

Intraguild predation models: how relevant are they for aphidophagous insects?

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Introduction

Intraguild predation has become a major research topic in biological control and conservation ecology. It occurs when two predator species compete for the same prey and one of them also feeds upon its competitor (Polis *et al.*, 1989) and is assumed to be a widespread interaction within many, but not all, communities of biological-control agents (Rosenheim *et al.*, 1995, Holt & Pollis, 1997). As a consequence, intraguild predation combines two important structuring forces in ecological communities: competition and predation (Polis and Holt, 1992; Polis and Winemiller, 1996), and may generate a diversity of indirect effects among co-occurring species (Miller & Brodeur, 2002).

Theoretical treatments have suggested that intraguild predation has a uniformly negative effect on the ability of predatory biological control agents to suppress populations of herbivores in agroecosystems (Rosenheim & Harmon, 2005). This result follows from key assumptions in the models, namely that (i) the system is at equilibrium, and (ii) the two predators compete for only a single species of shared prey (Fig. 1). With these assumptions, an intraguild predator that was more effective at suppressing the target herbivore population would drive an intraguild prey population extinct through a combination of competition and predation (Rosenheim & Harmon, 2005). In other words, the intraguild prey must be superior in the competition for the shared prey in order to make coexistence possible (Revilla, 2002). This leads to a prediction that intraguild predation is uniformly disruptive to biological control (Pollis *et al.*, 1989; Rosenheim *et al.*, 1995; Holt & Pollis, 1997), which was sometimes supported by empirical data (Finke & Denno, 2003).

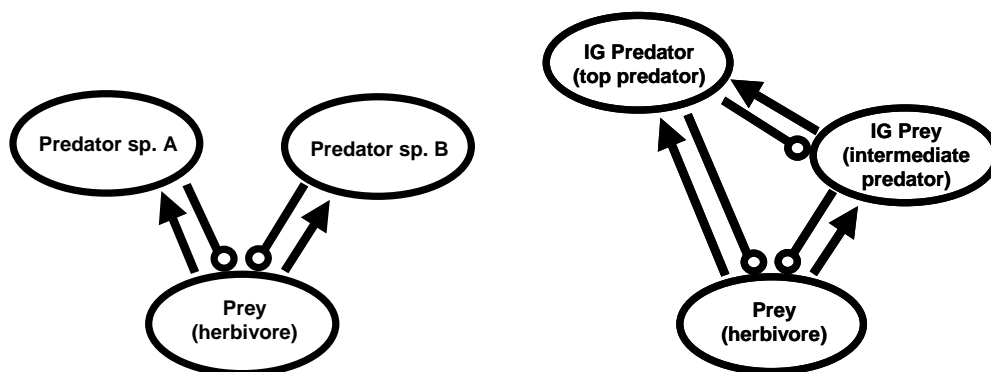


Figure 1. Two possibilities of interactions between two predators and shared prey.

A review of experimental field studies of intraguild predation by Rosenheim & Harmon (2005), however, revealed that inclusion of an intraguild predator can have a range of possible effects, including opportunities for enhancing herbivore suppression. In the context of this paper, experiments on aphidophagous guilds by Snyder *et al.* (2004), showing that the top predator, *Harmonia axyridis*, can complement aphid biocontrol by the parasitoid *Aphelinus asychis*, rather than disrupting control through intraguild predation, are especially important. This all supports the view that intraguild predators can, in many cases, enhance suppression of a target herbivore population, which contradicts the theoretical predictions. How can this discrepancy between theoretical predictions and empirical evidence be explained? One possible explanation is that the direct intraguild interactions among aphid predators are not frequent enough in nature, to have a significant influence on the aphid-natural enemy interactions. Here we aim to pursue this hypothesis.

In the context of the hypothesis above, it is notable that the lots of empirical data on the interactions between possible intraguild predator and intraguild prey, even within the aphidophagous predators guild, were obtained under artificial conditions: either in microcosms, cages, or in the laboratory (e.g., Pell *et al.*, 1997; Losey & Denno, 1998; Lucas *et al.*, 1998; Hindayana *et al.*, 2001; Burgio *et al.*, 2002, Agarwala *et al.*, 2003; De Clercq *et al.*, 2003; Roy *et al.*, 2003; Sato & Dixon, 2003; Sato *et al.*, 2003, 2005; Snyder *et al.*, 2004). While there is strong evidence that intraguild interactions are widespread in aphid-parasitoid or aphid-parasitoid-predator communities and mostly detrimental to aphid parasitoids (Brodeur & Rosenheim, 2000, Colfer & Rosenheim, 2001), nothing is known about how often these interactions really occur in nature among aphid predators. Therefore we develop here

a simple theoretical model predicting the strength of interspecific interactions among predator guilds in aphidophagous systems and further support our claims by empirical data collected in undisturbed field conditions.

