The Ubiquity of Intraguild Predation among Predatory Arthropods

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Abstract

Intraguild predation (IGP) occurs when one predator species attacks another predator species with which it competes for a shared prey species. Despite the apparent omnipresence of intraguild interactions in natural and managed ecosystems, very few studies have quantified rates of IGP in various taxa under field conditions. We used molecular analyses of gut contents to assess the nature and incidence of IGP among four species of coccinellid predators in soybean fields. Over half of the 368 predator individuals collected in soybean contained the DNA of other coccinellid species indicating that IGP was very common at our field site. Furthermore, 13.2% of the sampled individuals contained two and even three other coccinellid species in their gut. The interaction was reciprocal, as each of the four coccinellid species has the capacity to feed on the others. To our knowledge, this study represents the most convincing field evidence of a high prevalence of IGP among predatory arthropods. The finding has important implications for conservation biology and biological control.

Introduction

Contemporary ecologists struggle with complexity. Communities involve thousands of species interacting in many diverse ways within the spatial and temporal variability of natural ecosystems [1]. In the late 1980’s it became apparent that models based on functional trophic levels were not sufficiently universal to understand the dynamics and structure of communities [2]. The necessity of integrating non-trophic and indirect relationships has prompted theoretical and empirical work aimed at examining the role of omnivores. One form of omnivory is intraguild predation (IGP), where one predator species attacks another predator species with which it also competes for a shared prey species [3].

Following the pioneering field study of Polis and McCormick [4] on species of desert scorpions that feed on each other, a fertile and rapidly growing literature on IGP has led to a reconsideration of several classical topics in ecology such as stability and diversity of communities, trophic cascades in food webs, niche shift and species exclusion, as well as the effects of ecosystem productivity on species interactions [3,5–8]. IGP also rapidly became relevant to understanding the existence (presence/absence) of trophic linkages between species [13]. IGP and significance of IGP in nature [20].

Some studies have examined IGP in more natural settings using different methodological techniques and are important in complementing the less natural enclosure-based experiments. First, a number of semi-quantitative food-web studies document the existence (presence/absence) of trophic linkages between omnivores have shown that predators also include predatory species in their diet [4]. Second, purely observational field studies have quantified predator-predator interactions [21]. Third, experimental studies have been conducted in which the full, natural community of predators and prey were retained, and there was little if any constraint imposed on predator foraging [22]. Finally, a range of biochemical and molecular techniques have been developed to analyze gut contents and assess the diet of predatory arthropods under field conditions [23].

In this study we assess the nature and incidence of IGP among four species of coccinellid predators (Coleoptera: Coccinellidae) in soybean fields under natural conditions. This system has several
favourable attributes for the study of IGP. Coccinellids are generalist predators, voracious both during their larval and adult stages. In soybean fields of Quebec, Canada, they can be abundant and naturally play a role in aphid control [24]. They show an aggregative response to prey density [25–27], thereby increasing encounter rates with conspecific or heterospecific coccinellids. Furthermore, a number of laboratory or exclusion cage experiments have shown that IGP is a potentially common interaction among coccinellids [14,28] and have identified major ecological determinants of IGP such as relative size of the protagonists, mobility and aggressiveness, feeding specificity and aphid density [14,29].

A second advantage for using coccinellids as a model system is that we have developed molecular gut-content analyses to assess levels of IGP [30]. This approach uncovers predation events without interfering with the behavior of predators and prey and without disrupting ecosystem processes [31,32]. Gut-contents analysis using the polymerase chain reaction (PCR) has recently been applied to the study of IGP between predator species [33] and between predators and parasitoids [17,34].

Methods

Ethics statements

No specific permits were required for the described field studies and it did not involve endangered or protected species. Permission to sample invertebrates in the fields was obtained by each grower.

