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Movement, sex ratio, and population density in a dwarf male spider species, *Misumenoides formosipes* (Araneae: Thomisidae)

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Abstract. Crab spiders in the subfamily Thomisinae rank among the most extreme animals in terms of sexual size dimorphism (SSD). Hypotheses regarding the apparent selection for dwarfing of males relative to females generally reference advantages of small male size for mobility. Specific proposals claim that selection should be strongest in species with limited male-male combat, which would otherwise favor larger males. We aimed to determine if the predicted traits of low densities, female biased sex ratios, more movement by males, and limited male-male conflict characterized a population of *Misumenoides formosipes* Walckenaer 1837. New and previous assessments of these characteristics in this extremely dimorphic spider revealed a mix of support and discordance with the predicted set of traits. Repeated plot censuses over 2 years, together with daily monitoring of females and collections of males, documented relatively low densities with males outnumbering females by as much as 2.37:1. The movements of marked males were measured upon rediscovery during daily searches using two methods: tracking individuals from their point of discovery and trials in which males were moved to predetermined positions relative to females. Female movements were measured by marking their hunting positions followed by daily searches of these locations. Female average tenure across their locations was twice that of males (5.05 versus 2.45 days) and the initial moves made by marked males in trials were six times further than initial moves by monitored females (1.76 versus 0.29 m). Male-male conflicts over positions near females are frequent and intense in *M. formosipes*. By contrast, male fights are rare in the female biased populations of *Misumena vatia*, a species with similarly extreme SSD. Thus, while extreme SSD may be associated with enhanced mobility of small males during searches for females, it is not precluded by extensive male agonistic encounters.

Keywords: Crab spider, sexual size dimorphism, gravity hypothesis

Members of the thomisine subfamily of crab spiders have played prominent roles in ecological research on spiders. Decades of study by D. H. Morse and his collaborators has made the foraging ecology of *Misumena vatia* (Clerck 1757) among the most thoroughly understood of all predator systems (Morse 2007). The capacity for females of at least six crab spider species to change body color and its impact on foraging has also received substantial attention (e.g., Chittka 2001; Thery & Casas 2002; Heiling et al. 2004, 2005; Herberstein et al. 2009; Brechbühl et al. 2010; Anderson & Dodson 2014). We see a further opportunity for thomisines to play a more significant role in the ongoing investigation of extreme sexual size dimorphism (SSD) in animals. Crab spider females can be more than double the size of males and fully fecund females are many times heavier than adult males (Dondale & Redner 1978; Head 1995; Legrand & Morse 2000). The widely accepted explanation for large females in most invertebrates invokes natural selection for increased fecundity (Darwin 1871; Head 1995; Prenter et al. 1999; Hormiga et al. 2000). By contrast, multiple hypotheses have been proposed to explain small males. A recent phylogenetic analysis of the extremely dimorphic nephilid spiders supports the interpretation that larger body sizes evolved in both females and males, but at a lower trajectory for males (Kuntner & Elgar 2014). Thus, the appropriate question for these and perhaps most spiders might be "What has prevented males from growing as large as females?"

The greatest sexual size disparities among thomisids are represented by *Misumena vatia* and *Misumenoides formosipes* Walckenaer 1837. Small male size and protandry co-occur in both species, but it is uncertain whether one phenomenon determines the other or if selection acts independently on each (Legrand & Morse 2000). Indeed, the mechanisms driving the evolution of protandry across animals in general remain unresolved (Saino et al. 2010). Regardless of the developmental mechanism producing dwarf males, proposals for the selective advantages have been much debated. Ghiselin (1974), Vollrath & Parker (1992) and Vollrath (1998) argued that early maturation at smaller sizes would provide an advantage whenever mating success was determined by a race to find sedentary, unmated females. Elgar (1991) and Elgar & Fahey (1996) championed the notion that dwarf males would have a lowered risk of sexual cannibalism if their size helped them avoid capture or simply made them less attractive as prey. More recently Moya-Laraño et al. (2002) introduced the so-called gravity hypothesis with the basic tenet that males forced to search vertically for females in high habitats will be more successful at smaller body sizes. The latter hypothesis received multiple challenges regarding its applicability across species (e.g., Brandt & Andrade 2007a,b; Prenter et al. 2010) and has undergone subsequent revisions (Moya-Laraño et al. 2009; Corcobado et al. 2010).