Material and Methods

The model

We assumed that n aphid colonies are attacked at random by p_A (p_B) individuals of predatory species A (B) and that the attacks are independent of each other both intra- and interspecifically. Biologically this means that p_A (p_B) eggs (or egg batches) are laid independently in the total of n aphid colonies. We then calculated the number of cases, in which in this model species A (B) occur alone in the aphid colony and when these species occur together in one colony.

Based on these results, we calculated the expected population dynamics of these two species under the assumptions that the between-year growth rate of species A is 1.2 (i.e., an average individual in year t gives rise to 1.2 individuals in year $t+1$) and that of species B is 1, and that species B always wins in contest with A, i.e., if both A and B occur in one patch simultaneously, A does not survive in this patch, while B realizes its growth rate 1. Biologically this means that species A is able to grow more quickly, but is a worse competitor, compared with species B.

The species studied

Our model aphid species was *Macrosiphoniella tanacetaria*. It is a cyclical parthenogenetic species, which means that in its annual life cycle, several parthenogenetic generations are followed by a single sexual generation. Most of the individuals are wingless (apterae) during spring and summer, but some winged asexual females (alates) can be observed from time to time, and tend to colonize new plants. Sexual forms appear in autumn, alate males and apterous females. These females lay diapausing eggs that hatch in spring, giving birth to a new asexual lineage.

M. tanacetaria has been chosen for various reasons such as: they are not attended by ants, which limits the amount of interactions that have to be considered; they tend to form colonies and are relatively large, which facilitates their counting; they are specialized herbivores, which prevents their dispersal on other plants from the very start of the experiment and to stay in original patches during the whole experiment. This oligophagous species feeds mainly on tansy, *Tanacetum vulgare*, a perennial composite, and some of its relatives. It has the advantage of being a robust plant easy to manipulate.

Experimental design

One hundred of young tansy shoots of about 10 cm height were collected in the field in the middle of April, and grown in pots at 18°C, with 14 hours of light and 10 hours of dark for one month to regenerate. After that the plants were replanted into bigger pots (3 litres) and transferred outside. A mixture of half compost and half sand was used. As 50 plants were heavily devastated by slugs, fifty other shoots were collected afterwards near the experimental field and replanted at once. The pots were almost completely dug in the earth (only 5 cm of the pots were above soil surface), so that the earth predators were able to access or leave the tansy plants; for the same reason, but to keep the patches of aphids separated, the pots were placed at about 90 cm from each other. During the experiment, we watered the plants if needed and we trimmed new shoots and dead leaves to keep the patch simple to check.

The adults and fourth instar larvae of *M. tanacetaria* were also collected in the field at the beginning of June, and were raised in a greenhouse until a sufficient number of adult aphids and larvae of the fourth instar was obtained. Then, on the 12th of June, the 100 tansy plants were infested by groups of 5, 10 or 20 aphids, deposited at random, as shown in Fig. 2.

Afterwards, the number of aphids on each plant was counted once a day until their disappearance on August 1st. We distinguished the adults or IV instar larvae from the I-III instar larvae according to body size. When the alate aphids appeared, they were recorded separately as well. The number, type (species, genus) and stage of the predators encountered on the plants were also recorded. We paid particular attention to aphidophagous predators, but we noted also other possible consumers encountered, such as spiders, Cantharidae and Nabidae.

10	5	5	5	20	5	20	20	10	5
5	20	5	10	20	5	20	5	5	5
5	10	5	20	5	20	20	5	10	5
5	20	10	10	5	5	5	10	5	20
10	10	5	10	20	5	5	5	10	5
5	5	5	5	5	10	20	5	20	5
5	5	5	5	10	5	5	10	10	
5	5	20	5	5	5	5	10	5	
5	10	5	5	5	5	5	10		
20	5	5	5	5	20	5	5		
					20	5	5		
					5	10	20		

Figure 2. Infestation plan of tansy plants by fourth instar larvae and adults of *M. tanacetaria*.

