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# Specificity of attraction to floral chemistry in *Misumenoides formosipes* crab spiders

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**Abstract.** Although our understanding of arachnid olfactory physiology remains relatively limited, studies continue to reveal the importance of chemical cues for many spider behaviors. Olfactory cues for detecting prey, navigating to foraging sites, or finding mates might be especially beneficial to cursorial and ambush spiders living in structurally complex habitats. Previous field results suggested that volatile plant chemical cues were important in *Misumenoides formosipes* Walckenaer 1837 (Thomisidae) navigation and led us to design olfactometer bioassays to test this hypothesis in the laboratory. In our olfactometer trials, crab spider males were attracted specifically to the floral scent of *Rudbeckia hirta* (a species on which *M. formosipes* is commonly found in the field), but not to volatiles from foliage of the same plant species nor to volatiles from foliage of *Morus rubra*. Male spiders also failed to display any attraction to the floral scent of *Daucus carota*, even though they commonly reside on that plant in the field. Female *M. formosipes* did not move toward *R. hirta* inflorescences as a first choice over a control, although they did spend more time in the olfactometer arm with the *R. hirta* treatment. Males' use of olfactory cues to locate *R. hirta* inflorescences should increase encounters with potential mates, given that females in our population are found on that substrate more predictably than on any other.

**Keywords:** Floral scents, navigation, olfactometer, plant volatiles, spider olfaction, Thomisidae

Studies of the olfactory capacities of arachnids have lagged behind those of other arthropods, especially insects. The early recognition of antennae as a primary location of chemoreceptors in mandibulates and the absence of any clearly homologous structures in arachnids might in part account for this discrepancy. At this time, relatively few reports exist on the receptor anatomy and physiology of olfaction in spiders (e.g., Dumpert 1978; Foelix 1985, 2011). However, valid claims for the olfactory capacities of these animals come from demonstrations of behavior consistent with the reception of volatile chemicals, with studies combining behavior and receptor physiology being especially instructive (Tichy et al. 2001; Jiao et al. 2011).

Across spider families, there is substantial behavioral evidence for the existence of sex pheromones—either contact or air-borne or both (e.g., Schulz 2004; Gaskett 2007; Rypstra et al. 2009). Kairomones have been implicated in spiders' abilities to locate and discriminate among prey species, as well as avoid predators (Allan et al. 1996; Kaspi 2000; Hostettler & Nentwig 2006; Schonewolf et al. 2006; Cross & Jackson 2010). Olfactory or gustatory cues also enable spiders to find nectar sources (Patt & Pfannenstiel 2008), optimal hunting sites (Heiling et al. 2004; Junker et al. 2011) and substrates with greater prospects for locating mates (Stellwag & Dodson 2010). Among amblypygids, Hebets & Chapman (2000) recorded electrophysiological responses to a tremendous variety of volatile chemicals in the antenniform legs of one tropical species, and olfactory cues alone were sufficient for kin discrimination in a social species (Walsh & Rayor 2008).

Spiders that capture prey by stealth as opposed to webs might be especially likely to use chemical cues (animal kairomones and plant secondary compounds) to aid in locating prey, hunting sites or mates. For example, exposure to plant volatiles increased the number of *Thomisus spectabilis* Doleschall 1859 (Thomisidae) individuals attracted to inflorescences compared with visual cues alone (Heiling et al. 2004). Other *Thomisus* species were attracted to traps baited with eugenol, a component of many floral bouquets (Krell & Kramer 1998). Finally, males of the crab spider *Misumenoides formosipes* Walckenaer 1837 moved toward black-eyed susan (*Rudbeckia hirta* L.) inflorescences, the substrate upon which females were most commonly found, at a higher frequency when floral volatiles were available as opposed to visual cues alone (Stellwag & Dodson 2010).

