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Victoria R. Schmalhofer

Tritrophic interactions in a pollination system: impacts of species composition and size of flower patches on the hunting success of a flower-dwelling spider

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Abstract Size and species composition of flower patches were manipulated to determine whether these factors exerted indirect effects on the hunting success of flower-dwelling spiders via direct effects on insect pollinators. Multivariate analysis of variance (MANOVA) of two pollinator response variables (visitation rate and visitor size) revealed a significant pollinator preference for *Bidens aristosa* (tickseed sunflower) over *Solidago juncea* (goldenrod) and for large patches of a given plant species over small patches. *Bidens* received significantly more pollinator visits per floral unit per unit time and attracted significantly larger insects than *Solidago*. The significant patch size effect seen in the MANOVA was driven by the strong impact of patch size on the size of insects visiting the experimental patches: the size (mass) of insects visiting large patches was significantly greater than the size of insects visiting small patches of a given plant species, but visitation rates to large and small patches of a given plant species were similar. MANOVA indicated that hunting success of a flower-dwelling crab spider, *Misumenoides formosipes*, was also significantly affected by species composition and size of flower patches. Three measures of spider hunting success (rate of mass gain and its components, total prey mass captured per spider per day, and number of prey captured per spider per day) were evaluated, and the experimental treatments exerted similar effects on all three measures. Spiders occupying *Bidens* patches experienced greater hunting success than spiders occupying *Solidago* patches, and in patches of a given plant species, spiders occupying large patches experienced greater hunting success than spiders occupying small patches. The pattern of spider hunting success most closely paralleled the pattern described by the size of insects visiting the patches (BL>BS=SL>SS), suggesting that the size of visiting pollinators, rather than frequency of visitation, exerted a greater influence on spider hunting success. Taxonomic composition of a spider's diet varied with the plant species occupied. The size of insects captured by spiders was significantly greater than average size of insects visiting the patches, indicating that spiders selectively captured larger pollinator taxa. Spider movements among patches revealed a pattern of migration from *Solidago* to *Bidens*.

Keywords Crab spiders · Direct and indirect effects · Patch size · Pollinators · Predation

Introduction

Pollen- and nectar-feeding insects fall prey to other arthropods that use flowers as hunting sites. Flowers function as a long-distance attractants to pollinators (Kevan and Baker 1983; Scogin 1983; Barth 1991) and provide a mechanism by which pollinators can evaluate local resource abundance and quality. Discriminatory responses of insect pollinators to variations in the floral characteristics of plant communities are well-documented (Augspurger 1981; Stanton et al. 1986; Stanton and Preston 1988; Gori 1989; Ohara and Higashi 1994; Connor and Rush 1996; Strauss et al. 1996; Strauss 1997). Insects cue to a variety of floral characters such as color (Mulligan and Kevan 1973; Real 1981; Scogin 1983; Stanton et al. 1986; Jones and Cruzan 1999), odor (Mulligan and Kevan 1973; Galen and Kevan 1983), and symmetry (Møller and Sorci 1998), and discriminate among concurrently available plant species (Heinrich 1979; Morse 1981a; Schmalhofer 1996). Within a plant species, frequency and duration of pollinator visits increase with increases in corolla size (Stanton and Preston 1988), number of flowers per inflorescence (Willson and Price 1977; Morse and Fritz 1982; Thomson et al. 1982;

V.R. Schmalhofer (✉)
Graduate Program in Ecology and Evolution,
Rutgers University, Cook College, 14 College Farm Rd.,
New Brunswick, NJ 08901–8551, USA
e-mail: v.schmalhofer@worldnet.att.net
Fax: +1-302-8312281

Present address:
V.R. Schmalhofer, University of Delaware,
Department of Biological Sciences, Newark, DE 19716, USA

Morse 1986a; Schmid-Hempel and Speiser 1988; Gori 1989; Ohara and Higashi 1994), number of flowers/inflorescences per stem (Thomson et al. 1982; Jones and Cruzan 1999), and number of blooming individuals within a population (Augspurger 1981). These types of discriminatory responses by pollinators could affect the hunting success and fitness of flower-dwelling predators.

A growing body of literature has emphasized the need to examine the influence of plants on higher-level trophic relationships (e.g., Price et al. 1980; Faeth 1985; Kahn and Cornell 1989; Kareiva and Sahakian 1990; Hawkins 1992). Discriminatory responses of pollinators with respect to floral characters suggest that variation among flower patches may indirectly affect flower-dwelling predators via direct responses of pollinators to patch variation. The purpose of this study was to determine whether measurable direct and indirect effects could be discerned in a pollination system. An anthophilous crab spider, *Misumenoides formosipes*, and two plant species commonly occupied by the spider, *Bidens aristosa* (tickseed sunflower) and *Solidago juncea* (goldenrod), were used to investigate whether size and species composition of flower patches affected pollinator responses and spider hunting success. Two aspects of pollinator responses to the experimental manipulations were examined: number of visits per unit time and visitor size. These two measures may not contribute equally to hunting-site quality for crab spiders. Visitation rates permit an estimate of predation opportunities for spiders. However, because larger insect taxa make a greater contribution to the reproductive success of female crab spiders (Fritz and Morse 1985), the size of insects attracted to flower patches may have a stronger influence on a spider's rate of mass gain. I predicted that hunting success (rate of mass gain) of adult female spiders in the experimental patches would reflect pollinator preferences; in particular, spider hunting success was expected to mirror the pattern described by the size of visiting pollinators.

Materials and methods

Study organisms

Misumenoides formosipes, a semelparous, anthophilous member of the family Thomisidae (crab spiders), employs a sit-and-wait strategy to ambush flower-visiting insects. Enlarged raptorial forelimbs, rather than a web, are used to capture prey. Captured prey is consumed immediately. In central New Jersey, *Misumenoides* matures in mid- to late August, adult females hunt through September, and a single egg sac is laid in mid- to late September or early October. *Misumenoides* is generally white, but spiders turn yellow after approximately 2 days residence on a yellow flower (Schmalhofer 1996).

Only adult female spiders, which are relatively sedentary, were used in this experiment. Recently matured females average 44±15 mg, and immediately prior to egg laying females average 149±69 mg. Adult females are capable of capturing bumblebees (*Bombus* spp.), which have a mass approximately three times that of a recently matured spider. *Misumenoides* hunts both nocturnally and diurnally, but nocturnal predation events occur infrequently (personal observations). Diurnal activity consists mainly of hunting and feeding: spiders devote less than 3% of their time to other activities, such as changing hunting sites (Schmalhofer 1996).

