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SPIDER PREDATION: HOW AND WHY WE STUDY IT

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ABSTRACT. Predation is of great ecological, evolutionary and behavioral interest. For our present purposes the primary reason for studying it is to determine the role of spiders in suppressing pest populations. Research approaches have included laboratory studies of preference, feeding rate, and fitness; direct observation of predation events or accumulations of prey carcasses; gut analysis; and field experiments. Laboratory studies provide some uniquely useful kinds of information but cannot give reliable indications of the ''biological control potential'' of spiders against a given pest. Direct observation can be powerful; it has provided the best data on dietary range and predation rates in the field. Gut analytical methods include the use of radionuclides, electrophoresis, chromatography and serology. Serological techniques are preferred: antibodies can be made specific down to the level of prey stage or instar, and assays are simple, sensitive, and reliable. They can determine the relative importance of different predator species, and may be the most efficient methods to document predation on eggs. Problems in quantitation remain. Field experiments have demonstrated unequivocally that spiders can effectively reduce pest populations and the crop damage they cause.

Spiders are ubiquitous in terrestrial ecosystems and abundant in both natural and agricultural habitats (Dondale 1970; Turnbull 1973; Nyffeler & Benz 1987). They also have a suite of adaptations that enable them to wait out periods of low prey abundance rather than dispersing like some other groups of arthropod predators (Ford 1977; Greenstone & Bennett 1980). It has therefore been assumed that spiders play a major role in suppressing insect pest populations (Riechert & Lockley 1984; Young & Edwards 1990). However their small size, cryptic habit, and mode of feeding have made it difficult to determine whether this is so (Kiritani & Dempster 1973; Stuart & Greenstone 1990).

HOW PREDATION IS STUDIED

Predation data can be obtained by four means: laboratory feeding studies, direct observation in the field, gut analysis, and experimental field manipulations.

Laboratory studies.—There is a large literature in agroecosystem entomology and arachnology describing feeding trials of individual predators confined with prey in small containers in order to determine their ''predatory potential.'' For spiders this approach is problematic since most are oligophagous or polyphagous (Nentwig 1986), and neither choose nor survive and reproduce well on single-species diets (Miyashita 1968; Van Dyke & Lowrie 1975; Hydhorn 1976; Greenstone 1979; Lowrie 1987; Uetz et al. 1992; Toft 1996). Another difficulty is our lack of knowledge of the role of environmental variables in predator-prey behavioral interactions.

Web spider feeding trials are least apt to be compromised, because many of the critical environmental and behavioral elements are embodied in the web itself. But hunting spider feeding trials are generally performed in simple open arenas—rarely made more realistic by provisioning plant bouquets (Lingren et al. 1968)—and the spiders are usually starved for a day or even a week (Young 1989a; Punzo 1991; Sadana & Kumari 1991) to increase the likelihood of a result. Since a starved spider in a small, featureless arena is apt to attack any but the most unsuitable (noxious, venomous, too large or too well armored) arthropod placed before it, it is hardly surprising that such spiders usually feed, and sometimes consume large numbers of prey. However, lengthy starvation inflates feeding rates (Toft 1996); furthermore, starvation causes reductions in basal metabolic rate (Anderson 1974), which could change feeding latency or otherwise distort predatory behavior. Since spiders in the field usually consume about one appropriate-sized insect per day (Edgar 1969, 1970; Schaefer 1974; Morse 1979; Nyffeler 1982; Nyffeler & Benz 1988a, b; Nyffeler et

Table 1.—Studies in which direct observation was used to determine the spectrum of spider species attacking a pest, pest complex or biological control agent.

Prey	Reference
Acari	
Metatetranychus ulmi (Koch) & *Bryobia praetiosa* Koch	Chant 1956
Lepidoptera	
Helicoverpa zea (Boddie) & *Heliothis virescens* (Fabricius)	Quaintance & Brues 1905 Fletcher & Thomas 1943 Whitcomb & Bell 1964 Whitcomb et al. 1963 Whitcomb 1967
Anticarsia gemmatalis Hübner	Elvin et al. 1983 Godfrey et al. 1989 Gregory et al. 1989
Hyphantria cunea (Drury)	Whitcomb & Tadic 1963
Coleophora parthenica Meyrick	Nuessly & Goeden 1983
Coleoptera	
Diaprepes abbreviatus (L.)	Richman et al. 1983a,b
Ips and *Dendroctonus* spp.	Jennings & Pase 1975, 1986
Heteroptera	
Pseudatomoscelis seriatus (Reuter)	Dean et al. 1987

al. 1987a, 1992a), starved spiders may not behave normally (but see Bilde & Toft 1998). These same objections apply when more than one prey type is offered simultaneously to determine preferences (e.g., Provencher & Coderre 1987; Gillebeau & All 1989). Also, apparent preferences may be perversely misleading because a less preferred, even patently unpalatable prey species may, in combination with others, provide greater fitness than a pure diet of a preferred species (Toft 1995, 1996).

