SPIDER COMPETITION IN
STRUCTURALLY SIMPLE ECOSYSTEMS

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ABSTRACT. Spider competition has long been an elusive phenomenon for ecological study. Because
most spiders are generalist predators, they are predicted to overlap in resource use wherever they overlap
in space use and activity periods. However, despite this obvious potential for competition, the empirical
evidence for competition has been weak. Spider competition could potentially limit densities in agricultural
ecosystems, which would limit their effectiveness as biological control agents. We summarize the results
of five studies in a type of ecosystem which may be considered to be analogous to row crops in both the
physiognomy of vegetation and cyclic disturbance regimes, namely, wetlands. In addition, we summarize
the results of our own work in a soybean ecosystem.

Interspecific competition occurs whenever
the availability of a limiting resource is re-
duced by the presence of two or more species
which rely on the same resource. Species
which are more efficient or aggressive in re-
source use are predicted to prevail over other
species. Exploitative competition occurs when
one species has a negative effect on individ-
uals and/or populations of another because it
is more efficient at using a limiting resource.
However, competitive interactions can also be
behavioral, such as when one species alters
the space use or feeding behavior of a second
species, resulting in a reduction in access to
important resources by the second species.
This is termed 'interference competition'.

It seems intuitively obvious that resource
limitation by the action of other species
should be an important phenomenon influenc-
ing the success of species populations and, ul-
timately, community structure. However, just
how prevalent and significant competition is
has been the subject of extensive and often
contentious debate for decades (Strong et al.
1984). One of the key assumptions in com-
petition theory is that one of the species in a
community is better at exploiting some lim-
iting resource, and does so to the detriment of

other species. Because both resource avail-
ability and population densities of the com-
petitors may vary for reasons that have noth-
ing to do with the activities of the competing
species, competition may not be a persistent
phenomenon. Also, no two species will ever
use the same resource in precisely the same
way. Even small variations in resource ex-
ploitation strategies will reduce the intensity
of competitive interactions.

The most generally accepted paradigm in
spider ecology is that spiders are food-limited
generalist predators of arthropods, particularly
insects. Spiders rarely specialize in specific
prey taxa; however, the prey spectrum of any
spider species population will never be a per-
fect reflection of all potential prey in their en-
vironment. Some prey will either be rejected
as too risky because they possess defenses, or
will not be encountered at all as they are not
active in the same places at the same times of
the day as the spiders are foraging. However,
given these constraints on prey use, there is
still the potential for different species of gen-
eralist predators like spiders to share prey taxa
(Nyffeler & Sterling 1994). Intraspecific com-
petition would be predicted to be the stron-
gest, given that resource use should overlap
100% within a single species age/size class.
However, because many spiders are territorial,
and potentially cannibalistic, they will tend to
be self-limiting. Because of these population

regulation mechanisms, spider densities are predicted to rarely be high enough to set the stage for density-dependent resource limitation (Riechert 1974).

Evidence for interspecific competition in spiders has been rare enough that it may be viewed as the exception and not the rule (Wise 1993). However, there are similarities among the strongest examples of interspecific competition we found which suggest that competition may be more prevalent in structurally simple ecosystems which exhibit a gradient of habitat structure than those ecosystems which are more uniform and exhibit greater vertical stratification. Examples of structurally simple successional ecosystems are estuaries, wetlands, and an anthropogenic analog, agricultural ecosystems. Early research in spider community ecology documented the fact that early successional habitats had lower spider species diversity when compared to later seral stages nearby (Lowrie 1948; Barnes 1953). In these cases, this relatively low spider species diversity was functionally linked to the relative structural simplicity of the vegetation. The link between vegetation structure and spider species diversity was explicitly tested by Greenstone (1984). This link between structural simplicity and species poverty was extended to the litter layer by Uetz (1979). The link between the structural complexity of habitat and spider species diversity is so well-established as to be a paradigm in spider ecology (Uetz 1991; Wise 1993).

