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SCALE-DEPENDENT DISPERSAL AND DISTRIBUTION PATTERNS OF SPIDERS IN AGRICULTURAL SYSTEMS: A REVIEW

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ABSTRACT. A conceptual framework is presented for the study of the factors affecting the distribution, dispersal and abundance of spiders in agricultural systems. It is useful to consider how factors operate at three levels of a spatial hierarchy, namely micro-habitat, habitat and landscape. The size and distribution of spider populations are determined by factors influencing survival, reproduction and dispersal. Modes of dispersal vary in terms of the efficiency of sampling new habitats and the level of risk. A literature survey of proximal factors (micro-climate, habitat structure, disturbance, prey availability, predation, and territoriality) affecting micro-habitat usage by spiders showed that the relative importance of these factors varied according to spider species. Spider abundance and diversity were found, in general, to be positively correlated with environmental diversity at different spatial scales. Within-field habitat diversifications were found to be more effective in increasing spider populations when interspersed throughout the crop (e.g., polycultures and reduced tillage) than when spatially segregated (e.g., strip management). Two approaches (modeling and experimental) to studying the effects of landscape level phenomena on spider distribution and abundance are discussed. Manipulation of habitats at the edge of fields has not, in the main, resulted in increased spider density within fields. Opportunities were identified for increasing regional populations of spiders, and optimizing pest control, by management of the annual shift in the crop mosaic to maximize spider transfer rates from senescing crops to young crops.

Spiders are ubiquitous predators in terrestrial ecosystems and they have a substantial presence in the agricultural landscape. Species distributions of spiders in various agricultural habitats provide strong evidence that those assemblages are not just randomly collected from the local species pool (Topping & Lövei 1997). Spider diversity varies from being impoverished under intensive culture (Nyffeler et al. 1994) to being, under favorable agricultural management, even greater than in natural habitats (Toft 1989). Agricultural systems are, however, characterized by a relatively small number of highly dispersive dominant agrobiont species, which thrive under disturbed conditions (Luczak 1979). The potential role of spiders in controlling pest populations in agriculture has already been reviewed (Riechert & Lockley 1984; Nyffeler & Benz 1987). Here we depart from the proposition that spiders are useful components of agroecosystems. Our aims here are to determine, from the literature, how spiders are distributed in agricultural systems, to discover the factors which bring about the observed distributions, and to assess whether it might be feasible to manipulate some of these factors to increase the abundance and effectiveness of spider populations as antagonists of pests.

For the discussion of the different factors that influence spider distribution it may be useful to consider the distribution patterns in relation to three nested scales (Wiens 1989; Juhász-Nagy 1992): the *micro-habitat* (e.g., a weedy patch within a field, bare ground between rows of crop plants, or the air space between foliage), the *habitat* (e.g., the whole crop, the adjacent hedge, or an abandoned field), which comprises a collection of micro-habitats, and the *landscape*, which comprises a collection of habitats. For each scale, we will review dispersal modes, specific factors and farming practices that are relevant to the given level.

MICRO-HABITAT SCALE

Selection of micro-habitat by individual spiders is likely to be in relation to a specific biological need or collection of needs or may reflect avoidance of some factor, such as interspecific encounters (Post & Riechert 1977). The spider may, for example, assess a micro-habitat as a potential web site, oviposition site, overwintering site or as a safe haven from predators during the inactive phase of a diel cycle. Harsh physical conditions are common in agricultural habitats and the spider may need to seek temporary refuge in a favorable micro-habitat in order to maintain its physiological integrity. From this it follows that individuals of any spider population are harbored by specific micro-habitats which might vary over time, according to the current needs of the individuals.

The numbers of spiders to be found, at any instant of time, in each of the micro-habitats are determined by site selection (immigration into the micro-habitats), site-related rates of survival and reproduction (Sunderland & Topping 1993), and site abandonment (Gillespie & Caraco 1987) which, in turn, are determined by various abiotic and biotic factors. Studies aimed at the examination of specific factors can be useful in devising agricultural practices which, typically acting at the habitat scale, might create an improved quality and distribution of micro-habitats for the enhancement of natural enemies.

