

FORAGING PATTERNS AND TIME BUDGETS OF THE CRAB SPIDERS *XYSTICUS EMERTONI* KEYSERLING AND *MISUMENA VATIA* (CLERCK) (ARANEA: THOMISIDAE) ON FLOWERS

Douglass H. Morse

Division of Biology and Medicine
Brown University
Providence, Rhode Island 02912, USA

ABSTRACT

Xysticus emertoni Keyserling (Araneae: Thomisidae) hunted regularly for insects on flowers of common milkweed (*Asclepias syriaca* L.), but only infrequently on goldenrod (*Solidago juncea* Ait.) and rarely on pasture rose (*Rosa carolina* L.). Individuals usually remained less than two days on a milkweed stem and fed primarily on honey bees (*Apis mellifera* L.) and nocturnal noctuid and geometrid moths. The largest common prey, bumble bees (*Bombus* spp.) were very seldom captured. *Misumena vatia* (Clerck), a second species of thomisid that hunted on flowers in the study area, by contrast hunted frequently on milkweed, goldenrod, and pasture rose. Individuals remained over twice as long on milkweeds and captured bumble bees regularly, as well as honey bees and nocturnal moths. As a consequence, they captured over twice as much prey biomass per day as *Xysticus*. I hypothesize that the difference between the two species in time spent per stem and in frequency of using goldenrod and pasture rose is a consequence of the difference in success of prey capture, primarily a failure of *Xysticus* to include bumble bees regularly in their diet. *Xysticus emertoni*, a member of a largely litter-inhabiting genus, probably secures the majority of its food there, rather than at flowers.

INTRODUCTION

Xysticus emertoni Keyserling (Araneae: Thomisidae) is one of two crab spiders that regularly forage on milkweed (*Asclepias syriaca* L.) growing along the coast of Maine. *Xysticus* is an ambush hunter that lies in wait for the large numbers of insects that are attracted to milkweed when its flowers are producing nectar.

Xysticus emertoni is a medium-brown spider, with dark brown markings on its abdomen. It may range up to 12 mm in length (cephalothorax + abdomen) and immediately prior to egg-laying, females may weigh as much as 250 mg. Their robust cephalothorax and legs are relatively larger than those of the other common crab spider found on milkweed in the study area, *Misumena vatia* (Clerck), but their abdomen is relatively smaller. *Xysticus emertoni* is a member of a primarily litter-dwelling genus, which may account for these differences, although a few species of *Xysticus* do hunt regularly in flowers (Gertsch 1939, 1979).

Earlier (Morse 1981a) I reported on the foraging patterns and time budget of *M. vatia* on milkweed and other flowers in the study area. Since *Xysticus* is a member of a more

cursorial ground and litter-dwelling group of crab spiders than *Misumena* (Gertsch 1939, 1979), it seemed appropriate to compare its foraging on flowers with that of *Misumena*, which appears to hunt almost exclusively at flowers, at least when in its last instars. Given the somewhat different attributes but similar size of these two species, a comparison between them may provide useful insight into the factors that dictate the foraging patterns of crab spiders, as well as ambush predators in general.

In particular, I relate differences in their behavior on milkweed flowers to differences in hunting success. Hunting success has important implications for both giving-up times (Charnov 1976) of individuals on a given milkweed inflorescence or stem and the frequency with which they occupy other common flowers.

METHODS

This study was conducted in Bremen, Lincoln Co., Maine during July and August of 1979, 1980, and 1981. The spiders, all adults, occupied a field and some adjacent low brushy growth that supported clones of milkweed. Twenty of these individuals were marked with pens using indelible ink.

