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AFTERWORD

SUMMARY AND FUTURE DIRECTIONS FOR RESEARCH ON SPIDERS IN AGROECOSYSTEMS

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This symposium, using spiders as a focus, has explored a number of themes of general importance in ecology and biological control. These themes relate to grappling with the problems of scale in the distribution and dispersal of invertebrates, to gaining behavioral insights into the trophic biology of generalist predators, to understanding the functioning of communities and ecosystems, and to launching new initiatives in pest control based on ecosystem engineering. Each of these topics has been illuminated from a range of different angles by the participants, who each approached the symposium with a unique viewpoint and expertise, and the net effect (obtained by reading the full set of Symposium papers) is to provide the reader with a mature and well-rounded appreciation of the subject. The symposium presentations were nothing if not innovative and forward-looking, and they record the forging of some exciting new approaches to the study of ecological processes and the implementation of biocontrol.

Distribution and dispersal: from microhabitat to landscape.—Individual spiders can move between microhabitats within a habitat by walking. Some of the species characteristic of agricultural systems also have the ability to disperse over short and long distances through the air by ballooning, so they can move between habitats within the landscape during the lifetime of an individual (Samu et al., this volume). Annual recolonization of crops by spiders owes more, in many cases, to aerial deposition of aeronauts than to cursorial invasion from refugia adjacent to fields. The aerial arachnofauna is taxonomically rich, its composition is not representative of ground-based communities, and the size distribution of aeronauts is skewed in favor of small spiders (Suter, this volume). The small size of aeronauts might not be entirely a result of physical constraints, since a modeling exercise predicted that the optimal dispersal strategy is one of high juvenile dispersal (Topping, this volume). The probability of ballooning can increase in response to a decline in habitat quality, such as crop senescence; and the timing of these changes in habitat quality varies from habitat to habitat within the landscape (Thomas & Jepson, this volume). We have an increasingly detailed understanding of the proximate biological and meteorological constraints and cues for the initiation of aerial dispersal (Suter, this volume), but we know virtually nothing about the fate of aeronauts once they are airborne. Ballooning is risky for the individual. The unpredictable air movement at the time of ballooning could take the individual into danger zones. For the species, however, it is part of the equipment needed for efficient exploitation of the resources offered by ephemeral habitats (Thomas & Jepson, this volume).

To understand why particular strategies of dispersal have evolved it is necessary to consider large spatial areas and long spans of time, and the only practicable way of doing this is through modeling. This aspect of modeling is growing rapidly in sophistication and power (Topping, this volume), but it continues to rely on good-quality biological data. In addition to its contribution to developing ecological theory, landscape modeling could be of practical value if it can produce robust predictions about the optimal patterning of habitats within landscapes, i.e., patterning that will maximize regional populations of natural enemies, including spiders (Samu et al., this volume). Maybe it will also eventually be possible to incorporate a flavor of the topographical, political and economic factors that contribute to the farmer's decision making about the spatial distribution of crop types and other land use decisions.

Prey selection and pest control.—Predation and consumption of pests or alternative foods can be studied in the laboratory, or by direct observation in the field, by gut analytical methods (e.g., radionuclides, electrophoresis, chromatography, serology), or by field experiments (Greenstone, this volume). Laboratory studies are of limited value, serological gut analysis has proved to be the most efficient technique for large-scale studies of the consumption of selected prey species by spiders, and field experiments have demonstrated the value of spiders for biological control. Direct observation has provided good data on dietary range and predation rates in the field (Greenstone, this volume). This method has demonstrated that web-spiders are 99% insectivorous, whereas hunting spiders have a wider diet breadth (Nyffeler, this volume). It is not understood why, despite there being frequent agonistic encounters between web spiders, these rarely result in intra-guild predation (IGP). Many of the hunters, on the other hand are strongly araneophagic (Nyffeler, this volume). Linyphiidae have been found to feed mainly on small Diptera, Homoptera and Collembola, but hunting spiders (Oxyopidae, Thomisidae and Salticidae) eat Diptera, Hymenoptera, Heteroptera, Homoptera, Lepidoptera and Araneae (Nyffeler, this volume).

Some of the factors affecting prey selection have been studied in the laboratory. Active prey selection appears to be a compromise between maximizing energy intake, balancing nutrients and minimizing toxin consumption. Aversions to distasteful, toxic prey (e.g., some aphid species) can be learned by spiders, yet forgotten in less than a day (Toft, this volume). The intriguing possibility has been raised that in some situations pest control might even be improved if the pest is distasteful because of the operation of wasteful killing (= superfluous killing) and unsatisfied spider food demand (Sunderland, this volume). The role of prey quality in determining spider fitness is proving to be a very complex issue. This is a fertile area of current research that is revealing some unexpected facets of the trophic biology of spiders. For example, spiders do not always choose the optimal combination of prey from a mixture, toxic prey in a mixed diet may inhibit consumption of high quality prey, but if small quantities of other types of toxic prey are consumed they may even improve spider performance (Toft, this volume).

''Limit cycle'' control of pests, involving tracking of pest population density by the predator population, is not, generally, a mechanism of pest control that can be attributed to spiders. ''Stable equilibrium point or focal control,'' on the other hand, is a pest control mechanism suitable for spiders and other polyphagous predators that display prey switching and whose populations can be self-limited by cannibalism or territoriality. It relates more to pest control by assemblages of species, rather than to single species of spiders (Riechert, this volume). Spider species often have complementary niches and so an assemblage of species may be able to attack all growth stages of a pest, thus reducing ''enemy-free'' space and improving the prospects for effective biological control (Sunderland, this volume). Spiders have some additional attributes that increase their value as biocontrol agents. These include a) pest dislodgment, b) the capacity of webs to kill pests even when the spider is absent or unmotivated to attack, and c) wasteful killing and partial consumption (Riechert, this volume; Sunderland, this volume). Whatever the mechanism, solid evidence has accumulated, mainly from field experiments, that spider assemblages can be effective in reducing pest populations and the crop damage that they cause (Greenstone, this volume; Riechert, this volume; Rypstra et al. this volume; Sunderland, this volume; Wise et al., this volume).

