal food source for *Chrysoperla* spp. larvae (Tauber *et al.*, 2000; Pappas *et al.*, 2007). Second-instar larvae were used for the experiments because they exhibited higher survivorship than first-instar larvae (M.C.B., pers. obs.).

Sixteen aphid species (Hemiptera: Aphididae) (table 1) were tested as prey for *Chr. rufilabris* larvae. All aphid species were reared in plant growth chambers on their respective host plants at 25°C, 65% RH and 16:8 h L:D. These species were chosen to encompass a wide breadth of aphid taxonomy and contained species in two subfamilies – Aphidinae and Calaphidinae – including members of two aphidine tribes (Aphidini and Macrosiphini). To test the impact of host plant on prey suitability, we compared the survival and performance of *Chr. rufilabris* fed on the cotton aphid, *Aphis gossypii* (Glover, 1877) reared on two different host plant species, cotton (*Gossypium hirsutum* L., 1763) and milkweed (*Asclepias syriaca* L., 1753), the latter of which produces toxic cardenolides (Martel and Malcolm, 2004).

Experimental procedure

A plastic Petri dish (9 cm diameter) was lined with filter paper and a young leaf of the host plant was placed inside the dish with a wet cotton pad around its petiole to keep it turgid. This leaf was infested with *ad libitum* (about 300 individuals) 1st–4th instars of the appropriate aphid species as well as a single newly moulted second instar *Chr. rufilabris* larva that had been fed previously only on *E. kuehniella*. The Petri dish was then sealed with Parafilm (Bemis Company Inc., Wisconsin, USA) to maintain humidity and to prevent lacewing larvae or aphids from escaping. Each dish containing a single predator individual and multiple aphid individuals was considered the sampling unit for the experiment and replicated at least 12 times. Lacewing larvae were checked daily for survival and aphids were replenished every other day by adding a new infested leaf. Excess humidity inside the Petri dish was dried with a Kimwipe (Kimberly-Clark Corporation, Wisconsin, USA) if necessary, during daily evaluations. The Petri dish was cleaned and provided with fresh filter paper whenever necessary. Daily observations were made until *Chr. rufilabris* pupation.

The experiment was carried out in two groups of eight aphids. Every 10 days (the average time until pupation) a new group of eight aphid species was set up with two replicates per group. Aphid species for which more than 50% of larvae died before adulthood after 12 replicates were not used for further replicates. Additional replicates of the more suitable species were obtained until the emergence of ten females to obtain information on egg load (see below). Two control replicates in which 50 mg of frozen *E. kuehniella* eggs are a food source instead of aphids were established for each block of treatments.

Evaluations

Aphid consumption

We counted the number of aphids killed per *Chr. rufilabris* larva for a subsample of ten replicates of each aphid-species treatment. We observed larvae killing aphids in a preliminary trial to note the appearance of aphids consumed by *Chr. rufilabris* for each aphid species. These observations allowed us to recognize aphids that were preyed upon rather than dying of background mortality. Lacewing larvae feed by piercing the prey with both mandibles, injecting salivary secretions into the prey to liquefy the internal tissues, and then extracting the resulting fluid (Canard and Volkovich, 2001). This feeding process makes the attacked prey appear dry and shrivelled. Thus, dried and shrivelled aphids similar to the ones observed in the preliminary trial were considered attacked by *Chr. rufilabris*. Counting was carried out under a dissecting microscope (40× magnification, Leica Microsystems, Wetzlar, Germany) every 3 days until *Chr. rufilabris* pupation.

Survival, development time and pupal mass

Chrysoperla rufilabris larvae were checked daily for survival and the durations of three stages (second larval instar, third larval instar and pupa) were recorded. Additionally, pupae were removed from the Petri dish using a fine brush and weighed using an analytical scale (precision 0.1 mg). Only individuals that reached adulthood were considered for analysis of complete development (see below).

Egg load

In order to determine the effect of larval diet on the egg load of adult *Chr. rufilabris*, ten females that had been offered aphid species supporting at least 35% survivorship to adulthood were placed individually inside plastic vials (2.5 cm diameter, 7 cm height) upon eclosion. These females were provided honey (brushed on the side of the vial) and water (a piece of wet cotton placed in the bottom of the vial). Honey and water were replenished every other day and after 10 days, females were frozen and dissected to count the egg load. Mature eggs (fully yolked and chorionated oocytes) were green and of approximately the same size as deposited eggs, while immature eggs with yolk (yolked oocytes) were also green, but smaller. The sum of mature and immature eggs was used for statistical analyses.

Statistical analyses

The experiment took 225 days and so the data were separated into three blocks comprising 75 days each. The total aphid consumption was fitted using a Generalized Linear Mixed Model (GLMM) with Quasi-Poisson regression with block as a random variable. The effect of aphid species on the proportion of *Chr. rufilabris* reaching to adulthood was analysed using GLMMs with Binomial regression with block as a random variable (Crawley, 2013). To determine whether the effects of aphid species on lacewing survival were also influenced by aphid consumption, we regressed the per-aphid species survival rate on the average per-day aphid consumption rate using a linear model. Effects of aphid species on the number of days for the 2nd larval instar, 3rd larval instar, pupal stage and the sum of these times were analysed using separate GLMMs, with Poisson regression, with block as a random variable. We also assessed the effect of per-day aphid consumption on these times using linear models. The effect of aphid species on egg load of the adult lacewings (the sum or immature and mature eggs) was also fitted using a GLMM, with Quasi-Poisson regression with block as a random variable. We then performed separate regressions testing the effects of average per-day consumption rates and total development time on the egg load using linear models. Finally, the effect of aphid species on pupal mass was fitted using a linear model with Gaussian error distribution and experimental block included as a factor. We performed residue analyses to assess the appropriateness of models and error distributions for all analyses. Differences among treatments were compared via *a posteriori* contrast (Crawley, 2013). All statistical analyses were conducted in R (R Development Core Team, 2020).