Asclepias syriaca grows from rhizomes in clones of one to several thousand stems (Woodson 1954). The clones in which these spiders were studied contained 200-400 flowering stems. The flowering stems in the study area produced 1-5 inflorescences (umbels), each with 20 to 70 flowers. When in the peak of bloom milkweed attracts large

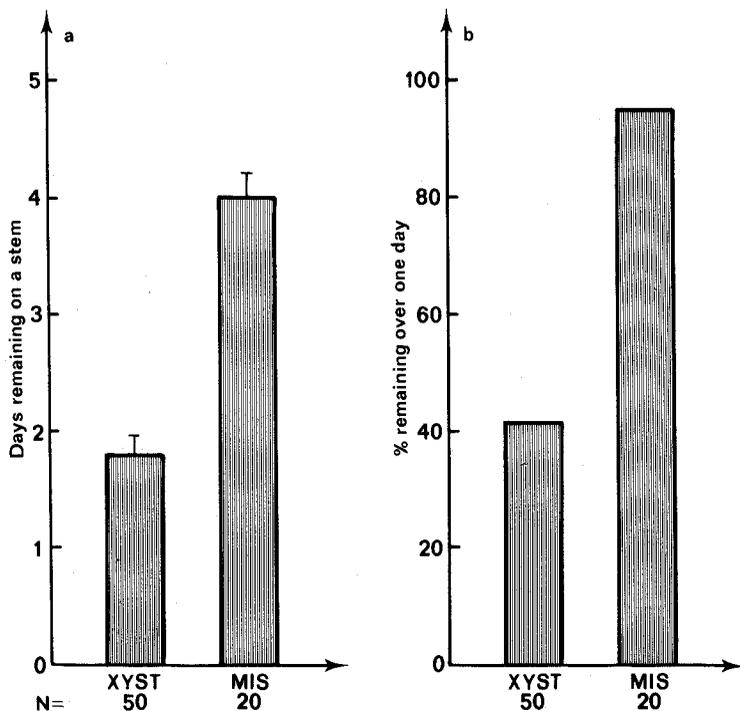


Fig. 1a.—Number of days that *Xysticus* and *Misumena* remained on a stem, \pm 2 S. D. ($p < 0.001$ in a two-tailed Mann-Whitney U Test). Fig. 1b. Percentages of *Xysticus* and *Misumena* remaining on a stem for more than one day ($X^2 = 14.29$, $p < 0.001$, $df = 1$, using original data).

Table 1.—Numbers of prey captured, with percentage of total biomass in parentheses.

Food item	<i>Xysticus</i>	<i>Misumena</i>
Moths (Noctuidae, Geometridae)	14 (32.8%)	21 (23.3%)
<i>Apis mellifera</i>	7 (21.4%)	25 (34.1%)
Other Hymenoptera (excluding <i>Bombus</i>)	6 (13.8%)	3 (4.1%)
Jumping spider (Salticidae)	1 (8.1%)	
Tachinid flies (Tachinidae)	10 (13.8%)	5 (3.1%)
Ladybird beetles (Coccinellidae)	5 (8.1%)	
Other	1 (2.1%)	7 (2.1%)
<i>Bombus</i> spp.		10 (33.3%)

numbers of insects, especially large social bees (Apidae) and nocturnal moths (primarily Noctuidae and Geometridae) in the study area (Morse 1982). Umbels bloom sequentially up a stem, and the different stems are not in perfect synchrony, so that large numbers of flowers are in nectar-producing condition at a clone for two weeks or more each year.

Spiders were monitored hourly between 0730 and 1730, the period during which they captured virtually all of their diurnal prey. In that *Xysticus* almost always retained their food items for over an hour (similarly to *Misumena*), it was possible to obtain an accurate estimate of the amount and type of foods taken. Limited nighttime observations were also made, and corpses of prey still being consumed or located below the spiders early the following morning were recorded. Total biomass captured was obtained by using the mean live weights of specimens of the various prey species (Morse 1979, 1981a).

Several spiders (8) were also monitored continuously for one day or more, permitting me to quantify the numbers of potential prey and attacks made on them during they day. This permitted calculation of foraging success and response to different prey species.

In the following sections I will first present the results of this study on *Xysticus* and then compare them with *Misumena*'s performance on milkweed. Unless otherwise indicated, the data on *Misumena* come from a companion study (Morse 1981a) that compared the foraging patterns and time budgets of that species on three different species of flowers that they regularly occupied.

RESULTS

Time spent on a stem.—*Xysticus* averaged less than two days on a stem (Fig. 1a), with a maximum of four days. Less than half of the individuals remained more than one day (Fig. 1b). In contrast, *Misumena* remained an average of four days on a stem (Fig. 1a), and virtually all individuals remained for more than a day (Fig. 1b). Both of these between-species differences were significant (Fig. 1). Since individual stems (or even umbels) usually attracted substantial numbers of insects for several days, changes in prey abundance were unlikely to account for any of these differences.

