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The Ecology of Wolf Spiders (*Lydosidae*) in Low Bush Bluberry (*Vaccinium angustifolium*) Agroecosystems

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THE ECOLOGY OF WOLF SPIDERS (LYCOSIDAE) IN LOWBUSH BLUEBERRY (*Vaccinium angustifolium*) AGROECOSYSTEMS

By

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An Abstract of the Thesis Presented
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The ecology of spiders (Araneae) in lowbush blueberry (*Vaccinium angustifolium* (Aiton)) fields in Washington County, Maine, was studied during the summers of 2000 and 2001. The abundance and distribution of spiders was investigated, and predation by one family of spiders, the wolf spiders (Lycosidae) was evaluated.

The abundance and distribution of spiders was examined by capturing spiders using pitfall traps. Traps were set in conventionally managed, reduced input, and organic fields at different distances from the field edge (forest border or windbreak). The most commonly captured spiders were in the family Lycosidae. More lycosids were captured in May, June, and July than in August. Lycosids were more abundant in reduced input fields than in conventional fields in 2000 and 2001. No differences in capture were detected among conventionally managed, reduced input, and organic fields for samples taken in the later part of

the season in 2001. Species composition of lycosid communities were not significantly different among fields and management practices in 2000, but the proportion of each species captured differed among management practices in 2001.

Significantly more lycosids were captured at field edges than the field interior. In both 2000 and 2001, there was a significant linear contrast with lycosid capture decreasing as distance from the edge increased. In each year, one conventional field showed this linear decline in lycosid capture as distance from the edge increased, but the reduced input and organic fields did not. There were no significant differences in community composition between distances from the edge, but some species were associated with specific distances. Field edges may be a more important habitat from lycosids in blueberry fields that are more intensely managed.

Predation by wolf spiders (Lycosidae) on pest and non-pest insects found in blueberry fields in Washington County, Maine, was investigated in the laboratory, greenhouse, and field. In laboratory experiments, four taxa of prey insects were evaluated as prey in no-choice arenas. Prey examined were blueberry spanworm *Itame argillacearia* (Packard) (Lepidoptera: Geometridae), blueberry flea beetle larvae, *Altica sylvia* Malloch (Coleoptera: Chrysomelidae), grasshopper (Acrididae) adults and nymphs, and field cricket (*Gryllus pennsylvanicus* Burmeister) (Orthoptera: Gryllidae) adults and nymphs. Lycosids consumed blueberry flea beetles, grasshopper nymphs, and field cricket nymphs but not blueberry spanworm, grasshopper adults, or field cricket adults. In

greenhouse mesocosms, both grasshopper and house cricket (*Acheta domestica* Linnaeus) densities were lower in no-choice cages containing a single lycosid compared to control cages with no spiders; blueberry spanworm larvae densities remained the same.

Two field experiments were conducted in which cages received known quantities of several prey species and either zero (control), four, or eight lycosids. Significant differences in numbers of grasshoppers or house crickets recovered were not detected among treatments. There were significant differences in field crickets recovered. Less field crickets remained in cages containing more predators (lycosids, carabid beetles, and ants). Although lycosids consumed some blueberry pest species, pest populations were not significantly lower in field cages containing lycosids.

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SPIDER PREDATION IN AGROECOSYSTEMS: CAN SPIDERS EFFECTIVELY CONTROL PEST POPULATIONS?

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). In order 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 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 (Pedigo 2001; Morin 1999). 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 lead to local extirpation of predators. Herbivores,

released from control by predators, 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.

Although the spiders (Araneae) are a diverse arachnid order consisting of over 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 34-58% 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 clearly capable of reducing populations of herbivores that may not be limited by competition and food availability.

Several studies have shown that insect populations significantly increase when released from predation pressure by spiders. Riechert and Lawrence (1997) found 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).

In addition, agricultural fields that are frequently sprayed with pesticides often have lower spider populations (Bogya and Markó 1998; 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. 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 1.1), and many have been documented as predators of major crop pest species and families (Table 1.2) (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).

Table 1.1. 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)

Table 1.2. 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*
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*

Table 1.2A continued.

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

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

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 and 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, 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 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 cutworm pests 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 much 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).

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 even be enhanced by the presence of other spiders. 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).

Because they differ in hunting strategies, habitat preferences, and active periods, a diverse group of spiders may potentially be highly efficient at biological control. The typical diversity of spiders in an agricultural ecosystem is such that there will probably be one or more species that will attack a given pest (Marc et al. 1999). Since different spiders feed on different insects at different times of the day, a loss in community diversity 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 that one is ensured of having predators of appropriate size classes and foraging modes to prey upon different prey life stages throughout the growing season. Since spiders usually have a long generation time compared to their prey, this size class effect can best be accomplished through an assemblage of species (Riechert and Lockley 1984; Riechert and Bishop 1990).

Prey Specialization

Some degree of specialization or monophagy by a predator on prey is assumed to be necessary in order 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 Hart 1987). 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.

Temporal differences in prey-capture activities are also 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. The spiders, therefore, will only catch prey that is encountered 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 as well. 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 make each species a fairly specialized predator (Nyffeler et al. 1994a; Marc and Canard 1997, Marc et al. 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 1-2.9 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 (Symondson et al. 2002). Young and Edwards (1990) suggest that hunting spiders might be better at controlling pests than web-weavers because this group of spiders tends to have few specialists, with most species capable of capturing a wide variety of prey types and sizes. For example, the lynx spider *O. salticus* consumes at least 34 species of insects in 21 families and 9 orders in Texas cotton fields (Nyffeler et al 1992). Web-weaving spiders, however, tend to be 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 chain or chains (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. 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. In other words, the existence of more than one pathway of energy flow may buffer the predator against oscillations in prey abundance. 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). Unlike species such as pest insects that feed on only one trophic level, spiders tend to exhibit 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 spiders 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) found that pest levels still remained below 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 excellent examples of this sort of learning behavior. This spiders 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 can be seen 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. *T. 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 seen in 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 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 specially 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 contributing 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 even 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.

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 utilize chemical pesticides to help manage 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, 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).

However, 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 influencing the effects of pesticides on spiders are solvent, soil type, moisture, percent organic matter, temperature, time of day of spraying, and the microhabitat, hunting style, prey preference and behavior of the spider (Marc et al. 1999). Wisniewska and Prokopy (1997) found 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 results 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 exert considerable top-down control, often catching more insects than they actually consume. Despite the potential for competition and intraguild predation, it is the diverse assemblage of spiders that is responsible for keeping pest densities at low levels, not any one particular species. Focus 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 had lead 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

In order to conserve and enhance spider populations, agricultural systems can 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 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 alternate 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) suspect that two species of *Pardosa* would not be present in the pasture they studied had the border zone 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 used than sprayed ones (Bogya and Markó 1998; 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 of high application rates destroy spider communities. 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 in fact 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) 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 ideal 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, if any. 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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Chapter 2

ABUNDANCE, DISTRIBUTION, AND COMMUNITY COMPOSITION OF SPIDER POPULATIONS IN LOWBUSH BLUEBERRY AGROECOSYSTEMS IN MAINE

Abstract

The abundance and distribution of spiders (Araneae) in lowbush blueberry (*Vaccinium angustifolium* (Aiton)) fields in Washington County, Maine were investigated during the summers of 2000 and 2001. Pitfall traps were placed in fields under different management practices and at different distances from the field edge (forest border or windbreak). The most commonly captured spiders were Lycosidae. More lycosids were captured in May, June, and July than in August. Lycosids were more abundant in reduced input fields than in conventionally managed fields in 2000 and 2001. There were no differences in capture among conventionally managed, reduced input, and organic fields during the later part of the season in 2001. Species composition of lycosid communities were not significantly different among fields and management practices in 2000, but the proportion of each species captured differed among management practices in 2001.

Significantly more lycosids were captured at field edges than the field interior. In both 2000 and 2001, there was a significant linear contrast with lycosid capture decreasing as distance from the edge increased. In each year, one conventionally managed field showed this linear decline in lycosid capture as

distance from the edge increased, but the reduced input and organic fields did not. There were no significant differences in lycosid community composition among distances from the edge, but some species were associated with certain distances. Field edges may be a more important habitat for lycosids inhabiting blueberry fields that are more intensely managed.

Introduction

With the growing interest in sustainable methods of insect pest management, more attention has been paid to a particular group of natural enemies, spiders (Araneae). Spiders are polyphagous, obligate predators that feed on a number of pest insects, including cotton bollworm (*Helicoverpa zea* (Boddie)), imported cabbage worm (*Pieris rapae* (Linnaeus)), and numerous species of aphids (Riechert and Bishop 1990; Young and Edwards 1990; Nyffeler et al. 1994a, 1994b). Investigations have demonstrated that spiders can be important biological control agents in crop ecosystems throughout the world (Riechert and Lockley 1984; Nyffeler et al. 1994b; Marc et al. 1999). However, modern farming practices, which rely on repeated chemical and physical disturbance of the habitat, often do not provide appropriate conditions for spiders (Young and Edwards 1990; Baines et al. 1998; Feber et al. 1998). Much of the recent research has focused on identifying habitat features that are important for attracting and maintaining spider populations. Such features include reduced use of insecticides, reduced physical disturbances such as tilling and burning, and increased diversification of plant communities instead of monocultures. These

features are more common in agroecosystems that are less intensely managed (Nentwig 1988; Bellini et al. 1994; Balfour and Rypstra 1998; Feber et al. 1998; Bogya and Markó 1999; Holland et al. 1999; Marshall and Rypstra 1999a; Rypstra et al. 1999; Amalin et al 2001).

Another important feature of sustainable agroecosystems is the presence of a permanent, undisturbed natural habitat adjacent to the field. These border or edge habitats form refuges from agricultural disturbances that may serve as a source of colonizers following disturbance (Baines et al. 1998; Huusela-Veistola 1998; Holland et al. 2000). Often spiders are more abundant at the edges, and certain species may be more commonly found in edge habitats than in the field itself (Alderweireldt 1989; Bogya and Markó 1999). Grassy strips and tree windbreaks can also serve as edge habitats and may be important features for spider conservation in more intensely managed fields (Nentwig 1988; Huusela-Veistola 1998).

In addition to differences in abundance, the species composition of spider communities is often affected by different agricultural management practices. Differences in the abundance and distribution of the species may also reflect complex species-specific habitat requirements (Bellini et al. 1999; Bogya and Markó 1999; Weeks and Holtzer 2000; Martin and Major 2001). Often it is not simply changes in species composition that differs between agricultural fields and their edge habitats but differences in relative abundances of individual species. Such differences would not be detected by analyses at the family level (Weeks and Holtzer 2000; Martin and Major 2001).

Little research has been conducted on spider communities in *Vaccinium* berry cropping systems. Collins et al. (1996) sampled spiders in mowed, burned, and bearing lowbush blueberry (*Vaccinium angustifolium*) fields in Washington County, Maine. They reported that hunting spiders were dominant, both in abundance and by species richness, and that the Lycosidae were the most abundant hunting spiders. In 1986, they found that both species richness and diversity was greater in bearing fields then non-bearing fields, but species were more evenly distributed in non-bearing burned fields. In 1987, species richness was greater in bearing and non-bearing burned fields, and diversity and evenness were greatest in non-bearing burned fields; mowed non-bearing fields scored the lowest overall. More individuals were captured in bearing fields than in mowed or burned non-bearing fields, and both bearing and non-bearing burned fields had more species than non-bearing mowed fields.

In wild and abandoned cranberry bogs (*Vaccinium macrocarpon* Aiton) in Massachusetts, the spider fauna consisted primarily of hunting spiders. The most common families found with prey in wild cranberry bogs were wolf spiders (Lycosidae) and orb-web-weaving spiders (Araneidae). At the abandoned commercial bogs, lynx spiders (Oxyopidae) and long-jawed web-weavers (Tetragnathidae) were the most common families collected with prey (Bardwell and Averill 1997).

In addition to their potential use as biological control agents, spiders are also important components of food webs. Despite their importance, few of Maine's natural habitats have been studied with respect to spiders and their

ecology. The collections in lowbush blueberry in 1986 and 1987 provided new habitat associations and extended the ranges of species of Linyphiidae, Philodromidae, Lycosidae, and Thomisidae (Collins et al. 1996). However, the spider community and their ecology of Maine's lowbush blueberry agroecosystems have not been further investigated for 13 years.

The present studies examined the following questions concerning spider populations in lowbush blueberry fields of Maine: 1) Which spider families and species are most abundant, and are their abundances consistent with earlier findings? 2) What is the seasonal pattern of lycosid abundance in the fields, and do any environmental or cultural factors affect this? 3) How are lycosids distributed within fields, and are distributions consistent between years and among management practices? 4) Does the lycosid community composition differ among fields, management practices, and distances from field edges?

Methods

Study Sites

Spiders were sampled from bearing blueberry fields of three different management practices – conventional, reduced input, and organic – in Washington County, ME during the growing seasons of 2000 and 2001. The conventionally managed fields were regularly sprayed with pesticides, including fungicides and organophosphate insecticides. Reduced input fields were categorized as those sprayed intermittently, when pest outbreaks occured.

Organic fields were those fields that did not use synthetic chemical input for fertilization or weed, insect, and pathogen management (MOFGA 2002).

Four fields were sampled in 2000 – three conventional fields (CF1, CF2 and CF3) and one reduced input field (BBH). All three conventional fields received applications of the fungicide propiconazole (Orbit®) on 2 May and 13 May and applications of the fungicide chlorothalonil (Bravo®) on 6 June. CF1 was sprayed with the organophosphate insecticide phosmet (Imidan®) on 21 July; CF2 and CF3 were sprayed with phosmet (4 hectares around perimeter) on 15 July. These fields were mowed (a standard pruning practice) in the fall following the bearing season. BBH was sprayed with propiconazole on 12 May and the herbicide clethodim (Select®) from 28 June to 30 June. This field was burned (a traditional pruning practice) in the spring following the bearing season. An application of the herbicide hexazinone (Velpar®) was added concurrent with burning.

Six fields were sampled in 2001 – two conventional fields (C-NL-5B and C-SL-8), two reduced input fields (BBH2 and Grant), and two organic fields (HI1 and HI2). C-NL-5B and C-SL-8 received applications of propiconazole on 7 May, chlorothalonil on 6 June, and phosmet on 14 July. Phosmet was applied to the entire field for C-NL-5B and on 2 hectares around the perimeter for C-SL-8. Both fields were mowed in the fall following the bearing season. Grant received applications of phosmet on 5 May, propiconazole on 12 May, and chlorothalonil on 21 May. This field was burned in the fall following the bearing season. BBH was sprayed with propiconazole on 4 May and clethodim from 19 June to 22

June. This field was burned in the spring following the bearing season. An application of hexazinone was added concurrent with burning.

HI1 and HI2 received no chemical pesticides, but the firebreak bordering HI2 received applications of hexazinone (Pronone®) prior to the 2001 growing season. HI1 was mowed along the edge and burned in the middle, and HI2 was burned in the spring following the bearing season.

Sampling Design

Spiders were sampled using pitfall traps consisting of a plastic container (ca. 7.5 cm h X 10 cm d) filled with 3-5 cm of propylene or ethylene glycol. An aluminum rain cover (18 X 18 cm) supported by three nails (9 cm length) was placed over each trap to prevent flooding.

In 2000, one trap was set at the edge of the field (BBH) or in a pine windbreak at the edge of field (CF1, CF2 and CF3). Subsequent traps were set at approximately 3, 15, and 30 m into the field (e.g., Alderweireldt 1989; Collins et al. 1996; Huusela-Veistola 1998; Martin and Major 2001). Traps at BBH were set at 4 m instead of 3, due to a dirt road around the perimeter of the field. There were three transects for each replicated set of pitfall traps set, resulting in 12 traps per field. Trap contents were collected every one to two weeks beginning in May (3 May for CF1, 16 May for CF2, and 30 May for CF3 and BBH) and continuing until 11 August. Two additional collections were made on 28 August and 8 September at BBH.

In 2001, one trap was set at the edge of the field (BBH2 and Grant) or in a pine windbreak at the edge of the field (C-NL-5B and C-SL-8), with subsequent traps set at 3, 15, and 30 m into the field. Traps at BBH2 were set at 7.5 m instead of 3, due to a dirt road around the perimeter of the field. There were three transects of 4 traps each, for a total of 12 traps per field (e.g., Alderweireldt 1989; Collins, et al 1996; Huusela-Veistola 1998; Martin and Major 2001). The traps were set out for approximately the first week of each month for May, June, July, and August, for a total of four collections. One additional collection was made on 2 May for BBH2. Traps at HI1 and HI2 were set at 3 and 30 m from the field edge, with three transects and 6 traps per field. Traps were set out for approximately the first week of June, July and August, for a total of three collections.

On each collection date, traps were removed from the ground and their contents passed through a fine mesh strainer. Captured organisms were sorted and placed in vials with 70% ethanol. Sexually mature spiders were identified to species, and immatures were identified to family or genus, when possible, by Dr. Daniel T. Jennings, USDA Forest Service (retired), following standard keys and species descriptions (Platnick 1975, 1989, 1993, 1997; Platnick and Shadab 1975, 1983; Dondale and Redner 1978, 1982, 1990; Kaston 1981; and Platnick and Dondale 1992).

Data Analysis

Captured spiders were tallied by family, genus and species (see Appendix A). For each study year, the percentages of spiders captured were calculated for two predatory groups (hunters or web weavers), and by spider family, and life stage and sex (adult male, adult female, and juvenile). Percentages of males, females, and juveniles of the most commonly captured family, Lycosidae, were also calculated.

All statistical analyses were performed using lycosid adults only. Adult spiders can be identified to species, whereas most juveniles cannot. Juveniles also were highly aggregated due to the maternal behavior of lycosids, i.e., spiderlings are transported on the dorsum of the female's abdomen for the first one to two weeks after hatching (Foelix 1996). For consistency among the samples taken in 2000, only data from 30 May – 11 August were used in statistical analyses. For samples taken in 2001, only data from 11 May – 9 August were used when comparing conventional and reduced input fields (two management practices comparison). Only data from 7 June – 9 August and from traps at 3 and 30 m, were used when comparing conventional, reduced input, and organic fields (three management practices comparison). When comparing management practices and distances from the field edge, each trap capture was pooled across dates to reduce zero counts and non-normal distributions.

Lycosid abundance (average number of adult lycosids per transect) each season was compared over each sampling date using analysis of variance (ANOVA) (PROC GLM, SAS Institute 1990). Linear regression analyses between

lycosid trap capture at each sampling date and average rainfall, low temperatures, and high temperatures during the sampling period were conducted to assess environmental factors that may have affected trap capture (PROC REG, SAS Institute 1990). Lycosid abundances (average number of adult lycosids per trap) in fields of each management practice were compared using ANOVA (PROC GLM, SAS Institute 1990). For 2001 data, separate ANOVAs were performed for the two management practices comparison and the three management practices comparison. This was necessary because of the different trapping dates. Lycosid abundances (average number of lycosid adults per trap) at each distance from a field edge were compared using ANOVA for overall abundance and for each field. A single degree of freedom linear contrast was also performed (PROC GLM, SAS Institute 1990) to determine if a linear relationship existed among trap capture levels and distance into a field. Samples taken at 4 and 7.5 m for BBH and BBH2 were included with the 3-m distance of other fields.

For the sampling date ANOVAs, the total number of lycosids per transect per sampling date was used in the analysis in order to reduce zero counts. For all remaining ANOVAs, the total number of lycosids per distance per trap was used in the analysis. Data were transformed using square root transformations. Non-transformed data were used in the figures and tables.

Differences in counts of species within each field management practice and within each distance from the edge were evaluated using Poisson regression with the General Linear Models procedure in SAS (PROC GENMOD, SAS

Institute 1990). Due to the assumptions of GENMOD, only species found in at least three fields or distances were used in the analyses. For the management practices comparison, 12 species were used in 2000 while 6 species were used in 2001. For the distance from the edge comparison, 9 species were used in 2000, while 8 species were used in 2001. Contrast statements were used to determine differences in mean number of individuals per species among management practices and trapping distances into a field.

Patterns in lycosid community composition by field and management practice, and by distance from the field edge, were analyzed with Canonical Correspondence Analysis (CCA) using the program PC-ORD (McCune and Mefford 1997; Ter Braak 1986). Due to assumptions of CCA, only species found in at least 2 fields in 2000 (12 species) and at least three fields in 2001 (9 species) were used in management practices comparisons. For the distance from the edge comparison, only species found in at least two distances were used. In 2000, 11 species were used, and in 2001, 10 species were used. Statistical significance of eigenvalues was assessed using the Monte-Carlo procedure supplied by PC-ORD (1000 randomized runs). If significant differences were found, the distributions of the treatments and species of lycosids were graphically inspected in order to determine associations among management practices and species, and among distances and species.

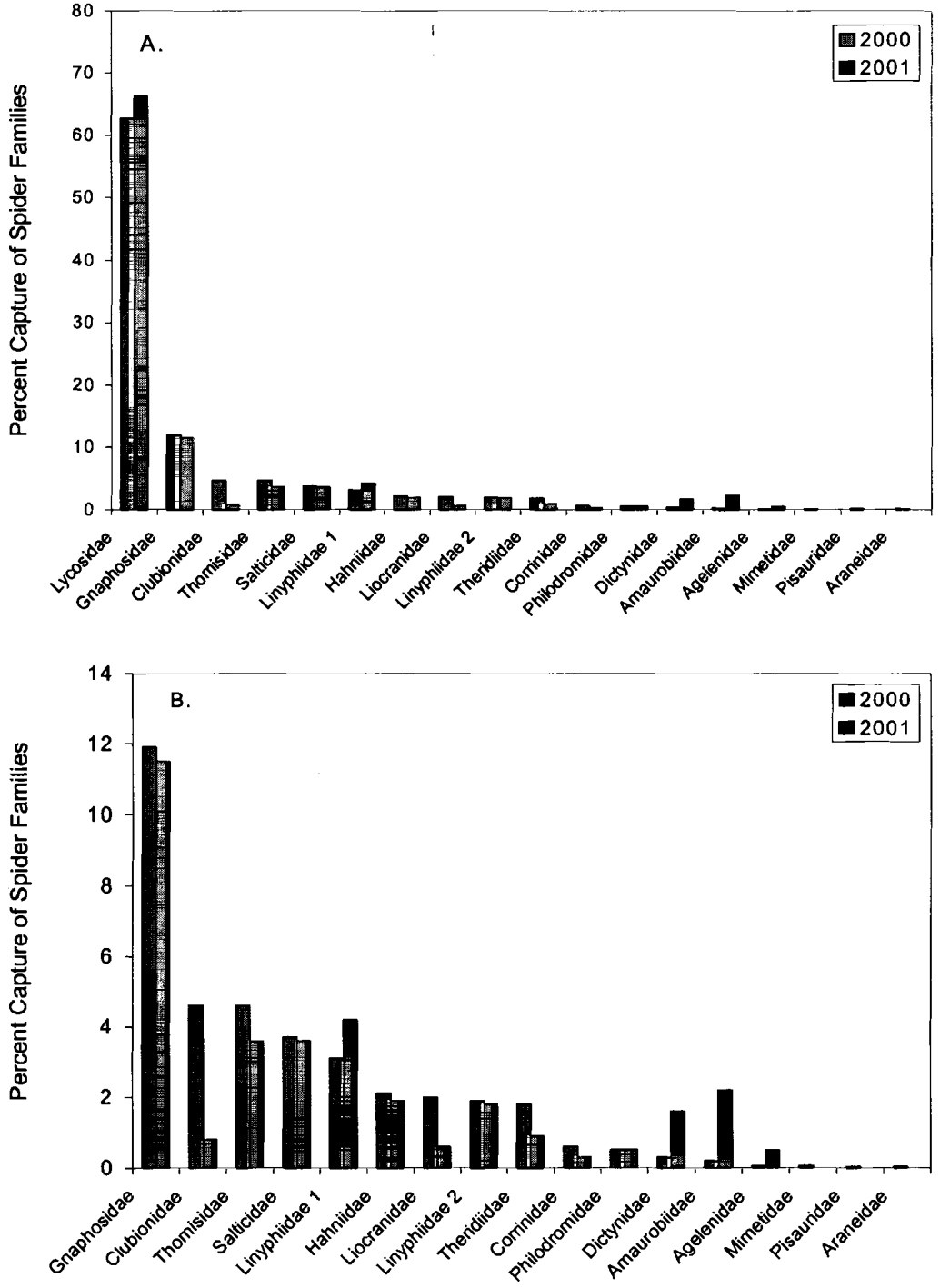
Results

Spider Taxa and Life Stages

Spiders of 17 families, 81 genera, and 133 species were captured in pitfall traps deployed in lowbush blueberry fields in Washington County, Maine during the summers of 2000 and 2001 (see Appendix A). Fewer taxa were captured in 2001 than 2000: 17 families, 72 genera, and 117 species in 2000 and 14 families, 49 genera, and 72 species in 2001. Species of Araneidae, Mimetidae and Pisauridae were trapped in 2000 but not 2001. However, trapping efforts were less intensive in 2001 than in 2000, with only five sampling periods instead of twelve.

For both study years, hunting spiders were numerically dominant, comprising 90.6% of all spiders captured in 2000, and 86.9% of spiders captured in 2001. In both years, the Lycosidae was the numerically dominant family, making up 62.7% and 66.2% of all spiders in 2000 and 2001, respectively. The next most common families in 2000 were Gnaphosidae (11.9%), Clubionidae (4.6%), and Thomisidae (4.6%). All other hunter families comprised 6.9% of the total number of spiders (n = 3108). The next most common families in 2001 were Gnaphosidae (11.5%), Linyphiidae, subfamily Erigoninae (web-weavers) (4.2%), Thomisidae (3.6%), and Salticidae (3.6%). The remaining hunter families comprised 2.2% of the total number of spiders, and the remaining web weaver families comprised 8.9% of the total number of spiders (n = 786) (Figure 2.1).

Figure 2.1. Percent capture of spider families trapped in pitfall traps in lowbush blueberry fields in Washington County, ME. Spiders were sampled from late April to early September in 2000, and during the last week of April and first weeks of May, June, July, and August in 2001. Linyphiidae 1 is subfamily Erigoninae. Linyphiidae 2 is subfamily Linyphiinae. A: Percent abundance of all spider families captured. B: Percent abundance of families captured, excluding the Lycosidae.



The rank order of abundances for the ten most commonly trapped spider species (adults) differed between study years (Table 2.1). Five lycosids and one hahniid were among the ten top ranked species during each study year. The numerical dominance of the hunter guild was evident in the rank order of species abundance – 80% of the top ten species were hunters in 2001, and 90% were hunters in 2000. The two web-weaver species, *Grammonota capitata* (Linyphiidae: Erigoninae) and *Neoantistea agilis* (Hahniidae) ranked seventh and tenth in abundance, respectively, in 2001; *N. agilis* ranked 9th in 2000. In 2000 and 2001, lycosids comprised fully 60% of the top ten most abundant species.

Table 2.1. Rank order of abundance for the 10 most commonly trapped adult spiders in lowbush blueberry fields of Washington County, ME, in 2000 and 2001. Total columns represent total number of individuals of each species, while percent columns represent percent of all spiders captured (n = 3108 in 2000 and n = 786 in 2001).

2000 Species	Total	% of Total	2001 Species	Total	% of Total
1. *Pardosa moesta* Banks	290	9.33	*Hogna frondicola* (Emerton)	70	8.91
2. *Schizocosa communis* (Emerton)	170	5.47	*Pardosa xerampelina* (Keyserling)	61	7.76
3. *Clubiona johnsoni* Gertsch	98	3.15	*Schizocosa communis* (Emerton)	52	6.62
4. *Pardosa xerampelina* (Keyserling)	98	3.15	*Zelotes hentzi* Barrows	22	2.80
5. *Pardosa distincta* (Blackwall)	93	2.99	*Pardosa moesta* Banks	21	2.67
6. *Hogna frondicola* (Emerton)	85	2.73	*Pardosa distincta* (Blackwall)	17	2.16
7. *Alopecosa aculeata* (Clerck)	66	2.12	*Grammonata capitata* Emerton	16	2.04
8. *Habronattus viridipes* (Hentz)	62	1.99	*Gnaphosa muscorum* (L. Koch)	15	1.91
9. *Neoantistea agilis* (Keyserling)	58	1.87	*Trochosa ruricola* (De Geer)	14	1.78
10. *Xysticus triguttatus* Keyserling	48	1.54	*Neoantistea agilis* (Keyserling)	14	1.78

For both study years, juveniles were the life stage trapped most frequently, followed by adult males and adult females, respectively. In 2000, 43.7% of all captured spiders were juveniles, 37.4% were adult males and 18.9% were adult females. In 2001, the percentages captured were 43.1% juveniles, 38.6% adult males and 18.3% adult females. Of the Lycosidae, 52.7% juveniles,

37.0% adult males and 10.1% adult females were trapped in 2000; 48.0% juveniles, 37.2% adult males and 14.8% adult females were trapped in 2001.

