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Spider Predation in Agroecosystems: Can Spiders Effectively Control Pest Populations?

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SPIDERS AS PREDATORS IN AGRICULTURAL ECOSYSTEMS

Recent trends in agriculture towards reduced pesticide use and ecological sustainability have lead to increased interest in spiders as potential biological control agents. Although the Chinese have augmented spider populations in field crops as a pest management strategy for centuries, much debate remains as to whether spiders will effectively control pest populations in U.S. agricultural ecosystems (Riechert and Lockley 1984; Riechert and Bishop 1990; Riechert 1999; Greenstone and Sunderland 1999). For a predator to effectively and economically control an insect pest, the predator must be capable of not only reducing pest densities to levels below an economic threshold, but also to stabilize those pest densities over time. If the pest population is not stable, the predator may drive the prey to local extinction, then die off itself, thus allowing for the potential of an unchecked secondary pest outbreak in the absence of this predator (Morin 1999; Pedigo 2001). Spiders may be capable of fulfilling both of pest reduction and pest stabilization requirements.

According to Hairston et al. (1960), herbivore populations are not limited by competition for food. This idea is supported by the observation that green plants are abundant. Therefore, it is theorized that herbivores must be limited by predation. However, in many agricultural systems repeated physical and chemical disruptions have led to local extirpation of predators. Herbivores, released from control by predators, sometimes become abundant to the point of severely damaging crop plants. If a predator could be established that would feed upon these herbivores, their numbers might be lowered. Spiders may be such a predator (Sunderland 1999).

Although the spiders (Araneae) are a diverse arachnid order consisting of more than 3500 species in North America (Young and Edwards 1990), all are obligate predators, and many feed upon herbivorous pest insects. The orb-web weavers Araneidae and Tetragnathidae feed upon Homoptera such as leafhoppers, Diptera, and Orthoptera, especially grasshoppers. The smaller, sheet-web weavers such as Linyphiidae, Dictynidae, and Theridiidae capture Diptera, Hemiptera, and Homoptera (especially aphids and leafhoppers), as well as beetles in the family Curculionidae. The funnel-web weavers (Agelenidae, Atypidae, Ctenizidae, and Eresidae) prey upon Orthoptera, Coleoptera, and Lepidoptera (Riechert and Bishop 1990; Nyffeler et al. 1994a). Hunting spiders, (Lycosidae, Oxyopidae, Thomisidae, and Salticidae) frequently capture Orthoptera, Homoptera, Hemiptera, Lepidoptera, Thysanoptera, Diptera, and some Coleoptera and Hymenoptera (Riechert and Bishop 1990; Young and Edwards 1990; Nyffeler et al. 1994a).

REDUCTION OF INSECT PEST DENSITIES BY SPIDERS

Many studies have demonstrated that spiders can significantly reduce prey densities. Lang et al. (1999) found that spiders in a maize crop depressed populations of leafhoppers (Cicadellidae), thrips (Thysanoptera), and aphids (Aphididae). The three most abundant spiders in winter wheat, *Pardosa agrestis* (Westring) and two species of Linyphiidae, reduced aphid populations by 34% to 58% in laboratory studies (Marc et al. 1999). Both web-weaving and hunting spiders limited populations of phytophagous Homoptera, Coleoptera, and Diptera in an old field in Tennessee (Riechert and Lawrence 1997). Spiders have also proven to be effective predators of herbivorous insects in apple orchards, including the beetle *Anthonomus pomorum* Linnaeus, and Lepidoptera larvae in the family Tortricidae (Marc and Canard 1997). In no-till corn, wolf spiders (Lycosidae) reduce larval densities of armyworm, *Pseudaletia unipunctata* (Haworth) (Laub and Luna 1992). Wolf spiders also reduced densities of sucking herbivores (Delphacidae and Cicadellidae) in tropical rice paddies (Fagan et al. 1998). Spiders are capable of reducing populations of herbivores that may not be limited by competition and food availability in some agroecosystems (Sunderland 1999).

Several studies have shown that insect populations significantly increase when released from predation by spiders. Riechert and Lawrence (1997) reported that plots in an old field from which spiders had been removed had significantly higher herbivorous insect numbers than in those plots that contained spiders. In Tennessee, vegetable garden plots from which spiders had been removed had higher pest numbers than those in which spiders remained (Riechert and Bishop 1990).

Agricultural fields that are frequently sprayed with pesticides often also have lower spider populations (Bogya and Markó 1999; Feber et al. 1998; Huusela-Veistola 1998; Yardim and Edwards 1998; Holland et al. 2000; Amalin et al. 2001). In general, spiders are more sensitive than many pests to some pesticides, such as the synthetic pyrethroids, cypermethrin and deltamethrin; the organophosphates, dimethoate and malathion; and the carbamate, carbaryl. A decrease in spider populations as a result of pesticide use can result in an outbreak of pest populations (Brown et al. 1983; Birnie et al. 1998;

Huusela-Veistola 1998; Yardim and Edwards 1998; Marc et al. 1999; Holland et al. 2000; Tanaka et al. 2000).

Spiders can lower insect densities, as well as stabilize populations, by virtue of their top-down effects, microhabitat use, prey selection, polyphagy, functional responses, numerical responses, and obligate predatory feeding strategies and we aim to review the literature on these topics in the following discussion. Nevertheless, as biological control agents, spiders must be present in crop fields and prey upon specific agricultural pests. Indeed, they are present and do eat pest insects. Spiders of several families are commonly found in agroecosystems (Table 1), and many have been documented as predators of major crop pest species and families (Table 2) (Roach 1987; Nyffeler and Benz 1988; Agnew and Smith 1989; Hayes and Lockley 1990; Riechert and Bishop 1990; Young and Edwards 1990; Fagan and Hurd 1991; Laub and Luna 1992; Nyffeler et al. 1992, 1994a, 1994b; Kumar and Velusamy 1997; Marc and Canard 1997; Wisniewska and Prokopy 1997; Fagan et al. 1998; Geetha and Gopalan 1999; Lang et al. 1999; Marc et al. 1999; Snyder and Wise 1999). Spiders may be important mortality agents of crop pests such as aphids, leafhoppers, planthoppers, fleahoppers, and Lepidoptera larvae. However, the same species of spider that feeds mostly on pests in one location may feed mostly on beneficial insects in another. Further research is needed to determine the extent of spider predation in a multitude of crops and climates under a variety of management practices before general conclusions about their efficacy as biological control agents can be justified (Nyffeler et al. 1994a, Rypstra et al. 1999).