Abiotic factors.—Structural complexity is usually determined by the vegetation. It provides support for webs and its degree of complexity has a bearing on the costs of exploration and web building (Zschokke 1996). The differential preference of spider species for various structural features can be demonstrated by the strong relationship between structure and the richness and density of spider assemblages (Rypstra & Carter 1995). Manipulations of shrub and tree structure were found to influence spider species diversity and abundance (Hatley & MacMahon 1980). Bultman & Uetz (1982) separated the effects of forest litter as a nutritional base for spider prey from its role as a spatially complex substrate by the use of artificial leaves. Web-builders were more abundant in structured artificial litter but hunting spiders preferred prey-rich natural litter. Other studies employing artificial micro-habitat structures showed that salticids preferred open geometries whilst theridiids selected dense ones (Robinson 1981). Web-builders are not entirely reliant on vegetation, and irregular ground surface features have also been found to meet the requirements of some species. Depressions in the soil of arable fields, for example, are attractive web sites for some linyphiids, and species segregate in relation to the diameter of such depressions (Alderweireldt 1994; Samu et al. 1996). Preference for different structures is also a size related phenomenon. Field data by Gunnarsson (1992) suggested a relationship between spider mean size and vegetation fractal dimension within a habitat, while Riechert (1974) observed change in the structural needs with growth within one species.

Although micro-climate and structure are often correlated (Cady 1984), manipulative experiments have been carried out in an attempt to separate the two factors. Such experiments demonstrated the strong effect of micro-climate: web-site selection occurred in relation to humidity for araneid, tetragnathid and linyphiid spiders (Enders 1977; Gillespie 1987; Samu et al. 1996) and in relation to temperature for the funnel web spider, *Agelenopsis aperta* (Riechert 1985).

Web destruction is often a precursor to web-site abandonment (Hodge 1987). Some micro-habitats may be more prone than others to destructive forces that endanger the web, such as foraging animals and meteorological factors (Enders 1976). Agrobiont species can cope with disturbances by life-history strategies compatible with disturbance patterns (Toft 1989; Samu et al. 1998) and by their high dispersal power. Mobility gives spiders the flexibility to vacate a locally disturbed area and re-invade later. This contrasts with many of their intra-guild competitors, such as carabid and staphylinid beetles, which often have eggs, larvae and pupae in earthen cells highly vulnerable to mechanical disturbance (Sunderland et al. 1996).

Biotic factors.—Cues from prey can (but do not always) play a role in micro-habitat selection and retention. The cues may be vibrational (Pasquet et al. 1994), olfactory (Riechert 1985) or visual (Persons & Uetz 1996). The relative importance of these cues varies with species, but Persons & Uetz (1997b) found visual cues to be the most significant for the wolf spider *Schizocosa ocreata*. Many authors (Gillespie 1987; Weyman & Jepson 1994) have reported spiders (belonging to a range of families) to have shorter residence times in micro-habitats where prey is scarce compared with sites where food is abundant. Riechert (1984) showed that if prey was experimentally supplemented in a poor quality web site of *Agelenopsis aperta*, the web owner made more effort to defend its web in territorial disputes. However, often weak or no relationship was observed between site quality and the tenacity of spiders to web-sites. In such cases spiders were demonstrated to follow a fixed probability random leaving strategy (Vollrath & Houston 1986; Persons & Uetz 1997a). An important factor affecting web-site tenacity and responsiveness to prey availability is the energetic cost of web construction, which varies between spider families (Janetos 1982).

A micro-habitat chosen by a spider can act as a refuge from its own natural enemies. In predator exclusion experiments, Gunnarsson (1996) demonstrated that, in the presence of bird predators, the abundance and mean size of spiders were greater on spruce branches where a high needle density provided a refuge from predation. Intraguild predation and cannibalism might affect micro-habitat selection as well. After spiders have reproduced, spatial separation of parents and offspring is often recorded, and this may be a mechanism to reduce cannibalism. Some species of adult lycosid, for example, move horizontally to occupy micro-habitats away from their offspring (Edgar 1971; Greenstone 1983), whilst age-specific vertical migration in *Clubiona phragmitis* may serve the same purpose (Nentwig 1982).

Spider territoriality may be generally uncommon (Wise 1993), but cases are known where agonistic interactions lead to spacing out of the spider population (Riechert 1981; Marshall 1995). In other instances, intra- and interspecific contests for webs and web-sites were observed frequently, without obvious influence on spider aggregation in a micro-habitat. Intraspecific contests between adult female *Lepthyphantes tenuis* for webs constructed in hollows in the earth of a wheat field were observed regularly (Samu et al. 1996), and they resulted in departure of more than 30% of web-owners from the web-site. An opposite trend can occur amongst less aggressive spiders, where a reduction in web construction costs can be obtained by attaching webs to each other, as was recorded for *Zygiella x-notata* (Leborgne & Pasquet 1987), and *Hypochilus thorelli* (Hodge & Storfer Isser 1997). Various degrees of communality are known in the Araneae, and this has concomitant implications for micro-habitat usage (Rypstra 1986; Hodge & Uetz 1995).