Bidens aristosa and *Solidago juncea* were selected for manipulation because, while both species are composites (Asteraceae), they had distinctly different floral architectures and provided spiders and pollinators with very different habitats. Also, adult *Misumenoides* are commonly found on *Bidens* and *Solidago* (Schmalhofer 1996). The floral architecture of *Bidens* is relatively simple: paired lateral branches arise along the length of the main stem, and long-peduncled inflorescences occur in loose clusters of 1–4 at the distal ends of the branches. The morphology of a *Bidens* inflorescence is typical of a composite: a central disk of small tubular florets is surrounded by larger, petal-like ray florets. The morphology of a *Solidago* inflorescence is also typical of a composite, but the floral architecture of *Solidago* is more complex than that of *Bidens*. A *Solidago* flowerhead is a compound inflorescence composed of multiple, apically clustered branches, each branch comprising multiple, short branchlets that bear many, small, short-peduncled inflorescences. Both species have yellow inflorescences and show a distinctive ultraviolet (UV) pattern in which the central disk and basal portion of the ray florets absorb UV, while the distal portion of the ray florets reflects UV. Flowering in the two species typically shows a high degree of overlap: *Solidago* blooms from mid-August through mid-September, while *Bidens* blooms from late August through late September. Height of *Bidens* plants varies greatly among individuals and is strongly influenced by water availability (Schmalhofer, unpublished data). The *Bidens* plants used in these experiments were approximately 1.5 times as tall as the *Solidago* plants, which were approximately 75 cm in height.

I refer to the portion of an inflorescence occupied by a spider as a "floral unit." For *Bidens*, an entire inflorescence comprised a floral unit, while for *Solidago*, an inflorescence branch served as a floral unit. Floral units of the two species presented comparable surface areas (*Bidens* 1,449±684 mm^2; *Solidago* 1,137±215mm^2), but their shapes differed: *Bidens* floral units were circular, while *Solidago* floral units were relatively linear.

Experimental design and field array

I used a replicated 2×2 factorial design to examine the effects of size and species composition of flower patches on insect visitation and spider hunting success in the field. Spiders were placed in large and small patches of *Bidens* and *Solidago*. Plants were not caged, so pollinator visitation was not restricted, and spiders were free to move among stems within patches and to move between patches. I measured pollinator responses (visitation rate and visitor mass) to the treatment combinations, and the effect of the treatment combinations on spider hunting success (rate of mass gain and its components: number of prey captured spider^{-1} day^{-1} and total prey-mass captured spider^{-1} day^{-1}).

A 10 m^2 grid centered in a 12 m^2 mown section of a 1 ha field at the William L. Hutcheson Memorial Forest Research Center, Somerset County, New Jersey, served as the experimental site. The field was a monoculture of foxtail grass (*Setaria* sp.), bordered to the north, east, and south by forest and to the west by another field (dominated by *Solidago* spp.). The experimental plot was surrounded by foxtail grass and located in the northwest quadrant of the field; 10 m wide bands of foxtail grass separated the experimental plot from the adjacent field and forest on the west and north sides of the plot.

At the beginning of the growing season, I collected *Solidago* rosettes and *Bidens* seedlings and potted multiple plants of a given species in individual 3 gallon containers. Plants were collected from the same areas from which I later collected spiders. Patch arrangement was randomized on the 10 m^2 grid and pots were randomly assigned to large (5 pots) and small (1 pot) patches. Four replicates of each plant species/patch size combination were used (*n*=16 patches). The experiment ran for 3 consecutive days during early September, 1994. Experiment duration was chosen to correspond to the average length of time female *Misumenoides* spent on

Table 1 Average numbers of flowering stems, floral units, and spiders in the experimental patches. Initial and final spider densities per patch, per stem, and per floral unit are given. Values are means (±1 SD)

	Patch type			
	Bidens, large	*Bidens*, small	*Solidago*, large	*Solidago*, small
No. stems per patch	45.5 (2.1)	13.0 (2.6)	45.3 (5.9)	10.8 (5.1)
No. floral units per patch	232 (11)	66 (13)	543 (70)	129 (61)
No. spiders per patch				
Initial	5.0 (0.0)	1.0 (0.0)	5.0 (0.0)	1.0 (0.0)
Final	6.5 (1.3)	2.0 (0.8)	4.0 (1.4)	0.5 (1.0)
Spider density (no. per stem)				
Initial	0.110 (0.005)	0.079 (0.016)	0.112 (0.014)	0.108 (0.046)
Final	0.144 (0.035)	0.163 (0.095)	0.088 (0.027)	0.029 (0.056)
Spider density (no. per floral unit)				
Initial	0.022 (0.001)	0.016 (0.003)	0.009 (0.001)	0.009 (0.004)
Final	0.028 (0.007)	0.032 (0.019)	0.007 (0.002)	0.002 (0.005)

a *Solidago* flowerhead (Schmalhofer, unpublished data). Observations were made of each patch at hourly intervals between 0900 and 1900 hours.

The density of *Solidago* stems per pot was not as great as that of *Bidens*, so during the experiment I supplemented *Solidago* patches with freshly cut *Solidago* stems (25 stems added to large patches, and 5 stems added to small patches) in order to make the number of stems per patch more similar (Table 1). Cut *Solidago* stems were added to the patches 30 min before spiders were released at the beginning of the experiment, and the cut stems were placed in 2-l containers of water interspersed among the potted plants. Cut stems remained fresh (no wilting or obvious color changes) throughout the experiment, and insect visitation to cut *Solidago* stems was similar to insect visitation to whole *Solidago* plants (χ^2=0.097, *df*=1, *P*=0.7551).

Insect data

I recorded visitation rates of insects that could serve as prey for the spiders. Insects were categorized according to size and taxonomic order (i.e., large dipterans, medium dipterans, small dipterans, etc.) unless they belonged to a readily identifiable and/or particularly common group (e.g., honeybees, bumblebees, syrphids, bombyliids). Large insects beyond the hunting capabilities of the spiders, such as *Polistes* spp. (paper wasps) and *Xylocopa* sp. (carpenter bees), or taxa not used by the spiders, such as beetles, were not counted. At each hourly observation interval, I recorded the number of visits made to a given patch by each prey taxon during a 1 min period. A "visit" consisted of an insect alighting on or otherwise occupying a floral unit. An individual insect could visit a patch multiple times as long as it left one floral unit and moved to another (or came back to the original floral unit). Hourly measures of visitation were divided by the number of floral units in the patch. Calculations of per floral unit visitation rates permitted an estimate of the number of opportunities a spider had to capture prey. Insect abundance (number of individuals visiting or number of floral units visited per individual per time period) was not measured. From a crab spider's perspective, the number of opportunities to capture prey and the size of potential prey are more relevant variables than is the actual number of foraging insects present. Risk of predation to individual insects by crab spiders is low: Morse (1986b) estimated that a given insect would be attacked only once every 4–10 days, and the predicted period until capture was 21–109 days. Spider densities in the present experiment were sufficiently low such that predation events would not deplete the local pollinator pool. Samples (*n*=10) of each visitor type were collected and weighed to calculate average fresh mass (mg). Mass estimates were used to calculate the average size of pollinators visiting the patches. Observations of insect visitation to each patch were made prior to searching patches for spiders: I stood approximately 1 m from a patch and used a small tape recorder to voice-record the identity of each visitor. A stopwatch was used to record the duration (s) of pollinator visits to *Bidens* and *Solidago* floral units.