The latter result led us to the present study in which we tested whether or not *M. formosipes* would navigate toward the chemical signatures of plants in the absence of associated visual and tactile cues. Laboratory bioassays were conducted in Y-tube olfactometers to address the following questions: 1) Are male *M. formosipes* attracted to plant volatiles from either the inflorescences or the foliage of *R. hirta*? 2) Are males attracted to volatiles from the inflorescences of Queen Anne's lace (*Daucus carota* L.)? 3) Are males attracted to volatiles from an arbitrarily chosen plant within their habitat [foliage of mulberry (*Morus rubra* L.)]? 4) Are female *M. formosipes* attracted to volatiles from the inflorescences of *R. hirta*? One of us (GND) has studied this population for many years and routinely found *M. formosipes* males and females hunting from the inflorescences of *R. hirta* and *D. carota* more than from any other substrates. If adult males use plant scents to locate females, we predicted that volatiles from these species should be attractive.

## METHODS

**Study organism.**—*Misumenoides formosipes* is an ambush predator that feeds primarily on insect visitors to inflorescences (Beck & Connor 1992; Dodson & Beck 1993), but males also ingest nectar as a secondary energy/water source (Pollard et al. 1995). Our study population is on a managed preserve in Delaware County, Indiana, containing habitats recently converted to prairie as well as successional fields and a forest patch. The spiders occur on a wide variety of flowering plants at the forest edges and in wildflower fields, with black-eyed susans (*Rudbeckia hirta*), brown-eyed susans (*R. triloba* L.), chickory (*Cichorium intybus* L.), and Queen Anne's lace (*Daucus carota*) the most predictable species on

