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Influence of extraguild prey density on intraguild predation by heteropteran predators: A review of the evidence and a case study

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ABSTRACT

Heteropteran predators constitute an important component of predatory guilds in terrestrial and aquatic ecosystems. Most heteropteran species have generalist diets, and intraguild predation has been documented in most heteropteran families. Zoophytophagous species also frequently engage in intraguild interactions. An increase in extraguild prey density is often predicted to reduce intraguild predation between guild members by providing abundant alternate prey. However, an increase of extraguild prey density may also be associated with an increase in the density of intraguild predators, which could instead strengthen intraguild predation. Evaluating the combined effect of these potentially opposing influences on intraguild predation is difficult. Most studies have been carried out in the laboratory, using artificially simplified communities of predators and prey and employing spatial and temporal scales that may not reflect field conditions. We review experimental studies examining how extraguild prey density influences the intensity of intraguild predation and then report an observational case study examining the influence of extraguild prey density on the intensity of intraguild predation at larger spatial and temporal scales in unmanipulated cotton fields. Fields with more abundant extraguild prey (aphids, mites) were not associated with elevated densities of intraguild predators, and were strongly associated with increased survival of intraguild prey (lacewing larvae). In this system, the ability of extraguild prey to relax the intensity of intraguild predation, as previously documented in small-scale field experiments, also extends to the larger spatial and temporal scales of commercial agriculture.

1. Intraguild predation in the Heteroptera

The present paper deals with intraguild predation (predation on a competitor, Polis et al., 1989) involving the true bugs (Hemiptera: Heteroptera) as intraguild predators, focusing mainly on terrestrial species. The Heteroptera suborder includes terrestrial predators in the infraorder Cimicomorpha (mainly Reduviidae, Miridae, Nabidae, and Anthocoridae) and the infraorder Pentatomorpha (Pentatomidae, Geocoridae, . . .), aquatic predators in the Nepomorpha (Belostomatidae, Nepidae, Corixidae, Notonectidae, . . .) and finally surface dwelling predators in the Gerromorpha (Gerridae, Veliidae, . . .) (Triplehorn and Johnson, 2004). There is an array of different heteropteran species with different habitats, morphologies, sizes, mobility, and feeding habits. Among these, many species may be involved as predators in an intraspecific (cannibalism), intraguild, or extraguild (classical predation) predation event.

Intraguild predation (henceforth "IGP") by heteropteran predators is widespread (Rosenheim et al., 1995; Schmidt et al., 1998; Arim and Marquet, 2004). Among predatory species, numerous studies have reported IGP and cannibalistic events involving terrestrial (Rosenheim et al., 1993; Wheeler, 2001), surface (Spence and Carcamo, 1991) and aquatic organisms (Miller, 1971; Dolling, 1991). Most aquatic heteropterans are generalist predators and select their prey more according to their size than to the guild to which they belong (see Hall et al., 1970); as a consequence, they may frequently be involved in IGP. In terrestrial systems, the Heteroptera includes a great number of generalist predators, which by definition constitute potential (and suspected) intraguild predators. Finally, some extremely generalist heteropteran predators, called zoophytophagous consumers (or true omnivores), may even exploit and develop on both plant and animal tissues. Formally, when these predators consume an herbivore they are engaging in IGP, since both the pest and the predator exploit the plant as a shared resource (However, this definition is not used in the present document). These predators may also compete with their extraguild prey for high-quality sites on the plant (Coll and Izraylevich, 1997). Their broad diet often includes some intraguild prey (i.e., their competitors; Lucas and Alomar, 2001, 2002a,b; McGregor and Gillespie, 2005; Provost et al., 2006; Fréchette et al., 2007).

Finally, according to the tremendous variability (in size, development stage, and mobility) of the different insect species belonging to

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the same predator guilds as heteropteran predators, IGP opportunities may be common. Eggs, younger (and smaller) instars, and molting individuals are especially susceptible to predation.

In terrestrial food webs, heteropteran predators may consume a diverse array of intraguild prey, including other predators (coccinellids, syrphids, neuropteran and dipteran predators, other heteropteran predators, ...), parasitoids (especially when consuming herbivores harboring developing parasitoid immatures), pathogens (when consuming infected hosts), and ants (Rosenheim et al., 1995; Kester and Jackson, 1996; Schmidt et al., 1998). IGP by heteropterans has been reported involving species in the families Geocoridae (Guillebeau and All, 1989, 1990; Wheeler, 2001; Rosenheim, 2005), Anthocoridae (Fauvel et al., 1975; Gillespie and Quiring, 1992; Cloutier and Johnson, 1993; Coll and Izraylevich, 1997; Erbilgin et al., 2004), Berytidae (Kester and Jackson, 1996), Miridae (Wheeler, 2001; Fréchette et al., 2007; Lucas et al., 2009), Nabidae (Whitcomb and Bell, 1964; Atim and Graham, 1984; Rosenheim et al., 1993, 1999), Reduviidae (Miller, 1971; Rosenheim et al., 1993, 1999) and Pentatomidae (Mallampalli et al., 2002; De Clercq et al., 2003; Herrick et al., 2008).

In aquatic-surface food webs, heteropteran intraguild predators include at least members of the families Nepidae, Notonectidae, (Dolling, 1991), and Gerridae (Spence and Carcamo, 1991).

