

THE ROLES OF PREY AND FLOWER QUALITY IN THE CHOICE OF HUNTING SITES BY ADULT MALE CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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ABSTRACT. Since adult male crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) feed sparingly and do not increase in mass, we wished to determine whether they responded to cues from hunting sites that would maximize their prospects of capturing prey. These spiders used cues from both prey and substrate as indicators of satisfactory hunting sites in the absence of females. They remained longer on red clover (*Trifolium pratense*) and ox-eye daisies (*Chrysanthemum leucanthemum*) in peak-condition flower than on senescent ones, and longer on daisies in peak-condition flower with prey than on peak-condition flowers without prey. They also remained as long on senescing daisies and clover with prey as on daisies and clover in peak-condition flower, but without prey. Thus, the effects of prey and substrate acted cumulatively on daisy, but not clover. However, they did not respond markedly differently on flowering and senescing branches of goldenrod (*Solidago canadensis*), although individuals on peak-condition flowers visited by prey remained somewhat longer than those at sites not visited by prey.

Current optimal foraging theory proposes that animals forage in a way that maximizes their rate of prey intake (Pyke et al. 1977; Morse & Stephens 1996). Adult male *Misumena vatia* (Clerck 1757) (Thomisidae) are particularly interesting in this regard since they do not increase in size during their adult stage (Gertsch 1939). The literature suggests that adult male spiders spend much of their time searching for females (Foelix 1996) or guarding penultimates prior to molt (Watson 1990; Dodson & Beck 1993), and they are often thought to take few or no prey during this period (Turnbull 1962; Vollrath 1987). We thus wished to establish whether precise hunting patch-choice behavior of adult male *Misumena vatia* would be reduced, relative to that of many other organisms whose individuals will grow rapidly at this time. This matter takes on added interest in that large females of this highly dimorphic (Gertsch 1939; Dondale & Redner 1979) species hunt voraciously and in some instances may increase in mass by as much as an order of magnitude as adults (Fritz & Morse 1985), a time during which they exhibit rather precise patch choice (Morse & Fritz 1982; Morse 1988).

In spite of these differences, male *Misumena* Latreille 1804 do hunt and capture prey in the field. We have observed that they frequently occupy flowers that attract nectar and pollen-seeking insects of a wide size and taxonomic range, including insects as small or smaller than male *Misumena*. We have also observed them with captured prey in the field, most often small Diptera ranging in size up to that of the spiders themselves. Further, they readily take prey in the laboratory. Thus, tests of flower choice should be both possible and realistic.

By testing the response of males to various hunting sites in the absence and presence of prey, we attempt to establish the importance of flower quality and prey presence in assessment of hunting sites by adult male crab spiders. We use giving-up times (Charnov 1976) as measures of site favorability. If male *Misumena* respond to predictions of this aspect of optimal patch choice theory (reviewed in Stephens & Krebs 1986), they should remain longer on high-quality flowers, even in the absence of prey, than on low-quality flowers, since high-quality flowers should eventually attract more potential prey than low-quality ones. (*Note:* This prediction depends on the ability of the males to evaluate flower condition in the absence of prey.) Quality may here be characterized by flower condition—nectar

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producing or senescent. Also, male spiders should remain longer on a substrate, regardless of quality as defined here, if a prey item is present, than in its absence. Visiting prey should also provide cues to a good hunting site, since a substrate capable of attracting one prey is likely to attract more. Both cues could also combine to produce a maximum response.

METHODS

We conducted this study in a 1 ha field in Bremen, Lincoln County, Maine from June–August, 1993 and 1994. The site contained several species of flowering plants and is described in greater detail elsewhere (Morse 1981a; Morse & Stephens 1996).

Adult male crab spiders were collected from flowers along roadsides in Lincoln County, Maine (Bremen, Bristol, South Bristol). Upon capture, they were maintained in clear 7 dram plastic vials (5 cm high, 3 cm diameter) and fed small moths and flies every other day. We removed discarded prey items and cleaned the vials twice weekly. All experimental individuals retained at least three of their four raptorial forelimbs, typical of adults in the field. Other experiments with males have revealed no differences associated with the loss of a single forelimb (A.R. Holdsworth & D.H. Morse unpubl. data). We used the small (*ca.* 4 mg) syrphid fly *Toxomerus marginatus* (Say) (Syrphidae) for the prey presentations. This extremely common species (Morse 1979, 1981a, 1981b) is one of the most frequent prey taken by adult male *Misumena*, and by females as well (Morse 1979, 1995).