Spider data

Penultimate instar juvenile and adult female spiders were collected in late July and early to mid-August. Because female crab spiders acquire 60–85% of their mass in the adult instar (Morse and Fritz 1987; Beck and Connor 1992; Schmalhofer, unpublished data), and physiological changes associated with egg maturation and insemination might strongly influence a female's hunger level and predatory motivation (Riechert and Harp 1987), I provided all females with mating opportunities in the laboratory prior to the field experiments. Each spider was assigned a unique two-digit number, which was marked in red indelible ink on the spider's abdominal dorsum. At the beginning of the experiment, marked spiders were randomly placed on inflorescences at 0800 hours. Each plant species was stocked with 24 spiders: 5 spiders per large patch and 1 spider per small patch (total *n*=48 spiders). Spider densities (Table 1) fell within the range of densities encountered for natural populations of *Misumenoides* (Schmalhofer, unpublished data). At each hourly observation interval, I recorded the identity of prey captured by individual spiders, and noted whether spiders remained in their original patches or shifted between patches. One hour observation intervals were adequate since prey handling time typically exceeded 1 h (average prey-handling time =3.4 h), and large prey items, such as honeybees and bumblebees, required several hours to consume. Spiders were weighed immediately prior to release and after collection at the end of the experiment to determine mass changes (mg day^{-1}) during the 3-day experimental period.

Some spiders emigrated from the experimental patches and were not recovered from the field site (3 spiders). These spiders were assumed to have left the study plot to find suitable egg-laying sites or to have fallen prey to other animals. Other spiders from outside the study plot immigrated into the experimental patches and were marked and incorporated into the study (6 spiders). Mass gains of immigrants and emigrants were estimated using a regression equation (spider mass gain versus mass of prey captured) based on data from recovered spiders: log y=0.775(log x)-0.026; R^2=68%, $P\leq0.001$. Spiders that shifted between plant species (7 spiders) or between patch sizes within a given plant species (1 spider) were counted as belonging to the patch in which they had originally been placed. Spiders that shifted between similar patches (2 spiders) were counted as belonging to the patch in which they captured prey. One spider that changed patches was excluded from the study because it fed nocturnally, so the patch in which it captured prey could not be determined.

Statistical analyses

Patches served as sampling units for statistical analyses. Data for individual spiders and hourly insect observations were subsamples. Subsamples were averaged within patches to obtain patch means. Transformations were used as necessary to achieve more normalized distributions of the data. The specific transformation used is indicated in the results.

To determine whether plant species composition and/or size of flower patches affected pollinator responses (visitation rates and size of visitors attracted), I used a two-factor multivariate analysis of variance (MANOVA). For this analysis, all pollinator taxa were grouped together under the rubric “pollinators.” To determine whether the results for “pollinators” as a group were driven by particular taxa, visitation rates of individual pollinator taxa were evaluated using ANOVAs. ANOVA was also used to compare the duration of insect visits to *Solidago* and *Bidens* floral units.

Spider body size may have a strong impact on the size of prey captured (Turner 1979; Murakami 1983; Vollrath 1987), and, hence, mass gain. Body condition may impact hunting success as well. ANOVAs were used to compare body condition and linear body size among spiders in the four treatment groups and between migrant and non-migrant spiders. The residual index, a metric advocated by Jakob et al. (1996) as the best estimate of spider nutritional state independent of body size, was used to assess body condition: linear regressions of mass against carapace width were performed, and residuals from the regressions were used in the ANOVAs. Carapace width and gape width served as measures of linear body size. Carapace width is a commonly used measure of spider body size (Hagstrum 1971; Marshall and Gittleman 1994; Jakob et al. 1996). Gape width (the length of the left and right raptorial forelimbs plus the width of the carapace) is a body size measure relevant to crab spiders; because crab spiders use their forelimbs to encircle and hold prey prior to biting, gape width may affect the size of prey crab spiders can capture.

To determine whether plant species composition and/or size of flower patches affected spider hunting success (rate of mass gain, number of prey captured spider^{-1} day^{-1}, and total prey mass captured spider^{-1} day^{-1}), I used a two-factor MANOVA. When calculating patch averages for the number of prey captured spider^{-1} day^{-1} and total prey mass captured spider^{-1} day^{-1}, spiders that were not observed with prey were scored as zeroes. Regression analysis was used to assess the relative importance of the pollinator responses in contributing to spider rate of mass gain. To determine whether spiders captured prey based on its relative availability or whether spiders were selective hunters, chi-square analysis was used to compare the proportionate visitation of various pollinator taxa with their proportionate representation in the diet of *Misumenoides*. A three-factor ANOVA using plant species, patch size, and insect status [a category that grouped insects as visitors (potential prey) or captures (actual prey)] as treatment factors was used to compare the size of insects available to *Misumenoides* with the size of insects actually captured by the spiders. Spiders not capturing prey were deleted from this calculation.

Results

Effects of species composition and size of flower patches on pollinator responses

A total of 1,065 pollinator visits to *Bidens* patches and 337 pollinator visits to *Solidago* patches were recorded. Both the identity of the plant species composing a patch and patch size influenced insect responses (Table 2). Univariate tests associated with the MANOVA indicated that the significant patch size effect on insect responses was due to the strong influence of patch size on the size of insects attracted to the patches. Visitation rates were significantly affected by plant species composition, but not by patch size, while the size of visitors attracted to the patches was significantly affected by both treatments (Table 2). *Bidens* attracted more insects floral unit^{-1} h^{-1} than *Solidago* (Fig. 1), and larger insects preferentially visited *Bidens* (Fig. 2). Large patches of a given plant species attracted significantly larger insects than small patches (Fig. 2), but visitation rates did not differ between large and small patches of a given plant species (Fig. 1). No significant interaction effects of plant species composition and flower patch size on pollinator visitation rates or size of pollinators attracted were found (Table 2). Pollinators spent significantly more time per floral unit foraging on *Solidago* (35.8±5.1 s) than on