Wetland ecosystems are structurally simple because they are biotically simple. Tidal estuaries, in particular, have few plant species which in turn supports a species poor community of herbivores and predators. In addition, there is an inshore-outshore gradient of the intensity and cycle of disturbance which results from cyclical disturbance by flowing water. Along this disturbance gradient habitat complexity varies from barren soil at the water's edge, to complex vegetation inshore (Cameron 1972; Uetz 1976). Agricultural ecosystems are structurally simple systems by design. Intensive cyclic disturbance regimes in tandem with the mechanized dispersal of seeds are all techniques used to attempt to create landscapes colonized by one species: The crop plant. However, despite the strenuous efforts of agriculturists, many species of plants and animals do colonize agricultural fields.

Because most crop plants have an annual crop cycle, and because of the disturbances inherent in crop management, most invading species of plants and animals are those naturally associated with early successional ecosystems (Wissinger 1997). The evolved ability of these pioneer species to invade and reproduce in a narrow window of time, tolerate abiotic extremes, and benefit from disturbance preadapts them to life in an agricultural field (Luczak 1979).

Spiders are common and often abundant incidental colonists of agricultural ecosystems. Young & Edwards (1990) found that 614 spider species are found in crop systems in North America. Studies of the spiders associated with crops found that the spiders found there are generally not species invading from local natural ecosystems, but those species found in the surrounding agricultural landscape (Duelli et al. 1990; Bishop & Riechert 1990). In our own fields at the Miami University Ecology Research Center in southwestern Ohio we found that the two dominant wolf spider species (*Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz) are absent from the native forest adjacent to the fields, but common in riparian and pond edge habitats in the area (Marshall & Rypstra unpubl. data).

Araneid competition in a California salt marsh.—Dave Spiller's 1984 study of the competitive interactions between two araneids, *Cyclosa turbinata* (Walckenaer) and *Metepeira grinneli* (Coolidge), in a salt marsh ecosystem near San Francisco remains one of the clearest experimental demonstrations of interspecific competition between spiders to date (Wise 1993). The higher and drier parts of this marsh are dominated by two plant species: *Salicornia pacifica* and *Baccharis Douglasii*. *Salicornia* is a low-growing woody perennial herb, and *Baccharis* a shrub (Cameron 1972). Spiller was motivated to study the potential for competition between these two species by both the high densities achieved by these spiders and the apparent absence of predators. Densities of these spiders are indeed high. In ten 1×1 m plots established to study the phenology of the focal species, *Metepeira* densities approximated 1 per m^2, and *Cyclosa* 10 per m^2 (Spiller 1984). *Metepeira* was the larger of the two, having approximately twice the body length of *Cyclosa* as an adult (Spiller 1984).

Spiller conducted his experimental studies in replicated 4 × 1 m plots, with three plots for each removal treatment and three controls. Across these plots the foliage height approximated 1.25 m. Spiller removed *Cyclosa* or *Metepeira* over a six month period and noted the response by the other species in numbers, web height, and fecundity. Spiller found evidence of both exploitative and interference competition in this pair of spiders. Removing the much more common *Cyclosa* resulted in an increase in the body size and fecundity of *Metepeira*. The mechanism to explain this result is the increased foraging success of *Metepeira* in plots free of *Cyclosa*. The much larger *Metepeira*, on the other hand, engaged in interference competition with *Cyclosa*. Both *Cyclosa* densities and web placement were affected by *Metepeira*. *Cyclosa* numbers were higher, and their webs were higher in the vegetation in the *Metepeira* removal plots.

Spiller's findings are significant because they represent clear evidence of how interspecific competition can influence both space use and fitness in spiders. However, it is also revealing that these results come out of a type of terrestrial ecosystem which is structurally simpler than most. The salt marsh ecosystem in which he worked was dominated by two plant species, and this vegetation had a low growth form. In addition, the densities of these two species were high enough that they were likely to have the opportunity to interact.

Wolf spider competition in a German salt marsh.—Schaefer (1972, 1974; summarized in English in Schaefer 1975 and Wise 1993) studied how competition might explain the patterns of space use exhibited by three lycosid species across a shoreline-salt marsh ecotone on a bay of the Baltic Sea near Kiel, Germany. These lycosids were: *Pirata piraticus* (Clerck)*, Pardosa purbeckensis* (F.O.P.-Cambridge), and *Pardosa pullata* (Clerck). The *Pirata* and *Pardosa purbeckensis* were more common in the salt marsh, and *Pardosa pullata* was more common on the dry ground fringing the salt marsh. However, all three overlapped in substratum use. *Pirata* was the largest of the three and would opportunistically prey upon the two *Pardosa* spp. Schaefer found that *Pardosa purbeckensis* comprised up to 8.2% of the diet of *Pirata*.

