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ORIGINAL ARTICLE

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The role of antipredator behavior in an experimental community of jumping spiders with intraguild predation

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Abstract The role of direct and indirect interactions in intraguild predation (IGP) was investigated in a laboratory study. The study system contained two spider species, *Phidippus audax* and *Phidippus octopunctatus*, and the fruit fly, *Drosophila melanogaster*. *P. audax* and *P. octopunctatus* eat *D. melanogaster*. *P. audax* (top predators) also eat *P. octopunctatus* (intermediate predators). Thus, *P. audax* and *P. octopunctatus* compete for the shared resource and also interact as predator and prey. Experiments consisted of two treatments: risk-IGP and full-IGP. In the risk-IGP treatments, I examined the effects of trait-mediated indirect effects generated by antipredator behavior of *P. octopunctatus* on the survival of fruit flies. *P. audax* chelicerae were waxed so that *P. audax* could not attack a prey. The result indicated a significant positive indirect effect of *P. audax* on the survival of *D. melanogaster* due to the antipredator behavior of *P. octopunctatus* (a trait-mediated indirect effect). In the full-IGP treatments, *P. audax* chelicerae were not restricted, so that it could attack prey; this resulted in decreased survival of *D. melanogaster*. Because of predation of *P. audax* on *P. octopunctatus*, even stronger positive interactions occurred between *P. audax* and *D. melanogaster* in full-IGP than in risk-IGP.

Key words Indirect interactions · Foraging behavior · Trophic interactions · Salticidae · *Phidippus*

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Introduction

In the course of survival activities such as foraging and mating, species interact with one another either directly or indirectly, leading to various modes of species interactions. These interactions are categorized as either direct interactions or indirect interactions. Indirect interaction can be further classified as a density-mediated interaction (DMI) or a trait-mediated interaction (TMI). The importance of indirect interactions, particularly trait-mediated indirect interactions (TMII), is being recognized more now than previously (Bolker et al. 2002) as evidence of the prevalence of such interactions accumulates (Kerfoot and Sih 1987; Lima 1998; Schmitz 1998; McPeek et al. 2001; Peacor and Werner 2001). The open question is whether TMI, which occurs on a short time scale (e.g., through behavior), can routinely affect community dynamics, which operate on a relatively long time scale (Abrams 1992; Bolker et al. 2002).

In this study, I examined TMII and their relations with other types of interactions [i.e., density-mediated indirect interactions (DMII) and direct effect] in a simple intraguild predation (IGP) system of jumping spiders in the laboratory. The presence of antipredator behavior in spiders and the occurrence of IGP is well known (Polis 1988). IGP creates interactions of competition and predation within a system, which facilitates the various modes of species interactions (i.e., each species is directly and indirectly affected by every other species in the system). Consequently, careful assessment of the types of species interactions is important to understand the IGP system (Holt and Polis 1997). In this study, I tested the following hypotheses: (1) intermediate predators reduce their foraging activity in the presence of top predators, which in turn increases the survival of prey species, and (2) top predators also benefit prey by eating intermediate predators. As spiders digest prey externally (i.e., long handling time), prey have more time to escape while intermediate predators are being eaten by top predators. In addition, intermediate predators, if eaten as prey, would satiate top predators, which will decrease the predation rate of top predators on prey. Furthermore, by eating intermediate predators, top predators decrease the number of potential predators for the basal prey. Combined with the behavior-mediated indirect effect, this density-mediated effect creates even higher levels of positive indirect interactions between top predators and the basal prey.

Materials and methods

Study animals

Intraguild predation is ubiquitous among cursorial spider species (Suwa 1986; Polis 1988). The jumping spider species *Phidippus audax* and *Phidippus octopunctatus* are no exception. Jumping spiders of the genus *Phidippus* are the largest among the jumping spider taxa (Kaston 1948). Both species hunt visually (Hill 1979). These jumping spiders are generalist predators, eat largely the same prey species, and also prey on each other depending on the difference in size between each of the species; smaller individuals become the victims of IGP. In the present study, I used adult *P. audax* as the top predator, immature *P. octopunctatus* as the intermediate predator, and the fruit fly, *Drosophila melanogaster*, as the prey species [carapace widths were 3.76 ± 0.11 (mm) for *P. audax* and 1.91 ± 0.29 (mm) for *P. octopunctatus* (mean ± SE)]. An asymmetrical relationship exists between the two species because of their size difference; *P. audax* eats *P. octopunctatus*, but *P. octopunctatus* does not eat *P. audax*. Both spiders eat *D. melanogaster*. Therefore, *P. audax* and *P. octopunctatus* share the same prey species (competition), and *P. octopunctatus* are also potential victims of predation by *P. audax*. Thus, the system exhibits IGP.