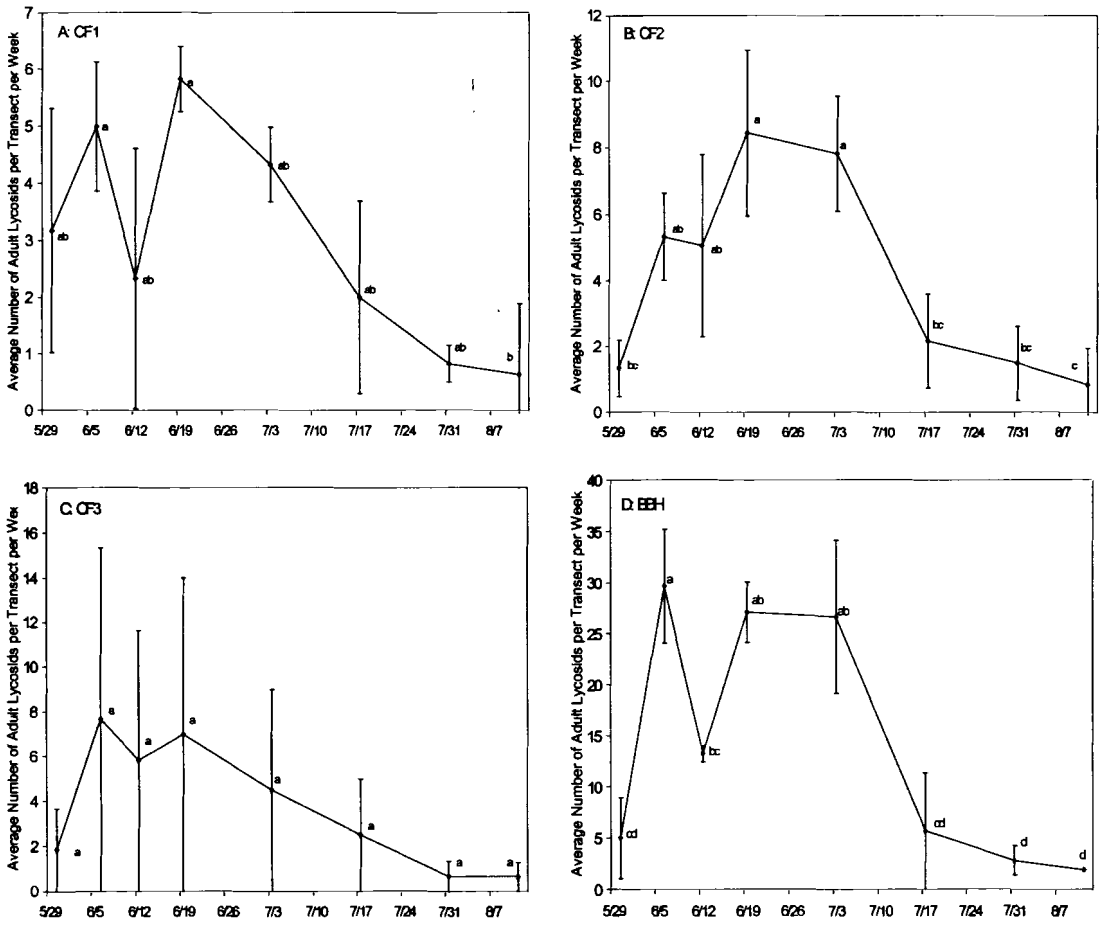
Lycosidae Adults Abundance and Distribution

Seasonal Patterns.

2000. Adult lycosid populations peaked in early July and sharply declined in late July and August in all four fields. There were significant differences in the numbers of lycosids captured among sampling dates in CF1, CF2 and BBH ($df=7,16$; $P<0.05$ for all three fields), with the 6 June and 19 June samples having more lycosids in CF1 (a conventional field), the 16 June and 3 July samples having more lycosids in CF2 (a conventional field), and the 6 June sample having more lycosids in BBH (a conventional field). The 11 August sample in CF1 and CF2 and the 31 July and 11 August samples in BBH had the fewest lycosids. There were no differences in trap capture among dates in CF3 as indicated by a Tukey's test (Figure 2.2).

Fewer lycosids were captured during rainy periods in 2000, although there was no significant relationship between lycosid capture and average rainfall during the sampling period ($df=1,6$; $F=0.40$; $r=0.251$; $P = 0.548$). There was also no significant relationship between lycosid capture and either average low temperatures ($df=1,6$; $F=0.00$; $r=0.014$; $P = 0.977$) or average high temperatures ($df=1,6$; $F=0.10$; $r=0.130$; $P=0.758$) during the sampling period in 2000.

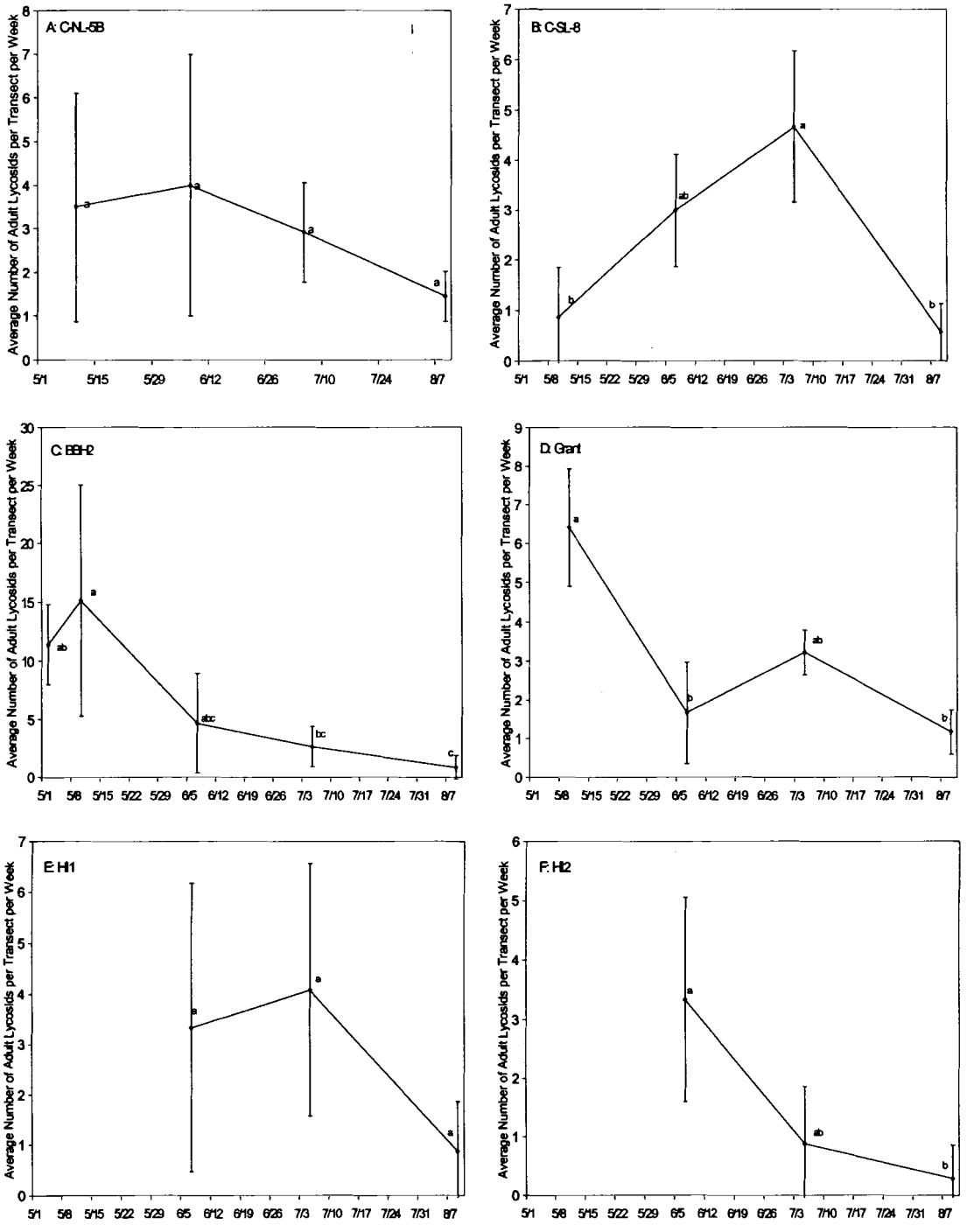
Figure 2.2. Average number of lycosids captured in pitfall traps at different lowbush blueberry fields in Washington County, ME, in 2000. A: Capture per transect per week in CF1. B: Capture per transect per week in CF2. C: Capture per transect per week in CF3. D: Capture per transect per week in BBH. Error bars represent 95% confidence intervals.



2001. Adult lycosid populations peaked in May in BBH2 and Grant, June in C-NL-5B and HI2, and July in C-SL-8 and HI1. August populations were low in all fields. There were significant differences in the numbers of lycosids captured among sampling dates in C-SL-8 (df=3,8; F=7.05; P=0.012), BBH2 (df=4,10, F=7.70; P=0.004), Grant (df=3,8; F=16.25; P<0.001) and HI2 (df=2,6; F=5.63; P=0.042). The 5 July sample had the most lycosids and the 10 May and the 9 August samples had the fewer lycosids in C-SL-8. The 10 May sample had the most lycosids, and the 9 August sample had the fewest lycosids in BBH2 and Grant. The 7 June sample had the most lycosids and the 9 August sample had the fewest lycosids in HI2 (Figure 2.3).

There was no significant relationship between lycosid capture and average rainfall during the five sampling periods in 2001 (df=1,3; F=0.84; r=0.467; P=0.428. There was a significant relationship between lycosid capture and average low temperatures during the sampling periods (df=1,3; F=17.34; r=0.924; P=0.025). Lycosid capture decreased as average low temperature increased. The relationship between lycosid capture and average high temperatures was not significant (df=1,3; F=7.21; r=0.840; P=0.075).

Figure 2.3. Average number of lycosids captured in pitfall traps at different lowbush blueberry fields in Washington County, ME, in 2001. A: Capture per transect per week in C-NL-5B. B: Capture per transect per week in C-SL-8. C: Capture per transect per week in BBH2. D: Capture per transect per week in Grant. E: Capture per transect per week in HI1. F: Capture per transect per week in HI2. Error bars represent 95% confidence intervals.



Patterns By Management Practice.

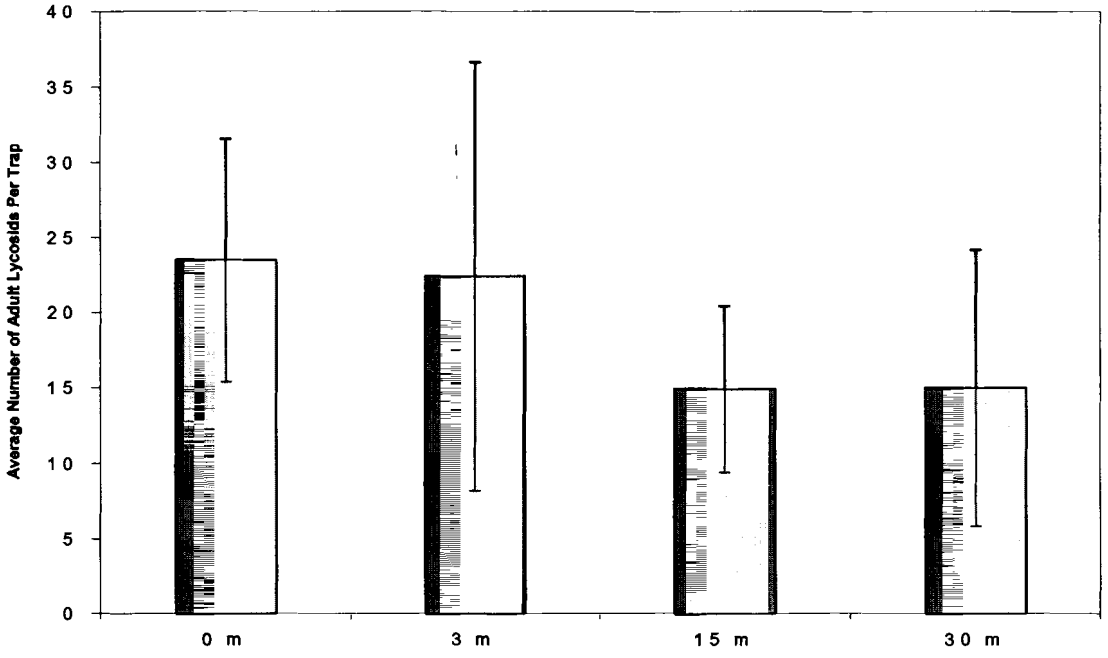
2000. There was a significant difference in lycosid capture between crop management practices (df=1,46; F=49.77; P<0.0001), with averages of 11.9 lycosids captured per trap in the conventional fields and 40.3 lycosids per trap in the reduced input field.

2001. In the two management practices comparison, there were significant differences in lycosids captured between management practices (df=1,46; F=6.14; P=0.017) with an average of 2.88 lycosids per trap in the conventional fields and 5.13 lycosids per trap in the reduced input fields. In the three management practices comparison, for traps at 3 m and 30 m, there was an average of 1.83 lycosids per trap in the conventional fields, 2.42 lycosids per trap in the reduced input fields, and 3.58 lycosids per trap in the organic fields. There were no significant differences in lycosids captured between management practices for this reduced sample set (df=2,33; F=0.69; P=0.508).

Spatial Patterns.

2000. For all fields combined, there was a significant linear trend (df=1; F=7.59; P=0.010), with the number of lycosids captured per trap decreasing as traps were placed further into the field (Figure 2.4).

Figure 2.4. Average number of adult lycosids captured per pitfall trap at different distances from the forest/windbreak edge of lowbush blueberry fields in Washington County, ME, in 2000. Error bars represent 95% confidence intervals.



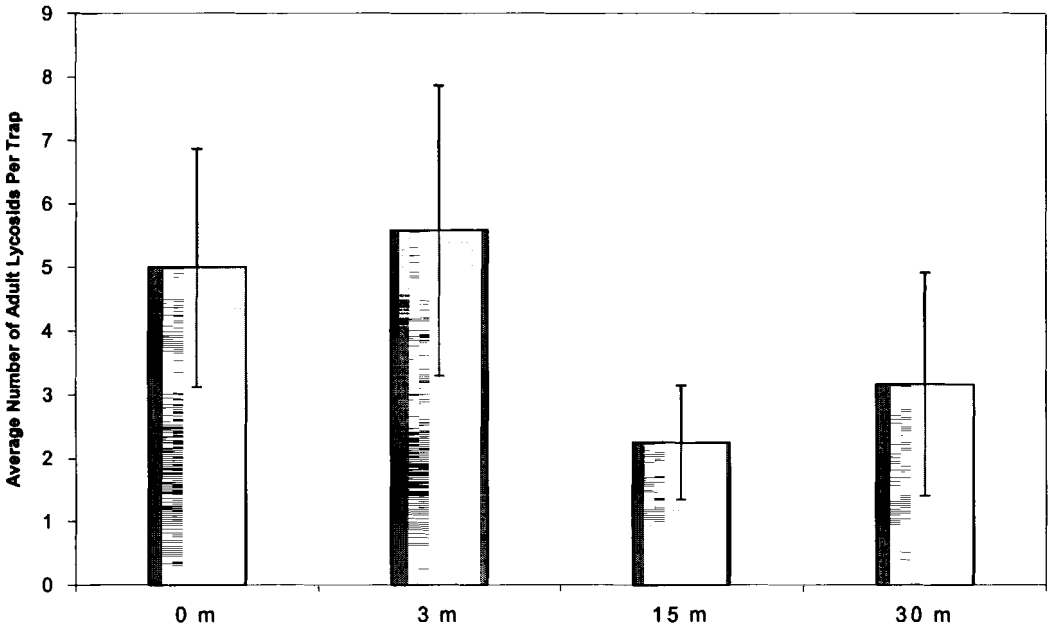
There were no significant differences in number of lycosids trapped at 0, 3, 15 and 30 m from the edge in CF1, CF3, or BBH (df=1; P>0.05 for all fields). There was a significant linear contrast in CF2 (df=1; F=16.08; P=0.004), with the number of lycosids captured per trap decreasing as traps were placed further into the field (Table 2.2).

Table 2.2. Average number of adult lycosids captured in pitfall traps at each of four distances from the field edge of four lowbush blueberry fields from May through August in Washington County, ME, in 2000.

	CF1		CF2		CF3		BBH	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
0 m	15.67	1.45	25.67	3.48	13.67	0.33	39.00	12.58
3 m	12.67	5.17	10.00	3.64	8.67	4.63	58.33	15.32
15 m	11.33	0.67	10.33	1.76	10.67	4.41	27.33	6.94
30 m	9.00	3.21	7.67	0.88	7.00	2.08	36.33	12.72

2001. For the four fields sampled in the two management practices comparison (BBH2, Grant, C-NL-5B and C-SL-8) combined, the average number of lycosids per trap was 5.00 at 0 m from the edge, 5.58 at 3 m, 2.25 at 15 m, and 3.17 at 30 m. There was a significant linear trend (df=1; F=6.87; P=0.013). Lycosid numbers decreased as distance from the edge increases (Figure 2.5).

Figure 2.5. Average number of lycosids captured in pitfall traps at different distances from the forest/windbreak edge of lowbush blueberry fields in Washington County, ME, in 2001. Error bars represent 95% confidence intervals.



There were no significant differences in number of lycosids trapped at 0, 3, 15 and 30 m from the edge in C-NL-5B, BBH2, or Grant (df=1; P>0.05 for all fields). There was a significant linear contrast in C-SL-8 (df=1; F=11.96; P=0.009), with the number of lycosids captured per trap decreasing as traps were placed further into the field (Table 2.3).

Table 2.3. Average number of adult lycosids captured in pitfall traps at each of four distances from the field edge of four lowbush blueberry fields during the first weeks of May, June, July and August in Washington County, ME, in 2001.

	C-NL-5B		C-SL-8		BBH2		Grant	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
0 m	4.00	0.00	5.33	1.33	5.33	3.93	5.33	1.45
3 m	5.33	1.33	2.67	0.88	10.33	3.18	4.00	0.58
15 m	1.67	0.88	1.33	0.67	3.67	1.20	2.33	0.67
30 m	2.00	1.53	0.67	0.33	6.67	1.76	3.33	1.45

For all six fields sampled in June, July, and August 2001, the average number of lycosids per trap was 2.5 at 3 m and 2.72 at 30 m. There were no significant differences between distances (df=1,24; F=0.20; P=0.659). There were also no differences between 3 and 30 m for each field in June, July, and August (df=1; P>0.05 for all fields) (Table 2.4).

Table 2.4. Average number of adult lycosids captured in pitfall traps at each of two distances from the field edge of six lowbush blueberry fields during the first weeks of June, July and August in Washington County, ME, in 2001.

	C-NL-5B		C-SL-8		BBH2		Grant		HI1		HI2	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
3 m	2.67	0.88	2.33	0.88	1.67	0.33	2.00	0.00	4.00	1.53	2.33	0.33
30 m	1.67	1.20	1.33	0.67	4.00	1.15	2.00	1.52	5.67	3.71	2.33	1.86

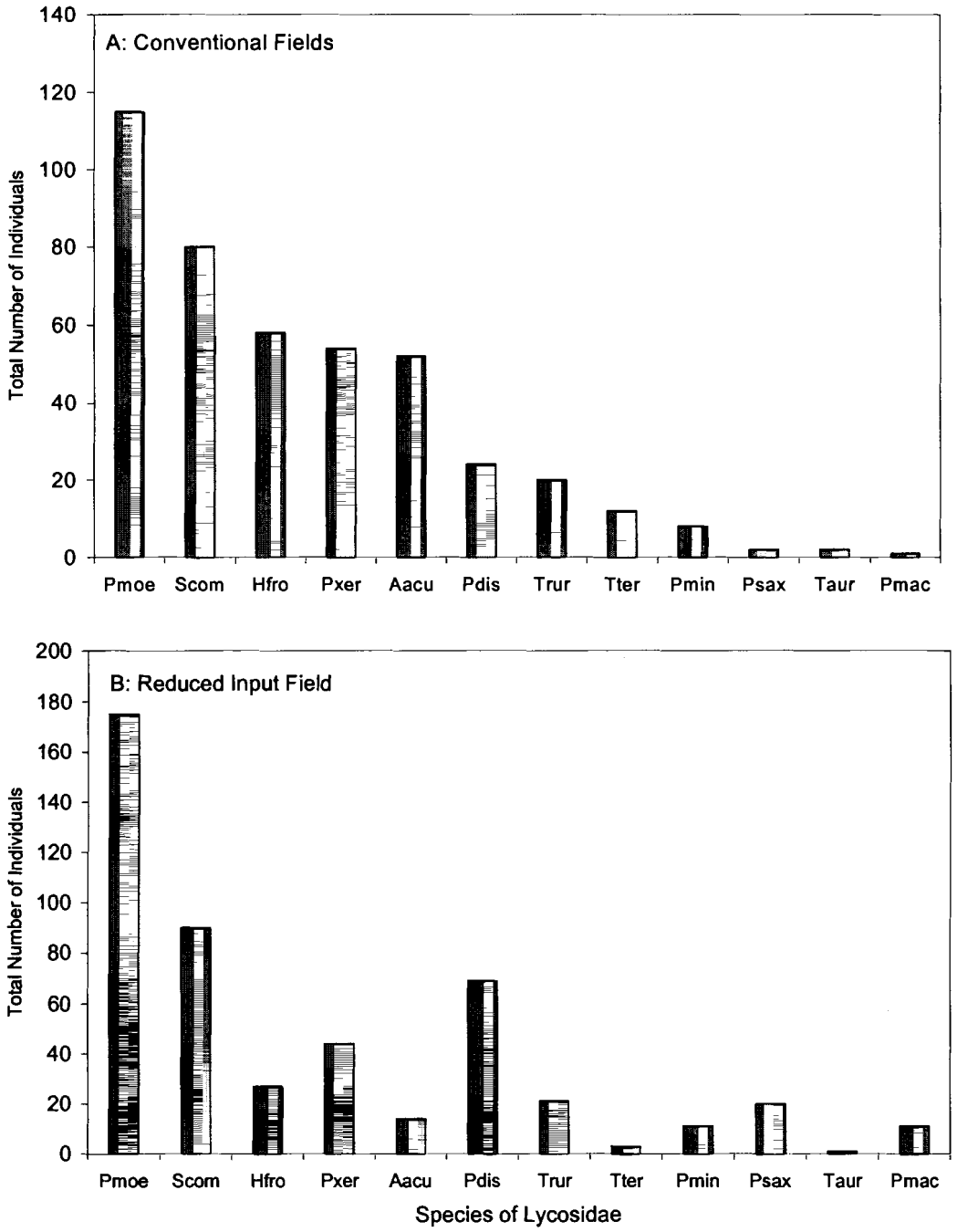
Community Composition

Among Fields and Management Practices.

2000. There was a significant species by treatment interaction determined by Poisson regression. Not only was the proportion of individuals within each species different, with the reduced input field having more individuals per species than the conventional fields (df=1, χ^2=26.27, P<0.0001), but the proportions of individuals in each species was different between management practices (df=11, χ^2=101.47; P<0.001) (Figure 2.6).

A Monte Carlo test associated with a CCA indicated that there were no significant changes in the spider community composition between management practices, or among fields (P=0.212; P=0.762; respectively).

Figure 2.6. Total number of lycosids of different species captured in pitfall traps in lowbush blueberry fields of different management practices in Washington County, ME, in 2000. A: Capture at the conventional fields. B: Capture at the reduced input field. Species designations are: Pmoe = *P. moesta*; Scom = *S. communis*; Hfro = *H. frondicola*; Pxer = *P. xerampelina*; Aacu = *A. aculeata*; Pdis = *P. distincta*; Trur = *T. ruricola*; Tter = *Trochosa terricola* Thorell; Pmin = *Pirata minutus* Emerton; Psax = *Pardosa saxatilis* (Hentz); Taur = *Trabeops aurantiaca* (Emerton); and Pmac = *Pardosa mackenziana* (Keyserling).



2001. The reduced input fields had more individuals per species than the conventional fields (df=1; χ^2=47.56; P=0.0005) and the organic fields (df=1; χ^2=12.21; P=0.0001). The conventional fields had more individuals per species than the organic fields (df=1; χ^2=11.51; P=0.0007). There was a significant species by treatment interaction determined by Poisson regression (P<0.001). The proportions of individuals in each species were different among management practices (Figure 2.7).

Axis 1 of the CCA – the difference among management practices – explains 61.5% of the variation. Axis 2 – the difference between fields within management practices – explains 22.9% of the variation. A Monte Carlo test indicated that there were changes in the community composition between management practices, but there were also differences in community composition between fields (P=0.046 for Axis 1; P=0.012 for Axis 2). Ordination of the fields results in three distinctly different groups, which correspond to the assigned management practices. Ordination of the species shows that certain species are associated with specific fields (Figure 2.8). *S. communis* was the dominant species in conventional fields, while *P. xerampelina* was the dominant species in reduced input fields. *T. terricola* and *T. ruricola* were also closely associated with the reduced input fields. *H. frondicola* was common in both conventional and reduced input fields. *P. moesta* and *P. distincta* were dominant in the organic fields, and *Schizocosa saltatrix* (Hentz) was only found in one of the organic fields.

Figure 2.7. Total number of lycosids of different species captured in pitfall traps in lowbush blueberry fields of different management practices in Washington County, ME, in 2001. A: Capture at the conventional fields. B: Capture at the reduced input fields. C: Capture at the organic fields. Species designations are: Scom = *S. communis*; Hfro = *H. frondicola*; Pxer = *P. xerampelina*; Trur = *T. ruricola*; Aacu = *A. aculeata*; Pmoe = *P. moesta*; Tter = *T. terricola*; Pdis = *P. distincta*; and Ssal = *S. saltatrix*.

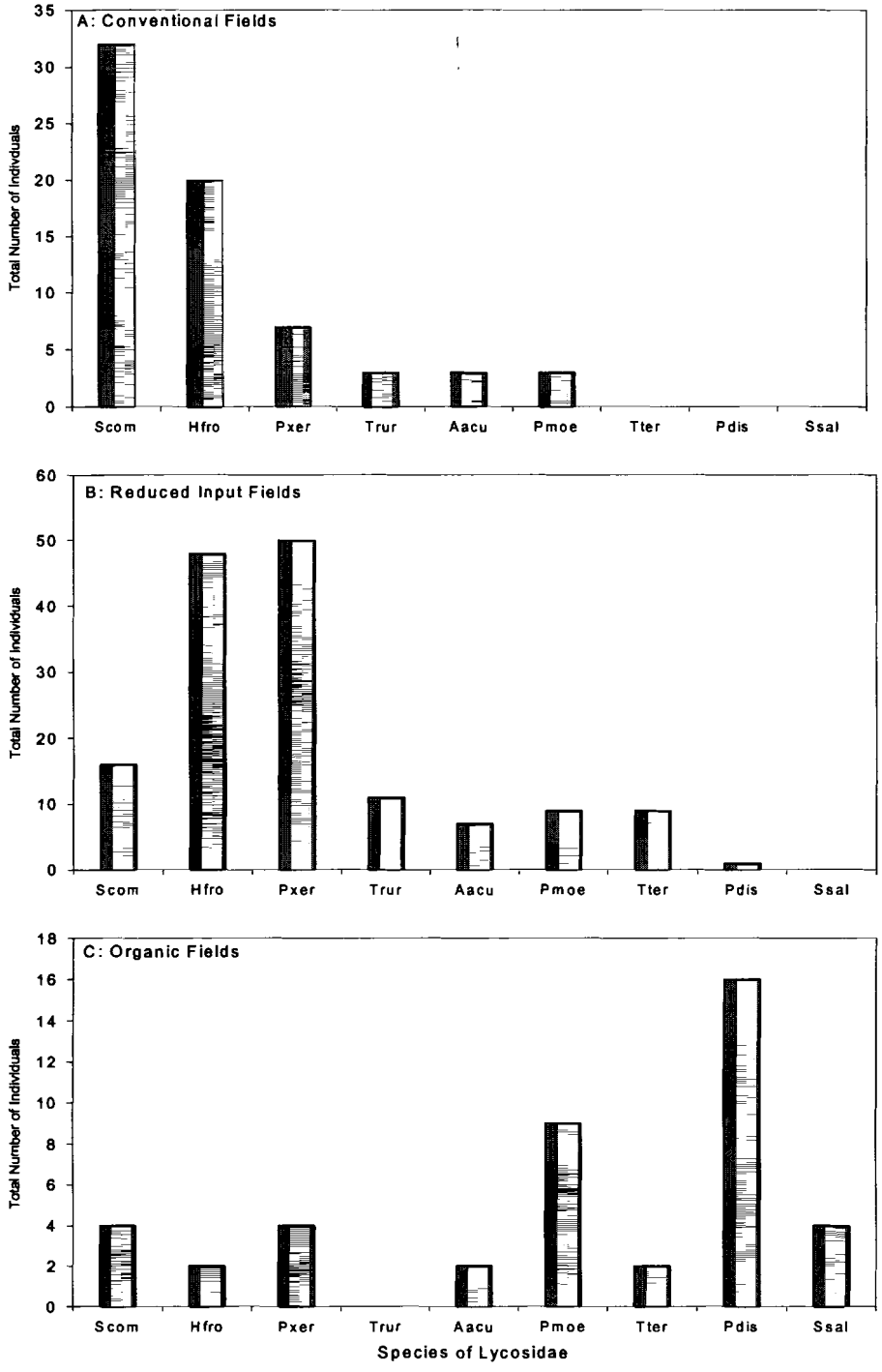
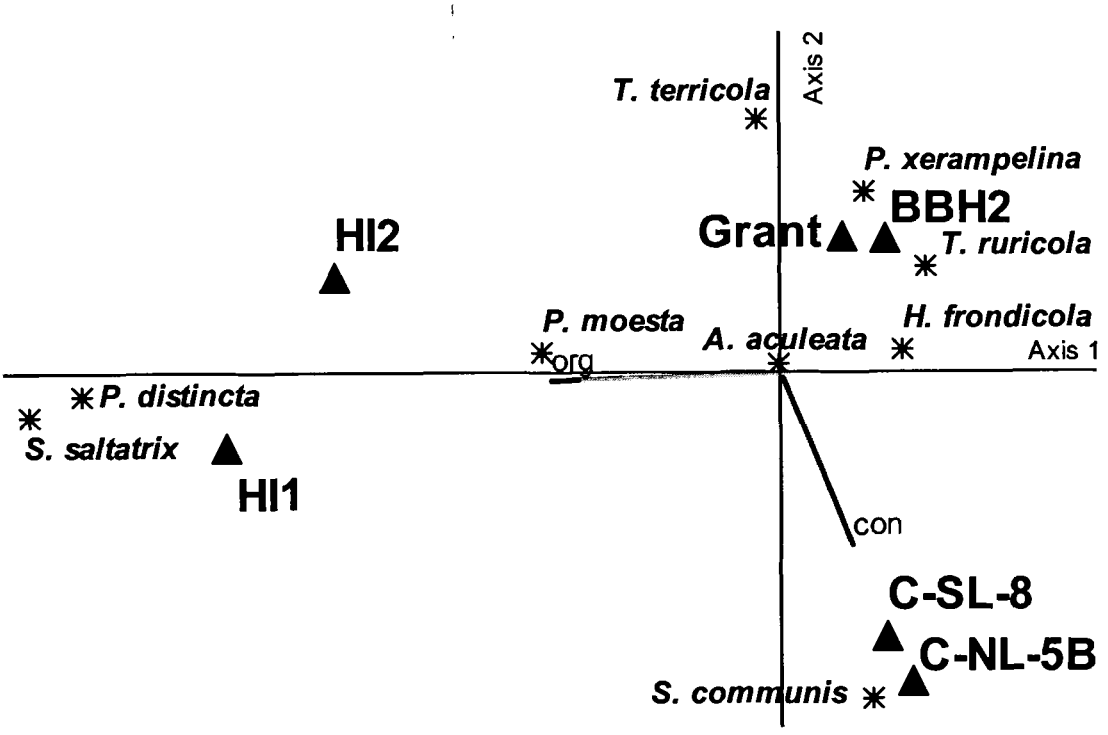


Figure 2.8. Ordination of spider species-field associations in 2001 determined by Canonical Correspondence Analysis. Stars represent lycosid species. Triangles represent lowbush blueberry fields in Washington County, ME, of different management practices. Conventional fields are plotted in quadrant II, reduced input fields are plotted in quadrant I, and organic fields are plotted in quadrants III and IV.