Phylogenetic analyses

A phylogeny of the 16 aphid species assessed in the study was used to determine whether some of the experimental outcomes showed phylogenetic signal. The phylogeny used for these analyses was pruned from the one presented by Desneux *et al.* (2012), although branch lengths are not included in the analyses reported here. Experimental outcomes analysed for aphid phylogenetic signal were: (i) survivorship of *Chr. rufilabris* from the 2nd instar to the adult stage, (ii) number of aphids consumed by *Chr. rufilabris* larvae per day, (iii) the development time of *Chr. rufilabris* larvae and pupae combined, and (iv) the egg load of *Chr. rufilabris* females. Since not all aphid species contributed to all data sets, the number of aphid species analysed (and therefore the phylogeny) was not the same for all of these analyses. Thus, the test on survivorship and aphid consumption included all 16 aphid species, but the test on development time included 11 species and the test on egg load included only eight. Tests of phylogenetic signal were conducted using the 'multiPhylosignal' function module in the R package Picante. This procedure randomizes trait values across the tips of the phylogeny and calculates Blomberg *et al.*'s (2003) *K* statistic as an indicator of conservatism of traits (phylogenetic signal). We ran 10,000 randomizations for

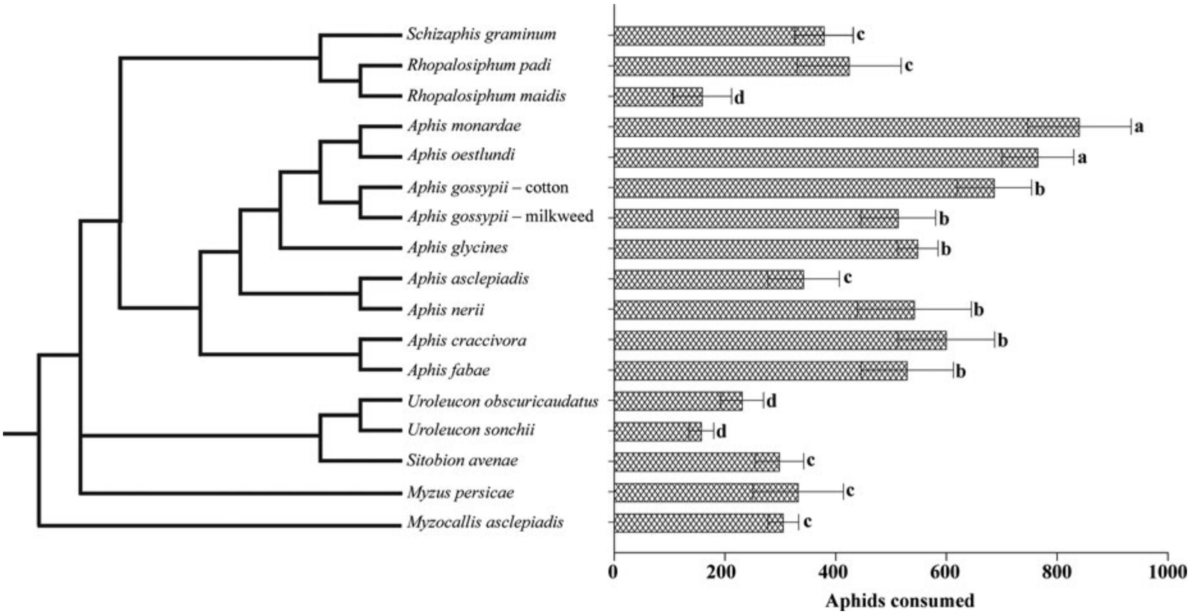

Figure 1. Mean number of total aphids consumed by *Chrysoperla rufilabris* larvae during the second and third instars. Means ± standard error are presented. Different letters indicate statistical differences among treatments (*a posteriori* contrasts $P < 0.05$). Phylogeny pruned from the one presented by Desneux *et al.* (2012).

each analysis. *Ephestia kuehniella* was not included in the phylogenetic analyses but it is presented in the figures to facilitate comparison.

