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Ontogenetic change of prey preference in the generalist predator *Zelus renardii* and its influence on predator–predator interactions

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Abstract. 1. Two field experiments were conducted to test the hypothesis that the intensity of predation by a generalist predator on two species of prey changes with the developmental stage of the predator. The generalist predator studied was *Zelus renardii* Kolenati (Hemiptera: Reduviidae) and the prey were the lacewing larva, *Chrysoperla carnea* Stephens, and the cotton aphid, *Aphis gossypii* Glover.

2. *Zelus renardii* and lacewings feed on aphids, thereby acting as potential competitors. In addition, *Z. renardii* feeds on lacewings. Thus, *Z. renardii* is an intraguild predator of lacewings.

3. *Zelus renardii* exhibited changes in prey preferences across developmental stages. The older stages of *Z. renardii* exerted greater mortality on lacewings and fed on larger lacewing larvae than did the younger stages.

4. Lacewings suppressed aphid population growth strongly. In contrast, none of the stages of *Z. renardii* was an effective control agent of the cotton aphid.

5. The addition of *Z. renardii* frequently disrupted the effective control of aphids generated by lacewings. In one of the two replicates of the experiment, the disruption increased with the developmental stage of *Z. renardii*, paralleling the increase in lacewing mortality.

6. Although the developmental stage of *Z. renardii* can influence the prevalence of intraguild predation and the intensity of the disruption of the aphid biological control, these experiments have demonstrated that even the youngest instars of *Z. renardii* can cause substantial lacewing mortality and release aphid populations from regulation.

Key words. *Aphis gossypii*, biological control, *Chrysoperla carnea*, intraguild predation, Reduviidae.

Introduction

Empirical evidence supports the hypothesis that food webs in many natural ecosystems are very complex, making it difficult to define discrete trophic levels (Polis, 1991; Strong, 1992; Polis & Strong, 1996). In comparison to natural ecosystems, annual agro-ecosystems, which are usually monocultures, contain relatively few species. Thus, agricultural food webs may be less complex, and a few strong trophic links may dominate the population dynamics of constituent species.

Generalist predators are frequently the most diverse and abundant members of the arthropod natural enemy community of many annual agro-ecosystems (van den Bosch & Hagen, 1966; Ehler & van den Bosch, 1974; Ehler, 1977; Byerly *et al*., 1978; Ehler & Miller, 1978; Wilson & Gutierrez, 1980; Bisabri-Ershadi & Ehler, 1981; Sterling *et al*., 1989; Braman & Yeargan, 1990; Wiedenmann & O'Neil, 1990). Traditionally, biological control theory for generalist predators has been based on the simple three discrete trophic level model proposed by Hairston *et al*. (1960). Under this model, individuals occupying the third trophic level (the predators) consume only individuals of the next lower trophic level (the herbivores), allowing plant populations to increase. Recently, experimental field studies have suggested an alternative model for generalist predators in agro-ecosystems, in which predators not only consume herbivores but also other predators (reviewed in Rosenheim *et al*., 1995).

Generalist insect predators may feed on any arthropod they

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are able to subdue, regardless of the nature of the prey. In general, a polyphagous predator may consume species that belong to different trophic levels within a community, acting as a primary predator (i.e. consuming herbivores) and as a secondary predator (i.e. consuming primary predators) (Menge & Sutherland, 1976, 1987; Polis & McCormick, 1987; Warren & Lawton, 1987; Moore *et al*., 1988; Polis *et al*., 1989; Polis, 1991; Polis & Holt, 1992; Strong, 1992; Hall & Raffaelli, 1993). In food web theory, feeding on more than one trophic level within a community has been termed omnivory (Pimm, 1982). One form of omnivory is intraguild predation, in which two species that compete for the same prey (e.g. a herbivore) also engage in trophic interactions with each other (a predator–prey interaction) (Polis & McCormick, 1987; Polis *et al*., 1989; Polis & Holt, 1992; Wise, 1993). Acting as a secondary predator, an intraguild predator may cause trophic cascades by suppressing populations of primary predators and releasing herbivores from biological control. Hence, intraguild predation can play an important role in the organization of many communities (Werner & Gilliam, 1984; Sih *et al*., 1985; Polis *et al*., 1989; Rosenheim *et al*., 1993; Wissinger & McGrady, 1993). Intraguild predators may be less likely to initiate trophic cascades when their preference for the intraguild prey is low relative to their preference for the shared prey (Diehl, 1993).

Ontogenetic change of prey preference

Most organisms experience increases in body dimensions from birth or hatching to adulthood. Accompanying these ontogenetic changes in body size, many species will undergo extensive shifts in food and/or habitat use (Keast, 1977; Polis, 1984; Ebenman, 1987; Mittelbach *et al*., 1988; Wissinger, 1988; Muotka, 1990). With generalist predators, changes in prey preference may occur gradually as the organism grows or may occur as a sudden shift (e.g. at metamorphosis in holometabolous insects). Changes in prey preference associated with the age of the predator have been well documented among fish, reptiles and amphibians (Werner & Gilliam, 1984) and have also been reported among invertebrates, including arachnids (Turner, 1979; Polis, 1984; Hallas, 1988; Lubin *et al*., 1991; Rayor & Uetz, 1993) and insects (Fedorenko, 1975; Thompson, 1975; Johannsson, 1978; McArdle & Lawton, 1979; Lockwood, 1989; Rowe, 1992).