Table 2 MANOVAs and associated univariate tests of the effects of plant species composition and flower patch size on pollinator responses and spider hunting success. Number of visits per floral unit per hour and pollinator size (mass) were log transformed, spider rate of mass gain (mg day^{-1}) and total prey mass captured per spider per day were log (x+1) transformed, and number of prey captured per spider per day was square root transformed

MANOVA results Source	*df*	error *df*	Lambda	*F*	*P*
Pollinator MANOVA					
Plant species	2	11	0.136	34.97	0.0001
Patch size	2	11	0.406	8.04	0.0071
Interaction	2	11	0.976	0.13	0.8757
Spider MANOVA					
Plant species	3	10	0.307	7.52	0.0064
Patch size	3	10	0.392	5.18	0.0205
Interaction	3	10	0.594	2.28	0.1414
ANOVA: summary of *P* values					
Variable	Plant Species		Patch Size		Interaction
Pollinator ANOVAs					
No. insect visits floral unit^{-1} h^{-1}	0.0001		0.1129		0.7125
Pollinator size	0.0003		0.0013		0.6249
Spider ANOVAs					
Spider rate of mass-gain	0.0120		0.0108		0.2171
No. prey captured spider^{-1} d^{-1}	0.0030		0.0045		0.0758
Prey mass captured spider^{-1} d^{-1}	0.0022		0.0035		0.1040

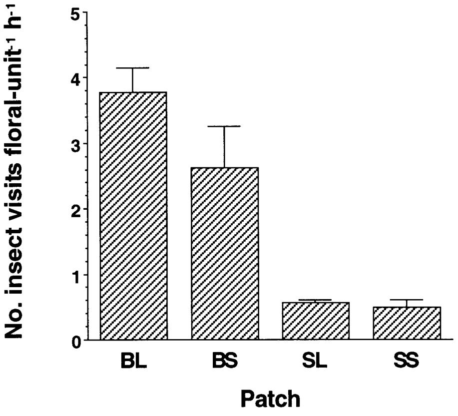

Fig. 1 Insect visitation rates (number of visits floral unit^{-1} h^{-1}) to the experimental patches. Raw data are presented. *Error bars* are ±1 SE. *BL* large *Bidens* patch, *BS* small *Bidens* patch, *SL* large *Solidago* patch, *SS* small *Solidago* patch

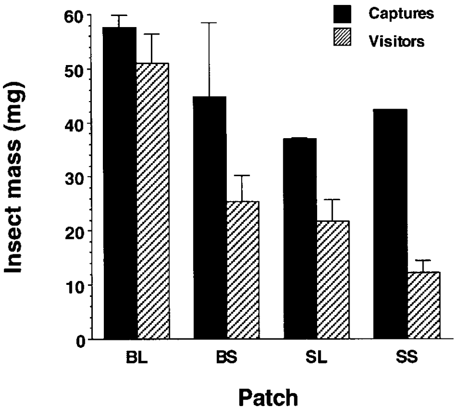

Fig. 2 Mass (mg) of insects visiting the experimental patches and mass of insects captured by spiders. Raw data are presented. *Error bars* are ±1 SE. SS captures lack an error bar because only one predation event occurred in the four SS patches

Bidens (10.8±2.4 s): ANOVA (log transformed data), $F=29.4$, $df=1$, $P\leq0.0001$.

An examination of visitation rates of individual pollinator taxa to the experimental treatments revealed that the general preference of insects as a group for *Bidens* was driven by bumblebees, honeybees, small bees, bombyliids (bee flies), and lepidopterans (Table 3). “Other flies” displayed a significant preference for *Solidago* (Table 3). Syrphids (hoverflies) also tended to visit *Solidago* more frequently than *Bidens*, but this preference was not statistically significant.

Individual pollinator taxa typically did not discriminate between patch sizes. Bumblebees and lepidopterans showed a significant preference for large patches, but in both cases patch size discrimination was strong only between large and small *Bidens* patches (Table 3). Table 3 should be interpreted cautiously. Many of the insect taxa observed were infrequent visitors to the experimental patches. These taxa were lumped into larger categories for analysis (e.g., all size classes of syrphids were grouped together). Even with lumping, some groups (indicated in Table 3) still had low frequencies of visitation. Larger sample sizes of individual pollinator taxa would be needed to accurately determine the responses of the less common taxa to the experimental treatments.

Spider size and body condition

Body size and condition did not differ among spiders in the four treatment groups or between migrant and non-migrant spiders (Table 4).

Effects of plant species composition and size of flower patches on spider hunting success

Both species composition and size of flower patches significantly affected the hunting success of *Misumenoides*

Table 3 Number of visits per floral unit per hour of various pollinator taxa, average taxon mass (mg), and summary of ANOVA results for taxon visitation rates. Raw data is presented, and values given are means (±1 SE). ANOVAs were performed on square root transformed data. “Medium bees” were predominantly megachiliids, but also included anthophorids and halictids. “Small bees” were predominantly andrenids. “Wasps” were predominantly yellow jacket workers (*Paravespula germanica*), but included occasional small ichneumonids. “Other flies” were predominantly calliphorids and muscids, but also included sarcophagids, tephritids, and simuliids. Small, medium, and large size classes of Lepidoptera were lumped. Similarly, small, medium, and large size classes of syrphids were lumped. Where multiple size categories were lumped, differences in the average mass of visitors to *Bidens* and *Solidago* are indicated (B/S)

Taxon	Mass (mg)	Patch type				ANOVA		
		BL	BS	SL	SS	Plant	Patch size	Interact.
Bumblebees	123	0.685 (0.054)	0.344 (0.099)	0.023 (0.020)	0.044 (0.035)	****	*	*
Honeybees	77	0.375 (0.126)	0.308 (0.098)	0.009 (0.007)	0.000 (0.000)	***	NS	NS
Medium bees[a]	58	0.059 (0.054)	0.030 (0.030)	0.055 (0.016)	0.043 (0.014)	NS	NS	NS
Small bees[a]	21	0.084 (0.126)	0.041 (0.028)	0.009 (0.005)	0.034 (0.014)	*	NS	NS
Wasps[a]	42/41	0.008 (0.005)	0.018 (0.010)	0.028 (0.013)	0.005 (0.005)	NS	NS	NS
Bombyliids	22	1.632 (0.179)	1.505 (0.497)	0.004 (0.004)	0.009 (0.005)	****	NS	NS
Syrphids	52/8	0.148 (0.049)	0.063 (0.016)	0.179 (0.029)	0.119 (0.045)	NS	NS	NS
Other flies	28/20	0.077 (0.015)	0.020 (0.012)	0.135 (0.025)	0.131 (0.044)	**	NS	NS
Lepidoptera[a]	109/27	0.186 (0.040)	0.016 (0.016)	0.021 (0.010)	0.023 (0.003)	**	**/	**/