In some agroecosystems, spiders may be unable to capture important pest species. In non-commercial cranberry bogs, hunting spiders comprised 61% of the total spider fauna, 87% of the hunters being lycosids. These spiders preyed predominately upon Collembola and small Diptera, which are not pests of cranberry. Very few hunting spiders captured pest insects such as cranberry weevils or Lepidoptera larvae. Many of these spiders occupy microhabitats on or near the ground surface so predominantly captured prey located on the ground (Bardwell and Averill 1997). Jumping spiders (Salticidae) may be ineffective predators of tephritid fruit flies, including major pest species such as apple maggot (*Rhagoletis pomonella* (Walsh)). Patterns on and specific movements of their wings make these flies resemble other salticids. Jumping spiders will respond to these displays by tephritids by backing away or giving threat or even courtship displays, allowing the fruit fly time to escape (Whitman et al. 1988). Various web-weaving spiders, despite having the ability to capture pest insects such as grasshoppers, weevils, and leaf beetles,

Table 1. Common spider (Araneae) families, genera, and species found in agroecosystems. These spiders are known predators of pest insects.

Family	Common Name	Genus or Species
Hunting Spiders		
Clubionidae	Sac Spiders	*Cheiracanthium inclusum* (Hentz) *Cheiracanthium mildei* Koch *Clubiona* spp.
Lycosidae	Wolf Spiders	*Rabidosa rabida* (Walckenaer) *Lycosa antelucana* Montgomery *Pardosa pseudoannulata* (Bösenberg et Strand) *Hogna* spp. *Pardosa* spp.
Oxyopidae	Lynx Spiders	*Oxyopes salticus* Hentz *Peucetia viridans* (Hentz)
Salticidae	Jumping Spiders	*Phiddipus audax* (Hentz) *Pelegrina galathea* (Walckenaer)
Thomisidae	Crab Spiders	*Misumenops* spp.
Web-Weaving Spiders		
Agelenidae	Funnel-Web Spiders	*Agelena labyrinthica* (Clerck)
Araneidae	Orb-Web Spiders	*Argiope* spp.
Linyphiidae	Sheet-Web Spiders	*Ummeliata insecticeps* (Bösenberg et Strand) *Erigone atra* Blackwall *Lepthyphantes tenuis* (Blackwall)
Pisauridae		*Pisaurina mira* (Walckenaer)
Tetragnathidae	Long-Jawed Spiders	*Tetragnatha laboriosa* Hentz
Theridiidae	Cob-Web Spiders	*Latrodectus mactans* (Fabricius)

usually capture aphids and small flies. They have little effect on non-flying pests such as lepidopteran larvae (Young and Edwards 1990).

Top-Down Effects

Spiders can also exert significant top-down effects, meaning that plant damage by insect herbivores is lower when spiders are present than when they are absent. Encouraging hunting spiders by the addition of mulch, which provides shelter and humidity, resulted in a

Table 2. Common crop pests and the spiders that are known to prey upon them. A: Common crop pest species and the spiders that are known to prey upon them.

Pest Species	Common Name	Spider Predators
Solenopsis invicta Buren	Red Imported Fire Ant	*O. salticus* *P. viridans* *P. audax* *P. mira* *L. mactans*
Helicoverpa zea (Boddie)	Cotton Bollworm	*Pardosa* spp. *O. salticus* *P. audax* *P. galathea* *Misumenops* spp. *P. mira*
Heliothis virescens (Fabricius)	Tobacco Budworm	*L. antelucana*
Trichoplusia ni (Hübner)	Cabbage Looper	*L. antelucana*
Spodoptera frugiperda (J.E. Smith)	Fall Armyworm	*P. galathea* *Misumenops* spp. *P. mira*
Pieris rapae (Linnaeus)	Imported Cabbageworm	Clubionidae* Lycosidae* Salticidae* Agelenidae*
Diabrotica undecimpunctata howardi Barber	Spotted Cucumber Beetle	*C. inclusum* *Hogna* spp. *Pardosa* spp. *P. viridans* *P. audax* *P. galathea* *Misumenops* spp. *P. mira*
Anthonomus grandis grandis Boheman	Boll Weevil	*P. audax* *P. galathea* *Misumenops* spp. *P. mira* *L. mactans*
Leptinotarsa decemlineata (Say)	Colorado Potato Beetle	Salticidae* Thomisidae* Agelenidae*
Epicauta vittata (Fabricius)	Striped Blister Beetle	Salticidae* Thomisidae* Araneidae* Theridiidae*

Table 2. Continued.

Pest Species	Common Name	Spider Predators
Lygus lineolaris Palisot de Beauvois	Tarnished Plant Bug	Salticidae* Linyphiidae* *C. inclusum* *L. antelucana* *Pardosa* spp. *O. salticus* *P. audax* *P. galathea* *Misumenops* spp. *P. mira*
Schizaphis graminum Rondani	Greenbug	*P. audax* *P. galathea*
Blissus leucopterus leucopterus (Say)	Chinch Bug	*C. inclusum* *Pardosa* spp. *P. galathea* *Misumenops* spp. *P. mira*
Spissistilus festinus (Say)	Three-Cornered Alfalfa Hopper	*C. inclusum* *L. antelucana,* *Pardosa* spp. *O. salticus* *P. audax* *P. galathea* *Misumenops* spp. *P. mira*
Nilaparvata lugens (Stal)	Brown Planthopper	*P. pseudoannulata* *U. insecticeps*
Pseudatomoscelis seriatus (Reuter)	Cotton Fleahopper	*O. salticus* *P. viridans*
Empoasca fabae (Harris)	Potato Leafhopper	*O. salticus* *P. audax*
Nephotettix cincticeps *Uhler*	*Green Rice Leafhopper*	*U. insecticeps*
Edwardsiana rosae (Linnaeus)	Rose Leafhopper	Salticidae*
Murgantia histrionica (Hahn)	Harlequin Bug	Lycosidae* Araneidae* Theridiidae*

*Spiders in these studies were not identified to genus and species

Table 2. Continued. B: Common crop pest families and orders and the spiders that are known to prey upon them.