Results

Aphid consumption and lacewing survival

All aphid species offered to *Chr. rufilabris* were accepted as prey, but the total number of aphids consumed differed significantly among species (fig. 1; $F_{16,155} = 164.058$, $P < 0.001$). The aphid species *Aphis monardae* (Oestlund, 1887) and *Aphis oestlundi* (Gillette, 1927) were consumed in highest numbers, followed by *A. gossypii* (both from cotton and milkweed), *Aphis glycines* (Matsumara, 1917), *Aphis nerii* (Boyer de Fonscolombe, 1841), *Aphis craccivora* (Kock, 1854) and *Aphis fabae* (Scopoli, 1763). Consumption of *Schizaphis graminum* (Rondani, 1852), *Rhopalosiphum padi* (L., 1758), *Aphis asclepiadis* (Fitch, 1851), *Sitobion avenae* (Fabricius, 1775), *Myzus persicae* (Sulzer, 1776) and *Myzocallis asclepiadis* (Monell, 1879) were intermediate while the lowest consumption was observed for *Rhopalosiphum maidis* (Fitch 1856), *Uroleucon obscuricaudatus* (Olive, 1965) and *Uroleucon sonchii* (L., 1767) (fig. 1). We detected significant phylogenetic clustering for aphid consumption ($K = 1.24$; $P < 0.001$). Measuring daily as opposed to lifetime aphid consumption provides almost identical results, with a highly significant linear regression of daily on lifetime consumption indicating across species ($F_1 = 7.05$, $P < 0.0001$, $r^2 = 0.87$) reflecting an overall average of 58.4 ± 6.7 (SEM) aphids consumed per day across species.

Developmental survival of *Chr. rufilabris* was significantly affected by the aphid species treatment ($X^2_{16,155} = 122.22$, $P < 0.0001$) with the highest survival achieved on the aphids *A. glycines*, *A. oestlundi*, *A. monardae* and *E. kuehniella* eggs (fig. 2). These three aphid species are closely related (fig. 2). *Rhopalosiphum padi*, *U. obscuricaudatus*, *Mzu. persicae*, *S. graminum*, *A. fabae* and *A. nerii* had the lowest survival proportion, with the three first species named above exhibiting larval survival rates of zero.

Larval-adult survival of the lacewings showed significant clustering on the aphid phylogeny ($K = 0.69$; $P < 0.001$; note that *E. kuehniella* was not included in the phylogenetic analysis but is included in fig. 2 and the contrast analysis to facilitate comparison).

There was a marginally significant positive effect of daily aphid consumption on *Chr. rufilabris* survival ($F_{1,15} = 4.53$, $P = 0.0504$, $r^2 = 0.232$, fig. 3)

Development time and pupal mass

Out of the 16 aphid species tested, only 11 allowed for the complete development of *Chr. rufilabris* from 2nd instar until adult emergence. There were no significant effects of aphid species on development times (2nd instar: $X^2_{12,232} = 5.104$, $P > 0.1$; 3rd instar: $X^2_{12,232} = 18.279$, $P > 0.1$; pupa: $X^2_{12,232} = 4.233$; $P > 0.1$; sum of all three stages: $X^2_{12,232} = 8.3716$; $P < 0.1$), and we could detect no significant effect of average daily aphid consumption on development times of any of the three stages ($P > 0.30$ for all analyses). Overall average development times were 3.33 ± 0.04 days for 2nd instar, 4.20 ± 0.06 days for 3rd instar, 11.89 ± 0.09 days for pupae and 19.42 ± 0.12 days for total development time. We also detected no significant phylogenetic signal of aphid development times of any of the three stages ($K = 0.45$, 0.65, 0.44 for 2nd instar, 3rd instar and pupa, respectively; $P > 0.2$ for all three).

Pupal mass of *Chr. rufilabris* did not differ significantly in association with aphid species consumed (mean = 10.48 ± 0.09 g, $F_{12,232} = 1.426$, $P > 0.1$) and no phylogenetic clustering was found for pupal mass ($K = 0.42$; $P > 0.05$).

Egg load

Total egg load (i.e. the sum of immature eggs with yolk and mature eggs) for emerged females was significantly affected by