* $P\leq0.05$ ** $P\leq0.01$ *** $P\leq0.001$ **** $P\leq0.0001$ NS no significant difference [a] Low frequency of visitation

Table 4 Comparison of linear body size (carapace width and gape) and body condition (residual index) among spiders in the four treatment groups and between migrant and non-migrant spiders. Raw data is presented. Values are means (±1 SE). For carapace width and gape, ANOVAs were performed on log transformed data. The residual index was based on ln transformed data

Treatment	Carapace width (mm)	Gape (mm)	Residual index
Patch type			
Bidens, large	3.36 (0.07)	28.38 (0.64)	0.024 (0.064)
Bidens, small	3.22 (0.15)	28.27 (0.68)	0.115 (0.112)
Solidago, large	3.38 (0.09)	28.00 (0.63)	–0.050 (0.063)
Solidago, small	3.50 (0.11)	29.23 (1.10)	–0.042 (0.059)
Migration status			
Migrant	3.45 (0.09)	28.18 (0.75)	0.089 (0.101)
Non-migrant	3.33 (0.05)	28.25 (0.45)	–0.040 (0.031)
ANOVA: summary of *P* values			
Patch type			
Plant species	0.2326	0.7904	0.2705
Patch size	0.9697	0.5466	0.6336
Interaction	0.2562	0.5590	0.6877
Migration status	0.2316	0.9156	0.1222

Table 2). Spiders in *Bidens* patches gained mass at a faster rate than spiders in *Solidago* patches, and spiders in large patches gained mass at a faster rate than spiders in small patches (Fig. 3). Similar patterns were found for number of prey captured spider^{-1} day^{-1} and mass of prey captured spider^{-1} day^{-1} (Fig. 4). No significant interaction effects of plant species composition and flower patch size on spider hunting success were found (Table 2).

Multiple regression indicated that variation in the rate of mass gain of spiders was only weakly correlated with pollinator responses: F=3.813, df=2, 13, R^2=27.3%, P_{total}= 0.0498; $P_{\text{no. visits/floral unit/h}}$=0.8858, $P_{\text{visitor-mass}}$=0.0949.

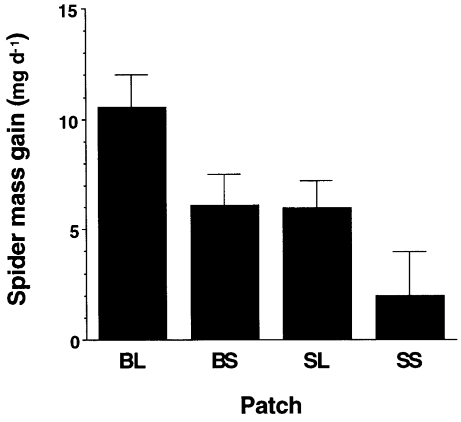

Fig. 3 Spider rates of mass gain (mg day^{-1}) in the experimental patches. Raw data are presented. *Error bars* are ±1 SE

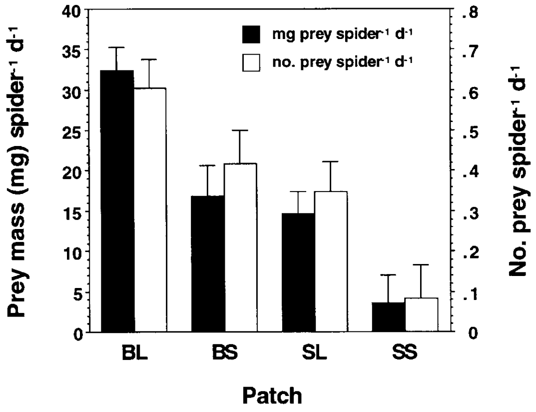

Fig. 4 Per-capita prey capture rates (number of prey captured spider^{-1} day^{-1}) and mass of prey captured spider^{-1} day^{-1} in the experimental patches. Raw data are presented. *Error bars* are ±1 SE

Prey availability versus prey captured

Misumenoides did not capture prey taxa in proportion to their availability: χ^2_{Bidens}=42.3, df=8, P≤0.0001; $\chi^2_{Solidago}$=27.0, df=8, P=0.0007. Spiders disproportionately captured larger taxa, with the exception of bumblebees (Fig. 5). Bombyliids, bumblebees, and honeybees were the most frequent visitors to *Bidens*. Spiders captured honeybees at a rate approximately 3 times that suggested by their proportionate representation among visitors, while bumblebees and bombyliids were under-represented in spider diets compared to their availability. Of the less common taxa visiting *Bidens*, small bees, medium bees, and “other flies” were captured at rates 3–4 times higher than that suggested by their proportionate representation among visitors, while lepidopterans were captured at a rate equivalent to their proportionate representation among visitors. On *Solidago*, syrphids and “other flies” were the most commonly available taxa. Spiders captured “other flies” in proportion to their availability, while syrphids were under-represented in spider diets. Of the less common taxa visiting *Solidago*, small bees, honeybees, and wasps were captured at rates approximately 2–7 times higher than that suggested by their proportionate representation among visitors, while medium bees were captured at a rate roughly equivalent to their proportionate representation among visitors. On *Solidago*, as on *Bidens*, bumblebees were under-represented in spider diets. Lepidopterans and bombyliids were conspicuous by their absence from the diets of spiders occupying *Solidago*.

Average mass of insects observed visiting the experimental patches was significantly lower than the average mass of insects actually captured by spiders (Table 5, Fig. 2). The data showed a tendency towards a greater disparity between the size of visiting insects versus captured insects in *Solidago* patches compared to *Bidens* patches. A tendency towards a greater difference between the size of visiting insects versus captured insects in small patches compared to large patches of a given plant species was also found.

