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HOW CRAB SPIDERS (ARANEAE, THOMISIDAE) HUNT AT FLOWERS

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ABSTRACT

The crab spider *Misumena vatia*, a sit-and-wait predator commonly found on flowers, did not specialize on prey, although the commonest prey (bumble bees *Bombus* spp. and tiny syrphid flies *Toxomerus marginatus*) on pasture rose differed so greatly in size that specialization was predicted. On milkweed the commonest prey (bumble bees and honey bees *Apis mellifera*) were more similar in size, and the predicted generalist strategy was observed.

Spiders on milkweed inflorescences usually selected the best hunting sites, but not all did so, as predicted. The sites chosen best match the frequency of prey visits to inflorescences of differing quality. Spiders on good stems moved more frequently than those on poor stems; however, their success was extremely variable.

INTRODUCTION

The foraging of spiders and many other animals is probably often affected by extreme heterogeneity in both food choices and the places in which food is found (Elton 1949, Weins 1976, Riechert and Luczak 1981). Much recent interest has focused on the proposition that animals forage in a way that optimizes their efficiency (optimal foraging theory), usually by maximizing their uptake of energy. However, relatively few attempts have been made to test prediction of optimal foraging theory under natural circumstances (reviewed by Pyke, Pulliam and Charnov 1977, Morse 1980), and most such efforts with spiders have used web-spinning species (Riechert and Luczak 1981, Janetos 1982a, 1982b, Olive 1982). In this paper I will discuss my studies on the prey captured (diet choice) and hunting sites (patch choice) of a sit-and-wait predator, the crab spider *Misumena vatia* (Clerck) (Thomisidae) (= *M. calycina* [L.]) (Morse 1979, 1981, unpubl.; Morse and Fritz 1982). Specifically, I will ask if *M. vatia* forages in a way consistent with certain predictions of optimal foraging theory, then comment on any discrepancies. In the process I will consider several variables relevant to the decisions that foraging spiders must make: size of prey, frequency of encountering prey, ability to capture prey, and the location of prey in space and time. I will then compare these results with recent studies on web-spinning spiders.

DESCRIPTION OF THE SYSTEM

Misumena vatia, a widely distributed species in the Holarctic Region, hunts on a wide variety of flowers, upon which it captures insect visitors (Gertsch 1939). Adult females, the subjects of this paper, sometimes reach 400 mg and over 12 mm total length when distended with food. They are either white or yellow, and often have red dorsolateral stripes along the sides of their abdomen. Characteristic of thomisids, they possess enlarged raptorial forelimbs.

In my study area in Maine, *Misumena* most commonly occupy flowers of pasture rose *Rosa carolina* L. (Rosaceae), common milkweed *Asclepias syriaca* L. (Asclepiadaceae), and goldenrod *Solidago juncea* Ait. (Compositae). I will discuss foraging on rose and milkweed here. These plants bloom sequentially (pasture rose, then milkweed, then goldenrod), although overlapping somewhat. They are also spatially separated in the study area, with the result that rarely do the different species flower simultaneously within 10 m of each other. Not only do these plants differ in the timing of their floral displays, but in the number and kind of insects attracted as well (Morse 1981). As a consequence, their quality as hunting sites differs. Pasture rose produces single large flowers that attract insects for only one day, but milkweed bears its flowers in large inflorescences that bloom sequentially from the bottom to the top of stems. Insects may visit such a stem for two weeks or more, and spiders on milkweed therefore experience a more stable resource than do those on rose.

Bumble bees (*Bombus terricola* Kirby and *B. vagans* Smith) were the commonest insect visitors to flowers in the study area. Syrphid flies (especially *Toxomerus marginatus* Say) and small solitary bees also frequented pasture rose, and honey bees (*Apis mellifera* L.) sometimes were common visitors on milkweed (Morse 1979, 1981).

CHOICE OF PREY

I tested a major prediction about optimal diet: whether a food is eaten is independent of its own abundance and is strictly a consequence of the abundance of higher-ranking items (Morse 1979). Two types of prey made up the great majority of captures on both rose and milkweed: bumble bees and tiny syrphid flies on pasture rose, bumble bees and honey bees on milkweed. Given the observed rates of intake and similar attack rates found in this study, one can calculate whether or not the spiders would have profited by specializing on one or the other prey species.