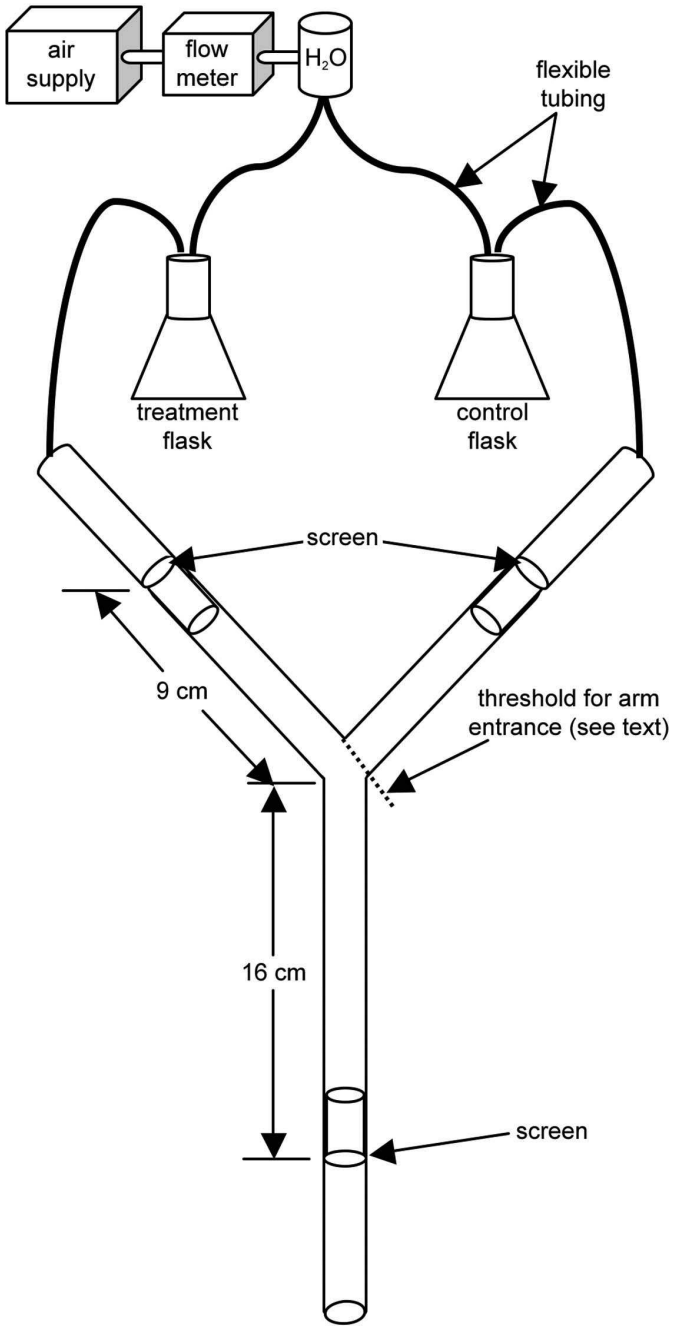


Figure 1.—Design of olfactometer used for biassays. Linear dimensions labeled indicate the distance from the mesh retaining screen behind the spider starting point to the point where each arm diverges and then the distance from the start of an arm to the screen preventing passage out of the olfactometer. The dotted line indicates the threshold a spider had to cross to be counted as having moved into the left or right arm.

which the late-instar juveniles and adults can be located (G.N. Dodson pers. obs.).

Males molt to the adult stage before females and begin searching the habitat for penultimate instar females that are nearing their own molt (Dodson & Beck 1993). The population sex ratio is strongly male-biased as the adult period begins [as high as 63% males in early August samples (Dodson & Stellwag unpubl. data)]. Adult males live only 2–3 weeks, after which females continue to hunt until laying eggs that hatch in the fall and give rise to overwintering spiderlings.

**Olfactometer set-up and protocol for all trials.**—Three olfactometers were assembled for each set of trials and laid out in parallel over white paper. Each olfactometer (Fig. 1) consisted of a glass Y-tube (Analytical Research Systems, Inc., Gainesville, FL), with both of its arms connected to a 50 ml treatment or control flask via flexible tubing. Air from a single source flowing at 20 ml/min was bubbled through 300 ml distilled water and this humidified air then traveled through both sides of the olfactometer before exiting through the base of the Y-tube. Factory inserted screens (Fig. 1) prevented spiders from moving out of the olfactometer.

For each bioassay trial, we placed one of the four treatments (*R. hirta* inflorescence, *R. hirta* leaves, *D. carota* inflorescence, *Morus rubra* leaves) into one of the two flasks along with 2 ml of water. The control flask contained only the 2 ml of water. We cut a single, typical inflorescence (ca. 5 – 6 cm diameter) for each trial in the *R. hirta* bioassays and took care to use a similar amount of plant material, whether inflorescence or leaves, across all treatments. The stem of the inflorescence or the petioles of the leaves were inserted into the water, with the remainder of the plant material resting above the water. We alternated the treatment flask between the left and right sides of the olfactometer in a pattern that resulted in equivalent numbers of trials conducted with plant material on each side. We positioned and shielded the flasks to eliminate the possibility of any visual cues for the spiders.

Spiders for the bioassays were collected daily from the field, held in vials with moist filter paper, and used in trials within 24 h or rarely 36 h. At the start of each trial, we allowed a spider to move from the vial to the introduction tube of the olfactometer on its own and gently prodded it only if it did not transfer after several minutes. Each spider was used in a single trial and then returned to the field site the next day. We collected new spiders well away from release sites, so there was a very small chance that we collected any male more than once. Trials were conducted between 25 July and 12 August in 2008, 2009, 2010, and 2011.

The temperature of the trial room varied minimally around 23° C. Standard florescent light bulbs remained on during all trials. All olfactometer glassware was washed using a bottle brush and detergent, rinsed thoroughly, and oven-dried between trials, with particular attention paid to clearing all residual silk from spider movements.

We started a set of trials each day at ca. 08:00 and a second set at ca. 20:00 and ran both undisturbed for 10 h. This trial duration was both expedient (typically no more than the required six males could be located within the search time available each day) and conservative (we had no way to predict beforehand how much time might pass before spiders began to move). We completed 30 trials for each treatment (two sets of 30 trials were conducted for males with *D. carota* inflorescences – see below). All trials were recorded with a digital video camera and then played back to determine 1) the time from the start of the trial until the spider entered an arm for the first time (= latency), 2) which arm (treatment or control) was visited first and 3) the total time spent within each arm during the trial. To be recorded as having entered an