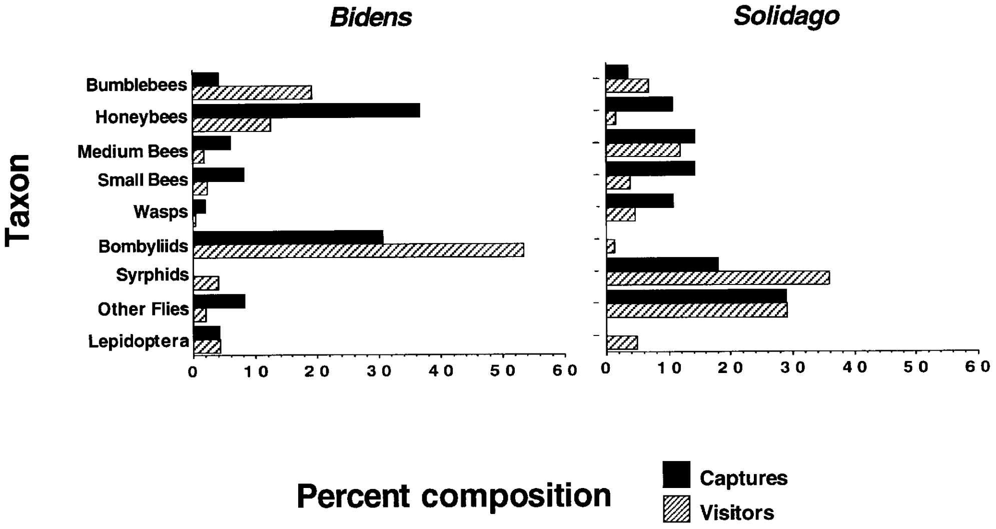

Fig. 5 Proportionate representation of the various pollinator taxa among *Bidens* and *Solidago* visitors and percent contribution of those taxa to the diets of *Misumenoides* hunting on *Bidens* and *Solidago*. Large and small patches of a given plant species were combined for this analysis

Table 5 ANOVA comparing insect mass (mg) with respect to experimental treatments and an insect's status (VC) as either a visitor or capture. ANOVA was performed on log (x+1) transformed data

Source	*df*	*SS*	*F*	*P*
Plant species	1	0.247	11.462	0.0028
Patch size	1	0.148	6.851	0.0161
VC	1	0.395	18.283	0.0003
Plant species × patch size	1	0.029	1.346	0.2590
Plant species × VC	1	0.091	4.215	0.0527
Patch size × VC	1	0.073	3.376	0.0804
Plant species × patch size × VC	1	0.007	0.306	0.5862
Residual	21	0.453		

Spider migration

Due to migration, spider densities in the patches changed over the course of the experiment (Table 1). All migration events were initiated by spiders placed in *Solidago* patches or by spiders outside the experimental plot. Seven spiders migrated from *Solidago* patches to *Bidens* patches during the course of the experiment: one SS to BS, two SS to BL, one SL to BL, and three SL to BS. Two spiders shifted between SL patches. One spider switched from a small to a large *Solidago* patch. All spiders placed in *Bidens* patches remained in their original patches. Spider movements indicated a preference for *Bidens* (χ^2=7.86, *df*=3, *P*=0.0490). Clear patch size preferences were not detected (χ^2=6.630, *df*=3, *P*=0.0847). Of the six spiders immigrating to the study plot from the surrounding vegetation, four chose BL patches, and two chose SL patches.

Discussion

Overview

Species composition and size of flower patches indirectly affected flower-dwelling spiders via direct effects on pollinators. *Misumenoides* experienced greater hunting success in *Bidens* patches compared to *Solidago* patches and in large patches of a given plant species compared to small patches. As a group, insects preferred *Bidens* over *Solidago*, but strong patch size discrimination was not evident in pollinator visitation rates. More pertinent to spider hunting success, however, was the fact that larger insects discriminated in favor of *Bidens* patches and in favor of large patches of a given plant species. Pollinator visitation rates predicted spider hunting success only with respect to the species composition of patches, while the average size of pollinators visiting the experimental patches predicted spider success with respect to both plant species and patch size.

Higher prey-capture rates and capture of larger prey taxa by spiders in *Bidens* patches offset the higher metabolic expenditures associated with occupation of this plant species (see below). In addition to having more predation opportunities and greater access to larger prey taxa, a further advantage gained by spiders using *Bidens* was that pollinator foraging movements were restricted to a much smaller area than were movements of pollinators on *Solidago*. On *Bidens*, foraging insects were confined to the central disk of an inflorescence, which had an average surface area of 74 mm^2. In the Asteraceae, disk florets mature over a period of several days, progressing from the outermost edge of the disk inward (Gilbert 1983). Pollinators circled a *Bidens* disk while feeding from the ring of nectar-producing florets. On *Solidago*, insects foraged in a straight line along the entire length of a floral unit (panicle branch), which had an average surface area of 1,137 mm^2. The different movement patterns displayed by pollinators on *Solidago* and *Bidens*, and the smaller furaging surface of a *Bidens* floral unit, suggested that insects had a greater likelihood of coming within range of a spider on *Bidens* than on *Solidago*, even though more time per visit was spent on *Solidago* floral units.

Pollinator responses to species composition and size of flower patches

The underlying cause of the general pollinator preference for *Bidens* was not determined, but likely reflected a greater reward per unit foraging cost for insects utilizing *Bidens*. Floral architectures of the two plant species were very distinct, and cues which insects may have used in long-distance orientation included total floral surface area presented by the plants, UV-reflecting surface area, and inflorescence symmetry.

Among the pollinator taxa displaying distinct plant species preferences, the largest and/or most common taxa (bumblebees, honeybees, and bombyliids) preferentially foraged on *Bidens*. Because bumblebees displace syrphids from flowers (Morse 1981b), the apparent preferences of syrphids and "other flies" for *Solidago* may have been a result of competitive exclusion of these smaller insects from *Bidens* by the large bees. Alternatively, shorter tongue lengths of syrphids and "other flies" may have enabled them to forage for nectar more efficiently on *Solidago*, which has smaller disk flowers with shorter corolla tubes than *Bidens* (Schmalhofer, unpublished data).

In terms of absolute numbers, large patches attracted more insects than did small patches. However, the greater number of visits was diluted among the greater number of floral units in large patches such that per floral unit visitation rates to large and small patches of a given plant species were similar. Only bumblebees and lepidopterans showed distinct preferences for large patches, and then only with respect to *Bidens*. Dipterans have generally been found to be less discriminating of floral-display size than hymenopterans (Thomson et al. 1982; Stanton and Preston 1988; but see Connor and Rush 1996 for an exception), so the lack of patch size effects on the visitation rates of bombyliids, syrphids, and "other flies" observed in the present study was not unusual. Conversely, the failure of most hymenopteran taxa to discriminate between patch sizes was unexpected. A particular surprise was the similarity in visitation rates of honeybees to large and small patches. In other studies, honeybees have shown strong preferences for larger patches or floral displays (Morse 1986a; Stanton and Preston 1988; Young and Stanton 1990; Schmalhofer 1996). Because patch size functions as a long-distance cue in attracting pollinators, the relative isolation of the study site, surrounded predominantly by foxtail grass and dense forest, may have contributed to the failure of most pollinator taxa to perceive and respond to patch size differences: the monochromatic grass background could have caused flower color to become a hyper-stimulus that overwhelmed patch size cues.

