THE IMPLICATIONS OF INTRAGUILD PREDATION FOR THE ROLE OF SPIDERS IN BIOLOGICAL CONTROL

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ABSTRACT. Evidence is growing that spiders can be effective biological control agents, particulary assemblages of several species. Other evidence finds that spiders prey on each other and other generalist predators, and as such are of limited value in biological control. Such predatory interactions between species which use similar resources have been dubbed intraguild predation (IGP) due to their potential to modify competition as well as cause direct mortality. IGP interactions can have unexpected effects at other trophic levels, and sometimes result in enhancement of a pest population. In this paper I review the evidence for intraguild predation interactions involving spiders in natural systems, and other generalist predators in agroecosystems. To date not much research has examined whether such interactions influence spider biological control potential. Some suggestions as to how we might begin to address these issues are presented.

Given their generalist arthropod diet and abundance in most terrestrial habitats, spiders likely inflict substantial mortality on insect populations. While the mechanisms by which spiders limit insect prey populations have been debated (Riechert & Lockley 1984; Wise 1993), it is generally agreed that they are important in reducing insect numbers, and as such are of potential value in biological control (Riechert & Lockley 1984; Nyffler & Benz 1987; Young & Edwards 1990; Wise 1993). Several studies have shown that assemblages of many predator species may be more effective at controlling agricultural pests than single species augmentation (Chiverton 1986; Riechert & Bishop 1990; Clark et al. 1994; Provencher & Riechert 1994; Chang 1996; Riechert & Lawrence 1997). On the other hand, different species of predators and/or parasitoids may compete with or prey on each other, potentially reducing their biological control potential (Force 1974; Ehler & Hall 1982; Spiller 1986; Briggs 1993; Rosenheim et al. 1995; Chang 1996; Ferguson & Stiling 1996; Kester & Jackson 1996; Cisneros & Rosenheim 1997; Rosenheim 1998).

The nature of the diet of spiders suggests that they can prey on each other and other arthropod predators (Polis 1981; Jackson 1992; Wise 1993), as well as overlap in prey taxa consumed, thus potentially competing for resources. Diet overlap is one distinguishing feature of a guild, a group of sympatric taxa

that use similar resources (Root 1967; Polis et al. 1989; Simberloff & Dayan 1991). Predatory interactions among members of the same guild are termed intraguild predation (IGP). This is distinguished from predation as traditionally defined because, by eating a guild member, an individual not only directly gains energy and nutrients, but also reduces potential competition for food (Polis et al 1989; Polis & Holt 1992). Intraguild predation and cannibalism (killing and eating a member of the same species), may have profound effects on community structure (Polis 1981, 1988; Polis et al. 1989; Polis & Holt 1992). Given their ubiquity in terrestrial ecosystems, spiders are model organisms to investigate the occurrence and consequences of IGP.

IGP: predation among potential competitors.—Intraguild predation and cannibalism have been shown to directly limit predator populations (Polis & McCormick 1986, 1987; Spiller & Schoener 1988; Wissinger 1989; Leonardsson 1991; Finke 1994; Wagner & Wise 1996; Wissenger et al. 1996). Since unsuccessful predation attempts represent extreme forms of interference competition (Polis et al. 1989; Elgar & Crespi 1992), IGP can also lead to behavioral adaptations to reduce mortality and conflict, resulting in habitat and diet shifts by IG prey (Fox 1975; Turner & Polis 1979; Doncaster 1992; Sih 1982; Ebenman & Persson 1988; Foster et al. 1988; Polis et al. 1989; Polis 1993; Dong & Polis 1992;

Holt & Polis 1997). These changes in foraging and habitat distribution may in turn have effects at other trophic levels (Polis 1984; Wilbur 1988).