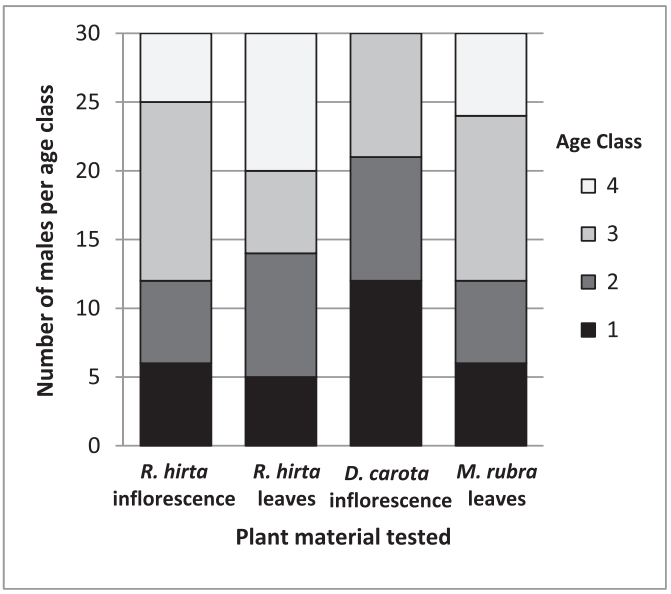


Figure 2.—Number of males used from each age group category across the four sets of trial treatments. Age classes represent the dates that males were collected and used in the trials from relatively youngest (Group 1) to oldest (Group 4). Collection dates were 30 July–2 August (Group 1), 3–5 August (Group 2), 6–8 August (Group 3), and 9–12 August (Group 4).

arm of the olfactometer, the entire body of the spider had to cross the threshold of the arm (see Fig. 1).

**Protocol specific to male trials.**—Adult males were collected from *R. hirta*, *R. triloba*, and *D. carota* plants, primarily from inflorescences, but from other parts of these plants as well. We did not record the exact proportion collected from each of the plant species, but a majority came from *Rudbeckia*. Following completion of a full set of trials with each of the four treatments, we conducted a second set of 30 trials with *D. carota* inflorescences using males collected exclusively from *D. carota*. The purpose was to assess whether or not males known to have had experience with *D. carota* as a substrate might behave differently when exposed to volatiles of that plant in our olfactometer. Thus, we addressed the possibility that males in the initial trials showed no attraction to *D. carota* (see Results), because at least some of them might not have experienced that plant in the field.

In anticipation of a potential effect of adult male age on the vitality of individuals, and thus their tendency to move within the olfactometer, we spread the four treatments across the trial dates as evenly as possible year to year. Although we could not know the age of a given male in the field, we assumed that the average adult age (time since adult molt) increased daily once molting began, since most of the initial adults in the population would still be alive as newly molted males entered the cohort. The only exception to this trend might be within the first few days if freshly molted individuals outnumber the adults from previous days. For the purpose of analysis, we divided the trial males into four groups based on date of collection (Fig. 2) and used these as a proxy for ''relative age'' of adult males.

**Protocol specific to female trials.**—Females were collected from *R. hirta*, *R. triloba*, and *D. carota* plants, exclusively from inflorescenses. All of the females were at least penultimate instar, and some of the last ones collected may have been adults (genital morphology was not examined in order to avoid extensive handling). We collected only females exhibiting the behaviors of active foraging to avoid the use of individuals in a molting phase, which would be less likely to move in the olfactometer.

**Statistical analyses.**—The data recorded for the time spent by spiders in the treatment and control arms, time spent in first choice and second choice arms, as well as male latency times were not normally distributed. Therefore, a Box Cox transformation was performed followed by the use of parametric tests wherever normality was achieved and nonparametric tests otherwise. We tested our data for normality with the Wilk-Shapiro test and homogeneity of variances with Levene's test. All statistical analyses were performed using IBM SPSS Statistics v. 19. All *P*-values are two-tailed with an alpha level of 0.05.