Natural communities of arthropods are often formed by populations that are highly size- or age-structured. It is widely recognized that the age of organisms can have a significant influence on species interactions and community structure in natural ecosystems (Wilbur, 1980; Polis, 1984, 1988; Werner & Gilliam, 1984; Polis & Strong, 1996). In agro-ecosystems, populations of generalist insect predators are also frequently formed by collections of immatures and adults (van den Bosch & Hagen, 1966; Ehler, 1977). In these systems, the age of the generalist predator may also be important in defining species interactions, including the prevalence of intraguild predation. However, field experiments examining the influence of the developmental stage of the predator on intraguild predation and the efficacy of biological control in agro-ecosystems have not been performed.

For this study, the generalist insect predator *Zelus renardii* Kolenati (Hemiptera: Reduviidae) was chosen. Direct observations in North American cotton fields have shown that adults of *Z. renardii* feed on a wide range of prey, including some herbivores but predominantly an array of beneficial arthropods (Whitcomb & Bell, 1964; van den Bosch & Hagan, 1966; Ables, 1978; Rosenheim & Cisneros, 1994, J. J. Cisneros & J. A. Rosenheim, unpublished observation). Field observations of nymphs of *Z. renardii* have shown, however, that they feed mostly on herbivores (Horton, 1918; J. J. Cisneros & J. A. Rosenheim, unpublished observation), suggesting that changes of prey preference associated with the developmental stage of this predator may occur. *Zelus renardii* has been found to be an important intraguild predator of larvae of the lacewing *Chrysoperla carnea* (Rosenheim *et al*., 1993). Lacewings are important biological control agents of a key pest in cotton, the cotton aphid *Aphis gossypii*. Field experiments have shown that adults of *Z. renardii* are capable of generating trophic cascades, disrupting the biological control of aphids generated by lacewings (Rosenheim *et al*., 1993; Rosenheim & Cisneros, 1994).

This study examines the changes in the impact of *Z. renardii* predation on lacewing larvae and aphid prey occurring across the developmental stages of *Z. renardii*. It addresses the three questions listed below. (i) Is there a change of prey preference associated with the developmental stage of *Z. renardii*? (ii) If a change in prey preference occurs, does *Z. renardii* developmental stage influence the prevalence of intraguild predation? (iii) Can *Z. renardii* developmental stage predict the intensity of the disruption of aphid population regulation?

Materials and Methods

Two manipulative field experiments were conducted in cotton fields in the San Joaquin Valley, California, U.S.A.

Experiment I

The experiment was carried out between 2 and 11 August 1994 at the University of California Cotton Research Centre, Shafter, California. *Gossypium hirsutum* cv. GC-510 was grown in rows separated by 102 cm without the use of any insecticides but otherwise following standard commercial practices. The crop was maturing fruit (small bolls) at the start of the experiment.

The experimental unit was the top five to seven nodes of individual plants harbouring natural aphid populations. Aphids and other economically important herbivores were counted. An index of the density of spider mites was obtained by estimating visually the percentage of each lower leaf surface covered by active mite colonies.

All resident natural enemies (predators and parasitoids) were removed from the plant by searching all plant structures carefully. It was not possible to remove the eggs of two predatory hemipterans, *Orius tristicolour* and *Nabis* spp., because they embed their eggs in plant tissues. The inspected portion of the plant was then caged in a tapered polyester mesh plant sleeve (height 58 cm, top width 19 cm, base width 50 cm; 'Fibe-Air Sleeve', Kleen Test Products). Bags were sealed with tape and staples and clipped shut at the base around the main stem of the plant.

Caged plants were assigned randomly to one of ten treatments, each replicated ten times. The treatments represent predatory lacewings and different developmental stages of *Z. renardii* tested singly and in combination. There was also a control treatment in which no predators were added. These treatments were:

1 aphids only;
2 aphids + a 'lacewing mix' (a combination of three lacewing eggs close to hatching, two young first-instar lacewing larvae [1–2 days old], and one mid first-instar lacewing larva [3–4 days old]);
3 aphids + six first-instar *Z. renardii* nymphs;
4 aphids + two third-instar *Z. renardii* nymphs;
5 aphids + one fifth-instar *Z. renardii* nymph;
6 aphids + one *Z. renardii* adult;
7 aphids + a lacewing mix + six first-instar *Z. renardii* nymphs;
8 aphids + a lacewing mix + two third-instar *Z. renardii* nymphs;
9 aphids + a lacewing mix + one fifth-instar *Z. renardii* nymph;
10 aphids + a lacewing mix + one *Z. renardii* adult.

The choice of densities of predators used in the experiment is explained below. *Zelus renardii* nymphs were obtained from a laboratory culture. Only the first-generation progeny from field-collected *Z. renardii* adults were used in the experiment. Nymphs were mass reared in large cages where they were separated by life stages to reduce the risk of cannibalism. They were fed on fruit flies, *Drosophila melanogaster*, and diluted honey. For the treatments that required *Z. renardii* adults, field-collected individuals were used (adults were hand collected or netted on the day that the experiment was set up).