Among Distances.

2000. There was a significant species by distance interaction determined with Poisson regression. The proportion of individuals within each species was different, with the forest border/windbreak (0 m) having more individuals per species than within the field (3, 15 and 30 m) (df=1, χ^2= 4.03, P=0.045). Additionally, the proportion of individuals in each species was different among distances (df=24, χ^2=206.99; P<0.0001), indicating that certain species are more common at specific distances (Figure 2.9).

Axis 1 of the CCA – the difference between the forest border/windbreak and the field – explains 69.0% of the variation. Axis 2 – the difference between distances not explained by the forest-field distinction – explains 22.9% of the variation. A Monte Carlo test indicated that there were no significant changes in the community composition between the forest edge and the field, but there was a trend (P=0.087). There were also no differences between distances (P=0.252). Ordination of the species shows that certain species may be associated with specific distances (Figure 2.10). *P. mackenziana*, *T. terricola*, *A. aculeata*, and *P. xerampelina* were associated with the forest edges and windbreaks, while *P. distincta* and *P. moesta* were associated with the 3 m distance. *T. ruricola*, *Pardosa saxatilis* (Hentz), *H. frondicola* and *S. communis* were associated with 15 and 30 m.

Figure 2.9. Total number of lycosids of different species captured in pitfall traps at different distances from the field edge of lowbush blueberry fields in Washington County, ME, in 2000. A: Capture at the field edge (0 m). B: Capture at 3 m from the edge. C: Capture at 15 m from the edge. D: Capture at 30 m from the edge. Species designations are: Pmoe = *P. moesta*; Pxer = *P. xerampelina*; Aacu = *A. aculeata*; Pdis = *P. distincta*; Scom = *S. communis*; Hfro = *H. frondicola*; Trur = *T. ruricola*; Pmin = *P. minutus*; and Psax = *P. saxatilis*.

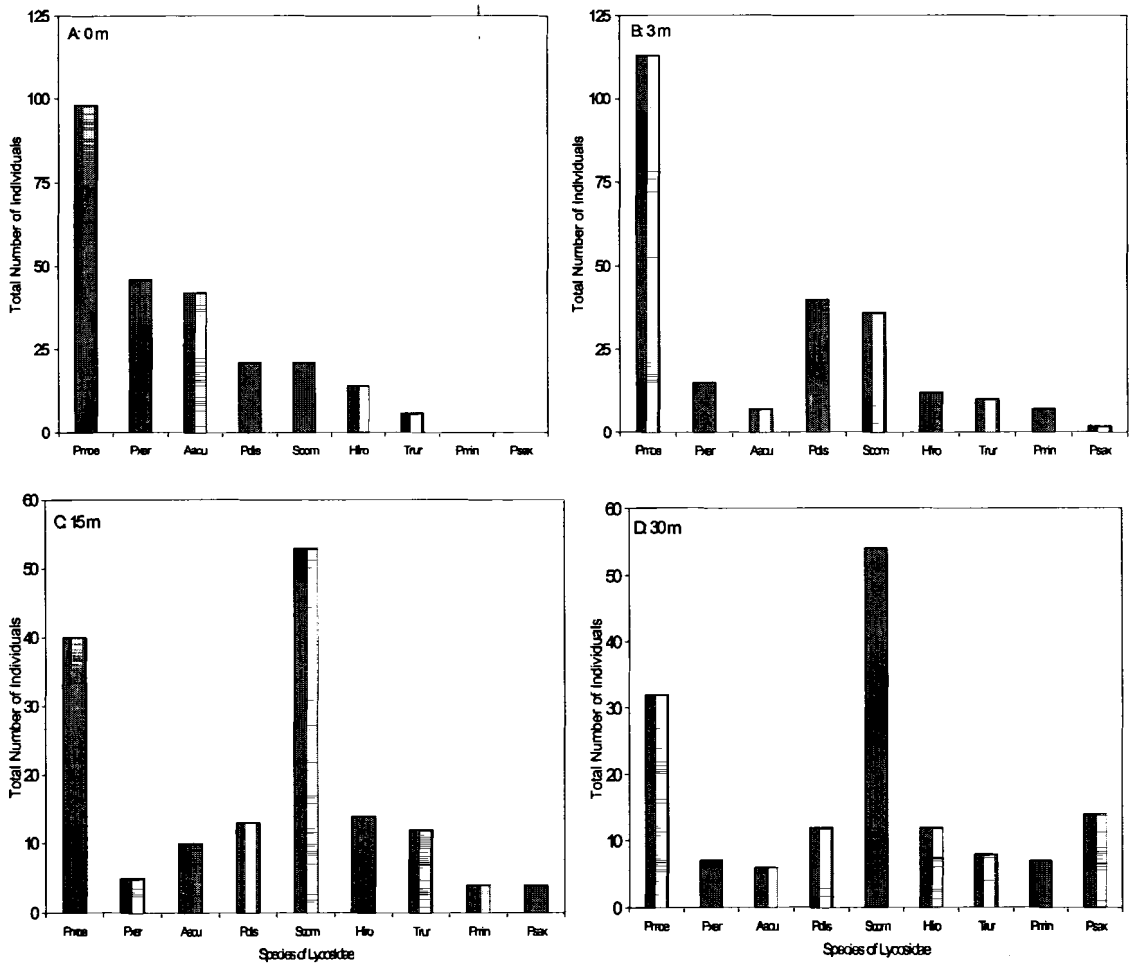
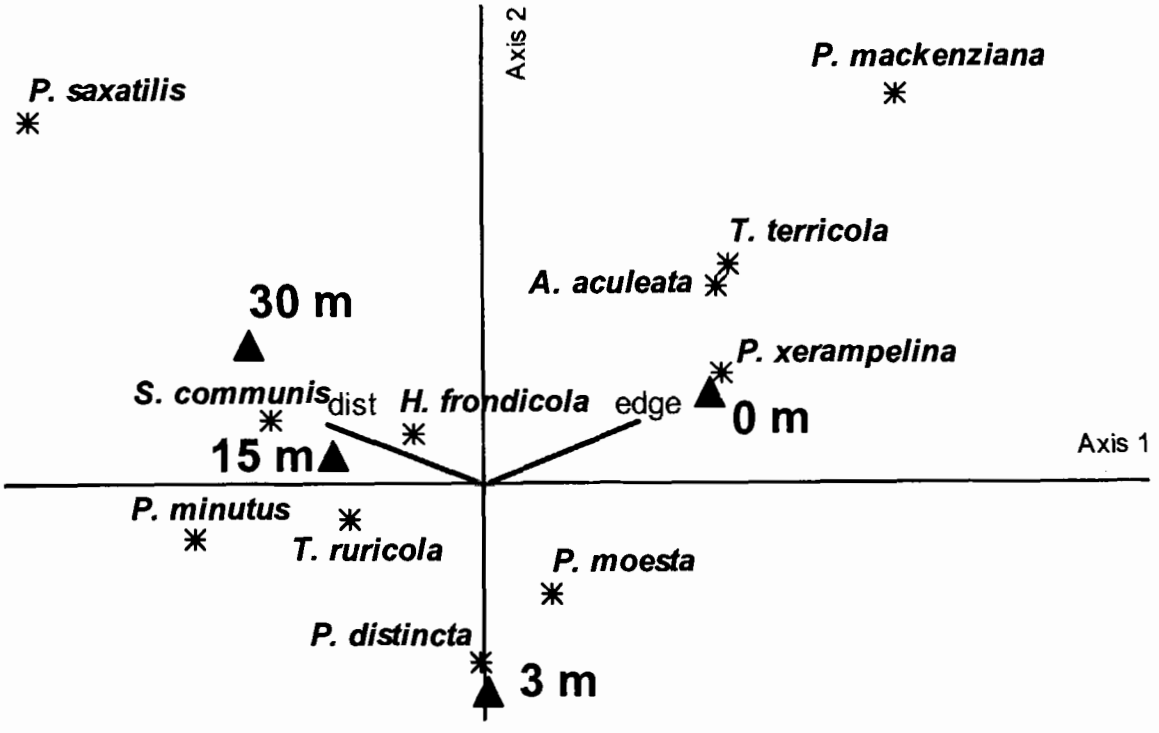


Figure 2.10. Ordination of species-distance associations in 2000 determined by Canonical Correspondence Analysis. Stars represent lycosid species. Triangles represent distances from the edge in lowbush blueberry fields in Washington County, ME.



2001. There was a significant species by distance interaction determined with the Poisson regression. The proportion of individuals within each species was different, with the 0 and 3 m distances having more individuals per species than the 15 and 30 m distances (df=1, χ^2= 8.00, P=0.005). Additionally, the proportions of individuals in each species were different among distances (df=21, χ^2=38.27; P=0.012), indicating that there are higher proportions of some taxa at some distances and higher proportions of other taxa at other distances (Figure 2.11).

Axis 1 of the CCA – the difference between the field edge and the field interior – explains 64.0% of the variation. Axis 2 – the difference between distances not explained by the edge-interior distinction – explains 14.8% of the variation. A Monte Carlo test indicated that there were no significant changes in the community composition between the forest edge and the field, but there was a trend (P=0.088). There were also no differences between distances (P=0.589). Ordination of the species shows that certain species may be associated with specific distances (Figure 2.12). *T. terricola* and *P. xerampelina* were associated with field edges (0 and 3 m), while *P. distincta* and possibly *A. aculeata* and *P. moesta* were associated with field interiors (15 and 30 m).

Figure 2.11. Total number of lycosids of different species captured in pitfall traps at different distances from the field edge of lowbush blueberry fields in Washington County, ME, in 2000. A: Capture at the field edge (0 m). B: Capture at 3 m from the edge. C: Capture at 15 m from the edge. D: Capture at 30 m from the edge. Species designations are: Hfro = *H. frondicola*; Pxer = *P. xerampelina*; Scom = *S. communis*; Tter = *T. terricola*; Pmin = *P. minutus*; Aacu = *A. aculeata*; Trur = *T. ruricola*; and Pmoe = *P. moesta*.

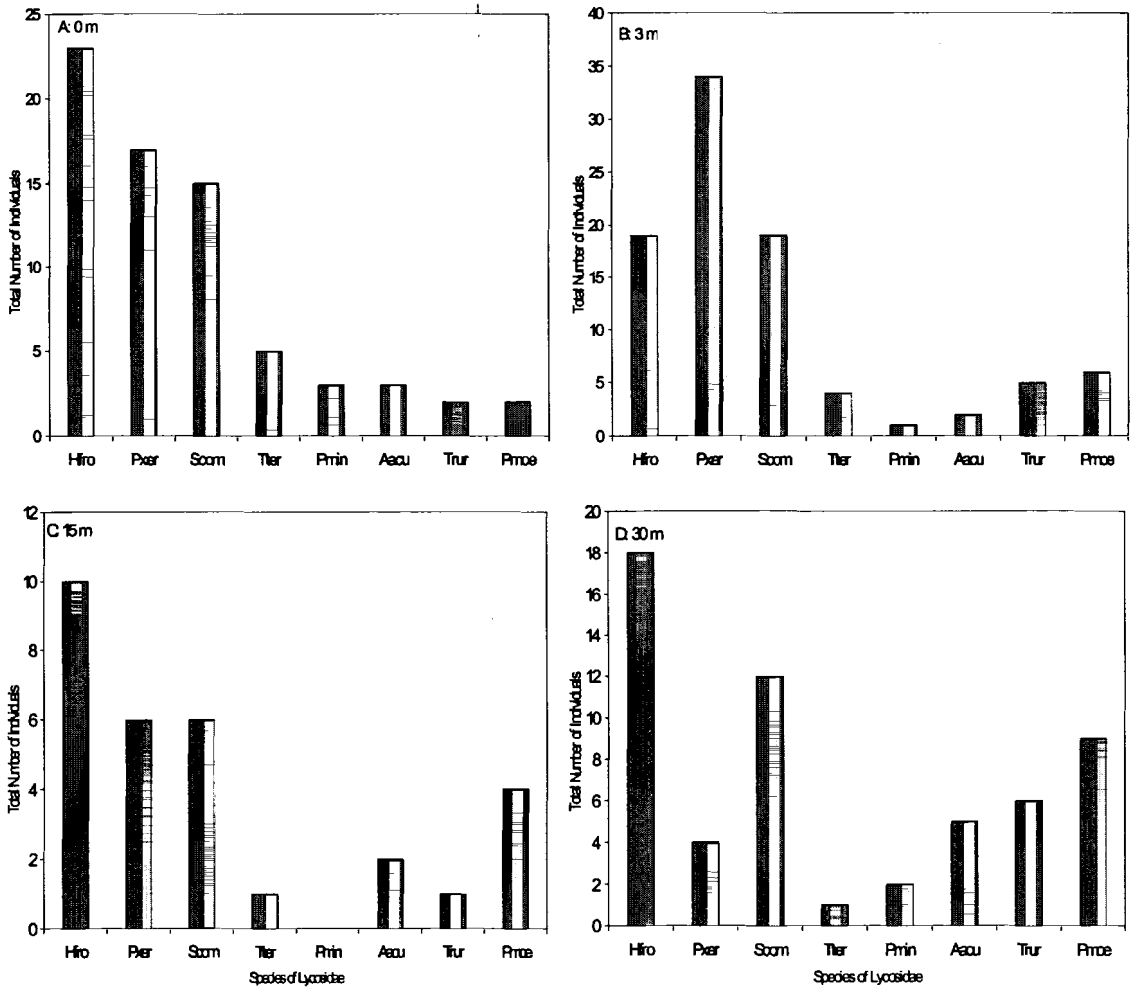
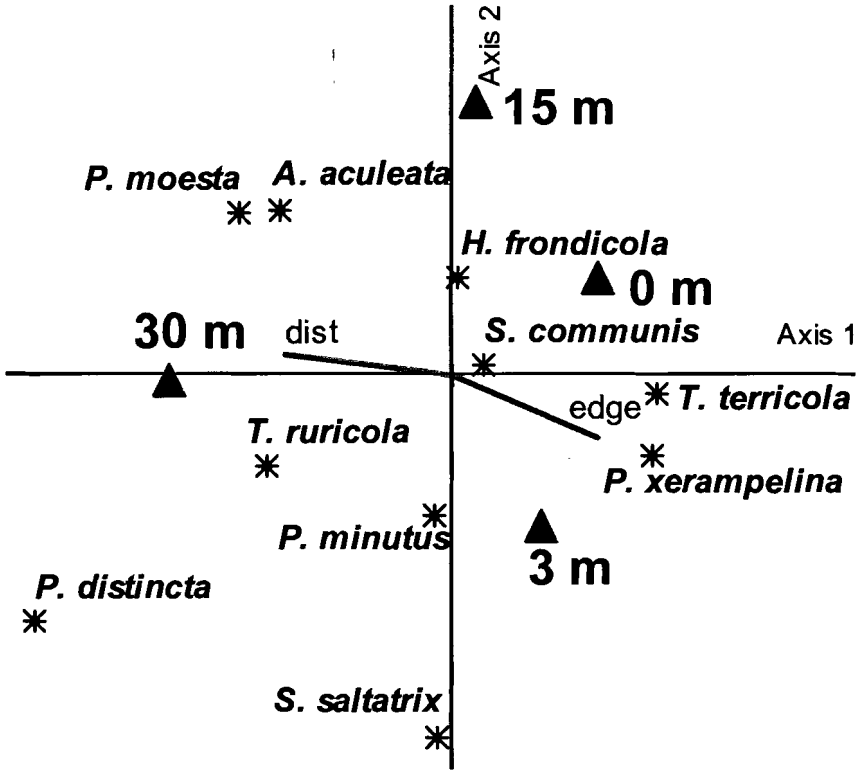


Figure 2.12. Ordination of species-distance associations in 2001 determined by Canonical Correspondence Analysis. Stars represent lycosid species. Triangles represent distances from the edge in lowbush blueberry fields in Washington County, ME.



Discussion

Spiders of 17 families, 81 genera, and 133 species were captured by pitfall traps in lowbush blueberry fields in Washington County, Maine during the summers of 2000 and 2001. These results are similar to those of Collins et al. (1996), who trapped spiders in 17 families, 53 genera, and 87 species in 1986 and 1987. More genera and species were found in 2000 and 2001 than in 1986 and 1987, possibly because trapping was conducted only in bearing fields in the present study. Collins et al. (1996) trapped in bearing, burned, and mowed fields and found significantly more individuals and species in bearing fields than in mowed or burned fields in 1987, although there were no differences in mean numbers of individuals or species richness between bearing and non-bearing fields in 1986.

In the present study, hunting spiders were numerically dominant in both years, making up 90.6% of the total spider fauna in 2000 and 86.9% in 2001. This dominance is also in close agreement with Collins et al. (1996), who found 94.5% hunters in 1986 and 95.5% hunters in 1987. The Lycosidae were the dominant family both in the present study and in earlier studies (Collins et al. 1996). Lycosidae are also the dominant epigeal family in many other crop systems throughout the world, including maize, mixed vegetable gardens, apple orchards, winter wheat, root vegetables, peanuts, cotton, and rice (Agnew and Smith 1989; Alderweireldt 1989; Bishop and Riechert 1990; Hayes and Lockley 1990; Feber et al. 1998; Huusela-Veistola 1998; Bogya and Markó 1999; Holland et al. 1999, 2000; Hussein 1999; Jalaluddin et al. 2000).

In 2000 and 2001, as well as 1986 and 1987, 90% of the ten most abundant species captured were hunters. Sixty percent were lycosids in 2000 and 2001, and 70% were lycosids in 1986 and 1987 (Collins et al. 1996). Six of the ten most common species captured in 2000 or 2001, *P. moesta*, *P. xerampelina*, *P. distincta*, *S. communis*, and *A. aculeata* (Lycosidae), and *X. triguttatus* (Thomisidae), were also among the ten most common species captured in 1986 and 1987 (Collins et al. 1996). Unlike Collins et al. (1996), *H. frondicola* (Lycosidae), *C. johnsoni* (Clubionidae), *H. viridipes* (Salticidae), and the web-weaver *N. agilis* (Hahnidae) were also among the 10 most commonly captured species in 2000. *H. frondicola*, *T. ruricola* (Lycosidae), *G. muscorum*, *Z. hentzi* (Gnaphosidae), and *G. captitata* (Linyphiidae) were among the top 10 in 2001. In 1986 and 1987, the additional species were *P. saxatilis*, *P. minutus* (Lycosidae), *Haplodrassus signifer* (C. L. Koch) (Gnaphosidae), and the web-weaver *Enoplognatha marmorata* (Hentz) (Theridiidae) (Collins et al. 1996).

The most abundant web-weaver family captured was the Linyphiidae, or sheet-web weavers. Linyphiidae are often the most common web-weaving spiders in agroecosystems due to their small size and ability to rapidly recolonize disturbed areas through ballooning (Nentwig 1988; Alderweireldt 1989; Maelfait and De Keer 1990; Feber et al. 1998; Huusela-Veistola 1998; Holland et al. 1999). Capture of the linyphiids *Bathyphantes gracilis* (Blackwall) and *Idionella rugosa* (Crosby) in 2000, and *Islandiana flavoides* Ivie in 2001, represent new state records for Maine. Additionally, an undescribed male of the genus *Scotinotylus* was captured in 2001 (Jennings, personal communication).

Pitfall traps may overestimate lycosids and other cursorial ground-dwelling spiders, while they generally underestimate sedentary Linyphiidae and other web-weaving and canopy-dwelling spiders (Huusela-Veistola 1998; Holland et al. 1999; Lang 2000). Pitfall traps do not measure absolute densities, but rather measure relative densities as related to activity level. However, activity may be correlated to predatory activity of mobile hunters such as lycosids (Kharboutli and Mack 1993; Huusela-Veistola 1998; Holland et al. 1999; Kiss and Samu 2000; Lang 2000). Pitfall trap capture of individuals of the same taxa at different locations of the same habitat during the same time period can be compared as a measure of the relative abundance at each location (Nentwig 1988; Maelfait and De Keer 1990). Indeed, pitfall traps have been shown to be the best method for sampling lycosids because they are inexpensive, easily monitored, and sampling is continuous over time (Kharboutli and Mack 1993; Bogya and Markó 1998; Kiss and Samu 2000).

Juveniles were the dominant life stage captured in both 2000 and 2001. This abundance of juveniles was due to high numbers of lycosid spiderlings trapped each study year. Mother wolf spiders will carry their egg sacs on their spinnerets until the eggs hatch. Afterwards, the hatchlings climb onto the female's abdomen and are transported for one to two weeks (Foelix 1996). Often pitfall traps would contain one or more adult female lycosids and anywhere from 10 to more than 100 early instar juvenile lycosids.

Approximately twice as many males as females were trapped in both 2000 and 2001. Collins et al. (1996) captured about three times as many male as

female spiders. Of the lycosids, 3.5 times as many males as females were captured in 2000 and 2.5 times as many males as females in 2001. Males are often captured more frequently than females in pitfall traps, even though the expected sex ratio is 1:1. For example, Bogya and Markó (1999) captured 7 times more males than females of the lycosid *Pardosa agrestis* Westring in apple orchards in Hungary. The higher proportion of males is possibly due to mate searching behavior (Lang 2000; Pekar 1996; Collins et al. 1996). Pekar (1996) found that females of *P. agrestis* were less active than males not only because males are actively searching for mates, but because females have a greater tendency to hide. Furthermore, males of *P. agrestis* were killed faster than females in pitfall traps containing formaldehyde. This slower kill time may have allowed females of this species more time to escape. Pekar (1996) found that females did indeed escape traps more readily than males.

Lycosid populations peaked in June and early July of 2000 and in early May, early June, and early July of 2001. Populations declined after early July and were lowest in August in both years. This pattern agrees with earlier findings of Collins et al. (1996), in which mean numbers of individuals of all spiders declined after early July in all fields studied during 1986 and 1987. Similar seasonal patterns in lycosid abundance have been found in apple orchards in Hungary (Bogya and Markó 1999), winter wheat in the UK (Holland et al. 1999), cereal fields in Finland (Huusela-Veistola 1998), and in maize and ryegrass in Belgium (Maelfait and De Keer 1990).

Nentwig (1988) captured fewer arthropods in wet years and captured more lycosids in warm years from meadows in Germany. Although fewer lycosids were captured during rainy periods in the present study, there was no significant correlation between lycosid capture and average rainfall during the sampling period. There was a significant correlation between lycosid capture and average low temperatures during the sampling period in 2001. However, average temperatures increased as the growing season progressed, and captures of lycosids generally decline as temperatures increased. Such declines may result from species life-history patterns instead of temperatures.

The decline in lycosid populations after early July may be due to adult die-off, as lycosids in the post-reproductive stage have high mortality (Hof et al. 1994). However, in blueberry fields in Maine, the month of July is often associated with multiple applications of organophosphate insecticides for control of the blueberry maggot fly (Drummond, personal communication). Lycosid capture following applications of fungicides (propiconazole and chlorothalonil) and insecticides (phosmet) was significantly lower than capture prior to pesticide sprays in two of the four conventional fields sampled. However, fewer numbers of lycosids were also captured during the same sampling dates in fields that were not chemically treated. In addition, the highest numbers of lycosids were captured in a reduced input field (Grant) in 2001, immediately following application of the same three chemicals. Therefore, it does not appear that pesticide applications had an immediate lethal effect on lycosid populations in the blueberry fields under investigation. Collins et al. (1996) also found that

application of phosmet did not affect spider catches in bearing blueberry fields of Washington County, Maine. However, Wisniewska and Prokopy (1997) found that insecticides, including phosmet, had season-long negative effects on spider populations on apple trees in Massachusetts.

Although no significant temporal effects of pesticide use were detected, there were significantly fewer lycosids captured at conventional fields than at the reduced input field in 2000. There were also fewer lycosids captured at conventional fields than at reduced input fields in May, June, July and August of 2001. Agroecosystems that regularly receive pesticide treatments often have lower lycosid populations than those fields that are treated intermittently (Wisniewska and Prokopy 1998; Huusela-Veistola 1998; Feber et al. 1999; Holland et al. 2000; Amalin et al. 2001). Pesticide use can have many indirect effects in addition to direct effects such as lethality. Direct sublethal effects of pesticides include knockdown effects which may subsequently lead to death by desiccation or predation, and behavioral changes such as reduced walking speed and reduced predation rate (Huusela-Veistola 1998; Toft and Jensen 1988).

Conventional management practices such as pesticide use, burning and mowing can also have numerous indirect effects on lycosid populations. Insecticides can reduce populations of phytophagous insects, which results in less available prey for spiders (Bogya and Markó 1998; Huusela-Veistola 1998; Amalin et al. 2001). Reduction in plant complexity through herbicide applications, mowing, or burning can also lead to lower spider populations. Agroecosystems

with more weeds, more structural diversity, and higher plant community complexity offer more shelter and microhabitats for spiders. These fields also provide more prey species than conventional fields (Baines et al. 1998; Balfour and Rypstra 1998; Bogya and Markó 1998; Feber et al. 1998; Huusela-Veistola 1998; Holland et al. 1999; Marshall and Rypstra 1999a; Rypstra et al. 1999).

In general, organic fields have been shown to support a higher abundance of lycosids than conventionally farmed fields (Wisniewska and Prokopy 1997; Feber et al. 1998; Yardim and Edwards 1998). However, no differences were detected in numbers of lycosids captured in the latter part of the 2001 season between conventional, reduced input, and organic lowbush blueberry fields in the present study. High numbers of lycosids were captured in May at the conventional and reduced input fields, but the organic fields were not sampled in May. This missing sampling date may have been a peak time period for lycosid populations in 2001. Differences among the three management practices may have been statistically significant if the organic fields had been sampled in May. In addition, Lang (2000) suggested that lycosids are less active in fields with higher vegetation cover, so lycosids in densely covered organic fields may be less likely to be captured in pitfall traps.

The lycosid community differed among management practices in 2001, when conventional, reduced input, and organic fields were sampled. The differences were not in the addition or deletion of species, but rather changes in the proportions of individuals per species between fields. However, no differences were detected in lycosid community composition between

management practices in 2000, when only three conventional and one reduced input fields were sampled. Potential differences in community composition between management practices in 2000 might have been more apparent if more reduced input fields had been sampled. Still, certain species were associated with specific management methods. In 2000, *H. frondicola*, *A. aculeata*, *T. terricola*, and *T. aurantiaca* were associated with the conventional fields while *P. distincta*, *P. saxatilis*, and *P. mackenziana* were associated with the reduced input fields. *T. ruricola* and *S. communis* showed no specific associations by management practice in 2000. Apparently, some lycosid species have specific habitat requirements, and some species may be more sensitive to habitat disturbance than others. For example, *P. distincta* is the dominant species at the organic fields in 2001. This species prefers drier habitats (Jennings, personal communication); the organic blueberry fields were not irrigated, whereas the conventionally managed fields were (Drummond, personal communication). Other species, such as *S. communis*, were commonly captured at conventionally managed fields, and may be more tolerant to insecticide use, or better able to recolonize fields following disturbances.

Differences in spider communities between farming practices have been found in other agroecosystems as well. For examples, cereal fields in the UK have been shown to have more species of spiders in organic or unmanaged plots than in conventionally managed ones (Baines et al. 1998; Feber et al. 1999). However, the lycosids showed differences in community composition between fields of the same management practice as well (Feber et al. 1999). In the

present studies, not only do less intensely managed lowbush blueberry fields support more lycosids than conventional ones, but also, certain species are associated with certain management practices. However, the same species are not associated with similar types of fields each year. More studies are needed to determine relationships between patterns in the distribution of spider species and lowbush blueberry management practices, field locations, amount and diversity of ground cover, and other habitat features.

In both 2000 and 2001, there was a decline in lycosid abundance from the field edge; lycosid capture decreased as distance from the field edges increased. Lycosids are often found at field edges in other agroecosystems as well. More lycosids were found at grassy and weedy borders and strips than in the corresponding pastures (Maelfait and De Keer 1990), cereal fields (Alderweireldt 1989; Huusela-Veistola 1998; Holland et al. 1999) and apple orchards (Bogya and Markó 1998).