An obvious commonality across these hypotheses is that small size provides males with an advantage in mate acquisition due to agility or energy efficiency during travel. Several authors (e.g., Ghiselin 1974; Vollrath & Parker 1992; Legrand & Morse 2000) have highlighted the ecological characteristics expected to promote male dwarfism within spider species according to these hypotheses. They include 1) low population densities (i.e., widely spaced females), 2) protandry, 3) female biased sex ratios, 4) more frequent and longer distance travel by males compared with females

(primarily with vertical challenges vis-à-vis the gravity hypothesis), and 5) limited confrontations between males in cases where large size would otherwise prove advantageous. In this study, we apply new and previously obtained ecological data to examine whether or not the above expectations are met for the dwarf male species *Misumenoides formosipes.* We then compare our findings to those reported for the similar-sized dimorphic *Misumena vatia*.

METHODS

Study species.—*Misumenoides formosipes* is a semelparous species widely distributed in North America (Dondale & Redner 1978). Research on this species has focused on its foraging ecology (Schmalhofer & Casey 1999; Schmalhofer 2000; Anderson & Dodson 2014) and mating system; especially factors determining the outcome of male-male contests during pre-copulatory guarding behavior (Dodson & Beck 1993; Dodson & Schwaab 2001; Hoefler 2002) and navigation cues relevant for mate searches (Stellwag & Dodson 2010; Dodson et al. 2013). Male *M. formosipes* molt into the adult stage over a span that is 1 to 2 weeks ahead of the equivalent span for adult molts in females (G. N. Dodson, pers. obs.).

Spider censuses.—Population censuses were conducted at Ball State University's Cooper Field Area in Delaware County, Indiana between 24 July and 20 August of 2005 and 2006. Intensive searches of the field site by one of us (GND) over many years had revealed that this species has a patchy distribution as late instar juveniles and adults, with spiders typically found where clusters of their preferred pollinator-attracting plants occur. This observation led to the establishment of four census plots of varying sizes (4.6, 6.4, 23.6, and 270.0 m^2) whose dimensions were dictated by the occurrence of discrete clumps of black-eyed Susan (*Rudbeckia hirta*) and Queen Anne's lace (*Daucus carota*). Thus, our estimates reflect high-end population densities rather than average densities across the full field area, most of which has no hunting substrates. Plots were examined every four days unless prevented by inclement weather. When a scheduled census did not occur, it was conducted as soon as possible and the four-day interval resumed from that day. Censuses involved a thorough search of inflorescences, stems, and leaves within each plot, recording the location and sex of each spider discovered. Densities were calculated as the number of spiders divided by the total area of each plot. Overall estimates of both spider densities and sex ratios were then calculated as the mean of the four plots collectively.

We investigated the population sex ratio again in 2011 by taking advantage of data available from two concurrent projects. Between 24 July and 5 August, males were being collected daily for lab studies from the same area that females were being monitored (without collection) for a field study. Up to six males were collected each day and subsequently released far enough away to avoid being collected again. Meanwhile the locations of all females discovered were marked by hanging a wire clip beneath the inflorescence they occupied and then monitoring their status every 24 h. Females rarely changed location during this time frame and their short moves made it possible to keep track of individuals (see below). While this method of counting the larger, more conspicuous females should have yielded an estimate close to their absolute numbers, we acknowledge that the total number of males was likely underestimated. Even though the counts did not reveal the exact sex ratio, it still allowed us to demonstrate that the population was not female-biased.

Spider movement.—Distances traveled by individual male spiders were quantified using three methods. During August 2004 and 2005 and July 2007 we conducted a total of 16 trials in which four adult males were collected in the field and given unique, dorsal paint marks. Each male was then placed in one of the four cardinal directions at a distance of 2 m from a naturally occurring penultimate female (the stage of females they guard normally). Searches for these marked males were conducted each subsequent day at the same time of day as the original release until none could be located for three consecutive days. The straight line distance between their initial locations (or the last known position if a move had already been recorded) and the location of rediscovery were used to calculate a minimum distance traveled per unit time together with the time that had elapsed. During August 2005 and 2006, >120 marked adult males were released after having been participants in field trials assessing navigational cues (Stellwag & Dodson 2010). Eleven of these males were rediscovered by chance after 24–216 h and their locations relative to initial release points measured. Finally, between 14 July and 8 August 2012 we marked adult ($n = 11$), penultimate ($n = 18$), and undetermined ($n = 4$) males *in situ* and then measured all moves until they could not be relocated for at least three consecutive days.