Schaefer conducted density manipulation experiments in the salt marsh as did Spiller

(1984). His treatment consisted of reducing *Pirata* densities by applying insecticide (a Parathion™ spray) to four 10 × 10 m plots. He had a fifth untreated control plot. The Parathion™ treatment initially eliminated all spiders, however, as *Pirata* was much slower to reinvade the plots than the *Pardosa* spp., its populations were never able to recover from the treatments (as he intended). Additionally, he sprayed the edges of the plots weekly to further limit recolonization by *Pirata* (Schaefer 1974, reported in Wise 1993). Schaefer (1975) reported a significant and impressive reduction in *Pirata* numbers as a result of his manipulations. Mean densities of *Pirata* in the Parathion plots was 2.2 per m^2, and in the control plot, 14 per m^2 (Schaefer 1975, table 1). On the other hand, both *Pardosa* spp. densities were higher in the Parathion plots than in the control plots (*P. purbeckensis*; Parathion, 9.6 per m^2, control 8.3 per m^2; *P. pullata*; Parathion 3.5 per m^2, control 2.8 per m^2). Schaefer found no statistically significant increase of *Pardosa* spp. numbers in the Parathion (i.e., *Pirata* removal) plots. As Wise (1993) notes, it is hard to interpret these results in light of the fact that Schaefer had only one control plot. However, it is nonetheless interesting to note that the two *Pardosa* spp. were in higher numbers in the Parathion plots despite the insecticidal application, when *Pirata* numbers were so low.

Schaefer conducted a second experiment in six 2 × 2 m enclosures in the salt marsh. He had six treatments, with one replicate each (Schaefer 1975). In each he added either each *Pardosa* spp. alone, each alone with *Pirata,* the two *Pardosa* spp. alone together, and all three together. All spiders where added in natural densities (*Pirata*: 2.5 per m^2, *P. purbeckensis*: 2.0 per m^2, *P. pullata*: 0.5 per m^2). He found that the mean densities of *P. purbeckensis* were higher in the enclosures where it was alone or with *P. pullata* (9.7 per m^2) than in the two enclosures with *Pirata* or the open control plots (6.5 per m^2. He also found that *P. pullata* was more common in the enclosures where it was alone, or with *P. purbeckensis* only (3.3 per m^2 than in the two enclosures with *Pirata* or in the single open control plot (2.5 per m^2). Based on his statistical analysis Schaefer concluded that he did not have any basis to invoke competition in the patterns he observed. However, in his reanalysis of the

data, Wise (1993) suggests that Schaefer was too conservative in drawing his conclusions and that in fact he had evidence for interspecific competition.

Schaefer found limited, but compelling evidence that the larger *Pirata piraticus* had an impact on numbers of the two *Pardosa* spp. where they co-occurred. This interaction was primarily mediated by predation by *Pirata* on the *Pardosa* spp., as well as presumably some interference interactions. Like the two araneids in Spiller's (1984) study, these combative lycosids lived at relatively high densities in a structurally two-dimensional ecosystem.

Space use by lycosids on the New Jersey shore.—Döbel et al. (1990) examined the relationship between vegetation structure and tidal flooding with spider community structure in a salt marsh near Tuckerton, New Jersey. This study was specifically designed to examine species diversity as a function of habitat structure and disturbance. However, they also uncovered indirect evidence of competition between two lycosid species, *Lycosa modesta* (Keyserling) and *Pardosa littoralis* Banks. This study was entirely correlative, and consisted of a series of D-VAC samples taken in two replicates of four categories of *Spartina* spp. vegetation. On the shore was *S. patens*, a low growth form type of grass with a thick thatch base. Below the mean high water mark were three growth forms of *S. alterniflora*: short, intermediate, and tall. Every two weeks between early May and October they D-VAC'd four sites within each of the eight plots. Each sample was four, 15 sec applications of the D-VAC head to the vegetation. They found that *L. modesta* and *P. littoralis* were the numerically dominant hunting spiders in this salt marsh ecosystem (Döbel et al. 1990). The authors concluded that the patterns they observed for most species were in fact correlated with the architecture of the *Spartina*, the depth of the thatch, and the cycle of tidal disturbance. One exception was for the habitat use patterns of *L. modesta* and *P. littoralis*. *Pardosa littoralis*, alone among the species graphed (Döbel et al. 1990), exhibits a dip in densities in the short form *Spartina*. This is the second of the four successive categories of *Spartina* habitat going from higher to lower elevations. This is noteworthy as all the other species graphed exhibit single peak in abundance across the inshore-outshore gra-