However, each field differed in lycosid distribution patterns. In 2000, there were no differences between lycosid capture at different distances in the reduced input field (BBH) and two of the conventional fields (CF1 and CF3). However, in one of the conventional fields, CF2, significantly more lycosids were captured at the field edges than in the field interior. Similar results were found in 2001; there were no differences in lycosid capture at different distances from the edge in the reduced input fields (BBH2 and Grant) and one conventional field (C-NL-5B), but there were differences in one conventional field (C-SL-8). Fewer lycosids were captured as distance from the windbreaks increased. In addition, there were

more lycosids captured at the edge than the field interior. These results suggest that field edges may be a more important refuge in conventional fields than in less intensely managed ones. Permanent edge habitats can provide shelter, overwintering sites, and alternate food sources for spiders in frequently disturbed habitats such as conventional agricultural fields (Nentwig 1988; Huusela-Veistola 1998). Pesticide sprays can disrupt the spatial distribution of beneficial arthropods, such as lycosids, and the edge zone of these fields may be crucial for protection of and reinvasion of fields by these organisms (Holland et al. 2000).

During the first week of June, July, and August 2001 no difference was detected in lycosid capture for traps placed at 3 and 30 m from field edges in conventional, reduced input, and organic fields. These results suggest that the month of May is a key time period for detecting edge effects and that lycosids overwinter at and colonize the field from the edge. Bishop and Riechert (1990) found that edge was not an important source of spider colonizers, as most new colonizers balloon in from long distances. However, their study site was adjacent to natural habitats. In conventional blueberry barrens, there may not be sites from which spiders can balloon; windbreaks or adjacent fields may be the only sources for some fields. Other studies have found that border zones and grassy strips do affect spider abundance in the field, and that the species composition in the field is a reflection of the species composition in the nearest source of colonists (Nentwig 1988; Maelfait and De Keer 1990; Huusela-Veistola 1998).

Community composition of lycosid spiders was not significantly different between the field edges and interior in either 2000 or 2001, but there is a trend

towards certain species being associated with either the edge or within the field. *P. mackenziana*, associated with the forest edge in 2000, is a known forest spider and is usually found on ground with an overstory canopy. *P. moesta* is usually found in open areas or edge habitats, and was commonly captured at 3 m, 15 m, and 30 m from the edges of blueberry fields. *P. distincta* and *P. saxatilis* are species that inhabit open areas, and were most often captured at 15m and 30 m from the blueberry field edges (Jennings, personal communication).

Differences in spider species composition between fields and field borders have been shown in other cropping systems as well. Alderweireldt (1989) found low similarity in spider species composition between the edge and field in maize and ryegrass, with the lycosid *Pardosa pullata* (Clerck) showing a preference for the edge zone. Lycosids species composition significantly changed between pastures and their associated wooded edges in Australia, with more species found at the edges (Martin and Major 2001). Similarly, Bogya and Markó (1999) found low similarity in the spider fauna between apple orchards and their borders. There were more spider species in the borders of apple orchards than in the tree rows and alleys. The lycosid *P. agrestis* was more abundant at the orchard edge than in the orchard itself (Bogya and Markó 1999).

Lycosid species associated with the edge in 2001 were also associated with the edge in 2000. However, the three species most closely associated with the field interior in 2001 were associated with the edge in 2000. Differences in species distribution between 2000 and 2001 may be attributed to numerous features, including competition, species territorial ranges, prey abundances, and

changes in microclimate (Nentwig 1988; Marshall and Rypstra 1999b; Rypstra 1999). For example, *P. moesta* was the most abundant lycosid in 2000, and was commonly captured only 3 m into the field. However, in 2001, *P. moesta* was the fourth most common lycosid, and was associated with the field interior. Another edge species, *P. xerampelina*, was more abundant in 2001, and may have outcompeted *P. moesta* for that preferred habitat (Marshall and Rypstra 1999b). Differences in species distribution may also be attributed to decreased migration into the field during the wetter summer of 2000 compared to the dry summer of 2001, as lycosids are less active during rainy periods (Nentwig 1988)

Differences in lycosid abundance, distribution, and community composition among fields, management styles, and distance from the field edges may be explained by characteristics associated with each microhabitat. The composition of the plant communities and amount of litter may be especially important in explaining patterns in lycosid communities (Bellini et al. 1994; Collins et al. 1996; Holland et al. 1999; Marshall and Rypstra 1999a; Martin and Major 2001). Lycosid capture in conventional fields was reduced following pesticide applications. However, capture was also low during those same sampling periods in fields that were not treated with chemical pesticides. Capture was also highest in one field (Grant) following application of pesticides. Therefore, it does not appear that herbicide, fungicide, or insecticide sprays in conventional fields had a direct lethal effect on lycosid populations. However, indirect effects such as lower lycosid populations due to reduced weed cover, reduced spatial variability, or reduced prey availability should be investigated.

The organic fields were not sampled as extensively or as early in the season as the conventional and reduced input fields. However, since the organic fields supported different lycosid communities than the conventional or reduced input fields, it is worthwhile to continue to research the spider populations of organic blueberry fields. Both the native *T. terricola* and the non-native *T. ruricola* were sampled from conventional and reduced input fields, although only *T. terricola* was sampled from organic fields. The invasive species, *T. ruricola*, may be better able to colonize and succeed in intensely managed agricultural fields, as introduced species are often successful in areas that have undergone disturbances. In addition, interactions and competition between these two very similar *Trochosa* species may be of ecological importance (Cox 1999; Prentice 2001). Differences in the community compositions between fields and management practices both in Maine and in other lowbush blueberry growing regions should continue to be studied so that we may gain a better understanding of environmental factors that are important in determining the spider inhabitants. Perhaps this knowledge can be used to manipulate agricultural habitats in order to enhance and maintain spider populations for use in integrated pest management.

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Chapter 3

PREDATION BY LYCOSIDAE IN LOWBUSH BLUEBERRY AGROECOSYSTEMS

Abstract

Predation by wolf spiders (Lycosidae) on pest and non-pest insects found in blueberry fields in Washington County, Maine was investigated in the laboratory, greenhouse, and field. In laboratory experiments, four taxa of prey insects were evaluated as prey in no-choice arenas. Prey examined were blueberry spanworm *Itame argillacearia* (Packard) (Lepidoptera: Geometridae), blueberry flea beetle larvae, *Altica sylvia* Malloch (Coleoptera: Chrysomelidae), grasshopper (Acrididae) adults and nymphs, and field cricket (*Gryllus pennsylvanicus* Burmeister) (Orthoptera: Gryllidae) adults and nymphs. Lycosids consumed blueberry flea beetles, grasshopper nymphs, and field cricket nymphs but not blueberry spanworm, grasshopper adults, or field cricket adults. In greenhouse mesocosms, both grasshopper and house cricket (*Acheta domestica* Linnaeus) densities were lower in no-choice cages containing a single lycosid compared to control cages with no spiders; blueberry spanworm larvae densities were not significantly different between control and treated cages.

Two field experiments were conducted in which cages received equal quantities of several prey species and either zero (control), four, or eight lycosids. Significant differences in numbers of grasshoppers or house crickets recovered were not detected among treatments. There were significant differences in field

crickets recovered. Fewer field crickets remained in cages containing more predators (spiders, carabid beetles, and ants). Although lycosids consumed some blueberry pest species, pest populations were not significantly lower in field cages containing lycosids.

Introduction

Wolf spiders (Lycosidae) consume a high diversity of pest insect species in many crop ecosystems throughout the world. Lycosids consume imported cabbageworm, *Pieris rapae* (Linnaeus), and harlequin bugs, *Murgantia histrionica* (Hahn), in vegetable garden plots in Tennessee (Riechert and Bishop 1990). *Pardosa pseudoannulata* (Bösenberg et Strand) consume planthoppers, including *Sogatella furcifera* Horvath and *Nilaparvata lugens* Stal, and leafhoppers, including *Nephotettix virescens* Distant and *N. cincticeps* Uhler, in Asian rice fields (Nyffeler et al. 1994a; Kumar and Velusamy 1997; Fagan et al. 1998; Geetha and Gopalan 1999). In Mississippi cotton fields, *L. antelucana* Montgomery consume hemipteran and homopteran pests such as *Lygus lineolarus* (Palisot de Beauvois), *Spissistilus festinus* (Say) and *Oncometopia orbana* (Fabricius), as well as the lepidopteran pests *Heliothis virescens* (Fabricius) and *Trichoplusia ni* (Hübner) (Hayes and Lockley 1990). *Pardosa* spp. consume aphids in winter wheat in Europe (Nyffeler and Benz 1988; Nyffeler et al. 1994a; Marc et al. 1999), cicadellids and aphids in alfalfa fields in California (Nyffeler et al. 1994a), and hemipteran and lepidopteran pests in peanut ecosystems in Texas (Agnew and Smith 1989).

In addition to simply consuming pests, wolf spiders can reduce some insect pest population levels. *Rabidosa rabida* (Walckenaer) and *Pardosa milvina* (Hentz) significantly lowered populations of pestiferous coleopterans, homopterans, lepidopterans, dipterans, and orthopterans in old-field habitats in Tennessee (Riechert and Lawrence 1997). Predation by *Pardosa* spp. and *Schizocosa* spp. was a major contributor to grasshopper nymph mortality in grass prairies in Montana and Nebraska (Chase 1996; Oedekoven and Joern 1998). Similarly, in pastures in Delaware, the combination of *R. rabida*, *Pirata insularis* Emerton, and *Trochosa terricola* Thorell resulted in reduced grasshopper populations (Fagan and Hurd 1991). A combined presence of wolf spiders and carabid beetles resulted in decreases in larval densities of armyworm, *Pseudaletia unipuncta* (Haworth), in no-till corn in Virginia (Laub and Luna 1992); and in reduced spotted cucumber beetle, *Diabrotica undecimpunctata howardi* Barber, numbers on cucurbits (Snyder and Wise 1999). These two predator groups also significantly reduced biomass of cicadellids and thysanopterans in maize (Lang et al. 1999).

Laboratory studies of predation can provide valuable information on predatory behavior and prey preferences. Simple feeding assays and more complex mesocosms representing the spiders' natural habitat can be used to observe interactions between predators and prey (e.g., Nentwig and Wissel 1986; Roach 1987; Bardwell and Averill 1996; Snyder and Wise 2000). However, pests that are readily preyed upon by a spider in laboratory or greenhouse situations may not be prey of the spider in the field. Due to spatial or temporal

isolation, spiders may behave differently in lab than in the field, and results from these studies cannot be easily extrapolated to the field (Nyffeler and Benz 1987). In addition, lycosids in the field often have a choice of prey and, therefore, may reject those prey items that are lower quality or more difficult to capture (Punzo 1991; Nyffeler et al. 1994a).

One method of evaluating predation in the field is with the use of cages. Luck et al. (1988) found that cages and barriers were effective in evaluating the impact of natural enemies. This technique is well suited for evaluating either the actual or potential impact of individual natural enemy species or natural enemy communities, natural enemy multiplication, and killing rate (Luck et al. 1988). Belovsky and Slade (1993) found that cages made of aluminum screen did not significantly alter the abiotic environment. Snyder and Wise (1999) found that adult lycosid activity densities, lycosid spiderling numbers, and numbers of non-lycosids sampled did not differ between caged and open plots. Therefore, field cages can be an accurate controlled representation of true field conditions.

The Lycosidae were chosen as the focus of the present studies because they are the dominant spider family in Maine blueberry fields (Collins et al. 1996; Chapter 2). Natural predation has not been well studied in native North American *Vaccinium* cropping systems, such as blueberry or cranberry. Bardwell and Averill (1997) found that in wild and abandoned cranberry (*Vaccinium macrocarpon* Aiton) bogs in Massachusetts, the numerically dominant lycosid, *Pardosa saxatilis* Hentz, primarily consumed non-pest insects in the orders Diptera and Collembola. They concluded that spiders probably did not have a

high impact on insect pests, especially in commercial bogs where spider numbers were already depressed (Bardwell and Averill 1997).

Lycosids are cursorial spiders, foraging for prey items on the surface of the ground and rarely climbing up onto plant foliage to hunt. Therefore, the prey species these spiders are most likely to encounter are those that spend time on the ground surface as well as on plants (Nyffeler and Benz 1988; Agnew and Smith 1989; Hayes and Lockley 1990; Bardwell and Averill 1996, 1997; Kumar and Velusamy 1997; Punzo and Kukoyi 1997; Lang et al. 1999; Snyder and Wise 1999; Williams et al. 2001). Because their life cycles and daily habits include both ground dwelling and canopy dwelling stages, the following species of pest insects in lowbush blueberry in Maine are considered candidate prey for lycosids: blueberry spanworm larvae, *Itame argillacearia* (Packard) (Lepidoptera; Geometridae), blueberry flea beetle larvae, *Altica sylvia* Malloch (Coleoptera: Chrysomelidae), and grasshopper (Acrididae) adults and nymphs (Belovsky et al. 1990; Quinn et al. 1993; Collins et al. 1995a, 1995b, 1995c; Lang et al. 1999).

The present studies examined the following questions concerning lycosid predation on insects found in lowbush blueberry fields: 1) Are any of the insect species commonly found in blueberry fields suitable prey for wolf spiders? 2) What is the predation rate of lycosids on these insect species? 3) Do lycosids that have prior experience with a certain prey species consume a different amount of that prey species than lycosids with unknown experience? 4) Do lycosids reduce blueberry pest and non-pest insect numbers in the field? 5) Do lycosids consume more of one type of insect than another (do lycosids make a

choice)? 6) Do different densities of lycosids have different effects on prey populations?

Methods

Study Species

The most common lycosid species collected from Maine blueberry fields are *Schizocosa communis* (Emerton), *Pardosa moesta* Banks, and *P. xerampelina* (Keyserling) (Collins et al. 1996, Chapter 2). The present studies are focused on *S. communis* instead of *Pardosa* spp. because *Schizocosa* are larger spiders and are more likely to consume larger prey items (Provencher and Riechert 1994).

Wolf spider predation was investigated on the following blueberry pest insect life stages: blueberry spanworm larvae, blueberry flea beetle larvae, and grasshopper adults and nymphs. These blueberry pests spend time on both the ground and on the plant, and are, therefore, more likely to be preyed upon by wolf spiders than those pests that remain on the fruit or foliage (Collins et al. 1995a, 1995b, 1995c). Furthermore, these pest species were abundant during the 2001 field season. A non-pest species, field cricket (*Gryllus pennsylvanicus* Burmeister) adults and nymphs, was also studied, since it is abundant in blueberry fields and occupies the same microhabitat as wolf spiders (Quinn et al. 1993; Punzo and Kukoyi 1997).

Spider and Prey Collection

During May, June, July and August 2001, adult and penultimate lycosids were collected from bearing blueberry fields in Jonesboro and Columbia Falls, Maine using dry funnel-pitfall traps (1-liter plastic soda bottles with tops cut off and inverted inside cup). A rain cover (18 X 18 cm) made of aluminum with 3 nails (9 cm length) as support was placed over each trap to prevent flooding. Traps were emptied twice a week from May through August (e.g., Clark et al. 1994; Pekar 1996; Birnie et al. 1998).

Spiders were taken to the laboratory and placed in opaque plastic containers (8.75 cm diameter, 3.75 cm height) containing crumpled paper towel for shelter and a moisture wick. Containers were covered with a mesh cloth and secured with rubber bands around the lip of the container. Spiders were maintained at 20° $\pm$ 2° C and a 16L:8D photoperiod (Punzo 1991; Persons and Uetz 1997; Searcy et al. 1999). Species captured from the field were *S. communis*, *Hogna frondicola* (Emerton), *Alopecosa aculeata* (Clerck), *Trochosa* spp. and *Pardosa* spp.

Spiders were held without food for at least seven days to standardize hunger levels before use in any trials (e.g., Bardwell and Averill 1996; Birnie et al. 1998; Toft and Wise 1999). Adult female lycosids that were carrying egg sacs were not used, as they exhibit a lower feeding rate than females not involved in maternal care (Nyffeler and Breene 1990; Nyffeler 2000). Both male and female spiders were used in trials, as not enough of a single sex was collected. Male wolf spiders have been reported to have a lower feeding rate than females in the

field (Nyffeler and Benz 1988; Nyffeler and Breene 1990), but lab studies on other lycosid species demonstrated that males and females consume the same amount of prey (Kielty et al.1999).

Spiders were identified to genus when captured. For "Prey Suitability Tests" and "Feeding History and Predation Rate Studies", spiders were identified by Dr. Daniel T. Jennings, USDA Forest Service (retired), to species, post-experiment. For "Field Predation Studies", spiders were identified to genus only, as spiders can only be reliably identified to species, post-mortem by examining genitalia, and this was not feasible for this study (Kaston 1981; Dondale and Redner 1990).

Pest insect prey and field crickets were captured from blueberry fields in Washington County, Maine, using sweep nets and maintained in plastic and cardboard containers containing blueberry foliage (Roach 1987; Chase 1996; Punzo and Kukoyi 1997; Schmitz et al. 1997). House crickets (*Acheta domestica* (Linnaeus)), another non-pest prey species, were purchased from a local pet store and maintained in a plastic container containing commercial high-protein cricket food (from Carolina Biological Supply™) and a moisture wick.

Prey Suitability Tests

Initial Prey Suitability Tests were conducted by placing a single adult lycosid and an individual live prey in a plastic petri dish (14 cm diameter, 2.5 cm height) and recording the prey status (healthy, fed upon, completely consumed) after 24 hours. Absent prey individuals were assumed to have been eaten (e.g.,

Roach 1987; Punzo 1991; Wise and Chen 1999). Petri dishes were kept in a Percival™ environmental chamber (16L:8D photoperiod, 18-22° C temp) during the trial period. Prey species used were: blueberry spanworm larvae (2^{nd} – 4^{th} instars), blueberry flea beetle larvae (2^{nd} – 3^{rd} instars), grasshopper adults and nymphs, and field cricket adults and nymphs.

The number and species of lycosids entered into a feeding trial depended upon availability from field capture. Individual blueberry spanworm larvae and individual blueberry flea beetle larvae were offered to 8 lycosids each. Individual grasshopper nymphs were offered to 18 lycosids, and individual grasshopper adults were offered to 9 lycosids. Individual field cricket nymphs were offered to 11 lycosids and individual field cricket adults were offered to 4 lycosids. For these trials, an individual spider was not used more than once. House crickets were not used as a prey item in any of these trials, but spiders were fed house cricket nymphs once a week following use in trials to maintain lycosid cultures for use in other assays. All prey suitability trials took place between 11 June and 27 August 2001.

Feeding History and Predation Rate

Experimental Design. To investigate actual predation rate by wolf spiders on each of the prey insects deemed edible from the Prey Suitability Tests, mesocosms were set up in a greenhouse (ambient light conditions) at the University of Maine, Orono, ME. Mesocosms consisted of 45 cm by 45 cm by 45 cm wire mesh cages with removable covers. A ring of aluminum flashing

approximately 35 cm in diameter and 30 cm in height was placed inside the cages. Five to ten blueberry shoots were planted in 2-3 inches of potting soil inside each aluminum flashing ring. Blueberry plants were collected from non-bearing fields at Blueberry Hill MAFES Experimental Farm in Jonesboro, ME. To prevent prey and spiders from burrowing, the top of the soil was covered with a circle of wire mesh screen that reached to the perimeter of the flashing, with a hole cut out of the center through which the plant was placed. An additional 1 cm of soil was spread over this screen. The tops of the flashing were covered with mesh cloth secured with lab tape (FisherBrand™ colored label tape, 1" width) for all orthopteran trials to prevent them from jumping out of the arena (Bardwell and Averill 1996; Geetha and Gopalan 1999; Snyder and Wise 2000). Plants were watered lightly when needed, about two to three times a week. All experiments took place between 24 May and 14 September 2001. Approximately one replicated trial a week was conducted.

Several prey insects were tested over the course of the summer, and those experiments conducted with a single prey species are referred to as a set. The collection of mesocosm cages used at one given time is considered to be one trial, and each cage served as a replicate.

Eight to ten individuals of the same species of prey insects were placed in each of up to 11 mesocosm cages. Prey insects were added 24 hours before spiders to give the prey insects time to acclimate. After the 24-hour acclimation period, 1 lycosid was added to each treatment cage; control cages were left with 0 lycosids (Geetha and Gopalan 1999; Snyder and Wise 2000). At the end of

each trial period (3-7 days), mesocosms were hand searched, and spiders and prey were removed and counted. Spiders were scored either as present or absent. The topsoil was sifted with a sieve with 2 mm openings (USA Standard Testing Sieve No. 10) to find any prey that may have burrowed. Prey position (inside or outside flashing) and condition (dead or alive) were recorded. Any prey not found and not accounted for by control cages were assumed to have been eaten by spiders. Prey that were dead and/or partially eaten could not be attributed to spider predation, as both crickets and grasshoppers will consume their dead (personal observations). Therefore, for the purpose of analysis, any insects present, whether alive or dead, were considered not to have been preyed upon by spiders.

Experiment 1: Spiders with Unknown Feeding History. For the mesocosm experiments performed using spiders with unknown feeding history, the lycosids were captured from the field, held without food, and used in trials a minimum of 7 days later.

The first set of experiments used blueberry spanworm larvae as prey. For the first trial (24 May – 31 May), 10 spanworm larvae were added to each of 10 cages. Larvae were given 24 hours to acclimate, and then 1 lycosid was added to each of 8 cages, the remaining 2 serving as a control cages. Lycosid species used were *S. communis* (n=4), *A. aculeata* (n=1), *H. frondicola* (n=1), and *Trochosa* sp. (n=2). Cages were then resealed and held for 6 days. For the second trial (20 June – 27 June), 8 spanworm larvae were added to each of 5

cages. One *S. communis* individual was added to each of 4 cages, the 5th cage serving as a control. Cages were then resealed and held for 6 days.

The second set of experiments (13 June – 19 June) used blueberry flea beetle larvae as prey. 10 flea beetle larvae were added to each of 11 cages and again given 24 hours to acclimate. One *S. communis* was then added to each of 9 cages, the remaining 2 cages serving as controls. Cages were then resealed and held for 5 days.

The third set of experiments used grasshopper nymphs as prey. For the first trial (5 July – 10 July), 8 grasshoppers were added to each of 3 cages. One *S. communis* was added to each of 2 cages 24 hours later, the 3rd cage serving as a control. Cages were then resealed and held for 5 days. For the second trial (23 July – 27 July), 10 grasshoppers were added to each of 6 cages. 24 hours later, one *S. communis* was added to each of 5 cages, the 6th serving as a control. Cages were then resealed and held for 3 days.

The fourth set of experiments used house cricket nymphs as prey. For the first trial (9 July – 13 July), 8 crickets were added to each of 4 cages. One *S. communis* was added to each of 3 cages 24 hours later, the 4th cage serving as a control. Cages were then resealed and held for 3 days. For the second trial (16 July – 20 July), 10 crickets were added to each of 11 cages. One lycosid was added to each of 8 cages, the remaining 3 serving as controls. Lycosid species used were *S. communis* (n=3), *H. frondicola* (n=2), and *Trochosa* sp. (n=3). Cages were then resealed and held for 3 days. For the third trial (13 August – 17 August), 10 crickets were placed in each of 11 cages. One lycosid was added to

each of 9 cages, the remaining 2 serving as controls. Lycosid species used were *S. communis* (n=3), and *Trochosa* sp. (n=6). Cages were then resealed and held for 3 days.

Experiment 2: Spiders with Known Feeding History. This series of mesocosm experiments used *S. communis* that had been fed a certain prey item once per week since 29 June. Spiders in Group 1 had been fed grasshopper nymphs, and spiders in Group 2 had been fed house cricket nymphs. Prey remains were removed and spiders were starved for at least 7 days before use in any trial. For the first trial (20 August – 24 August), 10 grasshopper nymphs were placed in each of 7 cages. One *S. communis* from Group 1 was added to each of 6 cages, the 7^{th} serving as a control. Cages were then resealed and held for 3 days. For the second trial (10 September – 14 September), 10 house cricket nymphs were added to each of 11 cages. One *S. communis* from Group 2 was added to each of 9 cages, the remaining 2 cages serving as controls. Cages were then resealed and held for 3 days.

Statistical Analyses. For all mesocosm experiments, any replicates in which the spiders were not recovered (or when 2 spiders were recovered from 1 cage) were not included in the analysis. Only treatments in which there was more than one replicate of a given spider species were analyzed.

For series A, set 1, trial 1, analysis was performed on *S. communis* and control groups only because there was only one replicate each for *A. aculeata*

and *H. frondicola*. Replicates using *Trochosa* were also not included in the analysis because one individual was never recovered, reducing the number of replicates for this treatment to one. In set 3, trial 2, analysis was performed using *S. communis* and *H. frondicola* as treatments. Replicates using *Trochosa* were not included in the analysis because two individuals were never recovered, reducing the number of replicates for this treatment to one.

Because some prey escaped the flashing arena and were not subject to spider predation, only data for the number of prey remaining inside the cage divided by the total number of prey added to the cage minus the escapees was used. Since some of the proportions were lower than 0.2 or higher than 0.8, data were transformed using the arcsine of the square root of the proportion so that the variances would be homogeneous around the mean.

For trials in which only one lycosid species was used and control cage sample size was greater than 1 (series 1: set 1, trial 1, and series 2: trial 2), data were analyzed using a t-test to test for differences between control and treated cages (PROC TTEST, SAS Institute 1990). For trials in which only one lycosid species was used, but the number of control cages per trial was 1 (series A: set 1, trial 2, set 3, trials 1 and 2, set 4, trial 1, and series B: trial 1), data were analyzed using a one-sample t-test (PROC MEANS, SAS Institute 1990), in which the control cage value was set to zero and the treated cages were adjusted accordingly and tested to see if they were significantly different from zero. For trials with more than one spider species (series A: set 4 trials 2 and 3), data were analyzed using one-way analysis of variance (ANOVA) to test for

differences between species 1, species 2, and control (PROC GLM, SAS Institute 1990).

Field Predation Studies

Experimental Design. Experiments were conducted at the Blueberry Hill Farm MAFES Experiment Station in Jonesboro, ME during the growing season of 2001. Nine caged enclosures were positioned in three areas (3 enclosures in each area) in the bearing blueberry fields. Enclosures measured approximately 1.5 meters in length, 1 meter in width and 1 meter in height, and were nylon screen on wooden frames. The tops of these cages were removable and could be secured by hooks. Cages were placed in trenches 10-12 cm deep. Aluminum flashing (30 cm in height) was placed around the inside perimeter of the cages and soil was piled around the frames and flashing for stability (Fagan and Hurd 1991; Belovsky and Slade 1993; Clark et al. 1994; Provencher and Riechert 1994; Riechert and Lawrence 1997; Snyder and Wise 1999). A pitfall trap consisting of a plastic container (ca. 7.5 cm h X 10 cm d) filled with 3-5 cm of ethylene glycol (antifreeze) was placed inside each enclosure to aid in arthropod removal. This trap was covered with a plastic cover during experimental periods, and the cover was removed during collection periods (Fagan and Hurd 1991; Clark et al. 1994; Snyder and Wise 1999).

The experimental design was a randomized complete block design with each block (area) receiving three treatments. Each treatment was replicated three times. Lycosid densities added to cages were determined by using the

original average number of spiders removed from cages (Fagan and Hurd 1991). Treatments were 0 times the estimated density (treatment 0), 1 times the estimated density (treatment 1), and 2 times the estimated density (treatment 2) (Fagan and Hurd 1991; Belovsky and Slade 1993; Snyder and Wise 1999).

Prey densities were determined by availability of insects and by approximating how many prey items the wolf spiders could eat based on estimated predation rate of 1 prey item per spider per day (if lycosids eat 1 prey item /day, and there are 4 lycosids/cage, then there should be at least 48 prey items available for a 12 day period) (Nyffeler and Benz 1988; Nyffeler and Breene 1990; Nyffeler et al. 1994b). All cages received the same number of prey.

Experiment 1: Early Season Predation. All arthropods were removed from enclosures twice a week from 29 May to 14 June, using pitfall traps, sweep nets, and hand collecting (Fagan and Hurd 1991; Riechert and Lawrence 1994; Lang et al. 1999; Snyder and Wise 1999). On 14 June, 40 blueberry flea beetle larvae, 10 blueberry spanworm larvae, and 20 house cricket nymphs were placed in each cage. Spider treatments were randomly assigned within each block. Zero, four, or eight *Schizocosa* were added to each cage 24 hours later (Snyder and Wise 2000). Cage tops were then hooked in place, and any gaps in the frame were taped with duct tape. Twelve days later (on 26 June), arthropods were removed and tallied; removals continued twice a week through 12 July (Fagan and Hurd 1991; Snyder and Wise 1999). Again, arthropods were removed using pitfall traps, sweep nets, and hand collection.

Experiment 2: Late Season Predation. All arthropods were removed from enclosures twice a week from 17 July to 31 July using the pitfall trap, sweep nets, and hand collecting (Fagan and Hurd 1991; Riechert and Lawrence 1994; Lang et al. 1999; Snyder and Wise 1999). On 31 July, 30 field cricket nymphs, 30 house cricket nymphs, and 30 grasshopper nymphs were placed in each cage. Zero, four, or seven Lycosidae were added to each cage 24 hours later. *Schizocosa* were less abundant in July and August, so other lycosid species, including *Hogna* and *Trochosa*, were used in addition to *Schizocosa*. Also, not enough lycosids were captured to double densities in cages receiving treatment 2, so enhanced densities are 1.75 times the estimated natural densities.

Spider treatments were randomly assigned within each block. Cage tops were then hooked in place, and any gaps in the frame were taped with duct tape. Ten days later (10 August) arthropods were removed and tallied, and removals continued twice a week through 23 August (Fagan and Hurd 1991; Snyder and Wise 1999). Again, arthropods were removed using pitfall traps, sweep nets, and hand collection.