Pest Families	Common Name	Spider Predators
Aphididae	Aphids	Salticidae*
		Thomisidae*
		Linyphiidae*
		Clubiona spp.
		Pardosa spp.
		O. salticus
		E. atra
		L. tenuis
		T. laboriosa
Acrididae	Grasshoppers	*R. rabida*
		P. audax
		A. labyrinthica
		Argiope spp.
Cicadellidae	Leafhoppers	Salticidae*
		Thomisidae*
		Theridiidae*
		P. pseudoannulata
		Pardosa spp.
		O. salticus
		P. viridans
		P. audax
		T. laboriosa
Chrysomelidae	Flea beetles	Salticidae*
		Agelenidae*
		Araneidae*
		Theridiidae*
Pest Orders	Common Name	Spider Predators
Thysanoptera	Thrips	Salticidae*
		Theridiidae*
		Pardosa spp.
		P. audax
Lepidoptera larvae	Caterpillars	Linyphiidae*
		C. mildei
		Clubiona spp.
		L. antelucana
		Hogna spp.
		O. salticus
		P. audax
		Misumenops spp.
		A. labyrinthica

*Spiders in these studies were not identified to genus and species significant decrease in plant damage in vegetable gardens (Riechert and Bishop 1990). Carter and Rypstra (1995), working in soybean agroecosystems, augmented web-weaving spider numbers by placing wooden crates in fields. These crates served both as sites for web construction and as retreats from unfavorable conditions such as rain. They found that leaf damage was significantly reduced in areas surrounding the crates compared to control areas without crates. Total leaf damage was negatively correlated to the biomass of insect remains found in and around the crates.

Top-down effects are evident even when spiders do not (or cannot) actually feed upon the insect herbivores. Snyder and Wise (2000) found that spotted cucumber beetles, *Diabrotica undecimpunctata howardi* Barber, reduced their feeding upon squash plants when in the presence of a wolf spider *Hogna helluo* (Walckenaer) even though the spider was separated from the beetles by a mesh barrier. Similarly, Rypstra (1995) found that the presence of either *H. helluo* or a theridiid, *Achaearanea tepidariorum* (Koch), resulted in less feeding upon soybean plants by Mexican bean beetles, *Epilachna varivestis* Mulsant and Japanese beetles, *Popillia japonica* Newman, even if the spiders could not prey upon the beetles. Spiders are also important in the decline of Lepidoptera larvae in apple orchards, not only because they feed on the larvae, but also because the larvae will disperse or otherwise abandon the apple branch when spiders are present (Marc et al. 1999). Similar results have been found in tobacco, where spiders in the family Linyphiidae prevented damage to plants by the tobacco cutworm, *Spodoptera litura* (Fabricius). The cutworms abandoned plants that were occupied by spiders. Spider-caused abandonment of plants is also known for greenbug, leaf fly, leafhoppers, and planthoppers (Riechert and Lockley 1984).

Wasteful Killing

Spiders can also control prey populations because they often capture and kill more prey than they consume. Riechert and Lockley (1984) report that a spider may kill as many as 50 times the number of prey it consumes. Persons (1999) found that wolf spiders (*Schizocosa ocreata* (Hentz)) killed more crickets than they could feed upon, even when satiated. This “wasteful killing” has been documented in other lycosids as well (Riechert and Lockley 1984; Persons 1999). Some web-weaving spiders may also trap more insects than they are able to consume. The golden orb weaver *Nephila clavipes* (Linnaeus) spins yellow silks, which serves as a super-stimulus, attracting herbivorous insects that would normally be attracted to flowers and new leaves (Craig et al. 1996). Orb-web weaving spiders (Araneidae, Uloboridae), such as the large orb-weaver *Argiope*, as well as *Gastracantha, Salassinia, Micrathena,* and *Uloborus*, attract insects to their webs using ultra-violet reflecting designs (called stabilimenta) woven into the webs (Craig and Bernard 1990; Craig et al. 1996.) Up to 1000 insects may be present in a web at a given moment, and many are ignored by the spider (Nyffeler et al. 1994a). It has been demonstrated through mathematical modeling that superfluous killing of prey augment the influence of spiders on insect prey populations (Riechert 1999).

A form of wasteful killing, intraguild predation or cannibalism, is when spiders prey upon each other. Little research has been conducted on this phenomenon, but it has been suggested that this type of wasteful killing may benefit pest insect prey populations (Hodge 1999).

Spider Assemblages

Numerous researchers have stressed that an assemblage of spider species is more effective at reducing prey densities than a single species of spider (Greenstone 1999; Sunderland 1999). Provencher and Riechert (1994) used computer simulations and field tests to show that an increase in spider species richness leads to a decrease in prey biomass. Riechert and Lawrence (1997) found that insect numbers were lower in test plots that contained a sheet-web weaver (*Florinda coccinea* (Hentz)), an orb-web weaver (*Argiope trifasciata* (Forskal)), and two wolf spiders (*Rabidosa rabida* (Walckenaer) and *Pardosa milvina* (Hentz)) than in plots that contained only one of these species.

Foraging behavior may be enhanced by the presence of other spider taxa. In agricultural fields in Ohio, the cob-web weaver *A. tepidariorum* and the orb-web weaver *Nuctenea cornuta* (Clerck) caught more prey per spider when in groups than when alone. Prey capture also was higher in mixed-species groups than in single-species groups (Rypstra 1997). However, competition between some spiders may limit their effectiveness at decreasing prey densities (Marshall and Rypstra 1999b).

A diverse group of spiders may be effective at biological control because they differ in hunting strategies, habitat preferences, and active periods. Because of the typical diversity of spiders in an agricultural ecosystem, there will probably be one or more species that will attack a given pest (Marc et al. 1999). Different spiders feed on different insects at different times of the day, so a loss in community diversity of spiders can result in some prey species being released from predation pressure (Riechert and Lawrence 1997). Variation in body size of both predator and prey species also contributes to prey reduction, with larger spiders taking larger prey and smaller spiders taking smaller prey (Nentwig and Wissel 1986; Nyffeler et al. 1994a). In addition, larger spiders consume disproportionately more prey than smaller spiders (Provencher and Riechert 1994).