Lacewing eggs and larvae were also obtained from a laboratory culture. Only the first generation progeny from field-collected adults were used for the experiment. Females were fed a mixture of yeast, whey, sugar and water. They laid their eggs on waxed paper, which was placed in cages and replaced daily. For the treatments that required lacewing eggs, pieces of waxed paper bearing eggs were pinned onto the leaves of recipient plants with insect pins. Only lacewing eggs that were going to hatch on the day that the experiment was set up were used. Lacewing larvae were reared individually to avoid cannibalism. They were fed on freeze-killed fifth-instar larvae of the moth *Phthorimaea operculella*.

Cages were left in the field for 10 days. This was enough time for the lacewing eggs to hatch and develop through most of the third (and final) instar and for the immature *Z. renardii* to moult to the next instar (except for the fifth instars, which were able to go through the 10 days of the experiment without moulting). After the 10-day period, each plant's main stem was cut, and the cage was brought to the laboratory for final scoring. Cages were opened, and all live herbivores and predators were counted. Lacewing larval cadavers were collected and their head capsule widths were measured using an ocular micrometer mounted on a dissecting microscope. Five replicates from the 'aphids only' treatment were excluded from analysis due to the presence of lacewing larvae inside the cages (lacewing eggs and/or larvae were probably missed during the removal of predators). A replicate from the treatment where a single fifth-instar *Z. renardii* was added was also excluded from analysis due to improper sealing of the cage (the predator escaped from the cage).

Experiment II

The second experiment was conducted to repeat the same treatments at a different time and location to assess the robustness of the results. All procedures were identical to those described for experiment I except as noted below. The second experiment was conducted from 29 August to 8 September 1994 in a 0.4-ha experimental planting at the Kearney Agricultural Centre near Parlier, California. Row spacing was 76 cm. Plants bore medium-sized bolls at the start of the experiment.

Each treatment had ten replicates, except the 'aphids only' treatment, which had fifteen replicates. During the course of the experiment, fifth-instar *Z. renardii* suffered high levels of mortality in both treatments where they were tested singly and in combination with lacewings. Similar mortality of fifth-instar nymphs was observed in laboratory cultures at the same time. The cause of the mortality was unclear. Because the mortality appeared to be unrelated to predator–prey interactions, treatments involving fifth-instar *Z. renardii* were excluded from all analyses. In addition, four replicates from other treatments were excluded from the analysis due to improper sealing (in all cases predators escaped from the cages).

Relationship between treatments and natural densities of predators

To compare the ecological roles of different developmental stages of *Z. renardii*, different numbers of immatures per cage were used (six first instars, two third instars, one fifth instar) to reflect the natural age distribution observed in the field. A census of the cotton plants ($n = 118$) was taken at Shafter from 1 August to 27 September 1994; mean densities observed were: 0.245 first–second instars, 0.084 third–fourth instars and 0.04 fifth-instar nymphs per plant, paralleling the 6 : 2 : 1 ratio closely. The absolute density of *Z. renardii* nymphs was lower in the field samples than in the experimental treatments. However, because *Z. renardii* lays eggs in masses (mean number of eggs per egg mass $= 42.6 \pm 6.3$ [SD]), and because the young nymphal instars disperse very slowly (J. J. Cisneros & J. A. Rosenheim, unpublished observation), *Z. renardii* nymphs are distributed very patchily. Plants that harboured at least a single first-instar nymph bore an average of 6.2 ± 5.2 (SD) nymphal *Z. renardii* (J. A. Rosenheim, unpublished observation). Thus, the absolute densities of predators used in the immature *Z. renardii* treatments were within the range of natural densities found on plants inhabited by *Z. renardii*. Densities of lacewing eggs often reach high levels ($>$ five eggs per plant) in mature cotton plantings (Rosenheim *et al.*, 1993).

Table 1. Experiment I. Densities of live herbivores and hemipteran predators in the ten experimental treatments. Shown are the means ± SE. *P*-values are reported for Kruskal–Wallis rank-sum tests; NS = $P > 0.05$; *** = $P < 0.001$. For full details of treatments, see Materials and Methods.

Treatment	*n*	Initial aphid densities	Final aphid densities	Initial % leaf area with mite colonies	Final % leaf area with mite colonies	*Orius tristicolour* nymph densities	% survival *Zelus renardii*
Aphids only	5	77.6 ± 5.8	402.6 ± 116.7	3.7 ± 1.4	4.7 ± 1.6	8.2 ± 2.7	–
Lacewings	10	72.4 ± 5.9	50.7 ± 24.2	5.9 ± 1.5	13.8 ± 3.8	4.6 ± 1.7	–
1st instar *Zelus*	10	72.3 ± 7.9	269.0 ± 64.2	12.3 ± 3.8	18.9 ± 4.6	7.3 ± 0.9	93.3 ± 3.6
3rd instar *Zelus*	10	65.2 ± 4.7	275.3 ± 58.6	8.2 ± 2.4	16.2 ± 5.0	9.2 ± 1.9	80.0 ± 8.1
5th instar *Zelus*	9	67.9 ± 6.1	288.8 ± 88.5	9.7 ± 3.8	16.3 ± 3.3	13.1 ± 5.8	88.8 ± 11.1
Adult *Zelus*	10	76.1 ± 6.8	339.4 ± 57.1	6.1 ± 1.6	11.7 ± 3.7	9.2 ± 2.9	100.0 ± 0.0
Lacewings + 1st instar *Zelus*	10	79.2 ± 7.9	152.2 ± 76.7	8.5 ± 1.9	8.1 ± 2.2	3.1 ± 0.8	88.3 ± 4.3
Lacewings + 3rd instar *Zelus*	10	67.4 ± 2.6	133.2 ± 37.4	8.1 ± 1.9	8.3 ± 2.4	9.0 ± 2.2	80.0 ± 11.1
Lacewings + 5th instar *Zelus*	10	75.3 ± 8.1	351.4 ± 131.5	8.7 ± 3.6	15.2 ± 3.5	10.4 ± 2.2	100.0 ± 0.0
Lacewings + Adult *Zelus*	10	74.7 ± 7.3	360.0 ± 95.0	5.1 ± 1.8	13.5 ± 4.4	7.7 ± 2.3	90.0 ± 10.0
P		NS	***	NS	NS	NS	NS