Statistical Analyses. Statistical analyses were conducted on arthropods removed after the experimental period. Treatments were: a) the number of Lycosids added and b) the number of extra predators (other spiders, opiliones, carabid beetles, and ants) that were trapped out of the cage during the post-experiment collection period.

Changes in the proportion of individuals of total prey recovered were evaluated by Poisson regression. Changes in the proportion of individuals within

each prey taxon were also evaluated by Poisson regression, using the taxa x treatment interaction (PROC GENMOD, SAS Institute 1990). Changes in the proportion of lycosids recovered were evaluated using the same model.

Results

Prey Suitability Tests

None of the spiders in the tests consumed blueberry spanworm larvae. *S. communis* consumed blueberry flea beetle larvae, grasshopper nymphs, and field cricket nymphs, but not grasshopper or field cricket adults. *H. frondicola* consumed blueberry flea beetle larvae and grasshopper nymphs. *Trochosa* sp. consumed grasshopper nymphs and field cricket nymphs but not blueberry flea beetle larvae. *Pardosa* sp. consumed grasshopper nymphs, but not blueberry flea beetle larvae. *A. aculeata* did not consume field cricket nymphs. (Table 3.1).

Table 3.1. Percentage of prey items taken by Lycosidae in laboratory assays. Life cycle stage of prey indicated as adult (A) or immature (I).

Prey Species	Spider Species					
	S. communis	*H. frondicola*	*Trochosa* spp.	*Pardosa* spp.	*A. aculeata*	All Lycosids
Blueberry Spanworm (I)	0%	0%	0%	0%	0%	0%
Blueberry Flea Beetle (I)	100%	100%	0%	0%		63%
Grasshopper (I)	60%	100%	75%	67%		67%
Grasshopper (A)	0%					0%
Field Cricket (I)	43%		100%		0%	55%
Field Cricket (A)	0%					0%

Feeding History and Predation Rate

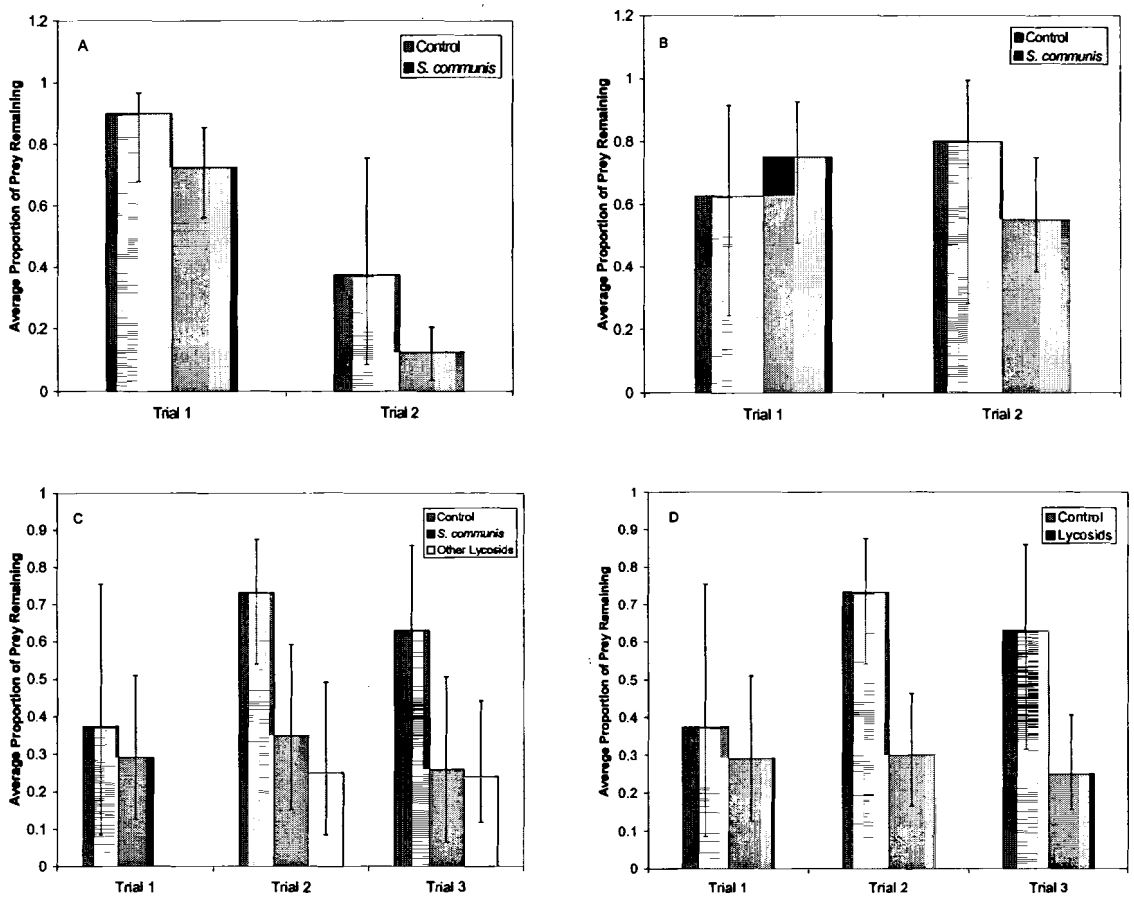
Experiment 1: Spiders with Unknown Feeding History. No blueberry flea beetle larvae were recovered in either control or treated cages. No significant differences were detected in average proportions of remaining blueberry spanworm larvae between control and *S. communis* cages for either trial (Trial 1: df=4; t= -1.13; P = 0.321; Trial 2: df=3; t= -2.54; P = 0.085) (Figure 3.1a).

S. communis did not reduce the proportion of grasshopper nymphs remaining in the first trial (df=1; t=0.68; P = 0.621). However, in the second trial, there was a significant difference in the proportion of grasshopper nymphs remaining between control and *S. communis* cages. (df=4; t= -2.87; P = 0.046) (Figure 3.1b). There were on average 53% of the original grasshopper total remaining in *S. communis* cages, and 80% remaining in control cages, indicating that each spider consumed approximately 30% of the available grasshoppers over a period of 3 days. Therefore, the estimated rate of predation by these spiders was 1 prey item per spider per day.

There were no significant differences in proportion of house crickets remaining between control and any of the treated cages when species treatments were analyzed separately (Trial 1: df=2; t= -1.00; P = 0.423; Trial 2: df=2,4; F=2.75; P = 0.177; Trial 3: df=2,8; F=3.04; P = 0.104) (Figure 3.1c). However, when the two species were combined into one treatment, as "lycosids", the difference between treated and control cages in trial 2 was marginally significant (df=1,5; F=6.39; P = 0.053), and the difference between treated and control cages in trial 3 was also significant (df=1,9; F=6.82; P = 0.028) (Figure

3.1d). There was on average 27% of the original cricket total remaining in the Lycosid cages for both trials, and 68% remaining in the control cages, indicating that each spider consumed approximately 40% of the available crickets over a period of three days. Therefore, the estimated predation rate on these house cricket nymphs is 1.3 prey items per spider per day.

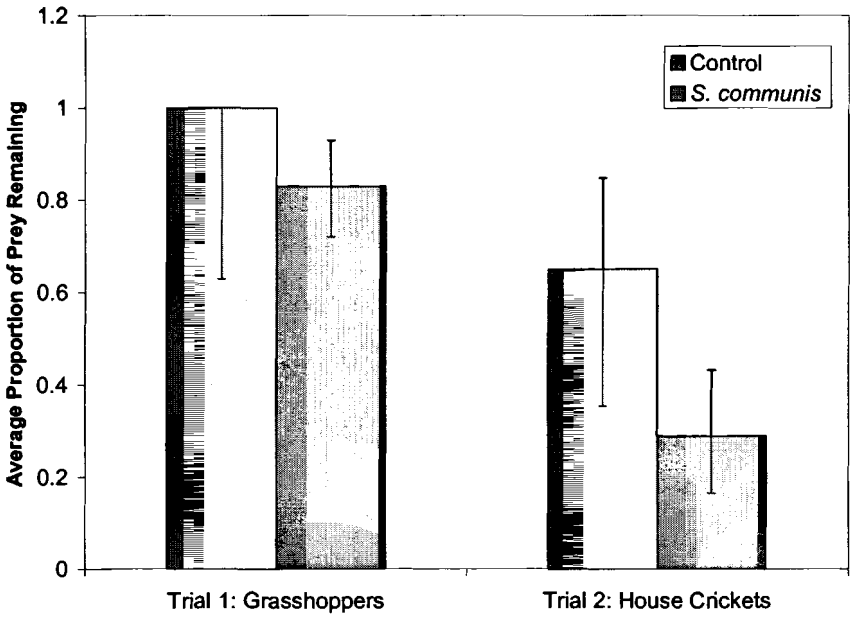
Figure 3.1. Average proportion of prey species remaining in greenhouse cages with lycosids and without (control). A: Prey were blueberry spanworm larvae and all lycosids were *S. communis*. B: Prey were grasshopper nymphs and lycosids were *S. communis*. C: Prey were house cricket nymphs and lycosids were *S. communis* and either *H. frondicola* (trial 2) or *Trochosa* (trial 3). D: Prey was house cricket nymphs and lycosids were *S. communis* (trial 1), *S. communis* and *H. frondicola* (trial 2), and *S. communis* and *Trochosa* (trial 3). Error bars represent 95% confidence intervals.



Experiment 2: Spiders with Known Feeding History. *S. communis* in Trial 1 (grasshopper feeding group) significantly reduced the proportion of grasshopper nymphs remaining when compared to control cages (df=4; t= -3.68; P = 0.021) (Figure 3.2). There were on average 86% of the original grasshopper total remaining in S. communis cages, and 100% remaining in control cages, indicating that each spider consumed approximately 15% of the available grasshopper nymphs over a period of 3 days. The predation rate of these spiders is estimated as 0.5 prey items per spider per day.

S. communis in Trial 2 (house cricket feeding group) did not significantly reduce the proportion of house cricket nymphs remaining, compared to control cages (df=5; t=1.72; P = 0.146) (Figure 3.2).

Figure 3.2. Average proportion of prey species remaining in greenhouse cages with *S. communis* and without (control). *S. communis* in Trial 1 had been fed grasshopper nymphs for 8 weeks and *S. communis* in Trial 2 had been fed house cricket nymphs for 8 weeks. Error bars represent 95% confidence intervals.



Field Predation Studies

Experiment 1: Early Season Predation. An average of 2.4 lycosids (in the genera *Schizocosa*, *Trochosa*, *Pardosa*, and *Alopecosa*) and 3.8 total spiders were originally removed from the cages.

No spanworm or flea beetle larvae were recovered. Therefore, the analyses were performed on house crickets, field crickets and grasshoppers recovered. A known number of field crickets and grasshoppers were not originally added into the cages, but it was assumed that entry into the cages by extra prey species was random and equal. Diptera, Dermaptera, Hemiptera, Homoptera, Lepidoptera larvae, Chilopoda and other Coleoptera besides Carabidae were not included in the analysis because they were not commonly found in the field and did not fit a distinct "predator" or "prey" category. Collembolans were not included as extra prey because often there were too many small ones to count (Table 3.2).

Table 3.2. Mean number and standard error of arthropods recovered from Early Season Predation field cages with different spider treatments from 6/26 – 7/12.

	0 *Schizocosa*		4 *Schizocosa*		8 *Schizocosa*	
Taxon	Mean	SE	Mean	SE	Mean	SE
Schizocosa	0.33	0.33	2.67	1.33	0.00	0.00
Pardosa spp.	0.00	0.00	0.67	0.67	0.33	0.33
Araneae (hunting)	0.00	0.00	0.67	0.67	0.33	0.33
Araneae (web weaving)	0.00	0.00	2.00	1.00	1.33	0.33
Opiliones	8.00	1.73	9.67	6.12	3.67	0.88
Formicidae	37.00	35.00	29.00	28.00	4.67	4.18
Carabidae	1.33	0.88	1.67	1.21	0.33	0.33
All Extra Predators	46.67	34.31	43.67	36.83	20.67	13.68
Acheta domestica	3.00	1.16	3.67	1.86	0.67	0.67
Gryllus pennsylvanicus	11.33	8.84	11.33	4.26	27.00	12.70
Acrididae	1.33	0.33	1.33	0.88	1.00	1.00
All Orthopterans	14.67	8.29	16.33	3.67	28.67	13.57
Hemiptera/Homoptera	1.00	1.00	0.67	0.33	0.00	0.00
Lepidoptera larvae	1.00	1.00	0.00	0.00	0.67	0.33
Other Coleoptera	1.00	0.58	0.00	0.00	1.33	0.88
Diptera	1.00	0.58	1.00	0.58	0.67	0.33
Collembola	2.67	2.19	>20*		7.33	5.90
Other Hymenoptera	0.33	0.33	0.00	0.00	0.00	0.00
Dermaptera	0.00	0.00	0.33	0.33	0.00	0.00
Chilopoda	0.67	0.67	5.00	3.06	3.00	2.52

* Not counted

The mean numbers of orthopterans recovered were 14.67 for treatment 0, 16.33 for treatment 1, and 28.67 for treatment 2. There were significant differences in numbers of orthopterans recovered between treatments, with more orthopterans found in cages with more *Schizocosa* (df=1; χ^2=7.69; P = 0.006). However, there was a significant treatment by taxa interaction, indicating that some amounts of orthopterans recovered were different between treatments while others were not (df=2; χ^2=112.90; P< 0.0001). Extra predators (ants, carabids, and other arachnids) may also have affected the number of prey recovered. More orthopterans were recovered from cages with fewer predators other than *Schizocosa* (df=1; χ^2=26.48; P< 0.0001) The extra predator by taxa interaction was significant, indicating that extra predators affected some taxa of orthopterans but not others (df=2; χ^2=10.26; P= 0.006) (Table 3.2).

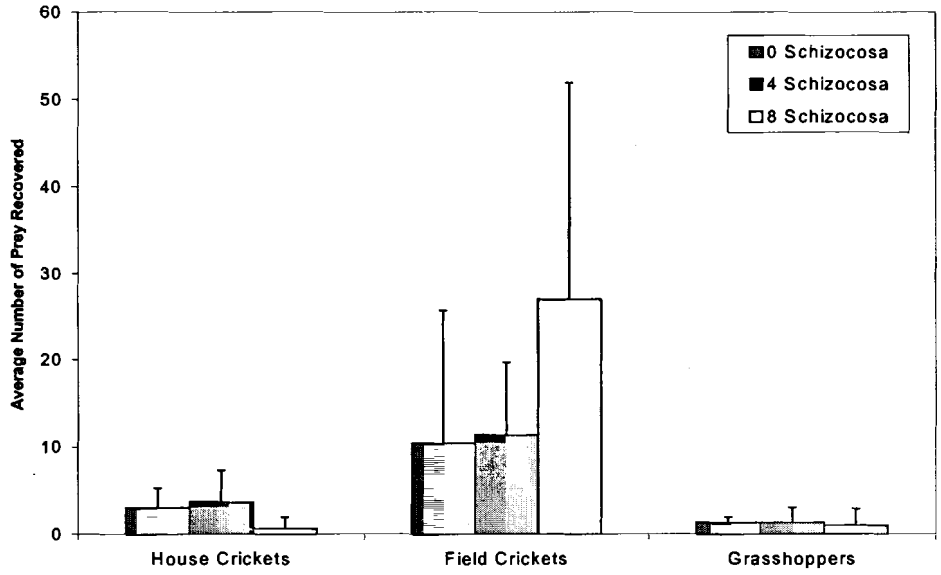
The mean numbers of house crickets recovered were 3.00 for treatment 0, 3.67 for treatment 1, and 0.67 for treatment 2. There were less house crickets recovered in the treatment with the highest numbers of *Schizocosa*, although the differences are not significant (df=1; χ^2=3.42; P= 0.065). Extra predators also did not affect the number of house crickets recovered (df=1; χ^2=0.04; P= 0.841). (Table 3.2, Figure 3.3).

The mean numbers of field crickets recovered were 10.33 for treatment 0, 11.33 for treatment 1, and 27.00 for treatment 2. There were significant differences in field crickets recovered between treatments, with more field crickets recovered in cages receiving the most *Schizocosa* (df=1; χ^2=10.54; P= 0.001). Extra predators also affected numbers of field crickets recovered, with

more field crickets recovered from cages with fewer extra predators (df=1; χ^2=15.22; P< 0.0001). (Table 3.2, Figure 3.3).

The mean numbers of grasshoppers recovered were 1.33 for treatment 0, 1.33 for treatment 1 and 1.00 for treatment 2. There were no significant differences in grasshoppers recovered between treatments (df=1; χ^2=1.06; P= 0.303). Extra predators also did not affect numbers of grasshoppers recovered (df=1; χ^2=1.31; P= 0.253). (Table 3.2, Figure 3.3).

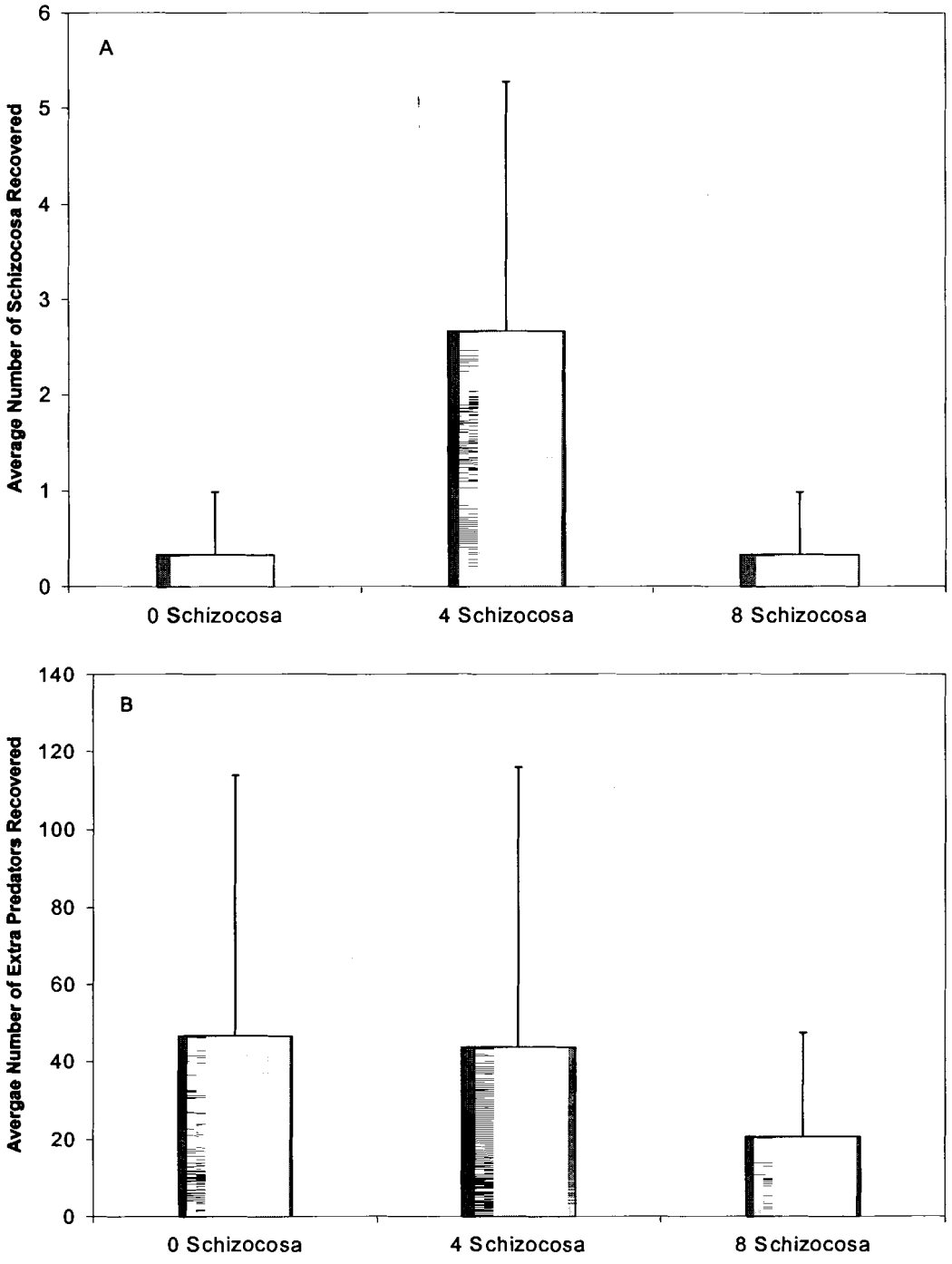
Figure 3.3. Average number of prey insects recovered from Early Season Predation field cages with different spider treatments from 6/26 – 7/12. Error bars represent 95% confidence intervals.



The average number of *Schizocosa* recovered did not differ between treatments (df=1; χ^2=0.00; P= 1.00). Higher populations of *Schizocosa* did not remain higher two weeks later; cages with no *Schizocosa* added had enhanced numbers (0.33 on average), and cages that had 4 and 8 *Schizocosa* added had lower numbers than originally added (2.67 and 0, respectively) (Table 3.2, Figure

3.4a) The number of *Schizocosa* recovered significantly differed with the number of extra predators recovered (df=1; χ^2=6.71; P= 0.010), but there was a significant extra predator by treatment interaction (df=1; χ^2=11.66; P=0.0006). There were more extra predators in cages that received fewer *Schizocosa* (Table 3.2, Figure 3.4b).

Figure 3.4. Average number of predators recovered from Early Season Predation field cages with different spider treatments from 6/26 – 7/12. A: Average number of *Schizocosa* recovered. B: Average number of ants, carabid beetles, opiliones, and other spiders recovered. Error bars represent 95% confidence intervals.



Experiment 2: Late Season Predation. All three prey species that were added to the cages were recovered. The analyses were performed on house crickets, field crickets and grasshoppers recovered. Other Hymenoptera besides ants, Dermaptera, Hemiptera, Lepidoptera, and other Coleoptera besides Carabidae were not included in the analysis because they were not commonly found in the field and did not fit a distinct "predator" or "prey" category (Table 3.3).

Table 3.3. Mean number and standard error of arthropods recovered from Late Season Predation field cages with different spider treatments from 8/10 – 8/23.

	0 Lycosidae		4 Lycosidae		7 Lycosidae	
Taxon	Mean	SE	Mean	SE	Mean	SE
Schizocosa communis	0.33	0.33	0.00	0.00	0.33	0.33
Hogna frondicola	0.00	0.00	0.00	0.00	0.33	0.33
Trochosa spp.	1.00	0.58	0.67	0.67	0.33	0.33
Pardosa spp.	1.00	0.58	0.00	0.00	0.67	0.33
All Lycosidae	2.33	0.88	0.67	0.67	1.67	0.33
Araneae (hunting)	0.00	0.00	0.67	0.67	0.33	0.33
Araneae (web weaving)	0.00	0.00	0.33	0.33	0.00	0.00
Opiliones	7.00	4.16	10.67	6.33	6.00	3.51
Formicidae	4.67	2.67	4.00	4.00	3.67	2.67
Carabidae	9.00	4.04	35.00	28.15	34.00	27.02
All Extra Predators	23.00	7.77	50.67	31.31	44.00	28.83
Gryllus pennsylvanicus	25.00	8.96	19.33	6.39	8.00	3.00
Acheta domestica	4.33	2.19	3.33	1.45	2.00	0.58
Acrididae	10.67	4.98	10.00	2.52	9.00	2.52
All Orthopterans	40.00	13.58	32.67	7.36	19.00	3.61
Other Coleoptera	1.00	0.58	0.00	0.00	0.33	0.33
Lepidoptera adult	0.33	0.33	0.67	0.67	0.00	0.00
Lepidoptera larvae	0.00	0.00	0.00	0.00	0.33	0.33
Hemiptera	0.33	0.33	0.00	0.00	0.00	0.00
Other Hymenoptera	0.33	0.33	0.00	0.00	0.33	0.33
Dermaptera	0.00	0.00	1.33	0.33	0.00	0.00

The mean numbers of all orthopterans recovered were 40.00 for treatment 0, 32.67 for treatment 1, and 19.00 for treatment 2. There were significant differences in numbers of all orthopterans recovered between treatments, with more orthopterans recovered from treatments with less lycosids (df=1; χ^2=31.40; P< 0.0001). However, there was also a significant treatment by taxa interaction, indicating that some amounts of orthopterans recovered were different between treatments while others were not (df=2; χ^2=41.51; P< 0.0001). Extra predators (ants, carabids, and other arachnids) did not affect the number of orthopterans recovered (df=1; χ^2=0.71; P= 0.401). (Table 3.3).

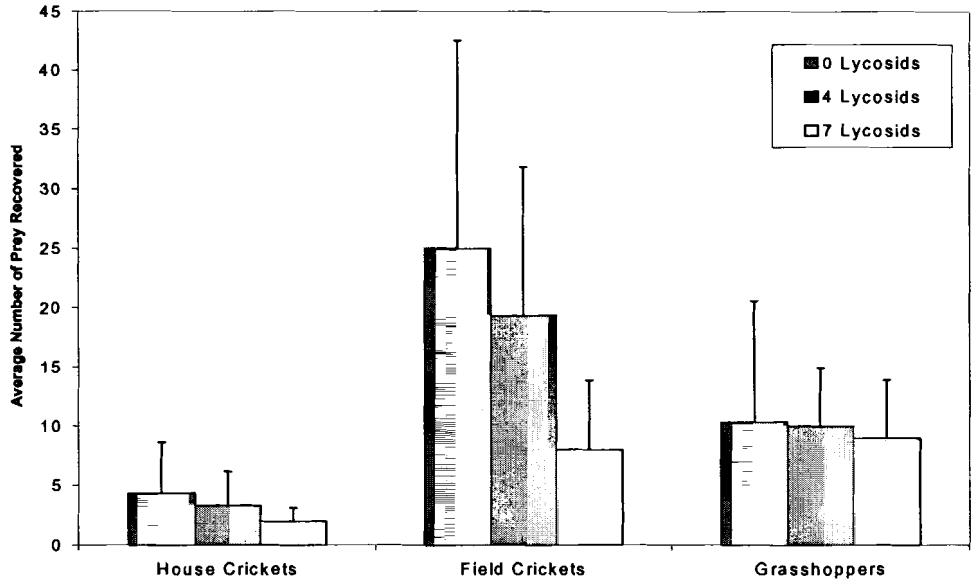
The mean numbers of house crickets recovered were 4.33 for treatment 0, 3.33 for treatment 1, and 2.00 for treatment 2. There were no significant differences between treatments in numbers of house crickets recovered (df=1; χ^2=2.08; P= 0.149). Extra predators also did not significantly affect numbers of house cricket recovered (df=1; χ^2=0.07; P= 0.786). (Table 3.3, Figure 3.5).

The mean numbers of field crickets recovered were 25.00 for treatment 0, 19.33 for treatment 1, and 8.00 for treatment 2. These values were significantly different, with less crickets recovered from cages with more lycosids (df=1; χ^2=25.04; P< 0.0001). Extra predators did not affect the numbers of field crickets recovered (df=1; χ^2=1.34; P = 0.248). (Table 3.3, Figure 3.5).

The mean numbers of grasshoppers recovered were 10.67 for treatment 0, 10.00 for treatment 1, and 9.00 for treatment 2. There were no differences in grasshopper numbers recovered for any treatments (df=1; χ^2=0.00; P= 0.956).

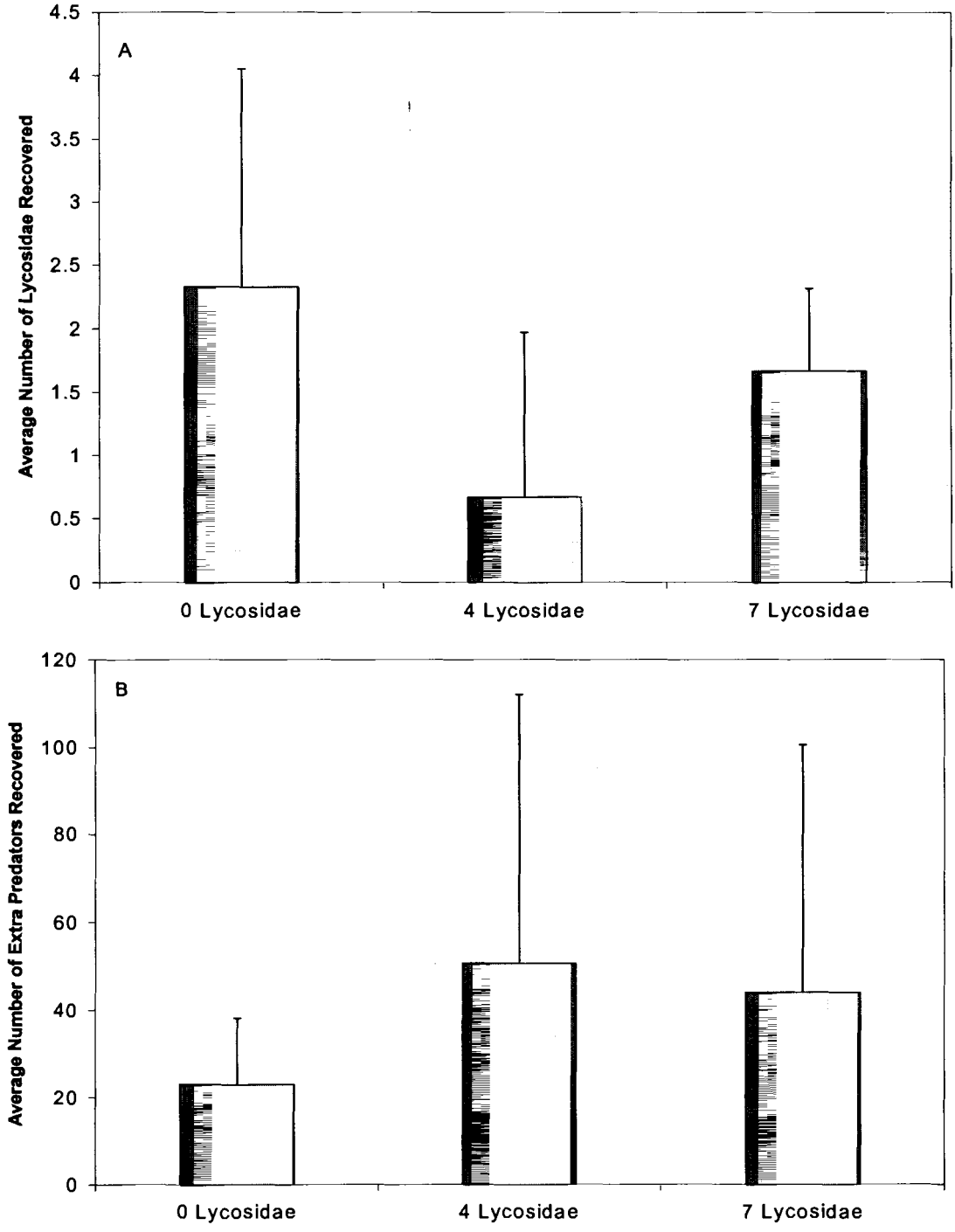
Extra predators also did not affect the number of grasshoppers recovered (df=1; χ^2=1.00; P = 0.317). (Table 3.3, Figure 3.5).