2. Theoretical effects of an increase of extraguild prey density on IGP

One of the key factors influencing the direction, symmetry and magnitude of IGP is the quantity and quality of extraguild prey that are available. At first sight, an increase in the density of extraguild prey might be expected to decrease the magnitude of IGP, simply by increasing the satiation of the predators. In this case, the extraguild prey essentially dilutes the effect of the IG predator on the IG prey. Of course, the situation in nature may be more complex, and may involve species other than just the three species that make up the intraguild predation community module (the extraguild prey, intraguild prey, and intraguild predator). Any change of population density within the trophic web may generate an array of direct and indirect effects on different members of the web, including either vertical effects (top-down or bottom-up) or more complex effects.

The whole system typically includes (1) the first trophic level, (2) the extraguild prey – the second trophic level, (3) both the intraguild predator and prey – the third trophic level, and (4) higher order natural enemies, the fourth trophic level (Rosenheim, 1998). Considering a classical terrestrial arthropod food web, the first trophic level is the plant. When extraguild prey density increases, more herbivores (extraguild prey, the second trophic level) attack the plant, which may elicit the expression of induced defences. The production of defensive compounds can have detrimental effects on the extraguild prey, and, when sequestered by herbivores, detrimental effects may also be extended to higher trophic levels (Rogers and Sullivan, 1986). Detrimental effects may reduce the nutritional value of the extraguild prey, and could theoretically increase their vulnerability to predators. On the other hand, sequestration of defensive compounds may reduce the susceptibility of herbivores to predators. Furthermore, zoophytophagous heteropteran IG predators involved in direct consumption of plant material could be affected by plant defensive mechanisms. Any reduction in host plant quality or availability of suitable feeding sites due to herbivory could increase competition (and IGP) between herbivores and omnivorous IG predators. Also, the integrity of the plant substrate may influence the oviposition decisions of those heteropterans that lay their eggs directly in plant tissues.

An increase in the density of herbivores (extraguild prey) may generate an increase of intraspecific and interspecific competition, and possibly cannibalism. Consequently, extraguild prey may also modify their behavior by exploiting the plant differently, for example by colonizing less productive plants or less productive microsites on the plant. The distribution of the extraguild prey may change from a contagious pattern to a regular pattern. Extraguild prey will also, most of the time, increase the efficiency of their colonial defences (dilution, encounter, and selfish herd effects) (Turchin and Kareiva, 1989; Lucas and Brodeur, 2001). These changes could affect the foraging efficiency of predators and consequently the magnitude of IGP.

Regarding the third trophic level, an increase in extraguild prey density may affect both the behavior and population density of the intraguild predators and the intraguild prey, with implications for overall guild structure and dynamics. For any particular predator, an increase of the shared resource could generate three types of responses: a numerical response, a functional response, or a developmental response. Predator density could increase both by increasing oviposition (reproductive numerical response) and by increasing the recruitment of individuals from other sites (aggregative numerical response). As a consequence, intraguild prey and intraguild predator densities can often be expected to increase. The ratio between both intra and extraguild prey types may shape the prey preferences of the intraguild predator, if preference increases for the most common prey (Chow et al., 2008). Also, as the shared resource becomes more common, predation efficiency may improve due to a decrease in handling and searching times (functional response). The intraguild predator may also be more likely to become satiated. As a consequence of the functional response, the development of the predators may accelerate (developmental response), and for the intraguild prey this may reduce the window of susceptibility to the intraguild predator. As the food required to reach a specific developmental stage may vary greatly among the different families of predators, and among species within a same family, the occurrence and duration of the predatory window (as intraguild predator) or prey window (as intraguild prey) will also change. In some cases, the intraguild prey may also benefit from the improvement of the extraguild prey's defensive traits. This may be especially likely for furtive predators (Lucas and Brodeur, 2001; Fréchette et al., 2008) and parasitoids (Chacón et al., 2008).

The composition of the predator guild may also respond to changes in extraguild prey availability. Guild composition and diversity may change according to the threshold density of extraguild prey required for particular predators to exploit extraguild prey populations. For example, some predators may only oviposit if herbivore densities exceed some density threshold (see for example Obrycki et al., 1998; Evans, 2004). In contrast, some predators may avoid sites already colonized by competitors (Janssen et al., 1997; Ruzicka, 1998) or emigrate from these sites (Briggs and Borer, 2005). These changes could be extremely important for a given intraguild prey species, since the arrival of a new intraguild predator may increase its susceptibility to IGP. Alternatively, a given intraguild prey could benefit from a release of IGP pressure if the new intraguild predator has a negative impact on another intraguild predator species that is an important predator of the intraguild prey. The latter hypothesis has been proposed for ladybirds: the arrival of a (second) invasive intraguild predator *Harmonia axyridis* Pallas in North America may have released some indigenous intraguild prey (smaller ladybirds) from predation by a previous invader *Coccinella septempunctata* L. (Brown, 2003). Extraguild prey density changes can also have an impact on guild dynamics (time of establishment, voltinism, and life-cycle duration of guild members) and thus on the probability of IGP occurrences (Lucas, 2005).

In conclusion, an increase in extraguild prey density may lead to (1) an increase intraguild prey density, with individuals developing more rapidly and spending less time moving about, and (2) a potential increase in predator guild richness and abundance with changes in guild composition.