It is important to have an assemblage of spiders rather than just one species so there will be predators of appropriate size classes and foraging modes to prey upon different prey life stages throughout the growing season. This size class effect can best be accomplished through an assemblage of species because spiders usually have a long generation time compared to their prey (Riechert and Lockley 1984; Riechert and Bishop 1990; Riechert 1999). Assemblages of spiders have usually been described within the ecological framework of guilds. However, applying the ecological guild concept to spiders has usually been taxon based instead of resource based and needs further investigation (Uetz et al. 1999). We do not understand whether mode of prey capture constitutes a "real" guild as suggested in many studies—i.e., a taxon-based guild—or whether the actual resource—prey type and its habitat and niche—make a better basis for guild classification. What has been suggested is that spider assemblages are the unit of predation pressure exerted by spiders and that mathematical modeling has shown that spider communities that naturally exhibit an uneven age-structure and have strong migratory and aggregation tendencies offer the greatest potential pest suppression (Riechert 1999).

Prey Specialization

Some degree of specialization or monophagy by a predator on prey is assumed to be necessary for the predator to reduce populations of that particular prey. Because of this assumption, spiders, which are polyphagous, generalist predators, were traditionally thought incapable of controlling prey populations (Riechert and Lockley 1984). However, spiders may be more specialized on particular prey than is often realized. It is common that when spiders have an excess of prey, they become more selective (Riechert and Harp 1987). Toft (1999) points out that it might be counter productive for a spider to feed on any prey since some might be toxic or deficient in nutrients. In addition, each species of spider occupies a specific region of the agricultural habitat, from the ground to the top of the canopy. Different prey species can be found in different microhabitats as well. Thus it might be concluded that prey specialization by spiders could be an attribute found in ecosystems, rather than in the laboratory. The question is whether this is true.

Temporal differences in prey-capture activities are found among spiders and may lead to specialization of diets. For example, some web-weavers are diurnal, spinning their webs during the day; others are nocturnal, spinning and capturing prey at night. Most hunting spiders that rely on visual and vibratory cues are diurnal, but there are exceptions, with some hunters active chiefly at night. Spiders, therefore, will only catch prey they encounter during their active period (Marc and Canard 1997; Riechert and Lawrence 1997; Marc et al. 1999). For example, in France, nocturnal and diurnal wandering spiders forage on the trunk and in the foliage of apple trees, while ambush species forage among the leaves and flowers. Tubular web species reside under the bark of the trees, while other web weavers occupy different microhabitat between leaves and branches (Marc and Canard 1997).

In addition to microhabitat preferences, spiders have feeding preferences. They usually only eat prey that is 50% to 80% of their size, with web weavers more adept at catching larger prey; smaller prey are typically ignored (Nentwig and Wissel 1986; Nyffeler et al. 1994a; Marc and Canard 1997; Marc et al. 1999). Some species of spiders also select insect prey that balance their amino acid requirements (Greenstone 1979). Although spiders are polyphagous predators, their hunting strategies and microhabitat preferences cause each species to be specialized (Nyffeler et al. 1994a; Marc and Canard 1997; Marc et al. 1999; Nyffeler 1999). The literature suggests that, in general, hunting spiders have a greater diet breadth than web-weavers (Nyffeler 1999).

Some types of spiders may be adapted towards catching a particular type of prey. The bolas spiders and ladder web spiders (Araneidae) have webs that are specially adapted to catch adult Lepidoptera. Smaller web weavers, such as Linyphiidae and Dictynidae, capture mainly soft-bodied insects such as aphids. Some cobweb weavers (Theridiidae) specialize on ants, including fire ants. A number of species of jumping spiders (Salticidae) are also behaviorally adapted to feeding on ants (Nyffeler et al. 1994a; Jackson and Pollard 1996). The water spiders (Argyronetidae) are highly specialized in that they forage underwater and feed on fly larvae, including mosquitoes (Nyffeler et al. 1994a). Other spiders show remarkable prey preference, despite a wide availability of prey. The lynx spider *Oxyopes salticus* Hentz preferentially feeds on prey organisms in the 1- to 2.9-mm-size class. This size class includes the cotton fleahopper, which was found to be the most important prey in the diet of this spider in Texas cotton fields (Nyffeler et al. 1992). Salticids in the genus *Phiddipus* prey upon a diverse assortment of arthropods, but seem biased towards flies and Lepidoptera larvae (Jackson and Pollard 1996). Some web-weavers also show similar preferences. Although insects of 17 different orders were caught in webs spun by *Argiope argentata* (Fabricius), 62% of prey consumed by this spider were stingless bees of the genus *Trigona* (Craig and Bernard 1990). Some web-weaving spiders also preferentially reject prey such as Coleoptera, either ignoring them or cutting them out of the web (Nyffeler et al. 1994a). Indeed, many spiders show behavioral specializations and prey preferences that make them able to effectively limit certain prey populations.

Role of the Generalist Spider

Some researchers and theorists argue, however, that generalist predators may be more effective than specialists at reducing and stabilizing prey densities (Riechert 1999; Symondson et al. 2002). Young and Edwards (1990) suggest that hunting spiders might be better at controlling pests than web-weavers because most species of hunting spiders are capable of capturing a wide variety of prey types and sizes. For example, in Texas cotton fields Nuffeler et al. (1992) found that the lynx spider *O. salticus* consumes at least 34 species of insects in 21 families and nine orders. Web-weaving spiders, however, are more specialized. Despite being capable of capturing grasshoppers and beetles, they usually only capture aphids and flies, and often have little to no impact on plant bugs, weevils, leaf beetles, and caterpillars (Young and Edwards 1990).