The study system

We studied the community of coccinellids associated with the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae), a recent invasive pest in North America [35]. The four dominant species in soybean fields in the province of Quebec are: *Coccinella septempunctata* Linnaeus, *Propylea quatuordecimpunctata* Linnaeus, *Harmonia axyridis* (Pallas) and *Coleomegilla maculata* lengi Timberlake, the only native species in this system [36]. These four coccinellid species are sympatric and present throughout the season, with *H. axyridis* arriving later than the others. Their abundance in soybean is mostly correlated with aphid densities, as commonly observed in agroecosystems [37].

Our primary objective was to estimate IGP levels within coccinellid assemblages in soybean fields. For the purposes of this paper, we define the IGP level as the proportion of a sample of a given predator species that contains measurable amounts of DNA of at least one different predator species in their guts. We do not attempt to examine the multitude of ecological factors that can promote the occurrence of IGP (predator and prey densities, predator:prey ratio, predator stage structure, etc) across fields or sampling dates; these analyses will be presented elsewhere. However, to place the present study in context we provide general information about aphid and coccinellid populations. *Aphis glycines* populations were relatively high with seasonal means of 266 and 371 aphids per plant in 2004 and 2005, respectively (A.E. Gagnon, unpublished data). The coccinellid community in 2004 was dominated by *H. axyridis* and *C. septempunctata* (representing 48 % and 41 %, respectively, of all species) with a small proportion of *C. maculata* (5 %) and *P. quatuordecimpunctata* (6 %). In 2005, the proportions of each species were as followed: *H. axyridis* (59 %), *C. septempunctata* (18 %), *C. maculata* (14 %) and *P. quatuordecimpunctata* (9 %).

Coccinellids were sampled in soybean fields in 2004 and 2005 with sweep netting, put in an electric icebox at 4°C, and brought to the laboratory. Specimens were frozen (–20°C) and then washed in 70% ethanol to prevent possible contamination stemming from the time that predators had been held together in the collecting bag [30,39]. In experiments done by Greenstone et al. [40], vigorous beating of plants followed by aspiration of insects into a common dry beaker led to incorrect assignment of gut contents – presumably due to regurgitant or feces from non-prey species contaminating the integument of predators. Contamination in our case is expected to be much lower because insects were immediately chilled rather than aspirated into a common beaker [30,39]. Also, contamination in the Greenstone et al. study was likely particularly high because the prey species they used (larvae of the Colorado potato beetle, *Leptinotarsa decemlineata*) is known to regurgitate readily and in large amounts, and is often covered with secretions and feces that may be particularly prone to generate contamination [40]. Finally, a substantial fraction of the control animals in the Greenstone et al. experiment showed contamination, which brings into question the validity of the study (as the authors themselves noted). Samples were preserved in vials with 70% ethanol at 4°C until DNA extraction. Coccinellids were sampled in four different fields, located within the municipalities of Maskinongé (46°12′39″, -73°02′02″), Hérouxville (46°39′50″, -72°37′27″), Nicolet-Sud (46°12′04″, -72°36′47″) and Saint-Augustin-de-Desmaures (46°44′19″, -71°28′43″) in the province of Quebec. A total of 188 and 180 coccinellid individuals were sampled in 2004 and 2005, respectively (Figure 1 provides details per species). Insects were sampled from mid-July to mid-September. We only used fourth larval instars in our analyses because they are more likely to be engaged in IGP than are other stages [28].