Study systems

Risk-IGP system

First, a risk-IGP system was studied (Fig. 1). The system contained *P. audax* (top predators), *P. octopunctatus* (intermediate predators), and *D. melanogaster* (prey). The chelicerae of *P. audax* were glued together with wax so that no true predation by *P. audax* occured. However, the presence of *P. audax* induced antipredator behavior by *P. octopunctatus*.

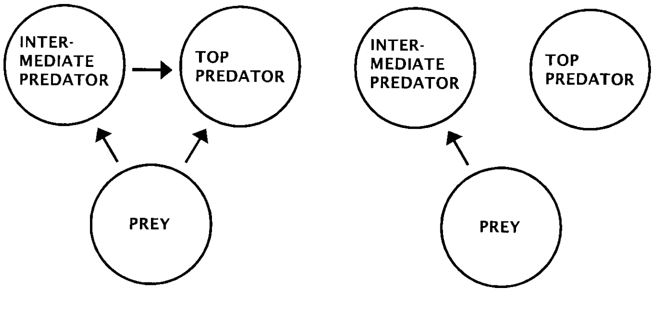

Fig. 1. Diagram of risk-IGP (*right*) and full-IGP (*left*). *Arrows* represent direction of energy flow by predation. IGP, intraguild predation

To observe the density dependence, four levels of *P. audax* densities (0, 1, 3, and 5 spiders) and three levels of *P. octopunctatus* densities (1, 3, and 5 spiders) were created. All possible density combinations were tested with 6 replications. In each trial, *P. audax*, *P. octopunctatus* and 20 *D. melanogaster* were introduced into a cylindrical container ($60\,\mathrm{cm}^2 \times 20\,\mathrm{cm}$) and left for 90 min. Preliminary observations indicated the vigilance behavior of *P. octopunctatus*. These spiders are so highly visual that they were also sensitive to the movement of the experimental observer. Therefore, to minimize external disturbance, the experiments were left unattended. At the end of the experimental period, the number of *D. melanogaster* that survived was scored. To control the satiation level of spiders, all the spiders except for *P. audax* were fed ad libitum for 2 days and subsequently starved for 2 days before being used in an experiment. *P. audax* were fed sufficiently until they were used in the experiment because even though their chelicerae were waxed, when they were starved, they still captured a prey and held it tightly and did not let go of it. By satiating *P. audax*, this nuisance effect was effectively removed. Feeding *P. audax* sufficiently could possibly alter their behavior from that of full-IGP system (described below). However, this effect would be negligible considering that the response of *P. octopunctatus* is highly visual and that just the presence of *P. audax* triggers their behavioral response.

Full-IGP system

This experiment was conducted to examine the results of various species interactions in IGP. The study system consisted of the same species as in the previous risk-IGP system, the only difference being that in full-IGP *P. audax* chelicerae were not manipulated. Hence, *P. audax* were free to attack both *P. octopunctatus* and *D. melanogaster* (see Fig. 1). Because risk-IGP and full-IGP are identical when there is no *P. audax*, this treatment (i.e., without *P. audax*) was not repeated in the full-IGP. Initially, cannibalism was anticipated and incorporated in the model. However, no cannibalism was observed so it was eliminated. The same satiation control was applied to all the spiders including *P. audax*.

Statistical analysis

The species interactions in the system were analyzed by using Poisson regression:

$$FL \sim \mathrm{Poisson}(\lambda)$$
$$\log(\lambda) = \beta_0 + \beta_1 PA + \beta_2 PO + \beta_3 PA \cdot PO$$

where FL is the number of *D. melanogaster* that survived from the initial population of 20 individuals; PA and PO are, respectively, the initial densities of *P. audax* and *P. octopunctatus*; $PA \cdot PO$ expresses the interaction between *P. audax* and *P. octopunctatus*; and β_0, β_1, β_2, and β_3 are the parameters of the model to be determined by regression.