Data analysis

We determined the empirical frequencies of the cases, when only one predator species or more predator species were found on the plant out of the total of 3000 observations (100 plants times 30 days of observations).

The expected frequencies of these cases were calculated as follows: the probability, p_i , of presence of predator i on one plant at one day, was derived from the total number of plants with predator i present, T_i , recorded during the experimental time: $p_i = \frac{T_i}{n.d}$, where $n = 100$ is number of experimental plants and $d = 30$ is number of

days, when the records of predators were complete. If the probabilities p and q be these probabilities of presence for a couple of predators A and B, then the expected number of plants with both A and B present is

$\hat{f}_{11} = p.q.n.d = p.q.3000$ and the expected number of plants with neither A nor B present is

$\hat{f}_{00} = (1-p).(1-q).3000$. The expected numbers of plants with only A and plants with only B were then

$\hat{f}_{10} = p.(1-q).3000$ and $\hat{f}_{01} = (1-p).q.3000$, respectively.

We then calculated the chi-square statistics for these frequencies. The null hypothesis for the 2x2 contingency table was “the presence of predator A is independent of presence/absence of predator B”. In other words, the distribution of individuals of any kind of predator within plants is random.

Results

Fig. 3 shows model predictions for two scenarios: 100 aphid colonies and 30 (50) ladybirds present. In realistic cases (when the number of predators is much lower than that of aphid colonies), the number of cases when both predator species are present is much lower than the number of cases when only one of the predatory species is present. This also accounts for the difference between predators and parasitoids in this respect: the proportion of colonies attacked by parasitoids tends to be much larger than that attacked by predators, and therefore the low frequency of common occurrence of two species, observed in Fig. 3, does not hold in the case of parasitoids (in their case, A+B would be large).

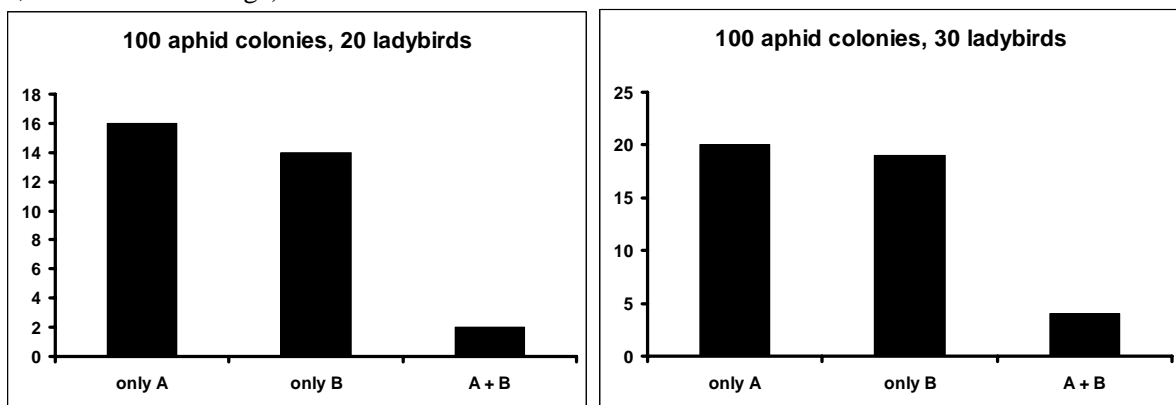


Figure 3. Model prediction of the number of plants with predator A (B) alone and with both predators present for two simulation runs with different numbers of ladybirds.

Fig. 4 shows the scenario of population dynamics of species A and B depicted in Fig. 3, if the between-year growth rate of species A is 1.2, that of species B is 1, and if B always wins, when occurs together with A. It is clear that when the common occurrence of both A and B in one patch is rare (as in Fig. 3), the decisive factor is growth rate, rather than competitive ability (winning in conflict with the other species).

