THE HOWS AND WHYS OF SUCCESSFUL PEST SUPPRESSION BY SPIDERS: INSIGHTS FROM CASE STUDIES

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ABSTRACT.   We can identify agricultural systems in which spiders might best be applied in pest suppression from study of the mechanisms by which spider populations influence prey in natural ecosystems. Theory predicts that prey control is achieved through the development of a stable interaction between predator and prey populations. Two models have been applied to predator control of prey, limit cycle and equilibrium point or focal control. Limit cycle control is exerted on a prey species population by a predator species that tracks the densities of its prey. Although the limit cycle approach is commonly applied to pest control situations, the long life cycles and generalist feeding habits of spiders limit their abilities to exhibit density-dependent tracking of their prey. Crops with short growing seasons and species-depauperate systems are the best candidates for limit cycle influences of spiders on prey. Spider populations that exhibit an uneven age-structure and have strong migratory/aggregational tendencies would offer the greatest pest suppression in these simple systems. Equilibrium point/focus control involves the limiting effects of an assemblage of polyphagous feeders on an assemblage of prey species. Spiders fit this model to a greater extent than they do a limit cycle model of prey control. Agricultural systems that conserve spider densities and species representation through minimal chemical application and the maintenance of ground cover are good candidates for equilibrium point control of prey by spiders. It is also important to recognize that many success stories in agroecosystems do not involve stable interactions between predator and prey populations. Indirect effects (e.g., the cessation of feeding in the presence of a predator) and superfluous killing of prey are two factors that augment the influence of spiders on targeted insect populations.

Field biologists search for patterns in natural ecosystems with the ultimate goal of applying the knowledge gained to human benefit. Of particular concern to the arachnologist is maximizing the potential of spiders to control insect pests in agroecosystems. Wang (1982) reports that as long as 2000 years ago, Chinese writing states that "If there is a large gathering of spiders, everything will be satisfactory." This contribution deals with how spider abundance and the mechanisms of prey control they exhibit affect their influence on prey populations in natural and agricultural systems.

SPIDER SIGNIFICANCE IN NATURAL ECOSYSTEMS

Energy and nutrient flow studies.—One problem inherent in assessing the predatory role of spiders is the logistical difficulty of determining not only what spiders eat, but in what quantities relative to other predators in a system. Our best estimates of spider significance in arthropod community dynamics actually are available from radioisotope tagging experiments completed on a reservation at the Oak Ridge National Laboratories in east Tennessee (van Hook 1971; Moulder & Reichle 1972). Van Hook (1971) identified wolf spiders of the genus *Lycosa,* (i.e., *Hogna* and *Rabidosa*) as the most important predators of herbivorous insects in the *Festuca-Andropogon* old field system he analyzed. These lycosids were prominent throughout the plant growing season, while other biomass prominent predators (i.e., other Araneae) were most important only in spring and early summer. Van Hook attributed 21.1% of the total mortality of herbivorous insects (i.e., orthopterans, hemipterans and homopterans) to predation by *Hogna* and *Rabidosa* wolf spiders. (Actually, the percentage of consumer biomass cycling through the two spider populations was underestimated in the study, because insect exuviae and egg clutches were included as part of the estimate of mortality attributed to non spider sources (van Hook 1971). Spiders in this grassland ecosystem exhibited a mean density of 56 individuals/m^2 and a mean biomass of 146 mg/m^2; other arthropod predators in the system "were not present in sufficient

biomass to warrant consideration'' in van Hook's (1971) analyses.

Moulder & Reichle (1972) followed the movement of the radionucleotide, cesium-137, through cryptozoan food chains on the laboratory's reservation. Forty spider species were represented in the samples collected from the litter community. They exhibited a mean density of 126 individuals/m^2 and a dry weight biomass of 43 mg/m^2. Thus the greater spider densities in this system compared to the grassland system van Hook (1971) investigated were offset by the smaller sizes of individual spiders. Centipedes (Chilopoda) and predaceous beetles (Coleoptera) were the other numerically and biomass prominent predatory groups in the forest floor community. Spiders, however, were both numerically more abundant (2.7 times that of either the centipedes or the predaceous beetles) and had a total biomass that was 1.4 times greater than the other classes of invertebrate predators. Moulder & Reichle (1972) attributed the numerical and biomass prominence of spiders in the forest floor system to their greater predatory effect on herbivorous insects: spiders consumed 77.8% of the herbivorous prey biomass lost to predation, while centipedes consumed 14.6% and coleopterans 7.7%, respectively.

