Intraguild predation in aphidophagous guilds : does it exist ?

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Introduction

The concept of intraguild predation (IGP) was presented in two papers in 1987-1989, in which the complex trophic interactions within a guild of scorpions, spiders and scopulgids preying upon insects in a sand dune desert are described (Polis & McCormick, 1987; Polis & Myers, 1989). The dominant scorpion, *Paruroctonus mesaensis*, not only ate insects but also other species of scorpions, spiders and scopulgids. That is, they were feeding at two trophic levels (Figure 1). The expression intraguild predation was coined to describe cases where a predator eats other species of predator as well as the common resource exploited by that guild. IGP was defined as "the killing and eating of species that use similar, potentially limiting resources". At that time the concept was perceived as rather novel because it combines the effects of predation with those of interspecific competition: the intraguild predator accrues an immediate benefit when eating a competitor in the exploitation of the extraguild resource.

However, IGP is very similar to omnivory as omnivores also feed at more than one trophic level. *P. mesaensis* is indeed an omnivore as heterospecific scorpions formed from 20 to 45 % of its diet (Polis & McCormick, 1897). These field observations contrast with the theoretical prediction that omnivory should be rare (Pimm, 1982).

Food webs with IGP raise questions about how intraguild predators and prey can coexist (Figure 1). According to theory, this can only occur if the intraguild prey is more efficient in the exploitation and conversion of the common resource than the intraguild predator. As a consequence, the common resource is subject to less predation in the presence than in the absence of the intraguild predator. It is therefore more abundant in the presence of this intraguild predator (Polis & Holt, 1992).

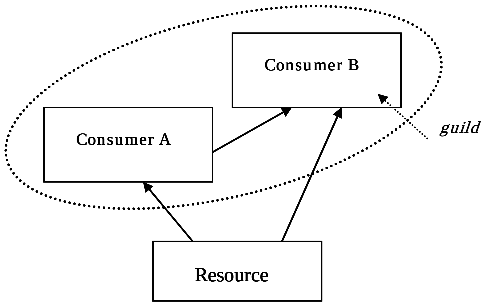

Figure 1. Representation of a simple case of intraguild predation: consumer A only eats the resource while consumer B eats A and the resource. Consumers A and B constitute a guild. The resource is sometime referred to as the extraguild prey; consumer A as the intraguild prey or the intermediate consumer and consumer B as the intraguild predator or top consumer.

Biological control of a pest is often achieved through the action of natural or man-made guilds of predators and parasitoids. Morevover, there is a long-standing debate among practitioners of biological control on whether a single or several natural enemies should be introduced to control a pest. The theory of IGP predicts that intraguild predators might disrupt the biological regulation of a pest. This probably explains the great interest shown by ecologists involved in biological control in IGP (Rosenheim et al., 1995). They questioned its impact on the population dynamics of biological control agents and on the success of biological control programmes.

In this paper, we firstly review the literature on guilds of natural enemies of aphids to determine whether intraguild predation is widespread and how it affects the population abundance of aphids. Secondly, the efficiency of the ladybirds *C. septempunctata* and *H. axyridis* in converting aphids and intraguild prey into their own biomass was measured

Material and methods

Literature survey

An electronic literature search in March 2005 yielded 56 papers on IGP in guilds of aphidophagous natural enemies : 5 are reports of field observations, 6 of field experiments and 45 of laboratory assessment of predation between different species of natural enemies[1]. All 5 of the field studies were analysed. Of the 6 reports of field experiments, 4 were specifically designed to test the prediction that the addition of intraguild predators would result in an increase in aphid abundance. Finally, 20 papers recording the results of laboratory experiments on aphidophagous ladybird beetles were reviewed.

[1] The complete list of references will be inserted in the extended version of this paper.

The efficiency of conversion of aphids and intraguild prey by two species of ladybirds

Stock cultures of *A. bipunctata*, *C. septempunctata* and *H. axyridis* were maintained on *Acyrtosiphum pisum* (Fréchette et al., 2004).

Upon hatching, first instars larvae of *C. septempunctata* and *H. axyridis* were isolated in 5 cm diameter Petri dishes and fed daily. Each dish was searched daily for exuviae, which were used to age the larvae. As soon as they reached the fourth instar, the larvae were weighed to an accuracy of 0.1 μg. Then, they were assigned to one of two groups, one of which was fed *A. pisum* and the other intraguild prey in the form of eggs of the other species. Those fed aphids, received an excess of aphids weighed to an accuracy of 0.1 μg. Those fed heterospecific eggs received a known quantity of eggs. Every day, the remaining aphids were weighed and eggs counted. The larvae were then put in clean Petri dishes and again given the same quantity of food. This was done until pupation or the larvae died. Pupae were detached from the Petri dishes and weighed to an accuracy of 0.1 μg. This procedure was repeated 16 times for each treatment. However, there were only 15 replicates of *C. septempunctata* fed *H. axyridis* eggs.