## RESULTS

**Effects of experimental design.**—We first examined the combined trial outcomes for the initial four treatments with males ($n = 120$) to determine if the position of the treatment, starting time of the trials, or relative age of the spiders had unintended impacts as factors in the experimental design. None did as revealed by statistically equivalent frequencies for first choice of the treatment arm whether it was on the left or right of the olfactometer (Pearson $\chi^2 = 1.17$, $df = 1$, $P = 0.28$), morning or evening trial starts (Pearson $\chi^2 = 0.57$, $df = 1$, $P = 0.45$) or date of collection of spiders used in the trials (Pearson $\chi^2 = 3.2$, $df = 3$, $P = 0.36$). Therefore, these parameters were not included as variables in the final analyses.

We also considered whether or not males collected from the field during our final days of testing (and therefore older on average) might be less ''active'' and potentially provide different results for that reason alone. Using latency (i.e., time from the beginning of a trial until an initial choice of olfactometer arm) as an indicator of activeness, we failed to detect a relationship between relative age and latency (Pearson correlation coefficient = 0.14, $df = 3$, $P = 0.12$) using the complete data set. However, the removal of a single outlier for latency (30% larger than any other value) produced a significant correlation upon reanalysis (Fig. 3; Pearson correlation coefficient = 0.184, $df = 3$, $P = 0.046$). As stated above, we intentionally distributed the four treatments across the trial dates as a control for this anticipated effect. Thus, we feel that any age related effects would have had little if any influence on our overall findings. We offer further discussion of this issue below.

**Male responses to volatiles.**—*Misumenoides formosipes* males entered the *Rudbeckia hirta* inflorescence treatment arm prior to the control arm of the olfactometer significantly more often than by chance (Fig. 4, binomial exact probability = 0.0014). They also spent more time in the *R. hirta* inflorescence treatment arm, although not at a statistically significant level (Fig. 5, Mann Whitney test, $z = 1.8$, $P = 0.069$). There were no significant differences in the frequencies with which *M. formosipes* males chose the treatment versus the control arm first for *R. hirta* foliar treatment (binomial exact probability = 0.36), *D. carota* floral treatment (binomial exact

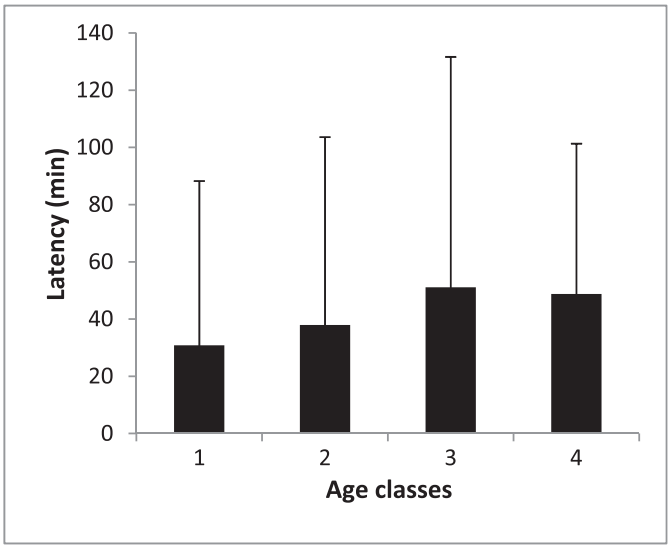


Figure 3.—Mean latency values for each male age class for the original four sets of trial treatments combined ($n$ = 120, error bars display one standard deviation; one outlier was removed from group 1). Latency was defined as the time from the start of a trial until the moment a male crossed into either of the two olfactometer arms. See Methods for a description of the rationale for this approximation of relative ages.

probability = 1.0) and *M. rubra* foliar treatment (binomial exact probability = 0.098) (Fig. 4). Likewise, the proportional time spent in treatment and control arms did not differ for these three treatments (Fig. 5, Mann Whitney tests: *R. hirta* foliage, $z$ = 0.57, $P$ = 0.56; *D. carota* floral, $z$ = 0.64, $P$ = 0.52; *M. rubra* foliage, $z$ = 0.87, $P$ = 0.38).

