Morse, D. H. 1985. Nests and nest-site selection of the crab spider *Misumena vatia* (Araneae, Thomisidae) on milkweed. J. Arachnol., 13:383-390.

NESTS AND NEST-SITE SELECTION OF THE CRAB SPIDER *MISUMENA VATIA* (ARANEAE, THOMISIDAE) ON MILKWEED

Douglass H. Morse

Graduate Program in Ecology and Evolutionary Biology
Division of Biology and Medicine, Brown University
Providence, Rhode Island 02912

ABSTRACT

Adult female crab spiders *Misumena vatia* that had previously hunted in large milkweed clones built nests on non-flowering milkweeds more often than predicted and used smaller than average leaves for their nests. These results suggest that they actively select nest sites at both stem and leaf levels. In commencing a nest, spiders first pulled the distal third of a leaf under the rest of the leaf, secured it with silk, and then rested inside this space. A few days later they laid their eggs there, sealed the edges of the leaf around the egg mass with silk and then guarded the nest, typically resting on its lower side. Spiders always left the last stem upon which they hunted before nesting and usually selected milkweed leaves on a stem several meters away from their hunting site for their nest site.

INTRODUCTION

The choice of a nest site is one of the most important decisions made by animals that deposit eggs. Not only must these nests be placed where physical conditions permit the development of eggs, and of hatchlings if they remain, but the location must also be satisfactory for the adults, if they latter guard them. Further, if the site is not guarded by parents, it is essential that if offer protection from egg parasites or predators. A poor choice subjects the eggs to a wide range of unfavorable factors. The stakes are particularly high if an individual lays many or all of its eggs at a single site, for the probability of all-or-none success at this stage of the life cycle is high. Not surprisingly, many species of animals exhibit precise nest-site selection behavior (Hildén 1965, Partridge 1978, Morse 1980).

Although considerable general information exists on where spiders place their egg sacs, much of it concerns web-building species (e.g., Comstock 1940, Bristowe 1958), and few quantitative data exist on egg placement for sit-and-wait spiders such as crab spiders (see Enders 1977). Here I report on the characteristics of nests and of nest sites selected by solitary, leaf-nesting crab spiders [*Misumena vatia* (Clerck (Thomisidae)] that hunt in common milkweed (*Asclepias syriaca*) immediately prior to nesting.

METHODS

I gathered data on the nests of *Misumena* in a one-ha field in Bremen, Lincoln Co., Maine, U.S.A., during July and August of 1980-1984. Although the vegetation is composed primarily of grasses, a large clone of common milkweed consisting of about 1500 flowering and non-flowering stems grows in the middle, and three smaller clones occur elsewhere in the field. Almost all of the nests were placed on milkweed. Several species of small forbs also grow throughout the field.

I recorded the height of the nest, the height of the milkweed stem, and the length and width of the leaf selected for the nest. If possible I recorded the distances that spiders moved between their last hunting site and their nesting site. I also measured stem height and leaf dimensions from random samples of flowering and non-flowering stems in the study area. Data for most of the variables came from 72 free-ranging spiders; however, I supplemented data on leaf choice and nest height with information on 50 individuals confined at the time of egg-laying to large screen cages placed over milkweed stems. Sample sizes often differ because I did not gather data on all of the variables from each spider.

RESULTS

Distance between last feeding site and nest site.—Spiders typically placed their egg-sacs several meters from their last hunting site, and many of them moved toward the outside of the milkweed clone at this time. Individuals moving to the periphery traveled over twice as far (9.6 ± 9.1 m S.D., N = 14) as did those remaining within a clone (4.2 ± 3.2 m, N = 8) ($P < 0.05$ in a one-tailed t-test). However, as indicated by the large standard deviations, distances moved were extremely variable. Part of the difference in distances travelled could be a consequence of milkweed stems, or other satisfactory nest-sites, being much less dense around the periphery of the clone than in the center. If so, individuals reaching the periphery would have to travel farther to reach the next stem than would spiders in the center of the clone.

Characteristics of nest-sites.—Spiders laid their egg masses on the leaves of both flowering and non-flowering milkweed stems. They selected stems that were significantly shorter than those of the clone as a whole (Table 1), in large part

Table 1.—Stem choice of free-ranging *Misumena vatia* for nest sites on common milkweed.