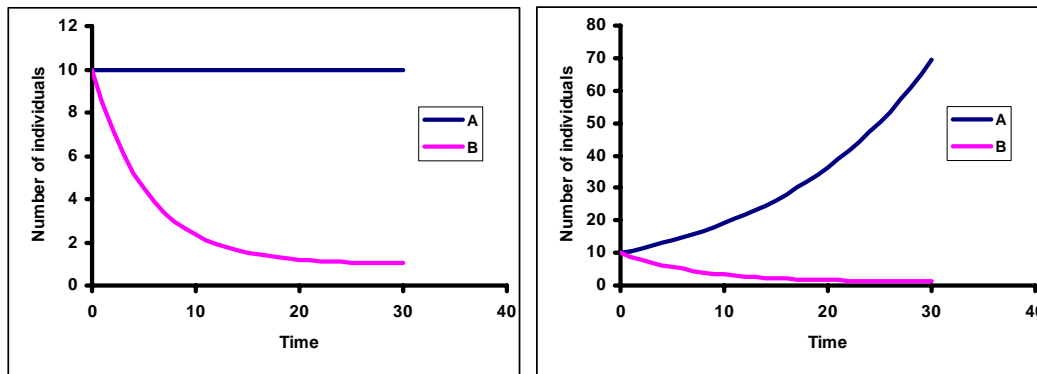


Figure 4. Model prediction of the population dynamics of predatory species A and B, if their occurrence on plants is given by Fig. 3, and if the between-year growth rate of species A is 1.2, that of species B is 1, and if B always wins, when it occurs together with A.

An example of empirical frequencies obtained is shown in Fig. 5 for the larvae of *Coccinella septempunctata* and adults of *Propylea quatuordecimpunctata*. Most of the chi-square statistics were significant, which means the observed number of plants without any of those predators was higher than expected, as was the number of plants with both species present. On the contrary, the observed numbers of predators alone were lower than expected. From comparison of Figs. 3 and 5 it is evident that the same pattern appears: the two predatory species only very rarely occur together.

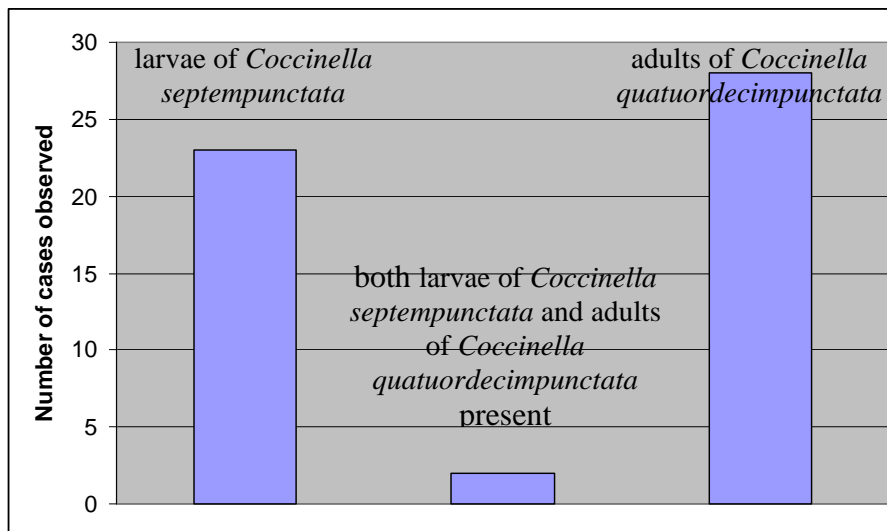


Figure 5. Distribution of larvae of *Coccinella septempunctata* and of adults of *Coccinella quatuordecimpunctata*.

Discussion

Our very simplistic model does not take into account the existence of the oviposition deterring pheromone, which enables the predators to avoid (or at least lower the degree of) cannibalism or intraguild predation (Dixon 2000). Inclusion of this assumption (as, e.g., in Houdkova and Kindlmann at this conference) would, however, lead to the frequency of A+B being even lower and the relative fitness of species A, compared with that of species B (as in Fig. 5) being even larger.

Thus both theory and empirical data support the hypothesis that direct interspecific conflicts between aphidophagous predators seem to be rather infrequent, even if we are aware of that the generality of this conclusion should be verified on a much larger scale than we did here. However, if it will be generally proven that direct interactions between different predatory species are rare in natural conditions, then the studies of direct interactions between different predatory species, although interesting academically, would not be applicable for explanation of the population dynamics of the predatory guilds.

Two suggestions for further research appear from this study: (1) more extensive field monitoring should be performed to correctly assess the true extent of direct interactions between different predatory species; and (2) predictions of population dynamics consequences stemming from laboratory, cage or microcosm experiments about relative competitive abilities of different predatory species in direct contests should be taken with caution.

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