Time budgets totalling over 450 hours were calculated for 24 spiders on pasture rose. These individuals were visited hourly during the period of prey capture, permitting an inventory of their food captures. Ten of them were also observed continually for a total of almost 80 hours, permitting determination of the frequency of visitors and the spiders' probability of attacking them. The data from milkweed resulted from 30 spiders that were continually observed for a total of 309 hours. Some of the individuals on pasture rose and all of the individuals on milkweed were individually marked.

Using the following equation (derived in Morse 1979), one can calculate the predicted daily biomass of prey captured by a predator that shifts from randomly attacking two species of prey to specializing on one prey species:

$$B'_1 = N_1 b_1 + \frac{(T_2 - x)(b_1)}{t_1},$$

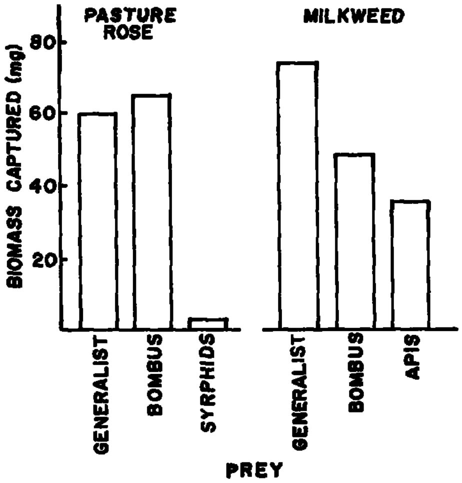

Fig. 1.–Actual and predicted daily capture of prey by generalist and specialist spiders hunting on pasture rose and milkweed. Data from Morse (1979, 1981).

where B'_1 = predicted biomass of food obtained per day by a predator from specializing on Prey Species 1, N_1 = number of Prey Species 1 captured, b_1 = biomass of Prey Species 1, T_2 = processing time for Prey Species 2, x = time saved by ignoring Prey Species 2 that can be applied to hunting for Prey Species 1, and t_1 = time spent processing an individual of Prey Species 1. If compared with the observed intake of randomly attacked prey ($B = N_1b_1 + N_2b_2$), the profitability of changing to a specialist strategy can be assessed. In the same way, one can calculate the daily biomass that the predator should capture if it specializes on Prey Species 2. The predicted intakes of specialists and generalists are presented in Fig. 1.

The spiders regularly attacked both bumble bees and syrphid flies on pasture rose, even though bumble bees were by far the more profitable of these prey both in terms of biomass captured per attack and biomass processed per unit time (Table 1). Further, the spiders would have captured 8% more prey if they had ignored the syrphid flies on pasture rose and concentrated on bumble bees (Fig. 1). The spiders regularly attacked the two commonest diurnal visitors on milkweek, bumble bees and honey bees (Table 1), in accordance with the prediction from Fig. 1, even though bumble bees were somewhat more profitable than honey bees.

Thus, the spiders performed according to prediction on only one of the flower species. A possible basis for their failure to specialize on bumble bees at pasture rose is that prey are not constantly available in large numbers on pasture rose. They visit mostly during mid-morning, when pollen is dehiscing. The best strategy for a spider to follow during the mid-morning would be to maximize its chances of capturing a bumble bee, upon which it could feed much of the rest of the day, when chances of capturing any food were low. Processing time of prey on pasture rose is substantial, even for a tiny syrphid fly (Table 1.) In fact, if a syrphid is captured at the beginning of the peak visitation period, processing may take much of the peak period (Fig. 2), diminishing greatly the chance of capturing a bumble bee that day. At this time spiders specializing on bumble bees realize an advantage of over 20% in intake; at other times of day generalist and specialist strategies are similar (Morse 1979). In that the predicted difference in overall intake of generalists and bumble bee specialists was less than 10%, this difference, combined with the great variance of intake at different times of day, may be inadequate to stimulate specialization, even if the spiders are capable of such discrimination.

Table 1.—Attacks, captures and processing of prey by *Misumena vatia*. Some of these data from Morse (1981).