3. Increasing extraguild and intraguild prey densities

An increase in extraguild prey density has been suggested to decrease the likelihood of predation events occurring among members of the predator guild, both for cannibalism (Fox, 1975; Polis, 1981) and IGP (Polis et al., 1989). Among terrestrial arthropod guilds, numerous studies have tested how adding extraguild prey to the system affects the intensity of IGP. In most cases, an increase of extraguild prey density leads to a decrease in IGP intensity (Polis and McCormick, 1987; Polis et al., 1989; Spence and Carcamo, 1991; Gillespie and Quiring, 1992; Lucas et al., 1998; Obrycki et al., 1998; Schellhorn and Andow, 1999b; Kajita et al., 2000; Hindayana et al., 2001; Burgio et al., 2002; Yasuda et al., 2004; Nóia et al., 2008; Shakya et al., 2009), but not always (Fincke, 1994; Lucas et al., 1998; Schellhorn and Andow, 1999a; Lucas and Brodeur, 2001; Fréchette et al., 2007; Chacón and Heimpel, 2010). Lucas et al. (1998) observed three different responses when testing how different densities of aphids (extraguild prey) affect IGP between lacewings, ladybirds and cecidomyids: (1) a strong decrease of IGP when there is a high risk of death/injury during aggressive interactions between similarly-sized predators; (2) a constant and high level of IGP when the intraguild predator experiences little or no risk of injury when attacking the intraguild prey and the two predators share similar searching behaviors, resulting in a high rate of mutual encounters, when extraguild prey increase from low to intermediate densities and (3) a decrease in IGP only at the highest extraguild prey, when the IG prey are not dangerous for the IG predator, but a dilution effect eventually occurs (see also Lucas and Brodeur, 2001).

On the other hand, an increase in intraguild prey density can increase the magnitude of predation events among guild members (cannibalism: Fox, 1975; Polis, 1981; IGP: Polis et al., 1989). This result may be observed any time an increased availability of extraguild prey leads to greater densities of predators, thereby increasing their encounter frequencies (Polis et al., 1989; Nóia et al., 2008; Lucas et al., 2009; Chacón and Heimpel, 2010).

Thus, increasing the availability of extraguild prey appears capable of producing two opposing effects, one that increases and the other that decreases the expected intensity of IGP. Can we predict the emergent net effect on IGP?

Turchin and Kareiva (1989) demonstrated that the risk for an individual aphid of being preyed upon by the ladybeetle *Hippodamia convergens* Guérin-Menneville decreased as aphid aggregations increased in size, despite a numerical response of the predatory guild to large aphid aggregations. Similarly, Lucas and Brodeur (2001) demonstrated that the furtive predator, *Aphidoletes aphidimyza* Rondani, which lives within aphid colonies without eliciting significant defensive reactions from the aphids, also benefits from a dilution effect in larger aphid colonies when facing the intraguild predator *Chrysoperla rufilabris* (Burmeister). This effect was however lost when the IG predators disrupted the aphid colony structure (i.e., caused aphids to disaggregate).

More recently, Nóia et al. (2008) tested four different extraguild prey densities with two different intraguild prey densities on IGP between predatory coccinellids. Overall, IGP decreased with an increase of extraguild prey density. At low extraguild prey density (extraguild prey for the predators for 12–24 h), increasing intraguild prey density leads to an increase in IGP, while at high extraguild prey density (extraguild prey for the predators for 48 h), no effect was reported. Finally, in a field study, Chacón and Heimpel (2010) demonstrated that higher extraguild prey density increased intraguild prey density and increased the intensity of IGP on parasitoid mummies (but see Meyhöfer and Hindayana, 2000).

Table 1
Intraguild (IGP) studies that explore the effect of extraguild prey and that allow (or not) spatial aggregation and reproductive recruitment of intragulid predators.

Reference	Allow spatial aggregation	Allow reproductive recruitment
Atim and Graham (1984)	No	No
Burgio et al. (2002)	No	No
Chacón and Heimpel (2010)	Yes	No
Cloutier and Johnson (1993)	No	No
De Clercq et al. (2003)	No	No
Fréchette et al. (2007)	No	No
Gillespie and Quiring (1992)	No	No
Hindayana et al. (2001)	No	No
Kajita et al. (2000)	No	No
Lucas and Brodeur (2001)	No	No
Lucas et al. (1998)	No	No
Mallampalli et al. (2002)	No	No
Meyhöfer and Hindayana (2000)	Yes	Yes
Nóia et al. (2008)	No	No
Polis and McCormick (1987)	Yes	Yes
Shakya et al. (2009)	Yes	No
Schellhorn and Andow (1999a)	Yes	Yes
Schellhorn and Andow (1999b)	Yes	Yes

Lucas (2005) proposed four types of IGP, which may be affected differently by extraguild prey density. IGP may be a fortuitous event (opportunistic type), or it may be specifically favored by natural selection, due to nutritional benefits (nutritional type) or benefits derived from decreasing the risk that the IG prey will grow up to become a competitor (competitive type) or even a predator of the IG predator (protective type). Under opportunistic IGP, the magnitude of the interaction is likely to be directly related to the probability of encounter between guild members, which will often be a function of the intraguild prey/extraguild prey ratio. Since this ratio decreases with an increase of extraguild prey density, the intensity of IGP should also decrease. By contrast, in the other types of IGP (nutritional, competitive and protective), the intraguild predator may search actively for the intraguild prey. In such situations, the impact of increasing the density of extraguild prey will often be less significant.

