



Line-following preferences of male crab spiders, *Misumena vatia*

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Male crab spiders locate cryptic females by methods that have proved elusive to researchers. Previous work has suggested that female draglines provide males with clues to the presence of females. Unlike other wandering spiders, however, *M. vatia* do not deposit mate-attracting pheromones on their draglines. Based on evidence that the size and strength of draglines vary predictably with the age and sex of the source spider, we tested the hypothesis that mechanical cues allow males to identify the age, sex and species of the dragline producer. We ran adult and penultimate male crab spiders through a series of trials to identify preferences for following different types of dragline. A spider's developmental stage influenced its response to draglines of other individuals, suggesting that these responses were influenced by the search for mates. Adult males preferred adult and juvenile female draglines and selected conspecific adult female draglines over draglines from adult females of a related species. Penultimate males did not show significant preferences in these tests. Mechanical cues may therefore moderate the responses of the adult males to foreign draglines. We consider dragline following in *M. vatia* as a model of how cues produced in a nonmating context may facilitate mate search, and we suggest that study of such species-specific environmental modifications may shed insight into the evolution of mate location systems.

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When encounters between conspecifics are infrequent and the search for mates competitive, selection is widely predicted to influence the mate-locating abilities of the searching sex (Darwin 1871; Ghiselin 1974; Andersson 1994). The reproductive advantage gained by an efficient searcher may help to explain a variety of traits in males, including size and locomotory morphology (Able 1999; Moya-Laraño et al. 2002) sensory capacity (Thornhill & Alcock 1983; Jumper & Baird 1991; Verrell et al. 2001) and cognitive characteristics (Schwagmeyer 1995; Jacobs 1996; Dukas 1998).

Much of our understanding of the role of mate search in shaping sensory systems and behavioural mechanisms derives from systems in which searchers respond to species-specific advertisement signals (Gerhardt & Huber 2002). However, the searching sex of many species locates mates in the apparent absence of distinct advertisements. Although mechanisms of mate location in systems

without obvious advertisements have typically been ignored, the details and dynamics of competitive mate search in these systems deserve consideration. For example, searcher behaviour in an advertisement-free system may depend on general, probabilistic strategies, such as searching for particular environments where females are likely to forage, oviposit, emerge or cluster at landmarks (Thornhill & Alcock 1983).

Cues left in the environment as the by-product of other behaviours may attain particular importance in the mate search of species that do not advertise their presence. Examples of such cues include tracks, trails (Clark et al. 1999), prey carcasses, faecal and urinary wastes, scent marks and shed exoskeletons. Although such cues can facilitate detection of prey (Koivula & Korpimäki 2001), hosts (Feener et al. 1996; Steidle & Ruther 2000) or predators (Chivers & Smith 1998; Kats & Dill 1998), the potential contribution of these cues to mate search remains relatively unexplored (but see Ruther et al. 2000, 2002). In spite of the hypothetical influence of such by-product cues in the process of signal evolution (Greenfield 2003), they have often been overlooked in studies of mate location. We investigated receiver response to such 'inadvertent stimuli' (Greenfield 2003, page 7), asking whether males that were engaged in a competitive search for

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females might exploit these cues, produced in a non-mating context and without apparent evolutionary specialization for such a behaviour.

The crab spider presents an ideal opportunity to study the contribution of such cues to mate search. A cryptic sit-and-wait predator, *M. vatia* is often sparsely dispersed (LeGrand & Morse 2000) in fields densely populated by other spiders. As a result, males should be strongly selected to develop tactics that facilitate the search for sexually mature females, which remain relatively sedentary in high-quality hunting sites (Morse 1993, 1999, 2000).

However, the apparent crypticity of females raises the question of how males find mates. Unlike other species of wandering spiders studied (Tietjen 1977; Yoshida & Suzuki 1981; Barth & Schmitt 1991; Taylor 1998), *M. vatia* females do not attract males with pheromones (Anderson & Morse 2001), nor do they adopt behaviours with the onset of sexual maturity to advertise their presence to males. However, nearly all females mate over the course of a summer (LeGrand & Morse 2000). Two hypotheses remain for how males locate females. First, males may find mates by seeking the same high-quality hunting sites as do adult females (Chien & Morse 1998; LeGrand & Morse 2000; Anderson & Morse 2001). Second, the silk draglines of sexually mature females may provide wandering males with types of information other than pheromones about female presence (Anderson & Morse 2001). These two hypotheses are not mutually exclusive, because draglines may provide a secondary cue to males already seeking out high-quality flowers that females are likely to exploit.

