

Intraguild predation: fiction or reality?

Pavel Kindlmann · Kateřina Houdková

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Abstract Intraguild predation has become a major research topic in biological control. Quantification of multipredator interactions and an understanding of the consequences on target prey populations are needed, which only highlights the importance of population dynamics models in this field. However, intraguild predation models are usually based on Lotka–Volterra equations, which have been shown not to be adequate for modeling population dynamics of aphidophagous insects and their prey. Here we use a simple model developed for simulation of population dynamics of aphidophagous insects, which is based on the type of egg distribution made by predatory females, to estimate the real strength of intraguild predation in the aphidophagous insects. The model consists of two components: random egg distribution among aphid colonies, and between-season population dynamics of the predatory species. The model is used to estimate the proportion of predatory individuals that face a conflict with a heterospecific competitor at least once during their life. Based on this, predictions are made on the population dynamics of both predatory species. The predictions are confronted with our data on intraguild predation in ladybirds.

Keywords Aphids · Biological control · Ladybirds · Model · Population dynamics

Introduction

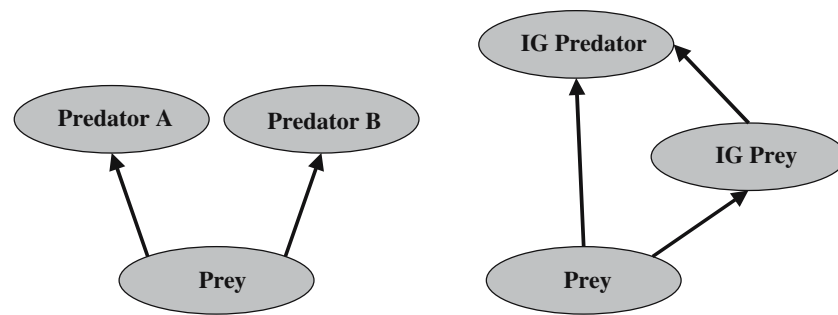
Intraguild predation has become a major research topic in biological control and conservation ecology. It occurs when two predator species compete for the same prey and one of them also feeds upon its competitor (Polis et al. 1989). It is assumed to be a widespread interaction within many, but not all, communities of biological-control agents (Rosenheim et al. 1995; Holt and Polis 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 cooccurring species (Miller and Brodeur 2002). However, intraguild predation models are usually based on Lotka–Volterra equations, which have been shown not to be adequate for modeling population dynamics of aphidophagous insects and their prey (Kindlmann and Dixon 1993, 1999a, b, 2001).

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 and Harmon 2005). This result follows from key assumptions in the models, namely, that (1) the system is at equilibrium, and (2) 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

P. Kindlmann
Agrocampus Rennes, UMR INRA/ENSA-R BiO3P,
65 rue de Saint-Brieuc, 35042 Rennes Cedex, France

P. Kindlmann (✉) · K. Houdková
Faculty of Biological Sciences, University of South Bohemia
and Institute of Systems Biology and Ecology AS CR,
Branišovská 31, 37 005 České Budějovice, Czech Republic
e-mail: pavel@entu.cas.cz

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



population extinct through a combination of competition and predation (Rosenheim and 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 (Polis et al. 1989; Rosenheim et al. 1995; Holt and Polis 1997), which was sometimes supported by empirical data (Finke and Denno 2003).

A review of experimental field studies of intraguild predation by Rosenheim and 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* (Pallas), can complement aphid biocontrol by the parasitoid *Aphelinus asychis* (Walker) 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? We hypothesize that the explanation may be hidden in another key assumption, which is implicit in the way that models are constructed, and additional to the “equilibrium” and “single-prey” conditions (1) and (2) mentioned above: (3) direct intraguild interactions are sufficiently frequent to be important for dynamics. If this condition is violated, then the predictions of the theoretical models may not be valid. Here we aim to pursue this hypothesis.

In the context of the hypothesis above, it is notable that the lots of empirical data on 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—where population densities of both predator and prey tend to be larger

than in field conditions (e.g., Pell et al. 1997; Losey and 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 and 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 and Rosenheim 2000; Colfer and 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 the aphidophagous systems and further support our claims by empirical data collected in undisturbed field conditions.

Materials 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 generated p_A (p_B) random integers, p_1, p_2, \dots, p_{p_A} and p_1, p_2, \dots, p_{p_B} , from the uniform distribution in the interval $< 0; n >$. We then numbered aphid colonies from 1 to n and assumed that colonies with numbers p_1, p_2, \dots, p_{p_A} were attacked by predator A and those with numbers p_1, p_2, \dots, p_{p_B} by predator B. We then calculated the numbers of cases predicted by this model, when 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. The growth rates 1.2 and 1 were chosen arbitrarily, just to illustrate the general trend; qualitatively, the same results would be obtained by other pairs of growth rates. Biologically, this model means that species A is able to grow more quickly but is a worse competitor than species B.