We used these spiders to run experiments on giving-up times, both 1) in the absence of and 2) in the presence of prey. To determine whether male spiders used flower quality alone as a cue in patch-choice decisions, we measured giving-up times of adult males in the absence of prey on high and low-quality red clover (*Trifolium pratense*), high and low-quality ox-eye daisy (*Chrysanthemum leucanthemum*), and high and low-quality goldenrod (*Solidago canadensis*). High-quality substrates were those whose flowers were in full bloom, and poor-quality substrates were those whose flowers had senesced. A close relationship exists between flower quality as here defined and numbers of visiting insects (Morse

& Fritz 1982). Spiders used in this experiment were not fed during the two preceding days, ensuring that they were in a similar non-satiated state (D.H. Morse unpubl. data).

We introduced each spider to the appropriate substrate by allowing it to climb onto a thin sable-hair brush and then slowly positioning the tip of the brush close to the flower until the spider climbed onto it. We terminated the experiment when the spider left the flower onto which it was introduced, or after 1 h. Tests were run only on clear or partly cloudy days between 0900–1700 h EDT. We did not monitor test flowers for previous insect visitation but refrained from using flowers containing spider silk from previous visitors.

We ran tests on clover and daisy using unscreened flowers, discarding tests if insects visited during the experimental period. This open-field test was quick and convenient, since insect visitors to the vicinity could almost always be chased from a surrounding flower before they would land on a focal flower. Spiders used in more than one experiment were never run on consecutive days, nor more than once in a particular experiment. All goldenrod experiments in the absence of insects were conducted in a large, walk-in screen cage (1.7 × 1.7 × 1.7 m) because the frequency of small insects on large inflorescences was so high that unscreened inflorescences seldom were without insects. Goldenrod inflorescences were thinned when in apposition to each other. High-quality branches were designated as those in which at least ¾ of the flower heads were in bloom. All of the flower heads had senesced on low-quality branches.

To assess the role of prey in determining patch choice, we tested in the same way the giving-up times of male crab spiders on the same flower species, to which small syrphid flies were introduced. We captured the syrphid flies used in the study with a large, open-mouthed jar (7 cm diameter, 17 cm height) that was slowly lowered over them as they fed at flowers. Flies were introduced onto test flowers within 5 min of the spiders, either by slowly lowering this upside-down jar containing syrphid flies over the flower until an individual climbed from the jar to the flower, or by slowly moving a fly from the jar on a sable-hair brush toward a test flower until it climbed onto that flower. The spiders did not respond to either the slowly-moving jar or

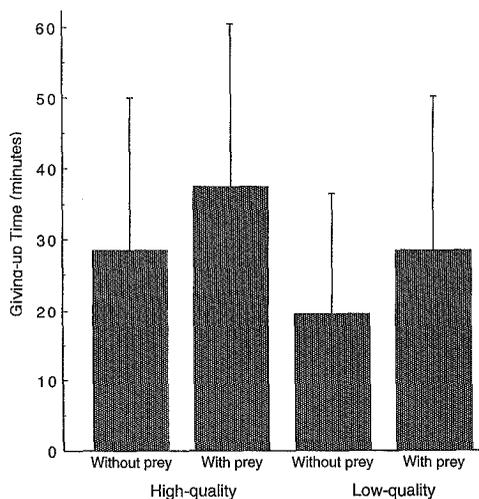


Figure 1.—Mean giving-up times \pm 1 SD of adult male crab spiders on daisy (*Chrysanthemum leucanthemum*) inflorescences. Inflorescences at peak flowering (high quality) or senesced (low quality); single syrphid fly *Toxomerus marginatus* present or absent. *n*'s as in Table 1.

brush, so runs were combined. Runs were discarded if the spider left the flower before prey were successfully introduced or if the fly left the flower before the spider responded to it. Giving-up times were measured from the moment the fly elicited a response from the spider (orientation toward prey or movement toward prey). We also discarded the occasional runs in which the spider captured the prey. Specimens of *M. vatia* were deposited in the American Museum of Natural History.