Potential influence of spiders on pollinator behavior

Slightly higher spider densities in some patches were not likely to have affected pollinator responses to the patches. Even in "high" density patches, spider density was actually rather low: 3% or less of floral units in any given patch were occupied by spiders, and spider densities per stem remained within the range of densities observed for field populations of adult and penultimate-instar *Misumenoides*: approximately 0.02–0.25 spiders per stem (Schmalhofer, unpublished data). Morse (1986b) provided compelling evidence that crab spider presence does not influence pollinator foraging behavior. Using common milkweed (*Asclepias syriaca*) and the crab spider *Misumena vatia* (a species very similar to *Misumenoides*), Morse found that pollinators showed no signs of avoiding spiders even at densities much higher than normal. Neither selection of milkweed umbels (a milkweed umbel is an inflorescence and is equivalent to a floral unit as defined in the present study) nor the length of time pollinators spent foraging on an umbel were affected by spider presence or absence (Morse 1986b). In addition, *Misumenoides* was extremely well-camouflaged on both *Solidago* and *Bidens*, so apparency to insects of spiders in the experimental patches was probably quite low. Spider crypsis was not dependent on the number of stems within a patch. Spiders were much smaller than *Bidens* and *Solidago* floral units and were cryptic at the level of the floral unit on both plant species. On *Solidago*, spiders typically positioned themselves among the small individual inflorescences that comprised a floral unit (rather than sitting exposed on top of the inflorescences) and only a portion of a spider's prosoma and forelimbs protruded from among the tiny *Solidago* inflorescences. On average 90% of spiders occupying *Solidago* were concealed in this manner (Schmalhofer and Casey, unpublished data). On *Bidens*, spiders generally constructed a "bower" by tying two ray florets together with silk. A spider hid within the bower where it waited to ambush prey. On average 69% of spiders occupying *Bidens* used bowers (Schmalhofer and Casey, unpublished data) Spider bowers were undoubtedly apparent to insects. Interestingly, spider alteration actually enhanced inflorescence attractiveness to insects (Schmalhofer, unpublished data).

Potential complications in evaluating indirect effects of plants on spider hunting success

Misumenoides occupying BL patches experienced the best hunting success. Placement of large spiders in BL patches, or preferential migration of large spiders to BL patches, could have led to an erroneous interpretation of enhanced hunting success in BL patches. If large spiders disproportionately occupied BL patches, rates of mass gain could have been high simply because large spiders were capable of capturing larger prey, not necessarily because these patches were better hunting sites. However, size and body condition of spiders were similar among patch types. Thus, the observed treatment effects on spider hunting success were real, not artifacts of a skewed size distribution of spiders among patches. Likewise, size and body condition of migrant and non-migrant spiders were similar, so spider movements between patches did not bias the results.

Another potentially complicating factor in evaluating indirect effects of the experimental patches on spider hunting success was the possibility of direct impacts of patches on spider energetics. Because spiders are strict ectotherms (Pulz 1987), occupation of patches allowing spiders to maintain lower body temperatures would have also lowered metabolic rates and provided these spiders with an energetic advantage. Body temperature of *Misumenoides* closely tracks environmental temperature (Schmalhofer 1996; Schmalhofer and Casey, unpublished data), therefore spider rates of mass gain could be influenced by patch residency. No differences were found in the body temperatures of spiders occupying large and small patches of a given plant species (Schmalhofer, unpublished data). However, spiders in *Bidens* patches had significantly higher body temperatures than did spiders in *Solidago* patches (Schmalhofer 1996; Schmalhofer and Casey, unpublished data): during the 3 days of the present study, average body temperatures of spiders occupying *Bidens* and *Solidago* patches were 22°C and 19°C, respectively. Thus, occupation of *Bidens* patches put *Misumenoides* at an energetic *disadvantage*. Also, *Misumenoides* prey-capture success is broadly insensitive to temperature (Schmalhofer and Casey 1999), so the higher metabolic rates experienced by spiders in *Bidens* patches were not likely to have imparted a predatory advantage.

Finally, the observed pattern of spider hunting success was not due to nocturnal predation. Only two instances occurred in which spiders (both occupying SL patches) experienced mass gains that could not be explained by diurnal prey capture. With respect to nocturnal predation opportunities, spiders occupying *Bidens* were at a disadvantage. *Bidens* inflorescences closed fully or partially at night. Spiders either stayed on the inflorescence disk and were enclosed within the inflorescence for the night (most spiders), or they moved to perch on the outside of the closed inflorescence. Spiders using *Solidago* could hunt throughout the night. Patch size should not have impacted nocturnal hunting success since night-flying pollinators could not use visual cues to orient to patches.

Spider hunting success

Misumenoides was a selective hunter. This aspect of the spider's predatory behavior explained the absence of strong correlations between variation in spider rate of mass gain and pollinator responses (visitation rate and visitor size) revealed by the multiple regression analysis. Another flower-dwelling crab spider, *Misumena vatia*, displayed low frequencies of attack (5–13% of visiting insects were attacked) and capture (0.5–2% of visiting insects were captured), and showed an inverse relationship between prey size and capture success (Morse 1981a, 1986b, 1986c). Given that attack success of *Misumenoides* likely shows a similar inverse relationship to prey size, hunting success of *Misumenoides* would be expected to be enhanced by occupation of patches offering more opportunities to capture larger prey taxa. Thus, selective predation by *Misumenoides* supplied evidence in favor of the hypothesis that flower patches indirectly impacted spiders through direct effects on pollinators and that the size and numbers of insects attracted to the experimental patches influenced spider hunting success. The experimental results supported this interpretation. Spider rates of mass gain paralleled the pattern described by average visitor size to the experimental patches: BL>BS=SL>SS.

Pollinator visitation rates predicted the plant species in which spiders would experience greater hunting success, but did not accurately reflect spider hunting success within different patch sizes of a given plant species. *Misumenoides* captured more prey per spider, a greater mass of prey per spider, and gained mass more quickly in large patches. Bumblebees and lepidopterans, the only insect taxa that discriminated between patch sizes (and then only with respect to *Bidens*) accounted for a small fraction of the prey captured by *Misumenoides* (see Fig. 5), so predation on these taxa did not explain the experimental results. Figures 2 and 5 clearly show that spiders were not indiscriminately attacking/capturing any insect that visited spider-occupied floral units. Rate of prey capture by *Misumenoides* has not been found to correlate with total insect availability (Schmalhofer and Casey 1999). Lack of a strong functional response to increasing pollinator availability is likely a consequence of the large prey types favored by *Misumenoides*. Large insects required long processing times (e.g. 5 h were needed to consume a honeybee), after which spiders would be satiated for some period of time and might be less likely to respond to additional predation opportunities. Given these constraints, the nonconformity between insect visitation rates and spider hunting success found in the present study was not surprising.