Prey captured.—Nocturnal moths and honey bees (*Apis mellifera* L.) made up the largest proportions of biomass taken by the *Xysticus* monitored (Table 1). Other frequently-captured prey included certain hymenopterans and tachinid flies (Tachinidae). *Xysticus* also captured several ladybird beetles (Coccinellidae), generally regarded as toxic (Wickler 1968). Perhaps *Xysticus* is not sensitive to toxic factors, since one individual was

observed feeding on a last-instar monarch butterfly (*Danaus plexippus* L.) larva (not included in the spiders censused for food captures). Additionally, one *Xysticus* captured a female jumping spider (*Phidippus* sp., Salticidae) larger than itself. Surprisingly, although bumble bees were the commonest visitors to the clones of milkweed upon which these observations were made (Morse 1981b; Morse and Fritz in press), none were captured in this sample.

Bumble bees and honey bees were the most important prey items of *Misumena*, with nocturnal moths also playing an important role. Thus, a major difference was the absence of bumble bees from *Xysticus*' prey items, but relatively higher proportions of other items, such as tachinid flies, solitary bees, and ladybird beetles (*Xysticus* have very occasionally been found feeding on bumble bees at other times, so this difference is not really absolute). Allocation of biomass from the various prey types (Table 1) differed highly significantly between *Xysticus* and *Misumena* ($X^2 = 20.52$, $p < 0.001$, $df = 5$, using all categories but the jumping spider and ladybird beetles). Although one might initially attribute this marked difference to niche partitioning, the densities of both spiders were so low [maximum count of 14 *Xysticus* ($\bar{x} = 9.5 \pm 3.6$ S.D. during 18-25 July) and 7 *Misumena* ($\bar{x} = 5.0 \pm 1.5$ D.S. during 18-25 July) on 387 flowering stems] that it is very unlikely that this factor played any role in the differences noted.

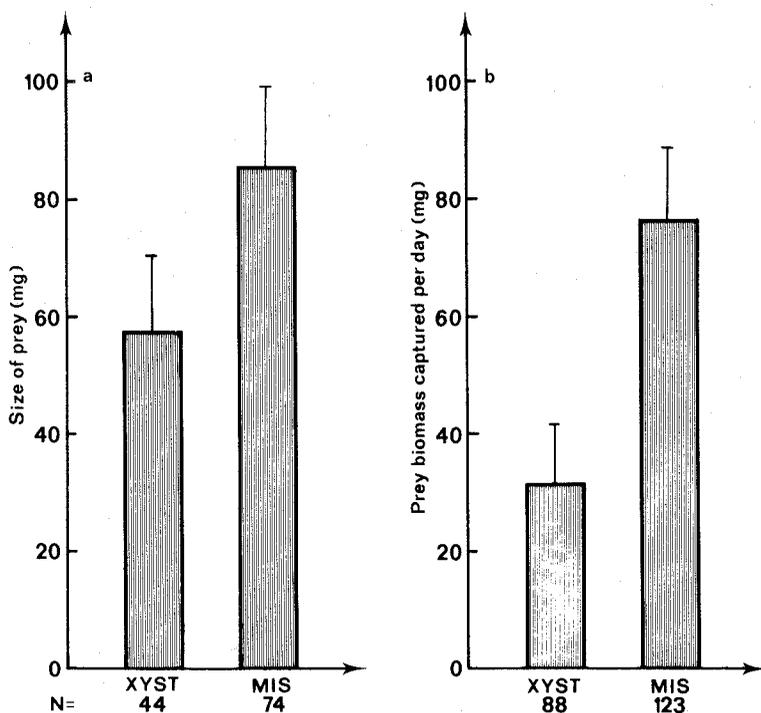


Fig. 2a.—Size of prey captured by *Xysticus* and *Misumena*, ± 2 S. D. ($U = 591$, $p < 0.002$ in a one-tailed Mann-Whitney U Test). Fig. 2b. Biomass of prey captured daily by *Xysticus* and *Misumena*, ± 2 S. D. Average rates of capture of *Xysticus* were significantly lower than those of *Misumena* ($U = 96$, $p < 0.025$ in a one-tailed Mann-Whitney U Test). Additionally, *Xysticus* observed only one day captured an average of 19.2 mg of prey/day ($N = 15$); *Misumena* observed only one day, 37.5 mg/day ($N = 2$).