RESULTS

Daisy.—A significant difference occurred among the experiments run on high and low-quality daisy inflorescences with and without prey (Fig. 1: $H = 13.65$, $df = 3$, $P < 0.01$ in a Kruskal-Wallis one-way ANOVA). Spiders on flowers without prey remained 1.5 \times as long on high-quality inflorescences as on low-quality inflorescences.

Introduction of prey to both high and low-quality inflorescences resulted in a nearly 50% increase in giving-up times over those without prey (Fig. 1). The difference between high and low-quality inflorescences with prey was also about 50%, with the result that low-quality inflorescences with prey exhibited giving-up times nearly identical to those of high-quality

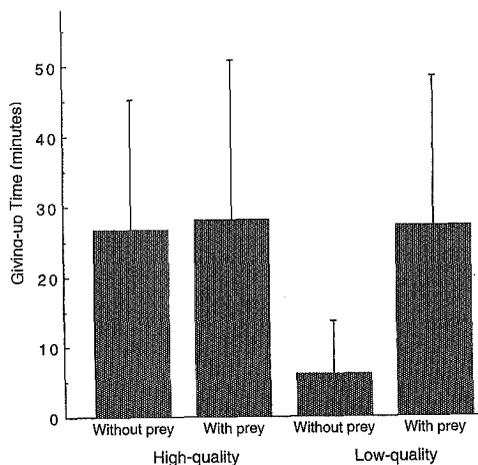


Figure 2.—Mean giving-up times \pm 1 SD of adult male crab spiders on red clover (*Trifolium pratense*) inflorescences. Flower quality and prey as in Figure 1, *n*'s as in Table 1.

inflorescences without prey. Thus, flower quality and prey acted in an additive way.

Clover.—A significant pattern also occurred among the experiments run on high and low-quality clover inflorescences with and without prey (Fig. 2: $H = 22.97$, $df = 3$, $P < 0.001$, same test). Spiders on flowers without prey remained over 4 \times as long on high-quality inflorescences as on low-quality ones.

Introduction of prey did not affect the time that spiders remained on high-quality clovers, but those on low-quality flowers remained over 4 \times as long if prey were introduced. However, giving-up times of spiders provided with prey on low-quality inflorescences were virtually identical to those of spiders in high-quality inflorescences, with or without prey introduction (Fig. 2).

Goldenrod.—No significant difference occurred among the experiments run on high and low-quality goldenrod inflorescences with and without prey (Fig. 3: $H = 6.71$, $df = 3$, $0.1 > P > 0.05$, same test). Spiders did remain 1.5 \times as long on high-quality goldenrod inflorescences with prey as on any of the other three choices, however, the only trend in the results (Fig. 3). Giving-up times of all three other experimental groups on goldenrod were virtually identical (Fig. 3). High-quality inflorescences without prey did not retain spiders any longer than low-quality inflorescences. Thus, the re-

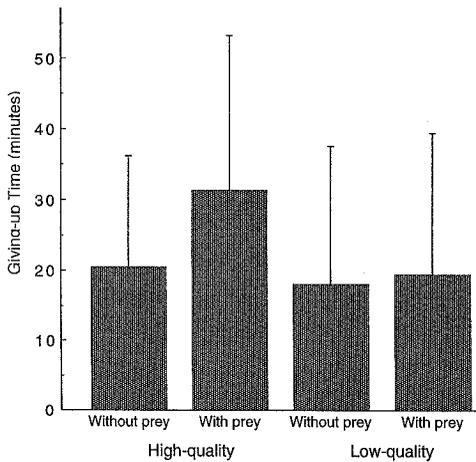


Figure 3.—Mean giving-up times \pm 1 SD of adult male crab spiders on goldenrod (*Solidago canadensis*) inflorescences. Flower quality and prey as in Figure 1, *n*'s as in Table 1.

sults for goldenrod differed somewhat from those of both daisies and clover.

Variance.—In general the results all exhibited high variance, primarily the consequence of varying numbers of individuals remaining on an inflorescence for the entire 60 min of an experiment. Not surprisingly, numbers of spiders remaining 1 h or more differed among treatments and among flower species in a way that closely matched the results illustrated in Fig. 1–3 (Table 1). It is also important to note that in almost every instance the mean times portrayed in Figs. 1–3 are underestimates, since the experiments were terminated after 1 h (Table 1).