The traditional view of feeding relationships has been to assign species in a community to a ''trophic-level'', such as secondary consumer (predator), primary consumer (herbivore), primary producer (plant), and so forth, with each level feeding on the former (Krohne 1998). Thus, in classic biological control, insect herbivore populations are reduced by addition of predators, and this in turn reduces damage to crop plants (van den Bosch et al. 1982). In reality, however, animals may feed from a variety of trophic levels, especially generalist predators, which take prey of whatever size they can handle (Polis 1988; Polis et al. 1989; Spence & Carcamo 1991; Dong & Polis 1992; Finke 1994). If these prey include younger conspecifics or other predators, then control of the herbivore population is not guaranteed. Various studies suggest that direct effects of one predator on another can indirectly affect a shared prey species by releasing it from intense predation or competition (Press et al. 1974; Pacala & Roughgarden 1984; Hurd & Eisenburg 1990; Polis & Holt 1992; Rosenheim et al. 1993; Wissinger & McGrady 1993; Wootton 1993; Cisneros & Rosenheim 1997; Fagan & Hurd 1994). If shared prey are herbivores then the indirect effects could cascade to plants, influencing primary productivity, an issue of agricultural relevance. The purpose of this paper is to review the theory and empirical evidence relevant to the implications of IGP for the potential role of spiders in biological control of herbivorous pests in agriculture.

IGP between spiders and other generalist predators.—Several studies of IGP in natural communities have uncovered direct and indirect interactions involving spiders. Polis & McCormick (1986, 1987) investigated a desert community of arachnids including spiders, solpugids and scorpions, all generalist predators that use similar prey and prey on each other. Scorpions were continually removed from experimental plots, but not from control plots, and the relative abundances of the spiders and solpugids were tracked over time. At the end of the experiment (29 months), significantly more spiders occurred in the scorpion removal plots than in the control plots.

Two alternative hypotheses could explain these results: removal of the scorpions could have resulted in competitive release by the spiders in experimental plots, or IGP (by scorpions) in the control plots may have reduced spider population size. There was no evidence of competitive release in that there were no differences between the experimental and control plots in insect prey abundance or spider reproduction. Release from scorpion predation was the most likely cause of the increased numbers of spiders.

Two independent studies on *Anolis* lizards examined evidence for intraguild predation on spiders cascading to populations of shared insect prey. Pacala & Roughgarden (1984) manipulated anole densities in a Carribean forest and found a direct effect of lizards on forest floor arthropods, their primary prey, and an indirect effect on flying insects, the prey of orb-weaving spiders. Since anoles also prey on orb-weavers, the increase in flying insects on the high density lizard plots was thought to be due to intraguild predation by the lizards on the spiders. On Bahamian islands Spiller & Schoener (1990) also found a direct effect of lizards on spiders, but no indirect effect on flying insects. They did, however, observe that more spiders were feeding on lizard removal plots than on plots where they co-existed with lizards. The authors hypothesized that interference competition or predation by lizards may displace spiders from prime web-sites, resulting in a reduction in prey capture for the spiders.

Although the generalist diet of most spider species suggests that exploitative competition for food should be important (Marshall & Rypstra, this volume), experimental tests have found little evidence (Schaefer 1978; Wise 1981; Horton & Wise 1983; Riechert & Cady 1983; see Spiller 1984 a, b for an exception). In spider removal experiments to test for exploitative competition among four genera of web-building spiders, Riechert & Cady (1983) not only found no competitive release, but on some of their removal plots they observed a negative effect of spider removals on the species remaining. They hypothesized that this may have been due to the fact that by removing the other species of spiders, they may have been removing potential prey.

Hodge & Marshall (1996) tested Riechert & Cady's hypothesis that intraguild predation

masked competitive release in their system of web-building spiders on rock outcrops in Tennessee. After 12 weeks of removing each of three species from experimental plots we found that one of the species, *Hypochilus thorelli* (Araneae, Hypochilidae) had lower body condition indices (indicating lower fecundity, Jakob et al. 1996) on spider removal plots as compared to control plots. This species was the major intraguild predator in the system, with spiders comprising over 40% of its diet (Riechert & Cady 1983; Hodge & Marshall 1996). These results support Riechert & Cady's interpretation of the lack of competitive release in their study. Another species, *Achaearanea tepidariorum* (Araneae, Theridiidae) exhibited greater spiderling populations on rock outcrops from which the other two species had been removed as compared to control plots, suggesting that the manipulation removed predators (Hodge & Marshall 1996). The fact that this study found IGP-related effects was striking given that the removals occurred over a relatively short time frame.