Locations of juvenile and adult females ($n = 84$) on the inflorescences of ten plant species were marked with color-coded clips between 18 July and 1 September, 2011. The distance of any subsequent moves were recorded when they were inspected the next day. It was not possible to mark the bodies of the females because they were being studied for color change properties at the same time (Anderson & Dodson 2014). So, while there is a chance that a female could have been misidentified when she moved, the very short average distances moved (see Results) made this unlikely. In 2005 and 2006, we marked and monitored the locations of females discovered in atypical positions (such as on plants with no inflorescences at the time) during routine searches of the field site outside the census plot areas. Tenures for such females are reported separately. All summary statistics are presented as means with standard errors.

RESULTS

Spider censuses.—Plot censuses in both years revealed a slightly female-biased sex ratio in the latter part of July that became male-biased before the end of the month (Fig. 1). During August, males outnumbered females by as much as 2.37:1, after which the numbers of males declined (probably due to male deaths) until well below the number of females (Fig. 1). Changes in the sex ratio were almost certainly due to males from outside the plots arriving at the location of females within the plots.

The male-biased sex ratio found in the 2005/2006 census plots was corroborated by the daily searches of a larger area of the habitat in 2011. The locations of 55 females were marked and monitored over the 13-d span, whereas 72 males were

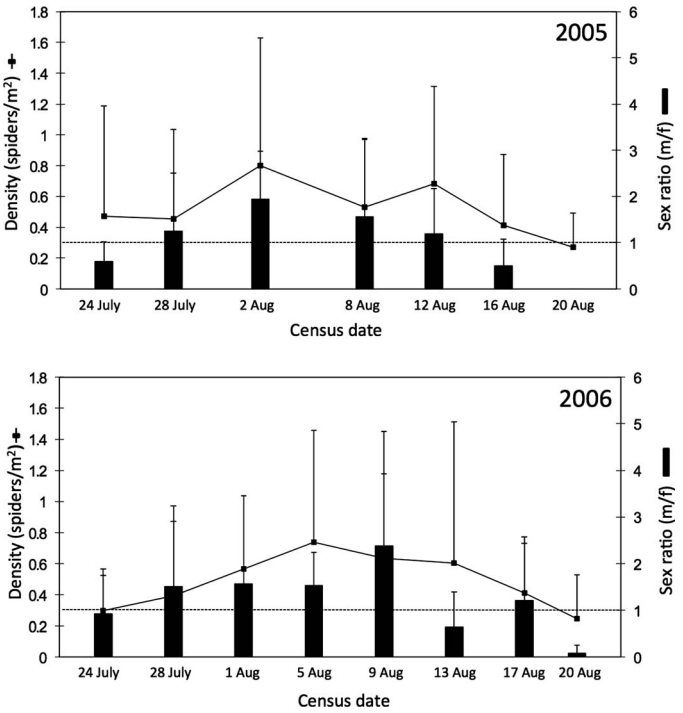

Figure 1.—Mean densities and sex ratios for a population of *Misumenoides formosipes* calculated from censuses of four study plots (see text for descriptions) on the dates noted in 2005 and 2006.

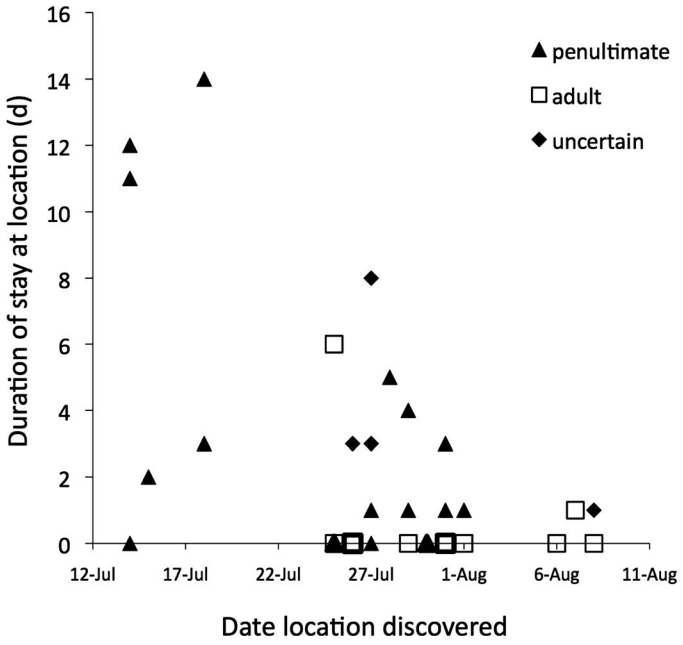

Figure 2.—Number of days *Misumenoides formosipes* males remained on the same plant following the day of discovery for each male in 2012. Symbol type indicates developmental status of each male. Symbols depicted in bold style represent two identical values.

permanently removed from this area over the same time period.