Our investigation focused on the second hypothesis, dragline-mediated female search. Dragline silk is produced by the major ampullate gland and adheres to the substrate by means of attachment discs secreted at regular intervals (Foelix 1996), thus functioning as a safety line. Male ground-dwelling spiders follow the draglines of females and are usually thought to be responding to pheromones laid down on these lines (Tietjen & Rovner 1980; Taylor 1998). Our research on *M. vatia* has shown that their draglines are produced by both sexes and all ages, whenever they move. The draglines persist under a variety of conditions, are readily followed by males (even to senescent flowers) and are common in hunting sites inhabited by females (Anderson & Morse 2001). However, these draglines do not convey directional information, carry pheromonal cues or indicate the sexual maturity (adult versus penultimate) of the female to these males (Anderson & Morse 2001).

One essential property of draglines, their structure, has yet to be considered. Female crab spiders undergo six moults after emergence from their egg sacs, during which their mass increases from 0.6 mg to 200 mg or more. The physical properties of draglines (diameter, elastic strength, breaking strength) vary with mass in other spider families (Osaki 1996, 1999; Vollrath & Kohler 1996), so *M. vatia* of different sizes probably produce draglines that provide structural cues about the identity of their producers. The importance of tactile cues in dragline recognition has been shown in other species of wandering spiders (Tietjen 1977; Tietjen & Rovner 1980), but more recent dragline-focused research has focused on the influence of chemical

rather than tactile cues (e.g. Barnes et al. 2002; Roberts & Uetz 2004). Even to the human eye, the draglines of adult female *M. vatia* are obviously thicker than the draglines of males and younger females (A.S. Leonard, personal observation). Despite the close relationship between spider size (and sex, in dimorphic species) and dragline structure, we are unaware of explicit evidence that tactile cues, in the absence of chemical cues, might provide males with information about the producer of the draglines. We tested whether these draglines provide information that might help males to locate females. *Misumena vatia* females do not deposit chemical cues that are used by males, so this species presents an opportunity to investigate this possibility.

In a series of line-preference trials, we investigated whether males distinguished between draglines of spiders of different ages, sexes and species. This range of choices probably reflects the actual experience of a male spider moving through a field filled with draglines, the majority of which have probably been produced by spiders whose age, sex or species is such that to follow such a dragline represents at least misdirected mating effort and, perhaps commonly, death.

Our first goal was to establish in behavioural trials whether draglines might provide males with potentially useful information about their producer in mate search. We predicted that, if so, adult males would preferentially follow adult female conspecific draglines over adult male conspecific draglines. We also predicted that adult males would prefer female conspecific draglines over the draglines of a heterospecific species of crab spider. We further predicted that penultimate males would show less line following, and no preference for or an aversion to female draglines, because males have little to gain and perhaps much to lose by doing so (cannibalism is not uncommon in *M. vatia*).

A second goal focused on the cues that males might use in dragline discrimination. Given that female *M. vatia* do not deposit pheromones on their draglines, we predicted that any cues used in intraspecific dragline discrimination would be structural. To investigate the possibility that large-scale structural cues informed males about the draglines' producers, we presented adult male subjects with a choice between the draglines of adult males and of similarly sized juvenile (2–3 moults away from maturity) female conspecifics. Although research has eliminated intraspecific chemical cues as likely sources of information for *M. vatia* males, we thought it possible that some measure of interspecific chemical responsiveness might mediate the response of males to foreign draglines. We therefore explored the responses of males to a heterospecific species of crab spider that is believed to use sex pheromones in intraspecific communication.

METHODS

Subjects

Misumena vatia are semelparous sit-and-wait predators; they are sexually dimorphic, with adult males averaging

4 mg and gravid adult females over 200 mg. They do not weave webs, but both sexes of all ages lay down a silken dragline when they move. The size and strength of this line is related to the spider's body mass (Osaki 1999), and the draglines of large females dwarf those of males (A. S. Leonard, personal observation). *Misumena vatia* are Holarctic (Gertsch 1939; Morse & Stephens 1996) and commonly occupy flowers, where they lie in wait for prey.

We collected spiders from roadsides and old fields in Lincoln County, Maine, U.S.A., from June to August in 2000–2004. Subjects were 98 adult and 26 penultimate male spiders that we housed indoors in individual 7-dram containers (length \times diameter 5 \times 3 cm), and provided with water to avoid desiccation. We maintained the spiders on a diet of *Drosophila melanogaster* and small moths. We did not feed subjects within 24 h of their trial.