Hurd & Eisenberg (1990) examined how interactions between praying mantises (*Tenodera sinesis*) and wolf spiders (*Lycosa* (*Rabidosa*) *rabida*) affected overall arthropod numbers in a temperate early successional field habitat. They established four treatments, each of which enclosed a cubic meter of old-field vegetation in screen cages: mantids alone, wolf spiders alone, mantids and wolf spiders, and a control with neither predator added, and then sampled the number and biomass of other arthropods after 10 days. The 'mantids alone' enclosures had lower arthropod biomass than any of the other treatments. Examining the arthropods on a taxa-by-taxa basis revealed that in the 'wolf spiders alone' treatments there was a significant increase in the density of crickets as compared to the other treatments. The explanation for this counter-intuitive result illustrates the complexity of direct and indirect effects that can result from IGP interactions. The authors concluded that interactions between wolf-spiders (as evidenced by some cannibalism) decreased their effectiveness as predators on crickets, and that in mantid/lycosid enclosures this effect was ameliorated because of mantid impact on spider numbers (an indirect effect of mantids on crickets). The presence of lycosids on the ground caused the crickets to move upward on vegetation (a direct effect of spiders on crickets); but when present with both mantids and lycosids, crickets were captured by mantids hunting in the vegetation. Finally, lycosids may have consumed other cricket predators (other spiders; an indirect effect of spiders on crickets); this was supported by the finding that there were significantly fewer heterospecific spiders in the lycosid enclosures. These results should be of interest to biological control because mantids are often augmented, at least in small scale crop systems. On the other hand one may question the reality of this experiment since many predators were packed into small enclosures, whereas normally they could flee from one another.

Enclosure effects were not a factor in the open-plot studies performed by Moran & Hurd (1994) in the same system. They added first instar mantids to 2 m × 2 m plots separated by 2 m wide barriers of black plastic sheeting which had a band of insect trapping compound painted down the middle to intercept arthropods leaving the plots. By comparing arthropods captured around mantid addition plots to those captured around control (no mantids) plots, they discovered a behavioral response by spiders to the presence of elevated mantid densities. Spiders dispersed from plots in which mantids were augmented. Smaller spiders (< 8 mm) are prey of the mantids whereas larger spiders (primarily wolf spiders) prey on the mantid nymphs and smaller spiders. Larger wolf spiders may have departed mantid addition plots because smaller spiders had dispersed. In this case the threat of IGP caused smaller spiders to leave, and scarcity of this IG prey caused the larger spiders to leave. Addition of supplemental food (*Drosophila*) reduced the tendency for spiders to emigrate from mantid augmented plots (Moran & Hurd 1997). This in turn increased IGP by spiders on mantids, as their numbers tended to decline in the food supplemented plots. As the authors point out, alternative prey does not always benefit generalist predators if they can prey on one another.

These authors extended their investigation to include the possibility of trophic cascades (Moran et al. 1996; Moran & Hurd 1998). Of interest was how a diverse plant community would respond in the context of an assemblage of many predator and herbivore species.

In these experiments, control plots had no mantids, and experimental plots had natural densities of mantids. Cursorial spiders emigrated from mantid plots throughout the course of the study (2 months) (Moran et al. 1996). Early emigration was probably due to the threat of IGP by mantids, whereas later emigration may have been a result of competition for prey, since mantid numbers at this point in time were too low to cause predator avoidance. Herbivore biomass was significantly lower and plant biomass was 30% higher in the mantid addition plots by the end of the experiment. Mantids therefore caused a trophic cascade that extended to plants.