Space does not permit a discussion of the numerous laboratory studies to generate spider functional response curves, but the same objections apply. The non-congruence of field and laboratory functional response data for one intensively studied insect predator (O'Neill 1997) should give us pause in contemplating the initiation of such lab studies.

Other feeding questions are well suited to laboratory study. Sunderland et al. (1986) determined escape rates of aphids from occupied linyphiid webs under varying conditions of falling frequency, aphid stage and spider satiation, necessary for converting field web density estimates into predation potential. Edgar (1969, 1970), Kiritani et al. (1972), Nyffeler & Benz (1988b) and Nyffeler et al. (1987a, b) determined the time during which prey items were carried and fed upon by spiders, a parameter needed to convert field observations on feeding to predation rates (see also below). A general case for which laboratory studies are defensible is where one needs to know about preferences of highly stenophagous predators (e.g., Morse 1984; Li & Jackson 1996).

Direct observation.—Our most extensive data on spider prey spectra, prey preferences and predation rates are derived from extensive field observations of spiders feeding and from the identification of prey carcasses taken from spiders' webs.

Prey spectrum: These studies focus on either the spiders attacking a particular pest or pest complex, or the prey spectrum of particular guilds of spiders. Table 1 lists studies of the first kind. In a paper on bollworm predation, Whitcomb (1967) pioneered the placement of eggs or larvae at regularly spaced stations to facilitate data collection, a method later used for studies of the velvetbean caterpillar (Elvin et al. 1983; Godfrey et al. 1989) and sugarcane rootstalk borer (Richman et al. 1983a,b). Whitcomb & Tadic (1963) surveyed spider predators of the fall webworm, a task facilitated by the arresting power of the webs

Table 2.—Rates at which field observations of feeding rate by hunting spiders have been collected by human observers. *Best estimate if investigators did not record exact number of hours. **Events/person-hour; in all cases only one author made observations (see Acknowledgments).

Spider species	Habitat	Events	Hours*	Rate**	Reference
Phidippus audax	cotton	58	10	5.80	Young 1989c
Oxyopes salticus	cotton	48	11.25	4.27	Lockley & Young 1987
Peucetia viridans	woolly croton	68	25.5	2.67	Nyffeler et al. 1987b
Lycosa anteleucana	cotton	147	91.4	1.61	Hayes & Lockley 1990
Dolomedes triton	ponds	625	~400	1.56	Zimmermann & Spence 1989
Pardosa spp.	wheat	106	104.5	1.01	Nyffeler & Benz 1988b
Oxyopes salticus	cotton	64	85	0.75	Nyffeler et al. 1987a
Phidippus audax	woolly croton	19	25.5	0.75	Dean et al. 1987
Pardosa ramulosa	salt marsh	32	~50	0.64	Greenstone 1976
Oxyopes salticus	cotton	63	108	0.58	Nyffeler et al. 1992b
Misumenops celer	woolly croton	11	25.5	0.43	Dean et al. 1987
Metaphiddipus galathea	woolly croton	9	25.5	0.35	Dean et al. 1987
Peucetia viridans	cotton	31	108	0.29	Nyffeler et al. 1992b
Peucetia viridans	cotton	25	85	0.29	Nyffeler et al. 1987b
Misumena calycina	old field	16	79.3	0.20	Morse 1979
Pardosa milvina	cotton	14	91.4	0.15	Hayes & Lockley 1990
Pisaurina mira	cotton	12	~300	0.04	Young 1989b
Phidippus johnsoni	various	33	~3,000	0.01	Jackson 1977

of the prey, which collected the spiders for the investigators' perusal.

The guild-centered prey spectrum literature comprises thousands of person-hours of direct observation (see Nyffeler 1999, this volume, for a thorough review and analysis). Hunting spiders pose the biggest challenge because they are less easily found and do not leave the carcasses of their prey where they can be identified and counted. Thirteen studies for which one can estimate the rate of discovery of hunting spider predation events by a human observer are summarized in Table 2. They reveal a surprising range, from about 0.01 to almost 6 events/person-hour of observation; rates for one species in cotton (*Oxyopes salticus*) varied seven-fold. These data demonstrate that direct observation can sometimes be an efficient way to learn about the prey spectrum of hunting spiders, and may enable the investigator to assess the effort likely to be involved in such an undertaking.

Predation rates: Predation rates for web spiders can be obtained directly from web densities and counts of prey carcasses in webs or in sticky traps, provided prey escape probabilities are determined; and an advantage of using traps is that they can obviate the need to work at night (Sunderland et al. 1986). Determining predation rates of hunting spiders by direct observation requires ingenuity; an approach was outlined by Edgar (1969, 1970) and formalized by Nyffeler & Benz (1988b). Their formula contains an estimate of the hours per day spent hunting. Such an estimate is implicit in all predation rate estimates, and must be stated explicitly if the investigator limits the time during which data are taken (Jmhasly & Nentwig 1995). Published predation rates for web and hunting spiders, variously expressed, are presented in Table 3.

