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MECHANISMS UNDERLYING THE EFFECTS OF SPIDERS ON PEST POPULATIONS

Keith Sunderland: Department of Entomological Sciences, Horticulture Research International, Wellesbourne, Warwick CV35 9EF, U.K.

ABSTRACT. Assemblages of spider species can make significant reductions in pest numbers that are of value to the farmer. A group of spider species with complementary niches leaves few refuges for the pest in space or time. Spiders usually exert an influence on pest numbers in concert with other natural enemies, and spiders are sometimes the dominant component. In addition to killing pests by direct attack, spiders cause pest mortality by dislodging them from plants or trapping them in webs. If the pest is distasteful, or if it is the dominant prey type available, spiders may kill more than they consume, which increases the rate of pest kill per unit of spider food demand. The implications for pest control, of various types of interaction between spiders and other natural enemies, are explored in this paper. Interactions with specialist natural enemies usually result in complementary effects, enhancing pest control. Specialists reduce the density of pests to levels where spiders can prevent resurgence. Specialists foraging on the crop may flush pests off the plant to be killed by ground-zone spiders. Although hyperpredation (i.e., predators killing other predators) may disrupt biological control occasionally, it is considered that the wide range of competitive interactions between natural enemies, in general, promotes diversity and stability of the natural enemy community and generates a robust basis for pest control.

There are currently in excess of 3000 described genera of spiders (Coddington *in lit.*), more than 50,000 species are predicted to be living on the planet, and they are the dominant insectivores in some terrestrial ecosystems (Thompson 1984). They are of economic value to man because of their ability to suppress pest abundance in agroecosystems. Faced with the need to reduce pesticide usage on the world's crops and optimize natural biological control, full investigation of the means by which spiders influence pest abundance is long overdue. Also, in recent years, there has been a realization by ecologists that components of agroecosystems are tractable to manipulate and that spiders are convenient model organisms. Consequently, there are a growing number of investigations in which spiders in agroecosystems are used as tools to gain fundamental insights into the role of generalist predators in community and ecosystem function.

This review is a brief exploration of the major routes by which spiders can influence the abundance of invertebrate pests.

DIRECT PREDATION BY SPIDERS

By spider assemblages.—Individual species of spider may, occasionally, make sufficient impact on a herbivore population for measurable effects on plant production to be registered (Louda 1982), but there is currently no evidence for this in agriculture. Consideration of some aspects of the biology of spiders (e.g., generation times and functional and numerical responses) leads to the conclusion that individual spider species are unlikely to regulate pest populations (Riechert & Lockley 1984; Riechert 1992; Wise 1993). However, when assembled into groups of species, as is the norm in agriculture (Sunderland et al. 1997), they often contribute to significant reductions in pest numbers that are of value to the farmer. In an individual-based model, increasing the number of spider species contributed significantly to prey limitation (Provencher & Riechert 1994). Nentwig (1982) found indications that the size-frequency structure of the arachnofauna matches that of their potential prey, and he suggested a significant role for spiders as a multi-predator complex for reducing a multi-prey complex. Experimental field manipulations, of the mean abundance of spider assemblages, has demonstrated a significant level of impact of spiders on leafhoppers in rice (Oraze & Grigarick 1989), on caterpillars in taro (Nakasuji et al. 1973), cotton (Mansour 1987) and orchards

(Mansour et al. 1980), scale insects in orchards (Mansour & Whitcomb 1986), and various pests in vegetables (Riechert & Bishop 1990) and old fields (Provencher & Riechert 1994; Riechert & Lawrence 1997). The effect of spider predation on pest populations can be sufficient to reduce significantly levels of crop damage (Riechert & Bishop 1990; Carter & Rypstra 1995). Spider species often have complementary niches (Whitcomb 1974; Nyffeler & Sterling 1994), segregating in terms of dimensions such as vertical location, diel cycle and foraging mode (Marc & Canard 1997), and, as an assemblage, may be able to kill all growth stages of a pest, including the eggs (Nyffeler et al. 1990). This means that there are fewer refuges for the pest in time or space (less ''enemy-free space''—Jeffries & Lawton 1984), and this is to the benefit of pest control (Murdoch 1990).