Site	Pasture rose (79.3 hr).		Milkweed (309 hr)	
Prey	Bumble bee	*Toxomerus*	Bumble bee	Honey bee
% of prey attacked (N)	68.1 (245)	54.8 (23)	45.9 (117)	50.0 (48)
Attacks/hour	3.1	0.3	0.4	0.2
Captures/hour (N)	0.05 (4)	0.11 (9)	0.03 (10)	0.04 (11)
Biomass	181.7 ± 9.1	3.0 ± 0.4	143.9 ± 47.0	85.0 + 21.6
Success (%)	1.6	39.1	8.5	22.9
Biomass captured/attack	2.9	1.2	12.2	19.5
Processing time (N)	5.5 ± 0.6 (8)	1.5 ± 0.4 (14)	4.2 ± 1.4 (6)	3.2 ± 1.0 (4)
mg ingested/hour when feeding	18.0	1.1	19.5	15.1

Given the rates of prey capture on milkweed flowers by *Misumena*, a generalist strategy would be dictated unless one of the prey was much larger than the other. Visitation rates of insects are more constant on milkweed than rose over a day (Fig. 2), so no particular time is especially important for prey capture. Thus, it may be that the combination of characteristics experienced on pasture rose (great variation in prey size, great fluctuation in rates of prey visitation) is an unusual one.

The generalist pattern observed on pasture rose might only be a small deviation from optimality in a generalist strategy if an individual then moved onto other kinds of flowers. Yet, many adult female spiders probably do not shift to other kinds of flowers. Only 1 of 175 marked adult spiders on my main study area switched to a new flower species during these studies. Many or all of them laid their single clutch of eggs as one of these flower sources senesced (Morse and Fritz 1982). Perhaps the uncertainty or danger of getting to a new flower source was the critical factor preventing a greater shift.

HUNTING SITES: CHOOSING BETWEEN INFLORESCENCES

The choice of a hunting site can be readily studied at two different scales on milkweed, within and between flowering stems. Milkweed stems have several sequentially flowering inflorescences, so that one inflorescence usually contains more nectar-producing flowers, and also attracts more insects, than other inflorescences (Morse 1981). One may therefore predict that spiders will occupy the inflorescence containing the most nectar-producing flowers, given their ability to respond to prey on adjacent inflorescences (they will orient to insects landing there), the short distance between adjacent inflorescence (ca. 2-5 cm: Morse and Fritz 1981), and the short time required to move between inflorescence (< 1 min after they begin to move: Morse, unpubl.).

To test this prediction, Morse and Fritz (1982) selected milkweed stems with three inflorescences: one with 25+ nectar-producing flowers (= high-quality), one with 5-10 such flowers (= middle-quality), and one with no nectar-producing flowers (= poor- quality). We then randomly assigned spiders to inflorescences, one per stem, releasing them in mid-morning after insect activity became high (Fig. 2). We allowed these spiders to shift sites over the next six hours, the period during which numbers of insect visitors remained high. Additionally, we determined the predicted distributions of spiders if they were to respond directly to any one of several variables at the flowers: the proportion of nectar-producing flowers on the different inflorescences, the number of times that insects visited inflorescences of different quality, the number of flowers visited per inflorescence, the total number of prey caught on different inflorescences, and the number of bees caught on different inflorescences. This regime thus provided a test of the optimal patch model and a simultaneous evaluation of any non-conformities.

Although the spiders occupied high-quality inflorescences significantly more frequently than predicted by chance, the choice was not absolute, for about 30% of the individuals did not perform as predicted (Fig. 3). Further, each of the alternative predicted distributions yielded closer fits to the experimental results than did the simple optimal patch model (Fig. 3). The frequency with which insects visited inflorescences of different quality fit the observed distribution of spiders most closely.

Given the ease of movement between inflorescences and the opportunity to monitor visiting prey, why didn't every spider choose the inflorescence that attracted the most insects, as predicted by the optimal patch model? Some variables seem extremely difficult to monitor and predict with precision, and it may be unrealistic to assume that the spiders can do so, as the simple model of patch use requires. Visits to high-quality inflorescences are not evenly spaced over time, even though they may appear to be so when summed over one-hour periods. Analysis of visits to a high-quality inflorescence may reveal periods of several minutes between consecutive visits, as well as instances when three or more insects may visit within a minute (Morse and Fritz 1982). Consider the poor-quality umbels upon which some of the spiders hunted. The time that an insect visited such an inflorescence relative to the time that a spider arrived on it might be of great importance to the spider. A randomly-selected inflorescence with no nectar-producing flowers attracted only one bee, at 11:14, during a day that it was monitored. Its quality might be assessed very differently by spiders arriving at 11:13 and 11:15, especially if the former spider succeeded in capturing this bee. Although inflorescences with no nectar-producing flowers are poor hunting sites, I have several records of spiders capturing prey on them, so the above example does not portray an improbable scenario. Thus, one might predict that the individual arriving at 11:13 would occupy a site for some time, even though the model would predict that it should soon leave.