DNA extraction and PCR cycles

DNA extraction and PCR protocols were modified from Hoogendoorn and Heimpel [41]. DNA was extracted from whole coccinellid larvae. Each insect was ground in a 1.5 ml micro-centrifuge tube using sterile plastic pestles (Ultrident Scientific Inc.) with 100 μl of grinding buffer [42]. PCR amplifications were done separately for each primer pair (*H. axyridis; C. septempunctata; C. maculata; P. quatuordecimpunctata*). Details of development and cross-reactivity tests of PCR markers are presented in Gagnon et al. [30]. All predators were screened against the primers of all three species in soybean fields in 2004 and 2005, respectively (Figure 1 provides details per species). Insects were sampled from mid-July to mid-September. We only used fourth larval instars in our analyses because they are more likely to be engaged in IGP than are other stages [28].
coccinellid species. Such a correction confers more importance to a “rapidly digesting” species combination where probability of detecting an intraguild prey is lower than for a “slowly digesting” species combination [44–46]. DS50 values for each predator-prey combination were weighted to obtain the DS50\textsuperscript{weighted} as follows: the shortest DS50 was assigned a value of 1.0 and other weighted DS50 values were obtained by placing this benchmark DS50 in the numerator and each other DS50 value in the denominator. The corrected predation value is calculated by multiplying the proportion of field-collected predators found to contain prey remains by their specific DS50\textsuperscript{weighted}. We did not attempt to estimate amount eaten per predator because no strong relationship had been found between the number of prey eaten and the duration of DNA in gut-contents of coccinellids [29,41].

**Results**

Three novel results emerge from our study. First, levels of IGP were extremely high with averages of 46.8% and 58.9% (non-weighted data) of all coccinellids containing DNA of other coccinellids in their gut in 2004 and 2005, respectively (Table 1). The intensity of IGP for each coccinellid-coccinellid interaction, expressed as the proportion of each species of IG prey detected in the gut of IG predators is shown in Figure 1. Using the weighted DS50 values changed the ranking of predators in terms of IGP strength quite drastically in 2004 but only slightly in 2005. In 2004, the ranking using raw data was as follows: *P. quatuordecimpunctata* > *C. maculata* > *H. axyridis* > *C. septempunctata* (Figure 2). Using weighted DS50 values revealed the following ranking: *H. axyridis* > *C. septempunctata* > *P. quatuordecimpunctata* > *C. maculata* (Figure 2). Thus, using raw data leads to an underestimation of the relative importance of IGP by *H. axyridis* and *C. septempunctata*. In 2005, relative IGP rates were more similar among species. The ranking using raw was: *C. maculata* > *H. axyridis* > *C. septempunctata* > *P. quatuordecimpunctata* (Figure 2), which was almost unaltered when weighted DS50 values were used, except that the relative strengths of IGP for *C. septempunctata* and *P. quatuordecimpunctata* were the same (Figure 2).

Second, the results indicate that IGP is reciprocal with each of the four coccinellid species feeding on each of the other three species (Figure 1). However, although levels of IGP were high in both years, the relative proportion of intraguild prey species varied between years. In 2004, *H. axyridis* was strongly represented as an intraguild prey species, whereas in 2005 *P. quatuordecimpunctata* and *C. septempunctata* were the dominant intraguild prey species.

Third, we report multiple prey detection (Table 1). When results from both years are combined, 11.8% of the intraguild predators contained the DNA of two other coccinellid species in their gut, and we detected three intraguild prey species simultaneously in the guts of 1.4% of the sampled coccinellids. Consumption of two intraguild prey species was most common in *H. axyridis* (48.1% of all cases) and *C. maculata* (35.7%), whereas only *H. axyridis* was feeding on three intraguild prey species.

**Discussion**

Our results indicate that IGP is very common among coccinellid species in soybean fields. Levels of IGP were high, with 52.9% of all sampled individuals containing the DNA of one, two and even three other coccinellid species in their gut. The interaction is reciprocal, as each of the four coccinellid species has the capacity to feed on the other three species. To our knowledge, this study represents the most convincing field evidence of the prevalence of IGP among predatory arthropods.