Statistical analyses

Kruskal–Wallis rank-sum tests were used to analyse lacewing survival and aphid population growth (expressed as per capita change in aphid population: [final aphid count – initial aphid count]/[initial aphid count]). Two-tailed Wilcoxon rank-sum tests were used for planned paired comparisons.

$\alpha = 0.05$ was allocated to each of two groups of treatment comparisons, and Bonferroni's inequality was used to provide a conservative adjustment of critical significance levels for multiple pairwise comparisons. The first group of tests compared single species of predators (*Z. renardii* and lacewings alone) with aphids alone. The second group of tests compared the effects of lacewings alone vs. combinations of *Z. renardii* and lacewings.

Two-way ANOVA was used to test for interactions between the action of lacewings and different life stages of *Z. renardii* on aphid population growth. Changes in aphid populations were transformed to ln (final number of aphids/initial number of aphids).

Spearman's rank correlation was used to test for trends in lacewing survival across the treatments where *Z. renardii* were included. To test the hypothesis that different instars of *Z. renardii* consumed different stages of lacewing larvae, trends in the size of head capsules of dead lacewings recovered from the *Z. renardii* + lacewings treatments were investigated. The percentages of cadavers recovered for experiments I and II were 26.3 and 32.7%, respectively.

Results

Experiment I

The mean initial number of aphids present per cage was similar across the ten treatments (Table 1; $\chi^2 = 5.7$, $P =$ NS), ranging from 65.2 ± 4.7 (SE) to 79.2 ± 7.9. Other arthropods were also present, including low densities of mites. Active mite colonies covered 7.8 ± 8.0 (SD)% of lower leaf surfaces at the beginning of the experiment. Other potential prey species observed (thrips, lepidopteran eggs and larvae, *Lygus* nymphs) were not abundant.

Lacewing survival

Lacewing survival differed across the five treatments to which lacewings were added (Fig. 1a; $\chi^2 = 16.04$, $P < 0.005$). Survival decreased from 0.35 ± 0.09 (SE) in the lacewings only treatment to:

0.15 ± 0.03 in the lacewings + first-instar *Z. renardii*
($\chi^2 = 1.9$, $P =$ NS),
0.07 ± 0.02 in the lacewings + third-instar *Z. renardii*
($\chi^2 = 4.6$, $P =$ NS),
0.017 ± 0.016 in the lacewings + fifth-instar *Z. renardii*
($\chi^2 = 7.9$, $P < 0.01$),
0.03 ± 0.02 in the lacewings + adult *Z. renardii*
($\chi^2 = 6.6$, $P = 0.01$).

Only the last two comparisons are significant (the critical *P*-value of 0.05 adjusted for four comparisons is 0.05/4 = 0.013; Bonferroni's inequality).

There was a significant trend of decreasing lacewing survivorship in the treatments with older life stages of *Z. renardii* (Fig. 1a; Spearman's rank correlation, $r = 0.448$, d.f. = 40, $P < 0.005$). The size of lacewing head capsules from the cadavers recovered at the end of the experiment tended to increase with the age of *Z. renardii* (Spearman's rank correlation, $r = 0.326$, d.f. = 60, $P < 0.02$). Thus, later developmental stages of *Z. renardii* tended to consume larger lacewing larvae. When the lacewing cadavers were sorted by instar (the three instars showed non-overlapping head capsule width distributions), the treatment with lacewings + first-instar *Z. renardii* did not show any third-instar lacewing cadavers (Fig. 1b).