Mean spider densities for the combined plots ranged from 0.26–0.8/m^2 between 22 July and 21 August 2005 (overall mean for all census dates in 2005 = 0.51/m^2) and 0.24–0.73/m^2 over the same time period in 2006 (overall mean for all census dates in 2006 = 0.51/m^2) (Fig. 1).

Spider movement and tenure.—Of the 64 males placed 2 m in the cardinal directions from a penultimate female, all but one had moved from their initial location within 24 h. We rediscovered 45% of these males at least once during daily searches beginning 24 h after release. Ten of these 29 males were rediscovered one to three additional times during further searching. Only two males were re-sighted in the immediate vicinity of the original female 2 m away, but eight males were rediscovered cohabiting with other females in their area. The initial move (i.e., the first time a male was rediscovered regardless of time since trial start) for all 29 males averaged 1.76 ± 0.35 m, which reflects a rate of 0.062 ± 0.012 m/h. Considering only those males that were rediscovered the next day after a trial was started (n = 22), the mean distance moved from the starting point was 1.55 ± 0.35 m for an average rate of 0.064 ± 0.015 m/h. Eight of those same males were relocated during subsequent searches and their new locations reflected greater movement with a mean rate of 0.32 ± 0.25 m/h. The fastest rate of travel measured for any of these trial males was 2.09 m/h, by a male who was relocated at a distance of 7.85 m in 24 h and 16.72 m after 48 h.

Males released after being used in separate navigation research (Stellwag & Dodson 2010) and then rediscovered ca. 24 h later (n = 7) were found an average of 2.86 ± 0.77 m from their release point. The inclusion of four additional males rediscovered 2–4 d after release revealed that the 11 males collectively had moved ca. 3.74 ± 0.97 m/d if their movement had been in a straight line. For comparison with the above "cardinal direction" trial results, this rate of movement would be ca. 0.15 m/h.

Movement by females was limited overall (see below), but we were able to measure moves made by 20 of the 84 immature and adult females monitored in 2011. The average distance from original location to where they were rediscovered the following day for the first move of the 20 females was 0.29 ± 0.049 m. Six of these females made one or two additional moves followed by rediscovery from 1–10 d later. The 29 total moves measured reflected a rate of 0.01 m/h if the spiders' movement was relatively constant and in a straight path. The longest distance from an initial location measured for any female within 24 h was 1.5 m and no other female was discovered more than a meter from her previous location.

Males (n = 33) whose initial location was monitored daily remained on the same plant for 2.42 ± 0.65 d. Forty seven percent of these males had moved from their initial location within 24 h. Of the 29 males whose developmental stage could be confirmed, 18 penultimate instars remained significantly longer (3.22 ± 1.05 d) on a single plant than did 11 adults (0.64 ± 0.54 d) (Mann-Whitney test, U = 50, P = 0.016). Adult male tenure averaged only 0.1 d with the omission of the single outlier who stayed on one plant for 7 days. Tenure on a single plant decreased as the season progressed and this result was driven by a change in the behavior of immature males rather than adults (Fig. 2).

Females monitored for tenure in 2011 (n = 84) remained significantly longer (5.05 ± 0.52 d) at each location than males (2.42 ± 0.65 d, see above) (Mann-Whitney test, U = 1858.5, P = 0.003). Twenty percent of these females had moved from