dient. This dip in densities exhibited by *P. littoralis* (to almost zero) corresponds to the single and very pronounced peak in *L. modesta* numbers. The authors note: "...it is likely that the larger (10–12 mm) and more aggressive *L. modesta* simply drives the smaller (6 mm) *P. littoralis* from short-form *S. alterniflora*." (Döbel et al. 1990). Unfortunately, the authors do not detail the basis for their assessment of the temperament of *L. modesta*. However, given the strength of the pattern they observed, it would be well worth an experimental study of the interactions of these two lycosids.

Lycosid competition in a hot springs ecosystem.—John Moeur studied the foraging consequences of competition between two lycosids (*Pirata maculatus* Emerton and *Pardosa altamontis* Chamberlin & Ivie) which live on bluegreen algal mats near hot springs in Serendipity Meadow at Yellowstone National Park (Moeur 1977). The ecosystem Moeur studied consists for the most part of the algal mats, a brine fly (Diptera: Ephydridae, *Paracoenia turbida*) which feeds on the algae, and the two lycosids which feed on the flies. Through direct observation, Moeur determined that the brine fly *P. turbida* comprised at least half the diet of both spider species (Moeur 1977). He also found that they overlapped broadly in activity periods, although the *Pirata* was more active early and late in the day, and the *Pardosa* was more active near midday (Moeur 1977). Moeur observed agonistic interactions between the two spiders, which led him to investigate the potential for competition between them: "When two meet, the larger spider invariably drives off the smaller, though it rarely kills it. Encounters between equal-sized individuals evoke much leg waving and feints by each animal before one routs the other. After a confrontation lasting a few seconds, *P. maculatus* usually drives away *P. altamontis*." (Moeur 1977, p. 30).

Moeur conducted enclosure experiments in which he tested for the impact of *Pirata* on *Pardosa* survival and fecundity. He constructed five artificial streams 1.22 × 2.44 m in area. He added vegetation (i.e., algae) from the surrounding hot springs habitats. He set up different ratios of 20 adult female *Pirata* and *Pardosa* in each. These ratios were: 20:0, 15:5, 10:10, 5:15, and 0:20 *Pardosa:Pirata*.

Moeur apparently added and removed the *Pardosa* from these systems on a weekly basis, although it is hard to tell from his description of the methods (Moeur 1977). Whatever the details of his methods, he found a clear pattern of reduced *Pardosa* survivorship in enclosures with more *Pirata* (Moeur 1977). He attributes this outcome to interference competition mediated by the agonistic interactions he observed.

Field and lab test for lycosid competition in soybean agroecosystems.—We have been studying the ecology and interactions of two lycosids, *Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz, in two soybean agroecosystems since 1994. These two spiders seemed to exhibit elements of some of the systems we have reviewed above: A larger, less vagile, and less common species (*Hogna*) which we predicted might engage in interference competition and intraguild predation with the smaller, more vagile, and more common species (*Pardosa*). In the first field season (1994) we recorded both species in high densities. Using a restricted-area search sampling method, we recorded a high of approximately 0.8 *Hogna* per m^2, and 2.0 *Pardosa* per m^2 (Marshall & Rypstra in press). We tested for competition in both the field and lab.