Allochthonous food sources.—The two classic studies described above are representative of the field of ecology that deals with the cycling of energy and nutrients through the ecosystem, consisting of both biotic and abiotic components. Ecosystem ecology's interest in top-down effects and trophic cascades (e.g., Hairston, Smith & Slobodkin 1960; Cohen et al. 1990; Hunter & Price 1992) has led to another example of the relationship between spider abundances and their effects on prey populations in natural systems. There is no general agreement as to the relative importance of top-down versus bottom-up control of food-web structure. Rather, the type of control appears to be system dependent. Polis & Strong (1996) proposed that trophic cascading (top-down effects) is most pronounced where there is an allochthonous source of food to predators. They argue that external food inputs will augment predator numbers to the extent that they can impose control on the lesser abundant resident prey and thus have cascading effects on the plants that these primary consumers forage

on. In Polis & Hurd's (1995) island food-webs, beached marine algae and carrion supported extremely large populations of arthropod detritivores. The detritivores, in turn, provided more than 90% of the food to spider populations of sizes that were 1–2 orders of magnitude greater than those observed for similar areas not influenced by the detritus. These large populations of island spiders strongly limited terrestrial herbivorous insects and the plant damage they would ordinarily have imposed. Henschel et al. (1996) suggest that emergents from aquatic habitats can have a similar subsidizing influence on spider populations. They found that spider community richness and biomass are significantly higher in the vicinity of water bodies with emergent insects than in comparable habitats away from water bodies. The authors conclude that such subsidies might be used to augment the role of spiders in agroecosystems.

POTENTIAL MECHANISMS OF SPIDER PREY LIMITATION

Non-consumptive effects.—In managing populations of pest insects and the damage they impose on crops, practitioners are interested in predator control of prey. Modeling approaches indicate that prey control by predators is achieved when a stable equilibrium is established between predator and prey population numbers. In practice, successful control commonly violates the assumptions of a stable equilibrium (Murdoch et al. 1985). 'Predator-induced effects' and 'superfluous killing' are two effects that spiders may have on prey population dynamics that fall outside of stable population interactions as they are non-consumptive effects. Predator-induced effects occur as a consequence of the fact that predators and prey are in an escalating evolutionary race. Predators become increasingly more efficient at capturing prey, while prey have evolved responses to predatory cues that permit escape from predation. Predator presence thus causes pests to cease feeding, to forage at less favorable sites, and to drop off host plants altogether in an escape response. The resulting effect is usually a slowing of prey population growth, which delays the outbreak phase. However, dropping from a plant to the forest or field crop floor may result in mortality as well due to desiccation and predation by generalist predators (ants and spiders in the

case of the hemlock woolly adelgid (McClure (1995)). Nakasuji et al. (1973) document the significance of predator-induced effects by linyphiid spiders on tobacco cutworm larvae, *Spodoptera litura*, by comparing spider exclusion cages to open cages. Only 4% of the 60% mortality rate suffered by cutworm larvae was attributed to actual spider predation, another 18% was not related to spider causation, and 38% involved predator induced effects (i.e., larval dispersal/dislodgement from the foraging site caused by spider presence). Since there is no ground cover in tobacco, dislodged larvae suffered starvation (Nakasuji et al. 1973).

There is evidence that trophic cascades can also be elicited through indirect predator-induced effects in which herbivores shift their foraging behavior in response to perceived predation risk. Schmitz et. al. (1997) found that 'risk' spider treatments (glued chelicerae) elicited similar avoidance behavior by grasshoppers feeding on herbaceous plants and grasses in an old field as did 'predation' (intact predators) spider treatments. Both treatments decreased the impact grasshoppers had on grass biomass, evidence for the existence of a trophic cascade in each case.

Superfluous killing, also referred to as wasteful killing and overkill, entails capture rates that significantly exceed rates of consumption: it includes the partial consumption of multiple prey items and the killing of prey that are never consumed at all. Samu & Biro (1993) observed killing without feeding and partial consumption of prey in the lycosid, *Pardosa hortensis*, when they offered test subjects high prey densities. Riechert & Maupin (1998) also observed high levels of these two facets of superfluous killing in all of the web spider species they tested: the theridiid *Achaearanea tepidariorum* (61%), the araneid *Argiope trifasciata* (49%), the dictynid *Dictyna volucripes* (20%), the agelenid *Agelenopsis aperta* (44%), and the linyphiid *Florinda coccinea* (43%). The numbers in parentheses following the test species names refer to the proportion of prey captured that were not consumed. Thus spider killing of prey was between 1.2 and 2.6 times greater than that required for feeding.

Combined then, predator-induced effects and superfluous killing can account for in excess of 80% of spider limiting effects on prey populations. These kinds of non-consumption influences must be considered in assessing the impact of spiders on pests in agroecosystems.