In conclusion, the effect of an increase of extraguild prey density on IGP intensity may be much more complex than it appears at first sight. Most studies have documented a reduction of IGP as extraguild prey abundance increases. However, those studies were often conducted in the laboratory on small temporal and spatial scales, and rarely considered the possibility that IG predator densities may increase in response to abundant extraguild prey (Table 1). Such increases in IG predator densities could occur either (i) through spatial aggregation of IG predators in areas with abundant extraguild prey, or (ii) through increased IG predator reproductive recruitment in areas where extraguild prey resources are rich. It is perhaps for these reasons that field experiments have produced much more mixed results regarding the influence of extraguild prey on IGP intensity than have laboratory studies.

4. Case study: an observational study of IGP by heteropteran predators in a cotton system

4.1. Goal

As previously stated, most of the work on IGP has been conducted within an experimental framework, and employing relatively small spatial and temporal scales. This creates some challenges in extending the lessons learned to the setting in which commercial agriculture is conducted, which usually involves larger spatial scales (i.e., the scale of whole fields) and larger temporal scales (i.e., a full growing season for annual agroecosystems, and multiple years for perennial agroecosystems). Two challenges that emerge in trying to apply lessons from small-scale experiments to the real setting of agriculture (or nature) are:

1. Some authors have questioned the importance of IGP, suggesting that strong predator-predator interactions are an artifact of confining predators within cages (Kindlmann and Houdková, 2006).
2. With respect to the study of the effect of extraguild prey on the intensity of IGP, it is possible that the effects observed in the short-term may differ from effects observed in the longer-term. In the short-term (i.e., a period of time that is too short for the IG predators to reproduce), extraguild prey may reduce IGP by satiating the IG predators or otherwise 'distracting' them from attacking the intermediate predator, or by reducing the mobility of the IG predators and intermediate predators, thereby reducing the likelihood of encounters. All of these effects should reduce the impact of IGP. In the longer-term, however, the IG predator populations may grow when extraguild prey are abundant, and this effect would be expected to act in the opposite direction, increasing the risk of IGP. This potential shift in the effect of extraguild prey has been discussed in the context of 'apparent competition' (see Harmon and Andow, 2004).

Previous small-scale and short-term field experiments employing enclosures have suggested that IGP by heteropteran predators (*Orius tristicolor* (White), *Geocoris* spp., *Nabis* spp., and *Zelus renardii* Kolenati) on larvae of common green lacewings (*Chrysoperla carnea* (Stephens), *Chrysoperla comanche* (Banks), and *Chrysopa nigricornis* Burmeister) is relaxed when extraguild prey, *Aphis gossypii*, are more abundant (Rosenheim, 2001). The goal of this work was to see if the signature of extraguild prey relaxing IGP is also observed in the setting of unmanipulated agroecosystems, observed at a larger spatial and temporal scale, and without the enclosures that preclude opportunities for aggregative responses of IG predators.

4.2. Methods

Details of the field sampling are given in De Valpine and Rosenheim (2008). Briefly, 20 cotton fields (*Gossypium hirsutum* L. and *Gossypium barbadense* L.) in California's San Joaquin Valley were sampled approximately weekly for 6–15 weeks (mean = 10.5 samples) during the mid- to late season (all samples fell between 21 June and 5 October), with 10 fields sampled in 1993 and another 10 fields sampled in 1994. Nine of the sites were commercial organic cotton fields, with the remaining 11 fields smaller plantings (none smaller than 1 ha) at experimental farms maintained by the University of California. Fields were planted to common commercial cotton varieties (all were nectaried and glanded), were left untreated for arthropod pests during the sampling period, and were conventionally tilled. The densities of the dominant herbivores (aphids, *A. gossypii* Glover, and spider mites, *Tetranychus* spp.) were measured in leaf samples (ca. 50 leaves per sample). Whereas aphids and mites were by far the dominant herbivores present in terms of numbers or biomass, cotton harbors a diverse arthropod community (University of California, 1996), and thus other potential prey were always present. The densities of the intraguild predators were measured in seven sweep samples (median; range 3–10), each comprising 10 swings of a standard insect net through the plant canopy. The age structure of lacewing populations was estimated by carefully searching seven (median; range 4–10) whole cotton plants, and recording the number of eggs, larvae of each of the three instars, and cocoons with lacewings (prepupae and pupae) present. An estimate of the daily mortality rate experienced by lacewing larvae, μ, was calculated from the age structure data as described in Fig. 1. The effects of the mean density of extraguild prey and intraguild predator taxa, averaged over the full period of sampling, on lacewing larval mortality rates was assessed using multiple regression.