Comparison of the proportionate contribution of various pollinator taxa to patch visitation and their representation in the diet of *Misumenoides* suggested that some taxa (e.g., honeybees) may have been attacked at every opportunity, while other taxa either were often ignored or frequently evaded capture (e.g., bumblebees, syrphids, and bombyliids). Direct measures of the number of attack opportunities experienced by spiders were not made, but data extrapolation suggested that BL, BS, SL, and SS patches received approximately 113, 77, 17, and 15 pollinator visits per floral unit, respectively, during the 3 days of the experiment, and that 1.7%, 1.1%, 8.2%, and 2.2%, respectively, of insect visits to occupied floral units ended in capture. Because a pollinator may not approach within striking range of a spider, a visit does not necessarily equate to an attack opportunity. Therefore, these percentages are conservatively low estimates of attack success. In laboratory tests with a representative dipteran prey-type (the house fly, *Musca domestica*), 85% of prey attacked were captured, but spiders did not always attack prey that came within striking range (Schmalhofer and Casey 1999). Coupled with the visitor size/prey size comparison data from the current experiment, the high success rate of *Misumenoides* attacks against *Musca* in the laboratory found by Schmalhofer and Casey (1999) supported the hypothesis that, in the field, *Misumenoides* ignored some of the smaller pollinator taxa in favor of larger taxa. However, physical capabilities of the prey taxa cannot be discounted: the extreme speed and agility of bombyliids and syrphids (Barth 1991) undoubtedly contributed to their under-representation in the diet of *Misumenoides*.

Attributing greater importance to the availability of large prey taxa as opposed to simply higher insect visitation rates explained why SL patches and BS patches appeared to be of similar value to *Misumenoides*. Spiders in these patch types experienced similar rates of mass gain, had similar-sized insects available to them, and captured prey of similar size, but visitation rates to SL patches were much lower than visitation rates to BS patches. Also, later in the season when the number of floral units per stem on *Bidens* had increased 5-fold, insect visitation rates to BL patches dropped to levels more comparable to that seen for *Solidago*, but visitor size and rate of mass gain among spiders remained high: late season BL visitation =0.77 visits floral unit^{-1} h^{-1}; late season BL visitor size =63.6 mg; late season spider mass gain in BL patches =12.0 mg day^{-1} (Schmalhofer, unpublished data). These findings argue for the greater importance of the size of potential prey over numbers of potential prey in contributing to crab spider hunting success.

Honeybees appeared to be preferred prey items, and predation on honeybees was largely responsible for the greater hunting success experienced by spiders in *Bidens* patches. The proportionate contribution of honeybees to the diet of *Misumenoides* as over 3 times that expected in both *Bidens* and *Solidago* patches given the proportionate availability of honeybees on these plants. However, per-floral unit visitation rates of honeybees to *Bidens* patches were approximately 38 times greater than to SL patches. Honeybees were conspicuous by their absence among the visitors to SS patches. *Misumenoides* experienced exceptionally poor hunting success in these patches, and all SS patches were eventually abandoned. Clumsiness of honeybees during foraging, and the apparent ease with which these insects are captured by crab spiders (Fritz and Morse 1985; Morse and Fritz 1987) coupled with their large size and availability, likely contributed to the status of honeybees as a preferred prey item. In contrast, bumblebees, although common visitors to both plant species, were seldom captured. The greater agility of bumblebees (Fritz and Morse 1985; Morse and Fritz 1987), and their larger size undoubtedly made bumblebees more difficult to handle. However, in the absence of honeybees, the number of bumblebees captured per spider increases dramatically (Schmalhofer, unpublished data), suggesting that bumblebees were ignored in the present study not because spiders could not catch them, but because the more easily captured honeybees were readily available.

Potential fitness consequences for spiders

Because spiders are often food-limited (Anderson 1974; Nakamura 1987; Riechert and Harp 1987; Vollrath 1987; Morse 1988a; Wise 1993) and growth is typically submaximal (Morse and Fritz 1987; Vollrath 1987), spiders choosing hunting sites resulting in an increase in the number or size of prey captured accrue fitness benefits. A strong correlation exists between maternal mass and reproductive success in *Misumenoides* (Beck and Connor 1992) and other flower-dwelling crab spiders (Fritz and Morse 1985; Morse and Fritz 1987; Morse 1992), and large prey make a greater contribution than small prey to these factors (Fritz and Morse 1985). Maternal mass of crab spiders is the primary factor affecting fitness of successive life-history stages and is strongly affected by maternal hunting-site choice and subsequent foraging success (Morse and Stephens 1996). *Misumena vatia* discriminated in favor of milkweed umbels with more nectar-producing flowers (Morse and Fritz 1982), and spiders selecting umbels with larger floral displays experienced greater mass gains, which led to increased reproductive output and other fitness benefits associated with having greater energetic reserves, such as longevity during egg-guarding and an increased ability to fend off potential predators of the spider's young (Fritz and Morse 1985; Morse 1988a, 1988b, 1992; Morse and Fritz 1987).

In the present study, *Misumenoides* clearly experienced differential hunting success in the various patch types. If patch quality was defined by the size of insects attracted to patches, then migration was equally likely to maintain a spider's current level of hunting site quality as to improve hunting site quality. Notably, spiders did not move to patches of lower quality. Migration patterns observed in the present study, and additional experiments (Schmalhofer 1996), revealed a preference of *Misumenoides* for *Bidens*. *Misumenoides* selecting *Bidens*, when both *Bidens* and *Solidago* are available, or selecting larger patches of a given plant species, should achieve fitness benefits similar to those documented for *M. vatia*. Discrimination among plant species is not unique to *Misumenoides*. Preferences have also been found in *M. vatia* and in the ambush bug, *Phymata americana* (Greco and Kevan 1994), and may be common among anthophilous predators. Discrimination by predatory arthropods among flower patches on the basis of patch size alone has not been documented. However, among patches of similar size, but differing quality, crab spiders preferentially selected higher quality patches (Morse and Fritz 1982).

Conclusion

Variation in the species composition and size of flower patches exerted indirect impacts on the hunting success of a flower-dwelling spider via direct effects on pollinators. Size of pollinators attracted to the patches had a stronger influence on spider rate of mass gain than did pollinator visitation rates. Consequently, spider reproductive success would also be affected by the size and species composition of flower patches available. *Misumenoides* not only had the potential to influence rates of energy acquisition, and hence fitness, through patch choice, but spiders actually selected hunting sites that enhanced, or at least maintained, average rates of mass gain. *Bidens* and *Solidago* often have contiguous or interspersed distributions, therefore *Misumenoides* may frequently have the opportunity to choose between these two species and among patches of varying size of a given plant species.

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