By a group of natural enemies including spiders.—Spiders need not act alone to be of value in agriculture. They also have a valid role as one component of a larger complex of natural enemies with the potential to keep pests at non-damaging levels. They play this role in the control of Colorado potato beetle (Cappaert et al. 1991) and mosquitoes (Service 1973), for caterpillar control on cotton (Gravena & Da-Cuhna 1991) corn (Coll & Bottrell 1992; Clark et al. 1994) and in forestry (Mason et al. 1983), against aphids on cotton (Chen et al. 1994) and apple (Wyss et al. 1995), and against hoppers and other pests on rice (Sawada et al. 1993; Kamal & Dyck 1994; Settle et al. 1996). As would be expected, the relative contribution of spiders compared to other natural enemies varies with crop and season and in response to many other factors. Spiders were not the dominant element in the predatory complex controlling *Helicoverpa* spp. caterpillars on cotton in Australia (Bishop & Blood 1981). However, on cotton in Texas more than 80% of predators observed to kill cotton fleahopper (*Pseudatomoscelis seriatus*) were spiders (Nyffeler et al. 1992); and they accounted for 73% of the net value of predators, compared to 27% for insects (Sterling et al. 1992). Spiders are the most abundant natural enemies in cotton fields throughout China (55–81% of all natural enemies); and they play a key role, together with the other dominant natural enemies, in suppressing pest populations (Zhang 1992).

ADDITIONAL ATTRIBUTES OF VALUE FOR PEST CONTROL

Pest dislodgement.—The foraging behavior of spiders on crop vegetation may disturb pest aggregations and may also cause the disturbed pests to walk or fall off the plants. This can reduce the pest population if the physical conditions on the ground cause rapid mortality (e.g., aphid survival times of only a few minutes at ground temperatures above 40 °C in North American field crops; Dill et al. 1990), or if they cannot easily regain the plants, or if they move into danger zones with greater probabilities of attack by natural enemies. It is possible that pest species belonging to many Orders are dislodged by spiders, but the literature emphasizes an effect on Lepidoptera. In manipulative experiments in apple orchards (Mansour et al. 1981) and in taro fields (Nakasuji et al. 1973; Yamanaka et al. 1973) approximately one third of caterpillars were dislodged, and the authors considered that the majority of dislodged individuals would be unable to regain the plant. In these examples dislodgement resulted in death of the pest. Under less extreme conditions the loss of feeding time resulting from dislodgement may be expected to reduce plant damage and also to reduce the rate of increase of the pest population.

Death of pests in webs not caused by spider predation.—Small pests, such as thrips, midges and aphids, may die by being caught in the webs of large spiders, even when they are ignored by the spider (Nentwig 1987). Alderweireldt (1994) identified 319 prey items in webs of linyphiid spiders in maize fields in Belgium. Spiders were feeding on only 184 of these prey items. Linyphiidae, Dictynidae, Theridiidae and Agelenidae do not renew their webs daily, and feed infrequently (Nyffeler et al. 1994a), so these families may contribute to pest control by the action of their webs. First instars of the cereal aphid *Sitobion avenae* did not escape from webs of non-attacking satiated adult female linyphiid spiders, *Lepthyphantes tenuis* (Sunderland et al. 1986). The proportion of *S. avenae* falling into webs (or sticky traps to simulate webs) that are first instars is typically 10–20% (Fraser 1982; Kennedy 1990). The mean duration of web-site tenacity in this species is less than two days (Samu et al. 1996), so the number of webs

may exceed the number of web-makers. In this study (Samu et al. 1996) nearly all *L. tenuis* webs contained uneaten *S. avenae* and none of the 60 observed spiders were feeding. Thus the potential of webs to kill pests, in the absence of spider attack, can be a relevant consideration for biological control.

Wasteful killing, partial consumption and the wounding of pests.—Under certain circumstances the predator may kill a pest but subsequently ingest little (partial consumption) or none (variously referred to in the literature as ''superfluous killing'' and ''wasteful killing'') of the pest's biomass. This is advantageous for pest control because it will result in more pests being killed per unit of spider food demand. These behaviors are usually observed when prey are plentiful (or when a small spider is able to overcome a large prey) and the spider is nearly or completely satiated. The seemingly inappropriate behavioral overshoot of continuing to kill when enough food to induce satiation has already been secured may be due to the time lag between prey capture and ingestion associated with the spider's extra-oral digestion system (Riechert & Lockley 1984). This is the arachnid equivalent of the gut compartmentalization theory proposed for insects (Johnson et al. 1975). There are examples of wasteful killing at high prey density for Clubionidae and Linyphiidae against aphids (Provencher & Coderre 1987; Mansour & Heimbach 1993), for Linyphiidae (DeKeer & Maelfait 1988) and Lycosidae (Samu & Biro 1993) against flies, and for Araneidae against hymenopteran parasitoids (Smith & Wellington 1983). Partial consumption has been recorded for Thomisidae and Lycosidae at high densities of *Drosophila* prey (Haynes & Sisojevic 1966; Samu 1993). These examples all refer to laboratory studies and it is not known how prevalent wasteful killing and partial consumption are under field conditions. Predators are not 100% efficient, and it is known that wounded prey may die following unsuccessful attacks by coleopteran (Doane et al. 1985) and dipteran (Griffiths et al. 1984) predators. It is likely that spiders, also, cause some pest mortality by wounding leading to fatal infection or loss of haemolymph, but this will be difficult to quantify in the field.