Our demonstration reflects the reality of the field situation. We used a sampling technique that entails no perturbation to the ecosystem or to the members of the community. Coccinellids were sampled *in situ*, without altering their behavior or distribution, thereby reducing potential artifacts that invariably arise through experimental manipulations conducted under laboratory conditions or within field cages. Molecular analyses allow the detection of minute amounts of prey material by PCR after DNA extraction. Molecular gut-contents analyses led to a demonstration of complex predation events between co-existing species and open the opportunity to better understand the dynamics and structure of communities. However, molecular gut-content analyses have their limits as well [23]. First, it is very difficult or impossible to determine the number of prey items a given predator has consumed, even using quantitative PCR [37,47]. This is because the size of prey items and the degree of digestion per prey item can vary so widely. For this reason, the ecological significance of intraguild predation can be difficult to determine because we cannot compare the amount of intraguild prey eaten in relation to the extraguild prey. However, using DS50 correction allowed a
comparison of intraguild predation rates between predator species that have different digestion times [30,43,46]. Second, scavenging or secondary predation (in which a predator eats another predator species containing the prey of interest in its gut) cannot be discriminated from true predation using PCR [48,49]. And lastly, PCR detection of cannibalism is not achievable because conspecific DNA cannot be discriminated from predator DNA. Thus, we still lack a basic understanding of the relative importance

**Table 1.** Number (N) of specimens tested and levels of intraguild predation (raw data) among four coccinellid species with molecular gut-content detection of one to three different intraguild prey species in a same predator, in 2004 and 2005.

|          | One intraguild prey species | Two intraguild prey species | Three intraguild prey species | Total IGP |
|----------|-----------------------------|-----------------------------|-------------------------------|-----------|
|          | n   | %     | n   | %     | n   | %     | n   | %     | n   | %     |
| 2004     | 188 | 72    | 14  | 7.45  | 2   | 1.06  | 88  | 46.81 |
| 2005     | 180 | 74    | 29  | 16.11 | 3   | 1.67  | 106 | 58.89 |

**Relative strength of IGP for each predator species**

**Figure 2.** Relative strength of intraguild predation by each of the four coccinellid species measured by molecular gut content analysis in soybean fields in Québec, Canada, in 2004 and 2005. Results are shown for raw and weighted data*. Ha = Harmonia axyridis, C7 = Coccinella septempunctata, Cmac = Coleomegilla maculata, P14 = Propylea quatuordecimpunctata.

* doi:10.1371/journal.pone.0028061.t001

* doi:10.1371/journal.pone.0028061.g002
of IGP and cannibalism, a common phenomenon in Coccinellidae [50, 51] for population dynamics. Monoclonal antibody-based ELISA could be useful in detecting cannibalism because it can be used to distinguish different life stages [52, 53].

While IGP models of predator–prey interactions, as well as the effects of omnivory on extraguild prey suppression have recently received considerable attention from both empiricists and theoreticians [2, 6, 7, 19, 54–57] very few studies have explicitly measured levels of IGP in arthropods under field conditions. To our knowledge only three other field studies using molecular techniques have directly quantified levels of IGP in arthropods. In the soybean agroecosystem, Harwood et al. [58] examined predation between H. axyridis and the predatory bug Orius insidiosus (Say) (Hemiptera: Anthocoridae) using molecular gut-content analysis. Less than 2.5% of O. insidiosus tested positive for the detection of H. axyridis. Chacon et al. [17] detected aphid parasitoid DNA in two predator species using PCR in a study examining IGP of released parasitoids of the soybean aphid. In this study, percentages of predators testing positive for parasitoid DNA ranged from 8 to 17. Hauiter et al. [59] reported that 9 out of 28 H. axyridis collected in potato fields had fed on heterospecific species of coccinellids, based on alkaloid quantification by gas-chromatograph-mass spectroscopy (GC-MS). Although this latter technique is promising, identification of prey species is only possible at the genus level and this method has also been estimated to be more expensive than other analyses of gut contents [60]. More information about IGP levels measured under natural conditions is available for larger predators from different taxa (see Table 2 for selected examples), probably because predation events can be more easily detected through different sampling techniques. The first published study quantifying the incidence of IGP in nature was conducted by Polis and McCormick [4] who observed relatively high proportions of intraguild prey in the diet of desert scorpions, from 8 to 21.9%, and up to 45% for the species Paruroctonus mesaeensis. Feeding information was easily collected on scorpions through observation because they digest their prey externally. Nevertheless, available data, both for arthropods and other taxa containing predators, are still too sparse to suggest patterns about the relative strength of IGP.