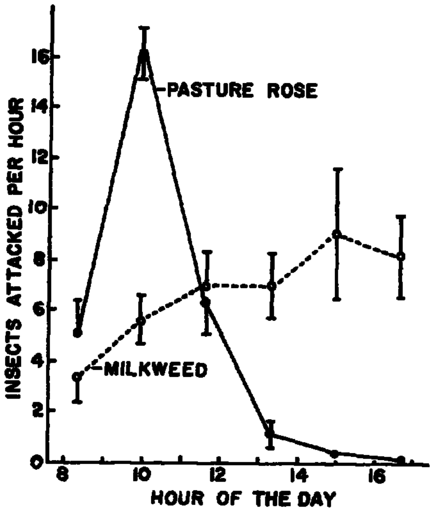

Fig. 2.–Numbers of insects attacked per hour on pasture rose (solid line) and milkweed (dashed line) ± one standard deviation. Modified from Morse (1981).

HUNTING SITES: CHOOSING BETWEEN STEMS

Moving to a better neighboring stem should be a more formidable task than moving between inflorescences, for that stem may lie some distance from the site occupied (e.g., 1 m or more), and it may be hidden from view. Even if identified, the difficulty of getting to it remains. This problem becomes particularly acute when most of the flowers are senescing. Nevertheless, as numbers of nectar-producing flowers decline, a point should be reached at which little is to be gained by remaining. Given the difficulties involved, one might predict that spiders' capability of responding to differences in stem quality is inferior to their capabilities of choosing at the between-inflorescence level. We examined this prediction in two ways: by comparing the condition of the stems occupied by free-ranging spiders with the condition of stems in the clone as a whole, and by testing the responses of experimental individuals released on stems of higher and lower quality (25+ and 0 nectar-producing flowers, respectively) than the average condition of the 10 stems nearest to the spider (25-125 cm away).

The average condition of the stems in the clone declined rapidly during the study period, but was followed closely by the average condition of the stems occupied by the spiders, a time during which nearly half of them moved each day (Fig. 4). Although some spiders improved their hunting sites by moving, variance was so high that improvement for spiders as a whole was not significant (Morse and Fritz 1982). However, some spiders prolonged their feeding period up to several days by moving.

Significantly more individuals placed on high-quality stems at this time remained (38 of 51) than did those placed on low-quality stems (10 of 28) (Morse and Fritz 1982). However, one is again struck by the high proportion of individuals that did not move from low-quality stems or remain on high-quality stems, especially since spiders on high-quality stems captured over four times as many prey in this experiment as did ones on poor quality stems (Morse and Fritz 1982).

The spiders may thus experience serious problems in responding to a resource that is variable at the between-stem level. Individuals were no more successful in improving their hunting site over a shot time period (one day) than predicted by chance. However, if they responded as did individuals choosing inflorescences, they would occupy a poor stem for a shorter period than a stem of high quality, with the result that additional random moves might improve their lot relative to their initial location. In this way they may prolong foraging a few days and perhaps capture one or two more large prey. Rewards of that size are important, permitting them to increase their reproductive output greatly. Nevertheless, the success of the spiders at this point is so highly variable that, given the difficulty of monitoring the environment, at some point a "decision" not to search further should be made. This may account for part of the high proportion (c 30%) of individuals that failed to move. A decision to lay a small clutch early should be advantageous to an individual in at least two ways, if its probability of capturing additional prey is low: the reproductive cycle can be moved ahead, and the energy spent in futile search can be used in reproduction. Further, it is likely that spiders on the move in the open are more vulnerable to predators than those situated on the plants, although I have no direct evidence of such predation at this time. The failure of last-instar spiders to move to other species of flowers at the end of a flowering period suggests that spiders make such a "decision" to cease searching.