Of course, spiders do not consume only pestiferous herbivores. Being generalists, they feed on more than one trophic level in a food web (Morin 1999). Although model food webs predict that polyphagy will lead to instability, studies of natural communities show that food chains containing generalists are more stable (Wise et al. 1999). Predators feeding on multiple prey species in multiple trophic levels are more likely to withstand declines in the abundance of one prey species than predators that specialize on that species (Reichert 1999). Species that feed on one prey fluctuate in abundance, while polyphagous species are less likely to fluctuate and more likely to maintain consistently high populations (Morin 1999). In agroecosystems, spiders, as generalist predators, may maintain populations in periods of low pest numbers by preying upon other insects, including harmless and beneficial insects (Riechert and Lockley 1984; Nyffeler et al. 1992, 1994a). Compared to irruptive species such as pest insects that feed on only one trophic level, some spiders exhibit relatively stable population dynamics (Riechert and Lockley 1984; Nentwig 1988).

Despite the potential to create stable predator populations, polyphagy may be a disadvantage in systems such as agricultural fields, where food chains may be short and simple. In a food chain consisting of three levels—primary predator, herbivore, and producer—the herbivore is not limited by competition but by predation. However, in a four-level food chain—secondary predator, primary predator, herbivore, and producer—the top (secondary) predator limits populations of the primary predator, thus releasing the herbivore from predation pressures. The herbivore may then be limited by competition alone and may become quite abundant (Hairston et al. 1960; Morin 1999). Spiders, which can feed on other predators, may be responsible for such trophic cascades. Fagan and Hurd (1991) increased wolf spider densities in pastures and found that cricket survivorship increased. It seems the spiders released crickets from predation by either reducing the numbers of some other cricket predator, or by cannibalizing each other (Fagan and Hurd 1991).

Spiders do indeed limit other predators. Roach (1987) found that in prey choice experiments, *Phiddipus audax* (Hentz) (Salticidae) consumed the predaceous hemipteran *Geocoris punctipes* (Say) before consuming any of the herbivores offered. In peanut agroecosystems, *O. salticus* also feed frequently upon *G. punctipes* (Agnew and Smith 1989). Agnew and Smith (1989) concluded that because of the high frequency of predaceous insects in their diet, spiders do not have an impact on pest populations in this system. In Texas cotton fields, lynx spiders frequently eat beneficial insects such as pollinating bees (23% of the diet of *Peucetia viridans* (Hentz)), other spiders, and other predators, including *G. punctipes, Hippodamia convergens* Guerin-Meneville, and *Chrysoperla rufilabris* (Burmeister). These spiders and entomophagous insects are key predators of bollworm and budworm eggs and larvae (Nyffeler et al. 1992). Since predation effects are diluted across many prey species and trophic links, generalist predators can maintain pest populations at low levels, but may not be able to control pest outbreaks (Riechert and Lockley 1984; Riechert and Lawrence 1997; Marc et al. 1999). Despite reduction of predator numbers by spiders, Agnew and Smith (1989) and Nyffeler et al. (1992) reported that pest levels still remained below an economic threshold. Natural enemies were adequate enough that no pest populations escaped predation pressure and increased to unacceptable levels.

Functional Response

A desirable biological control agent is a predator that not only reduces pest densities, but also stabilizes them at low levels, while maintaining stable populations itself (Pedigo 2001). Stability in predator-prey systems is achieved by density-dependent responses of the predator to the prey. As prey populations increase, predation pressure should increase, and predation pressure should lessen as prey populations decrease. Usually, the greater the importance of a given prey in the diet of a predator, the lower the population size the predator effectively controls. Density-dependent control is thereby affected by the functional response and the numerical response of the predator (Riechert and Lockley 1984; Morin 1999).

The functional response depends on feeding and hunting behavior and can be defined as the change in numbers of prey consumed per unit time by a single predator as prey density changes (Riechert and Lockley 1984). There are three commonly recognized types of functional response relationships that describe how consumption rates vary with prey density: Type I, Type II, and Type III. In the Type I response, prey intake is proportional to prey density until satiation. This response is typical of filter-feeding organisms and is not seen in spiders. In the Type II response, predators increase prey consumption at a decreasing rate, usually because of a reduction in capture rate associated with handling time (time needed to capture, kill, and consume prey). This type of functional response fails to produce stable populations, as prey are either driven to extinction at low densities, or escape predation at high densities. Type II responses are common in spiders, as they may eat fewer insects when insects are abundant (Rypstra 1995; Marc et al. 1999). The Type III response is a sigmoidal response, beginning with a lag time followed by an increase in prey consumption at an increasing rate. Type III responses are a strong stabilizing mechanism and are associated with either prey switching or learning by the predator (Riechert and Lockley 1984; Morin 1999).

Although it was historically thought that only vertebrates exhibit Type III functional responses, recent studies have show that many invertebrates, including spiders, show a sigmoidal response to prey densities (Riechert and Lockley 1984; Marc et al. 1999). Type III response relationships have been demonstrated for *Cheiracanthium mildei* Koch (Clubionidae) feeding on *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), *Philidromus rufus* Dondale (Philidromidae) feeding on *Drosophila*, and Lycosidae in rice paddies (Marc et al. 1999). Searching activity appears to rises exponentially above a certain threshold of prey density, thus producing the characteristic lag and acceleration response (Riechert and Lockley 1984).

The sigmoidal functional response is often associated with some form of learning on the part of the predator, such as recognizing and developing efficient searching and capture patterns towards prey. The jumping spiders (Salticidae) of the genus *Portia* provide examples of this sort of learning behavior. This spider uses trial and error to adjust its predatory strategy depending on the prey it is attacking, associating success with a particular course of action and remembering to keep using it. Other salticids seem to improve with practice their typical stalk-and-pounce routine (Jackson and Pollard 1996). The golden orb-weaver, *N. clavipes*, spins a web that reflects UV and appears yellow, thus attracting insects such as bees. However, bees have difficulty seeing UV reflectance in shaded areas. *Nephila*, therefore, will adjust web reflectance according to local light conditions, spinning white silk when exposed to light conditions similar to that of a forest understory and yellow silk when exposed to intense light. This change in silk reflectance occcurs after only three days (Craig et al. 1996).