Apparatus

Line-preference trials were conducted on an apparatus designed to simulate the draglines of a spider in the field. We followed the design of Anderson & Morse (2001), placing two 30-cm leafless grass stems (A and B) equidistant from a centre stem (C) on a 30 \times 20-cm experimental surface (Fig. 1a). Experiments were conducted on the windowsills of a room that provided natural light and moderate cross breezes. We deviated slightly from Anderson & Morse's arrangement of stems in a cross pattern by placing the stems in a 'V' arrangement.

Silk lines were strung between both A and C and B and C using source spiders as shuttles (Anderson & Morse

2001). The source spider was first placed on the outlying stem (A or B), where it attached line, and then was moved onto a sable-hair brush. The brush, with the spider on it, was then gently moved towards the centre stem (C), allowing the silk to trail behind. The silk was attached to the centre stem and made taut by winding it around the stem 1 cm from the top. In an identical manner, silk from the second source spider was strung from the other outlying stem to the centre (C). Lines were always strung towards the centre stem, although these spiders gain no directional information from silk lines (Anderson & Morse 2001). We recorded the positions of the silk lines on the centre stem relative to each other, but the lines were rarely more than 1 mm apart, so we assumed that subject spiders made contact with both lines. In addition to recording the direction of line followed by the subject, we also tracked the overall percentage of line following among our subject groups. In all trials that involved a choice between two different types of line, the placement of line on A or B was randomized for each trial. Individual male subjects were generally used in multiple types of trials; the order of trials was randomized for each subject, and each spider had at least a 40-min rest interval between trials. Stems were changed or wiped clean between trials to remove possible cues.

A series of control trials, conducted in concert with the experimental trials described below, presented adult and penultimate male subjects with a choice between two directions of male line. As in all trials that involved male dragline, penultimate male dragline was used for penultimate male subjects, and adult male dragline for adult male subjects. We found no preferences for crossing lines in a particular direction (C to A versus C to B). Thus, no external environmental factors encountered in the experiments (light, wind or temperature differences) influenced the choice of grass stem towards which a spider chose to move.

Dragline Trials

We presented 52 adult and 22 penultimate male subjects with a choice between male and adult female draglines, a straightforward test of whether males of either age class prefer to follow the lines of sexually mature females over those of males. We used as sources of dragline 40 randomly selected adult female spiders kept in the laboratory for short periods (mean \pm SD mass of females = 106.7 \pm 52.0 mg; adult males = 4.2 \pm 1.5 mg; penultimate males = 4.1 \pm 1.2 mg).

To establish whether sexually mature *M. vatia* prefer conspecific draglines, we presented 18 adult males with a choice between draglines of adult female *M. vatia* and *Xysticus* spp. (*X. emertoni* and *X. punctatus*, crab spiders that share old-field habitats with *M. vatia*). Adult females of the three species are of similar size (mean \pm SD mass of young adult *Xysticus* female subjects = 96.7 \pm 22.6 mg). *Misumena vatia* and *Xysticus* lay down lines in a similar manner, although, in contrast to *M. vatia*, female *Xysticus* probably use male-attracting pheromones (D. H. Morse, unpublished data).

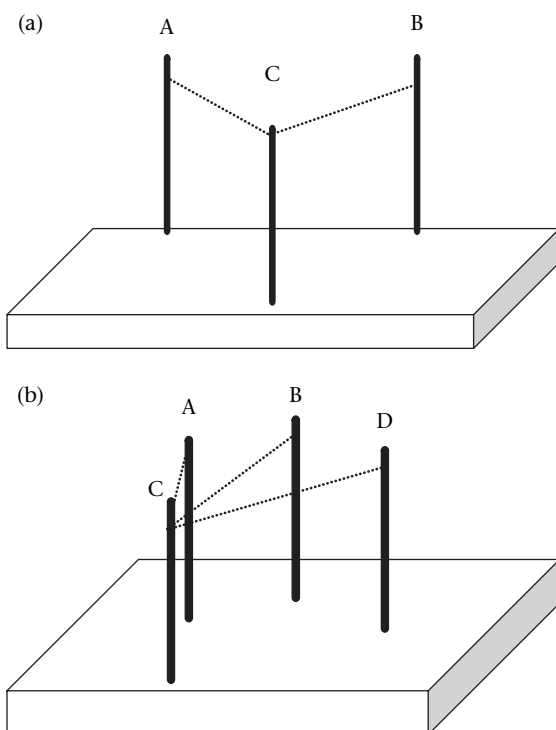


Figure 1. Line preference apparatus used in (a) most trials and (b) three-prong preference trial.