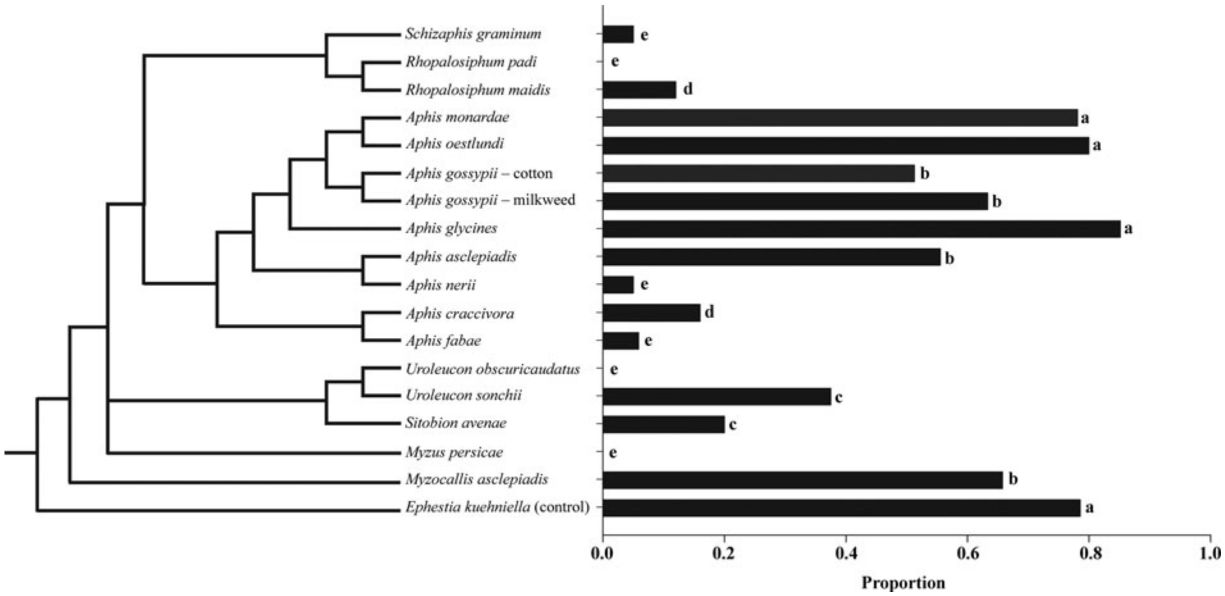

Figure 2. Proportion of individuals of *Chrysoperla rufilabris* larvae provided different aphid species which reached adulthood. Different letters indicate statistical differences among treatments (*a posteriori* contrasts $P < 0.05$). Phylogeny pruned from the one presented by Desneux *et al.* (2012). *Ephestia kuehniella* was not included in the phylogenetic analysis but it was included in the statistics and is presented in the figure to facilitate comparison.

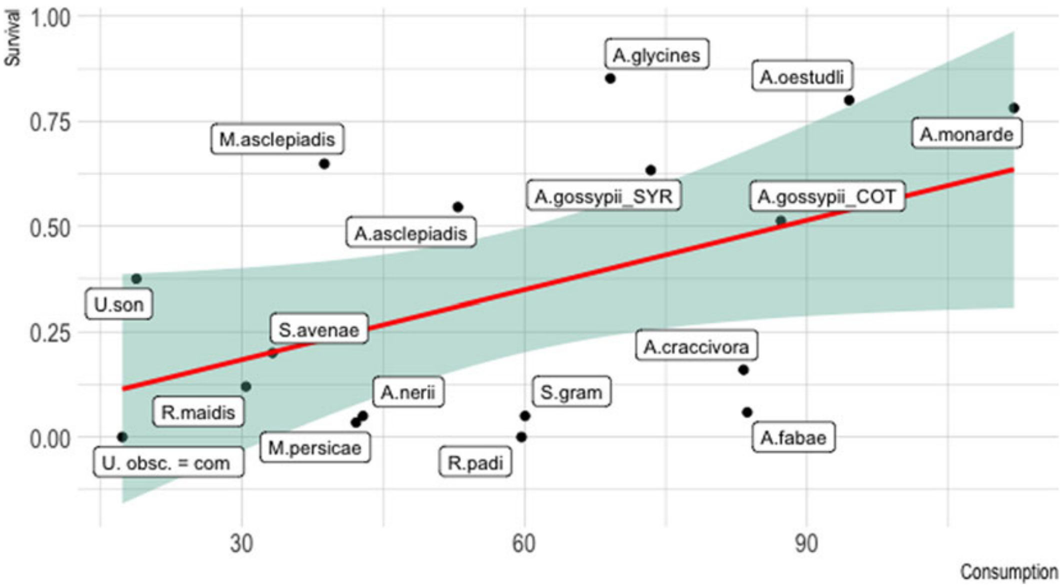

Figure 3. Linear regression of survival to adulthood of *Chrsysoperla rufilabris* on the number of aphids consumed for 16 species of aphids. See text for statistical details.

aphid species (fig. 4; $F_{8,95} = 8.556$, $P < 0.001$) but we detected no significant phylogenetic clustering *Chr. rufilabris* egg load-associated aphid species ($K = 0.43$; $P > 0.312$). The highest egg load was found for *Chr. rufilabris* females that had fed on *E. kuehniella* eggs as larvae and for *Chr. rufilabris* females that had fed on aphids as larvae, the soybean aphid, *A. glycines*, led to the highest egg loads while *A. oestlundi*, *A. gossypii*, *A. asclepiadis* and *U. sonchii* led to the lowest egg loads recorded (fig. 4). *Chrysoperla rufilabris* females that had fed on *A. monardae* as larvae produced no eggs. While we detected no significant effect of daily aphid consumption on *Chr. rufilabris* egg load ($F_{1,6} = 0.720$, $P = 0.429$), there was a significant negative effect of total development time on egg load ($F_{1,7} = 12.140$, $P = 0.010$; fig. 5).

Discussion

Although the green lacewing *Chr. rufilabris* is considered a generalist aphid predator and can indeed prey on a broad range of aphid species under laboratory conditions, our results demonstrate that the survival and performance of this species is limited by a relatively narrow aphid prey range. As a general pattern, the best survival rates and performance results were observed in

