

DISPERSAL OF THE SPIDERLINGS OF *XYSTICUS EMERTONI* (ARANEAE, THOMISIDAE), A LITTER-DWELLING CRAB SPIDER

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ABSTRACT. Dispersing spiderlings of *Xysticus emertoni* (Thomisidae), a litter-dwelling species, placed on sites similar to their nests on leaves usually descended quickly into the vegetation below. However, those placed on nearby goldenrod (*Solidago* spp.) flowers remained significantly longer, sometimes hunting, before dropping lower in the vegetation. They seldom ballooned from either site. *Xysticus* dispersal behavior differs markedly from that of the thomisid *Misumena vatia*, a flower-inhabiting species, which balloons regularly from leaves and remains much longer on goldenrod flowers than *Xysticus*.

Resource spacing and availability play an important role in an individual's predisposition to disperse (Southwood 1962; Richter 1970; Dingle 1984). In turn, dispersal patterns influence other aspects of the life styles of the individuals in question. Combined, these factors should exert a dominant impact on patterns of gene flow and consequent population structure. It is therefore instructive to compare the dispersal patterns of related species with extremely different life styles.

Two thomisid crab spiders, *Xysticus emertoni* Keyserling and *Misumena vatia* (Clerck), provide such a comparison. *Xysticus* is primarily an inhabitant of herbaceous vegetation and litter in fields and pastures of eastern North America (Comstock 1940; Dondale & Redner 1978). Although it sometimes hunts in flowers at the top of the herbaceous layer, *Xysticus* occurs much less frequently, remains for shorter periods, and as an adult experiences considerably lower hunting success in flowers than does *Misumena* (Morse 1983). The latter species concentrates its activities, especially as an adult, at flowers (Morse 1984). Nevertheless, *Xysticus* sometimes places its nests in emergent herbaceous plants, as does *Misumena*. This placement presents *Xysticus* spiderlings with an excellent opportunity to disperse.

Although thomisid spiders regularly occur in samples of aerial "plankton" (Glick 1939; Salmon & Horner 1977; Greenstone et al. 1987), reports often do not distinguish between species or genera. Most frequently, reference is made to

Misumenops F. Pickard-Cambridge and *Misumenoides* F. Pickard-Cambridge in these catches, because these are the thomisid genera that dominate the aerial fauna—*Xysticus* is extremely rare in aerial catches (M. H. Greenstone, pers. comm.). Other than for Richter's (1970, 1971), Greenstone's (1982), and Miller's (1984) studies on lycosids, no experimental effort has been made to compare the ballooning by different species of a spider family, although Tolbert (1977) provides some comparative information on two araneid species.

I therefore tested dispersal patterns of *Xysticus emertoni* spiderlings for comparison with recent results (Morse in press) on the dispersal of *Misumena vatia* spiderlings. In the latter study I established that *Misumena* readily balloon after emerging from their egg sacs, although the propensity to do so is strongly influenced by the substrate they occupy. If the nest sites offer rich foraging opportunities for the spiderlings, primarily flowering goldenrods (*Solidago* spp.) in my study area, they are very likely to remain and feed in them. Their consequent foraging success and subsequent growth at these sites decrease their probability of ballooning. However, *Misumena* of all ages live above the litter in their habitat, concentrating their activities in flowers, a characteristic associated with a nearly continuous quest for insect food. In light of the much less frequent occupation of the somewhat exposed sites by *Xysticus*, and the seemingly more homogeneous areas that they occupy low in the

vegetation, one may predict a considerably lower probability of ballooning than for *Misumena*, even though *Xysticus* nests are often placed in positions that make this type of dispersal possible.

In the present study, I tested the propensity of second instar *Xysticus* spiderlings, newly emerged from their egg sacs, to balloon in experimental situations similar to those under which I had tested *Misumena* spiderlings. I then compared the two species, paying particular attention to the implications of these differences for dispersal, potential gene flow and population structure in general.

METHODS

I found several *Xysticus emertoni* nests on broad-leaved vegetation in the study area while pursuing other work. I measured key parameters of their locations as I encountered them, but made no special attempt to hunt for them in the litter layer. Thus, I do not claim that those nests are typical of all *X. emertoni*. Young were taken from these nests for release experiments (discussed below), and others were taken from broods laid in the laboratory, for a total of 22 broods.