Equilibrium models of predator-prey interactions.—In the reductionist approach commonly applied to agroecosystems, there is an interest in dealing with a single pest species problem. The addition of a single predator or parasitoid species to control a particular pest is an attempt to establish a stable limit cycle between predator and prey population numbers (Hassell 1978). This reductionist approach involves the tracking of the size of a prey population by the selected predator/parasitoid population. Density-dependent tracking requires that the predator/parasitoid: 1) have a life span of similar length to that of its prey, 2) is a prey specialist, and 3) exhibits a search behavior pattern that concentrates foraging in patches of high prey densities while allowing prey refuges to survive (Hassell 1978; Murdoch et al. 1985).

In the food-web literature, top-down control and trophic cascades are achieved through another model involving stable predator-prey population interactions, stable equilibrium point or focal control. In this mathematical model, population sizes of predators and prey equilibrate at some relative level rather than cycling out of phase of one another, which is characteristic of limit cycle control (DeAngelis et al.1975; Tanner 1975). To achieve a stable equilibrium, there must be one or more polyphagous predator populations and an assemblage of prey types. As predator encounter rates with prey change in space or time, individual predators will switch feeding concentration among these prey types (Murdoch & Oaten 1975; Beddington et al.1978). In addition, the predators must not be limited by local prey availabilities in the immediate sense. Rather, they are expected to have some mechanism of self-damping that keeps their population numbers below the limits of prey availability (e.g., energy-based territoriality, cannibalism or forced migration) (DeAngelis et al. 1975; Tanner 1975; Post & Travis 1979; Erlinge et al. 1984). These behaviors often are evolutionarily adjusted to averages or lows in prey availabilities for particular habitats (e.g., the funnel-web spider, *Agelenopsis aperta* (Riechert 1981)).

IMPLEMENTING SPIDER CONTROL IN AGRICULTURAL SYSTEMS: THE NEED FOR SYSTEM SPECIFIC PROTOCOLS

Single spider species on single pest species: limit cycle control.—Many pest insects are *r*-selected and thus have short generation times and high reproductive potentials. Because spiders have much longer generation times and comparatively low fecundities, they generally will not develop stable limit-cycles with their insect prey. It may be possible to achieve stable cycling between a spider species and a particular pest in a simple system with just a few herbivores and/or a crop with a very short life cycle. An uneven age distribution exhibited by a spider population (e.g., the multivoltine lycosids (e.g., *Pardosa lugubris* (Walckenaer): Edgar 1971) and linyphiids (e.g., *Erigone arctica* (White): van Wingerden & Vugts 1974)) and a strong aggregational numerical response to prey densities (e.g., aerial ballooning by linyphiids in response to localized weather conditions and densities; see review in Riechert & Gillespie (1986)) would also permit some density-dependent tracking of the prey population by a spider species population. There would be fewer generations of pest population build-up in the short-season crop, and the predators would be concentrating foraging on encounter with the numerically prominent prey, the pest.

Obviously, the best case scenario for successful control by limit cycle would involve spider species with the characteristics listed above feeding on a pest in a crop with a short life cycle. An example of a system that meets the short-crop season criterion is spring barley in Sweden. Chiverton (1986) found that linyphiids successfully control cereal aphids, *Rhopalosiphum padi*, in this northern region because *R. padi* overwinters here only in the egg stage. The growing season is simply too short to permit the sowing of a fall grass or cereal crop that would permit the build-up of large *R. padi* populations of viviparae before spider emigration in May and June. Aphid densities in barley field plots enclosed early enough to prevent spider emigration were six times higher than those observed in unenclosed plots in Chiverton's (1986) study.

Spider species assemblage control of pest species assemblages: stable equilibrium point or focal control.—There are objective reasons for implementing a holistic approach (stable equilibrium point or focus control) to pest suppression by spiders as opposed to the reductionist approach, a single predator species acting on a single pest species (limit cycle). Stable equilibrium point control or focus (Tanner 1975) is the predator-prey model that is associated with top-down and cascading effects in natural food webs (Post & Travis 1979) and spiders exhibit the traits requisite to stable equilibrium point control of prey by predators (Riechert et al. 1999). They are, in fact the prominent predators of insects in natural ecosystems and this occurs despite the fact that they are self-damped by territorial and cannibalistic behaviors (Edgar 1969; Riechert 1981; Wagner & Wise 1996). Self-damping behavior is actually a necessary condition of stable equilibrium-point control of prey by polyphagous predators. Thus spiders are well-suited to this community level approach to prey control. In addition, the fact that suppression of a prominent pest is often followed by new problems with secondary pests favors a community approach where an assemblage of predators influences the entire assemblage of pest species in a local system.