Figure 3.5. Average number of prey insects recovered from Late Season Predation field cages with different spider treatments from 8/10 – 8/23. Error bars represent 95% confidence intervals.



Although different numbers of lycosids (0, 4, or 7) were added to each cage, the average number of lycosids recovered did not differ between treatments (df=1; χ^2=0.42; P = 0.519). Higher populations of lycosids did not remain higher two weeks later. Cages with no lycosids added had enhanced numbers (2.33 on average), and cages that had 4 and 7 lycosids added had lower average numbers than added (0.67 and 1.67, respectively) (Table 3.3, Figure 3.6a). Extra predators also did not significantly affect the number of lycosids recovered (df=1; χ^2=0.01; P= 0.905). There was no significant treatment by extra predator interaction (df=1; χ^2=0.09; P=0.768) (Table 3.3, Figure 3.6b).

Figure 3.6. Average number of predators recovered from Late Season Predation field cages with different spider treatments from 8/10 – 8/23. A: Average number of Lycosidae recovered. B: Average number of ants, carabid beetles, opiliones, and other spiders recovered. Error bars represent 95% confidence intervals.



Discussion

Blueberry flea beetle larvae, grasshopper nymphs, and field cricket nymphs are suitable prey for the wolf spider species found in Maine blueberry fields, as all these prey were readily killed and consumed in the laboratory. Wolf spiders are known to prefer small soft-bodied insects as prey (Punzo 1991; Nyffeler and Benz 1988; Nyffeler et al. 1994a, 1994b; Snyder and Wise 1999). Both grasshopper and field cricket adults were not consumed by the wolf spider species tested. Hunting spiders prefer prey items that are within 50-80% of the spider's body size, and, therefore, these orthopteran adults were too large for the wolf spiders to handle (Nentwig and Wissel 1986; Hayes and Lockley 1990; Punzo 1991; Nyffeler et al 1994a, 1994b). Although arthropods may be the principal predators of grasshopper nymphs, they are not usually the principal predators of grasshopper adults. Indeed, lycosids have been shown to exert no significant mortality on grasshopper adults in grasslands and prairies, although juvenile grasshoppers are readily consumed (Belovsky et al. 1990; Punzo 1991; Chase 1996; Oedekoven and Joern 1998, 2000).

Punzo (1991) found that the large wolf spider *Lycosa lenta* (16.4-22.3 mm in body length) does prey upon adult grasshoppers and crickets in both field observations and laboratory arenas. However, these spiders consumed only 10% of grasshoppers with a mean body length of 23.1 mm, compared to 95% of grasshoppers with mean body lengths of 10.9 mm; mean length of the adult crickets was 14.7 mm, well below the 18.1 mm body length of the *L. lenta* individuals that were feeding on them (Punzo 1991). The adult grasshoppers that

are pestiferous in lowbush blueberry have a mean body length of 31 mm, while the body lengths of the adult lycosids (*S. communis*, *Trochosa* spp., and *H. frondicola*) in these fields are 5.5 to 14 mm (Dondale and Redner 1990; Roberts 1993; Collins et al. 1995b).

Blueberry spanworm larvae were not consumed by wolf spiders either in lab or greenhouse trials. In cranberry mesocosms similar to the ones used in my study, wolf spiders did consume larvae of another spanworm larval pest, *Ematurga amitaria* Guenée. *E. amitaria* sometimes displays a secondary defense consisting of regurgitating a brown fluid and thrashing its body. These larvae were killed 80% of the time; however, those that remained in a motionless, cryptic posture were not attacked as frequently (Bardwell and Averill 1996). Although the cryptic nature of some geometrid larvae may prove an adequate defense in the field or in greenhouse mesocosms, it does not explain why the larvae were never eaten in petri dish arenas. Perhaps blueberry spanworm larvae have additional defenses such as urticating hairs or distasteful chemicals.

S. communis with unknown feeding histories ate a significant number of grasshopper nymphs in one trial but not the other. However, the trial in which there were no significant differences between control and *S. communis* cages had a very low sample size (n=2 for treated and n=1 for control) and a high amount of variation. Although house cricket numbers were lower in lycosid cages than in control cages, the differences were not significant. Low sample size and high variation may also explain the results from the house cricket trials that did not show significant effects of spider predation. In addition to having no more

than 5 replicates of any treatment, variation may have been high due to the tendency of crickets to escape the aluminum flashing arena. However, sample size was increased by combining species treatments into one treatment, as "lycosids". This increase in sample size resulted in detection of significant differences between treated and control cages. House cricket numbers were significantly lower in cages containing lycosids when data from the two spider species were combined.

A spider's daily prey capture rate (b) can be estimated using the equation $b = (T_f \bullet 60 \bullet w)/(T_h \bullet 100)$ where T_f is the time (hours per day) available for prey capture and feeding in the field, w is the average percentage of spiders with prey, and T_h is the average handling time (in minutes). Using this equation, researchers have estimated the predation rate of lycosids and other hunting spiders to be approximately 1 prey item per spider per day (Nyffeler and Benz 1988; Nyffeler and Breene 1990; Nyffeler et al. 1994b).

A crude predation rate can be estimated by dividing the number of individual prey items eaten by predators by the number of available individual prey items per unit time (Belovsky et al. 1990; Belovsky and Slade 1993). Using this crude method, the present study determined that the predation rates of lycosids on caged grasshopper nymphs (0.5 and 1 prey item/spider/day) and house cricket nymphs (1.3 prey items/spider/day) were in agreement with the published estimates of lycosid predation rate (Nyffeler and Benz 1988; Nyffeler and Breene 1990; Nyffeler et al. 1994b). However, this rate may be an overestimate of lycosid predation on orthopterans in blueberry crops, as the

mesocosm afforded less shelter or chance to escape for the grasshoppers than the natural environment (Belovsky et al. 1990).

Previous prey experience can affect foraging decisions made by wolf spiders. Lycosids that had been maintained in laboratory conditions spend longer time than spiders fresh from the field in an experimental patch that contained the same prey the spiders had been fed in the lab (Wagner and Wise 1997). Lycosids also increase residence time in patches containing chemical cues from prey that they have eaten recently (Punzo and Kukoyi 1997; Persons and Rypstra 2000). In addition, lycosids are more likely to reject low-quality prey items if they had been fed that item previously (Toft and Wise 1999). Toft and Wise (1999) did not examine whether spiders that have previous experience with a high quality prey item would accept that prey item more readily than spiders with no prior experience. If spiders are exposed to a high quality prey insect, perhaps they may become more efficient predators of that prey insect.

Because greenhouse trials took place at different times and under different atmospheric conditions, the present study was not able to explicitly test whether lycosids that had been feeding exclusively on a certain prey species (known feeding history) consumed more of that prey species than lycosids from the field (unknown feeding history). However, the crude predation rates of each group of lycosids can be compared. *S. communis* from the field had a predation rate of 1 grasshopper per spider per day while *S. communis* that had been fed grasshopper nymphs in the lab had an estimated predation rate of 0.5 grasshoppers per spider per day. Thus, these studies suggest lycosids do not

increase predation rate on orthopteran prey with which they have had fed upon previously. However, since spiders tend to prefer prey species with which they have had prior experience (Turnbull 1960; Kumar and Velusamy 1997), it would be worthwhile to see if lycosids exhibit any choice between a familiar and novel prey item. For example, spiders that have been feeding on pestiferous insects, such as grasshoppers, may be more likely to accept them as prey and reject non-pest insects, such as field crickets.

Although wolf spiders consume house crickets nymphs in the laboratory and greenhouse, no predation was detected on this prey species in the field. Such a low number of house crickets were recovered in both experiments that it can be concluded that house crickets are not a good model for a ground dwelling prey species in this field system.

These field cages may not have been appropriate to evaluate predation under the conditions of this study. Variation between cages was high, and there were only 3 replicates of each treatment. Furthermore, cages were obviously not sealed well enough, as numerous insects that had not been placed inside cages, including numerous field crickets, were removed post-experiment. In the Early Season Predation experiment, the most field crickets were recovered from those cages receiving the highest number of *Schizocosa*. However, cages receiving this treatment also had the lowest number of extra predators removed from the cages. High field cricket densities may be a response to the low number of ant and carabid predators and not the high number of *Schizocosa* predators.

In the Late Season Predation experiment, field cricket populations decreased as lycosid densities increased, while grasshopper populations remained the same. These results suggest that although lycosids consumed grasshoppers in the laboratory and greenhouse studies, these spiders may not prey upon grasshoppers and other herbivores when alternative, ground-dwelling prey are present.

These results conflict with other studies, which found that wolf spiders (including the genera *Schizocosa*, *Hogna*, *Trochosa*, *Rabidosa, Pardosa*, and *Lycosa*) are important predators of both grasshoppers and crickets (Punzo 1991; Nyffeler et al. 1994). Several field cage studies found that lycosids reduce prey biomass of populations of field crickets, grasshoppers and katydids (Fagan and Hurd 1991; Provencher and Riechert 1994; Chase 1996; Riechert and Lawrence 1997; Oedekoven and Joern 1998, 2000).

Studies suggest that spider predation on grasshoppers may act in a compensatory manner, i.e., spider predation on some grasshopper nymphs releases the remaining nymphs from competition for food, so that adult densities, and thus plant damage, remains the same. However, when plant production is high and competition for food is not important, a reduction in grasshopper number does result in a decrease in plant damage (Chase 1996; Oedekoven and Joern 2000). Alternatively, when grasshoppers were more food-stressed than usual by having fewer hours per day to feed, presence of spiders resulted in less plant consumption also (Oedekoven and Joern 2000; Schmitz et al. 1997). In the present studies, the number of grasshoppers remaining in treated and control

cages was lower than the original amount added. Perhaps in the Late Season Predation studies, where grasshoppers were likely to be food-limited due to a dry August, grasshopper mortality from starvation and predation were comparable.

Other predators, including carabid beetles, ants, and other arachnids can compete with lycosids for prey, or even engage in intraguild predation. Fagan et al. (1998) found that enhancing lycosid populations in rice paddies resulted in a reduction in populations of the other top predator in the system, mesovellids; pest densities increased as a result. In other systems, top predators, including carabids and lycosids, effectively reduce pest densities and have no negative effect on each other (Laub and Luna 1992; Lang et al 1999; Snyder and Wise 1999). The present studies indicate that predators other than lycosids may not impact either pest or lycosid populations in blueberry crops.

Cannibalism is another important mortality agent that limits spider densities, especially for lycosids. Lycosids will often self-regulate their density through cannibalism, and such self-limiting tendencies may result in increased prey populations (Riechert and Lawrence 1984; Fagan and Hurd 1991; Wise and Chen 1999). Snyder and Wise (1999) found that doubling lycosids densities in garden plots did not increase activity densities of wolf spiders; lycosid spiderling populations were also not increased. In addition, there was no difference in pest numbers or plant productivity between plots with natural and increased lycosid densities (Snyder and Wise 1999).

Late Season Predation studies found that increasing lycosid densities resulted in decreases in ground-dwelling prey species but not herbivorous

canopy-dwelling pest species. However, it must be pointed out that prey densities in these studies may not reflect actual prey availability in the field. If insufficient prey are available, lycosids may compete more strongly for food, resulting in cannibalism or increased territory size (Provencher and Vickery 1988). In such cases, wolf spider augmentation is not feasible, as they will either consume or drive away competing conspecifics. Indeed, elevated wolf spider densities in both Early and Late Season Predation studies did not remain for two weeks. Lycosids may have escaped the cages or have been cannibalized.

Although reduction of insect pest numbers is important, the ultimate measure of success of a biological control agent is decreased plant damage and increased yield (Snyder and Wise 1999). Presence of spiders in some garden and crop ecosystems can result in less plant damage by herbivores (Riechert and Bishop 1990; Clark et al. 1994). The present study did not measure whether the reduction in grasshopper numbers in greenhouse studies led to a subsequent reduction in plant and fruit damage.

Even though wolf spiders may not reduce blueberry pest insect numbers in the field, their presence in these agroecosystems is still beneficial. The presence of spiders can result in reduced plant damage, even when spiders do not (or cannot) actually feed upon herbivores. Several studies have shown that pest insects such as spotted cucumber beetles, Mexican bean beetles, *Epilachna varvestis* Mulsant, and Japanese beetles, *Popillia japonica* Newman reduce feeding on crop plants in the presence of lycosids, even when the spiders were physically prevented from preying upon the beetles (Rypstra 1995; Snyder and

Wise 2000). In addition to a decrease in plant damage, the presence of hunting spiders can also result in increased mortality of pest insects such as grasshoppers (Beckerman et al. 1997; Schmitz et al. 1997). Other pest insects, such as lepidopteran larvae, leafhoppers, and planthoppers will disperse or otherwise abandon the plants they are feeding on when spiders are present (Riechert and Lockley 1984; Marc et al. 1999). Spiders can reduce herbivore feeding, and thus plant damage, even without actually killing and consuming the prey. Therefore, further testing is needed to see if presence of lycosids in blueberry patches decreases insect damage to plants and fruit.

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Appendix A

SPIDER (ARANEAE) SPECIES ASSOCIATED WITH LOWBUSH BLUEBERRY AGROECOSYSTEMS IN WASHINGTON COUNTY, MAINE

Table A.1. Spiders (Araneae) associated with lowbush blueberry agroecosystems in Washington County, Maine, 2000. All spiders were sampled with pitfall traps from late April through early September. Spiders were identified by Dr. Daniel T. Jennings, USDA Forest Service (retired).

Spider taxa [1]	Number of individuals [2]		
	M	F	Juv.
WEB SPINNERS			
THERIDIIDAE			
Achearanea globosa (Hentz)	1	1	
Crustulina sticta (O. P.-Cambridge)	1	2	
Enoplognatha marmorata (Hentz)	24	2	
Enoplognatha sp.			11
Euryopis argentea Emerton	1	2	
Neottiura bimaculata (Linnaeus) [3]	2		
Robertus spinifer (Emerton)	7		
Robertus sp.			2
LINYPHIIDAE (Linyphiinae)			
Agyneta fabra (Keyserling)	4		
Agyneta simplex (Emerton)	11	5	
Agyneta zygia (Keyserling)	2	7	
Agyneta sp.			2
Bathyphantes gracilis (Blackwall) [3, 4]	1		
Bathyphantes pallidus (Banks)	1	6	
Centromerus comupalpis (O. P.-Cambridge)	5	1	
Centromerus persolutus (O. P.-Cambridge)	1	1	
Drapetisca sp.			1
Microlinyphia mandibulata (Emerton)	1	1	
Stemonyphantes blauveltae Gertsch	1		
Undet. genus, sp. 1 [5]	2		
Undet. genus, sp.			5
LINYPHIIDAE (Erigoninae)			
Ceraticelus emertoni (O. P.-Cambridge)		1	
Ceraticelus minutus (Emerton)	1	1	
Ceratinella brunnea Emerton	1	2	
Eperigone trilobata (Emerton)	8	3	
Eridantes erigonoides (Emerton)		1	
Gonatium crassipalpum Bryant		1	

Grammonota capitata Emerton	8	1	
Idionella rugosa (Crosby) [4]	1		
Islandiana flaveola (Banks)	18	3	
Metopobactrus prominulus (O. P.-Cambridge)	1		
Pocadicnemis americana Millidge		3	
Sciastes truncatus (Emerton)	2	1	
Scotinotylus exsectoides Millidge		1	
Scylaceus pallidus (Emerton)	1	1	
Tapinocyba simplex (Emerton)	1	2	
Walckenaeria communis (Emerton)		2	
Walckenaeria digitata (Emerton)	3	2	
Walckenaeria directa (O. P.-Cambridge)	1	4	
Walckenaeria pinocchio (Kaston)	6		
Walckenaeria placida (Banks)		2	
Walckenaeria sp. 7 (WBP- sp. 10) [6]	4		
Undet. genus, sp. 1 (WBP- sp. 1) [7]	1		
Undet. genus sp. 2 [8]		1	
Undet. genus, sp.			8
ARANEIDAE			
Araneus sp.			1
AGELENIDAE			
Agelenopsis potteri (Blackwall)	1		
Agelenopsis utahana (Chamberlin & Ivie)	1		
HAHNIIDAE			
Cryphoeca montana Emerton	1		
Hahnia cinerea Emerton	3		
Neoantistea agilis (Keyserling)	20	38	
Neoantistea magna (Keyserling)	2		
DICTYNIDAE			
Lathys pallida (Marx)	9		
AMAUROBIIDAE			
Callobius bennetti (Blackwall)	2		
Callobius sp.			4
Coras sp.			1
Web Spinner Subtotals	***161***	***98***	***35***
HUNTERS			
MIMETIDAE			
Ero canionis Chamberlin & Ivie		1	
Ero sp.			1
LYCOSIDAE			
Alopecosa aculeata (Clerck)	51	15	
Alopecosa sp.			80
Hogna frondicola (Emerton)	68	17	
Hogna sp.			73
Pardosa distincta (Blackwall)	68	25	
Pardosa hyperborea (Thorell)	1		
Pardosa mackenziana (Keyserling)	9	3	

Pardosa modica (Blackwall)	1		
Pardosa moesta Banks	238	52	
Pardosa saxatilis (Hentz)	15	7	
Pardosa xerampelina (Keyserling)	69	29	
Pardosa sp.			107
Pirata minutus Emerton	14	5	
Pirata sp.			6
Schizocosa crassipalpata Roewer		1	
Schizocosa communis (Emerton)	139	31	
Schizocosa saltatrix (Hentz)	1		
Schizocosa sp.			30
Trabeops aurantiaca (Emerton)	3		
Trabeops sp.			1
Trochosa ruricola (De Geer) [3]	34	7	
Trochosa terricola Thorell	10	5	
Trochosa sp.			34
Undet. genus, sp. [9]			700
PISAURIDAE			
Pisaurina mira (Walckenaer)	1		
LIOCRANIDAE			
Agroeca ornata Banks	3		
Agroeca pratensis Emerton	1	38	
Agroeca sp.			2
Phrurotimpus alarius (Hentz)	3	1	
Phrurotimpus borealis (Emerton)	1	1	
Phrurotimpus certus Gertsch	1		
Phrurotimpus sp.			3
Scotinella divesta (Gertsch)	6	2	
CLUBIONIDAE			
Clubiona johnsoni Gertsch	45	53	
Clubiona kastoni Gertsch	2	6	
Clubiona mixta Emerton	1		
Clubiona sp.			36
CORINNIDAE			
Castianeira cingulata (C. L. Koch)		3	
Castianeira descripta (Hentz)	4	1	
Castianeira gertschi Kaston	1	1	
Castianeira sp.			8
GNAPHOSIDAE			
Drassodes neglectus (Keyserling)	4		
Drassodes sp.			1
Drassyllus niger (Banks)	1		
Drassyllus socius Chamberlin	2	1	
Drassyllus sp.			3
Gnaphosa muscorum (L. Koch)	33	10	
Gnaphosa parvula Banks	12	2	
Gnaphosa sp.			77

Haplodrassus bicomis (Emerton)	1		
Haplodrassus hiemalis (Emerton)	1		
Haplodrassus signifer (C. L. Koch)	28	17	
Haplodrassus sp.			2
Herpyllus sp.			1
Micaria gertschi Barrows & Ivie	3		
Micaria pulicaria (Sundevall)	2	3	
Micaria riggsi Gertsch	9	6	
Zelotes exiguoides Platnick & Shadab	14	9	
Zelotes fratris Chamberlin	19	15	
Zelotes hentzi Barrows	8	13	
Zelotes puritanus Chamberlin		3	
Zelotes sp.			69
PHILODROMIDAE			
Ebo iviei Sauer & Platnick	1		
Ebo sp.			1
Philodromus pernix Blackwall	1		
Philodromus sp.			2
Thanatus fromicinus (Clerck)	4		
Thanatus sp.			4
Tibellus sp.			1
THOMISIDAE			
Bassaniana utahensis (Gertsch)	1		
Ozyptila distans Dondale & Redner	9		
Ozyptila sp. 2 [10]	1		
Ozyptila sp.			3
Xysticus ampullatus Turnbull, Dondale & Redner	8	1	
Xysticus discursans Keyserling	6	3	
Xysticus elegans Keyserling	5		
Xysticus ferox (Hentz)		1	
Xysticus fervidus Gertsch		1	
Xysticus luctans (C. L. Koch)	2		
Xysticus pellax O. P.-Cambridge	3	1	
Xysticus triguttatus Keyserling	39	9	
Xysticus winnipegensis Turnbull, Dondale & Redner	1	1	
Xysticus sp.			47
SALTICIDAE			
Euophrys monadnock Emerton	1		
Evarcha hoyi (Peckham & Peckham)	1		
Habronattus viridipes (Hentz)	40	22	
Habronattus sp.			31
Neon nelli Peckham & Peckham		1	
Pelegrina flavipedes (Peckham & Peckham)		1	
Phidippus purpuratus Keyserling	1		
Phidippus sp.			1
Talavera minuta (Banks)	9	8	
Hunter Subtotals	***1,060***	***432***	***1,324***

UNDETERMINED				
Undet. genus, sp. [11]				2
	Totals	***1,163***	***587***	***1,358***

[1] Enumeration of spider taxa follows "Advances in Spider Taxonomy..." by Norman I. Platnick (1989, 1993, 1997).

[2] Number of individuals by sex and development stage; where M = male, F = female, and Juv. = juvenile.

[3] Introduced species.

[4] NEW STATE RECORD for Maine.

[5] Possibly a species of *Meioneta* or *Agyneta*; specimens should be sent to Peter J. van Helsdingen in the Netherlands for species determination. The genus *Meioneta* needs revision.

[6] Adult males of an undetermined species of *Walckenaeria*, previously discovered by pitfall trapping in an open pitch-pine heath of the Waterboro Barrens Preserve (TNC), York County, Maine. Adult females of this apparently undescribed species are needed for species description. This is an early-spring spider with males trapped mostly in May, and absent thereafter in pitfall collections from mid-June to August.

[7] Adult male of an undetermined genus, species of the subfamily Erigoninae, previously taken by pitfall traps at the Waterboro Barrens Preserve (TNC), York County, Maine. Specimen needs to be compared with deposited material at CNC.

[8] Adult female of undetermined species of Erigoninae. Epigynum lost after dissection.

[9] Most of these juvenile lycosids are young spiderlings, no doubt aboard females that had fallen into the traps. Unfortunately, at this early life stage (i.e., first post-emergent instar) reliable characters for generic-species determinations are unknown.

[10] Adult male of *Ozyptila*; however, both palps are missing. Based on coloration, this undetermined species appears to differ from *O. distans* Dondale & Redner.

[11] Juvenile spiderlings that are damaged; insufficient characters available for family determination.

Table A.2. Spiders (Araneae) associated with lowbush blueberry agroecosystems in Washington County, Maine, 2001. All spiders were sampled with pitfall traps during the last week of April and the first weeks of May, June, July, and August. Spiders were identified by Dr. Daniel T. Jennings, USDA Forest Service (retired).

Spider taxa [1]	Number of individuals [2]		
	M	F	Juv.
WEB SPINNERS			
THERIDIIDAE			
Enoplognatha caricis (Fickert)		2	
Enoplognatha marmorata (Hentz)	3		
Robertus spinifer (Emerton)	2		
LINYPHIIDAE, Linyphiinae			
Agyneta fabra (Keyserling)	1		
Agyneta simplex (Emerton)	4	1	
Agyneta zygia (Keyserling)		1	
Centromerus comupalpis (O. P.-Cambridge)		1	
Centromerus persolutus (O. P.-Cambridge)	1		
Lepthyphantes sp.			1
Macrargus multesimus (O. P.-Cambridge)	3		
Undet. genus, sp.			1
LINYPHIIDAE, Erigoninae			
Ceratinella brunnea Emerton	1		
Eperigone trilobata (Emerton)	3		
Eridantes erigonoides (Emerton)	1		
Grammonota capitata Emerton	9	7	
Islandiana flavoides Ivie [3]	1		
Metopobactrus prominulus (O. P.-Cambridge)	3	1	
Scotinotylus n. sp. ? [4]	1		
? *Wabasso* sp.		1	
Walckenaeria pinocchio (Kaston)	1		
Undet. genus, sp.			4
AGELENIDAE			
Agelenopsis actuosa (Gertsch & Ivie)	2	1	
Agelenopsis sp.			1
HAHNIIDAE			
Cryphoeca montana Emerton	1		
Neoantistea agilis (Keyserling)	10	4	
DICTYNIDAE			
Argenna obesa Emerton	1		
Cicurina arcuata Keyserling	1		
Cicurina brevis (Emerton)	1	1	
Cicurina pallida Keyserling	4	1	
Cicurina placida Banks	1	1	
Cicurina sp.			1
Dictyna foliacea (Hentz)		1	

AMAUROBIIDAE			
Callobius bennetti (Blackwall)	1	2	
Callobius sp.			13
Wadotes calcaratus (Keyserling)		1	
Web Spinner Subtotals	**56**	**26**	**21**
HUNTERS			
LYCOSIDAE			
Alopecosa aculeata (Clerck)	8	4	
Alopecosa sp.			5
Hogna frondicola (Emerton)	59	11	
Hogna sp.			71
Pardosa distincta (Blackwall)	8	9	
Pardosa mackenziana (Keyserling)		1	
Pardosa moesta Banks	16	5	
Pardosa saxatilis (Hentz)	1	1	
Pardosa xerampelina (Keyserling)	42	19	
Pardosa sp.			67
Pirata minutus Emerton	1	5	
Pirata sp.			1
Schizocosa communis (Emerton)	43	9	
Schizocosa saltatrix (Hentz)		4	
Schizocosa sp.			56
Trabeops sp.			1
Trochosa terricola Thorell	7	4	
Trochosa ruricola (De Geer) [5]	9	5	
Trochosa sp.			11
Undet. genus, sp.			38
LIOCRANIDAE			
Agroeca ornata Banks	1		
Agroeca sp.			1
Phrurotimpus alarius (Hentz)		1	
Phrurotimpus borealis (Emerton)		1	
Phrurotimpus sp.			1
CLUBIONIDAE			
Clubiona canadensis Emerton	1		
Clubiona johnsoni Gertsch	1	3	
Clubiona sp.			1
CORINNIDAE			
Castianeira sp.			2
GNAPHOSIDAE			
Callilepis pluto Banks	1	1	
Drassodes sp.			1
Gnaphosa muscorum (L. Koch)	13	2	
Gnaphosa parvula Banks	1		
Gnaphosa sp.			12
Haplodrassus hiemalis (Emerton)	1		
Haplodrassus signifer (C. L. Koch)	3	2	

Haplodrassus sp.			11
Micaria riggsi Gertsch	2		
Sergiolus ocellatus (Walckenaer)		1	
Zelotes fratris Chamberlin	4	2	
Zelotes hentzi Barrows	11	11	
Zelotes puritanus Chamberlin	3	1	
Zelotes sp.			7
PHILODROMIDAE			
Philodromus pernix Blackwall		1	
Thanatus striatus C. L. Koch	1		
Thanatus sp.			1
Tibellus oblongus (Walckenaer)	1		
THOMISIDAE			
Xysticus elegans Keyserling	1	2	
Xysticus ferox (Hentz)	1	1	
Xysticus punctatus Keyserling	3		
Xysticus triguttatus Keyserling	1		
Xysticus winnipegensis Turnbull, Dondale & Redner		1	
Xysticus sp.			18
SALTICIDAE			
Euophrys monadnock Emerton	1		
Habrocestum pulex (Hentz)		1	
Habronattus viridipes (Hentz)	3	10	
Habronattus sp.			12
Phidippus sp.			1
Hunter Subtotals	**248**	**118**	**318**
Totals	**304**	**144**	**339**

[1] Enumeration of spider taxa follows "Advances in Spider Taxonomy..." by Norman I. Platnick (1989, 1993, 1997).

[2] Number of individuals by sex and development stage; where M = male, F = female, and Juv. = juvenile.

[3] NEW STATE RECORD for Maine.

[4] Possibly a new, undescribed species of *Scotinotylus*. Additional specimens of both sexes are needed for study and description.

[5] Introduced species.