Several factors may contribute to the very high levels of IGP we quantified in coccinellids. First, coccinellids respond numerically to high aphid densities [24–27] a condition that may favour encounters between predators; although high prey abundance may also lead to predator satiation and thereby a reduction in intraguild interactions. Second, by eating a heterospecific, intraguild predators eliminate a competitor and thereby improve access to the aphid resource. Third, aphids are a relatively low quality prey resource [61], and coccinellids may benefit by complementing their diet by feeding on other coccinellids. A recent study also showed high levels of predation on coccinellid eggs in soybean fields in Michigan, USA [18]. However we still have a poor understanding of ecological factors that influence the strength and direction of intraguild interactions, and there is a need for more empirical studies that examine the effect of factors such as seasonality, vegetation-structured complexity, habitat productivity, extraguild prey density, as well as the behaviors and life histories of protagonists.

Over the last 20 years, several models and experimental studies have examined the nature and role of intraguild interactions in both terrestrial and aquatic communities. Intraguild predation is now considered to be ubiquitous in most species assemblages [12]. However, previous studies conducted in natural or managed ecosystems have largely overlooked the prevalence of IGP among top predators. Our results on coccinellids emphasize the importance of quantifying IGP in the field. This basic information is central for understanding the role of top predators in population dynamics and community structure, and from a more applied perspective, to predict their impact in programs devoted to the biological control of pest species or the management of native endangered or invasive exotic species.

**Acknowledgments**

We are very grateful to Emilie Lemaire, Veronique Janelle and Julie Mainguy for assistance in the field and laboratory. Thanks to Jay A. Rosenheim and Edward W. Evans who provided valuable comments on an earlier version of the manuscript.

**Author Contributions**

Conceived and designed the experiments: AEG JB GEH. Performed the experiments: AEG JB GEH. Analyzed the data: AEG JB GEH. Contributed reagents/materials/analysis tools: AEG JB GEH. Wrote the paper: AEG JB GEH.

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**Table 2.** Selected examples of intraguild predation under field conditions among different taxa.

| IG predator            | IG prey                        | Extraguild prey | % IGP          | Method of detection       | Region            | Authors                                    |
|------------------------|--------------------------------|-----------------|----------------|---------------------------|------------------|-------------------------------------------|
| White-tailed sea eagle (Haliaeetus albicilla L.) | Mink (Mustela vison Schreb.) | Fish and birds | <7% (for all mammal species) | Behavioral observation | Finland          | [62, 63]                                   |
| Cougar, wolf            | Coyote                         | Small mammals   | 43–67%         | Radio-tracked animals     | Alaska, Idaho     | [64]                                      |
| Lion, spotted hyena     | African wild dog               |                 | 13–50%         |                           | South Africa, Tanzania |                           |
| Red fox                 | American marten                |                 | 4%             |                           | Ontario           |                                           |
| Scorpion Paruroctonus mesaeensis | P. luteolus                      | Insects         | 8–22% (in some months higher than 40%) | External digestion (direct observation) | Italy            | [65]                                      |
| Eagle owl               | Tawny owl                      | Mammals, birds, fish, invertebrates | 0.6%        | Pellets and prey remains found under nests and roost sites | Italy            | [65]                                      |
| Dingo                   | Feral cat                      | NA              | 1.2–6.1%       | Dissection of gut-content | Australia         | [66]                                      |
| Many intertidal herbivores | Many intertidal herbivores | NA              | 0.37–10%       | Dissection of intestinal content | Chile            | [67]                                      |

**doi:10.1371/journal.pone.0028061.t002**
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