An example of a holistic approach to pest suppression by spiders is offered in Riechert & Bishop's (1990) study of spider assemblage effects on herbivorous insects in mixed vegetable garden systems. Riechert and Bishop observed a highly significant spider assemblage effect on pest insects (60–80% reduction in pest-induced plant damage) across a wide variety of vegetable types. The effect was achieved by grass-hay mulch applications, which augmented spider population densities thirty-fold over those observed in tilled control plots. Contrasts completed on spider predation effects in the mulched plots indicated that spiders significantly suppressed insects and thereby afforded less plant damage in mulched than in bare-ground control plots. On the other hand, pest numbers and plant damage were not significantly different between controls and mulched plots from which spiders were systematically removed.

Although the analysis of variance was completed on spider densities alone, Riechert & Bishop (1990) presented additional analyses of the quadrat sampling of spiders as well as the results of timed watches of foraging activity within the same system. Calculations made

on the data set from the quadrat sampling produced an average spider diversity (Shannon-Wiener H') in the tilled control plots of 0.94 compared to an average of 2.48 in the mulch and mulch + flowers plots (Pielou 1974). In a five guild system, the nocturnal running spider guild was totally absent from the tilled control plots, while all guilds were well represented in the mulch and mulch + flowers plots. Fifteen families of spiders were observed during the course of the foraging observations, six of which were web-building families. Most of the spider families were observed feeding on more than one pest species with six families feeding on almost the entire range of 13 insect pests observed during the course of the watches. Riechert & Bishop (1990) conclude from these results that the significant effect of spiders on pest insects in the mixed vegetable system was an assemblage effect, rather than the effect of just a few prominent spider species.

Augmentation: sheer numbers versus species richness.—Regardless of the mechanisms by which control is achieved, all evidence indicates that successful pest suppression by spiders will best be achieved through the maintenance of high spider densities and in many cases also high species diversities. Maximization of spider densities and species richness are steps that logically must be taken in agricultural systems to increase the beneficial functioning of spiders in them.

Numerous studies support the idea that spider effects on prey are approximately a function of spider versus prey densities/biomasses in a system (e.g., natural communities: Moulder & Reichle 1972; Polis & Hurd 1995; Henschel et al. 1996; Kajak 1997; coconut: Sathiamma 1995; corn: Laub & Luna 1991; Clark et al. 1994; Coll & Bottrell 1995; cotton: Sterling et al. 1989; mixed vegetables: Riechert & Bishop 1990; old fields: Riechert & Lawrence 1997; pastures: DeBarro 1992; rice: Sasaba et al. 1973; Wang 1982; Oraze & Grigarick 1989; Litsinger et al. 1994; soybeans: Carter & Rypstra 1995; wheat: Hausamman 1996). The significance of increasing species diversity is less clear. From summary analyses of the performance of prominent single spider species versus spider species assemblages, Provencher & Riechert (1994) and Riechert & Lawrence (1997) in different experiments found that more than 70% of total reduction

in prey biomass and numbers (over that exhibited in spider removal controls) is contributed by single spider species. This would seem to indicate that having different foraging strategies represented is less important than mere numbers or biomass. However, Riechert et al. (1999) encountered very different results when they considered the predatory performance of spider species assemblages versus those of single prominent spider species over time (i.e., a four month period). The spider species assemblage was far more temporally consistent in its predation effects on the broad spectrum of prey types encountered in the old field system than was any single spider species (four numerically/biomass prominent species tested). Further, no single spider species performed as well over time towards a particular prey category as did the spider species assemblage, despite the fact that all of the predators used in the single species treatments were maintained at high densities throughout the four months of the study. Each spider species did show changes in linear dimensions, mass, and reproductive status that corresponded to its own unique life cycle at various times during the period of the study. Therefore, spiders show changes in their diets over time, a factor that makes it important to have a diversity of spider species in longer-lived crop systems.

Sathiamma (1995) reached a similar conclusion in a study of natural enemy suppression of the white spider mite, *Oligonychus iseilemae* on coconut foliage (See also Agnew & Smith 1989 for spider suppression of pests in peanuts). The total predator density (seven prominent species) corresponded closely over time to the density of the mite and control was adequate to eliminate the need for chemical applications. No single predator, however, was abundant at all potential peak periods of mite density and Sathiamma concluded that the suppression effect of any single predator species by itself on the pest would be insignificant.

This is not to say that single spider species might not be able to exert sufficient control to eliminate the need for chemical intervention in some systems (see also section on limit cycle control). It may be that in exhibiting high population densities at critical times in the life cycle of a pest, a single spider population may suppress that pest sufficiently to require only

minimal chemical intervention during periods when the predator's life cycle is out of phase with the pest. Such a special case may account for the successful use of *Lycosa pseudoannulata* in controlling green rice leafhopper in Japan (Kiritani & Kakiya 1975). This predator imposes highly significant reductions of overwintering leafhoppers that prevent the early season transmission of rice diseases. A systems model has been developed that incorporates the densities of this predator and those of the pest in determining when particular paddies need to be treated with insecticides (Kiritani & Sasaba 1978).