The quality of both kinds of food was estimated by calculating the rate of biomass conversion (RBC), the relative growth rate (RGR), the survival of fourth instar larvae and pupae and duration of the fourth larval instar. RBC is: (pupal weight – initial larval weight)/total weight of ingested food; RGR is: log(pupal weight) – log(initial larval weight)/ duration of the fourth instar

Results

Review of the incidence of IGP in aphidophagous guilds

Field observations

In Japan, the ladybird *Harmonia axyridis* frequently eats eggs and pupae of *Coccinella septempunctata bruckii* (Takahashi, 1989; Hironori & Katsuhiro, 1997). However, the latter was never seen eating the former. In addition, all the active stages of *H. axyridis* readily eat conspecific individuals. A similar asymmetrical interaction occurs among predators of *Aphis gossypii* in cotton fields in California, where the lacewing *Chrysoperla carnea* is the intraguild prey of *Zelus renardii* (Reduviidae) (Rosenheim et al., 1993). Shelhorn & Andow (1999) also recorded interspecific predation between *Adalia bipunctata* and *Coleomegilla maculata* in maize fields. Both species appear to suffer equally from interspecific predation, which was similar to or greater than the losses due to cannibalism. Interestingly, both cannibalism and IGP were only recorded when aphids were extremely rare, i.e., well after their peak in abundance. That is, asymmetrical interspecific predation occurs in some guilds but it is not a general phenomenon.

Field experiments

These were not designed to measure whether or not intraguild predators are less efficient in exploiting aphids than intraguild prey. However, one of Rosenheim et al.'s (1993) three experiments suggests that this might be the case. The objective of all these field experiments was to determine whether the intraguild predators increased aphid abundance. In only 2 out of the 7 trials was this the case (Rosenheim et al., 1993; Snyder & Ives, 2001). That is, although interspecific predation occurs in aphidophagous guilds there is no good empirical support for the notion that this predation fulfils the criteria of intraguild predation.

Interspecific predation among aphidophagous natural enemies in the laboratory

The objective of all these studies was to assess the potential for interspecific predation among aphid predators. In some of these studies the effect of the presence of aphids on the intensity of the interactions between predators was tested. The choice experiments, however, were never designed to assess whether or not extraguild prey is preferred to intraguild prey. Similarly, the relative importance of cannibalism and interspecific predation was not determined. When present, aphids were treated as background noise rather than a potentially important factor influencing the mortality of the predators. In addition, only 7 studies went further than just comparing interspecific predation in the presence or absence of aphids. Two densities of aphids were used in 5 studies and 3 in two. They generally show a reduction in predation with increase in aphid density. In 10 studies the interaction between predators was measured in the absence of extraguild prey. That is, the ratio of extraguild to intraguild prey was rarely if ever varied, as occurs in the field.

Symmetrical interspecific predation was recorded 11 times and asymmetrical 12 times, with some papers recording both symmetrical and asymmetrical interactions. When *H. axyridis* was involved (9) it was always the winner. The three remaining cases are of predation by *C. septempunctata* on native North American species. In all 12 papers, *H. axyridis* is reported to be cannibalistic. The intensity of interspecific predation recorded is generally high for *H. axyridis,* but low for other species.

Assessments of the cost of attacking intraguild prey are rarely made. *C. septempunctata* suffers a mortality of greater than 80 % after eating *H. axyridis,* whereas the mortality of *H. axyridis* is low and independent of whether it feeds on aphids, conspecifics or *C. septempunctata* (Yasuda & Ohnuma, 1999). *C. septempunctata* was more reluctant to eat the eggs of *A. bipunctata* than the reverse. In addition, fourth instar larvae of *C. septempunctata* failed to complete their development on a diet of *A. bipunctata* eggs. Only 30 % of the larvae of *A. bipunctata* completed their development when fed *C. septempunctata* eggs (Hemptinne et al., 2000). These results support the high proportion of laboratory tests reporting the effectiveness of *H. axyridis* as an intraguild predator. This indicates that some species are better adapted for intraguild predation and that, in aphidophagous guilds, such species are probably rare.

The efficiency of conversion of aphids and intraguild prey by two species of ladybirds

When fed eggs of *H. axyridis*, *C. septempunctata* had a lower RBC and very low RGR compared with when fed aphids (Figure 2). Eight larvae even lost weight and were lighter at the end of their development then at the beginning. Two thirds of the larvae fed heterospecific eggs died before they completed their development. Those that survived spent significantly longer in the fourth instar (Table 1).

The RBC of *H. axyridis* was significantly better when fed *C. septempunctata* eggs than aphids. Its RBC when fed aphids was also less than that of *C. septempunctata* fed the same diet (t = 4.2831; 30 d. f.; P = 0.0002). (Figure 2). However, its RGR was higher when fed aphids rather than intraguild prey and similar to that of *C. septempunctata* (t = 1.1156; 30 d. f.; P = 0.2734). The consumption of intraguild prey did not result in the death of any of the larvae but did result in a significant increase in the duration of the fourth larval instar (Table 1). This might indicate that there is a cost in eating *C. septempunctata* eggs for *H. axyridis*.