Orius tristicolour nymphs were abundant in the cages at the end of the experiment, probably as a result of hatching from

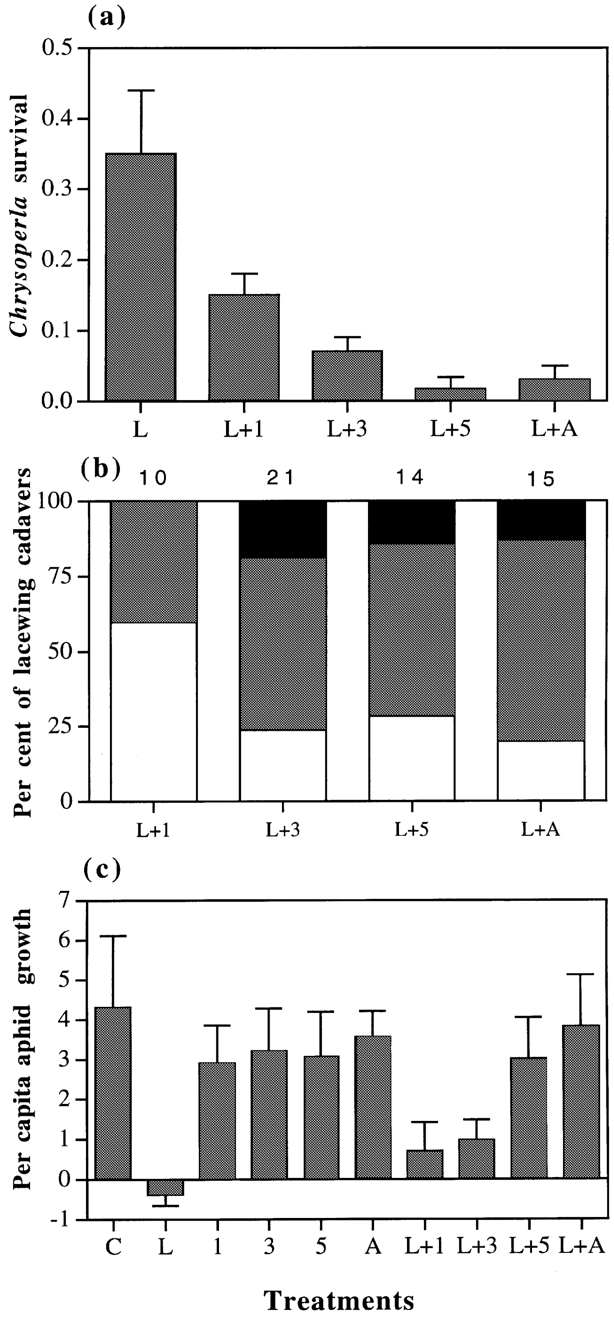

Fig. 1. Experiment I. (a) Mean (+ 1SE) proportion of *Chrysoperla carnea* survival. (b) Instar distribution of lacewing cadavers recovered from cages harbouring *Zelus renardii*. Numbers of cadavers recovered are indicated above each bar. White area, first instar; grey area, second instar; black area, third instar. (c) Mean (+ 1SE) per capita rate of aphid population growth. Treatments: C, aphids only (i.e. no predators); L, 'lacewing mix' (a combination of three lacewing eggs, two young first-instar lacewing larvae 1–2 days old, and one first-instar lacewing larva 3–4 days old); 1, six first-instar *Zelus* nymphs; 3, two third-instar *Zelus* nymphs; 5, one fifth-instar *Zelus* nymph; A, one *Zelus* adult; L + 1, lacewing mix plus six *Zelus* first instars; L + 3, lacewing mix plus two *Zelus* third instars; L + 5, lacewing mix plus a *Zelus* fifth instar; L + A, lacewing mix plus a *Zelus* adult.

eggs embedded in the plant (Table 1). Despite their abundance, *O. tristicolour* did not have a significant effect on lacewing survival (ANCOVA, $F_{1,44} = 0.057$, P = NS in which the dependent variable was the arcsin of percentage lacewing survival, the treatment was the main factor, and the number of *O. tristicolour* nymphs was the covariate).

Herbivore population growth

To examine the effect of predation on aphid population dynamics, the treatments were separated into two groups. The first group, comprising the first six treatments (Fig. 1c), was used to test the effects of single species of predators (either lacewings or the different life stages of *Z. renardii*) on aphid population growth. Lacewings were the only treatment that exerted suppression of aphid population growth ($\chi^2 = 7.9$, $P < 0.01$; critical P-value is 0.05/5 = 0.01). None of the treatments with *Z. renardii* alone had a significant effect on per capita aphid population growth: first instars ($\chi^2 = 0.4$, P = NS), third instars ($\chi^2 = 0.4$, P = NS), fifth instars ($\chi^2 = 0.2$, P = NS), and adults ($\chi^2 = 0.0$, P = NS).

The second group of treatments comprised lacewings alone and in combination with *Z. renardii* (Fig. 1c). These treatments allow quantification of the extent to which different developmental stages of *Z. renardii* disrupt the lacewing-generated biological control of aphids. Each treatment that combined *Z. renardii* and lacewings was compared with the treatment with lacewings alone. As in the first group of treatments, per capita aphid growth rates were compared using two-tailed Wilcoxon rank-sum tests. All the treatments where *Z. renardii and* lacewings were present together showed some degree of disruption of aphid control compared with the control generated by lacewings alone. This effect was not significant for first-instar *Z. renardii* ($\chi^2 = 2.06$, P = NS), nearly significant for third instar *Z. renardii* ($\chi^2 = 5.9$, $P = 0.015$) and significant for fifth instar ($\chi^2 = 8.7$, $P < 0.01$) and adult *Z. renardii* ($\chi^2 = 14.3$, $P < 0.001$; critical P-value is 0.05/4 = 0.013). The intensity of the disruption of aphid control increased with older stages of *Z. renardii* (Fig. 1c; Spearman's rank correlation, $r = 0.538$, d.f. = 40, $P < 0.001$).