Lycosids exhibit a particularly interesting learning behavior – they are preferentially attracted to substrate chemical cues associated with recent prey (Persons and Uetz 1996; Punzo and Kukoyi 1997; Persons and Rypstra 2000; Persons et al. 2001). Persons and Uetz (1996) demonstrated that wolf spiders (*S. ocreata*) previously fed crickets spent significantly longer periods of time on pieces of paper that crickets had walked upon than on clean paper. Punzo and Kukoyi (1997) found that field-collected wolf spiders (*Trochosa parthenus* (Chamberlin)) increased patch residence time on substrate containing chemical cues from two insects naturally found in its habitat—field crickets (*Gryllus assimilis* (Fabricius)) and grasshoppers (*Schistocera obscura* (Fabricius)—compared to substrate containing chemical cues from mealworms (*Tenebrio obscurus* Fabricius) or no chemicals. Furthermore, *T. parthenus* preferred the cricket odors to the grasshopper odors. *Trochosa parthenus* usually hunts on the ground and would encounter crickets more frequently than grasshoppers. The plant dwelling lynx spider, *O. salticus*, showed similar results, preferring grasshopper and cricket odors to mealworm and control, and preferring grasshopper odors to cricket odors. Lab-reared *T. parthenus* and *O. salticus*, having no previous exposure to any of the prey tested, showed no preference for any particular odors (Punzo and Kukoyi 1997). Further research has shown that the large wolf spider *H. helluo* fed house crickets (*Acheta domestica* (Linnaeus)) prefers cricket cues to those of another wolf spider, the smaller *Pardosa milvina* Hentz. *Hogna* fed *P. milvina* prefer *P. milvina* cues to those of crickets (Persons and Rypstra 2000). Interestingly, *P. milvina* avoids substrates containing cues from *Pardosa*-fed *Hogna* (Persons et al. 2001). This type of learning behavior is similar to that reported for parasitoid wasps, which first must learn the particular odors of its host before becoming an effective predator (Punzo and Kukoyi 1996; Tumlinson et al. 1993).

In addition to learning behaviors, a change in preference from one prey type to another as prey numbers of one type increase or decrease can also elicit a Type III response. This phenomenon, known as "switching," was thought to not generally occur in spiders (Riechert and Lockley 1984). However, more recent studies have demonstrated spiders can exhibit significant levels of density-dependant switching (Nyffeler et al. 1994b; Riechert and Lawrence 1997). Nyffeler et al. (1994a) state that the lynx spider, *O. salticus,* switches dietary composition in response to prey availability. Salticids will narrow their prey spectrum when a suitable prey species reaches high numbers. For example, in a roach-infested building, roaches made up over 90% of the diet of these spiders. In addition, in field cages the salticid *P. audax* has shown a Type III response to fleahopper prey (Nyffeler et al. 1994a). Some web-weaving spiders (*Argiope* spp., *Nephila* spp.) will design their webs specifically to attract flower-visiting insects in areas where flowers, and thus pollinating insects, are abundant. They will then preferentially consume the pollinators (Craig and Bernard 1990; Craig et al. 1996). In shaded areas where flowers and pollinating insects are not common, these spiders show no prey preference (Craig et al. 1996). The omnivorous habits of spiders may also result in Type III functional responses. Spider numbers may be maintained in periods of low pest numbers by predation on other trophic levels (Nyffeler et al. 1994a). However, the switching behavior of a generalist predator, in theory, may also lead to stability of prey populations through feedback loops. This can lead to coexistence of competing insect prey (Yodzis 1986).

A stabilizing factor to the functional response is a high plateau—the point at which rate of attack ceases to increase relative to rate of encounter with prey. Spider functional responses often have a very high plateau, since often spiders will kill many prey items before the first one is digested. Numbers of prey killed may be much greater than the amount needed for the spider to reach satiation (Riechert and Lockley 1984; Nyffeler et al. 1994a; Persons 1999).

Functional responses can be modified by intraspecific interactions between generalist predators such as spiders. Many spiders cannibalize and interfere with one another. While interference reduces the functional response, cannibalism reduces predator density and thus reduces the probability of interference (Nilsson 2001). This interplay between interference and cannibalism may determine whether it is effective to increase densities of certain species of spiders or whether increased densities result in diminishing returns. This might result in a decrease of the effectiveness of a spider community in controlling pest populations (Hodge 1999).

Numerical Response

Both Type II and Type III functional responses can lead to regulation of prey fluctuations if a strong numerical response is also present. A numerical response can be defined as an increase in predator numbers after a rise in prey density. This response may be in the form of aggregation, increased reproduction, or both (Marc et al. 1999). Spiders exhibit both aggregative and reproductive responses to prey numbers (Riechert and Lockley 1984; Marc et al. 1999). Predator recognition of patches of high prey density and the concentration of foraging activity in these areas can lead to stabilization, since predation pressure will be high where prey numbers are high and low where prey numbers are low. In the field, spiders do inhabit areas where prey are abundant and will migrate from patches of decreasing prey density to patches of higher prey density (Riechert and Lockley 1984; Harwood et al. 2001). For example, the funnel-web weavers of the species *Agelenopsis aperta* (Gertsch) aggregate in areas where prey are abundant. The theridiid *A. tepidariorium* will relocate its web if prey density is insufficient, leading to a clustering of individuals in areas where prey are more numerous. Some crab spiders (Thomisidae) behave similarly in response to low prey densities (Marc et al. 1999). Persons and Uetz (1998) reported that adult female wolf spiders (*S. ocreata*) use visual and vibratory cues to assess prey density and spend more time in patches with higher prey density.

Competition, intraguild predation, and cannibalism can limit the aggregation response of spiders. Spiders are usually territorial and will compete for space and prey at high spider densities, limiting the number of spiders that can coexist in the same area. The result may be migration from a patch of high prey densities and, therefore, less pest control (Riechert and Lockley 1984; Provencher and Vickery 1988; Marc et al 1999; Marshall and Rypstra 1999b). Intraguild predation—predation upon members of the same trophic level—is a major factor limiting aggregation and spiders' pest control abilities (Fagan et al. 1998; Marc et al. 1999; Wise and Chen 1999). Fagan et al. (1998) found that the addition of the wolf spider *Pardosa pseudoannulata* (Bösenberg et Strand) to rice patties sprayed with insecticide resulted in a reduction of the other top predator in the system, mesoveliids. Mesoveliids and wolf spiders both exert significant top-down control on phytophagous insects in this crop. However, when *P. pseudoannulata* numbers were enhanced, they preyed upon mesoveliids and pest densities increased (Fagan et al. 1999). Other spiders such as gnaphosids and ctenids reduce lycosid (*Schizocosa* spp.) numbers on forest floors, and reduction of intraguild predation improved *Schizocosa* survival by 75% (Wise and Chen 1999). However, competition and intraguild predation may not be present between predators in some agroecosystems. Lang et al. (1999) found that the combined predation of lycosids and carabid beetles showed the strongest negative effect on leafhopper (Cicadellidae) populations in maize fields. The two predators did not seem to have a negative effect on each other (Lang et al. 1999).