DISCUSSION

Under some circumstances adult male *Misumena* appear to use both flower quality and prey cues in assessing hunting sites. Daisies and clover both closely fit our original prediction that spiders would spend longer times on high-quality flowers than on poor ones. However, when prey were present, poor-quality daisies and clover retained spiders as long as high-quality clover in the absence of prey, demonstrating that more than one cue can serve as an indicator of good hunting sites. Although showing a qualitatively similar pattern, performances of the spiders nevertheless differed somewhat on the two flowers: the results from daisies suggested an additive effect of flower quality and prey; i.e., high-quality

Table 1.—Percentage of individuals in different experiments that remained on an inflorescence one hour or more, with sample size in parentheses.

Species	No prey		Prey	
	High-quality	Low-quality	High-quality	Low-quality
Daisy	23 (30)	12 (26)	43 (28)	32 (25)
Clover	13 (15)	0 (16)	27 (15)	27 (15)
Goldenrod	6 (18)	7 (15)	28 (32)	13 (31)

sites with prey > high-quality sites without prey = low-quality sites with prey. In contrast, those from clover suggested a substitutive effect: high-quality sites with prey = high-quality sites without prey = low-quality sites with prey. This difference between the two flower species is most evident in the response to low-quality flowers without prey: senescent daisies without prey retain some attraction for the spiders, while one of the two characters is necessary to generate more than momentary adherence to clover.

Spiders did not clearly discriminate between low and high-quality goldenrod in the absence of prey, although they exhibited a modest trend to remain longer on high-quality goldenrod when prey were present than when absent. Thus, this male performance resembles that of adult female *Misumena* in the sense that flower quality does not play a significant role in choice of hunting site (Morse 1988). The role of prey as a cue for males on goldenrod thus remains tentative, though consistent with their responses on daisies and clover (Morse 1988).

Because daisies and clovers have compact inflorescences and goldenrod has much larger ones, the physical-temporal arrangement of prime flowers may be of major importance in accounting for differences in choice. Parts of a goldenrod inflorescence bloom asynchronously, so that some branches are in full bloom while others have not yet bloomed or have already senesced (Morse 1977). The spiders may thus have disregarded the flower quality of individual goldenrod branches, since a poor-quality branch may not characterize an entire inflorescence. If adjacent branches of the same inflorescences still attract prey, these prey may frequently land on a senescent branch occupied by a spider. This argument, however, fails to explain why spi-

ders showed no tendency to respond differently to the poor-quality inflorescences visited by prey.

In contrast, daisy and red clover inflorescences do not exhibit internal patchiness on the scale of the goldenrod. Individual clover inflorescences bloom and senesce within 10 days, and the ring of nectar-producing florets remains relatively constant over much of the life of a clover inflorescence (S.A. Chien pers. obs.); further, clover inflorescences are much smaller than goldenrod inflorescences. Therefore, spiders may assess a clover inflorescence in an all-or-none way; i.e., as one patch, while they assess a goldenrod inflorescence as a mosaic of patches. Our results suggest that where floral quality accurately reflects the ability to attract prey, male crab spiders will use flower quality independently as a cue for assessing the quality of hunting sites. This tactic would be potentially advantageous in allowing individuals to choose hunting sites when insect prey are not visiting flowers, thereby increasing considerably the period during which choices may be made.

These data establish that adult male spiders will respond directly to flower cues independently of the presence of females. The response to prey on daisies and clover demonstrates that they will react directly to another potentially critical resource—food—although the presence of prey should simultaneously increase the probability of finding females. Whether the increased time on sites with prey would be necessary to find such a female on a daisy or clover inflorescence seems questionable, judging from the short discovery times (a few sec to less than 5 min) exhibited in most male-female interactions we have staged on these substrates (A.R. Holdsworth & D.H. Morse unpubl. data). The similar attention of females to sites with prey simultaneously positions them on these favorable sites, enhancing probability of contact, even if the sexes do not actively search for each other. The giving-up times of males are all markedly shorter than those of either adult or penultimate-instar females, which appear to be involved totally in sit-and-wait foraging at such times (Morse & Fritz 1982; D.H. Morse unpubl. data). Males in the present study remained at high-quality sites for 1 h or more only 27–43% of the time (Table 1), far less than adult females, which remained over 2 h

at high-quality milkweed *Asclepias syriaca* inflorescences 69–80% of the time (Morse & Stephens 1996). Adult females also exhibited long tenure times on goldenrod and pasture rose, *Rosa carolina* (Morse 1981a).

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