To test whether lacewings and *Z. renardii* had an additive, independent effect on aphid control or whether significant interactions occurred between them, the treatments where predators were present singly and in combinations were grouped. Two-way ANOVA revealed non-significant interactions between lacewings and first-instar *Z. renardii* ($F_{1,34} = 2.6$, P = NS) and between lacewings and third instar *Z. renardii* ($F_{1,34} = 3.2$, P = NS). Highly significant interactions were found between lacewings and fifth instar *Z. renardii* ($F_{1,33} = 8.9$, $P < 0.01$) and between lacewings and adult *Z. renardii* ($F_{1,34} = 9.9$, $P < 0.005$).

Mite population growth was analysed by calculating the relative change in the percentage of the lower leaf surface covered with active mite colonies ([final percentage – initial percentage]/[initial percentage]). Mite populations grew slowly across the experiment (active mite colonies covered 13.0 ± 11.7 [SD]% of lower leaf surfaces at the end of the experiment). There were no

Table 2. Experiment II. Densities of live herbivores and hemipteran predators in the eight experimental treatments. Shown are the means ± SE. *P*-values are reported for Kruskal–Wallis rank-sum tests; NS = $P > 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. For full details of treatments, see Materials and Methods.

Treatment	*n*	Initial aphid densities	Final aphid densities	*Orius tristicolour* nymph densities	% survivors *Zelus renardii*
Aphids only	15	77.7 ± 4.2	188.4 ± 34.1	5.4 ± 0.8	–
Lacewings	9	79.2 ± 3.0	7.8 ± 5.8	1.4 ± 0.5	–
1st instar *Zelus*	9	85.2 ± 4.7	194.1 ± 41.6	1.6 ± 0.6	85.1 ± 4.3
3rd instar *Zelus*	9	68.6 ± 4.3	144.4 ± 36.8	5.2 ± 1.1	88.9 ± 7.3
Adult *Zelus*	10	76.0 ± 2.8	123.0 ± 25.6	6.6 ± 1.1	90.0 ± 10.0
Lacewings + 1st instar *Zelus*	10	86.1 ± 3.2	98.4 ± 52.2	2.9 ± 0.7	78.3 ± 5.6
Lacewings + 3rd instar *Zelus*	10	65.4 ± 3.6	39.2 ± 8.9	2.5 ± 1.1	80.0 ± 8.2
Lacewings + Adult *Zelus*	9	70.3 ± 3.0	63.6 ± 18.0	3.7 ± 2.6	88.9 ± 11.1
P		**	***	***	NS

significant differences among the treatments (Table 1; $\chi^2 = 8.3$, $P =$ NS), suggesting that the lacewing larvae and the different life stages of *Z. renardii*, alone and in combination, had minimal influences on mite population dynamics, at least in the presence of aphid populations.

Experiment II

The mean number of aphids present per cage at the beginning of the experiment varied significantly across treatments (Table 2; $\chi^2 = 20.5$, $P < 0.01$), ranging from 65.4 ± 3.6 (SE) to 86.1 ± 4.4. This was an accidental variation, because treatments were assigned randomly to plants. However, this variation in initial aphid densities across treatments did not affect the outcome of the experiment as demonstrated below. Other potential prey species (mites, thrips, Lepidoptera eggs and larvae, *Lygus* nymphs) were almost absent.

Lacewing survival

As in experiment I, the survival of lacewings varied across the four treatments in which lacewing larvae were added (Fig. 2a; $\chi^2 = 24.5$, $P < 0.001$). Lacewing survival decreased from 0.24 ± 0.04 (SE) in the lacewings only treatment to:
0.08 ± 0.02 in the lacewings + first-instar *Z. renardii*
($\chi^2 = 7.6$, $P < 0.01$),
0.016 ± 0.016 in the lacewings + third-instar *Z. renardii*
($\chi^2 = 13.9$, $P < 0.001$),
0.0 in the lacewings + adult *Z. renardii*
($\chi^2 = 15.2$, $P < 0.001$).
All the comparisons were significant (critical *P*-value is 0.05/3 = 0.017). The initial aphid densities did not have a significant effect on lacewing survival (ANCOVA, $F_{1,33} = 3.6$, $P =$ NS, in which the dependent variable was the arcsin percentage lacewing survival, the main factor was the treatment, and the covariate was the initial aphid density).

Lacewing survival decreased in treatments with older life stages of *Z. renardii* (Fig. 2a; Spearman's rank correlation, $r = 0.501$, d.f. = 29, $P < 0.01$). The size of lacewing larval head capsules from cadavers recovered at the end of the experiment increased with the age of *Z. renardii* (Spearman's rank correlation, $r = 0.408$, d.f. = 55, $P < 0.005$). When the lacewing larval cadavers were sorted by instar, no third-instar lacewing larval cadaver was found in the lacewings + first-instar *Z. renardii* treatment (Fig. 2b). As in the first experiment, first-instar *Z. renardii* killed primarily first-instar lacewings, whereas adult *Z. renardii* killed primarily second-instar lacewings.

Even though *Orius* nymphs were not manipulated experimentally, there were significant differences in their final densities among treatments (Table 2; $\chi^2 = 29.1$, $P < 0.001$). However, they did not have a significant effect on the lacewing survival among the treatments (ANCOVA, $F_{1,33} = 0.9$, $P =$ NS, in which the dependent variable was the arcsin percentage lacewing survival, the main factor was the treatment, and the covariate was the number of *Orius* nymphs).