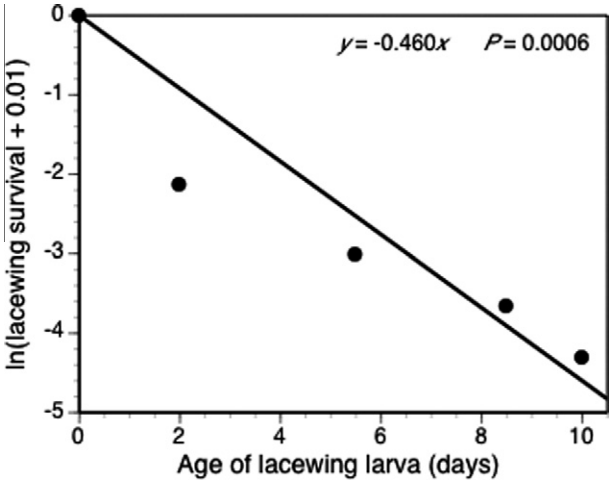

Fig. 1. Example of how an estimate of lacewing larval mortality rate (μ) was obtained from lacewing age structure observed in the field. These data describe lacewing larva survival at one cotton field, sampled between 22 June and 5 October, 1993. A total of 493 eggs, 37 first-instar larvae, 10 second-instar larvae, 4 third-instar larvae, and 3 prepupae/pupae (in cocoons) were collected. Based on previously measured rates of egg mortality, we estimate that 425 eggs survived to hatch. Eggs require 5 days to hatch under field conditions (Rosenheim, 2001); thus, we estimate that our cohort was initiated with 85 eggs hatching/day. 37 first instar larvae (corresponding to 9.25 larvae per day, across the 4-day duration of the first instar), represent a proportional survival of 0.109; analogous estimates were generated for each developmental stage, assuming that 4, 3, 3, and 10 days were required to complete the first, second, and third larval instar, and the pupal stage, respectively. μ was then estimated by fitting a linear regression (forced through the origin) through estimates of the proportion of lacewing larvae surviving to reach the midpoints of each larval instar (at days 2, 5.5, and 8.5) and the time at which cocoons are formed (day 10). We added 0.01 to all survival values to cope with zeroes. For this field, the estimated value of $\mu = 0.46$ (the absolute value of the slope of the regression). This approach rests upon several assumptions that are almost certainly not satisfied precisely (e.g., that the lacewing population has reached a stable age structure, and that mortality is constant across the different larval instars), but nevertheless provides a useful, albeit coarse, metric of lacewing larva mortality that can be compared across fields.

4.3. Results and discussion

Perhaps surprisingly, none of the four genera of heteropteran predators (*Orius*, *Geocoris*, *Nabis*, or *Zelus*) exhibited higher population densities in fields that harbored larger populations of aphids (linear regressions, $n = 20$, $-0.39 < r < 0.28$; $0.09 < p < 0.86$) or spider mites ($-0.28 < r < 0.24$; $0.23 < p < 0.63$), suggesting that some factor other than prey availability was responsible for controlling their populations. As observed previously in small field cage experiments, we found that lacewing mortality was significantly reduced in the face of intraguild predation in fields harboring abundant extraguild prey (aphids and spider mites combined; Fig. 2A). A regression analysis that evaluated the effects of aphids and mites separately revealed that increasing densities of each generated a significant ($p < 0.05$) reduction in lacewing mortality (data not shown). The effect of total intraguild predator density (*Orius* + *Geocoris* + *Nabis* + *Zelus* combined) on lacewing larva mortality rates was not significant in the multiple regression ($p = 0.62$; Fig. 2B). This result appears to be explained in part by the fact that densities of the two most common intraguild predators, *Orius* and *Geocoris*, were themselves strongly negatively correlated ($n = 20$, $r = -0.73$, $P = 0.0002$), consistent with the earlier-reported result that *Geocoris* is a major intraguild predator of *Orius* (Rosenheim, 2005). As a result, the total density of these two numerically-dominant intraguild predators traded off, one