It is important to note that while simulation models may key on the densities of prominent spider species in the management of a particular pest, it is probable that any conservation scheme designed for a prominent spider will also foster other spider species populations as well. While these other species might have lesser individual roles, their cumulative effect on pests and crop damage can be significant.

Spiders and agroecosystem practices.—Successes with spider suppression of pests in agroecosystems are correlated most frequently with increased predator densities, though recent studies indicate that species richness may be an important component as well. Augmentation of spider densities and accompanying species richness in agroecosystems could include the following three practices: 1) restriction of chemical pesticide applications to an as needed basis, 2) habitat diversification, and 3) maximization of allochthonous inputs.

1). Restriction of chemical pesticide use.—The literature on the deleterious effects of chemical insecticides on spider communities is too substantial to attempt to cover here. I include only two systems (rice and cotton) for which simulation models have been developed that favor the conservation of spiders through the monitoring of pest and predator ratios and selective use of pesticides where warranted. Spiders are used effectively in the control of rice pests in southeast Asia. Kiritani (1977) reported that the regular application of a broad spectrum insecticide to control a rice stem borer in Japan decimated spider populations but had little effect on the leaf- and planthoppers that transmit viral diseases in rice. It took ten years for the spider populations to sufficiently recover from exposure to the insecticide to be useful in suppressing the

major new problem of insect transmitted viral diseases. In China, Wang (1982) found that when spiders moved into an area of planthopper infestation, they reduced the pest: predator ratio from 9 to 1.5:1 within 10 days in one study area and from 5:1 to 0.03:1 within 5 days in another. After implementing conservation practices that fostered spider density increases (e.g., encouraging the movement of predators from early rice plantings to 2nd plantings and using cultural practices that limited the frequency of pesticide application and quantities of chemicals used), the need for chemical pesticides decreased as much as 80% with no measurable loss in rice yields. Monitoring programs of predator density/pest density ratios and weather are used in rice in Japan to determine when pesticide applications are required (Sasaba et al., 1973). A similar systems model has been developed for cotton by researchers at Texas A&M University (e.g., Hartstack & Sterling 1989; Sterling et al. 1992). The TEXCIM model is widely used in Texas cotton to predict when it is economically beneficial to apply chemical insecticides rather than to rely on natural enemy (primarily spider) suppression of pests. Breene et al. (1990) tested the predation component of the TEXCIM model for cotton, obtaining evidence that natural enemies protect the Texas cotton crop for 95% of the crop days, whereas chemical pesticides provide control for only 5% of the season (See also Mansour (1987) on spider control of cotton pests in Israel).

2). Habitat diversification.—This problem has been addressed in a number of ways, including the addition of weed strips, the maintenance of uncultivated borders, intercropping, and the application of mulch and other ground covers. The first three approaches have produced mixed results. Jmhasly & Nentwig (1996) report that the addition of weed strips to winter wheat did lead to higher web-spider densities in the vicinity of the strips, but that this increase did not lead to protection of the wheat crop from pest damage. Riechert & Bishop (1990) did not find that alternation of rows of vegetables with flowering buckwheat augmented spider numbers compared to bareground controls, nor was plant damage less in the plots containing the flowering buckwheat.

A potential increase in spider diversity is one pest suppression benefit of intercropping,

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but this suppression effect may be confounded by the fact that intercropping also reduces oviposition sites for the pests. Roltsch & Gage (1990) report that tomatoes intercropped with beans in the control of the potato leafhopper, *Empoasca fabae*, did not increase natural enemy densities nor species richness, but nevertheless suppressed pest densities. The availability of oviposition sites was the important factor in this study. On the other hand, Coll & Bottrell (1995) found that spiders and nabid hemipterans had a greater effect on Mexican bean beetle (*Epilachna varivestis*) populations in dicultures of maize and bean vegetation than in bean monocultures. The lower bean beetle numbers were correlated with the higher abundances of the predators in the diculture.

The problem I have with all three of the above habitat management techniques concerns the question of whether the augmented spiders will move into the crop where the pest problem exists versus stay in more structurally complex natural habitats. Bishop & Riechert (1990) did not find that spiders from surrounding natural communities (i.e., old field, oak-hickory woods, and briar) colonized a mixed vegetable garden system. Over 60% of the species present in the garden system were not even collected in neighboring habitats and experimental limitation of ground dispersal indicated that most of the colonization occurred through ballooning.