Category	Height of sample of stems in clone N	Height of sample of stems in clone $\bar{x} \pm$ SD (cm)	Height of stems used by spiders N	Height of stems used by spiders $\bar{x} \pm$ SD (cm)	P (Wilcoxon two-sample test)
Flowering and non-flowering	143[1]	68.0 ± 17.2	65	62.6 ± 19.1	<0.01
Flowering	103	76.8 ± 10.4	25	84.4 ± 11.2	<0.01
Non-flowering	101	49.2 ± 15.3	40	51.1 ± 10.5	>0.3

[1]Initially, I measured randomly-selected samples of 103 flowering and 101 non-flowering stems. However, because the clone averaged 72% flowering stems and 28% non-flowering stems over the study period, I produced the profile of flowering and non-flowering stems tested here by using the entire sample of 103 flowering stems (72% of the sample) and 40 non-flowering stems randomly chosen from the sample of 101 (the remaining 28% of the sample.)

the result of using significantly more non-flowering stems (40 of 65: Table 1) than predicted from the numbers of flowering and non-flowering stems during this study. Differences between the observed and predicted patterns of nest-site choice ranged from $P < 0.02$ to $P < 0.001$, $G = 6.61$ to 23.50, respectively.)

In spite of their apparent preference for non-flowering stems, spiders used a large number of flowering stems for nest sites. Because the clone is a rough rectangle of 20 x 30 m, and because most flowering stems are located in the center and non-flowering stems about the periphery (Fritz and Morse 1985), the relatively immobile, egg-laden spiders hunting in the middle of the clone may often not travel far enough to find a non-flowering stem. None of the spiders whose last hunting site was unambiguously known (N = 22) used that site for its nest.

Flowering stems used by spiders were significantly taller than the non-flowering stems that they used (Table 2). I then tested whether the spiders exhibited height preferences within these two categories of stems. They used flowering stems significantly taller than predicted by the heights of flowering stems within the clone, but the heights of non-flowering stems that they used did not differ significantly from the height predicted by the numbers of non-flowering stems within the clone (see Table 1). Thus, although spiders showed clear preferences for non-flowering stems, they also exhibited height preferences among flowering stems.

Spiders also placed their nests higher on flowering than non-flowering stems (Table 2). Egg masses were most frequently placed near the tops of milkweed stems (Table 2), often on the uppermost leaf wide enough to enclose them. Usually this leaf lay no more than 3-4 cm below the top of the terminal shoot of the stem. In few instances (8 of 93: 8.6%) did the spider build its nest more than 10 cm below the tip of the terminal shoot. In one such instance an egg sac was placed 45 cm up a 75 cm stem in a small axillary leaf that had developed subsequent to the loss of an original leaf.

On both flowering and non-flowering stems spiders used significantly shorter and narrower leaves than predicted by the mean sizes of leaves on these two stem types (Table 3). These results suggest that the spiders actively selected relatively small leaves, although they might also select leaves at the top of the stems, since most of the small leaves grow there. Further, they also used significantly longer

Table 2.—Characteristics of nest sites on common milkweed. N's not all equal because not all variables were measured each year.

	Flowering stems		Non-flowering stems		
Variable[1]	N	$\bar{x} \pm$ SD (cm)	N	$\bar{x} \pm$ SD (cm)	p[2]
Height of stem	25	83.4 ± 12.4	40	51.1 ± 10.5	<0.0001
Height of egg mass	25	76.6 ± 15.3	90[3]	47.8 ± 10.5	<0.0001
Length of opposite leaf	16	10.2 ± 1.9	65[3]	7.4 ± 1.5	<0.03
Width of opposite leaf	16	3.0 ± 0.8	65[3]	3.1 ± 1.8	>0.7

[1]No significant between-year differences occurred in any of these variables ($P > 0.1$ in each Kruskal-Wallis Test)

[2]Difference between flowering and non-flowering stems; one-tailed Wilcoxon two-sample tests

[3]Includes 50 nests on caged, non-flowering stems. These nests were included since they did not differ from those of free-ranging individuals in height of stem ($P > 0.7$). Neither did they differ in height of egg mass ($P > 0.9$), length of opposite leaf ($P > 0.4$), and width of opposite leaf ($P > 0.4$) (Wilcoxon two-sample tests).

Table 3.—Leaf choice of *Misumena vatia* for nest sites on common milkweed.