Communities and ecosystems.—A major theme here, picked up by various contributors (Riechert, this volume; Sunderland, this volume; Wise et al., this volume) and treated in different ways, is the realization that spiders, as polyphagous predators, can get a subsidy from the detritivore food chain, and that this can boost their impact on herbivores, including pests. It can be argued that ways should be found to apply this principle in agriculture and that there should be research into farming-compatible techniques to increase the detritivore component in a wide range of crops. There could, however, be the penalty that more choice of food may mean that spiders and other generalist predators refuse to eat the pests, especially in cases where the pest species are distasteful and toxic (Toft, this volume). Clearly, there is a need for studies directed at determining the outcome of increasing the amount of prey biodiversity in agroecosystems, and at determining the mechanism by which this affects pest control (Wise et al., this volume). There is some evidence that spider predation on detritivores and fungivores can depress rates of litter decomposition and nutrient mineralization in agroecosystems, but this negative effect is expected to be more than offset by the positive effect of spider predation on pests (Wise et al., this volume).

A promising approach to the study of how spider assemblages, as part of a community, affect pest populations, is to see how they fit into functional guilds, rather than always treating them taxonomically. There are indications that this approach is already throwing up some commonalities of community organization that apply across a spectrum of crops (Uetz et al., this volume), but knowledge of the mechanism(s) underlying these findings awaits further research. There is still a dearth of behavioral and life history information for many species, and this is hindering the development of guild classifications and of quantitative comparative guild studies (Uetz et al., this volume). The suggestion that the exact taxonomic composition of these guilds depends heavily on the composition of assemblages in nearby non-agricultural habitats (Uetz et al., this volume) underscores the need for a better understanding of the role of dispersal in the assembly of spider guilds in agro-ecosystems (Samu et al., this volume), especially since the contrary has been observed in experimental garden systems (Riechert, this volume).

A rich complexity of interactions (including various types of competition and intraguild predation (IGP)) can occur between natural enemies in agroecosystems. Some of these interactions are thought to buffer the community from change, while others have been shown to destabilize pest control (Sunderland, this volume; Wise et al., this volume). Both exploitation and interference competition can occur between spider species, especially where preferred microhabitats overlap (Marshall & Rypstra, this volume). Subtle competitive interactions may also be occurring, but investigations of these are still at an early stage. For example, preliminary results from laboratory mesocosm experiments with two lycosid species suggested that foraging activity of *Pardosa milvina* was reduced in the presence of *Hogna helluo*, even though the two species have contrasting diel activity cycles. A kairomone that alerts *Pardosa* to the presence of a potential predator may be involved (Marshall & Rypstra, this volume). It is hypothesized that complete elimination of a competing species from the crop may be averted if a top predator (such as the strongly araneophagic green lynx spider, *Peucetia viridans*) reduces the density of the dominant competitor (i.e., exploiter-mediated coexistence, as applied to predators) (Sunderland, this volume). Cannibalism and IGP may also enable populations of spiders and other predators to persist in a habitat during periods of low abundance of herbivore and detritivore prey (Marshall & Rypstra, this volume). IGP involving spiders has been studied in natural communities, and IGP involving predators other than spiders has been studied in agroecosystems (sometimes demonstrating that intense predation by one predator on another may release a pest from a former level of satisfactory biological control); but IGP involving spiders in agroecosystems has not yet been investigated experimentally (Hodge, this volume). IGP by lycosid spiders on the insect predators of squash bug eggs was, however, suspected as the explanation for reduced squash production in summer vegetable garden experiments (Wise et al., this volume), and there is a wealth of observational data on the involvement of spiders in IGP relationships in agroecosystems (Nyffeler, this volume). Quantification of density, activity and diet of spiders and co-occurring predators in agroecosystems will enable prediction of the probability of IGP and competition which can then be used to guide the design of rigorous and meaningful field experiments (Hodge, this volume).

Modifications to agricultural practice.— Ways are being sought to promote the effective use of spiders in biological control; but it should be noted that spiders will, for the foreseeable future, be embedded in integrated management systems which are likely to continue to include some use of pesticides. The selective use of pesticides so that they work with, rather than against, natural enemies

(Riechert, this volume), needs development, and can only be based on a sound understanding of the ecotoxicology of spiders and other natural enemies. Our knowledge of the ecotoxicology of spiders is lagging significantly behind that of some other generalist predators, such as carabid beetles. A strong relationship between spider density and habitat structure has been demonstrated by correlations and experimental manipulations. Measures that increase the structural complexity of the habitat, such as intercropping, mulching and conservation tillage, are known to enhance spider density and diversity (Rypstra et al., this volume). Diversification is most likely to be effective if it comes in the form of interspersed microhabitats, rather than spatially-segregated microhabitats or habitats (Samu et al., this volume). How the specific details of habitat structure influence the effectiveness of spiders as biological control agents has yet to be worked out. Conservation tillage and mulches are examples of approaches that could simultaneously provide spiders with a more diversified habitat structure and a nutrient and energy boost from the detritivore food chain (Samu et al., this volume; Riechert, this volume; Rypstra et al., this volume; Wise et al., this volume). This topic justifies theoretical, experimental and applied research in the future (Wise et al., this volume).