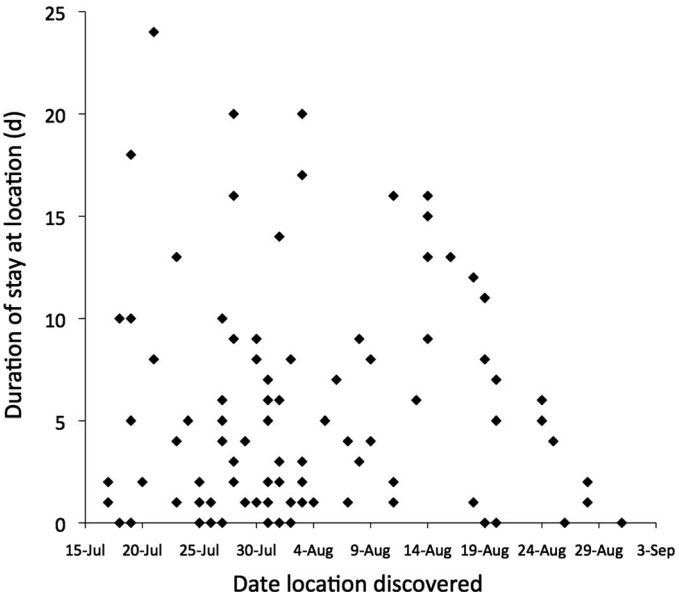

Figure 3.—Number of days *Misumenoides formosipes* females remained on the same plant following the day of discovery in 2011. Data include immature and adult females.

their initial location within 24 h of discovery. Female instar status could not be determined with certainty in many cases and therefore we cannot confirm distinctions between juvenile and adult tenures. The duration of stay for females at a given location decreased across the time period monitored (Fig. 3), most likely a result of adult females moving off inflorescences to preferred locations for depositing egg sacs.

Residencies of females were not limited to positions on inflorescences. Intensive searches from 3–14 August 2006, in areas outside the census plots, revealed 24 females hidden within leaves sealed with silk on plants bearing no open inflorescences at the time. Five plant species were involved with 58% of the sightings on goldenrod (*Solidago altissima*). These females remained at the locations where discovered for an average of 4.12 d (an underestimate since some remained in the same location when monitoring ended).

DISCUSSION

The magnitude of SSD within spiders, particularly in certain families, has been well documented (e.g., Dondale & Redner 1978; Head 1995; Fairbairn 1997; Vollrath 1998; Legrand & Morse 2000). Comparative analyses (Prenter et al. 1999) and phylogenetic studies (Kuntner & Elgar 2014) have supported Darwin's (1871) original thesis that giant females result from natural selection for increased fecundity. In contrast, the selective context for the dwarfism of males in most orb weaver and crab spider species continues to be debated, especially the assumptions and predictions of the gravity hypothesis (Moya-Laraño et al. 2002, 2009; Brandt & Andrade 2007a,b; Prenter et al. 2010; Corcobado et al. 2010). While the significance of climbing to find females deserves investigation, it is only one of many factors suggested to influence male body size in these extreme SSD species.

The mobility enhancement (Ghiselin 1974) and differential mortality (Vollrath & Parker 1992) hypotheses for male dwarfism both imply that traits favoring speed and long distance movement are more important for males than those favoring fighting prowess. Thus, extreme SSD would be more likely in species with low density populations, female biased operational sex ratios (OSR), and scramble competition mating systems with limited male-male agonism. The only one of these expected attributes that characterizes our *M. formosipes* population, however, is the low density, and even that is uncertain (see below). In contrast, we have documented a male biased sex ratio (this study), precopulatory guarding behavior by males (Dodson & Beck 1993), and an advantage of larger size in the frequent and occasionally lethal male-male contests (Dodson & Schwaab 2001; Hoefler 2002). Yet the dwarfed size of males relative to females in this species ranks as one of the most extreme cases across all spiders (Dondale & Redner 1978; Head 1995).

The contrasts between *Misumenoides formosipes* and *Misumena vatia*, the two most dimorphic thomisid species, provide insight into the debate over the causes of male dwarfism. While their foraging ecologies are essentially identical, *M. vatia* differs from *M. formosipes* in having a female biased OSR and scramble competition mating system in which male-male aggressive interactions rarely occur (Holdsworth & Morse 2000; Legrand & Morse 2000; Morse 2007). By contrast, *M. formosipes* males routinely fight over positions near the scarce late-penultimate females (Dodson & Beck 1993; Dodson & Schwaab 2001). The fact that the two most dimorphic crab spider species exhibit divergent population and mating system characteristics is perhaps our most instructive result. Finding females first or finding females at all during the short adult male lifespan, regardless of the degree of aggressive interference that might follow, seems to be the major driver underlying selection for protandry and small, mobile males.