Herbivore population growth

The eight treatments were separated into two groups as in the analysis of experiment I. The first group considered the first five treatments (Fig. 2c). The lacewings-only treatment produced a large decrease in aphid populations compared with the aphids-only treatment ($\chi^2 = 15.2$, $P < 0.001$; critical *P*-value is 0.05/4 = 0.013), driving the aphid population close to extinction (the aphid population decreased on average by 91.3%). The other three treatments where *Z. renardii* were present alone had little effect on per capita aphid population growth (first instars, $\chi^2 = 0.04$, $P =$ NS; third instars, $\chi^2 = 0.2$, $P =$ NS; and adults, $\chi^2 = 3.2$, $P =$ NS).

The second group included the treatments in which lacewings were combined with *Z. renardii* (Fig. 2c). All *Z. renardii* developmental stages produced a significant disruption of the aphid control generated by lacewings alone (for first-instar *Z. renardii*, $\chi^2 = 9.6$, $P < 0.005$; third-instar *Z. renardii*, $\chi^2 = 9.6$, $P < 0.005$; and for adult *Z. renardii*, $\chi^2 = 0.017$, $P < 0.001$; critical *P*-value is 0.05/3 = 0.017). Two-way ANOVA revealed significant interactions between lacewings and first-instar *Z. renardii* ($F_{1,42} = 14.6$, $P < 0.001$), lacewings and third-instar

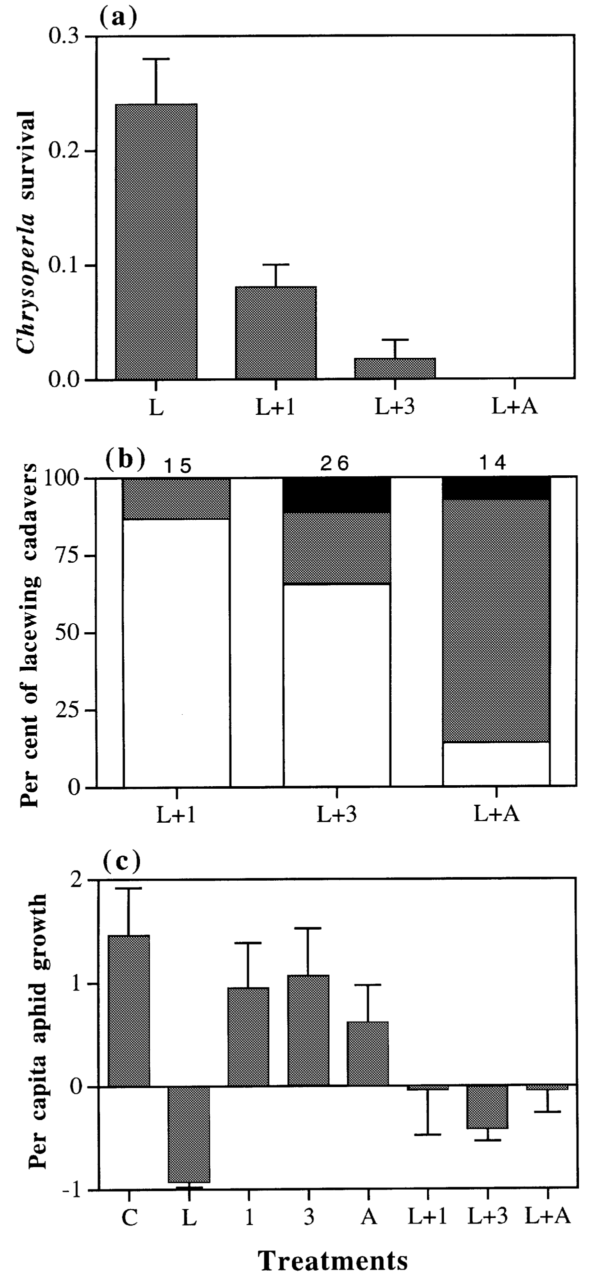

Fig. 2. Experiment II. (a) Mean (+ 1SE) proportion of *Chrysoperla carnea* survival. (b) Instar distribution of lacewing cadavers recovered from cages harbouring *Zelus renardii*. Numbers of cadavers recovered are indicated above each bar. White area, first instar; grey area, second instar; black area, third instar. (c) Mean (+ 1SE) per capita rate of aphid population growth. Treatment abbreviations (each replicated ten to fifteen times) as in Fig. 1.

Z. renardii ($F_{1,42} = 18.6$, $P < 0.001$), and lacewings and adult *Z. renardii* ($F_{1,42} = 24.2$, $P < 0.001$).

Neither the final *Orius* nymph density nor the initial number of aphids had a significant effect on per capita aphid growth after controlling for treatment effects (ANCOVA, $F_{1,72} = 0.03$, $P =$ NS; and $F_{1,72} = 1.3$, $P =$ NS, respectively).