**Test for effect of prior experience with floral volatiles.**—Males collected exclusively from *D. carota* inflorescences exhibited the same non-preference for *D. carota* floral treatment as did the males in the original trials with that plant species. Seventeen of 30 males moved into the inflorescence arm before the control arm (binomial exact probability = 0.54). Thus, we found no evidence to suggest that familiarity with a particular substrate influences subsequent responses to its chemical signature, further support for the lack of a behavioral response to any volatiles from *D. carota* inflorescences.

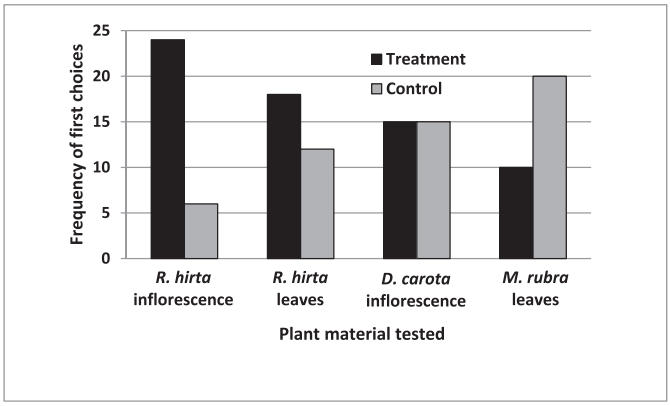


Figure 4.—Frequencies of males choosing to move first into the treatment versus the control arm of the olfactometer. Only the *R. hirta* inflorescence treatment arm was chosen first significantly more often than the water control. N = 30 for each treatment.

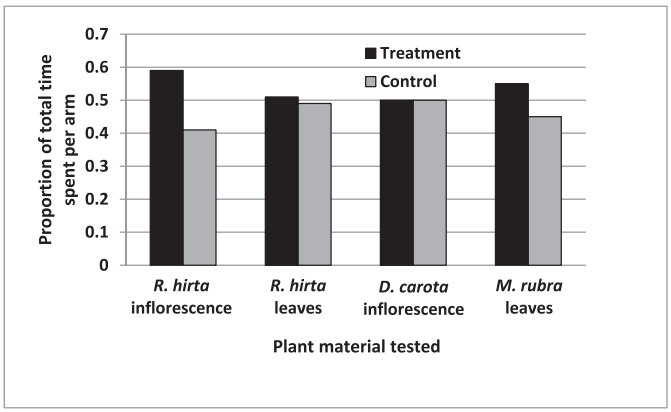


Figure 5.—Time spent by males in the treatment arm versus the control arm as proportions of the total time spent in both. No significant differences were found between treatment and control arm times based on 30 trials for each of the four treatment types. Proportional values shown correspond to the following average total time per trial in the arms: *R. hirta* inflorescence = 171.8 min, *R. hirta* leaves = 395.1 min, *D. carota* inflorescence = 368.0 min, *M. rubra* leaves = 317.7 min.

**Female responses to floral volatiles.**—Females showed no significant preference for the *R. hirta* floral treatment arm versus the control arm as a first choice (50% of 30 females entered the treatment arm first, binomial exact probability = 1.0). However, they spent significantly more time (61% of the total time in the two arms) in the arm with the floral treatment [medians and first quartiles: 192.1 (108.9) min for treatment arm, 72.9 (26.0) min for control arm; Mann Whitney test, $z$ = 2.07, $P$ = 0.036].

## DISCUSSION

Studies are increasingly revealing the ways in which spider behavior is influenced by olfaction, particularly in foraging and mating systems (e.g., Hostettler & Nentwig 2006; Gaskett 2007; Cross & Jackson 2010). We submit that non-web building spiders should benefit the most from the use of airborne chemical cues for navigation to hunting sites and potential mates. Locomotion represents an obviously large part of their energy expenditure, and visual targets might be difficult to locate within the complex three-dimensional space occupied by most of these species. Variety in the use of chemical cues for hunting is illustrated by a cursorial spider that finds its ant prey by detecting their alarm pheromone (Allan et al. 1996) and a nectarivorous ghost spider that locates its nectar source via scent cues (Patt & Pfannenstiel 2008). In field trials on *M. formosipes*, the availability of chemical cues in addition to visual ones increased the attraction of males to the kind of inflorescences that often harbor females (Stellwag & Dodson 2010), which led us to the hypotheses tested herein.