Cannibalism is another important mortality agent that limits spider densities, especially for lycosids. Reducing other arthropod predators may not improve survival of juvenile *Schizocosa* because they will self-regulate their density through intra-cohort cannibalism (Riechert and Lawrence 1984; Wise and Chen 1999). Such self-limiting tendencies of lycosids may result in increased prey populations via depressed numerical responses to prey density (Fagan and Hurd 1991).

The reproductive response of spiders is less studied. Some spiders, especially web-weavers, do show an increase in fecundity with increasing amounts of prey ingested. Such spiders include *Neriene radiata* (Walckenaer) (Linyphiidae), *Mecynogea lemniscata* (Walckenaer), *Metepiera labyrinthea* (Hentz) (Araneidae), and *Agelenopsis aperta* (Agelenidae) (Riechert and Lockley 1984; Marc et al. 1999). The extent to which this increase in fecundity can permit tracking of prey populations is limited by long generation times compared to those of pest insect species. Spiders are usually univoltine while generation times for many insect pests are a few weeks (Riechert and Lockley 1984; Provencher and Vickery 1988).

EFFECTS OF PESTICIDES

Many farmers use chemical pesticides to help control pests. An ideal biological control agent, therefore, would be one that is tolerant to synthetic insecticides. Although spiders may be more sensitive to insecticides than insects due in part to their relatively long life spans, some spiders show tolerance, perhaps even resistance, to some pesticides. Spiders are less affected by fungicides and herbicides than by insecticides (Yardim and Edwards 1998). Spiders such as the wolf spider *P. pseudoannulata* are highly tolerant of botanical insecticides such as Neem-based chemicals (Theiling and Croft 1988; Markandeya and Divakar 1999). They are also generally more tolerant of organophosphates and carbamates than of pyrethroids, organochlorines, and various acaricides, although this tolerance may be due to genetic resistance bred over a period of continuous exposure (Theiling and Croft 1988; Wisniewska and Prokopy 1997; Yardim and Edwards 1998; Marc et al. 1999; Tanaka et al 2000). For example, *P. pseudoannulata* (Lycosidae), *Tetragnatha maxillosa* Thorell (Tetragnathidae), *Ummeliata insecticeps* (Bösenberg et Strand) and *Gnathonarium exsiccatum* (Wider) (Linyphiidae) were highly sensitive to the pyrethroid deltamethrin, but very tolerant of the organophosphate diazinon and the carbamate carbaryl (Tanaka et al. 2000).

Some broad-spectrum organophosphates are highly toxic to spiders. For example, dimethoate sprays resulted in 100% mortality to the lycosid *Trochosa ruricola* (De Geer) at concentrations below recommended field application rates (Birnie et al. 1998). The organophosphate methyl parathion and the pyrethroid cypermethrin are highly toxic to spiders in the genus *Erigone* (Linyphiidae), while the carbamate pirimicarb is almost harmless (Brown et al. 1983; Huusela-Veistola 1998). Toft and Jensen (1989) found that sublethal doses of dimethoate and cypermethrin had no effect on development and predation rates of the wolf spider *Pardosa amentata* (Clerck). In fact, with very low doses of cypermethrin, killing rates of the adult and penultimate females increased. However, the insecticides did have knockdown effects that, although not influencing survival in the laboratory, would likely result in death in the field due to desiccation or predation (Toft and Jensen 1998).

Other factors that influence effects of pesticides on spiders are type of solvent, soil type, moisture, percent organic matter, temperature, and time of day of spraying. Further, the microhabitat, hunting style, prey preference, and behavior of the spider also influences their response to pesticide application (Marc et al. 1999). Wisniewska and Prokopy (1997) reported that if pesticides were only used early in the growing season, spider populations increased. Presumably, spiders have a chance to recolonize the field if pesticide use ceases after early June. Spatial limitation of pesticides (such as only applying the pesticides to certain plants or certain plots) also result in higher spider numbers, since they can move out of the treated areas and return when the chemicals dissipate (Riechert and Lockley 1984; Balança and de Visscher 1997).

CAN SPIDERS BE EFFECTIVE BIOCONTROL AGENTS?

In summary, spiders can be effective predators of herbivorous insect pests, and can exert considerable top-down control, often catching more insects than they actually consume. Despite the potential for competition and intraguild predation, a diverse assemblage of spiders may have the greatest potential for keeping pest densities at low levels. The focus on much spider research has mainly been on wandering spiders, as web weavers may either be unable to establish webs or catch pest insects. The spiders that are most efficient at capturing pest insects are those that forage on the plant itself. Spiders show both functional responses and numerical responses to prey densities, although they may not be able to display long-term tracking of any one particular prey species. By virtue of these density-dependent responses, as well as polyphagy in times of low pest levels, spider populations in agroecosystems are stable and can be maintained at low levels when pests are absent. Spiders exhibit the ability to both lower and stabilize pest populations, making them excellent biological pest management candidates.