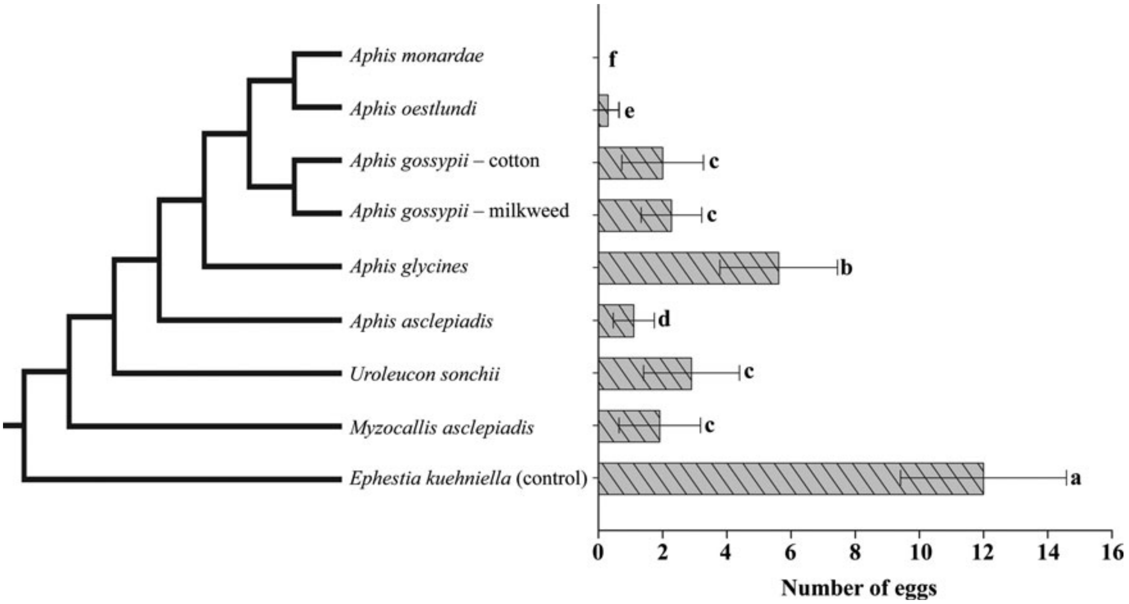

Figure 4. Mean number of eggs (the sum of yolked immature and mature eggs) counted in the ovaries of dissected females of *Chrysoperla rufilabris*. Mean ± standard errors are presented. Different letters indicate statistical differences among treatments (*a posteriori* contrasts $P < 0.05$). Phylogeny pruned from the one presented by Desneux *et al*. (2012). *Ephestia kuehniella* was not included in the phylogenetic analysis but it was included in the statistical analysis of egg load.

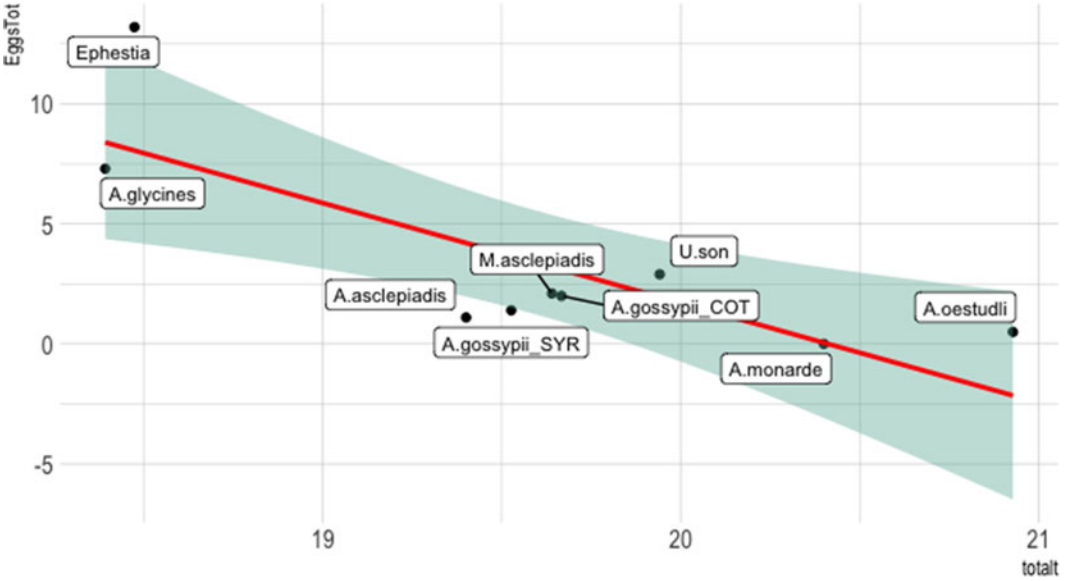

Figure 5. Linear regression of total egg load of *Chrsysoperla rufilabris* females (mature + immature eggs) on the total immature development time for eight species of aphids. See text for statistical details.

association with species in the genus *Aphis*, which is a narrower prey range than has been reported so far (Legaspi *et al.*, 1994; Cohen and Smith, 1998; Tauber *et al.*, 2000), but even within *Aphis*, there were strong and significant differences in performance.

Survival and consumption rates

The highest survival and consumption rates of *Chr. rufilabris* were achieved when larvae were fed on a clade within *Aphis* that includes the soybean aphid *A. glycines*, and the cotton aphid *A. gossypii*. Outside of this clade, feeding on the milkweed-feeding aphid *M. asclepiadis* also led to high survival rates. Chen and Liu (2001) found higher *Chr. rufilabris* survival and consumption rates for *A. gossypii* and *Mzu. persicae* than for *Lypaphis erysimi* (Kalt., 1843) (Hemiptera: Aphididae). In our study, except for *U. sonchii*, species that experienced lower consumption rates were also the ones associated with lower larval survival of *Chr. rufilabris*, such as *R. maidis* and *R. padi*. Surprisingly, some species that had been previously considered suitable prey species for *Chr. rufilabris* and other green lacewing species, such as *Mzu. persicae* and *R. padi* (Chen and Liu, 2001; Daane, 2001; Pappas *et al.*, 2007; Khuhro *et al.*, 2012) did not support high survival of *Chr. rufilabris* survival in our study. *Chrysoperla rufilabris* could not complete its development in five aphid species: *A. fabae*, *A. nerii*, *Mzu. persicae*, *R. padi* and *U. obscuricaudatus*. Both *A. fabae* and *A. nerii* are known to be inadequate for the development of other lacewing species, so failure to complete larval development was not unexpected (Daane, 2001; Pappas *et al.*, 2007). In fact, *A. fabae* and *R. padi* are considered a poor feeding resource to other aphid predators that have been termed 'generalists' such as coccinellid beetles (Rana *et al.*, 2002; Toft, 2005).