I released over 200 newly-emerged, second instar *Xysticus* spiderlings from locations that resembled one of their frequent nest sites, leaves of the common milkweed *Asclepias syriaca*; and inflorescences of nearby goldenrod clones (*Solidago juncea* and *S. canadensis*) that attracted large numbers of tiny insects. Five young from a single brood were placed on a substrate (milkweed leaf or goldenrod inflorescence) at a time, the maximum number that an observer could carefully watch and record under these conditions. These densities frequently occur when they emerge from a nest. All statistics were run on the responses of groups of spiderlings, with only one group used from a brood in any experiment. Prior to release the spiderlings were lightly dusted with powdered red micronite dye, which increased their visibility to the observer. Earlier experiments with *Misumena* spiderlings had demonstrated that this manipulation did not affect their subsequent behavior (Morse in press). The studies were carried out in a field in Bremen, Lincoln Co., Maine, an area that I have described in detail elsewhere (Morse 1979, 1981).

I observed these spiderlings continuously during the first two hours following release, or until they had all dispersed. If any remained at the

end of two hours I censused them twice or more daily to determine the approximate time at which they dispersed from the substrate on which they were released. I recorded movements of these spiderlings, the time they remained on the substrates to which they were introduced, and the methods by which they left these sites (ballooning, dropping on lines, etc.). I then compared these results with those for *Misumena* spiderlings that had been exposed to similar experiments (Morse in press).

RESULTS

Location of *Xysticus* nests in the field.—I found nine *Xysticus emertoni* nests during 1989–1991, of which a majority (five) were on milkweed, two on aster (*Aster* sp.), one on chokecherry (*Prunus virginiana*), and one on raspberry (*Rubus* sp.). The nests were constructed at the ends of leaves, and on all but the aster the distal tip was turned under the rest of the leaf and secured, the eggs laid between the two resulting thicknesses of leaf, and the sides drawn tight by silk into a compact nest. These nests resembled those of *Misumena* (figure 1, Morse 1985), except that *Xysticus* mothers ensconced themselves inside their nests, rather than guarding the nests from the outside. In contrast, *Xysticus* folded the narrow aster leaves twice, permitting a nest to be fashioned by essentially providing a third side from plant material. In a sample now exceeding 1500, I have never seen a *Misumena* nest built by folding a leaf in the latter way.

Nests were all located in low vegetation at a mean height of 54.9 (\pm 12.1 SD) cm, in vegetation of 71.3 \pm 17.8 cm. The nests on milkweed most frequently occupied the third pair of leaves from the top, ranging from the second to the fifth from the top.

Movement of *Xysticus* spiderlings on various substrates.—*Xysticus* spiderlings have a strong tendency to descend into the litter when placed on substrates similar to the ones on which their parents normally build their nests. This behavior occurred both in young placed on the normal sites (milkweed leaves) and on nearby goldenrod flowers at the peak of bloom (Table 1), a source at which large numbers of tiny insects, potential prey of these spiderlings, often congregate. However, they responded quantitatively differently to these two substrates, remaining significantly longer on goldenrod than on milkweed (Table 1) (P < 0.05 in a two-tailed Mann-Whitney U -test).

Table 1.—Time (min) that newly emerged *Xysticus* spiderlings remained on different substrates, with similar results on *Misumena* for comparison (Morse in press). a = *Misumena* remained 176.1 ± 251.5 min on milkweed, 3820.0 ± 3435.5 min on goldenrod (Morse in press); b = 19 of 50 *Misumena* released on milkweed were observed to balloon, but none of 50 released on goldenrod were observed to balloon (Morse in press).

Substrate	Year	N	Time remained ($\bar{x} \pm SD$)	Method of dispersal			
				Drop	Line	Balloon	Not Known
Milkweed ^a	1987	92	8.1 ± 11.9	64	17	8 ^b	3
	1990	65	18.0 ± 21.0	53	4	0	8
Goldenrod ^a	1990	38	114.8 ± 169.1	11	0	2 ^b	25
	1991	10	144.4 ± 203.8	5	0	0	5

Further, numbers of spiderlings observed quickly dropping on lines directly to the litter from milkweed far exceeded those dropping from goldenrod ($P < 0.002$ in a two-tailed Mann-Whitney U -test). This difference, combined with observations of two *Xysticus* spiderlings capturing tiny midges on goldenrod during these periods, suggested that they used these flowers as hunting sites. This result is consistent with occasional observations of early-instar *Xysticus* on these sites under unmanipulated conditions (Table 2).

The most frequent movement from the release sites was directly into the litter, either on vertical lines or by crawling down the vegetation (Table 1). These movements occurred significantly more frequently than dispersal via horizontal lines to adjacent grass stems ($P < 0.01$ for milkweed, $P = 0.05$ for goldenrod in Wilcoxon matched pairs signed ranks tests). The outcome of most moves on horizontal lines probably did not differ in function from the vertical movements, however, since all such individuals that I could follow on horizontal lines used their new locations as staging sites from which to move into the litter, rather than for aerial dispersal. Some of the latter movements could have been a consequence of

the wind moving the line-laying spiders from a vertical to horizontal position while they were leaving the original sites. Although the results clearly indicated that *Xysticus* does balloon, it was the least common of the activities recorded in these releases (Table 1).