Category	Size of sample of leaves in clone[1] N	$\bar{x} \pm$ SD (cm)	Size of leaves used by spiders N	$\bar{x} \pm$ SD (cm)	P (Wilcoxon two-sample test)
Flowering stems, length	124	14.2 ± 2.2	16	10.2 ± 1.9	<0.0001
Flowering stems, width	124	5.3 ± 1.9	16	3.0 ± 0.8	<0.0001
Non-flowering stems, length	135	11.7 ± 4.1	65[2]	7.4 ± 1.5	<0.0001
Non-flowering stems, width	135	4.5 ± 1.9	65[2]	3.1 ± 1.8	<0.0001

[1]Mean length and width of leaves from 15 randomly-chosen flowering stems and 15 randomly-chosen non-flowering stems. Leaves are paired: only one leaf of a pair, randomly selected, was measured. Some of the lower leaves had fallen from flowering stems by the time spiders laid their eggs.

[2]Includes 50 nests on caged, non-flowering stems. These nests were included since they did not differ from those of free-ranging individuals in height of stem ($P > 0.7$). Neither did they differ in length of opposite leaf ($P > 0.4$) or width of opposite leaf ($P > 0.4$). (Wilcoxon two-sample tests).

leaves on flowering stems than on non-flowering stems; however, these leaves were not wider than those used on non-flowering stems (Table 2). This result suggests that leaf width is a more important factor than leaf length in determining leaf choice.

I observed three spiders unsuccessfully attempting to fashion a large leaf into a nest. Each one subsequently used a smaller leaf as a nest site. Although nests in this study were invariably placed on milkweed leaves, no other plants within the study site had leaves or leaflets nearly as large as those routinely used by the spiders. Common forbs and shrubs in the area included cow vetch (*Vicia cracca*), yellow-rattle (*Rhinanthus crista-galli*), goldenrod (*Solidago* spp.), red clover (*Trifolium pratense*), pasture rose (*Rosa carolina*), and meadow-sweet (*Spiraea latifolia*). All were periodically searched carefully for *Misumena* nests.

General description of nests.—On milkweed, *Misumena* initially bent under the distal tip of a leaf, securing it to the under side of this leaf with a few strands of silk. Typically they remained inside the resulting folded leaf for a day or more (2.1 ± 1.6 S.D. days, N = 56 nests censused each morning and evening) before laying their eggs there and completing the nest. However, a few individuals left this site and moved to another site (N = 9), where they subsequently laid their eggs.

Spiders turned under about one-third of a leaf in making a nest on milkweed. In seven nests that I measured, the turned-under tissue averaged 2.7 cm (± 0.3 cm S.D.) in length.

Spiders always laid their eggs at night (N = 122), and by morning had completed the majority of their nest construction. Although I did not observe them exhaustively at night, I saw two different individuals laying eggs, at 23:30 and 01:30, respectively. By the time I observed spiders the following morning (05:30 - 09:00), almost all of them had pulled the distal part of the leaf tightly to the under side of the rest of the leaf (fig. 1). However, in three of 122 instances (2.5%), spiders had not completed this process by morning, and the filmy silk surrounding the egg sac proper remained visible. Spiders that laid their eggs the preceding night had invariably positioned themselves on the under side of the nest by morning (Fig. 1). The three spiders that did not completely close their nests during the first night finished the task on the following night.

Within two to three days several spiders secured their nests with strands of silk to surrounding vegetation. With few exceptions they attached it to an adjacent leaf of the stem bearing the nest, especially the one immediately under the leaf in which the nest was placed. Fig. 1 illustrates a typical pattern. This extra silk increases the stability of the nest, and pulling it closer to the lower leaf may provide the attending female with a hiding place (Fig. 1). However, it also facilitates access to the nest from the flat surface of the leaf below.

Numerous additional lines of silk were often subsequently produced in the immediate vicinity of the nest (Fig. 1). They do not play a major role in stabilizing the nest, but are probably a mere consequence of the attending spider