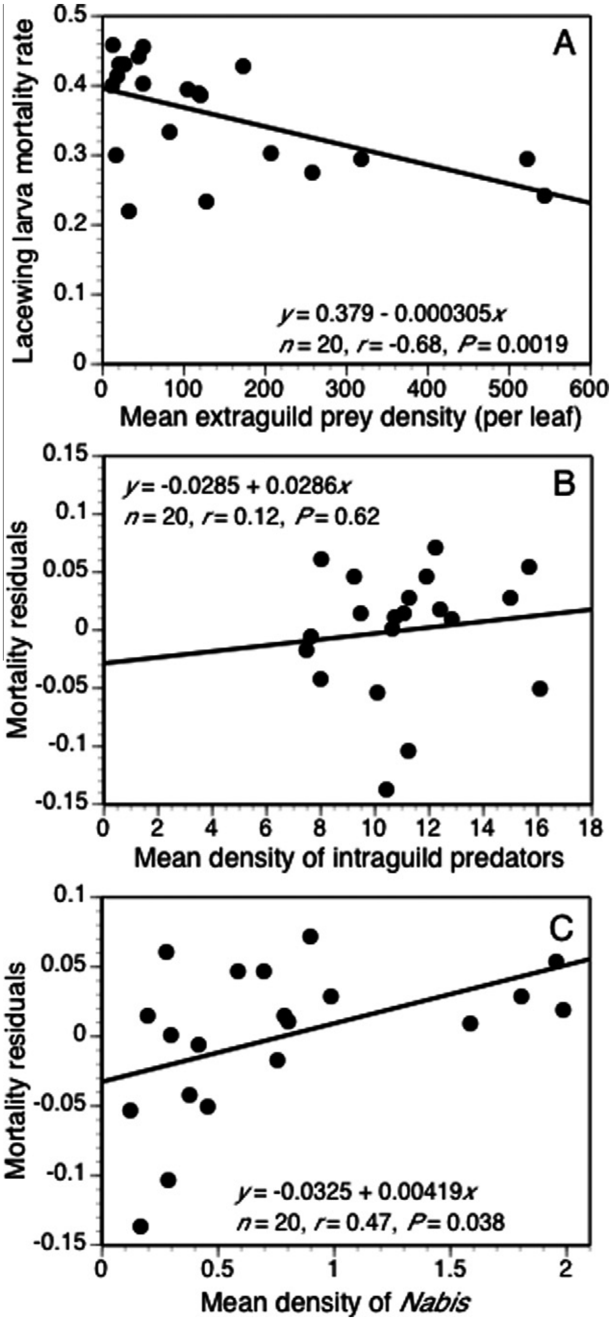

Fig. 2. Influence of variation in densities of extraguild prey and intraguild predators on the mortality rates of lacewing larvae in California cotton fields. (A) Lacewing larva mortality rates decrease as the mean density of extraguild prey (aphids and spider mites combined) increase. (B) Variation in the total density of intraguild predators (*Orius*, *Geocoris*, *Nabis*, and *Zelus* densities combined) does not explain the residual variation in lacewing larval mortality, after removing the explanatory effect of extraguild prey. (C) Variation in the density of *Nabis* does explain a significant amount of the residual variation in lacewing larva mortality; increasing *Nabis* densities are associated with increased lacewing mortality, as expected from their role as intraguild predators.

against the other, and total intraguild predator density varied only 2.1-fold across fields (range of observed densities: 7.5–16.1 per sweep sample), in contrast to the total density of extraguild prey, which varied 43.1-fold (range of observed densities: 12.7–544.8 extraguild prey per leaf). A regression of the density of the different intraguild predator genera, considered individually, against the residuals from the regression of lacewing larva mortality (μ) against extraguild prey density revealed that lacewing mortality was significantly negatively correlated with *Nabis* densities (Fig. 2C), consistent with *Nabis*' role as a significant intraguild predator of lacewing larvae in small-scale field experiments (Rosenheim et al., 1993; Rosenheim, 2001).

The decrease in lacewing mortality observed when extraguild prey are more abundant (Fig. 2A) could be interpreted as a reduction in lacewing larva starvation when prey are more abundant, rather than being connected with IGP. Whereas such a direct effect of prey availability on lacewing survival is possible, we suggest for two reasons that a reduction in lacewing starvation is unlikely to be the main cause of increased lacewing survival when extraguild prey are abundant. First, a prior experiment conducted in small enclosures showed that whereas lacewing mortality increased dramatically in the presence of IG predators when extraguild prey were less abundant (initial aphid densities were 5–10 aphids/leaf), lacewing performance in the absence of IG predators did not reveal any signs of nutritional stress: lacewing survival, development rate, and weight at pupation were not reduced (Rosenheim, 2001). Thus, even with low extraguild prey densities, lacewings did not appear to be directly prey-limited. Second, when prey are scarce in cotton, lacewing larvae have been shown to increase their consumption of extrafloral nectar, which is produced by cotton in copious quantities. Extrafloral nectar does not appear to support lacewing development, but does support foraging activity and dramatic increases in longevity (Limburg and Rosenheim, 2001). Such a prolongation of development would change lacewing age structure by increasing the ratio of larvae to eggs; all other things being equal, this would tend to increase, rather than decrease, our estimates of lacewing survival (Fig. 1). Thus, we think it unlikely that lacewing starvation was an important contributor to the observed increases in our estimates of lacewing mortality when extraguild prey were less abundant. Rather, we interpret this result as the field-scale expression of the intensification of intraguild predation when IG predators are hungry, and both IG predators and lacewings must forage extensively in search of scarce prey, thereby increasing opportunities for encounters between these predators.

5. Conclusion

In the literature, numerous studies have reported heteropteran predators engaged in IGP. The wide trophic range of numerous terrestrial and of most aquatic species combined with the large size of several species may provide abundant opportunities for predatory interactions. One of the main factors influencing the magnitude of IGP is the density of extraguild prey. Most laboratory and field mesocosm studies have reported a decrease in IGP intensity as extraguild prey density increases. However, an increase in extraguild prey density may, in the long term, lead to an increase in the density of the intraguild predator. This increase could, in theory, act to amplify the impact of the intraguild predator population. The case study described here suggests, however, that experimental results observed in small enclosures and over small time frames may, in some cases, still scale up to predict field-wide patterns. Perhaps because intraguild predator populations did not increase in response to more abundant extraguild prey, the ability of abundant extraguild prey to dilute the impact of an intraguild predator on an intraguild prey in cotton was still clearly expressed at the field level.

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References

Arim, M., Marquet, P.A., 2004. Intraguild predation: a widespread interaction related to species biology. Ecology Letters 7, 557–564.

Atim, A.B., Graham, H.M., 1984. Predation of *Geocoris punctipes* by *Nabis alternatus*. Southwestern Entomologist 9, 227–231.

Briggs, C.J., Borer, E.T., 2005. Why short-term experiments may not allow long-term predictions about intraguild predation. Ecological Applications 15, 1111–1117.

Brown, M.W., 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. BioControl 48, 141–153.

Burgio, G., Santi, F., Maini, S., 2002. On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Biological Control 24, 110–116.

Chacón, J.M., Heimpel, G.E., 2010. Density-dependent intraguild predation of an aphid parasitoid. Oecologia 164, 213–220.

Chacón, J.M., Landis, D.A., Heimpel, G.E., 2008. Potential for biotic interference of a classical biological control agent of the soybean aphid. Biological Control 46, 216–225.