Movement of males versus females.—A clear prediction of the enhanced mobility hypothesis for small male size is that males should be moving more frequently and for longer distances than females. Accordingly, we found that the males were more than twice as likely as females to have moved from their initial locations of discovery within 24 h. Those initial moves were six to ten times further for males than females. Other species of non-web building spiders have also exhibited more activity by adult males than females (e.g., Cady 1984; Sullivan & Morse 2004). It should be noted, however, that Vollrath & Parker's (1992) proposal that male dwarfism reduces the risk of mortality was not supported by sexual differences in locomotor behavior *per se* in wolf spiders (Walker & Rypstra 2003).

Sex ratios and densities.—The ease with which these small organisms can disappear from view in their complex habitat forces us to accept that our censuses underestimate the true densities. At the same time, we are confident that our numbers reflect high-end densities across the full field area given that repeated searches always revealed many more spiders at patches of flowers than in between. When *M. formosipes* individuals do show up in flower-less areas, it is more often males than females. Locations chosen for separate navigation trials (Stellwag & Dodson 2010) contained no spiders initially; but as spiders subsequently showed up in the plots, males outnumbered females 48 to 6 over two years. The higher number of males encountered in these "remote" locations,

coupled with the likelihood of overlooking small, stealthy males versus the more conspicuous females, suggests our male biased sex ratio is also an underestimate.

It is again worth emphasizing the contrast between *M. formosipes* and *M. vatia* populations. Legrand & Morse (2000) reported a range of 2.5–5.1 adult females for every adult male in their populations. Thus, the bias towards females in *M. vatia* was even greater than the bias towards males in our *M. formosipes* population (2.3 males per female at its greatest). The operational sex ratio in our population would be even more biased towards males than the overall sex ratio since the majority of males are adults by the first week of August, whereas most females undergo their adult molts over the next two weeks (G.N. Dodson, pers. obs.).

Comparison of population density values among spider species is hampered by the variation in how they have been measured. In the only other thomisid population density data found, Holdsworth & Morse (2000) completed a month-long census of adult *M. vatia* throughout a 0.5 ha plot via mark/resighting. Their finding of 0.019 spiders/m^2 is an order of magnitude lower than our minimum average densities, but we are confident the difference would be much less if we sampled large plots rather than flower patches. In fact, the largest of our plots (270 m^2) had a lower average density across the two years (0.013 spiders/m^2) than the *M. vatia* counts. Are thomisine crab spider densities low compared with other spiders? Jakob et al. (2011) recorded lower densities than ours for three native linyphiid species in forest habitats, but substantially higher densities for two of the three species in shrubby, coastal habitat. Censuses of two alfalfa field sites revealed densities of ca. three and nine spiders per m^2 for the lycosid *Pardosa agrestis* (Westring 1862) (Kiss & Samu 2000). Both linyphiids and lycosids are much less sexually dimorphic in size than thomisids.

Dwarf males.—Our findings are not the only ones to contradict the prediction that species with dwarf males should exhibit reduced levels of male interactions, especially when large size is an advantage. Foellmer & Fairbairn (2005) also found a male biased OSR and large male fighting advantage in the highly dimorphic orb weaver *Argiope aurantia* Lucas 1833. Kuntner & Elgar (2014) examined studies on sexual selection in nephilid species (the most dimorphic of all spider families) and reported that five out of six documented an advantage for large males in contests on female webs. Given the contrasting patterns for both OSR and the frequencies of male-male interactions in the only two thomisid species measured thus far, more studies of crab spider mating systems are needed for comparison with the orb weaver results.

Male *M. formosipes* are remarkably adept at locating widespread females within a complex habitat. We have documented through field and lab experiments that males are helped in this task at least in part by floral cues (Stellwag & Dodson 2010; Dodson et al. 2013), but this does not account for our observations of males gathering around females on plants far from flower patches. The possibility that female sexual pheromones might aid crab spiders in this quest is contradicted by strong circumstantial evidence in both *M. formosipes* (Dodson & Schwaab 2001) and *M. vatia* (Holdsworth & Morse 2000; Legrand & Morse 2000; Leonard & Morse 2006). Whatever the navigational cues allowing males to find females, the speed at which they are able to climb plant stems and traverse silk lines (bridging) appears to be enhanced by their small size. For both *M. formosipes* and *M. vatia,* the race to find females in these mating systems seems to have a greater influence on male size than does any competitive interactions between rival males should they meet.

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