Discussion

The experiments support two primary conclusions. First, adding *Zelus renardii* into a community comprised of lacewings and aphids can increase the rate of aphid population growth, through negative interactions between predators. Thus, this study supports theoretical predictions for increased equilibrium of a shared prey following the introduction of an intraguild predator (Polis & Holt, 1992), and corroborates the experimental results obtained by Rosenheim *et al.* (1993). Second, *Z. renardii* has shown not only a change in prey preference associated with its developmental stage but also an intensification of the intraguild predation on lacewings. In both replicates of the experiment, older stages of *Z. renardii* not only preyed on larger *Chrysoperla* larvae but also exerted higher overall mortality. This result is consistent with studies of other predatory species in which mean prey size increased with body size of the predator (Hespenheide, 1973; McArdle & Lawton, 1979; Rathet & Hurd, 1983; Werner & Gilliam, 1984). No third-instar lacewing larval cadavers were recovered from the treatments in which first-instar *Z. renardii* were added (Figs 1b, 2b). It may be that the young instars of *Z. renardii* (first and second instars) are unable to subdue third-instar *Chrysoperla* larvae; therefore, the window of vulnerability of lacewings to predation by *Z. renardii* may have been shorter in the lacewings + first-instar *Z. renardii* treatment. Lacewing survival was consistently highest in the treatment with first-instar *Z. renardii*.

The increase in lacewing mortality in the presence of *Z. renardii* can be inferred to be a result of predation rather than enhanced competition, because the availability of aphid prey was higher in the treatments where *Z. renardii* were present. *Zelus renardii* alone were unable to regulate aphid populations, and by preying on many lacewings actually relaxed the overall intensity of competition for prey.

Lacewing survivorship in the lacewings-only treatment was relatively low in both replicates of the experiment (35% and 24% in experiments I and II, respectively, Figs 1a and 2a). Two factors that may have contributed to this low survivorship are starvation and cannibalism. Despite the low availability of prey at the end of the experiment, starvation may not be the main cause of the high lacewing mortality. J. A. Rosenheim and D. D. Limburg (unpublished observation) found that lacewing larvae were able to survive for ⊤ 2 weeks (longer than the total duration of the experiments reported here) by consuming nectar from extrafloral nectaries present on the lower surfaces of cotton leaves. Duelli (1981) and Bar & Gerling (1985) have demonstrated that the probability of cannibalism in *C. carnea* is increased when encounters occur between larvae of different ages and under conditions of limited heterospecific prey availability. The experiments reported here were initiated with lacewings of different ages (i.e. three lacewing eggs close to hatching, two 1–2-day-old lacewing larvae and one 3–4-day-old lacewing larva) and, in the lacewings-only treatment, eventually led to conditions of limited prey availability. In addition, encounters between lacewing larvae may have been increased by the cage confinement. Thus, cannibalism may have been an important factor in the low lacewing survival.

Cannibalism may also have occurred in the treatments where

Z. renardii were added, despite the abundance of prey in these treatments at the end of the experiment. However, cannibalism cannot explain by itself the elevated lacewing mortality in these treatments compared with the lacewings-only treatment. On the contrary, lacewing cannibalism may have been reduced in the treatments where *Z. renardii* were present. The lacewing mortality exerted by *Z. renardii* reduced the number of competing lacewings, potentially reducing the probability of an encounter between cannibalistic larvae.

Tests of the effect of *Z. renardii* developmental stage on the likelihood of disrupting the regulation of aphid populations produced by lacewings showed inconsistent results. While experiment I suggested that the intensity of the disruption increased with older *Z. renardii*, in experiment II there was no obvious trend. Variation in these results may be related to variation in aphid population growth rates. Wilhoit & Rosenheim (1993) showed that variation in aphid population growth rates can be attributed to a polyphenism in *A. gossypii* that is associated with major effects on fecundity and developmental rates. Aphid populations in the aphids-only treatment grew much more rapidly in experiment I, with per capita growth rates of 4.3 ± 1.8 (SE) (Fig. 1c), compared with experiment II, where per capita growth rates were 1.5 ± 0.5 (Fig. 2c). Lacewing larvae that were eaten at a later stage of development (e.g. in treatments with older stages of *Z. renardii*) could have consumed a substantial number of aphids before being killed. It appears that only when aphid populations were growing rapidly (in experiment I) were the surviving aphids capable of rebuilding high densities of aphids before the end of the 10-day experiment.

The present study supports the need to develop ecological theory for generalist predators in agro-ecosystems that is more flexible than the three discrete trophic level model proposed by Hairston *et al*. (1960). General analytical models of predators exhibiting intraguild predation (Rosenzweig, 1966; Levins, 1979; Polis *et al*., 1989; Polis & Holt, 1992), as well as empirically based simulation models have been developed (reviewed in Rosenheim *et al*., 1995). The present study has demonstrated that the age of a generalist predator (e.g. the intraguild predator) can influence the prevalence of intraguild predation. Thus, predator age is an important factor that should be taken into consideration when developing new models.

In this study, an attempt was made to minimize the extent to which the arthropod community in the cages differed from the natural community (i.e. all herbivore populations naturally present in the field were used with natural densities of predators). However, the limitations of the experiments are recognized (e.g. their short duration, and the possibility that the cage may have imposed restrictions on the natural foraging behaviour of the predators or prey). Future work will include direct observations of predators foraging freely in the field to identify factors that influence prey selection for different developmental stages of *Z. renardii*.

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