Our field studies of competition were conducted in replicated field plots (Marshall et al., unpubl. data). In six, 0.42 ha soybean plots we created eight 6 × 6 m islands of enhanced wolf spider microhabitat using wild bird seed (to increase vegetation) and wheat straw mulch. We enhanced prey availability by adding composted vegetable waste to selected subplots. We had three treatments and a control, repeated for each species (for a total of eight subplots): 1) spiders added, 2) prey attractants added, 3) spiders and prey attractants added, and 4) control. Each two weeks from June to September we added the compost and/or the spiders. We added *Pardosa* and *Hogna* in numbers similar to natural densities we observed in the field (Marshall & Rypstra in press); 25 *Hogna* and 36 *Pardosa* per 36 m^2 subplot. At the end of the season we censused a third of the area of each subplot using a restricted area search method. We found no significant decrease in *Pardosa* numbers in the *Hogna* addition plots, although these were the lowest *Pardosa* densities we recorded (Marshall et al. unpubl. data). Interestingly,

we collected more *Pardosa* than we added to most plots, but recovered far fewer *Hogna*. This indicates that something was limiting *Hogna* densities, perhaps intraspecific competition. The extremely low densities of *Hogna* when compared to *Pardosa* may also explain the limited evidence for interspecific competition we found.

We also conducted laboratory mesocosm tests for competitive interactions between the two species. We compared the weight gain of eight *Pardosa* held alone to the weight gain of six *Pardosa* in enclosures with a single *Hogna*. We applied a paraffin muzzle to the *Hogna* to prevent them from preying on the *Pardosa*. This was done using a protocol devised by Jerome Rovner (Rovner 1980). These mesocosms were 40 liter aquaria (25 cm × 50 cm × 32 cm). Each aquarium was filled with soil from the soybean fields to a depth of 3.5 cm. One half the soil surface in each aquarium was then covered in 3.5 cm of pine bark mulch. A house plant (*Syngonium podophyllum*), 17–25 cm, high was placed in the mulched half of the tank to offer vertical stratification. The tanks were lit on a 12:12 light: dark cycle by standard fluorescent lights suspended over the tops of the tanks. The *Hogna* were placed in randomly assigned tanks one day before the *Pardosa* were added. *Pardosa* were randomly assigned to treatments, and weighed and placed into their assigned tank. This was done in the early evening; data collection began the following morning and lasted one week. Vestigial-winged fruit flies (*Drosophila melanogaster*) were introduced into the tanks twice during the week as food for the *Pardosa*. The flies were added in sufficient numbers to assure a constant supply of prey. We misted the soil often enough to keep the soil moist. At the end of seven days the spiders were removed from the tanks and weighed.

We found a significant reduction in weight gain by *Pardosa* in the presence of *Hogna*. *Pardosa* alone gained 45.3 ± 10.6 ($\bar{x}$ ± 1 S.D.) percent of their body weight, compared to 24.3 ± 5.1% when housed with *Hogna* (one-tailed *t*-test on the residuals of a regression of ln transformed weight gain on ln transformed carapace width, $t = -1.784$, $df = 12$, $P < 0.05$). Despite the small sample size, the results are clear: *Pardosa* alone gained almost twice the weight of *Pardosa* in the presence

of *Hogna*. This was interesting, given that the *Hogna* were hidden in refuges during the 'daylight' hours when the *Pardosa* were most active.

We have good evidence that *Hogna* has a negative influence on a fitness associated behavior, foraging, in *Pardosa*. Our field test did not reveal a strong negative effect of *Hogna* on *Pardosa*; however, *Hogna* numbers remained low in spite of repeated *Hogna* additions. It may be that *Hogna* is more prone to engage in intraspecific interactions than *Pardosa*, and so be more self-limiting. Our finding of a negative effect in the small laboratory mesocosms but not in the field coupled with the low density of *Hogna* in the field may mean that there is only a local negative effect of *Hogna* on *Pardosa*.

CONCLUSIONS

Spiders are conspicuous components of agricultural ecosystems wherever found. However, most work to date on spiders in agroecosystems has focused on the ecology of their predation on arthropod pests rather than competitive interactions. In general, the most compelling evidence for interspecific competition in spiders comes from studies undertaken in structurally simple successional habitats such as salt marshes. Can we draw any general conclusions about the likelihood and consequences of interspecific competition among spiders in agroecosystems?