**Male responses.**—The strong attraction of *M. formosipes* males to *R. hirta* floral volatiles in our laboratory trials was expected following the aforementioned field trial results (Stellwag & Dodson 2010). Likewise, it seems appropriate that 60% of the trial males moved toward the foliage of this

same plant, since that also would ultimately bring them toward *R. hirta* flowers. Finally, moving away from the *Morus rubra* plant volatiles is also unsurprising, given that these crab spiders depend on flower-visiting prey and *M. rubra* flowering occurs more than two months prior to these spiders becoming adults. Any direction that takes them away from a "wrong" choice might be efficient. The one result that contrasted with our expectations was the males' indifference to the odor of *Daucus carota*. Females are routinely found on this plant as juveniles and adults, so it would seem to be an appropriate target for mate-seeking males to pursue. Given that adult males mostly forego prey capture to hunt for mates, an additional incentive is that *M. formosipes* uses *D. carota* for nectar feeding (Pollard et al. 1995). Indeed, when returning them to the field after the indoor trials we often observed males spend several minutes in a nectar feeding posture on this plant species.

The lack of attraction to *D. carota* by the spiders in our initial trails made us consider whether past experiences of the males might have influenced their responses. Collecting males as they were encountered in the field meant that we took a minority from *D. carota*, making it possible they had no experience with that plant substrate. Perhaps they had not learned to "recognize" its chemical signature. At least one case of olfactory imprinting has been demonstrated in spiders. Punzo (2002) fed separate groups of a lynx spider an exclusive category of prey and found that they subsequently displayed a preference for odors matching their prey type. However, our follow-up olfactometer trials using males collected exclusively from *D. carota* revealed the same lack of attraction to that plant species as in the initial trials. At face value, these results indicate that the spiders may not locate all favored plant species by floral scents. We acknowledge, however, that the act of cutting the floral stems for our bioassays may have altered the production or release of chemical compounds compared with the intact plant.

Our finding that a coarse measurement of relative male age (i.e., timing of collection from the field) was a predictor of latency times was not surprising. Given their long distance travel in search of females coupled with male-male aggressive interactions over mating opportunities (Dodson & Beck 1993; Dodson & Schwaab 2001), we might expect male vigor to decrease with time. Notably, in the closely related *Misumena vatia* Clerck 1757, older males lost 70% of staged contests with younger males (Hu & Morse 2004). Any influence that this variable might have had on male behavior in our trials, however, should have been mitigated by our equitable distribution of trial types across the dates of spider collection. Indeed, the pattern for first choice of treatment versus control in the olfactometers did not vary among the relative age categories.

**Female responses.**—Crab spider species that forage by ambushing pollinators are logical candidates for exploiting floral scents to locate hunting sites. This is particularly expected of females since their fecundity ultimately depends on foraging success (Schmalhofer 2001; Morse 2007). Indeed, the choice of hunting substrates by female *Thomisus spectabilis* Doleschall 1859 depended on whether or not floral scents were made available to them (Heiling et al. 2004). When floral scents were presented, *T. spectabilis* chose the same inflorescences favored by one of their primary prey species, *Apis mellifera*. By contrast, our results were somewhat ambiguous regarding *M. formosipes* females' preferences for the floral scents of a plant on which they are commonly found. Females displayed no tendency to move first toward the *R. hirta* inflorescence over a water control, but they did spend significantly more time in the floral treatment arm during the trials. When Junker et al. (2011) gave *Misumena vatia* females the choice between inflorescences and leaves of five species in laboratory trials (via intact plant material as well as hexane extracts of the plant parts), they reported no significant preferences for floral over foliar options. The latter finding does not preclude floral scent attraction, however, since the lack of a preference between the two parts of the plant does not rule out equivalent levels of attraction to both. Trials with a control that contained no volatile plant chemicals would be necessary to rule out this alternative. At this point, it is not possible to draw generalizations on the olfactory tendencies of crab spider females at the subfamily level given the differing results reported in these three studies.