Table 2.—Number of prey within attack range (within one spider body-length), prey attacked, and capture success of *Xysticus* and *Misumena*. Observations made during constant monitoring of *Xysticus* (84.25 hr) and *Misumena* (107.50 hr) throughout the day. The total number of observations is in parentheses.

Prey	<i>Xysticus</i>			<i>Misumena</i>		
	Prey within range	Prey attacked	Prey captured	Prey within range	Prey attacked	Prey captured
<i>Bombus</i>	0.78 (66)	0.18 (15)	— (0)	0.80 (86)	0.26 (28)	0.02 (2)
Diptera	0.05 (4)	0.05 (4)	0.02 (2)	0.02 (2)	0.02 (2)	0.02 (2)
<i>Apis</i>	0.10 (8)	— (0)	— (0)	0.30 (32)	0.14 (15)	0.01 (1)
Other	0.07 (6)	0.05	0.04 (3)	0.03 (3)	0.01 (1)	— (0)

Xysticus' prey were significantly smaller than those of *Misumena* (Fig. 2a). This difference occurred largely because *Xysticus* failed to capture bumble bees, the largest common prey at these flowers.

Rate of capture of biomass.—*Xysticus* captured an average of 23.1 mg of diurnal prey per day and additional 8.5 mg of nocturnal moths, for a total of 31.6 mg of prey per day. *Misumena*, on the other hand, captured, over 2.5 times as much diurnal prey and over twice as much nocturnal prey biomass. The overall difference is significant (Fig. 2b).

Daily time budget.—*Xysticus* spent about 85% of their time hunting on the plants and 15% of the time feeding (Fig. 3). The greatest proportions of the hunting time were spent under the umbels and the flowers of the umbels. The times allotted to hunting and feeding were nearly identical to those of *Misumena* (Fig. 3); however, the locations of the hunting sites were markedly and significantly different (Fig. 3). Most of *Misumena*'s hunting was done on top of the inflorescences, rather than under or in the inflorescences, as with *Xysticus*.

Attacks on prey and success of capture.—The frequency of attacks and success of capture were determined from studies on continually-observed individuals (Table 2). Bumble bees were the most frequent visitors, and the most frequent species to come within strike range (defined as one spider body-length). Only about one-fourth of these bumble bees were attacked, and none were captured. Numbers of other visitors during the observation period were too small to make detailed comparisons, but they tended to be attacked with considerably higher frequency than the bumble bees. However, *Xysticus* attacked nearly as high a proportion of bumble bees that came within range as did *Misumena* (25.8% vs. 32.6%). This difference is not significant ($X^2 = 0.53$, $p > 0.3$, $df = 1$, using data in Table 2). The data suggest a possible trend for *Misumena* to respond to honey bees more frequently than do *Xysticus*, but the frequency of honey bees available to *Xysticus* was too low to permit testing.

Use of other flowers by *Xysticus*.—No observations were made of marked *Xysticus* individuals moving between milkweed and other species of flowers, although *Xysticus* were occasionally seen on other species of flowers, including cow vetch (*Vicia cracca* L.) growing within a few meters of the milkweed. Given the frequency with which they moved on and off milkweeds, one would expect them to shift between plant species where it would be profitable. However, of the other flowers attracting the most potential prey (and *Misumena*), *Xysticus* was seen only twice on pasture rose (*Rosa carolina* L.) over several summers of intensive observations of *Misumena*. Although observed more

frequently on goldenrod (*Solidago juncea* Ait.), it was not seen often enough there to obtain data for quantitative analysis. A *Xysticus* observed on goldenrod did, however, capture a bumble bee.