Some aphid species can sequester secondary metabolites from their host plants and thus affect the survival and development of their natural enemies (Helms *et al.*, 2004; Desneux *et al.*, 2009; Erb and Robert, 2016; Mohl *et al.*, 2020; Monticelli *et al.*, 2021). To test this possibility, we evaluated the performance of *Chr. rufilabris* larvae on *A. gossypii* reared in cotton and in milkweed; there were no significant differences between the two host plants for larval survival, total aphid consumption, developmental time or egg load. In fact, *Chr. rufilabris* exhibited high performance on three out of four aphid species reared on milkweed, cardenolide-producing plant species which may be sequestered by some herbivores, including some aphids (Helms *et al.*, 2004; Mooney *et al.*, 2008; Opitz and Müller, 2009). However, *Chr. rufilabris* performance was slightly worse when feeding on aphids reared on milkweed than when compared to when fed on *A. glycines*. Although some studies have demonstrated that *A. asclepiadis* and *A. gossypii* can concentrate plant allelochemicals in their bodies, such as cardenolides and terpenoids (Mooney *et al.*, 2008; Hagenbucher *et al.*, 2014), it seems that such chemicals do not interfere with the palatability or suitability of these species for *Chr. rufilabris*. Interestingly, for some herbivore species, secondary metabolite sequestration has a role in protecting immature stages from negative effects of host plant chemicals while offering no reduction in mortality caused by natural enemies (Poreddy *et al.*, 2015). Our study suggests such a pattern in the case of *A. gossypii*, *A. asclepiadis* and *M. asclepiadis*.

Larval development and egg load

The larval developmental times of *Chr. rufilabris* were not affected by aphid species consumed. Other studies on green lacewings, such as *Dichochrysa prasina* (Burmeister, 1839), have found that suitable prey species may increase the survival rates of these predators and promote a shorter preimaginal development compared to nutritionally poor prey species (Canard and Volkovich, 2001; Pappas *et al.*, 2007). Surprisingly, we found no such pattern in our study.

Finally, of all 16 aphid species tested, only seven could be assessed for egg load, based on their survival rates. Five of those species were in the genus *Aphis* and closely related to *A. glycines*, the species that provided for the highest egg load in *Chr. rufilabris*. It is worth mentioning though that female *Chr. rufilabris* that fed on *E. kuehniella* eggs as larvae presented the highest egg loads recorded in this study, indicating that food sources other than aphids can be highly nutritious.

Prey phylogeny and its implications

Information on prey phylogeny has been used in several studies as a tool to understand and predict predator–prey interactions and food webs for generalist predators in different ecosystems (Gordon and Weirauch, 2016; Goodheart *et al.*, 2017; Brousseau *et al.*, 2018). Including phylogeny in predator–prey studies can help, for instance, to understand how fitness cost in generalist species may be more related to taxonomic range than to the number of hosts/prey species avalilable (Straub *et al.*, 2011) or to predict possible food web interactions that may drive species distribution and ecological processes (Brousseau *et al.*, 2018).

Our significant results of phylogenetic signal for survival, aphid consumption and egg load with the clustering on the genus *Aphis* indicate that *Chr. rufilabris* have a more restricted diet than was previously assumed (Cohen and Smith, 1998; Legaspi *et al.*, 1994; Tauber *et al.*, 2000). Closely related species are presumed to share characters that can make them suitable for a given consumer, being an indication of a certain level of specialization. In fact, it is expected that specialists feed on closely related species, while generalists feed on more distantly related ones (Futuyma and Moreno, 1988; Bulgarella and Heimpel, 2015; Eklof and Stouffer, 2016; Brousseau *et al.*, 2018; Monticelli *et al.*, 2019; Abram *et al.*, 2021; Heimpel *et al.*, 2021).

Although *Chr. rufilabris* fed on all aphid species tested, development could not be completed on all of those species, which limits the extent to which a broad prey range can benefit this green lacewing species. Such a finding can be important to help understand the interaction of this species in agroecological food webs, where it is commonly found, and provides insights into why natural or conservation biological control may succeed or fail. For instance, although *Chr. rufilabris* may be present in a crop, it might not be able to prevent or suppress outbreaks of *S. avenae*, *S. graminum*, *R. maidis* or *A. craccivora*, even if farmers take measures to benefit *Chr. rufilabris* populations such as increasing vegetational diversity. From this standpoint, our findings are also relevant for planning the use of this green lacewing species in biological control programmes, especially those based on augmentative releases. Insectaries usually market *Chr. rufilabris* as biological control agents against aphids in general without regard to the species that may be present at the crop/home garden. As we demonstrate in this study, aphid consumption by *Chr. rufilabris* varies according to the aphid species and thus the success of releases will vary depending on the target species.