In the risk-IGP experiment, the interpretations of the coefficients β_1, β_2, and β_3 are as follows. β_1 indicates the predation of *P. audax* on the flies. Because *P. audax* cannot eat in this experiment, *P. audax* should have no direct effect on *D. melanogaster*. Thus, we would expect the coefficient β_1 to be zero. β_2 indicates the magnitude of the predation of *P. octopunctatus* on flies; a large negative value indicates *P. octopunctatus* eats many *D. melanogaster*. β_3 describes the joint effect of the two species of the spiders on the flies. Because *P. audax* does not eat *P. octopunctatus*, the only interaction between the two species is the antipredator behavior of *P. octopunctatus*, a TMII; that is, there is an effect due to the perception of *P. octopunctatus* of a threat by *P. audax*. Therefore, a positive value for β_3 indicates that *P. octopunctatus* antipredator behavior increases the survival of the flies.

The full-IGP model was evaluated in the same way as in the risk-IGP model, and the interpretations of the coefficients are similar to those in the risk-IGP model. However, β_1 now represents the direct predation of *P. audax* on *D. melanogaster*, β_2 still describes the magnitude of predation of *P. octopunctatus* on *D. melanogaster*, and β_3 now combines both a TMI and a DMI. The interaction term between the two spider species now includes (1) reduction of the number of *P. octopunctatus* by *P. audax* from predation (DMII), and (2) effects of antipredator behavior by *P. octopunctatus*, due to the perception of threat from *P. audax* leading to reduced foraging activity (TMII). Because there are two effects involved rather than just the trait-mediated effect, β_3 may be higher in the full-IGP model compared with the risk-IGP model, if these indirect effects are additive. To compare the value of β_3 in the two models, a model with a dummy variable Z was formed:

$$\log(\lambda) = \alpha_0 + \alpha_1 PA + \alpha_2 PO + \alpha_3 PA \cdot PO + \alpha_4 PA \cdot PO \cdot Z + \alpha_5 PA \cdot Z$$

where $Z = 1$ for the risk-IGP trials and $Z = 0$ for the full-IGP trials. Under this model, the coefficient of $PA \cdot PO$ for the risk-IGP becomes $\alpha_3 + \alpha_4$, and the coefficient for the full-IGP is α_3. Therefore, by testing the significance of the parameter α_4, it is possible to determine whether the estimated values of β_3 from the risk-IGP and the full-IGP are significantly different.

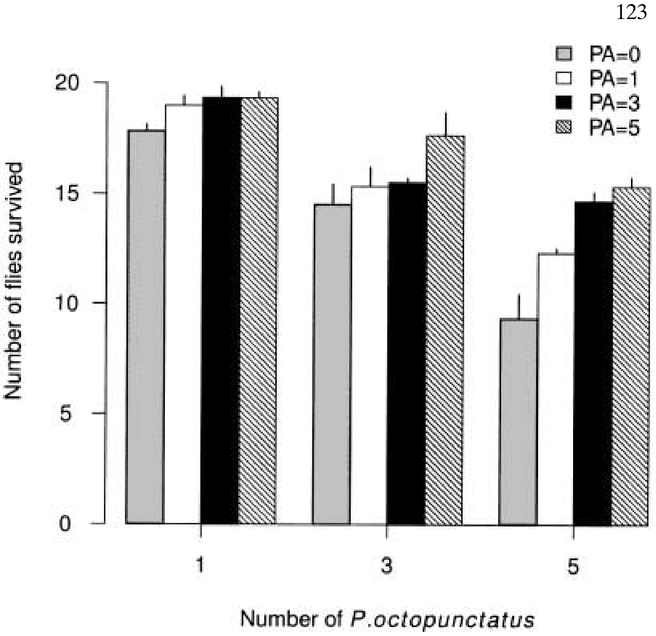

Fig. 2. Average number of flies that survived after the risk-IGP experiments. *PA*, number of *Phidippus audax*

Table 1. Coefficient table of the Poisson regression models

Experiment	Predictor	Coefficient	SE	χ^2	P
Risk-IGP	Constant	3.0561	0.0914	1117.752	0.0001
	PA	−0.008	0.0302	0.0696	0.7961
	PO	−0.1374	0.0293	21.947	0.0001
	PA·PO	0.0177	0.0094	3.5321	0.0602
Full-IGP	Constant	3.0173	0.0950	1008.3306	0.0001
	PA	−0.1351	0.0352	14.7406	0.0001
	PO	−0.1208	0.0299	16.3105	0.0001
	PA·PO	0.0325	0.0105	9.6018	0.0019