Chow, A., Chau, A., Heinz, K.M., 2008. Compatibility of *Orius insidiosus* (Hemiptera: Anthocoridae) with *Amblyseius* (*Iphiseius*) *degenerans* (Acari: Phytoseiidae) for control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse roses. Biological Control 44, 259–270.

Cloutier, C., Johnson, S.G., 1993. Predation by *Orius tristicolor* (Hemiptera: Anthocoridae) on *Phytoseiulus persimilis* (Acarina: Phytoseiidae): testing for compatibility between biocontrol agents. Environmental Entomology 22, 477–482.

Coll, M., Izraylevich, S., 1997. When predators also feed on plants: effects of competition and plant quality on omnivore-prey population dynamics. Annals of the Entomological Society of America 90, 155–161.

De Clercq, P., Peters, I., Vergauwe, G., Thas, O., 2003. Interaction between *Podisus maculiventris* and *Harmonia axyridis*, two predators used in augmentative biological control in greenhouse crops. BioControl 48, 39–55.

De Valpine, P., Rosenheim, J.A., 2008. Field-scale roles of density, temperature, nitrogen and predation on aphid population dynamics. Ecology 89, 532–541.

Dolling, W.R., 1991. The Hemiptera. Oxford University Press, New York.

Erbilgin, N., Dahlsten, D.L., Chen, P., 2004. Intraguild interactions between generalist predators and an introduced parasitoid of *Glyscaspis brimblecombi* (Homoptera : Psylloidea). Biological Control 31, 329–337.

Evans, E.W., 2004. Habitat displacement of North American ladybirds by an introduced species. Ecology 85, 637–665.

Fauvel, G., Rambier, A., Cotton, D., 1975. Activité prédatrice et multiplication d'*Orius* (*Heterorius*) *vicinus* (Het.:Antocoridae) dans les galles d'*Eriophyes fraxinivorus* (Acarina : Eriophyidae). Entomophaga 23, 261–270.

Fincke, O.M., 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. Oecologia 100, 118–127.

Fox, L., 1975. Cannibalism in natural populations. Annual Review of Ecology and Systematics 6, 293–302.

Fréchette, B., Rojo, S., Alomar, O., Lucas, E., 2007. Intraguild predation among mirids and syrphids. Who is the prey and who is the predator? BioControl 52, 175–191.

Fréchette, B., Larouche, F., Lucas, E., 2008. *Leucopis annulipes* larvae (Diptera: Chamaemyiidae) use a furtive predation strategy within aphid colonies. European Journal of Entomology 105, 399–403.

Gillespie, D.R., Quiring, D.J.M., 1992. Competition between *Orius tristicolor* (White) (Hemiptera: Anthocoridae) and *Amblyseius cucumeris* (Oudemans) (Acari: Phytoseiidae) feeding on *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). Canadian Entomologist 124, 1123–1128.

Guillebeau, L.P., All, J.N., 1989. *Geocoris* spp. (Hemiptera: Lygaeidae) and the striped lynx spider (Araneae: Oxyopidae): cross predation and prey preferences. Journal of Economic Entomology 82, 1106–1110.

Guillebeau, L.P., All, J.N., 1990. Big-eyed bugs (Hemiptera: Lygaeidae) and the striped lynx spider (Araneae: Oxyopidae): Intra- and interspecific interference on predation of first instar corn earworm (Lepidoptera: Noctuidae). Journal of Entomological Science 25, 30–33.

Hall, D.J., Cooper, W.E., Werner, E.E., 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography 15, 839–928.

Harmon, J.P., Andow, D.A., 2004. Indirect effects between shared prey: predictions for biological control. BioControl 49, 605–626.

Herrick, N.J., Reitz, S.R., Carpenter, J.E., O'Brien, C.W., 2008. Predation by *Podisus maculiventris* (Hemiptera: Pentatomidae) on *Plutella xylostella* (Lepidoptera: Plutellidae) larvae parasitized by *Cotesia plutellae* (Hymenoptera: Braconidae) and its impact on cabbage. Biological Control 45, 386–395.

Hindayana, D., Meyhöfer, R., Scholz, D., Poehling, H.M., 2001. Intraguild predation among the hoverfly *Episyrphusbalteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. Biological Control 20, 236–246.

Janssen, A., Bruin, J., Jacobs, G., Schraag, R., Sabelis, M.W., 1997. Predators use volatiles to avoid prey patches with conspecifics. Journal of Animal Ecology 66, 223–232.

Kajita, Y., Takano, F., Yasuda, H., Agarwala, B.K., 2000. Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. Applied Entomology and Zoology 35, 473–479.

Kester, K.M., Jackson, D.M., 1996. When good bugs go bad: intraguild predation by *Jalysus wickami* on the parasitoid, *Cotesia congregata*. Entomologia Experimentalis et Applicata 81, 271–276.

Kindlmann, P., Houdková, K., 2006. Intraguild predation: fiction or reality? Population Ecology 48, 317–322.

Limburg, D.D., Rosenheim, J.A., 2001. Extrafloral nectar consumption and its influence on the survival and development of an omnivorous predator, larval *Chrysoperla carnea*. Environmental Entomology 30, 595–604.

Lucas, É., 2005. Intraguild predation among aphidophagaous predators. European Journal of Entomology 102, 351–364.

Lucas, É., Alomar, O., 2001. *Macrolophus caliginosus* (Wagner) as an intraguild prey for the zoophytophagous *Dicyphus tamaninii* Wagner (Heteroptera: Miridae). Biological Control 20, 147–152.