Greater success has been achieved with the addition of ground cover and structure in annual crop systems (e.g., mulch in vegetables (Riechert & Bishop 1990), artificial habitat structure in soybeans (Carter & Rypstra 1995), and in no-till corn through the mowing of the winter cover crop (Laub & Luna 1991)). In the first two studies, experimental increases in spider densities and suppression of pest numbers and crop damage were noted. Laub & Luna (1991) found that by mowing a winter rye cover crop rather than spraying it at corn planting time, they achieved a significant net economic benefit (US $91–$113/ hectare). They attribute the benefit of the mulch produced by mowing rye to suppression of army worm populations through the conservation of natural enemies in the mowed treatment. (Other work by this lab (Clark et al. 1994) used predator exclusion arenas in corn to demonstrate significant carabid and

staphylinid beetle, ant, and spider predation effects on armyworm damage.) The application of mulch to an agroecosystem early in the season may provide more favorable thermal environments to the spider populations before crop growth is sufficient to provide cover. It also may provide an abundance of early food in the form of subsidies from the detritivore food chain (e.g., collembola).

3). Maximization of allochthonous inputs.—It is clear from Polis & Hurd's (1995) study that allochthonous inputs from detritivore food chains may also subsidize spider population densities, permitting them to have greater cascading effects on crop production. Little is known about the detritivore community in temporary systems. Turnbull (1966) reported that 38% of the food of spider communities in overgrazed pastures was contributed by the detritivore food chain; and Kajak (1995) reports that linyphiid, araneid and lycosid spiders generally feed to a large extent on detritivorous dipterans. Sunderland (1975) and Sunderland et al. (1986) demonstrate the significance of the contribution of collembola from the detritivore food chain to linyphiid spiders in cereals. These serve as alternative food to polyphagous predators early in the growing season of the crop when pest numbers are low. The build up of the linyphiid populations supported by the collembola permits effective suppression of pest numbers later in the season when warm temperatures caused the collapse of the collembola populations and the predators switched to feeding on aphids.

Although De Barro (1992) does not directly address the role of detritivores in supporting spider populations in irrigated perennial pastures in Australia, this system too is likely subsidized by input from decomposer food chains. De Barro (1992) experimentally demonstrated that lycosids and linyphiids significantly limit the population growth of a prominent pest, the cereal aphid *Rhopalosiphum padi,* in its summer pasture refuges. The removal of spiders led to a 15–16 fold increase in *R. padi* numbers in experimental plots. The limiting effect spiders imposed on the aphids reduced the number of alates produced in the fall that could colonize and transmit diseases to cereal crops. *Rhopalosiphum* populations fluctuate greatly with local weather conditions in the pastures, as this aphid suffers 90% mor-

tality when exposed to temperatures in excess of 39 °C, whereas the spider populations are not affected by summer temperature extremes. The system has no specialist predators or parasitoids, probably because of the degree to which population numbers of *R. padi* fluctuate during the summer months. During periods of low cereal aphid densities, the spider community, which consists of approximately 11 species, is supported by alternative prey which I suggest comes from detritivores in the soil and litter. The reader should consult Wise et al. (this volume) for further discussion of the topic of external subsidies.

Whatever the mechanism, spiders as agents of biological control can be used in combination with no-till agriculture for the kind of whole ecosystem approach to habitat management that should be encouraged in modern agriculture. While it may be difficult to suggest that a grower decrease pesticide use and apply mulch for its benefits to natural enemies alone, a favorable cost/benefit ratio that might result from these practices in terms of reduced chemical costs; and greater water retention and organic matter accumulation may make the whole ecosystem approach both attractive and practical.

LITERATURE CITED

Agnew, C.W. & J.W. Smith, Jr. 1989. Ecology of spiders (Araneae) in a peanut agroecosystem. Environ. Entomol., 18:30–42.

Beddington, J.R., C.A. Free & J.H. Lawton. 1978. Characteristics of successful enemies in models of biological control of insect pests. Nature, 273:513–519.

Bishop, L. & S.E. Riechert. 1990. Spider colonization of agroecosystems: source and mode. Environ. Entomol., 19:1738–1745.

Breene, R.G., W.L. Sterling & M. Nyffeler. 1990. Efficacy of spider and ant predators on the cotton fleahopper (Hemiptera: Miridae). Entomophaga, 35:393–401.

Carter, P.E. & A.L. Rypstra. 1995. Top–down effects in soybean agroecosystems: spider density affects herbivore damage. Oikos, 72:433–439.

Chiverton, P.A. 1986. Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Hom.: Aphididae) in spring barley. Ann. Appl. Biol., 109:49–60.

Clark, M.S., J.M. Luna, N.D. Stone & R.R. Youngman. 1994. Generalist predator consumption of armyworm (Lepidoptera: Noctuidae) and effect of predator removal on damage in no–till corn. Environ. Entomol., 23:617–622.