Appendix B

ADDITIONAL RESULTS CONCERNING THE ADUNDANCE, DISTRIBUTION, AND COMMUNITY COMPOSITION OF LYCOSIDS IN LOWBUSH BLUEBERRY AGROECOSYSTEMS IN WASHINGTON COUNTY, MAINE

Figure B.1. Average number of lycosids captured in pitfall traps in four different lowbush blueberry fields in Washington County, Maine, in 2000. CF1, CF2 and CF3 represent conventional fields and BBH represents a reduced input field. Fields were sampled every 1-2 weeks from May through August. Bars with different letters are significantly different from each other at $P<0.0001$. Error bars represent 95% confidence intervals.

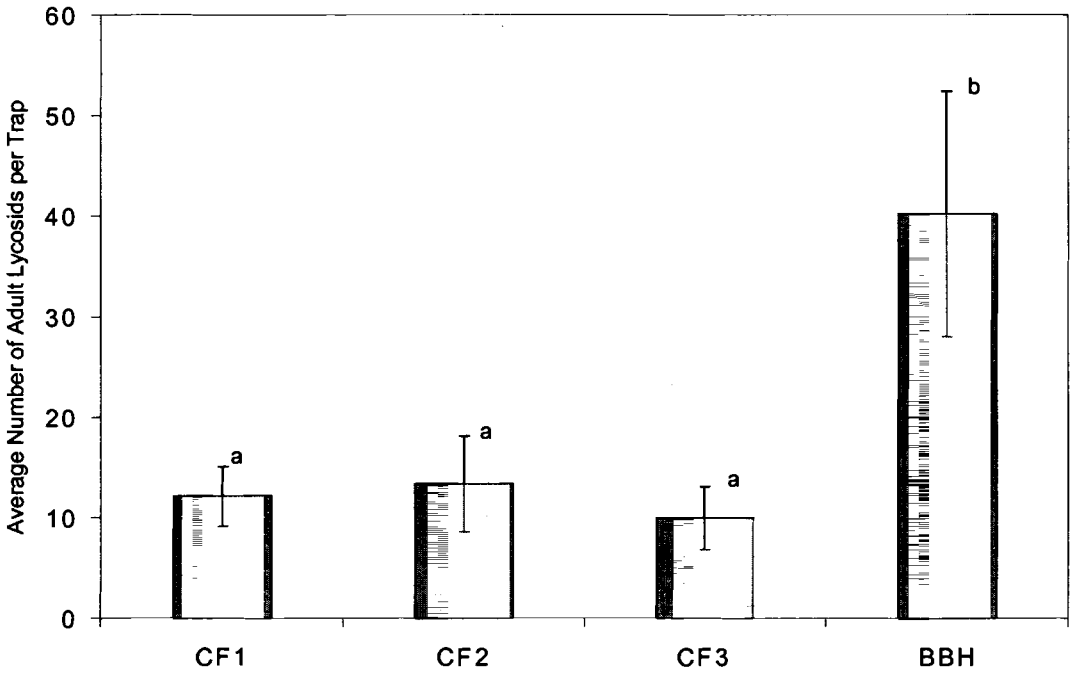


Figure B.2. Average number of lycosids captured in pitfall traps in different lowbush blueberry fields in Washington County, Maine, in 2001. A: Comparison of two conventional (C-NL-5B and C-SL-8) and two reduced input (BBH2 and Grant) fields sampled the first weeks of May, June, July and August (12 traps per field). There were significant differences between fields at $P<0.05$. B: Comparison of two conventional, two reduced input, and two organic (HI1 and HI2) fields sampled the first weeks of June, July, and August (6 traps per field). There were no significant differences between fields. Bars with the same letter are not significantly different from each other. Error bars represent 95% confidence intervals.

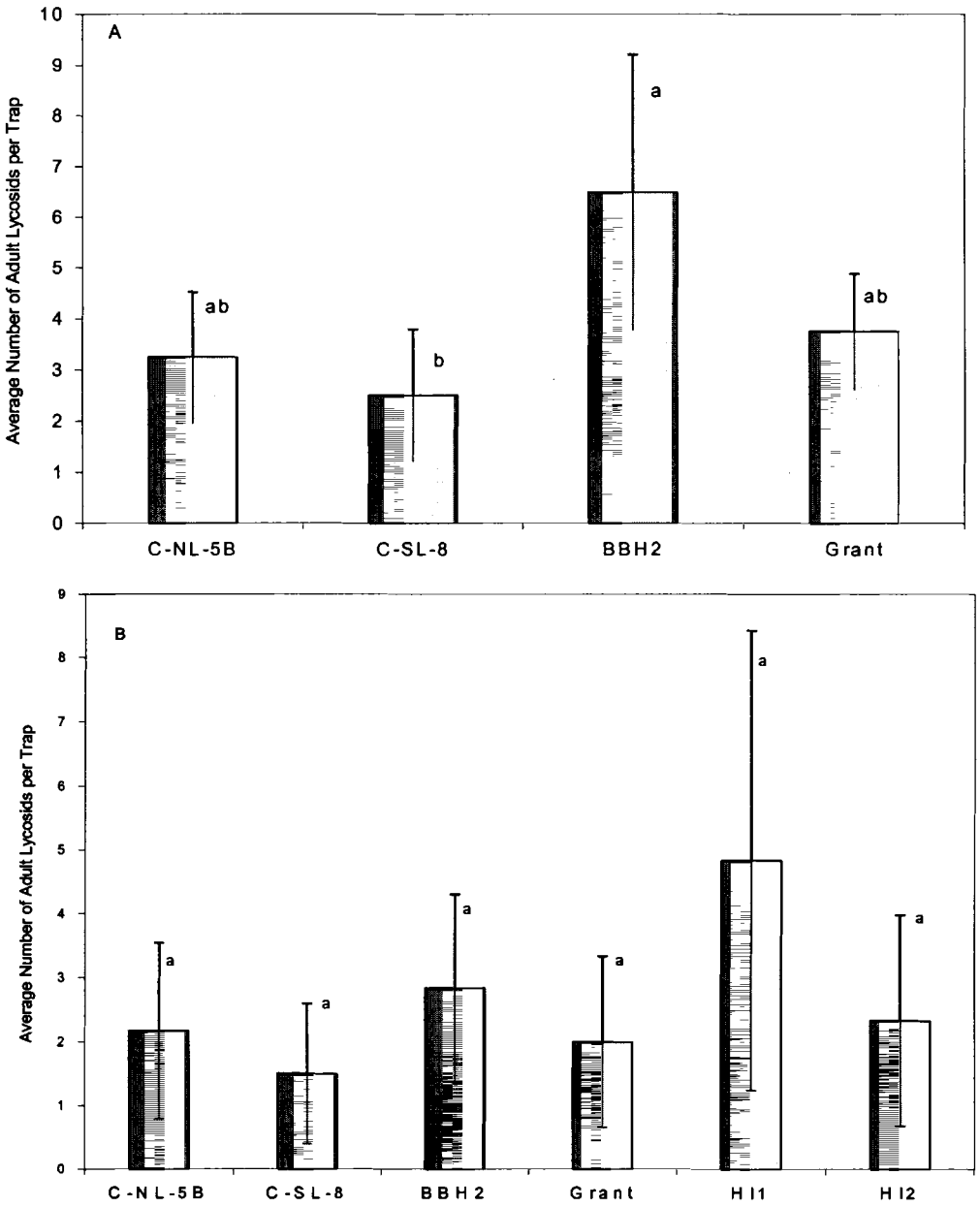


Figure B.3. Average number of lycosids captured in pitfall traps at different locations within lowbush blueberry fields in Washington County, Maine, in 2000. A: Comparison of lycosid capture between the field edges (0 and 3 m from the forest/windbreak) and the field interior (15 and 30 m from the forest/windbreak). There were significant differences at $P<0.05$. B: Comparison of lycosid capture between the forest/windbreak (0 m) and the field (3, 15, and 30 m). There were significant differences at $P<0.05$. Error bars represent 95% confidence intervals.

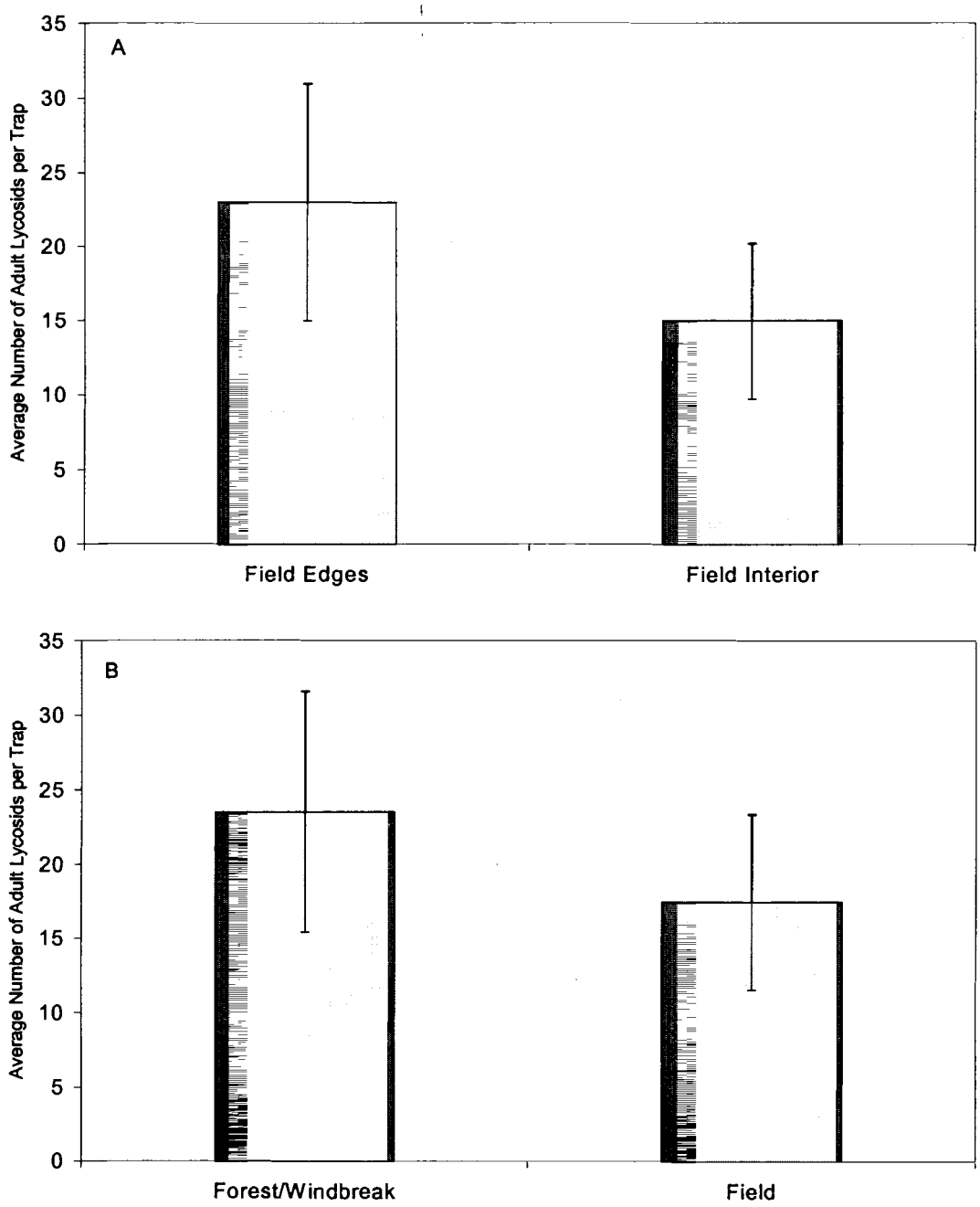


Figure B.4. Average number of lycosids captured in pitfall traps at different locations within the conventional lowbush blueberry field CF2 in Washington County, Maine, in 2000. A: Comparison of lycosid capture between the field edges (0 and 3 m from the windbreak) and the field interior (15 and 30 m from the windbreak). There were significant differences at $P<0.05$. B: Comparison of lycosid capture between the windbreak (0 m) and the field (3, 15, and 30 m). There were significant differences at $P<0.05$. Error bars represent 95% confidence intervals.

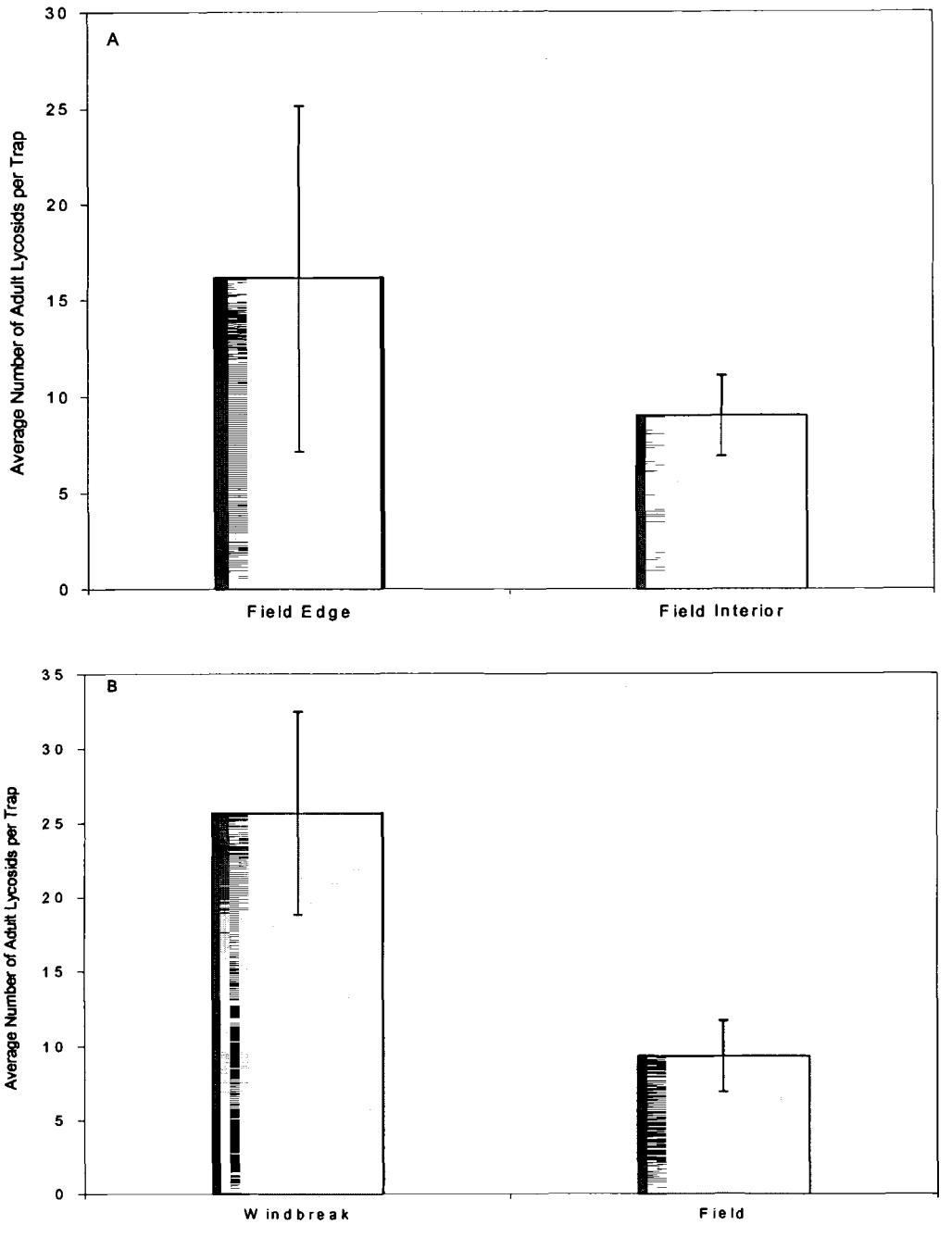
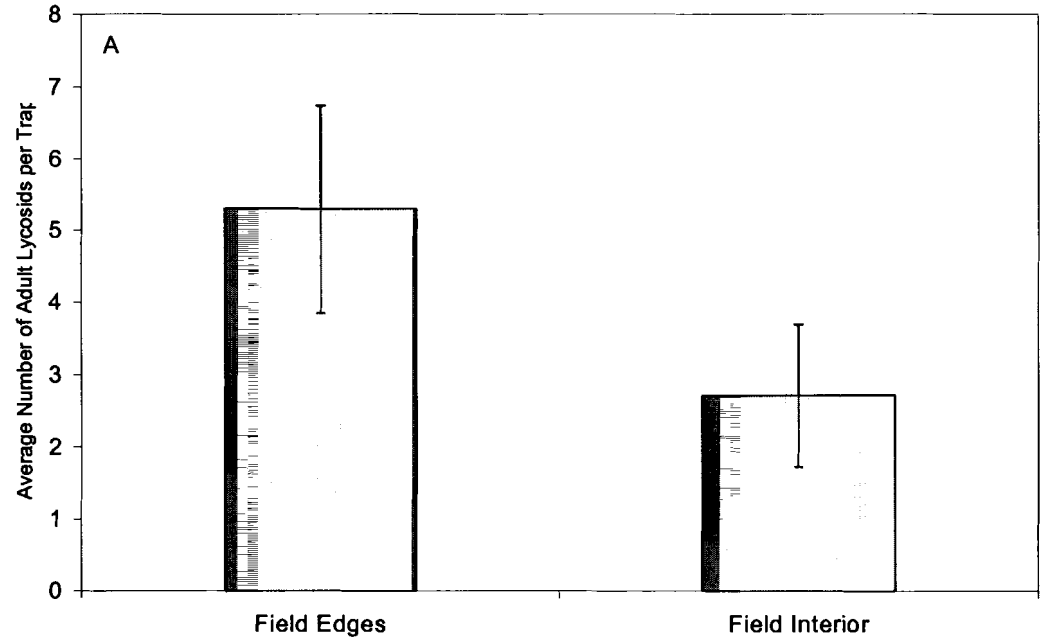


Figure B.5. Average number of lycosids captured in pitfall traps at different locations within lowbush blueberry fields in Washington County, Maine, in 2001. A: Comparison of lycosid capture between the field edges (0 and 3 m from the forest/windbreak) and the field interior (15 and 30 m from the forest/windbreak). There were significant differences at $P<0.01$. B: Comparison of lycosid capture between the forest/windbreak (0 m) and the field (3, 15, and 30 m). Difference in capture between these locations was not significant ($P>0.05$). Error bars represent 95% confidence intervals.



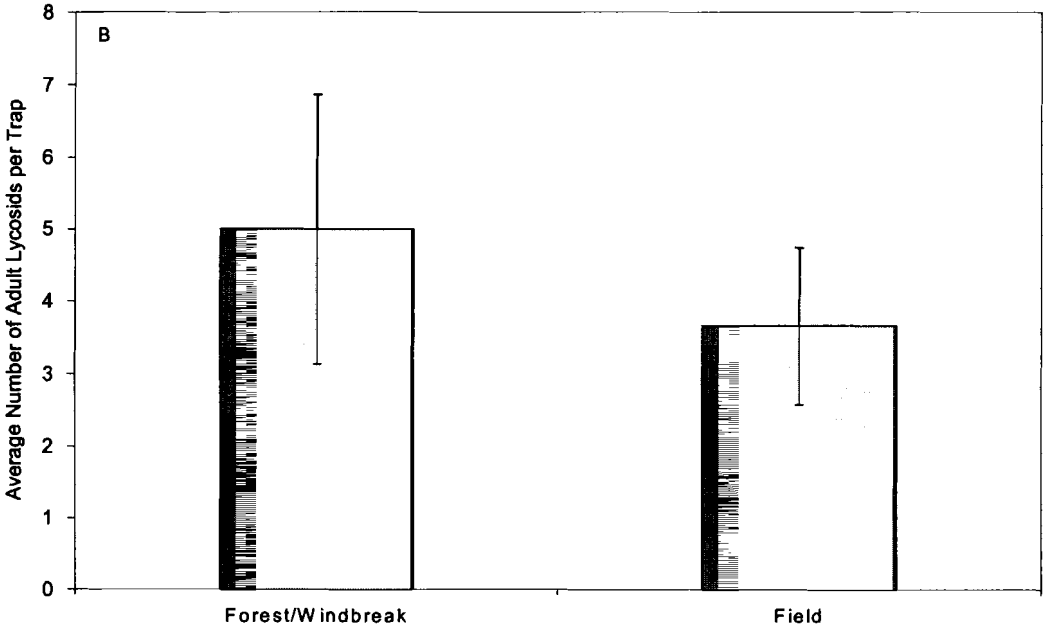


Figure B.6. Average number of lycosids captured in pitfall traps at different locations within the conventional lowbush blueberry field C-SL-8 in Washington County, Maine, in 2001. A: Comparison of lycosid capture between the field edges (0 and 3 m from the windbreak) and the field interior (15 and 30 m from the windbreak). There were significant differences at $P<0.05$. B: Comparison of lycosid capture between the windbreak (0 m) and the field (3, 15, and 30 m). There were significant differences at $P<0.05$. Error bars represent 95% confidence intervals.

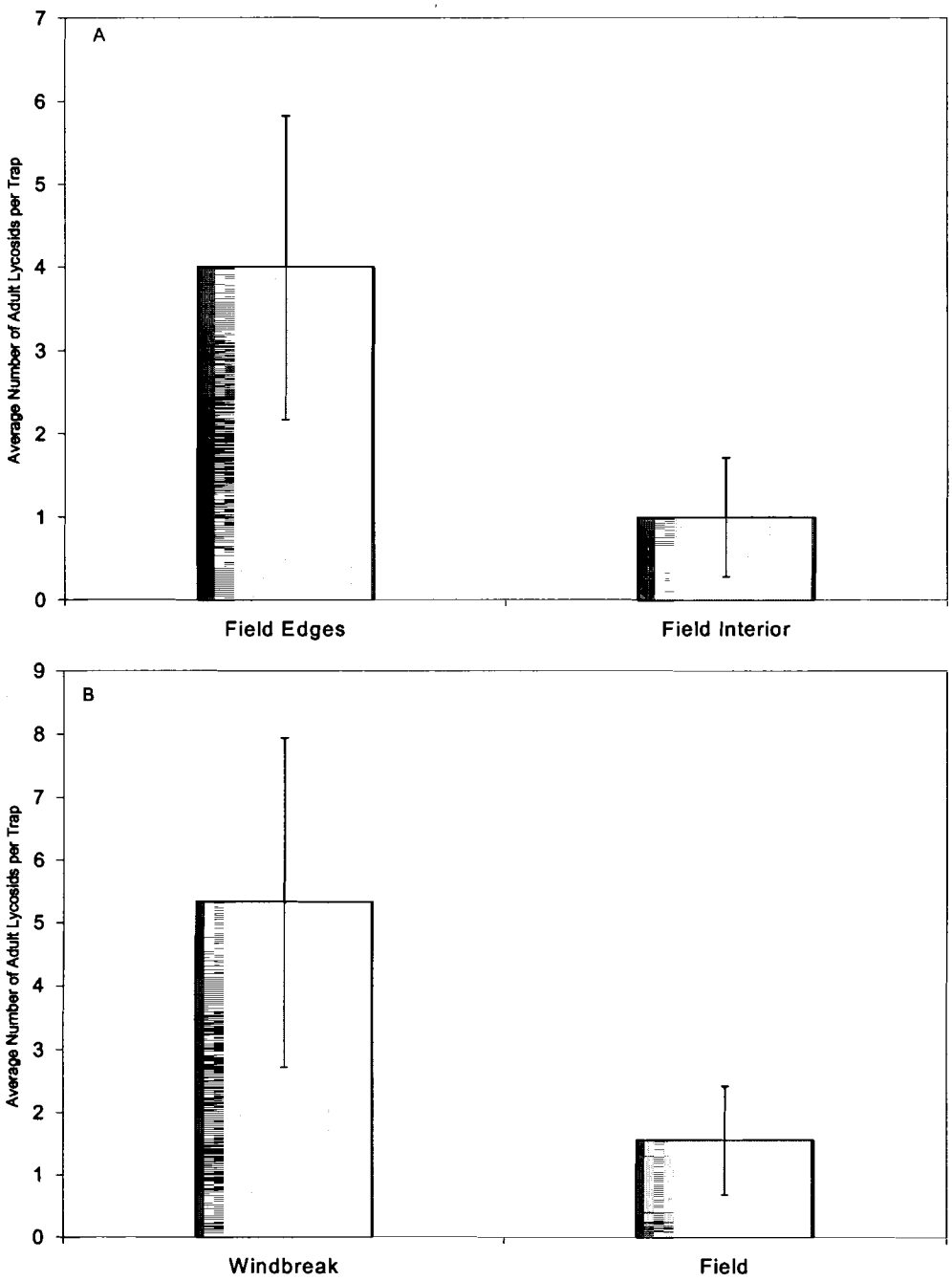


Figure B.7. Average number of lycosids captured in pitfall traps at different locations within the conventional lowbush blueberry field C-NL-5B in Washington County, Maine, in 2001. A: Comparison of lycosid capture between the field edges (0 and 3 m from the windbreak) and the field interior (15 and 30 m from the windbreak). There were significant differences at $P<0.05$. B: Comparison of lycosid capture between the windbreak (0 m) and the field (3, 15, and 30 m). Difference in capture between these locations was not significant ($P>0.05$). Error bars represent 95% confidence intervals.

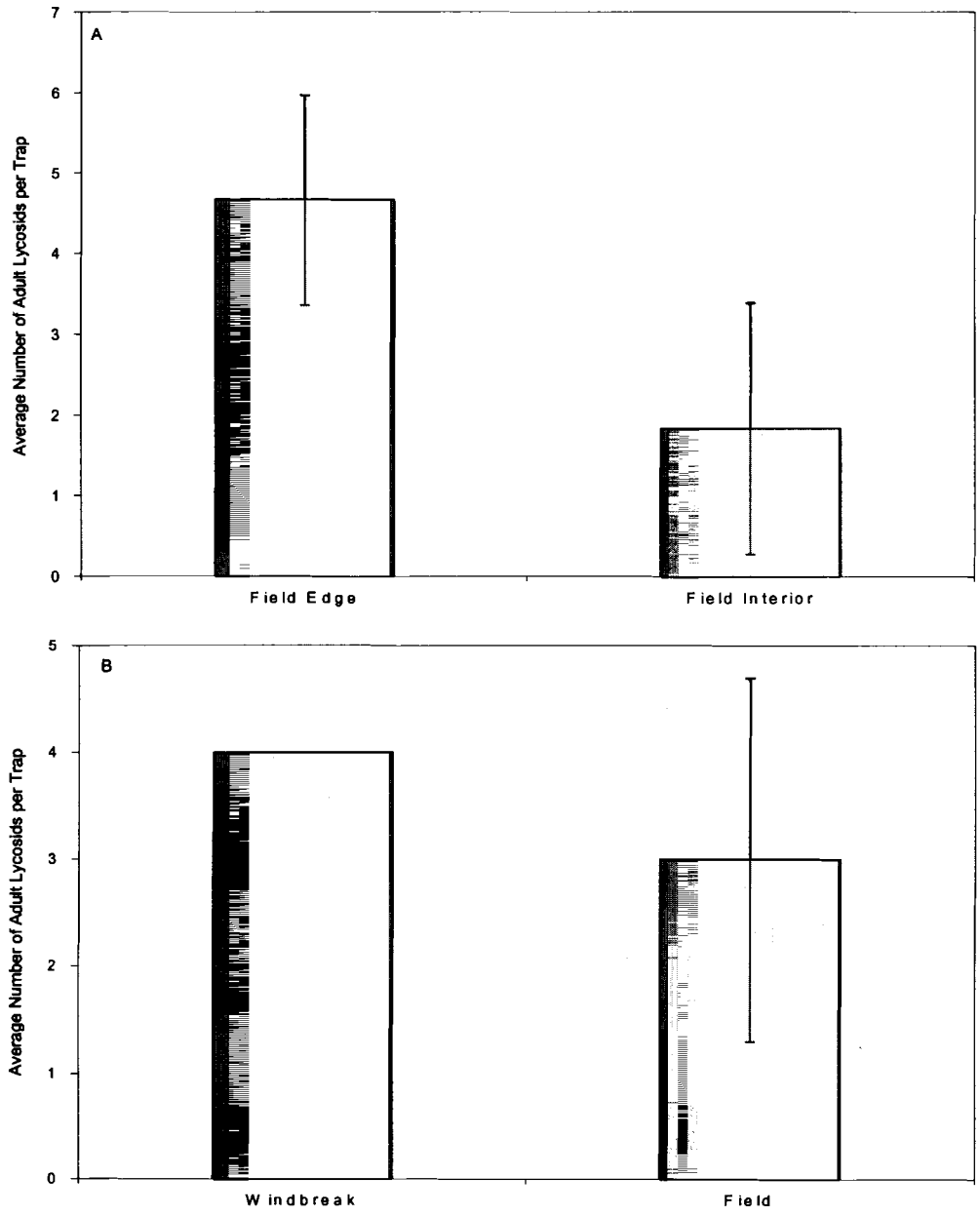


Figure B.8. Total number of lycosids of different species captured in pitfall traps in four lowbush blueberry fields in Washington County, Maine, in 2000. BBH is a reduced input field and CF1, CF2, and CF3 are conventional fields. Species designations are: Pmoe = *P. moesta*; Scom = *S. communis*; Pdis = *P. distincta;* Pxer = *P. xerampelina*; Hfro = *H. frondicola*; Trur = *T. ruricola*; Psax = *P. saxatilis;* Aacu = *A. aculeata*; Pmac = *P. mackenziana*; Pmin = *P. minutus*; Taur = *T. aurantiaca*; and Tter = *T. terricola*.