The species studied

Our model aphid species was *Macrosiphoniella tanacetaria* Kalténbach. 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 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—alate males and apterous females—appear in autumn. These females lay diapausing eggs that hatch in spring, giving birth to a new asexual lineage. *M. tanacetaria* was 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 means they stay in original patches during the whole experiment. This oligophagous species feeds mainly on tansy, *Tanacetum vulgare* L., a perennial composite, and some of its relatives. It has the advantage of being a robust plant easy to manipulate.

Experimental design

One hundred 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 h of light and 10 h of dark for 1 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. The pots were almost completely dug into the earth so that the ground-dwelling predators were able to access or leave the tansy plants. 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 trimmed new shoots and dead leaves to keep the patch simple to check. The adults and fourth instar larvae of *M. tanacetaria* were collected in the field at the beginning of

June and raised in a greenhouse until a sufficient number of adult aphids and larvae of the fourth instar was obtained. Then, on 12 June, the 100 tansy plants were infested by groups of 5, 10, or 20 aphids, deposited at random. Afterward, the plants were monitored once a day until the disappearance of aphids on 1 August. The numbers, species, and stages of the predators encountered on the plants were recorded.

Data analysis

We determined the empirical frequencies of the cases when only one or more predators were found on the plant out of the total of 3,000 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: $p_i = T_i/n \cdot d$ where $n = 100$ is the number of experimental plants and $d = 30$ is the number of days on which the records of predators were performed. If p and q are these probabilities for a couple of predatory species A and B, and if the null hypothesis H_0 “The presence of predator A is independent of presence/absence of predator B” is assumed, then the expected number of plants with both A and B present is $\hat{f}_{11} = p \cdot q \cdot n \cdot d = p \cdot q \cdot 3,000$. We compared the observed and predicted frequencies of cases when two species of predators occurred together.

Results

Figure 2 shows model predictions for two scenarios: 100 aphid colonies and 20 (30) ladybirds of each species distributed at random among them. 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, depicted in Fig. 2, does not hold in the case of parasitoids (in their case, $A + B$ would be large).

Figure 3 shows the predicted population dynamics of species A and B depicted in Fig. 2, 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. From Figs. 2 and 3 it is clear that when the common

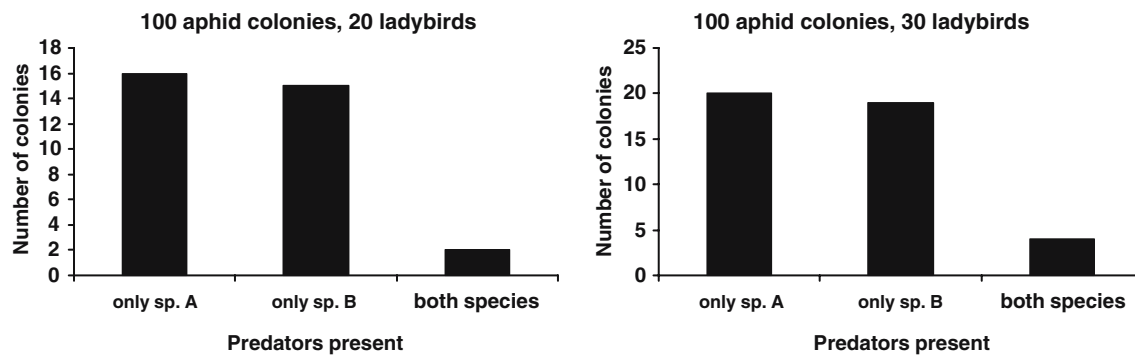


Fig. 2 Model prediction of the number of aphid colonies with predator A (B) alone and with both predators distributed at random for two simulation runs with $n=100$ aphid colonies and different numbers of ladybirds: $p_A = p_B = 20$ (left), $p_A = p_B = 30$ (right)

occurrence of both A and B in one patch is rare (as in Fig. 2), the decisive factor is growth rate, rather than competitive ability.

A comparison of empirical and predicted frequencies of predators occurring individually and together is shown in Fig. 4. The same pattern as in Fig. 2 appears here: two different predatory species only very rarely occur together. In addition, the observed numbers of cases when two predatory species occur together is in most cases even lower than expected just by random distribution of both species, as in our simplistic model.