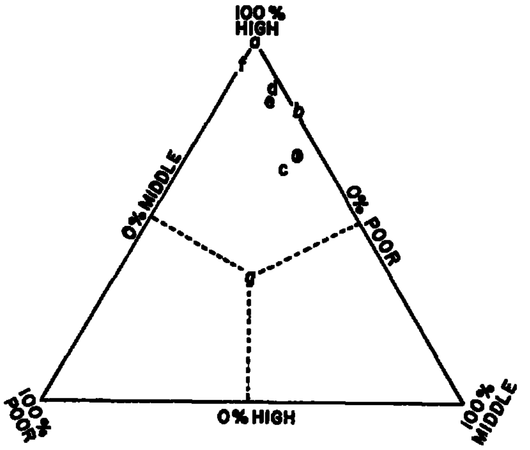

Fig. 3.–Observed and predicted frequencies (%) of spiders occupying inflorescences of high (25+ nectar-producing flowers), middle (5-10 nectar-producing flowers), or poor (0 nectar-producing flowers) quality. Predicted frequencies are based on O) observed; a) optimal patch choice; as well as several variables that spiders might monitor; b) number of nectar-producing flowers; c) inflorescences visited by prey; d) flowers visited by prey; e) total prey captured; f) bees captured; g) null hypothesis (Data from Morse and Fritz 1982). Depicted is a method of plotting frequencies falling into each of 3 mutually exclusive categories. Perpendiculars dropped from any point within the triangle to each of the 3 sides sum to 100%. In this instance, the categories refer to inflorescences of 3 different qualities. The null hypothesis (g), for example, predicts equal occupation of each kind of inflorescence, so all 3 perpendiculars will be of equal length. By contrast, total prey captured (e), predicts that most of the spiders will occupy high-quality inflorescences; therefore, the perpendicular dropped to that side (bottom side of triangle) is by far the longest of the 3 perpendiculars that one can construct.

GENERAL DISCUSSION

Comparison of foraging by crab spiders and web-building spiders.–Giving-up times at hunting sites differ as a function of several variables. Rates of insect visitation to hunting sites are of central importance to crab spiders, and to other spiders as well (Janetos 1982a, Olive 1982). Janetos (1982b) has predicted that the orb-weavers he studied should give up an unsatisfactory site more rapidly than sheetweb weavers, in major part a consequence of their three-fold lower energy expenditure per web. This difference is largely the consequence of orb-weavers, but not sheetweb weavers, ingesting their old web (Janetos 1982a). According to this line of reasoning, *Misumena* and other flower-dwelling spiders, having low moving costs, should remain even shorter periods at an unsatisfactory site, and exhibit even lower variance in their giving-up times. Although conditions were not directly comparable to Janetos', the mean residence time of two hours at poor-quality inflorescences (Morse and Fritz 1982) is consistent with this interpretation.

Additionally, Janetos (1982b) noted that orb-weaver sites have a more variable supply of prey than those of sheet web weavers. Hunting sites of *Misumena* also show a great variation in numbers of visiting prey (Morse and Fritz 1982).

Other factors play a major role in crab spiders' decisions about which sites to occupy. Residence times of *Misumena* on milkweed stems were significantly greater than those of *Xysticus emertoni* (Thomisidae) and were directly correlated with the major differences in prey biomass taken at similar hunting sites. *Xysticus* were largely unsuccessful in capturing bumble bees and honey bees (Morse 1983), the commonest visitors to these flowers.

In general, *Misumena* is thus more like mobile predators than web-spinning spiders in patch choice, although clearly not as mobile as most vertebrates or flying insects. It may, therefore, provide a useful intermediate condition for testing the role of different factors in choosing hunting sites.

In studies with other animals, if foragers do not always occupy the most profitable hunting sites, workers have usually explained the result as the consequence of the foragers sampling the environment for potential future use (e.g., Smith and Sweatman 1974). One would only expect this behavior in individuals with a future stake in the hunting site. Although some spiders clearly exhibit territoriality (e.g., Riechert 1981), and web sites may be limiting factors (Riechert 1981, Riechert and Cady 1983), the sampling explanation does not seem likely for either web-spinners or *Misumena.* Web sites of spiders may be analogous to an entire territory of a highly mobile predator, such as a bird (Olive 1982), and it seems doubtful that their mobility is high enough to exhibit such sampling regimes, even if they possessed the ability to make such decisions. Further, hunting sites on flowers retain high quality for only short periods relative to even a crab spiders' mobility. Therefore, such non-conformities seem more likely a consequence of spiders' inability to monitor their immediate vicinities than assessment of resources for the future.