IGP, intraguild predation; PA, initial density of *Phidippus audax*; PO, initial density of *Phidippus octopunctatus*

Results

Risk-IGP model

The results from the risk-IGP experiments are summarized in Fig. 2. Fewer *D. melanogaster* survived when there were more *P. octopunctatus*. However, fewer flies survived when there were fewer *P. audax*, which indicates the positive indirect effect of *P. audax* on the flies. The regression coefficients for the risk-IGP model are shown in Table 1. Based on the Pearson chi-square ($Q_P = 13.231$, $df = 68$), the model fit was adequate. The interaction coefficient, β_3, was marginally significantly positive ($P = 0.0602$), indicating that the interaction between *P. audax* and *P. octopunctatus* may have a positive influence on *D. melanogaster* survival. To visualize the effect, results of the regression model obtained above were plotted (Fig. 3). It is clear from the figure that as the density of *P. audax* increases, the negative effect (predation) of *P. octopunctatus* on flies decreases.

Full-IGP model

Results from the full-IGP trials are summarized in Fig. 4. Overall, more flies were consumed by spiders in full-IGP than in risk-IGP experiments. The parameter estimates for full-IGP are shown in Table 1, and the number of *P. octopunctatus* eaten in the full-IGP experiment is shown in Table 2. Based on the Pearson chi-square ($Q_P = 20.771$, $df = 68$), the model fit was adequate. All the coefficients were significant (Table 1). As in the risk-IGP model, the regression model was plotted by the densities of *P. audax* to visualize the effects (see Fig. 3). As the density of *P. audax*

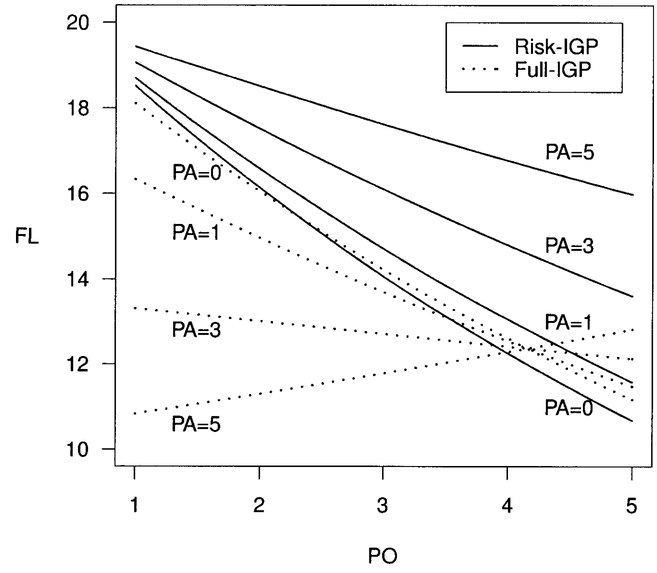

Fig. 3. Regression plots of the IGP systems. *PA*, number of *P. audax*; *PO*, number of initial *P. octopunctatus*; *FL*, number of flies that survived

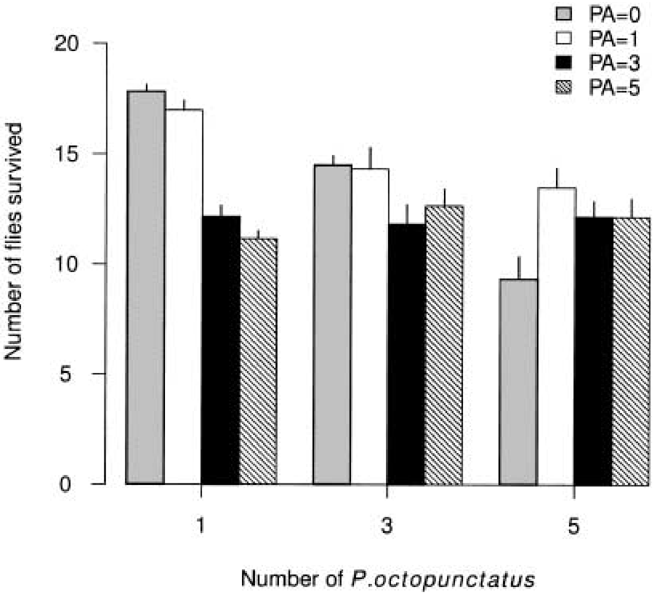

Fig. 4. Average number of flies that survived after the full-IGP experiments. *PA*, number of *P. audax*