Discussion

Our very simplistic model does not take into account the existence of the oviposition-detering 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 Houdková and Kindlmann, this issue) 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. 3) being even larger. Thus, both theory and empirical data support the hypothesis that direct interspecific conflicts between aphidophagous predators seem to be rather infrequent in field conditions even if we are aware that the generality of this conclusion should be verified on a much larger scale than we did here. However, if it is 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.

It should also be noted that in the system considered only condition (2) mentioned in the introduction is satisfied. The two predators compete for a single species of shared prey [i.e., (2) is satisfied], but the system is not at equilibrium [i.e., (1) is not satisfied]. However, when direct contacts between predators are very infrequent [i.e., (3) is not satisfied], as in our system, this becomes unimportant.

The observed numbers of cases when two predatory species occurred together in our experiment was, in

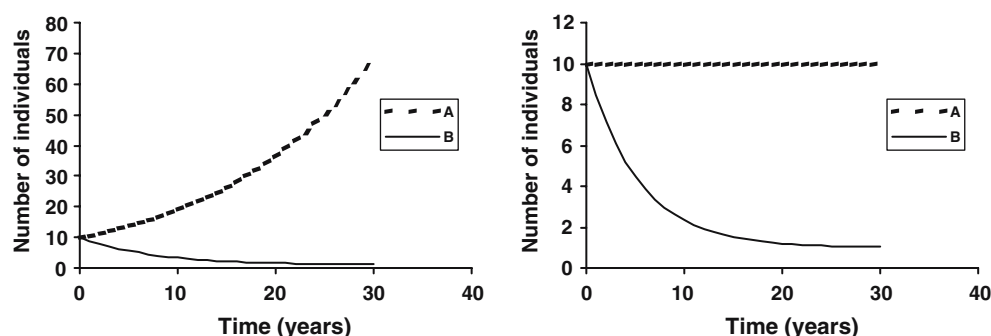


Fig. 3 Model prediction of the population dynamics of predatory species A and B, with $n=100$ aphid colonies and different numbers of predators: $p_A = p_B = 20$ (left), $p_A = p_B = 30$ (right), if the between-year growth rate of species A is 1.2, that of species

B is 1, and if B always wins when it occurs together with A. See Fig. 2 for predicted frequencies of patches with one or both species present

		Coccinellid eggs	Chrysopid eggs	<i>Coccinella septempunctata</i> , larvae	<i>Propylea quatuordecimpunctata</i> larvae	<i>Adalia bipunctata</i> , larvae	Chrysopid larvae	Syrphid larvae	<i>Coccinella septempunctata</i> , adults	<i>Propylea quatuordecimpunctata</i> , adults	<i>Adalia bipunctata</i> , adults
		264	85	51	2	9	10	417	115	59	2
Coccinellid eggs	264		0	20	0	0	0	0	0	0	0
Chrysopid eggs	85	7		2	0	0	0	9	0	4	0
<i>Coccinella septempunctata</i> , larvae	51	4	1		1	0	0	5	1	2	0
<i>Propylea quatuordecimpunctata</i> , larvae	2	0	0	0		0	0	0	0	0	0
<i>Adalia bipunctata</i> , larvae	9	1	0	0	0		0	0	0	0	0
Chrysopid larvae	10	1	0	0	0	0		1	0	0	0
Syrphid larvae	417	37	12	7	0	1	1		12	2	0
<i>Coccinella septempunctata</i> , adults	115	10	3	2	0	0	0	16		7	0
<i>Propylea quatuordecimpunctata</i> , adults	59	5	2	1	0	0	0	8	2		0
<i>Adalia bipunctata</i> , adults	2	0	0	0	0	0	0	0	0	0	

Fig. 4 Comparison of the observed (*above the main diagonal*) and predicted (*below the main diagonal*) numbers of cases, when two types of predators occurred together on one plant. Total numbers of observations of each type of predators are **boldfaced**

most cases, lower than expected just by random distribution of both species. This may be because the predatory mothers, when smelling the oviposition-detering pheromone, were reluctant to oviposit in aphid colonies already attacked by another predator. The low rates of cooccurrence in the field are similar to those predicted by our theoretical model, which only strengthens our point that competitive ability (e.g., intraguild predation) is unlikely to be important in field settings.

In our predictions in Fig. 4, we assumed that all predatory species are equally likely to arrive at any time. This may not be true. Predators have different phenologies, and therefore, some species may tend to arrive earlier and some later. If this is the case, then the expected rate of encounters among different predatory species is even lower than predicted in Fig. 4, which makes our predictions even closer to the observed values and further supports our claim that intraguild predation may be a rare event.

Two suggestions for future research appear from this study: (1) more extensive field monitoring should be performed to correctly assess the true extent of

in the *first row and first column*. Cases when the predicted numbers of cooccurrences was higher than or equal to the observed one are *shaded*

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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