These studies demonstrate that, contrary to theoretical predictions that interactions between trophic levels in complex communities will be diffuse and buffer the intensity of responses of any given species to another (Strong 1992), a single predator in a speciose natural assemblage can indeed initiate a trophic cascade. Perhaps this bodes well for potential predator influences on primary production in less speciose agroecosytems: that is, despite the potential for IGP, strong interactions can cascade through trophic levels in such a way as to benefit crops. On the other hand, these strong interactions could be such that IGP interactions disrupt rather than enhance the control of herbivore populations (Rosenheim et al. 1993; Rosenheim 1998).

IGP in agroecosystems.—The fact that the self-limiting nature of spiders (via interference, territoriality or araneophagy) can decrease their potential as biological control agents has been recognized (Reichert & Lockley 1984; Wise 1993), but rarely quantified. The bulk of my review will therefore cover experimental studies involving IGP among arthropod generalist predators other than spiders, since they have as yet not been well studied.

Rosenheim et al. (1993) examined interactions between three species of predatory hemiptera (*Geocoris* spp., *Nabis* spp., and *Zelus renardii*) and green lacewing larvae (*Chrysoperla carnea* (Neuroptera)), all of which eat aphid pests (*Aphis gossypii*) of cotton. To determine whether hemipteran predators exert mortality on lacewings, they caged cotton plants with aphids alone (control), and aphids with various combinations of the hemipterans. Lacewing survival was significantly reduced in the presence of bugs. To isolate the influences of predation cotton plants were caged with a variety of combinations of predators: each hemipteran species alone or in combination with lacewing larvae (with appropriate controls). Lacewing survival was significantly lower in the *Z. renardii* and *Nabis* spp. treatments. Comparing aphid population growth among the single-predator species treatments, only in those cages with lacewing larvae alone was there a significant impact on aphids, suggesting that of all of these predator species, lacewings are the most effective at aphid control. Given these results, it is not suprising that cages with lacewing larvae and *Z. renardii* or *Nabis* spp. exhibited a non-additive effect on aphid population control. Not only were the effects non-additive, but aphid populations actually increased in these treatments. Therefore, predator interference generated a trophic cascade, increasing the abundance of herbivores.

They also examined the effect that nymphal hemipterans can have on lacewing eggs. The presence of hemipterans reduced the proportion of lacewing eggs surviving to larval stages. Cisneros & Rosenheim (1997) examined the effect of predation by *Z. renardii* of different age-size classes on control of cotton aphid populations by lacewing larvae. Survival of lacewing larvae was significantly lower in the presence of larger, older *Zelus*, and this produced a significant disruption of lacewing control of aphid populations. Observations of freely foraging bugs in the field showed an ontogenetic shift in foraging height and foraging behavior resulting in higher encounter rates between *Zelus* adults and other predators (Cisneros & Rosenheim 1998).

Another study of aphidophagous predators examined interactions between generalists and specialists and evaluated predator mobility as a potential factor influencing vulnerability to IGP (Lucas et al. 1998). The predators were lacewings (*Chrysoperla rufilabris*), spotted lady beetles (*Coleomegilla maculata*), both generalists, and larvae of the gall midge (*Apidoletes aphidimyza*), a specialist on the shared prey, potato aphids (*Macrosiphum euphorbiae*). The lacewing and lady beetles are very active foragers as larvae and adults, whereas gall midge larvae are slow-moving predators.

IGP interactions between all three predators

were investigated in the absence of aphid prey. Various combinations of predators at different developmental stages (egg-adult) yielded 37 different test combinations. Symmetric IGP occurred between lacewings and lady beetles; that is, larger developmental stages of one predator fed on smaller developmental stages of the other. A few exceptions were explained by behavioral and morphological differences between the predators. Third instar lacewings were able to prey on larger fourth instar lady beetles as well as adult beetles. It may be that a more aggressive hunting style and effective grasping mouthparts of lacewings allow them to defy the general trend that the larger predator wins (Lucas et al. 1998). Interactions between both lacewings and lady beetles with gall midges were asymmetric: gall midges were almost never IG predators. This confirmed the authors' prediction that more mobile predators have an advantage over slow moving predators.

