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

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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.

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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, Cocicidae, Notonectidae, . . .) and finally surface dwelling predators in the Gerromorpha (Gerridae, Velidae, . . .)(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
the same predator guilds as heteropteran predators, IGP opportuni-
ties may be common. Eggs, younger (and smaller) instars, and molt-
ing individuals are especially susceptible to predation.

In terrestrial food webs, heteropteran predators may consume a
diverse array of intraguild prey, including other predators (coccin-
ellids, syrphids, neuropteran and dipteran predators, other heter-
opteran 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 het-
eropterans 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 Carmaco, 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 extra-
guild 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) high-
er 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 in-
creases, more herbivores (extraguild prey, the second trophic level)
attack the plant, which may elicit the expression of induced de-
defences. The production of defensive compounds can have detri-
mental effects on the extraguild prey, and, when sequestered by
herbivores, detrimental effects may also be extended to higher tro-
phic levels (Rogers and Sullivan, 1986). Detrimental effects may re-
duce 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 sus-
ceptibility of herbivores to predators. Furthermore, zoophytopha-
gous 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 feed-
ning 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 exam-
ple by colonizing less productive plants or less productive micro-
sites 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 conse-
quently 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 re-
sponses: a numerical response, a functional response, or a develop-
mental 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 pre-
frences 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 pre-
dators may accelerate (developmental response), and for the intra-
guild prey this may reduce the window of susceptibility to the
intraguild predator. As the food required to reach a specific develop-
mental stage may vary greatly among the different families of preda-
 tors, 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 extra-
guild prey’s defensive traits. This may be especially likely for furtive
predators (Lucas and Brodeur, 2001; Fréchette et al., 2008) and par-
asitoids (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 extra-
guild 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 Obrzycki et al., 1998; Evans, 2004). In contrast, some pre-
dators 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 intra-
guild 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). Extra-
guild 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; Obyrcki et al., 1998; Schellhorn and Andow, 1999b; Kajita et al., 2000; Hindayana et al., 2001; Burgio et al., 2002; Yausuda et al., 2004; Nöia 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 cecidomyiids: (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; Nöia 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-Ménéville 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, Nöia 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).

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
Some authors have questioned the importance of IGP, suggesting that strong predator-predator interactions are an artifact of confining predators within cages (Kindlmann and Houdkává, 2006).

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 (White), 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, Tetramychus 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.

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 larval 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...
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.

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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