HABITAT SCALE

Habitats are comprised of a number of micro-habitats within a delimited area. Animals which move from one micro-habitat to another within a habitat can usually do so by low-risk dispersal modes. Agricultural fields with their artificial homogenous vegetation can typically be viewed as habitats.

Dispersal within habitats.—Micro-habitat relocations within a habitat are part of the foraging strategy of actively hunting spiders (Ford 1978), but abandonment of web-sites can occur with high frequency in web spiders as well (Samu et al. 1996). To change micro-habitat, walking over the ground (*cursorial dispersal*) is relatively low-risk, as the spider can withdraw rapidly if it accidentally enters inimical territory. However, in extreme environments, even short distance movements, such as within-habitat web-relocation, can significantly increase mortality in a desert widow spider (Lubin et al. 1993). Increased daily movement rates had similar effects for a wolf spider species. In a tidal flood area *Pardosa lapidicina* migrates back and forth with the tides, and the mortality of the population in this habitat was higher than in a nearby salt marsh habitat where the animals moved less (Morse 1997). Cursorial movement could be ineffective for moving across or into large areas of monoculture (Thomas et al. 1990). An alternative dispersal mode is that of ‘‘rigging.’’ This entails the spider climbing to the top of the vegetation, letting out strands of silk which fall onto the top of the canopy, then running along the silken line for a few meters and then repeating the process. It is likely to be relatively low-risk and is intermediate between aerial and cursorial dispersal in terms of habitat sampling rate.

Farming practices.—Many farming operations result in major habitat-scale disturbance for spiders. Harvesting, plowing, pesticide spraying and forest clearcutting are likely to affect most micro-habitats within a given habitat; and they are known to cause severe reductions in spider populations (Nyffeler et al. 1994; Thomas & Jepson 1997). Conversely, disturbances of intermediate strength and frequency may actually increase the diversity of a spider community (Johnson 1995). This effect may operate by increasing the diversity of micro-habitats within a habitat. Another type of diversification might be achieved through the selection of appropriate farming practices which alter vegetation/structure in areas within habitats (fields) that are either spatially segregated (e.g., strip farming) or fully interspersed (e.g., intercropped polycultures, mulching).

Interspersed diversification is frequently attained by planting multiple crop species in one field. This in a number of instances resulted in spider densities greater than those found in monocultures, and an associated suppression of pest species (Letourneau & Altieri 1983; Coderre et al. 1989; Coll & Bottrell 1995). Lycosid abundance, for instance, was increased; and corn borer (*Ostrinia furnacalis*) decreased, in peanut intercropped with maize, compared with monocultures (Altieri 1994). Reduced-tillage systems often provide a diversification of interspersed micro-habitats by engendering a rough or heterogeneous soil surface, plus structural complexity in the form of plant residues conserved from previous-year crops (House & Stinner 1983; Clark et al. 1993; Robertson et al. 1994). Other authors (Thornhill 1983; Alderweireldt 1994; Samu et al. 1996) have experimentally demonstrated that linyphiid density can be increased by creating depressions in the surface of arable soils. Clover, as a living mulch (Altieri et al. 1985), and mulches experimentally applied to a garden system (Riechert & Bishop 1990) have been found to increase spider densities significantly, probably by simultaneous effects on structure, micro-climate and prey availability (see above).

Strip management contributes to micro-habitat diversification within crops, but the spatial separation of micro-habitats is greater than for interspersed treatments. In a Swiss orchard, the density of spiders and their webs on the apple trees was greater in plots where weeds had been planted in strips below the trees, than in weed-free control plots (Wyss et al. 1995). However, in many cases, spider density on and under crop plants is unaffected by strip management (Nentwig 1989; Riechert & Bishop 1990; Samu et al. 1997), perhaps because spiders aggregate in the favorable micro-habitats (such as weed and flower strips) and do not disperse out onto the crop plants.

LANDSCAPE SCALE

The distribution of spiders is least studied at the landscape scale. This is mostly because it is extremely labor intensive to obtain even a coarse picture of spider distribution over a large area. To study the effect of landscape level phenomena on spider distribution two approaches are possible. One is to model landscape scale distribution of spiders using information on the biology of specific species and incorporate that into spatially explicit metapopulation models (Topping & Sunderland 1994b; Halley et al. 1996; Topping, this volume). The other approach is to select smaller scale landscape fragments, a meaningful subset of landscape structures such as a field and its margin, to experimentally study the distribution and movement of spider populations.