Cohen, J.E., F. Briand & C.M. Newman. 1990. Community food webs: data and theory. Biomathematics. Vol. 20. Springer Verlag, New York.

Coll, M. & D.G. Bottrell. 1995. Predator-prey association in mono- and dicultures: effect of maize and bean vegetation. Agric. Ecosyst. & Environ., 54:115–125.

DeAngelis, D.L., R.A. Goldstein & R.V. O'Neill. 1975. Stability and connectance in food web models. Ecology, 56:238–245.

DeBarro, P.J. 1992. The impact of spiders and high temperatures on cereal aphid (*Rhopalosiphum padi*) numbers in an irrigated perennial grass pasture in south Australia. Entomologist, 122:19–26.

Edgar, W.D. 1969. Prey and predators of the wolf spider *Lycosa lugubris*. J. Zool., London, 159:405–411.

Edgar, W.D. 1971. The life cycle, abundance, and seasonal movement of the wolf spider *Lycosa (Pardosa) lugubris* in central Scotland. J. Anim. Ecol., 40:303–322.

Erlinge, S., G. Goransson, G. Hogstedt, G. Jansson, O. Liberg, J. Loman, I.N. Nilson, T. von Shantz & M. Sylven. 1984. Can vertebrate predators regulate their prey? American Nat., 123:125–133.

Hairston, N.G., F.E. Smith & L.B. Slobodkin. 1960. Community structure, population control, and competition. American Nat., 94:421–425.

Hassell, M.P. 1978. The Dynamics of Arthropod Predator-Prey Ssystems. Princeton Univ. Press, Princeton, New Jersey.

Hartstack, A.W. & W.L. Sterling. 1989. TEX-CIM30: The Texas cotton insect model. Texas Agric. Exp. Stn. Publ. MP 1646.

Hausammann, A. 1996. The effects of weed strip-management on pests and beneficial arthropods in winter wheat. J. Plant Dis. Prot., 103:70–81.

Henschel, J., H. Stumpf, & D. Mahsberg. 1996. Increase of arachnid abundance and biomass at water shores. Proc. XIII Intern. Congr. Arachnol., Geneva, Rev. Suisse Zool., vol. hors serie. Pp. 269–278.

Hunter, M.D. & P.W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology, 73:724–732.

Jmhasly, P. & W. Nentwig. 1995. Habitat management in winter wheat and evaluation of subsequent spider predation on insect pests. Acta Oecol., 16(3):389–403.

Kajak, A. 1997. Effects of epigeic macroarthropods on grass litter decomposition in mown meadow. Agric. Ecosyst. & Environ., 64:53–63.

Kajak, A. 1995. The role of soil predators in decomposition processes. European J. Entomol., 92:573–580.

Kiritani, K. 1977. Recent progress in pest management for rice in Japan. Japanese Agric. Res. Quart., 11:40–49.

Kiritani, K. & N. Kakiya. 1975. An analysis of the predator-prey system in the paddy field. Res. Popul. Ecol., 17:29–38.

Kiritani, K. & T. Sasaba. 1978. An experimental validation of the systems model for predation of rice dwarf virus infection. Appl. Entomol. Zool., 13(3):209–214.

Laub, C.A. & J.M. Luna. 1991. Influence of winter cover crop suppression practices on seasonal abundance of army worm (Lepidoptera: Noctuidae), cover crop regrowth, and yield in no-till corn. Environ. Entomol., 20:749–754.

Litsinger, J.A., N. Chantaraprapha, A.T. Barrion & J.P. Bandong. 1994. Natural enemies of the rice caseworm *Nymphula depunctalis* (Guenee) (Lepidoptera: Pyralidae). Insect Sci. Applic., 15(3): 261–268.

Mansour, F. 1987.Spiders in sprayed and unsprayed cotton fields in Israel, their interactions with cotton pests and their importance as predators of the Egyptian cotton leaf worm, *Spodoptera littoralis*. Phytoparasitica, 15(1):31–41.

McClure, M.S. 1995. *Diaterobates humeralis* (Orbatida: Ceratozetidae): An effective control agent of the woolly adelgid (Homoptera: Adelgidae) in Japan. Environ. Entomol., 24(5):1207–1215.

Moulder, B.C. & D.E. Reichle. 1972. Significance of spider predation in the energy dynamics of forest-floor arthropod communities. Ecol. Monogr., 42:473–498.

Murdoch, W.W. & A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res., 9:1–131.

Murdoch, W.W., J. Chesson & P.L. Chesson. 1985. Biological control in theory and practice. American Nat., 125:344–366.