Acknowledgements. We thank Jonathan Dregni for help in rearing aphids, and the following organization for funding assistance: the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) in Brazil, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) in Brazil, Fundação de Amparo a Pequisa do Estado de Minas Gerais (FAPEMIG) in Brazil, and Minnesota Agricultural Experiment Station in the United States.

Conflict of interest. None.

References

Abram PK, Labbe RM and Mason PG (2021) Ranking the host range of biological control agents with quantitative metrics of taxonomic specificity. *Biological Control* **152**, 104427.

Agrawal AA and Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters* **6**, 712–715.

Albuquerque GS (2009) Crisopídeos (Neuroptera: Chrysopidae). In Panizzi RA and Parra JRP (eds), *Bioecologia e nutrição de insetos: base para o manejo integrado de pragas*. Brasília, BRA: Embrapa Informações Tecnológicas, pp. 969–1022.

Asplen MK, Bruns E, David AS, Denison RF, Epstein B, Kaiser MC, Lacroix C, Mohl EK, Quiram G, Prescott K, Stanton-Geddes J, Vincent JB, Wragg PD and May G (2012) Do trade-offs have explanatory power for the evolution of organismal interactions? *Evolution* **66**, 1297–1307.

Bilde T and Toft S (2001) The value of three cereal aphid species as food for a generalist predator. *Physiological Entomology* **26**, 58–68.

Blomberg SP, Garland Jr T and Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.

Brooks SJ (1994) A taxonomic review of the common green lacewing genus *Chrysoperla* (Neuroptera: Chrysopidae). Bulletin of the British Museum (Natural History). *Entomology* **63**, 137–210.

Brousseau PM, Gravel D and Handa TI (2018) Trait-matching and phylogeny as predictors of predator–prey interactions involving ground beetles. *Functional Ecology* **32**, 192–202.

Bulgarella M and Heimpel GE (2015) Host range and community structure of bird parasites in the genus *Philornis* (Diptera: Muscidae) on the Island of Trinidad. *Ecology and Evolution* **5**, 3695–3703.

Canard M and Volkovich TA (2001) Outlines of lacewing development. In Mcewen PK, New TR and Whittington AE (eds), *Lacewings in the Crop Environment*. New York: Cambridge University Press, pp. 130–154.

Cavender-Bares J, Kozak KH, Fine PVA and Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* **12**, 693–715.

Chen TY and Liu TX (2001) Relative consumption of three aphid species by the lacewing, *Chrysoperla rufilabris*, and effects on its development and survival. *BioControl* **46**, 481–491.

Cohen AC and Smith LK (1998) A new concept in artificial diets for *Chrysoperla rufilabris*: the efficacy of solid diets. *Biological Control* **13**, 49–54.

Crawley MJ (2013) *The R Book*, 2nd Edn. New York: John Wiley and Sons.

Daane KM (2001) Ecological studies of released lacewings in crops. In Mcewen PK, New TR and Whittington AE (eds), *Lacewings in the Crop Environment*. New York: Cambridge University Press, pp. 338–350.

Desneux N, Barta RJ, Hoelmer KA, Hopper KR and Heimpel GE (2009) Multifaceted determinants of host specificity in an aphid parasitoid. *Oecologia* **160**, 387–398.

Desneux N, Blahnik R, Delebecque CJ and Heimpel GE (2012) Host phylogeny and specialisation in parasitoids. *Ecology Letters* **15**, 453–460.

Dhandapani N, Pallavi S and Mishra G (2016) Chrysopids. In Omkar (ed.), *Ecofriendly Pest Management for Food Security*. San Diego, USA: Elsevier, pp. 331–327.

Eklof A and Stouffer DB (2016) The phylogenetic component of food web structure and intervality. *Theoretical Ecology* **9**, 107–115.

Erb M and Robert CAM (2016) Sequestration of plant secondary metabolites by insect herbivores: molecular mechanisms and ecological consequences. *Current Opinion in Insect Science* **14**, 8–11.

Forister ML, Dyer LA, Singer MS, Stireman JO and Lill JT (2012) Revisiting the evolution of ecological specialization, with emphasis on insect-plant interactions. *Ecology* **93**, 981–991.

Futuyma DJ and Moreno G (1988) The evolution of ecological specialization. *Annual Review of Ecology, Evolution and Systematics* **19**, 207–233.

Giles KL, Madden RD, Payton ME and Dillwith JW (2000) Survival and development of *Chrysoperla rufilabris* (Neuroptera: Chrysopidae) supplied with pea aphids (Homoptera: Aphididae) reared on alfalfa and faba bean. *Environmental Entomology* **29**, 304–311.

Goodheart JA, Bazinet AL, Valdés A, Collins AG and Cummings MP (2017) Prey preference follows phylogeny: evolutionary dietary patterns within the marine gastropod group Cladobranchia (Gastropoda: Heterobranchia: Nudibranchia). *BMC Evolutionary Biology* **17**, 221.

Gordon ERL and Weirauch CE (2016) Efficient capture of natural history data reveals prey conservatism of cryptic termite predators. *Molecular Phylogenetics and Evolution* **94**, 65–73.

Hagenbucher S, Wäckers FL and Romeis J (2014) Indirect multi-trophic interactions mediated by induced plant resistance: impact of caterpillar feeding on aphid parasitoids. *Biology Letters* **10**, 20130795.

Heimpel GE and Mills NJ (2017) *Biological Control: Ecology and Applications*. Cambridge, UK: Cambridge University Press.

