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Leaf choices of nest-building crab spiders (*Misumena vatia*)

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Summary. Crab spiders (*Misumena vatia*, Thomisidae) selected leaves of common milkweed (*Asclepias syriaca*) over those of spreading dogbane (*Apocynum androsaemifolium*), pasture rose (*Rosa carolina*), and chokecherry (*Prunus virginiana*) as nest-sites in pairwise experiments among these four substrates. Nesting success was higher on milkweed than on the other three plant species. Early survival of the clutches was thus correlated with the preferences exhibited by their mothers. The major source of nest failure was parasitization by the ichneumonid wasp, *Trychosis cyperia*, which accounted for over 50 per cent of the nest losses.

Introduction

One of the most important decisions made by gravid females that lay eggs is where to place them (Dingle 1981; Morse 1985). This decision becomes critical for those that lay only one clutch, since their entire reproductive output is compressed into this one effort.

Given the importance of such a decision, selection would normally be expected to remove variation for choice (Falconer 1981), and, indeed, many species of animals exhibit precise site-selection for egg deposition (Hildén 1965; Partridge 1978; Morse 1980). However, recent work has revealed the frequent presence of substantial variation in presumably critical traits within populations. Little direct information exists on how selection affects such traits under natural circumstances and what factors are responsible for members of a population performing differently (Endler 1986; Singer et al. 1988). In particular, there is little direct evidence that correlations between behavioral choices of animals (preference) and their resulting success (performance) even exist. Most studies on this subject have concentrated on variation in either preference or performance, have confounded within- and among-population variation for these variables, or have confounded components of preference and performance (reviewed in Singer et al. 1988). I report here the results of experiments and observations designed to test whether members of a crab spider (*Misumena vatia* (Clerck): Araneae: Thomisidae) population select among leaves of different plant species for their nest sites and the success of nests placed on different substrates.

Nest site choice may be important to these spiders for at least three reasons: relative vulnerability to parasitoids, egg predators, and spiderling predators; proximity to hunting sites for the spiderlings; and microclimatic differences. I will concentrate here on factors associated with nest construction, but will also discuss spatial differences in nest predation.

Earlier (Morse 1985) I found that crab spiders exhibit clear preferences in the leaves they use for nests. Choice of sites is especially important for *Misumena* because they are semelparous. Spiders in the study area usually made their nests on leaves of the common milkweed (*Asclepias syriaca*) however, milkweed was the commonest plant with leaves of the size and shape used by the spiders. Other records (Gertsch 1939; D.H. Morse unpubl.) indicate that this spider accepts leaves from a wide variety of plant species for its nests. Spiders in the study area hunt primarily on milkweed immediately before laying; therefore, the study concentrates on individuals with this experience.

Methods

This study was carried out in a field in Bremen, Lincoln County, Maine, during July and August 1984–1989. The field is about one ha in size and surrounded by mixed coniferous-deciduous woodland and pasture. I have described it in detail elsewhere (Morse 1979, 1985).

The four common, emergent, broad-leafed species of plants in the study area were chosen for these studies: milkweed, chokecherry (*Prunus virginiana*), spreading dogbane (*Apocynum androsaemifolium*), and pasture rose (*Rosa carolina*). I have found nests of *Misumena* on all of these species, (D.H. Morse, unpubl.).

Broody spiders that had previously hunted on milkweed were placed on naturally growing plants enclosed in 50 cm × 50 cm × 150 cm cages (length × width × height) of metal screening (0.2 cm × 0.2 cm) before 1200 h. (Broody individuals move from their hunting site, turn under the ends of leaves that they eventually use for nests, and refuse to attack prey. They lay their eggs within a few days.) These cages had no bottoms, but fit snugly against the level ground, thus preventing the spiders from escaping. Each cage provided a choice of two of the four species noted above. Plants of both species selected for an experimental pair were of similar size. All combinations of the four species were used in the experiments. A minimum of 40 different spiders (one per plant) was used for each combination of plant species in an experiment; thus in comparing milkweed and dogbane, 20 or more spiders were placed on the milkweed within the cages and 20 others on dogbane. Similar methods were used for each pair of plant species presented. To control for the tendency of the spiders to move freely on both plant species in an experiment, I tested 20 other individuals in a similar way, except that their choice was between two similar milkweed plants. These pairs of milkweed plants were from the same clone and of the same size.