Rates for individual spider species and species complexes suggest relatively low proportions of pest populations being destroyed, but one must remember that spiders constitute an assemblage of species that may, in aggregate, exert effective control (Riechert & Bishop 1990; Riechert & Lawrence 1997). Furthermore, spiders kill many more insects than they consume (see Sunderland 1999, this volume). Finally, in conjunction with parasitoids, pathogens, and other polyphagous predators, spiders may tip the balance in biological control.

Intraguild predation: Prey spectrum studies reveal that some spiders consume large numbers of beneficial arthropods, including other spiders and parasitic and predatory Hymenoptera and Diptera (see Hodge 1999, this volume); most notorious is the green lynx spider, *Peucetia viridans* (Turner 1979; Randall 1982;

Table 3.—Spider predation rates and prey population impacts derived by direct observation. *Data collection restricted to hours of daylight. **Based on calculation from raw data in Edgar 1969.

Species or Complex	Rate	Impact	Reference
Web Spiders			
All foliage web spiders	0.2–1.2 $\times 10^6$ insects/ha/year		Nyffeler (1982)
	0.2–1.2 kg insects/ha/year		
Araneidae only	38 insects/m^2/day		
	150 fresh kg insects/ha/year		
Araneus spp.	12 insects/m^2/day		Kajak 1965
Linyphiidae, Araneidae & Tetragnathidae	3.5–5.8 prey /m^2/9 h day*		Jmhasly & Nentwig 1995
Linyphiidae only	1.5–1.7 aphids/m^2/9 h*	4% of aphid population	
Linyphiidae	0.023–31.2 aphids/m^2/day		Sunderland et al. 1986
	105.6 aphids/m^2/season		
Micryphantidae	42 insects/m^2/day	2% of aphid population	Nyffeler & Benz 1988a
	20 aphids/m^2/day		
Hunting Spiders			
Pardosa spp.	$\sim$1.3 insect/day		Nyffeler & Benz 1988b
	2 aphids/m^2/week		
Pardosa lugubris	0.8 insect/day**		Edgar 1969
Pardosa amentata	1.17 insect/day		Edgar 1970
Peucetia viridans	0.25–0.5 insects/day		Nyffeler et al. 1987b
Oxyopes salticus	120,000 insects/ha/week	4.5% of available prey	Nyffeler et al. 1987a
Oxyopes salticus	0.9 insects/day	15–18% avail. fleahoppers	Nyffeler et al. 1992a
Phidippus audax		5% of available prey	Young 1989c

Nyffeler et al. 1987b). Randall (1982) asserted that the green lynx is ‘‘counterproductive’’ as a biological control agent, but the only sure way to determine this would be to study the agroecosystem in its presence and absence. Louda (1982) performed just such a study of predation by *P. viridans* in a natural system and found that its net effect was beneficial to plants.

Gut analysis.—Identifying and quantifying prey remains in the gut are the first steps in determining spider predation rates (Sunderland 1996). However, because spiders are liquid feeders and the remains of several meals may be found concurrently, this presents formidable technical problems (Stuart & Greenstone 1990).

Radionuclides: Breene et al. (1988) showed that when mosquito larvae irradiated with ^{32}P were made available to three amphibious spider species in simulated ponds, spider feeding could be documented by acquired radioactivity. Similar approaches were used to document spider predation on moth eggs and larvae (Buschman et al. 1977; McCarty et al. 1980; McDaniel & Sterling 1979; Elvin et al. 1983; Godfrey et al. 1989). To use this approach in the field, one must label and release large numbers of potential prey and then determine the proportion of total prey that are labeled. One must also assume that the released animals and those of the natural population are equally susceptible to predation, and that radioactivity is not being made available to the spiders by other routes. Finally, this approach would be difficult to employ given environmental concerns and regulations (Elvin et al. 1983); besides, there are better alternatives (below).

Chromatography: In a unique application, Putnam (1967) used paper chromatography to detect the pigments of mites that had been consumed by spiders.

Electrophoresis: Gel electrophoresis of prey allozymes has been used for insect and mite gut analysis but not yet for spider gut analysis. One must pay serious attention to the choice of enzyme system and gel medium, and be a competent bench scientist (Solomon et al. 1996). If it could be made to work, an advantage would be relative economy and, with luck, the ability to distinguish a wide range of prey species with a single analytical system.

Nucleic acid probes: Probes employing species-specific DNA sequences have been used to diagnose a number of arthropod interspecific interactions, including pathogen host and parasitoid host (Greenstone & Edwards 1998), and could, in principle, be used to identify prey remains in a spider's gut.