Heimpel GE, Abram PK and Brodeur J (2021) A phylogenetic perspective on parasitoid host ranges with implications for biological control. *Current Opinion in Insect Science* **44**, 95–100.

Helms SE, Connelly SJ and Hunter MD (2004) Effects of variation among plant species on the interaction between a herbivore and its parasitoid. *Ecological Entomology* **29**, 44–51.

Hydorn S and Whitcomb WH (1979) Effects of larval diets on *Chrysopa rufilabris*. *Florida Entomologist* **62**, 293–298.

Khuhro N, Chen H, Zhang Y, Zhang L and Wang M (2012) Effect of different prey species on the life history parameters of *Chrysoperla sinica* (Neuroptera: Chrysopidae). *European Journal of Entomology* **109**, 175–180.

Legaspi JC, Carruthers RI and Nordlund DA (1994) Life history of *Chrysoperla rufilabris* (Neuroptera: Chrysopidae) provided sweetpotato whitefly *Bemisia tabaci* (Homoptera: Aleyrodidae) and other food. *Biological Control* **4**, 178–184.

Leppla NC, Johnson MW, Merritt JL and Zalom FG (2018) Applications and trends in commercial biological control for arthropod pests of tomato. In Wakil W, Brust GE and Perring TM (eds), *Sustainable Management of Arthropod Pests of Tomato*. Cambridge, USA: Academic Press, pp. 283–303.

Martel JW and Malcolm SB (2004) Density-dependent reduction and induction of milkweed cardenolides by a sucking insect herbivore. *Journal of Chemical Ecology* **30**, 545–561.

Michalko R, Pekár S and Entling MH (2019) An updated perspective on spiders as generalist predators in biological control. *Oecologia* **189**, 21–36.

Mohl EK, Stenoien CM and Heimpel GE (2020) The effects of host plant species on adult oviposition and larval performance of the aphid predator *Aphidoletes aphidimyza*. *Ecological Entomology* **45**, 606–616.

Monticelli LS, Le Thu Ha N, Amiens-Desneux E, Luo C, Lavoir A-V, Gatti J-L and Desneux N (2019) The preference-performance relationship as a means of classifying parasitoids according to their specialization degree. *Evolutionary Applications* **12**, 1626–1640.

Monticelli LS, Desneux N and Heimpel GE (2021) Parasitoid-mediated indirect interactions between unsuitable and suitable hosts generate apparent predation in microcosm and modeling studies. *Ecology and Evolution* **11**, 2449–2460.

Mooney KA, Jones P and Agrawal AA (2008) Coexisting congeners: demography, competition, and interactions with cardenolides for two milkweed-feeding aphids. *Oikos* **117**, 450–458.

Opitz SW and Müller C (2009) Plant chemistry and insect sequestration. *Chemoecology* **19**, 117–154.

Pappas ML, Broufas GD and Koveos DS (2007) Effects of various prey species on development, survival and reproduction of the predatory lacewing *Dichochrysa prasina* (Neuroptera: Chrysopidae). *Biological Control* **43**, 163–170.

Pappas ML, Broufas GD and Koveos DS (2011) Chrisopid predators and their role in biological control. *Journal of Entomology* **8**, 301–326.

Perring TM, Stansly PA, Liu TX, Smith HA and Andreason SA (2018) Whiteflies: biology, ecology, and management. In Wakil W, Brust GE and Perring TM (eds), *Sustainable Management of Arthropod Pests of Tomato*. Cambridge, USA: Academic Press, pp. 73–110.

Poreddy S, Mitra S, Schöttner M, Chandran J, Schneider B, Baldwin IT, Kumar P and Pandit SS (2015) Detoxification of hostplant's chemical defence rather than its anti-predator co-option drives [beta]-glucosidase-mediated lepidopteran counteradaptation. *Nature Communications* **6**, 8525.

R Development Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL https://www.R-project.org/.

Rana JS, Dixon AFG and Jarosik V (2002) Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology* **71**, 15–22.

Straub CS, Ives AR and Gratton C (2011) Evidence for a trade-off between host-range breadth and host-use efficiency in aphid parasitoids. *American Naturalist* **177**, 389–395.

Symondson WOC, Sunderland KD and Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Plant Science* **47**, 561–594.

Tauber MJ, Tauber CA, Daane KM and Hagen KS (2000) Commercialization of predators: recent lessons from green lacewings (Neuroptera: Chrysopidae: Chrysoperla). *American Entomologist* **46**, 26–38.

Toft S (2005) The quality of aphids as food for generalist predators: implications for natural control of aphids. *European Journal of Entomology* **102**, 371–383.

Tscharntke T, Bommarco R, Clough Y, Crist TO, Kleijn D, Rand TA, Tylianakis JM, van Nouhuys S and Vidal S (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control* **43**, 294–309.

van Driesche R, Hoddle M and Center T (2008) *Control of Pests and Weeds by Natural Enemies: An Introduction to Biological Control*. Victoria, AUS: Blackwell Publishing Ltd.

van Lenteren JC (2012) The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. *BioControl* **57**, 1–20.

Woolfolk SW, Cohen AC and Inglis GD (2004) Morphology of the alimentary canal of *Chrysoperla rufilabris* (Neuroptera: Chrysopidae) adults in relation to microbial symbionts. *Annals of the Entomological Society of America* **97**, 796–808.