DISCUSSION

Characteristics of *Xysticus*.—*Xysticus*' visitation patterns on milkweed differed markedly from those of *Misumena*. Individuals remained at a site for a much shorter period of time, and once marked individuals disappeared they were only seldom resighted, as opposed to *Misumena*, in which individuals leaving a foraging site were frequently rediscovered when stems were carefully searched. This suggests that adult *Xysticus* spend much of their time in the litter, as opposed to adult *Misumena*, which spend virtually all of their time on flowering plants, and most of that on the flowers, or at least in searching for flowers. This difference is perhaps not surprising, in that *Xysticus* is a member of a large genus composed primarily of litter-dwelling species (Gertsch 1939). The dull brown coloration of *Xysticus* is similar to that of many litter-dwelling spiders, and its larger legs probably contribute to making it more cursorial than *Misumena*.

Suitability of different flower species as hunting sites.—There is, however, another aspect to *Xysticus*' brief appearances on these flowers. Their rate of prey uptake on milkweed was markedly lower than that of *Misumena*, and it is thus possible that these sites are simply not highly profitable ones for them. *Xysticus* were almost completely

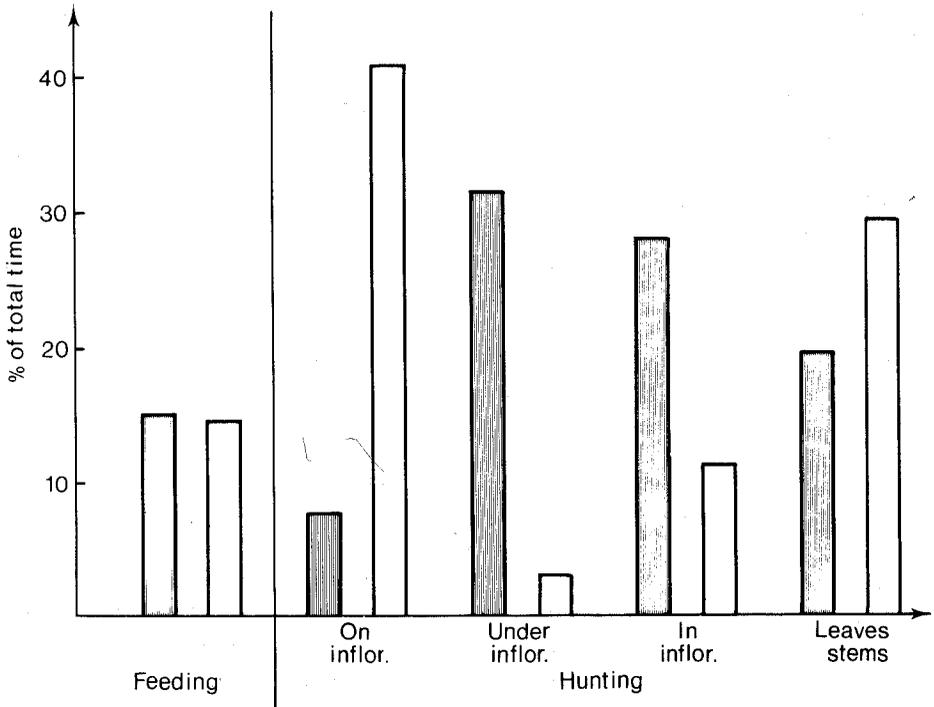


Fig. 3.—Diurnal time budget of *Xysticus* (black bars) (544.5 hr) and *Misumena* (white bars) (716.0 hr) on milkweed. The hunting positions of the two species differed significantly from each other ($X^2 = 29.23$, $p < 0.001$, $df = 3$, using an arcsine transformation).

unsuccessful in capturing bumble bees, although these bees were the commonest visitors to the flowers, and constituted one of the two most important items (over 40%) in the food of *Misumena* on milkweed (the other being honey bees). Failure to incorporate these prey into their diet may make the difference between milkweed inflorescences being a profitable or unprofitable hunting site for *Xysticus*. Further, milkweed was a more profitable hunting site for *Misumena* than either goldenrod or pasture rose (Morse 1981a), suggesting that it may provide the richest source of food for ambush hunters. It was also the only one of the three flower species at which bumble bees were not the overwhelmingly most important prey item for *Misumena*. *Misumena* captured nearly twice as much biomass per day on goldenrod as on pasture rose, and further, its diet was more varied there than on pasture rose, where virtually the entire biomass was composed of bumble bees. Thus, there was progressively less available food, and markedly fewer prey other than bumble bees, on goldenrod and pasture rose than on milkweed. These two factors are consistent with the only occasional appearance of *Xysticus* on goldenrod, and its virtual absence from pasture rose.