Mansour & Heimbach (1993) recorded a high rate of wasteful killing of the cereal aphid *Rhopalosiphum padi* by spiders, even at low aphid density. *R. padi*, in common with other species of cereal aphid, is a poor quality food for spiders (Toft 1995). They may find it distasteful and can develop an aversion to it, but such aversions persist for only a few hours (Toft 1997). Prey that cause an aversion response by the spider may be ignored, or attacked and released intact, or released wounded or dead, or killed and partially consumed (Nentwig 1985), depending on many variables, including spider hunger and degree of naivete (Toft 1997). Such behavior would not be expected from a specialist natural enemy. When food availability is dominated by a non-preferred pest species (e.g. aphids constituting 83% of prey items in webs of *L. tenuis* in maize; Alderweireldt 1994) the spider population might even kill more pests than if the pests were a high-quality preferred food, because spiders would remain unsatiated. This prey sampling-aversion-wasteful killing syndrome also raises questions about our methodologies for determining the kill rate of spiders on pests, especially for species that do not construct webs. Post-mortem methods, such as electrophoresis, radio-tracers and antibody techniques (Sunderland 1988; Greenstone 1996), would fail because no ingestion has taken place. Quantitative methods based on direct observation of food being eaten by spiders in the field (e.g., Edgar 1970) would underestimate the impact on pests, because the probability of observing a kill and rejection incident is much lower than that of a kill and consume incident (the former being of shorter duration than the latter).

SPIDERS IN COMMUNITIES

Spiders in agroecosystems are components of species-rich communities of herbivores, detritivores and natural enemies. The effect of a spider species on a pest population may be enhanced if the spider population increases rapidly in response to a rich supply of nutritious alternative prey (Jeffries & Lawton 1984; Axelsen et al. 1997). However, if the pest species is less-preferred than the alternative prey, the net effect of these opposing processes on the level of pest control will be difficult to predict (Bilde & Toft 1994). Selective predation by spiders in relation to the size of pest taken (Nentwig & Wissel 1986) can alter the mean body size of the pest pop-

ulation, modifying its vulnerability to other size-dependent natural enemies in the community (Strauss 1991). Some additional examples of interactions between spiders and other natural enemies, with implications for pest control, are described below.

Predation of moribund pests.—Predation by spiders of moribund parasitized pests (i.e., living pests that will be killed eventually by the developing parasitoid) is counter-productive to biological control because the mortality of these pest individuals is already assured, and spider predation will reduce the size of the next generation of parasitoids. Predation of moribund parasitized pests could, however, be of value to the farmer in cases where the moribund pest continues to damage the plant significantly, or reproduces before death (Sunderland 1996). Moribund pests often have phenologies, distributions, activity, defenses and palatability that are different from the healthy pest (Sunderland 1996), but there is very little information in the literature concerning how this influences the probability of capture by spiders (Coll & Bottrell 1992). Predation of moribund diseased pests could be beneficial if the spider spreads the disease to other individuals in the pest population. For example, it is considered likely that *Oxyopes salticus* is an important disseminator of *Anticarsia gemmatalis* Nuclear Polyhedrosis Virus in USA soybean (Kring et al. 1988). It is regrettable that interactions between predators and moribund pests are rarely taken into account in comparisons of the relative effectiveness of predators, parasitoids and pathogens in biocontrol (Hawkins et al. 1997).