In the presence of shared or extraguild prey (potato aphids) IGP was lower in several of the predator/life-stage combinations. Some of the IGP interactions persisted though, except when extraguild prey densities were very high. Based on the outcomes of IGP interactions between their different predators at various levels of extraguild prey, Lucas et al. (1998) developed some general predictions as to the effect of extraguild prey and predator characteristics on the direction and outcome of IGP interactions. In cases where both predators forage randomly, IGP will decrease steadily with increasing extraguild prey. Random search will, in this case, bring predators into contact with extraguild prey more often. When IGP interactions are risky for both predators, IGP should decrease exponentially as extraguild prey increases in density. Abundance of alternative prey has similarly been observed to influence the tendency towards cannibalism in many animals (Elgar & Crespi 1992). In some cases IGP may remain constant despite increasing extraguild prey, especially if IG prey are vulnerable, sessile and/or aggregated. Finally, IGP may remain high at low extraguild prey densities, and only decline at very high extraguild prey densities. When extraguild prey are at low density, IG predators may benefit from removing potential competitors, whereas at high prey density this benefit disappears. Overall, the theme that

unifies all of these predictions, and all of the experimental studies presented above, is that a detailed understanding of the ontogeny, behavior and ecology of predators and prey is required to understand the role that IGP plays in the dynamics of complex communities, including agroecosystems.

IGP & spiders in agroecosystems.— Though some research has been conducted evaluating the effectiveness of spiders as biocontrol agents in agroecosystems (Riechert & Bishop 1990; Clark et al. 1994; Provencher & Riechert 1994; Carter & Rypstra 1995; Riechert & Lawrence 1997), there has been scant research on their potential interactions with other predators. Fagan et al. (1998) discovered an unpredicted interaction between IGP, pesticide application and biological control. They set out to examine the compatibility of insecticide-based and natural enemy-based pest control methods in tropical rice. Using opentop cages (to ameliorate enclosure effects) they established four treatments: insecticide added, wolf spiders added, both insecticide and wolf spiders added, nothing added. As would be predicted, rice pests were lower in the insecticide and wolf spider treatments, and each reduced pest densities to similar levels. The combination of insecticide and wolf spider addition, however, resulted in an increase in pests such that these enclosures were indistinguishable from the controls. They attribute these results to the additive impact of spiders and insecticide on predatory hemipterans (mesoveliids) which are also important biological control agents of rice pests. The combination spider-insecticide treatment lowered the densities of these alternative predators below the threshold of effective biological control. This study has important implications for integrated pest management, and further illustrates the importance of a clear understanding of the role of IGP in agricultural systems.

Given the general lack of experimental studies, what evidence (beyond Fagan et al. 1998) do we have that IGP involving spiders might be important in agroecosystems? Several studies have documented that spiders do engage in IGP interactions with other generalist predators, and many of these observations come from crop systems (Table 1). These data were gleaned from tables in primary research papers and from several reviews of spider diets by Nyffeler and col-

Table 1.—A survey of the literature containing field observations of the spectrum of prey captured by a variety of spider species focusing on taxa that are potentially intraguild prey. The percent of the total observed diet for the majority of species in the list is obtained from a total number of observed prey exceeding 50.