The difference in hunting behavior of *Xysticus* and *Misumena* in the milkweed inflorescences could in part account for the differences in prey capture patterns. *Xysticus* remained more concealed than did *Misumena*, which could either be a consequence of its hunting patterns in the litter, or be associated with concealment from prey or predators. *Xysticus* should be more conspicuous against the white background of milkweed inflorescences than *Misumena*, which is typically white on milkweed and cryptic both at visual and ultraviolet wave lengths (Morse, unpubl.). In spite of this, the proportion of approaching bumble bees attacked by *Xysticus* was not significantly lower than that of *Misumena*.

Giving-up times.—The short times (= giving-up times of Charnov 1976) spent on milkweed by *Xysticus* are probably best explained in the context of environmental patchiness, given this spider's presence both on milkweed stems and in the litter layer. Assuming that *Xysticus* have energetic demands comparable to those of similar-sized *Misumena*, their relatively low success and short giving-up times on milkweed stems suggest that their rates of prey capture often fall below those to be obtained at hunting sites away from the flowers (see Charnov 1976; Pike, Pulliam and Charnov 1977). In fact, these *Xysticus* exhibited giving-up times that were similar to those of *Misumena* on senescent milkweed stems (Morse and Fritz, 1982), suggesting that the two species responded to very different densities of prey. Morse and Fritz (1982) found that numbers of insect visitors, rather than more direct measures (e.g., attack or capture frequency), provided the best correlation between observed and predicted frequencies of umbel occupation by *Misumena*. However, since umbels occupied by *Xysticus* were visited by insects at frequencies similar to those occupied by *Misumena*, actual capture rates may play an important direct role in *Xysticus*' choice of umbels. If the two species responded in different ways to these various cues, this would be of major interest in untangling the web of variables that dictate the choice and continued occupation of a hunting site. One could experimentally test whether frequency of visitation to an umbel does play an important role in determining *Xysticus*' giving-up time by increasing the frequency of prey visitation, probably in a screened flight cage. The predicted frequency of insect visits necessary to extend *Xysticus*' giving-up time to that of *Misumena* can be determined by calculating the number of insect visits necessary for *Xysticus* to realize a hunting success comparable to that of *Misumena*. Fig. 2b suggests that an increase in visitation frequency of over two-fold would be required.

ACKNOWLEDGMENTS

I thank R. S. Fritz for comments on the manuscript. R. Bartlett generously permitted use of his property. C. Duckett, D. Fleming, R. S. Fritz, C. Jacobs, A. Keller, and E. K. Morse assisted in the field. W. J. Gertsch identified the spiders. Supported by the National Science Foundation (DEB78-02256 and DEB80-08502).

LITERATURE CITED

- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.*, 9:129-136.
- Gertsch, W. J. 1939. A revision of the typical crab-spiders (Misumeninae) of America north of Mexico. *Bull. American Mus. Nat. Hist.*, 76:277-442.
- Gertsch, W. J. 1979. *American spiders*, 2nd ed. Van Nostrand Reinhold, New York, 274 pp.
- Morse, D. H. 1979. Prey capture by the crab spider *Misumena calycina* (Araneae: Thomisidae). *Oecologia*, 39:309-319.
- Morse, D. H. 1981a. Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three native flowers. *Amer. Midl. Natur.*, 105:358-367.
- Morse, D. H. 1981b. Modification of bumble bee foraging: the effect of milkweed pollinia. *Ecology*, 62:89-97.
- Morse, D. H. 1982. Patterns of pollinia accretion and loss on bumble bees, and their implications for outcrossing. *Oecologia*, 53:187-196.
- Morse, D. H. and R. S. Fritz. 1982. Experimental and observational studies of patch choice at three scales by the crab spider *Misumena vatia*. *Ecology*, 63:172-182.
- Pyke, G. H., H. R. Pulliam and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.*, 52:137-154.
- Wickler, W. 1968. *Mimicry*. Weidenfeld and Nicolson, London, 255 pp.
- Woodson, R. E. 1954. The North American species of *Asclepias*. *Ann. Missouri Bot. Gard.*, 41:1-211.

Manuscript received December 1981, revised February 1982.