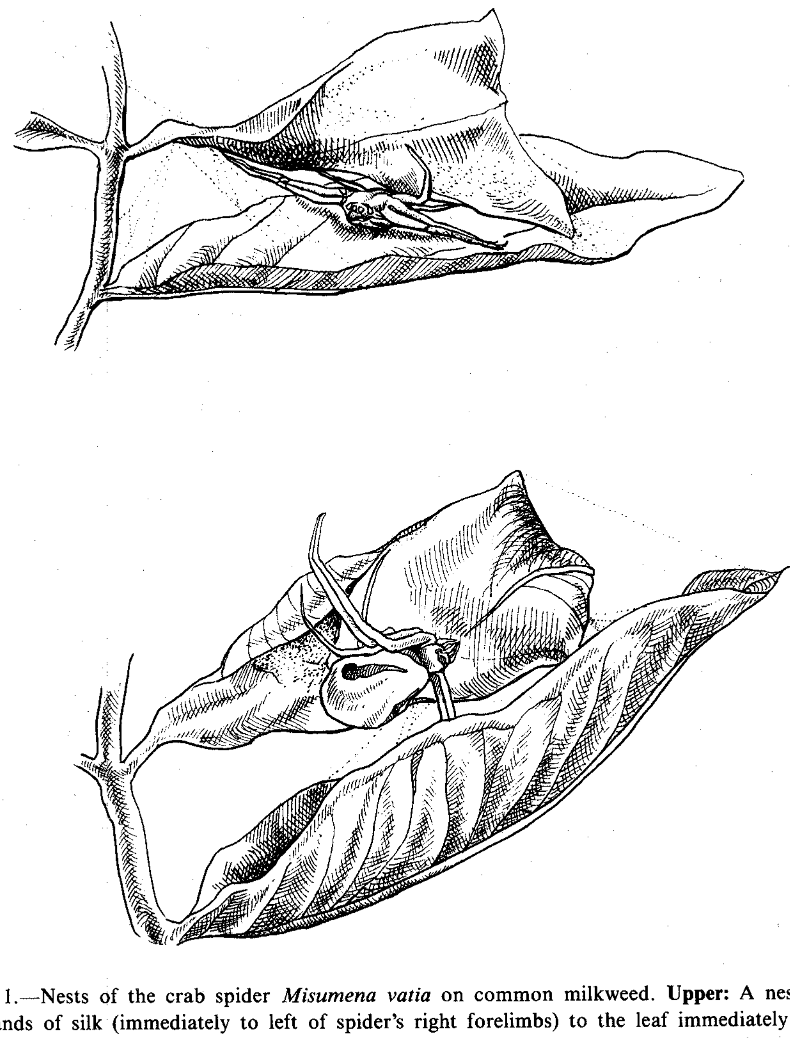

Fig. 1.—Nests of the crab spider *Misumena vatia* on common milkweed. **Upper:** A nest secured by strands of silk (immediately to left of spider's right forelimbs) to the leaf immediately under it, with the postreproductive female attending it in a position often assumed on nests drawn close to other leaves. However, many of the nests are made on leaves that do not grow closely to other leaves, and are therefore not attached to other structures. Strands of silk near the stem are intermittently laid down over the life of the nest and are unlikely to play a major role in stabilizing the nest. **Lower:** Nest rotated 90° to illustrate the position most frequently assumed by *Misumena* while attending nest. This extremely large postreproductive individual was 10 mm long (abdomen + cephalothorax) and weighed 110 mg. Illustrations by Elizabeth Farnsworth.

moving about near the nest. These post-reproductive individuals invariably left lines behind them wherever they moved.

I have occasionally found egg sacs of *Misumena* on other plants. Species used as nest-sites included pasture rose (*Rosa carolina*), spreading dogbane (*Apocynum androsaemifolium*), chokecherry (*Prunus virginiana*), and sensitive fern (*Onoclea sensibilis*).

DISCUSSION

Leaf choice.—Although crab spiders do not select milkweed leaves randomly, the mechanism governing this choice is not explicit. Spiders might either choose the highest leaves possible, or the leaves that provide ideal characteristics for a nest. However, a few data do suggest that leaf characteristics, rather than location, serve as the major basis for selection. Twice I have found spiders using small axillary leaves well down on the stem as nest sites. These leaves, which follow the loss of a main leaf, occur infrequently on milkweeds. They are also often the only medium-sized leaves below the tops of flowering plants. Additionally, individuals that used extremely large leaves experienced difficulty in manipulating them, probably because these leaves were thicker and larger than the ones usually used. All free-ranging individuals subsequently selected medium-sized leaves for nests. Only caged spiders confined to large leaves eventually fashioned nests out of them (Morse, unpubl.). In no instance did spiders using large leaves appose the two parts of the leaf closely, and, consequently, large areas of their nests were protected only by silk, probably making them extremely vulnerable to attack by parasitic insects (see Eason, Peck and Whitcomb (1967).