Table 2. The number of *P. octopunctatus* eaten in the full-IGP experiments

	PO		
PA	1	3	5
1	5-1-0-0	3-3-0-0	3-3-0-0
3	2-4-0-0	2-2-1-1	1-2-3-0
5	3-3-0-0	2-2-1-1	1-2-1-2

The maximum number eaten in a trial was 3; in each cell, the numbers are the numbers of trials in which 0, 1, 2, or 3 *P. octopunctatus* were eaten, respectively (i.e., the number of each cell add up to 6 trials)
PA, number of *P. audax*; PO, initial number of *P. octopunctatus*

increased from 0 to 5, the risk of density-dependent mortality of *D. melanogaster* by *P. octopunctatus* shifted from a negative relationship to a positive relationship when $PA = 5$.

The estimated value for α_4 was -0.019 and was significant ($z = -2.078$, $P = 0.0377$), indicating β_3 that from the risk-IGP model and the full-IGP model were significantly different.

Discussion

The results of the experiments clearly show the significant effects of TMII. I hypothesized that the presence of *P. audax* would decrease foraging activity by *P. octopunctatus*, which in turn would decrease predation by *P. octopunctatus* on *D. melanogaster*. The results of these experiments support this hypothesis. It is especially clear in the risk-IGP trials. In the risk-IGP system, a TMII had a beneficial influence on the survival of flies. This TMII was caused by a change in the foraging behavior of *P. octopunctatus*. *P. octopunctatus* was expected to decrease foraging behavior when *P. audax* were present because of the predation risk, and this response was density dependent. Because there was no predation by *P. audax*, the effect is a pure TMII.

In the full-IGP experiment, the effect of the interaction between *P. audax* and *P. octopunctatus* was even greater than that of the risk-IGP trials, which may be attributed to the addition of DMII in the full-IGP. The DMII in this system is explained by *P. audax* eating *P. octopunctatus*, decreasing the number of potential predators of flies. Furthermore, because spiders digest food externally, while a spider is eating it is unable to begin foraging. In other words, *P. octopunctatus* not only helped flies by being eaten (i.e., reduction of the effective predators) but also helped the flies to survive longer. As discussed earlier, the satiation level of top predators is also affected by the intraguild predation. These results may be criticized as an artifact of the short experimental time. However, the feeding behavior of spiders is real, and we would expect different modes of TMII to arise depending on such behaviors (e.g., external feeders as opposed to filter-feeding organisms). Unlike TMI, a density-mediated effect is propagated by deaths of transmitter species, and thus the structure of the food web is more drastically altered by DMI. In TMI, on the other hand, the basic organization of the food web is affected only minimally. For this reason, for a food web as a whole, TMI might play an important role in the stability of the community.

In this study, I did not consider the antipredator behavior of *D. melanogaster* as an important factor because these flies were insensitive to the presence of the spiders. Flies walked often toward a spider and even walked on a spider.

Adaptive foraging behavior by *P. octopunctatus* has both positive and negative influence on *D. melanogaster*. The positive effect is TMII, as already discussed. The negative effect arises by *P. octopunctatus* avoiding predation by *P. audax*. It becomes more difficult for *P. audax* to capture *P.*

octopunctatus, which may make *P. audax* attack *D. melanogaster* more. Because the present study was conducted in a small arena, the presence of such an interaction is not obvious. However, in the field, *P. octupunctatus* would be able to avoid the predator more effectively, which may cause different interactions among direct and indirect effects and result in different population dynamics.

Although it will require more thoughtful experiment, in the full-IGP trial, it is valuable to quantify the relative contribution of TMII and DMII to the positive indirect interactions. Careful evaluation of the characteristics of the interactions (e.g., linear vs nonlinear) is important. For example, we have to keep in mind that the additive terms under the log-linear link of the Poisson regression are multiplicative in real space. Does the relative composition of TMII and DMII change according to some rule? If so, quantifying such characteristics will benefit our understanding of indirect interactions in community processes.

Due to the rather artificial setting used in this experiment, the results found here cannot be extrapolated to a jumping spider community in the field. However, these jumping spiders coexist in high abundance in the field, and vigilance behavior is commonly observed. Consequently, the present study implies a potentially significant role of these indirect interactions in the jumping spider community, and further studies are awaited.

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