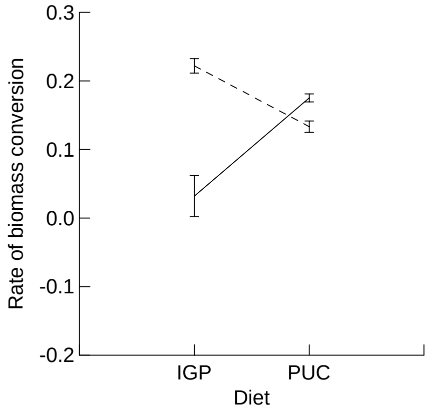

Figure 2a. Rate of biomass conversion by fourth instar larvae of *Coccinella septempunctata* (solid line) and *Harmonia axyridis* (dotted line) fed either pea aphids (PUC) or the eggs of the other species (IGP).

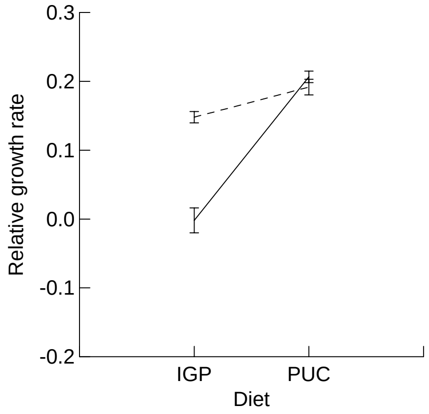

Figure 2b. The relative growth rate of fourth instar larvae of *Coccinella septempunctata* (solid line) and *Harmonia axyridis* (dotted line) fed either pea aphids (PUC) or the eggs of the other species (IGP).

Table 1. Survival (%) and length of development of fourth instar larvae of *C. septempunctata* and *H. axyridis* fed either the other species eggs or pea aphids.

	C. septempunctata		*H. axyridis*	
	Eggs	Aphids	Eggs	Aphids
Survival rate (%)	33.3	87.5	100	87.5
Duration of the 4th instar (days)	12.2	6.9	6.7	5.6

Conclusions

Interspecific predation in aphidophagous guilds occurs in the field, mainly when aphids are scarce (Takahashi, 1987; Shellhorn & Andow, 1999). Interestingly, *H. axyridis* consistently arrives in aphid colonies after *C. septempunctata bruckii* and is a frequent predator of the later.

Laboratory experiments confirm the potential for interspecific predation between the natural enemies of aphids. They also show that the presence of aphids tends to reduce the intensity of this interaction. *H. axyridis* stands out as a very aggressive ladybird and is better at converting intraguild prey into its own biomass than are other species of ladybird. In comparison, ladybirds such as *C. septempunctata* and *A. bipunctata* rarely survive after feeding on one an others' eggs. This might indicate that intraguild predation is probably rarer in the field than these laboratory experiments indicate.

The design of the experiments used to assess the incidence of intraguild predation has several weaknesses. Firstly, the number of prey is rarely manipulated in order to create ratios of intraguild and extraguild prey similar to those observed in the field. If anything, these experiments show that IGP only occurs when aphids are rare. Secondly, the predators are never presented with a choice. Finally, the cost of hunting and eating intraguild prey is rarely measured. When it is, it reveals that most species cannot survive on a diet of intraguild prey.

Finally, field experiments only detected a positive effect of the "top predator" on aphid abundance in 2 out of 7 experiments. Therefore, although interspecific predation may be widespread in aphidophagous guilds, it rarely meets the criteria of IGP. On the other hand, the high incidence of cannibalism in laboratory experiments and in the field indicate that this is the mechanism, rather than IGP, which accounts for the coexistence of many predators in aphidophagous guilds.

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References

Hemptinne, J-L., Dixon, A. F. G. & Gauthier, C. 2000. Nutritive cost of intraguild predation of *Coccinella septempunctata* and *Adalia bipunctata* (Coleoptera, Coccinellidae). European Journal of Entomology, 97, 559-562.

Hironori, Y. & Katsuhiro, S. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga, 42, 153-163.

Pimm, S. L. 1982. Food webs. Chapman & Hall, 219 p.

Polis, G. A. & McCormick, S. J. 1987. Intraguild predation and competition among desert competitions. Ecology, 68, 332-343.

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

Polis, G. A. & Holt, R. D. 1992. Intraguild predation : the dynamics of complex interactions. TREE, 7, 151-154.

Rosenheim, J. A., Wilhoit, L. R. & Armer, C. A. 1993. Influence of intraguild predation among generalist insect predators on hte 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.

Shellhorn, N. A. & Andow, D. A. 1999. Mortality of coccinellids (Coleoptera : Coccinellidae) larvae and pupae when prey become scarce. Environmental Entomology, 28, 1092-1100.

Snyder, W. E. & Ives, A. R. 2001. Generalist predators disrupt biological control by a specialist parasitoid. Ecology, 82, 705-716.

Takahashi, K. 1989. Intra- et inter-specific predations of Lady Beetles in spring alfalfa fields. Japanese Journal of Entomology, 57, 199-203.

Yasuda, H & Ohnuma, N. 1999. Effects of cannibalism and predation on the larval performance of two ladybird beetles. Entomologia Experimentalis et Applicata, 93, 63-67.