IG predator	IG prey taxon	% of diet	Habitat	Source
Araneidae:				
Argiope bruennichi	Araneae	3.3	Grassland	Nyffeler 1982
Linyphiidae:				
Oedothorax insecticeps	Araneae	16.3	Rice	Kiritani et al. 1972
Theridiidae:				
Latrodectus mactans	*Solenopsis invicta*	75.3	Cotton	Nyffeler et al. 1988
Achaearanea tepidariorum	Araneae	22	Rock outcrop	Hodge & Marshall 1996
Lycosidae:				
Paradosa spp.	Araneae	6.8	Winter Wheat	Nyffeler & Benz 1988
Paradosa ramulosa	Araneae	19.6	Alfalfa	Yeargan 1975
Lycosa pseudoannulata	Araneae	8.9	Rice	Kiritani et al. 1972
Lycosa antelucana	Lycosidae	4	Cotton	Hayes & Lockley 1990
Lycosa antelucana	Staphylinidae	6.7	Cotton	Hayes & Lockley 1990
Lycosa antelucana	Carabidae	10.9	Cotton	Hayes & Lockley 1990
unspecified	Araneae	19.2	Peanuts	Agnew & Smith 1989
Pardosa lugubris	Araneae	24	Forest	Edgar 1969
Pardosa lugubris	Araneae	34	Forest	Hallander 1970
Pardosa amentata	Araneae	11	?	Edgar 1970
Pardosa pullata	Araneae	38	Meadow	Hallander 1970
Pardosa purbeckensis	Araneae	23	Salt Meadow	Nyffeler & Benz 1988
Pardosa ramulosa	Araneae	20	Alfalfa	Yeargan 1975
Pardosa hokkaido	Araneae	12	Forest	Suwa 1986
Pirata piraticus	Araneae	22	Salt Meadow	Schaefer 1974
Pirata piraticus	Araneae	28	River Bank	Gettmann 1977, 1978
Pardosa agrestis	Araneae	16	?	Nyffeler 1982
Lycosa osceola	Araneae	27.5	Florida scrub	Hodge, unpublished
Lycosa pseudoceratiola	Araneae	9	Florida scrub	Hodge, unpublished
Oxyopidae:				
Oxyopes salticus	Araneae	15.9	Cotton	Nyffeler et al. 1992
Oxyopes salticus	Araneae	14.1	Cotton	Nyffeler et al. 1987a
Oxyopes salticus	Araneae	9	Cotton	Nyffeler & Sterling 1994
Peucetia viridans	Araneae	40	Cotton	Nyffeler et al. 1987b
Peucetia viridans	Hemiptera	8	Cotton	Nyffeler et al. 1987b
Peucetia viridans	Neuroptera	8	Cotton	Nyffeler et al. 1987b
Peucetia viridans	Araneae	16	Croton	Nyffeler et al. 1987b
Peucetia viridans	Araneae	13.3	Peanuts	Agnew & Smith 1989
Peucetia viridans	Araneae	7	shrubs	Turner 1979
various	Araneae	15	?	Nentwig 1986
Thomisidae:				
Xysticus spp.	Araneae	6.4	Meadow: Plants	Nyffeler 1982
Xysticus spp.	Araneae	26	Meadow: Soil Surface	Nyffeler 1982
Misumenops spp.	Araneae	16.7	Peanuts	Agnew & Smith 1989

Table 1.—Continued

IG predator	IG prey taxon	% of diet	Habitat	Source
Salticidae:				
Phidippus audax	Araneae	22.2	Wild Plants & Cotton	Dean et al. 1987; Nyffeler et al. 1994
Phidippus audax	Araneae	15.5	?	Young 1989
Phidippus johnsoni		27	?	Jackson 1977
various	Araneae	20	?	Nentwig 1986
Amaurobiidae				
Coras montanus	Araneae	24	Rock outcrop	Hodge & Marshall 1996
Hypochilidae				
Hypochilus thorelli	Araneae	46	Rock outcrop	Hodge & Marshall 1996
Pisauridae				
Pisaura mirabilis	Araneae	18	?	Nitzsche 1981
Pholcidae				
Pholcus phalangiodes	Araneae	6	Cellars	Nentwig 1983
Scytodidae				
Scytodes longipes	Araneae	17.4	outside buildings	Nentwig 1985
Unspecified Araneae	Hemiptera	14.5	Peanuts	Agnew & Smith 1989
	Araneae	17.3	Peanuts	Agnew & Smith 1989

leagues. Higher levels of IGP might have been reported in some cases if more specific taxonomic categories were used, for example, breaking insect orders into families which often exhibit characteristic feeding habits (e.g., Carabidae rather than Coleoptera). Even so, it is not uncommon to find spider diets consisting of almost one-fifth IG prey (mean for Table 1 = 18.3% ± 12.7%).