To test whether individuals that last hunted on milkweed differed in plant choice from those that last hunted on other plant species, I ran a similar experiment on a group of spiders that last hunted on rose flowers, rather than milkweed. Because rose-frequenting spiders were not abundant, I confined these experiments to rose-milkweed comparisons. Numbers of spiders found foraging on dogbane and chokecherry were inadequate for testing. Although these spiders not infrequently hunt on dogbane, they only incidentally forage on chokecherry. The small chokecherry bushes growing in the field do not bloom.

Broody spiders were assigned randomly to pairs of plant species that were available, and monitored daily. The day the spiders laid, or folded under the distal end of a leaf in preparation for laying, and the plant species chosen were recorded.

The act of folding the distal end of a leaf was adopted as the criterion for nest site choice in the latter parts of the study because earlier work demonstrated that virtually without exception spiders in these experiments eventually laid their egg masses on the leaf that they folded. Once the latter spiders turned under a leaf, they were used in other experiments (to be described elsewhere).

Individuals permitted to lay their eggs in these experiments were monitored for nesting success. Since these spiders always laid at night (Morse 1985), I inspected the cages before 0800 each day and removed cages from individuals that had laid. Early removal of the cages minimized the probability that they would artificially protect the new egg masses from attacks by diurnal parasitoids and predators. Since numbers of individuals building nests on pasture rose initially appeared inadequate to permit analysis of nesting success, I supplemented them with spiders similarly caged, but with only rose available as a substrate.

Table 1. Experimental choices of spiders for nest sites

Placed on	Alternate choice	Site selected		G^a
		Same as placed on	Alternate choice	
Last hunted on milkweed				
Milkweed	Chokecherry	18	2	20.17***
Chokecherry	Milkweed	5	16	
Milkweed	Dogbane	18	2	5.06*
Dogbane	Milkweed	12	8	
Milkweed	Rose	21	1	36.80***
Rose	Milkweed	6	27	
Dogbane	Chokecherry	15	9	0.69^{NS}
Chokecherry	Dogbane	10	10	
Dogbane	Rose	19	2	35.66***
Rose	Dogbane	1	19	
Chokecherry	Rose	20	4	13.47**
Rose	Chokecherry	6	14	
Last hunted on rose				
Milkweed	Rose	18	4	27.38***
Rose	Milkweed	2	21	

[a] *G*-tests; *$P<0.05$, **$P<0.01$, ***$P<0.001$, NS = not significant

Table 2. Tendency of broody spiders to lay on the plant species they were placed on as a function of time in cages

Days	Species used for nest-site	
	Species placed on	Other species of experiment
1[a]	30	25
2	35	24
3	23	14
4	9	9
5	5	5
6	8	7
$7\text{–}7^+$	8	9

[a] One-day individuals are those that lay on the night following their introduction to the cages

Results

These spiders exhibited significant preferences for milkweed in each instance that it was available, even if they had last hunted on pasture rose (Table 1). Dogbane and chokecherry, occasional natural nest sites, were intermediate in their attractiveness between milkweed and pasture rose, and in turn they were significantly more attractive to the spiders than pasture rose (Table 1). Spiders placed on the plant species tested with milkweed exhibited these differences in preference most clearly, by moving from that species to milkweed; very few spiders initially placed on milkweed selected any of the other species. The dogbane/rose experiments demonstrated a preference for dogbane as strong as that between milkweed and rose.

Thirteen of the 20 spiders presented with two similar milkweed plants built their nests on the plant they were placed on, and seven shifted. This result raises the possibility that some of the spiders that did not shift from one plant species to the other may have simply accepted the species they were placed on. However, since the vast majority of the randomly chosen individuals placed on rose and chokecherry in tests with milkweed as the alternate nest-site moved to milkweed, it is apparent that they responded effectively to plant-species specific cues in these tests. Also, if individuals that laid quickly, as on the night following their introduction into the cages, were less likely to shift plants than those that waited longer before laying, this behavioral difference would bias the results. However, no such differences occurred in the sample in which I recorded numbers of days between release and egg-laying (Table 2: $G=1.89$, $df=6$, $P>0.9$ in a *G*-test).