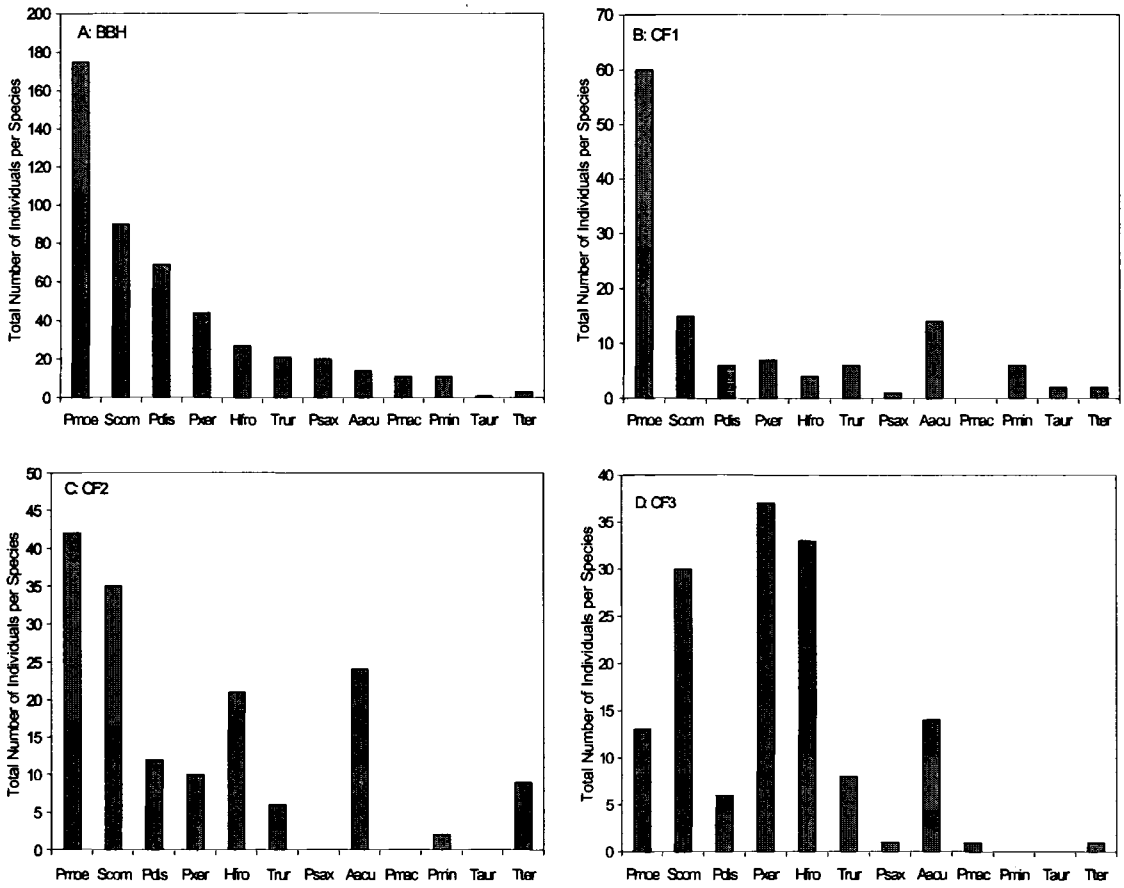


Figure B.9. Total number of lycosids of different species captured in pitfall traps in six lowbush blueberry fields in Washington County, Maine, in 2001. C-NL-5B and C-SL-8 are conventionally managed fields. BBH and Grant are reduced input fields. HI1 and HI2 are organic fields. Species designations are: Scom = *S. communis*; Hfro = *H. frondicola*; Pxer = *P. xerampelina*; Trur = *T. ruricola*; Aacu = *A. aculeata*; Pmoe = *P. moesta*; Tter = *T. terricola*; Pdis = *P. distincta*; and Ssal = *S. saltatrix*.

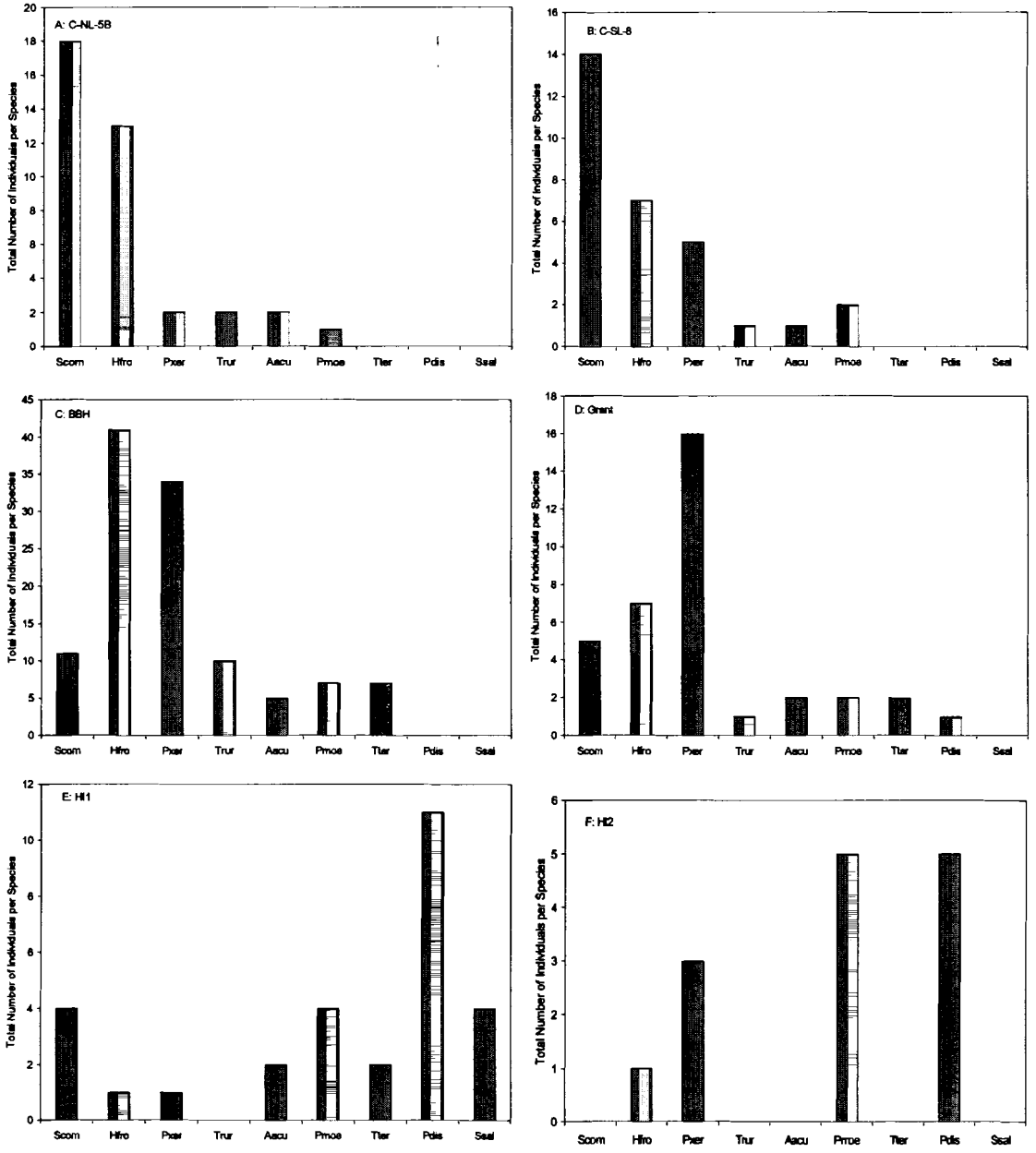


Figure B.10. Average lycosid capture (left y-axis) and average rainfall, high temperatures, and low temperatures (right y-axis) in lowbush blueberry fields in Washington County, Maine, in 2000 and 2001. Lycosids were captured in pitfall traps. A: Lycosid capture and average rainfall during the sampling period in 2000. B: Lycosid capture and average high and low temperatures during the sampling period in 2000. C: Lycosid capture and average rainfall during the sampling period in 2001. D: Lycosid capture and average high and low temperatures during the sampling period in 2001. Error bars represent 95% confidence intervals.

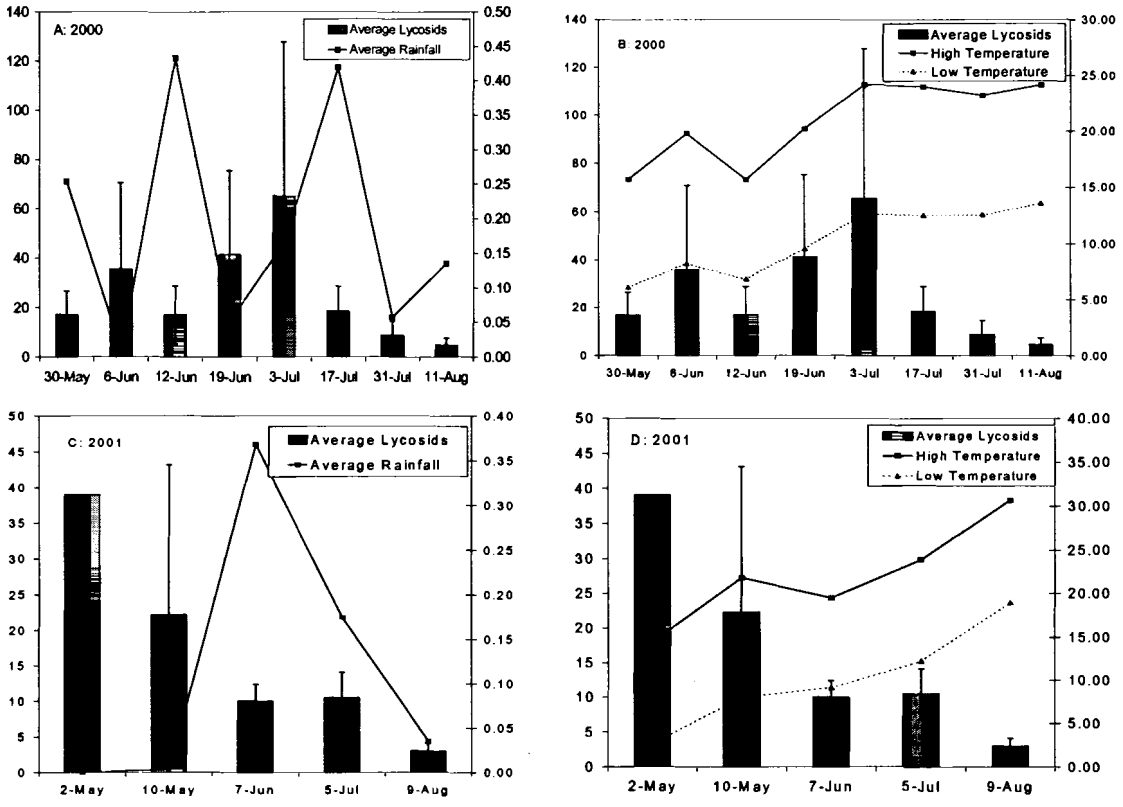
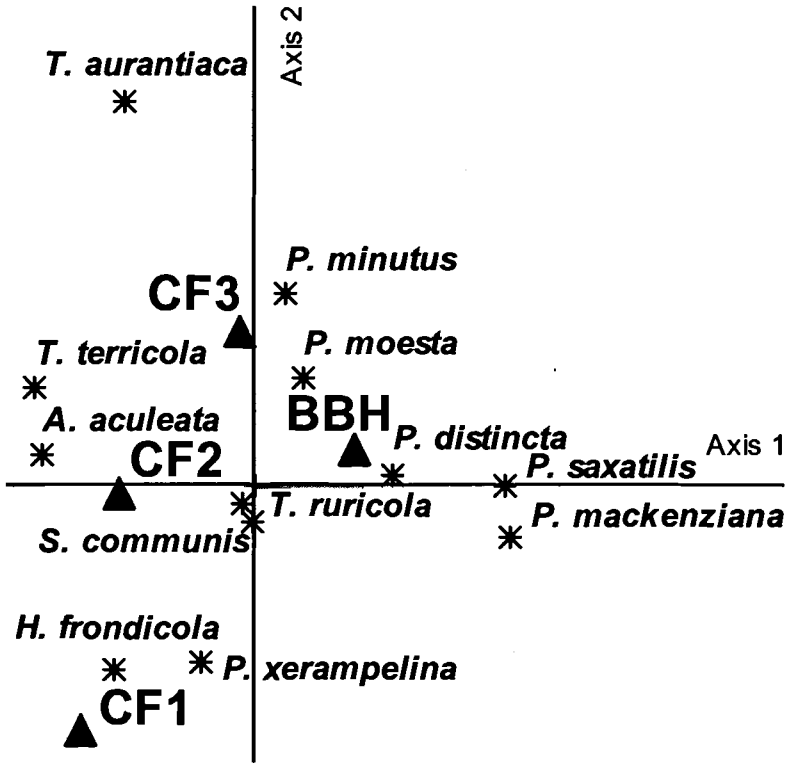


Figure B.11. Ordination of species-field associations in 2000 determined by Canonical Correspondence Analysis. Stars represent lycosid species. Triangles represent lowbush blueberry fields in Washington County, ME, of different management practices. Conventional fields are plotted in quadrants I and IV, and the reduced input field is plotted in quadrant II. Axis 1 of the CCA – the difference between management practices – explains 41.4% of the total variation in spider abundance. Axis 2 – the difference between fields within management practices – explains 46.2% of the variation.



Appendix C

PRELIMINARY STUDIES ON THE RESPONSE OF LYCOSIDS TO CHEMICAL CUES FROM INSECT PREY

Introduction

Wolf spiders (Lycosidae) have been shown to respond to chemical cues from prey. For example, *Schizocosa ocreata* (Hentz) spend more time in patches containing chemical cues from house crickets (*Acheta domestica* (Linnaeus)) than in patches with no sensory information (Persons and Uetz 1996). In addition to responding to the presence of prey odors, lycosids also show a preference for chemical cues deposited by the prey species they have most recently consumed over prey species with which they have no previous experience (Punzo and Kukoyi 1997; Persons and Rypstra 2000). These chemical cues may be in the form of silk, feces or other metabolic byproducts, volatiles associated with metabolic waste, and airborne or contact chemicals such as pheromones (Punzo and Kukoyi 1997; Sinha and Kumar 1998; Persons and Rypstra 2000; Persons et al. 2001; Allan and Sonenshine 2002). If lycosids show a preference for chemical cues for prey they have most recently consumed, this response to specific prey odors may be able to be used to determine which prey species the spiders are consuming in the field.

The present study was conducted using lycosids and prey species captured from lowbush blueberry (*Vaccinium angustifolium* (Aiton)) agroecosystems in Washington County, Maine. The objectives of this study were

to determine if lycosids a) respond to chemical cues deposited by live prey they have been recently consuming, b) respond to chemical cues deposited by live prey from their natural habitat, and c) respond to extracts of prey they have recently consumed.

Methods

Lycosids and prey species were collected and maintained as described in Chapter 3: Spider and Prey Collection. Lycosids used were *Schizocosa communis* (Emerton), *Hogna frondicola* (Emerton), and *Trochosa* spp. Prey used were grasshopper (Acrididae) nymphs, field cricket (*Gryllus pennsylvanicus* Burmeister) nymphs, and house cricket nymphs.

Two sets of experiments were conducted with chemical cues from live prey. For Set A, *S. communis* had been fed either house cricket nymphs or grasshopper nymphs once a week since 29 June. Prey remains were removed and spiders were starved for at least 7 days before use in any trial. For Set B, spiders (*S. communis*, *H. frondicola*, and *Trochosa* spp.) were captured from the field and held without food for at least 7 days before use in any trial (Persons and Uetz 1996; Punzo and Kukoyi 1997; Persons and Rypstra 2000). No spider was used more than once in these trials. These experiments took place between 17 August and 7 September.

Test arenas were constructed of two 9-cm petri dishes from which a portion of the side (ca. 5-cm arc) had been removed. Petri dishes were adjoined where the side was removed. The exposed paper ("Scented") was randomly assigned to side A or B, and the remaining side was lined with a clean,

unexposed piece of filter paper ("Blank"). Paper was trimmed on one side so that the two papers did not overlap, thereby providing an untreated space in the center for a starting point (Figure C.1) (Persons and Uetz 1996; Punzo and Kukoyi 1997; Persons and Rypstra 2000).

Chemical cues were collected by allowing a single prey individual to move on a piece of 11 cm filter paper (Whatman #1) for a 48-hour period. All insects used were approximately the same size as the adult lycosids, 0.8 – 1.5 cm in length (Persons and Uetz 1996; Punzo and Kukoyi 1997; Persons and Rypstra 2000).

Spiders in Set A were tested for responses to filter paper associated with the prey they had been feeding upon in the laboratory, Spiders in Set B were tested for response to filter paper from house crickets, field crickets, and grasshopper nymphs. Filter paper for Set B were randomly assigned based on prey availability.

For each experimental trial, a single spider was introduced in the center of the arena within an inverted clear glass vial. Spiders were allowed to acclimate for 1 minute, after which the vial was removed and the entry hole was covered with parafilm. The spider was given an additional minute to acclimate, and then the spider was allowed to move freely for 30 minutes. For each spider, the position (Side A, Side B, or Center), and the amount of time (mm:ss) spent in each position was recorded. Test arenas and release vials were swabbed with 75% ethanol and allowed to dry for 30 minutes between trials to remove residual

odors and spider silk. All spiders were tested between 0900 and 1700 h (Persons and Uetz 1996; Punzo and Kukoyi 1997; Persons and Rypstra 2000).

Experiments were also conducted using extracts of house crickets. For these assays, lycosids were fed house crickets since 16 September. Although some spiders had produced viable egg sacs while in the laboratory, no spiders were carrying egg sacs at the time of the experiment. All spiders were starved at least 7 days before trial. No spider was used with same extract twice.

Chemical cues were extracted from house crickets using the following protocol. The digestive tracts had been removed, and the crickets were placed in deep freeze (-70° C) for at least 1 hour. Crickets were then ground up in methanol, pentane, or water as a solvent (3 ml solvent for every 2 crickets). Extracts were stored in airtight vials at 4-10° C until use (Alla et al. 2001;Schaffner and Müller 2001; Allan and Sonenshine 2002).

Extract was pipetted onto filter paper (Whatman #1) and placed in a fume hood to dry (5 min for pentane, 15 min for methanol, and 30 to 60 min for water). These filter papers were used in trials as soon as they were dry. Testing arenas were set up, spiders were released, and data were recorded as described above. For preliminary trials, the amount of extract used was 100 μl and 300 μl for methanol and pentane extracts, and 300 μl for water extracts. For experimental trials, two trials were run concurrently each time – one using the extract paper and a blank paper and one using a solvent-only paper and a blank paper. The amount of extract and solvent used was 500 μl. Experiments took place between 26 October and 16 November.

Results

Lycosids did not respond to filter paper held with prey with which they had previous feeding experience in the laboratory. Spiders often did not initiate searching behavior, remaining in one location for the duration of the trial (Table C.1).

Lycosids from the field did not initiate searching behavior in response to house cricket or field cricket scented paper. Searching behavior was also not initiated in one out of eight grasshopper scent trials (*Schizocosa* α) and was not initiated until more than 10 minutes into the 30-minute trial in three trials (*Trochosa* μ, *Schizocosa* δ, and *Hogna* k). In one of those three trials, *Hogna* k, searching behavior ceased after 1 minute and 49 seconds. *Trochosa* ο, *Trochosa* ρ, and *Trochosa* σ spent more time on the grasshopper scented paper than on the blank. *Schizocosa* b spent approximately the same amount of time on scented and blank paper (Table C.2).

In preliminary trials, using cricket extract, spiders did not initiate searching behavior in trials using pentane or methanol as a solvent. The spider *Schizocosa* ρ spent more time on filter paper containing cricket extract and water than on blank paper (Table C.3).

For trials using pentane as a solvent, *Schizocosa* ι did not initiate searching behavior in response to pentane only. *Schizocosa* x spent approximately equal amount of time on scented and blank paper (Table C.4a).

For trials using methanol as a solvent, three spiders spent approximately the same amount of time on both scented and blank paper, and three spiders

ceased searching behavior after less than 15 minutes. In two methanol-only trials, the spiders *Schizocosa* υ and *Trochosa* ε spent approximately the last 20 minutes on the scented paper, while in one cricket extract trial the spider *Trochosa* υ spent the last 27 minutes on the blank paper (Table C.4b).

For trials using water as a solvent, two out of three spiders (*Schizocosa* ω and *Trochosa* z) spent the same amount of time on the cricket extract paper as the blank paper, and the third spider (*Schizocosa* η) did not initiate searching behavior. For the water-only trials, one spider (*Schizocosa* f) did not initiate searching behavior until 17 minutes after the trial began, and the other two (*Schizocosa* z and *Trochosa* ρ) spent approximately the same amount of time on both blank and water-only papers (Table C.4c).

Figure C.1. Spider chemical trial arena. Filter paper that was either marked with prey chemical cues (scented) or clean (blank) was randomly assigned to side A or B. The circle in the position between sides A and B represents the position of release of the spider.

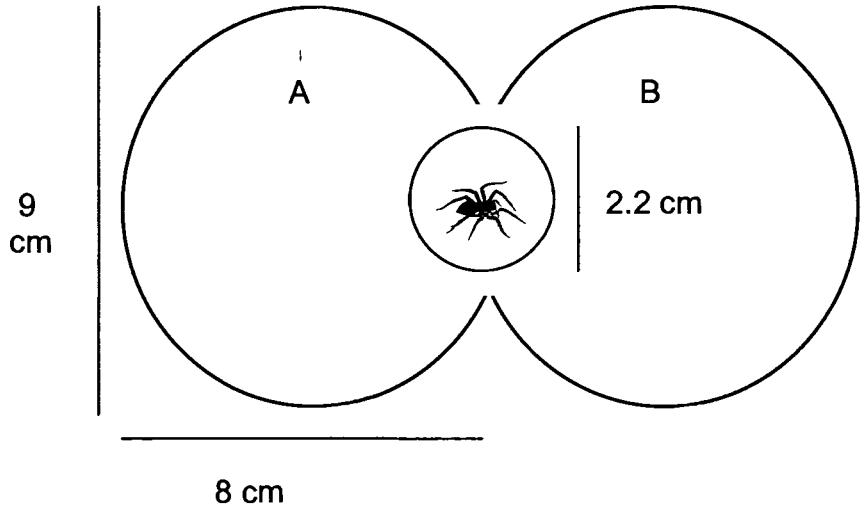


Table C.1. Total residence time on filter papers with and without prey scent by spiders with known feeding history. Each spider was assigned an alphabetical ID letter and was fed the same prey insect used in "Scent". Scent indicates the insect that marked the filter paper, with HC = house cricket, and GH = grasshopper. The "*" indicates the position (scented, center, or blank) in which the spider began the trial.

		Total Residence Time (mm:ss)			Total number of
Spider ID	**Scent**	**Scented**	**Center**	**Blank**	**position changes**
Schizocosa u	HC	02:15	02:03*	25:42	2
Schizocosa c	GH	30:00*	00:00	00:00	0
Schizocosa d	GH	03:52	26:07*	00:01	2
Schizocosa a	GH	10:12	00:03	19:45*	2
Schizocosa n	GH	00:00	30:00*	00:00	0
Schizocosa υ	GH	00:00	00:00	30:00*	0

Table C.2. Total residence time on filter papers with and without prey scent by spiders with unknown feeding history. Spiders were caught from the field, assigned an alphabetical ID letter, held without food, and used in trial at least 7 days later. Scent indicates the insect that marked the filter paper, with HC = house cricket, FC = field cricket, and GH = grasshopper. The "*" indicates the position (scented, center, or blank) in which the spider began the trial.

		Total Residence Time (mm:ss)			Total number of
Spider ID	**Scent**	**Scented**	**Center**	**Blank**	**position changes**
Schizocosa k	HC	30:00*	00:00	00:00	0
Trochosa λ	FC	00:00	00:00	30:00*	0
Hogna i	FC	05:25	24:35*	00:00	1
Trochosa π	FC	29:26*	00:02	00:32	4
Schizocosa α	GH	30:00*	00:00	00:00	0
Schizocosa b	GH	15:28	00:14	13:57*	60
Schizocosa δ	GH	08:30	00:13	21:16*	13
Trochosa o	GH	21:06*	00:05	09:49	16
Trochosa μ	GH	12:54	00:02	17:04*	10
Trochosa ρ	GH	21:47*	00:19	07:54	19
Trochosa σ	GH	21:36	00:12	8:12*	11
Hogna k	GH	01:45	00:04	28:11*	3

Table C.3. Total residence time on filter papers with and without prey scent in preliminary cricket extract trials. Each spider was assigned an alphabetical ID letter and fed house crickets (HC). Extract indicates the solvent-plus-cricket solution applied to the filter paper with PEN = pentane, METH = methanol, and H_2O = water. The "*" indicates the position (scented, center, or blank) in which the spider began the trial.

			Total Residence Time (mm:ss)			Total number of
Spider ID	**Conc. (μl)**	**Extract**	**Scented**	**Center**	**Blank**	**position changes**
Schizocosa η	100	PEN+HC	00:00	00:00	30:00*	0
Schizocosa u	300	PEN+HC	30:00*	00:00	00:00	0
Schizocosa ι	100	METH+HC	00:00	00:00	30:00*	0
Schizocosa x	300	METH+HC	00:00	00:00	30:00*	0
Schizocosa ρ	300	H_2O+HC	20:23	06:13*	03:24	27

Table C.4. Total residence time on filter papers with and without prey scent in cricket extract trials. Each spider was assigned an alphabetical ID letter and fed house crickets (HC). Extract indicates the solution applied to the filter paper. Solvent only trials are represented with PEN, METH, or H_2O, while cricket chemicals extracted with solvent are represented with "+HC" after the solvent with PEN = pentane, METH = methanol, and H_2O = water. The "*" indicates the position (scented, center, or blank) in which the spider began the trial. Trials were paired with one set of solvent+cricket and solvent-only trials running simultaneously.

C.4A: Pentane as a solvent

			Total Residence Time (mm:ss)			Total number of
Spider ID	**Conc. (µl)**	**Extract**	**Scented**	**Center**	**Blank**	**position changes**
Schizocosa x	500	PEN+HC	16:40*	01:04	11:16	34
Schizocosa ι	500	PEN	25:25*	00:11	04:24	2

C.4B: Methanol as a solvent

			Total Residence Time (mm:ss)			Total number of
Spider ID	**Conc. (µl)**	**Extract**	**Scented**	**Center**	**Blank**	**position changes**
Schizocosa ρ	500	METH+HC	17:15	02:15	14:04*	72
Schizocosa η	500	METH	09:31	00:54	18:37*	21
Schizocosa k	500	METH+HC	12:43	00:14	16:03*	17
Schizocosa υ	500	METH	22:45	00:00	7:15*	3
Trochosa υ	500	METH+HC	00:53	00:18	28:49*	7
Trochosa ε	500	METH	27:56*	01:10	00:54	10

C.4C: Water as a solvent

			Total Residence Time (mm:ss)			Total number of
Spider ID	**Conc. (µl)**	**Extract**	**Scented**	**Center**	**Blank**	**position changes**
Schizocosa ω	500	H_2O+HC	13:29*	01:06	12:36	48
Schizocosa f	500	H_2O	12:14	00:24	17:22*	5
Schizocosa η	500	H_2O+HC	30:00*	00:00	00:00	0
Schizocosa z	500	H_2O	12:16*	03:47	13:57	12
Trochosa z	500	H_2O+HC	11:39	01:08	14:13*	21
Trochosa ρ	500	H_2O	18:55	02:48	08:17*	23

Conclusions

This study represents a preliminary study on the potential use of chemical cues by lycosids to detect prey. Cues were in the form of either prey extracts or cues deposited by live prey. Although lycosids have been shown to increase patch residence time in the presence of chemical deposits by prey (Persons and Uetz 1996; Punzo and Kukoyi 1997; Persons and Rypstra 2000; Persons et al. 2001), response to prey chemical cues by lycosids in this study was not detected.

The live crickets may not have deposited enough chemical cues, such as pheromones or feces, for the spiders to detect. The concentration of odors could be increased by allowing multiple prey individuals to deposit chemicals onto the filter papers. Alternately, the prey individual could be provided with food during the period of chemical collection, to increase the amount of defecation.

Hunting spiders increase searching rate when they are hungry. Although researchers suggest that 7 days starvation time is adequate to both standardize and sufficiently increase hunger levels (Persons 1999; Persons and Rypstra 2000), this time period may not have been long enough for the lycosids in the present study. Spiders often did not initiate searching behavior, or ceased to search before half the allotted time period had passed. It is possible that these spiders were not searching because they were employing a sit-and-wait method of prey capture, that is, they detected the presence of prey and were simply waiting for it to walk by. It is more likely, however, that the spider had ceased

searching behavior in favor of grooming, resting, or other behaviors unrelated to the acquisition of food (Persons and Uetz 1998).

Because response by lycosids to both contact and airborne chemical cues from prey is well documented, it is unlikely that the lycosids in the present study do not naturally respond to chemical signals from potential prey or prey with which they have had previous experience (Persons and Uetz 1996; Punzo and Kukoyi 1997; Sinha and Kumar 1998; Persons and Rypstra 2000; Persons et al. 2001). The lycosids in the present study, therefore, may not have responded to chemical cues because such cues were not present in adequate concentrations, the spiders were not sufficiently hungry and therefore not searching for prey, appropriate chemicals were not extracted from or deposited by prey, or a combination of these factors.

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Darlene Maloney was born in Milford, Massachusetts on October 24, 1977. She was raised in South Grafton, Massachusetts and graduated from Grafton High School in 1995. She attended Cornell University and graduated in 1999 with a Bachelor's degree in Biology. She then entered the Ecology and Environmental Sciences graduate program at the University of Maine in the fall of 1999, where she concentrated her studies in Entomology.

After receiving her degree, Darlene plans to pursue a career in entomological research or environmental education. Darlene is a candidate for the Master of Science degree in Ecology and Environmental Sciences from The University of Maine in August, 2002.