Agroecosystems and littoral ecosystems, like other early successional ecosystems, are structurally simple when compared to later seral stages. This is because both are subject to regular cycles of disturbance, be it plowing in agricultural fields, or tidal or seasonal flooding as in estuarine or littoral ecosystems. Disturbance will inevitably limit the species diversity, and select for colonists which are vagile, fecund, or in other words 'weedy' (Gibson et al. 1992; Wissinger 1997). Because of the nature of the community structure in these simple ecosystems, the commonest species found there tend to occur in high densities. This, coupled with the structural simplicity of the vegetation, also increases the opportunity for interactions. The consequence is the potential for competition. Because littoral zones are ecotones between highly disturbed and less disturbed microhabitats, spider species with divergent but overlapping micro-

habitat associations may come into contact. This kind of fine-scale microhabitat segregation has been documented in lycosids (den Hollander & Lof 1972; Greenstone 1980). The zone of overlap is where we would be most likely to see competition occur, based on the studies reviewed herein. The wetland-cropland analogy is more than functional, as Luczak (1979) reports that many of what she terms 'agrobiont' spiders in Poland are naturally found in littoral ecosystems. We have likewise found that *Pardosa milvina* and *Hogna helluo* co-occur in littoral and riparian habitats as well as in the soybean agroecosystems in southwest Ohio.

The studies we reviewed, as well as ours, indicate that both exploitation and interference competition can occur between spiders. Spiller (1984) found that his species pair engaged in both, with the larger and rarer *Metepeira* dominating the smaller and more common *Cyclosa* in behavioral interactions. However, because *Cyclosa* occurred in much higher densities, it did engage in exploitation competition with *Metepeira*. This makes it unclear just which species is the competitive dominant of the pair. If we conclude that it is *Cyclosa*, by virtue of its greater densities, then the mechanism of its success is its smaller body size and apparent greater toleration of conspecifics allowing it to attain greater densities and so deplete prey. The dominant of the trio of lycosids Schaefer studied (1975) exhibited the highest densities, and engaged in interference competition with the two inferior competitors. However, in this study, as in Döbel et al. (1990), there was separation by substratum type. Competition, if observed, occurred in areas where the preferred microhabitats overlapped. This pattern of a commoner competitive dominant was not seen for the lycosids studied by Döbel et al. (1990) or Moeur (1977). In these two studies, the more aggressive competitive dominant was no more common, or in fact rarer, than the less aggressive species. In our own studies with *Hogna* and *Pardosa* we found that while *Hogna* did have a local negative effect on *Pardosa* activity, it is the rarer species in the fields (Marshall & Rypstra in press). Which is the superior competitor? *Hogna* may engage in interference competition and intraguild predation with Pardosa; however, we have no evidence that *Par-*

dosa exploits the prey base to the detriment of *Hogna* populations.

What is the implication of interspecific competition for biological control of arthropod pests in agroecosystems? Because spiders are generally self-limiting via agonistic interactions and cannibalism, they may have limited utility as biocontrol agents (Riechert & Lockley 1984). Between species competitive interactions could likewise limit species diversity and abundance. However, as Breene et al. (1993) note, the ability to engage in cannibalism and intraguild predation during times of low pest abundances may help maintain spider populations at some minimum in the crop fields. Spiller (1986) found that competition limited the predatory efficiency of the two species salt marsh system he worked on. He proposed that *Cyclosa* alone would better limit herbivore numbers than a combination of *Metepeira* and *Cyclosa* because the interference interactions between the two would limit *Cyclosa* densities. Luczak (1979) also proposes that spider competition should reduce prey-limitation by spider populations. However, Luczak also suggests that spider competition should be lower in littoral and agroecosytems than in ecosystems with higher spider species diversity (1979). Riechert & Lawrence (1997) on the other hand, found evidence that a multispecies spider assemblage would better reduce pest insect abundances because a group of species would occupy a wider range of niches than any single species could. In our own studies we uncovered limited evidence that *Hogna* could affect both *Pardosa* densities as well as foraging efficiency. We would predict that *Pardosa* alone would achieve greater abundances and prey population control.

Spider competition potentially occurs in agroecosystems because the community structure and physical structure of these engineered ecosystems may promote high densities of a few spider species. How important competition is in moderating the impact of spider populations on pest insect populations will depend on the spider species present in the fields.

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