Movement of *Xysticus* and *Misumena* spiderlings.—Although *Xysticus* spiderlings resembled *Misumena* spiderlings in remaining significantly longer on goldenrod (foraging substrate) than on milkweed (nest substrate), they stayed on both of these sites only a small fraction of the time that *Misumena* did (Table 1), differences that are highly significant ($P < 0.002$ for goldenrod, $P < 0.001$ for milkweed in two-tailed Mann-Whitney U -tests). These results are consistent with their parents' habits and with the relative scarcity of *Xysticus* spiderlings on goldenrods and other flowers. In censuses of spiderlings on goldenrods only two *Xysticus* spiderlings were found on over 900 inflorescences, in comparison to over 600 *Misumena* spiderlings (Table 2).

Also striking is the difference in dispersal modes of *Xysticus* and *Misumena* spiderlings from the release sites. Although a majority of *Xysticus* spiderlings left these sites for the litter, either directly by lines or by crawling down the vegeta-

Table 2.—Numbers of *Xysticus* and *Misumena* spiderlings on flowering goldenrod. a = Each clump is distinct from others and probably a clone. b = Involves daily counts over 2½ to 3½-week period following release of a total of 404 *Misumena* spiderlings.

Sample of goldenrod	Number of clumps ^a	Number of flowering stems	Number of <i>Xysticus</i> spiderlings	Number of <i>Misumena</i> spiderlings
Randomly chosen	25	277	1	248
> 5 m from <i>Misumena</i> nest	10	151	0	27
< 1 m from <i>Misumena</i> nest	12	439	0	359
Release of 4 <i>Misumena</i> broods ^b	4	42	1	—

tion, *Misumena* spiderlings never descended to the litter (Table 1). This difference is highly significant ($P < 0.002$ for both milkweed and goldenrod in two-tailed Mann-Whitney U -tests), as is the difference in frequency with which the two species balloon from milkweed ($P < 0.002$ in a two-tailed Mann-Whitney U -test) (Table 1). Although a few *Xysticus* were observed to balloon off goldenrod as well as milkweed in the trials, *Misumena* were observed to balloon only off milkweed. Nevertheless, the frequency of ballooning from goldenrod by *Xysticus* was so low that the two species did not differ significantly ($P > 0.05$ in a two-tailed Mann-Whitney U -test). Since many *Xysticus* left goldenrod within the two-hour period of continuous observation (Table 1), the probability of observing them ballooning from goldenrod was far higher than for *Misumena*. *Misumena* remained for long periods, often several days, on goldenrod (Table 1), and they were only censused a few times a day after the original observation period.

DISCUSSION

The behavior of *Xysticus* spiderlings resembled that of *Misumena* spiderlings in that dispersal time was related to substrate in both species. This difference strongly suggests that they discriminate between sites. However, actual times required to disperse were considerably shorter for *Xysticus* than for *Misumena*. This brief tenure is consistent with *Xysticus*'s distribution at similar heights as adults (Morse 1983).

Richter (1970) and Greenstone (1982) have provided the only previous experimental studies on between-species differences in ballooning patterns, although they have all been performed in the laboratory using artificial wind, heat, and light sources. Young wolf spiders of different *Pardosa* species vary in their ballooning tendencies, which Richter attributed to the abundance and stability of their habitats, and Greenstone to the predictability of the habitats. Propensity to balloon differed inversely with each of these traits. Abundant habitats often have a low level of patchiness.

This study thus suggests that spatial patchiness may be added to the variable of temporal patchiness as a factor affecting ballooning. Both thomisids live in similar habitats, but as a result of their markedly different demands on these habitats, they probably view patchiness at strikingly different scales. For most or all of its stages, *Misumena* depends on insects drawn to extremely

patchy flower resources, but *Xysticus* does not depend primarily on this resource. Even when *Xysticus* does hunt on flowers, it remains there for much shorter periods than *Misumena*, with a periodicity suggesting that its poor hunting success may account for the short tenure (Morse 1983). Because *Xysticus* obtains a major part of its prey away from the flowers, within the vegetation and litter layers, its resources are not likely to be as patchy as those of *Misumena*. *Xysticus* should therefore balloon less frequently than *Misumena*, as observed. Thus the two species appear to respond to the same habitat in distinctly different ways, notwithstanding their similar size and close phylogenetic relationship.

These results, plus the infrequent natural presence of *Xysticus* spiderlings on goldenrod, suggest that the latter spider seldom moves above the litter layer. Consequently, its dispersal distances as juveniles are likely to be low. Gene flow should thus be much lower in *Xysticus* than in *Misumena*, which should in turn generate differences of population structure in the two species. Nevertheless, since *Xysticus* sometimes ballooned, it clearly retains the ability to initiate long-distance movement.

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