Nakasuji, F., H. Yamanaka & K. Kiritani. 1973. The disturbing effect of micryphantid spiders on the larval aggregation of the tobacco cutworm *Spodoptera litura* (Lepidotera: Noctuidae). Kontyu, 41:220–227.

Oraze, M.J. & A.A. Grigarick. 1989. Biological control of aster leafhopper (Homoptera: Cicadellidae) and midges (Diptera: Chironomidae) by *Pardosa ramulosa* (Araneae: Lycosidae) in California rice fields. J. Econ. Entomol., 82:745–749.

Polis, G.A. & S.Hurd. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proc. Natl. Acad. Sci. USA, 92:4382–4386.

Polis, G.A. & D. Strong. 1996. Food web complexity and community dynamics. American Nat., 147:813–846.

Post, W.M. & C.C. Travis. 1979. Quantitative stability in models of ecological communities. J. Theoret. Biol., 79:547–553.

Provencher, L. & S.E. Riechert. 1994. Model and field tests of prey control effects by spider assemblages. Environ. Entomol., 23:1–17.

Riechert, S.E. 1981. The consequences of being territorial: spiders, a case study. American Nat., 117:871–892.

Riechert, S.E. & R.G. Gillespie. 1986. Habitat choice and utilization in web-building spiders. Pp. 23–48. *In* Spiders: Webs, Behavior and Evolution. (W.B. Shear, ed.). Stanford Univ. Press, Stanford.

Riechert, S.E. & L. Bishop. 1990. Prey control by an assemblage of generalist predators in a garden test system. Ecology, 71:1441–1450.

Riechert, S.E. & K. Lawrence. 1997. Test for predation effects of single versus multiple species of generalist predators: spiders and their insect prey. Entomol. Exp. Appl., 84:147–155.

Riechert, S.E. & J. Maupin. 1998. Spider effects on prey: Tests for superfluous killing in five web builders. Pp. 203–210 *In* Proc. 17th European Colloquium Arachnol. (P.A. Selden, ed.). Bull. British Arachnol. Soc.

Riechert, S.E., L. Provencher, & K. Lawrence. 1999. The potential of spiders to exhibit stable equilibrium point control of prey: Tests of two criteria. Ecol. Appl., 9:365–377.

Roltsch, W.J. & S.H. Gage. 1990. Influence of bean-tomato intercropping on population dynamics of the potato leafhopper (Homoptera: Cicadellidae). Environ. Entomol., 19:534–543.

Samu, F. & Z. Biro. 1993. Functional response, multiple feeding and wasteful killing in a wolf spider (Araneae: Lycosidae). European J. Entomol., 90:471–476.

Sasaba, T., K. Kiritani & T. Urabe. 1973. A preliminary model to simulate the effect of insecticides on a spider-leafhopper system in a paddy field. Res. Popul. Ecol., 15:9–22.

Sathiamma, B. 1995. Biological suppression of the white spider mite *Oligonychus iseilemae* (Hirst) on coconut foliage. Entomon, 20:237–243.

Schmitz, O.J., A.P. Beckerman & K.M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology, 78:1388–99.

Sterling, W.L., K.M. El–Zik & L.T. Wilson. 1989. Biological control of pest poulations. Pp. 155–189. *In* Integrated Pest Management Systems and Cotton Production. (R. Frisbie, K. El-Zik & T. Wison, eds.). Wiley, New York.

Sterling, W.L., A. Dean & N.M. ABD El-Salam. 1992. Economic benefits of spider (Araneae) and insect (Hemiptera: Miridae) predators of cotton leafhoppers. J. Econ. Entomol., 85:52–57.

Sunderland, K.D. 1975. The diet of some preda-

tory arthropods in cereal crops. J. Appl. Ecol., 12:507–515.

Sunderland, K.D., A.M. Fraser & A.F.G. Dixon. 1986. Distribution of linyphiid spiders in relation to capture of prey in cereal fields. Pedobiologia, 29:367–375.

Tanner, J.T. 1975. The stability and the intrinsic growth rates of prey and predator populations. Ecology, 56:855–867.

Turnbull, A.L. 1966. A population of spiders and their potential prey in an overgrazed pasture in eastern Ontario. Canadian J. Zool., 44:557–583.

van Hook, R.I. Jr. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecol. Monogr., 41(1):1–26.

van Wingerden, K.R.E. & H.F. Vugts. 1974. Factors influencing aeronautic behaviour of spiders. Bull. British Arachnol. Soc., 3:6–10.

Wagner, J.D. & D.H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. Ecology, 77:629–652.

Wang, H. 1982. Conservation and utility of paddy field spiders to control pests. Pp. 274–281. *In* Proc. Chinese Acad. Sci.–US Natl. Acad. Sci. Symposium on Biological Control of Insects. (P.L. Ackleson, ed.).