Why would *M. formosipes* females fail to exhibit the strong attraction displayed by males toward *R. hirta* floral scents? It was not due to differences in how quickly a decision was made in the Y-tube apparatus, as the latency times were virtually identical (67.8 ± 95.1 min for males and 65.4 ± 96.9 min for females, mean ± SD). Sexual differences in the species' life history may be a factor. *Misumenoides formosipes* is protandrous, with the peak in adult male molts occurring at least 1 wk prior to the earliest maturation of females (G. N. Dodson pers. obs.). Coincident with adulthood, male activity is focused on searching for potential mates, primarily penultimate females close to their adult molt (Dodson & Beck 1993), whereas females continue to operate as ambush predators and exhibit substantial site fidelity (Beck & Connor 1992). We can see how males would benefit from continuously seeking the next inflorescence until a female is located, which may require many meters of travel. Females, on the other hand, move only when a new foraging site is needed and are likely to find an appropriate inflorescence nearby – making visual cues potentially sufficient for guidance, at least during the day. Female olfactory tendencies at night need further investigation, however. Of the 15 trials during which females moved into the *R. hirta* inflorescence arm first, 10 were night trials (although lights stay on). V.R. Schmalhofer (pers. comm.) has determined that *M. formosipes* females often make their hunting site moves nocturnally.

**Conclusions.**—Are we prepared to argue that the chemical signature of a single plant species is the major navigational cue for *M. formosipes* males seeking mates? Our current answer has to be "no" given the many potential cues in this process that remain uninvestigated. However, we now have laboratory results corroborating the original field study findings (Stellwag & Dodson 2010) on the significance of this specific olfactory signal. As part of ongoing bioassay work, we removed any potential effect of the physical plant body and found that 70.5% of 17 males chose the whole chemical extract from the *R. hirta* inflorescence over a water control. We intend to isolate and characterize the compounds in the extracts that elicit responses from spiders.

Certainly, females are found on other plant species including *D. carota*, and males converge quickly around near-adult females on these substrates (G.N. Dodson pers. obs.). Further

olfactometer trials with additional plant species are warranted, including a protocol that uses intact flowers on whole plants. For now, however, we are left to assume that males in our population benefit by seeking *R. hirta* inflorescences because of greater prospects for finding potential mates there. *D. carota* inflorescences have always been abundant over the years at our field site, but a lower percentage of them harbor females compared to *R. hirta.* Females also remained only half as long on *D. carota* (5.8 ± 6.1 d) as on *R. hirta* (12.6 ± 8.8 d) during field surveys (A.G. Anderson & G.N. Dodson unpublished data). In a roll of the dice that would seem to make the latter a better search target.

Our focus on phytochemical cues for male searches should not be seen as an argument that pheromone release by *M. formosipes* females is not important in mate finding. Given the growing documentation of sexual pheromones in spiders (Gaskett 2007), it is a reasonable conjecture that *M. formosipes* females might advertise their locations to males. At this point, however, several observations suggest the lack of a pheromone. In trials in which marked males ($n = 68$) were placed in the proximity of penultimate-instar females who were within days of their adult molt (and thus the target of searching males), fewer than 3% of these males moved to the nearby females (G. N. Dodson unpublished data). When males were placed directly onto the inflorescence housing a penultimate female for male-male contest trials (Dodson & Schwaab 2001), their behavior indicated a failure to recognize her presence until they happened to make physical contact with her body. Lastly, D.H. Morse and coworkers have found no evidence of a sex pheromone in the related species *Misumena vatia* (Holdsworth & Morse 2000; Legrand & Morse 2000; Leonard & Morse 2006). Even if a female sex pheromone were eventually identified in this species, it would not alter our interpretation that phytochemicals are important cues given that males are attracted to flowers with no females present.

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