It is hard to form any general conclusions based on the data in Table 1 since the list is not comprehensive, and the methodology and intensity of data collection vary among studies. The most striking feature, however, is the number of studies involving lycosids and oxyopids in agricultural systems, and the sometimes high percentage of IG prey reported from these spiders (e.g., 40% Araneae in the diet of *Oxyopes salticus*). It may be that cursorial spiders dominate as IG predators due to their active hunting style (Lucas et al.1998; Cisneros & Rosenheim 1998). It would be quite informative to have greater taxonomic resolution to the IG prey reported, to see if they are represented disproportionately by less mobile predators. This type of resolution would also suggest the types of direct and in-direct effects that might cascade to herbivores and crops.

CONCLUSIONS

How can we determine the implications of IGP for the role of spiders in agroecosystems? How does one begin to identify which of a suite of predators present in a particular crop have the potential for IGP interactions? Classification systems exist for spider guilds (Uetz et al., this volume), predator and herbivore guilds in crops (Breene et al. 1993) and structural zones in crop plants which may support distinct suites of predator and prey species (e.g., LeSar & Unzicker 1978). Using these as a starting point, one can begin to define potential predator-predator and predator-herbivore interactions in which IGP may be of consequence. Quantification of the potential for IGP and/or competition should be achieved by careful study of the relative densities, habitat use, activity period and space, and diet. From these measures one can calculate indices of the opportunity for predation (IOP) and the opportunity for competition (IOC), as derived by Wissinger (1992) from pre-existing indices of resource overlap (Hurlbert 1978). Wissin-

ger's indices allow for comparisons of the relative strengths of predation, cannibalism, and resource competition between and within species by quantifying these interactions in the field and laboratory (Wissinger 1992). In a sense, they simply involve collecting the relevant natural history information about each species, and quantifying this information to make specific predictions of the relative importance of cannibalism, IGP and intra- or interspecific competition. This allows the design of more rigorous and meaningful field experiments (Wissinger 1992).

Future field experiments should heed lessons from the past regarding the use of enclosures and the duration of experiments. Stocking closed cages with predators may not reveal information relevant to the real world; and responses in the short term may lead to very different conclusions than might be reached from experiments of duration more similar to the actual seasonality of the particular system (Wise 1993; Moran & Hurd 1994, 1998), and should be repeated across years to detect the effects of temporal variability (Polis et al. 1998).

Despite the recent revival of interest in food web interactions, (''top-down'' versus ''bottom-up'' effects) and the complex nature of feeding relationships (Strong 1992; Polis 1994; Polis & Strong 1996; Polis & Winemiller, 1996; Holt & Polis 1997), the scenario still generally used for biocontrol is that of a 3-tiered system in which herbivores eat plants, and in turn are eaten by predators. As the studies reviewed in this paper demonstrate, animals do not recognize these artificial trophic boundaries, and often feed from several trophic levels. This can generate a complex array of direct and indirect effects which can have important and unexpected consequences for the effectiveness of generalist predators as biological control agents. The paucity of experimental research on the potential web of IGP interactions involving spiders is surprising since they are widely recognized as model organisms for the types of manipulative field studies used to investigate these interactions (Polis 1993; Wise 1993). Other generalist predators studied to date (hemiptera, lacewings, beetles) are similar in nature to spiders in that they include animals with a both sit and wait and active foraging hunting styles, and also involve animals with distinct size

classes, generating possibilities for both cannibalism and intraguild predation between different life stages of different predator species. Given the variety of crop systems, management practices (e.g., tillage versus no-tillage), and diverse predator and prey assemblages, agricultural systems provide models for investigating the role of IGP from both pure and applied perspectives.

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