Interactions between spiders and specialist predators.—*Pest density:* Spiders, as generalist predators, can be present in a crop, feeding on alternative prey, before the pest arrives. High spider-pest ratios early in the season (e.g., Wheeler 1973; Zhang 1992) may reduce the pest increase rate sufficiently to enable later-arriving specialist natural enemies to suppress the pest population below the economic threshold, a conclusion also reached from metabolic pool modeling exercises (Axelsen et al. 1997). This is a finely-balanced relationship that can also have a negative outcome if synchronization is inadequate. For example, if generalists depress pest density below the oviposition threshold of immigrant specialists (Honek 1980; Ghanim et al 1984), the specialists are likely to leave the field in search of higher pest densities elsewhere, and the generalists may then be unable to prevent a pest outbreak occurring. Generalists and specialists do, however, work together harmoniously, if not synergistically, in many agroecosystems (e.g., Zhang 1992). In perennial systems, this is sometimes because specialists reduce pest density, in one year, to a level from which generalists are able to prevent resurgence in later years (Mason & Torgersen 1987; Roland & Embree 1995). Specialist predators, by themselves, tend to be unreliable (except for crops with economics that permit rear-and-release strategies) because their densities are highly variable from year to year (Aebischer 1991). In contrast, it has been suggested (Sunderland et al. 1996) that the densities of generalists (e.g., spider assemblages) are buffered, in that a deficiency in the numbers of any one species in a given year is very likely to be counterbalanced by a superabundance of another species within the same guild.

Spatial effects: Pests, such as aphids and caterpillars, are dislodged by foraging parasitoids and predators, and especially by specialists such as aphidophagous coccinellids (see review in Sunderland et al. 1997). Spider assemblages are often vertically stratified in crops (e.g., Provencher et al. 1988; Marc & Canard 1997), and many spider species are confined to the ground zone or lower strata of vegetation (Wheeler 1973; Leathwick & Winterbourn 1984; Heong et al. 1990). In U.K. winter wheat, the proportion of fallen aphids that climb back onto plants is negatively related to the density of ground predators (Winder 1990; Duffield et al. 1996). Sixty-one out of 109 species of spider in this crop are confined to the ground zone (Sunderland et al. 1988), and the webs of linyphiids can cover 50% of the ground surface below the crop (Sunderland et al. 1986). Thus it is clear that spiders, and other ground predators, will make a greater contribution to aphid control in this crop in situations where aphids are flushed off the crop by specialist natural enemies.

Competitive interactions between predators.—Cannibalism, intra-specific competition and territoriality (Wise 1993) may result in self-limitation of the density of a given spider species, and inter-specific interactions, including interference competition (Spiller

1984; Moran & Hurd 1994), can result in further reductions in density. Complete elimination of a competing species from the crop may be averted if the intensity of competition is ameliorated by the action of a top predator reducing the density of the dominant competitor (i.e., exploiter-mediated coexistence, as applied to predators). An example of a top predator that might fulfil this role, in USA cotton, is the green lynx spider (*Peucetia viridans*), which is strongly araneophagous (Nyffeler et al. 1987). Interactions such as these promote spider biodiversity and, in addition, cannibalism and hyperpredation (i.e., predators killing predators) may buffer the spider community (i.e., prevent localized species extinctions) during short-term dearth of herbivore and detritivore prey. These mechanisms reduce the availability of enemy-free space to pests, and their effects are enhanced by a behavioral flexibility on the part of predators that permits them to make short-term niche shifts (Jeffries & Lawton 1984; Polis et al. 1989). For example, hunting spiders in USA field crops are highly polyphagous, but can narrow their feeding niche significantly when a suitable prey species reaches high numbers (Nyffeler et al. 1994b).

Some species of spider have been shown to make little impact on other predators (Nentwig 1975; Lockley & Young 1987; Jmhasly & Nentwig 1995), but others are significant predators of spiders, ants, lacewings, ladybirds, and predatory Heteroptera (Nentwig 1986; Nyffeler et al. 1987; Sengonca & Klein 1988; Heong et al. 1992; Nyffeler et al. 1994b; Dinter 1998). Hyperpredation is valuable in promoting diversity and stability of the natural enemy community, but is occasionally detrimental to pest control when intense predation of one predator by another releases a pest from a former level of satisfactory biological control (Rosenheim et al. 1995). Spiders are included in the natural enemy complex implicated as reducing the effectiveness of lacewing release for leafhopper control in vineyards (Daane et al. 1996) and of pentatomid release for suppression of Colorado potato beetle (Hough-Goldstein et al. 1996).

CONCLUSIONS

There are indications from the literature of many mechanisms whereby spiders can affect the abundance of invertebrate pests. Direct predation, pest dislodgement and wasteful killing (by both spider and web) reduce pest abundance, whilst predation of moribund pests and IGP may destabilize existing natural control and trigger indirectly an increase in the pest population. The relative importance of these various pathways in any given agroecosystem, and whether major pathways differ between agroecosystems, is not known. Answering these questions is consistent with the development of a ''community approach'' to biological pest control and spiders are especially apt subjects of study in this context because they are known to exert their influence on pest populations as species assemblages and in concert with other groups of natural enemies.

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