Usefulness of optimal foraging models in this system.—It should not be surprising that simple optimal foraging models did not make highly accurate predictions of the spiders' behavior under the field conditions experienced. These models do not incorporate constraints upon foragers resulting from limits to their analytical or perceptual capacities. Great temporal and spatial fluctuation of resource availability exists in this system and provides the most likely basis for the non-conformities observed. Other possible confounding factors (predators, special nutrient requirements, competition) seem less likely to influence crab spiders than many other foragers. The low disappearance rate of adult spiders, the low frequency of would-be predators, and the low frequency of likely predator-avoidance patterns (hiding under flowers, etc.) (Morse 1979) suggests that predation was not a major factor inhibiting them. Their tendency to strike indiscriminately at prey of all types on pasture rose suggests that they did not experience nutrient constraints. The low density of conspecifics and other similarly foraging species, combined with a large surplus of hunting sites, argues against competition of any sort being an important constraint.

The relative effects of diet and patchiness.—It is of interest to ask whether the foraging regimes of the spiders were influenced more by dietary choice or by the patchiness of these resources. Although I have not specifically tested these alternatives, the predictions from patch theory appear to fit the results more closely than do those from diet theory. This could be a true reflection of a sit-and-wait predator's world, in which choice of hunting site is of extreme importance in an environment as patchy as the spiders' appears to be. Great

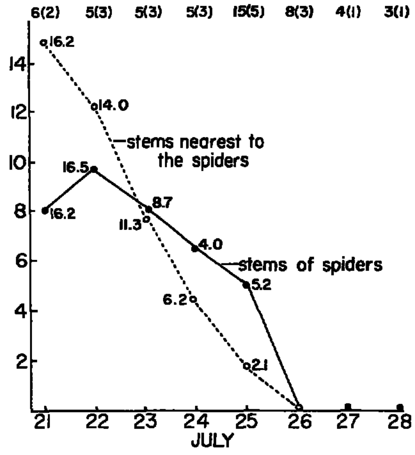

Fig. 4.—Number of nectar-producing flowers on stems occupied by spiders (solid line) and number of nectar-producing flowers on 10 stems nearest to spiders (dashed line). Two standard errors of the mean appear next to data points. Differences were not significant on any day ($p > 0.05$ in one-tailed Wilcoxon matched-pairs, signed-ranks tests). N = number of spiders, with the number of spiders changing stems each day in parentheses. Modified from Morse and Fritz (1982).

as the variety in prey attributes may be, it may be modest in relation to the patchiness, both spatial and temporal, that spiders experience at and between their hunting sites. However, given the differences in size distributions of the commonest visitors to pasture rose and milkweed, the 1.7-fold difference in mean size of prey captured on the two flowers (Morse 1981) and the differences in scales of patchiness at these flowers, one may predict that the relative importance of diet and patchiness will also differ from flower species to flower species.

Attributes of the system and opportunities for additional studies.—The crab spider-flower system has many admirable attributes for studies of foraging. It is a relatively simple system, in which the currency (food) can be measured readily in the way that the predator measures it and can be manipulated easily. It is possible to accumulate the data sets necessary to test either deterministic or stochastic models. Although obtaining the necessary data for stochastic models is much more tedious than for deterministic models, this is one of the few systems I know in which such data could be gathered without undue difficulty. Further, an independent estimate of fitness can be readily made, since one can measure the reproductive output from the single clutch of eggs and relate it to foraging success. Typically, it is merely assumed that efficient foraging behavior will result in enhanced fitness. It should be possible to extend this measure at least through the second instar, at which point the young disperse by ballooning. In that way one can incorporate benefits and costs of adult guarding behavior and the impact of egg predators and parasites.

Having worked out basic patterns of *Misumena* foraging on one species of flower, one may predict the patterns that individuals will exhibit on other species of flowers, based on differences in prey abundance and variance at those flowers. One may test the generality of the results further by predicting the foraging performances of two other ambush foragers at these sites that differ in their dispersal capacities, the brown crab spider *Xysticus emertoni* and the ambush bug *Phymata americana* (Melin) (Hemiptera: Phymatidae). Such a combination of studies should provide a basis for assessing the variables that affect sit-and-wait predators and how these predators respond to them.

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