Spiders have been successfully used as biocontrol agents in two groups of crop ecosystems throughout the world—orchards, primarily apple, and rice paddies. Spiders have been shown to both suppress populations of major pest insects and significantly decrease insect damage to harvest in apple orchards in Israel, Europe, Australia, and Canada. They are also important predators of many pests of citrus. However the pest management strategy in orchards has been one of spider conservation, through reduced pesticide use, rather than enhancement (Marc and Canard 1997; Wisniewska and Prokopy 1997; Amalin et al. 2001). In rice paddies in Asia, however, spiders are often purposefully introduced into fields. In China, farmers build straw or bamboo shelters for spiders and then move these shelters to whichever paddies are experiencing pest outbreaks. This method of spider augmentation led to a 60% reduction in pesticide use (Riechert and Bishop 1990; Marc et al. 1999). In Japan, spider populations are maintained and enhanced by the release of *Drosophila* fruit flies into fields when pest insects are not abundant (Marc et al. 1999). Ground-dwelling spiders such as lycosids are one of the most important predators of leafhopper and planthopper pests of rice, and the addition of wolf spiders to rice paddies can result in reductions in pest populations similar to that seen with insecticide use (Nyffeler and Benz 1987; Fagan et al. 1998; Geetha and Gopalan 1999; Jalaluddin et al. 2000)

CONSERVATION AND ENHANCEMENT OF SPIDER ASSEMBLAGES

To conserve and enhance spider populations, agricultural systems should be manipulated in ways beneficial to the needs of the spiders. The structural complexity of the environment is directly related to spider density and diversity. Highly varied habitats provide a greater array of microhabitats, microclimatic features, alternative food sources, retreat sites, and web attachment sites, all of which encourage colonization and establishment of spiders (Riechert and Lockley 1984; Agnew and Smith 1989; Young and Edwards 1990; Rypstra et al. 1999). Wandering spiders respond to the depth and complexity of the litter layer. For example, adding mulch to vegetable gardens can significantly enhance spider densities (Riechert and Bishop 1990; Rypstra et al. 1999). Spider densities are also increased in potato fields where straw mulch is used as a ground cover (Brust 1994). In this experiment, Colorado potato beetle populations and potato plant damage were significantly reduced compared to plots of potato where no straw mulch was applied.

In soybeans, conservation-tilled fields had more vegetable debris on the soil surface and more weeds than conventionally tilled fields, resulting in greater numbers of wolf spiders in the conservation-tilled fields (Marshall and Rypstra 1999a). In tropical rice cropping systems, weed residues have been shown to result in increased spider densities and a significant reduction in insect pest damage (Afun et al. 1999). Increasing weed densities also enhanced the numbers of web weaving spiders (Balfour and Rypstra 1998).

In apple orchards, increasing foliage and plant complexity leads to increases in hunting spiders, presumably because the lush foliage provided a more complex hunting habitat for the spiders (Wisniewska and Prokopy 1997). Living mulches planted in strips within apple orchards have been shown to increase web spider densities in apple trees and to reduce the number of alate aphids (Wyss et al. 1995). Dense foliage can also offer shade, protection, and humidity favorable to hunting spiders (Agnew and Smith 1989). Intercropping enhances spider populations by increasing spatial complexity and providing more favorable habitats for spiders (Provencher and Vickery 1988; Young and Edwards 1990; Rypstra et al. 1999). Crop diversity also leads to an availability of alternative prey, which may increase spider diversity as well as reduce territory size of spiders, leading to a stable population of spiders at high densities (Provencher and Vickery 1988).

Promoting colonization of fields by predators is an important aspect of pest management. In addition to providing refuges and overwintering sites, field edges and marginal habitats are important components of the spiders' ecosystems because they serve as corridors for dispersal into the field (Riechert and Lockley 1984; Maelfait and De Keer 1990; Marc et al. 1999). Maelfait and De Keer (1990) suspected that two species of *Pardosa* would not have been present in the pasture they studied if the border zone had not been present. Agnew and Smith (1989) also attribute field colonization by wandering spiders to the presence of adjacent natural habitats. Ballooning is also essential to recolonization, especially in annual crops where farming practices can destroy overwintering sites for spiders. Ballooning spiderlings are often the earliest predaceous colonizers of agricultural fields (Agnew and Smith 1989; Young and Edwards 1990; Marc et al. 1999).

Conservation of predators in the field can be accomplished by reducing both chemical and physical disturbance of the habitat. Spider density and diversity are significantly higher in orchards and fields where no pesticides have been sprayed (Bogya and Markó 1999; Feber et al. 1998; Huusela-Veistola 1998; Yardim and Edwards 1998; Marc et al. 1999; Holland et al. 2000; Amalin et al. 2001). Restricting insecticide treatment to crucial periods in the pest life cycle or limiting spraying to midday when many wandering spiders are inactive and in sheltered locations can help conserve spider numbers (Riechert and Lockley 1984). Spiders can recolonize if the interval between chemical applications is long enough, but several applications per season can destroy spider communities. Some pesticides are also retained in the webs of spiders and can be detrimental to those spiders that ingest their webs daily (Marc et al. 1999).

Besides pesticides, other human practices that can disrupt spider populations are mowing, plowing, harvesting, and crop rotation (Nyffeler et al 1994b; Collins et al. 1996; Marc et al. 1999). Soil disturbance by plowing destroys overwintering sites and can kill any spiders already present in the soil (Marshall and Rypstra 1999a). The movement of farm equipment through a crop field damages spider webs and may destroy web attachment sites (Young and Edwards 1990). Consequently, spider density and diversity is higher in organic fields than in conventional ones. For example, in cereal fields, Lycosidae made up only 2% of the community in conventional fields, but 11% in organic fields. Most lycosids were found in field edges (Marc et al. 1999). Clearly, human input is harmful to spiders, and the best spider conservation strategy may be non-intervention (Young and Edwards 1990).

Traditional biological control efforts have focused on using specialist predators to control pest outbreaks, which Riechert and Lockley (1984:300) liken to “putting out fires rather than preventing their conception”. Encouraging spider populations may have the effect of keeping pest levels low and not letting them get out of control. Spiders may be potential biocontrol agents because they are relatively long lived and are resistant to starvation and desiccation. Additionally, spiders become active as soon as conditions are favorable and are among the first predators able to limit pests. The risks associated with using spiders to control pests are minimal. Since diverse species of spiders are naturally present in an agricultural system (thus avoiding the problems associated with introductions) and predaceous at all stages of their development, they fill many niches, attacking many pest species at one time (Agnew and Smith 1989; Marc et al. 1999). Because they are sensitive to disturbance, spiders may best be used in perennial agroecosystems, such as orchards, that suffer the least disruption and human intervention (Riechert and Lockley 1984; Marc et al. 1999). Spiders do have the potential to be highly effective pest management agents, but the overall level of control is specific to each combination of crop and management style.

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