I registered the nesting success of spiders allowed to complete their nests and lay their eggs. Success on milkweed was greater than that for the other three species (Table 3). This difference resulted both from low parasitism by the ichneumonid wasp *Trychosis cyperia* and low rates of failure from a variety of other factors (Table 3). Other failed nests were parasitized by scuttle flies (*Megaselia* sp., Phoridae), preyed on by ants (*Formica* sp., Formicidae), preyed on by an earwig (*Forficula*

Table 3. Success of spider egg masses laid on leaves of milkweed, dogbane, rose, and chokecherry. Percentages in parentheses

Substrate	Number of egg masses	Number successful[a]	Number with *Trychosis* cocoons	Other sources of loss
Milkweed	104	86* (82.7)	10 (9.6)	8 (7.7)
Dogbane	48	29^{+} (60.4)	10 (20.8)	9 (18.8)
Rose	25	15^{+} (60.0)	8 (32.0)	2 (8.0)
Chokecherry	27	13^{+} (48.2)	7 (25.9)	7 (25.9)

[a] Differences among species are significant, using *G*-test ($G = 17.57$, $df = 3$, $P < 0.001$). Means that are significantly different from each other are indicated by different symbols (unplanned test for heterogeneity following *G*-test: Sokal and Rohlf 1981)

auricularia, Forficulidae) (one nest that was only partly closed by the parent), or the eggs simply failed to hatch. All eggs in parasitized or preyed-on clutches were lost or failed to hatch.

Discussion

The spiders' choices in these experiments resembled those of free-ranging individuals in similar situations (Morse 1985). This choice is not just a consequence of previous experience with a substrate, since spiders most recently hunting on rose did not differ from those that had most recently hunted on milkweed. The preference for milkweed over the other species suggests that choice may be governed by characteristics of the leaves. Milkweed leaves differ distinctively from all the others by their rubbery, pliable, and strongly pubescent character. Additionally, they differ in shape from dogbane and pasture rose. The latter two species have compound leaves: although single leaflets of dogbane are usually used as nests, they are typically smaller than most milkweed leaves selected. In contrast, more than one rose leaflet is almost always used to construct a nest. Nests on milkweed are typically tightly constructed, at least if the leaves available are of the size they select in the field (Morse 1985; Fig. 1). The spiders seldom accomplished the perfect symmetry characteristic of milkweed nests on the similarly ovate chokecherry leaves. Nests built on rose were characterized by large spaces protected only by silk, in comparison with most nests on the other three species, which had relatively little or almost no space protected only by silk.

The choice of milkweed over the other species correlates with overall differences in nesting success and, inversely, with levels of egg predation by *Trychosis*. Clear relationships in choice and predation-parasitism did not occur among the other three nest substrates, however. The basis for those relationships is not obvious from the results. Clearly, their choice mechanisms are relatively sophisticated, because these spiders exhibit strong preferences in leaf location and size within a single milkweed plant (Morse 1985).

The observations on nest construction suggest that leaf characteristics could be associated with success of the egg masses. Given the importance of *Trychosis cyperia* as an egg parasitoid in the study area (Morse 1988a), it might play an important role in the behavior of *Misumena* at this stage of its life cycle. Prospectively ovipositing *Trychosis* concentrate on inspecting the leaf edges that have been drawn together with silk, and ovipositor probing is largely confined to these areas (Morse 1988b). This behavior should select for nests that minimize the area through which the wasps can easily probe. Tendencies to probe the leaf itself could also be minimal on milkweed because of the sticky latex-like consistency of its leaves, which might clog the ovipositor if contact was made with one of the latex canals in the process (Dussourd and Eisner 1987). A single *Trychosis* larva typically consumes all of the eggs in a nest (Morse 1985, 1988a).

This study differs from most others on parental choice of nesting substrate (e.g., Singer et al. 1988) in testing predators, rather than phytophages. It is also concerned with predation pressures on the offspring, rather than the quality of food available to them. Thus, these results extend considerably the generality of this type of selection problem.

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