Problems of nest construction could also account for *Misumena*'s absolute choice of milkweed leaves as nest sites within the study area. Although the sample of free-ranging spiders I studied used milkweed leaves exclusively under natural circumstances, spiders that I confined to cages containing only pasture rose, spreading dogbane, or meadow-sweet fashioned nests of these leaves (Morse, unpubl.). None of these nests incorporated as much leaf material into the covering as did nests on medium-sized milkweed leaves; thus, larger areas were covered only by silk than in typical nests built on milkweed. It would be of interest to determine the spiders' relative preference for these different leaves as a function of the area of the resulting nests covered only by silk, and also as a function of the level of parasitism that such nests would experience. These nests, and nests on large milkweed leaves as well, could also be subject to greater desiccation than tightly-constructed nests. Hatching success of crab spider eggs in nests that I opened soon after laying was significantly lower than that of unmanipulated eggs (Morse, in prep.).

Movement to nest site.—The movement of spiders from their last hunting site, despite a mobility that was often inadequate to reach a different habitat, suggests a strong selective pressure for leaving the hunting site. Moving may minimize vulnerability to egg parasites. Egg parasitism by an ichneumonid wasp (*Trychosis cyperia*) and a phorid fly (*Megaselia* sp.) was relatively constant between 1980 and 1984, averaging about 15% per year (Morse and Fritz, in press). Simply moving away from the previously-used site might on average be advantageous. Moving is unlikely to bring a spider into a yet higher density of flowering stems and other spiders, and possibly higher concentrations of parasites, and it could take the spider to an area of lower density.

However, because some individuals moved much greater distances than the mean distance between the last hunting site and the nest site, conflicting pressures, rather than absolute mobility, may constrain the length of their move. Dangers to the adults may be played off against those associated with egg parasitism and egg predation. I do not have quantitative data on spider mortality at this time, but because relatively long movements require descending into the grass year, spiders may become vulnerable to predators unlikely to disturb them on the milkweed stems. Two likely predators sometimes common in the study area are the meadow vole (*Microtus pennsylvanicus*) and the garter snake (*Thamnophis sirtalis*). Both species regularly prey on arthropods (Zimmerman 1965; Hamilton 1951). Further, during the one year of this study in which a *Microtus* outbreak occurred, twice as many spiders disappeared after leaving their last hunting site, not to be found again, than in any other year (Morse, unpubl.)

ACKNOWLEDGMENTS

I thank J. Eccleston and R. S. Fritz for comments on the manuscript. H. Townes identified the ichneumonid wasp, and E. Fisher identified the phorid fly. R. Bartlett generously permitted the use of his property. E. Cravey, C. Duckett, E. Farnsworth, D. Forbes, R. S. Fritz, J. Hoffman, E. K. Morse, and A. Raynsford assisted in the field. E. Farnsworth drew Fig. 1. This work was supported by the National Science Foundation (DEB80-08502, DEB81-18105, and BSR81-18105-A01).

LITERATURE CITED

Bristowe, W. S. 1958. The world of spiders. Collins, London.

Comstock, J. H. 1940. The spider book. Revised and edited by W. J. Gertsch. Doubleday, Doran, New York.

Eason, R. R., W. B. Peck and W. H. Whitcomb. 1967. Notes on spider parasites, including a reference list. J. Kansas Entomol. Soc., 40:422-434.

Enders, F. 1977 Web-site selection by orb-web spiders, particularly *Argiope aurantia* Lucas. Anim. Behav., 25:694-712.

Fritz, R. S. and D. H. Morse. 1985. Reproductive success, growth rate and foraging decisions of the crab spider *Misumena vatia*. Oecologia, 65:194-200.

Hamilton, W. J., Jr. 1951. The food and feeding behavior of the garter snake in New York State. Amer. Midland Nat., 46:385-390.

Hildén, O. 1965. Habitat selection in birds. Ann. Zool. Fennici, 2:53-75.

Morse, D. H. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Mass.

Morse, D. H. and R. S. Fritz. *In press*. The consequences of foraging for reproductive success. *In* Foraging Behavior II. (A. C. Kamil *et al.*, eds.). Plenum, New York.

Partridge, L. 1978. Habitat selection. *In* Behavioral Ecology: an Evolutionary approach. First edition (J. R. Krebs and N. B. Davies, eds.). Sinauer. Sunderland, Mass.

Zimmerman, E. G. 1965. A comparison of the habitat and food of two species of *Microtus*. J. Mammal., 46:605-612.

Manuscript received March 1985, revised June 1985.