Lucas, É., Alomar, O., 2002a. Impact of *Macrolophus caliginosus* presence on damage production by *Dicyphus tamaninii* (Heteroptera: Miridae) on tomato fruits. Journal of Economic Entomology 95, 1123–1126.

Lucas, É., Alomar, O., 2002b. Impact of the presence of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on whitefly (Homoptera: Aleyrodidae) predation by *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae). Biological Control 25, 123–128.

Lucas, É., Brodeur, J., 2001. A fox in a sheep-clothing: dilution effect for a furtive predator living inside prey aggregation. Ecology 82, 3246–3250.

Lucas, É., Fréchette, B., Alomar, O., 2009. Resource quality, resource availability, and intraguild predation among omnivorous mirids. Biocontrol Science and Technology 19, 555–572.

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.

Mallampalli, N., Castellanos, I., Barbosa, P., 2002. Evidence for intraguild predation by *Podisus maculiventris* on a ladybeetle, *Coleomegilla maculata*: Implications for biological control of Colorado potato beetle, *Leptinotarsa decemlineata*. BioControl 47, 387–398.

McGregor, R.R., Gillespie, D.R., 2005. Intraguild predation by the generalist predator *Dicyphus Hesperus* on the parasiotoid *Encarsia Formosa*. Biocontrol Science and Technology 15, 219–227.

Meyhöfer, R., Hindayana, D., 2000. Effects of intraguild predation on aphid parasitoid survival. Entomologia Experimentalis et Applicata 97, 115–122.

Miller, N.C.E., 1971. The biology of Heteroptera, second ed. E.W. Classey Ltd., Hampton.

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.

Obrycki, J.J., Giles, K.L., Ormord, A.M., 1998. Experimental assessment of interaction between larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in field cages. Environmental Entomology 27, 1280–1288.

Polis, G.A., 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12, 225–251.

Polis, G.A., McCormick, S.J., 1987. Intraguild predation and competition among desert scorpions. Ecology 68, 332–343.

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20, 297–330.

Provost, C., Lucas, E., Coderre, D., 2006. Prey preference of *Hyaliodes vitripennis* as an intraguild predator: active predator choice or passive selection? Biological Control 37, 148–154.

Rogers, D.J., Sullivan, M.J., 1986. Nymphal performance of *Geocoris punctipes* (Hemiptera: Lygaeidae) on pest resistant soybeans. Environmental Entomology 15, 1032–1036.

Rosenheim, J.A., 1998. Higher-order predators and the regulation of insect herbivore populations. Annual Review of Entomology 43, 421–447.

Rosenheim, J.A., 2001. Source-sink dynamics for a generalist insect predator in a habitat with strong higher-order predation. Ecological Monographs 71, 93–116.

Rosenheim, J.A., 2005. Intraguild predation on *Orius tristicolor* by *Geocoris* spp and the paradox of irruptive spider mite dynamics in California cotton. Biological Control 32, 172–179.

Rosenheim, J.A., Wilhoit, R., Armer, C.A., 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96, 439–449.

Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Marois, J.J., Jaffee, B.A., 1995. Intraguild predation among biological control agents: theory and evidence. Biological Control 5, 303–335.

Rosenheim, J.A., Limburg, D.D., Colfer, R.G., 1999. Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. Ecological Applications 9, 409–417.

Ruzicka, Z., 1998. Further evidence of oviposition-deterring allomone in chrysopids (Neuroptera: Chrysopidae). European Journal of Entomology 95, 35–39.

Schellhorn, N.A., Andow, D.A., 1999a. Cannibalism and interspecific predation: role of oviposition behavior. Ecological Applications 9, 418–428.

Schellhorn, N.A., Andow, D.A., 1999b. Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. Environmental Entomology 28, 1092–1100.

Schmidt, J.M., Taylor, J.R., Rosenheim, J.A., 1998. Cannibalism and intraguild predation in the predatory Heteroptera. In: Coll, M., Ruberson, J.R. (Eds.), Predatory Heteroptera: Their Ecology and Use in Biological Control. Thomas Say Publications in Entomology, Lanham, Maryland, pp. 131–170.

Shakya, S., Weintraub, P.G., Coll, M., 2009. Effect of pollen supplement on intraguild predatory interactions between two omnivores: the importance of spatial dynamics. Biological Control 50, 281–287.

Spence, J.R., Carcamo, H.A., 1991. Effects of cannibalism and intraguild predation on pondskaters (Gerridae). Oikos 62, 333–341.

Triplehorn, C.A., Johnson, N.F., 2004. Borror and DeLong's an introduction to the study of insects, seventh ed. Sauders College Publishing, Montréal.

Turchin, P., Kareiva, P., 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. Ecology 70, 1008–1016.

University of California, 1996. Integrated Pest Management for Cotton in the Western Region of the United States. Publication 3305, Division of Agriculture and Natural Resources, University of California, Oakland, CA.

Wheeler Jr., A.G., 2001. Biology of the Plant Bugs (Hemiptera: Miridae): Pests, Predators, Opportunists. Cornell University Press, New York.

Whitcomb, W.H., Bell, K., 1964. Predaceous insects, spiders, and mites of Arkansas cotton fields. Arkansas Agricultural Experiment Station Bulletin 690, 1–84.

Yasuda, H., Evans, E.W., Kajita, Y., Urakawa, K., Takizawa, T., 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. Oecologia 141, 722–731.