Dispersal.—For both above-mentioned research strategies, knowledge of the scale-dependent dispersal of spiders is essential. In fact, Topping's (1997) simulation model appeared to be more sensitive to assumptions about dispersal than to field size or timing of agricultural operations. Spiders can vary dispersal modes, such as cursorial movement, rigging or ballooning, by applying the most effective mode for the given scale of movement, although not all dispersal modes are available in each stage or taxon (Plagens 1986). The most efficient dispersal mode at the landscape scale is ballooning (*aerial dispersal*), which provides the individual spider with the potential to sample different widely-separated habitats in a short period of time (Weyman 1993). If it lands in a safe habitat the spider may have the option to re-balloon immediately, sample the new habitat and re-balloon after a short period of time, or it may choose to stay. As far as is known, the destination of the aeronaut is determined purely by meteorological factors (Bishop 1990; Thomas 1996). It is, therefore, a high-risk activity; individuals which land at unfavorable destination areas will not be able to reproduce, thus these places act as a reproductive sink (Meijer 1977; Crawford et al. 1995).

Farming practices.—At the landscape scale the effect of basic landscape structure (size and distribution of different habitat types, e.g., fields) and the cumulative impact of field-scale farming practices, (including their timing and distribution), are of primary interest. Root's ''enemies hypothesis'' (Root 1973), which predicts generalist and specialist natural enemies to be more abundant in diversified agricultural systems, was tested by spatially explicit models at the landscape scale. The maintenance of grass habitats that are not demolished by crop rotation (Topping & Sunderland 1994b) and the presence of set-aside fields (Topping & Sunderland 1994a) significantly increased the viability of the modeled *Lepthyphantes tenuis* metapopulation (Topping 1997). In a simulated linear landscape the inclusion of small amounts of grassland considerably increased overall spider population sizes (Halley et al. 1996). These models were also useful at pointing out the importance of the pattern and timing of destructive agricultural practices. Crop rotation was generally detrimental, but the re-scheduling of plowing could decrease this negative effect on spiders (Topping & Sunderland 1994b).

Using the experimental approach many attempts have been made to increase the abundance of natural enemies in field habitats by manipulation of habitats at the edges of fields. In the majority of such studies (including soybean, cereals and orchards), increases in spider densities at the edges were not translated into increases in the fields themselves, and especially in the centers of large fields (Altieri & Schmidt 1986; Alderweireldt 1989; Kemp & Barrett 1989; Dennis & Fry 1992; Kromp & Steinberger 1992; Altieri 1994; Vangsgaard 1996; Tóth & Kiss 1997). Landscape fragments studied by transect sampling show this phenomenon as the 'edge effect.' Edges are often considered as distinct ecological systems, ecotones, where the local fauna consist of species specific to the ecotone, and a mixture of the two neighboring faunas which overlap there. The width of the overlap was typically not found to be greater than a few meters for farmland and forest spiders (Bedford & Usher 1994; Downie et al. 1996). Between wheat and various grassy areas the penetration of spiders into neighboring habitats was also limited (Duelli et al. 1990; Kajak & Lukasiewicz 1994). For spiders the absence of certain species from specific habitats is usually due to the lack of habitat suitability, rather than a limitation of dispersal capacity. Bishop & Riechert (1990) found that about half of the spider species found in a garden system were not found in nearby habitats, but arrived by long-distance migration.

Larger scale landscape models suggest that the maintenance of habitat diversity and preserve areas are important for the subsistance of spider metapopulations. On the other hand, smaller scale experimental studies reveal the overriding importance of within field habitat quality. Perhaps these two phenomena could be combined by finding ways to provide ''time-specific habitat diversity,'' such that natural enemy populations build up in favorable non-crop habitats and micro-habitats initially, but are forced to transfer to crop plants (at a time when pests start their increase) by strategically timed destruction of the favorable non-crop habitats. It will be a challenge to develop practical management systems to achieve these goals. Large numbers of natural enemies do, however, emigrate from senescing crops (Whitcomb & Bell 1964); and, since the various crop species in a landscape tend to senesce asynchronously, there is an opportunity to manage the annual shift in the crop mosaic to maximize transfer rates of beneficials from senescing crops to young crops (Burel & Baudry 1995).

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