Serology: Vertebrate antibodies have been used for spider gut analysis for 35 years (Loughton et al. 1963). I have recently reviewed this approach (Greenstone 1996) and shall here emphasize just three points. First, these are proven technologies with stable, reproducible protocols. Second, assay technology is getting cheaper and simpler; and ELISA, which requires expensive equipment, could be replaced by the immunodot (Stuart & Greenstone 1990; Greenstone & Trowell 1994; Agustí in press). Finally, any level of prey specificity is achievable, down to stage and even instar (Ragsdale et al.1981; Greenstone & Morgan 1989; Greenstone & Trowell 1994; Goodman et al. 1997). Although most directly achieved by monoclonal antibody technology, the same specificities might be achieved more cheaply by affinity chromatography of conventional antisera (Greenstone 1996).

Serological assays have been used to study spider predation on all manner of arthropod prey (Greenstone 1996). They are particularly useful for studying oophagy, a poorly documented phenomenon because of the small size and cryptic habit of eggs and short spider handling times (Nyffeler et al. 1990). For example, a single monoclonal antibody has revealed the extent of bollworm egg predation by two *Cheiracanthium* species in India and North America (Sigsgaard 1996; Ruberson & Greenstone 1998).

Two problems in quantitating serological data remain. First, predators differ in digestive rates and are therefore differentially likely to contain detectable remains of a prey item at any interval post-feeding. Weighting factors, based on temperature-dependent detectabilities, are necessary to determine the relative importance of different predator species. Maximum detectability intervals (Sunderland et al. 1987) and detectability half-lives (Greenstone & Hunt 1993; Agustí in press) have been proposed as weighting factors. Second, due to the extraordinary sensitivity of contemporary assays, one generally cannot know the number of prey items represented by a serological positive (Greenstone 1996). If one assumes that the number of prey contained in any given predator gut is a Poisson variate, then the proportion of negatives can be used as the zero class to calculate the mean number of prey individuals per gut (Nakamura & Nakamura 1977; Greenstone 1979; Lister et al. 1987). Since Poisson assumptions may not always be met, the model needs to be tested. Other models have been suggested by Ashby (1974), Sunderland & Sutton (1980), and Sopp et al. (1992).

Field experiments.—Direct evidence for the effectiveness of spiders in biological control comes from field experiments in which spider numbers are manipulated and the resultant pest populations and attendant crop damage are compared to those in controls.

Mansour et al. (1980) removed all of the spiders from half of a sample of apple trees in an abandoned orchard and then infested them with Egyptian cotton leafworm egg masses. After five days, damage to egg masses was significantly greater; and larval populations and leaf feeding damage were significantly lower on the controls. Analogous experiments were performed with the same insect on cotton (Mansour 1987) and a scale insect on citrus (Mansour & Whitcomb 1986), with similar results.

Itô et al. (1962) used heptachlor to reduce spider numbers in a rice ecosystem. Spider densities were lower and planthopper and leafhopper densities and population growth rates were greater where plots had been sprayed. In a northern California rice ecosystem, Oraze & Grigarick (1989) used floating rings with sticky tops to manipulate the numbers of *Pardosa ramulosa* within. Rings with higher spider densities had significantly reduced densities of the aster leafhopper.

Carter & Rypstra (1995) added artificial web sites (crates) and an inoculum of *Achaearanea tepidariorum* to some soybean plots and removed all spiders and uninhabited webs from others. Crates increased spider density, which was significantly correlated positively with insects killed and negatively with leaf area damaged.

Riechert & Bishop (1990) increased the hospitability of a vegetable garden ecosystem by adding mulch, which significantly increased spider density and decreased pest densities and plant damage. After spider removal, the mulch treatments were no longer different from bare ground controls. Riechert & Lawrence (1997) manipulated numbers of the entire spider assemblage and also of four individual species (an abundant small lycosid and linyphiid and less abundant but large lycosid and araneid), in an old field ecosystem. The entire assemblage significantly reduced insect herbivore numbers relative to spider removal controls, but individually the abundant small species could also significantly reduce the densities of some insect taxa.

CONCLUSIONS

All four approaches to studying spider predation have some value, but laboratory feeding studies are only useful in selected cases; before succumbing to the temptation to perform them, one should ask whether the resulting data are likely to be informative (Howell & Pienkowski 1971). Direct observation is a powerful tool that will continue to provide useful information on prey spectrum and feeding rates. Serological gut analysis is the most efficient and least disruptive method available for gathering large-scale spider predation data on selected prey species. Experimental field manipulations provide the most powerful demonstrations of the efficacy of spider species and assemblages as biological control agents, and they can also serve as realistic trials for proposed management approaches (e.g., Riechert & Bishop 1990).

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