In a related experiment, designed to determine whether line preferences would persist in a more complex environment, we ran 14 adult males through a three-pronged preference test in which three stems (A, B, D) were placed equidistant from the centre stem (C), and three kinds of line were strung to the centre (Fig. 1b). We used adult female *Xysticus* lines, adult female *M. vatia* lines and the lines of the adult male subject. Pilot experiments revealed that males did not prefer to follow their own dragline over those of other males (A. S. Leonard, unpublished data). The positions of the three kinds of line were rotated for each trial. The only difference between this trial and the previous three trials was the choice of three lines rather than two.

In a third category of trials ($N = 40$ adult and 26 penultimate males), we presented male subjects with a choice between male and juvenile female draglines, with the female lines taken from the smallest available third- or fourth-instar females. We used 22 juvenile females as sources of line, whose average mass (mean \pm SD = 8.7 ± 4.1 mg) was far less than that of adult females. The diameter of line is correlated with the mass of the spider (as in other spider families: Vollrath & Kohler 1996; Osaki 1996, 1999), so the line of the less massive juvenile females used in this trial helped to establish the effect of line size on the males' propensity to follow female line.

We ran line-preference trials on clear days within one week of capturing the males, conditions that promote activity levels comparable to those recorded from individuals in the field (Anderson & Morse 2001). A trial began when the subject spider was placed on the centre stem (C) 2 cm below the lines, facing upwards. Trials lasted 20 min, and were aborted only if a spider was lost. We recorded every movement of a subject during a trial, as well as the time and length of its first contact with the lines and the direction of the crossing. We considered the first directional choice of the subject as an indication of preference.

We explored male *M. vatia*'s response to *Xysticus* line in further detail by observing 20 males' responses to a single *Xysticus* dragline strung between two grass stems. In this no-choice trial, we recorded the number of males who crossed and their latency to cross the *Xysticus* line. To determine whether males' response to *Xysticus* draglines in the above trials mirrored their response to substrate (chemical or tactile) cues, we placed 20 adult males in 9-cm diameter petri dishes; one-half of the substrate consisted of filter paper upon which we had previously placed a female *Xysticus* for 30 min and the other half consisted of fresh filter paper. In 20-min trials, we recorded the time spent by each male on the two sides of the dishes.

RESULTS

Adult Female *M. vatia* Lines

Adult males preferred adult female lines when presented with a choice of adult male lines or adult female lines (two-tailed binomial test: $N = 41$, $P < 0.05$; Fig. 2a). Penultimate males, in contrast, showed no such preferences

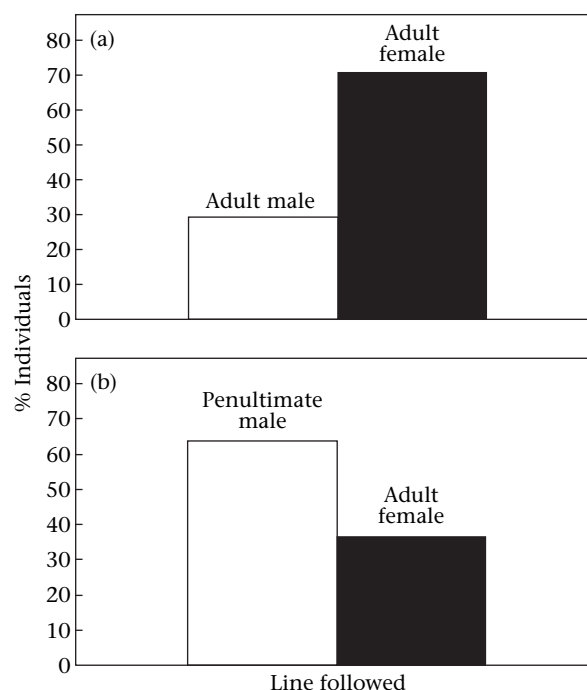


Figure 2. Responses of (a) adult and (b) penultimate males to a choice between adult female and male draglines.

($N = 11$, $P < 0.548$). When presented with a choice between penultimate male lines and adult female lines, their response was in the opposite direction; more males followed the lines of penultimate males than those of adult females (Fig. 2b). Adult males were more likely than were penultimate males to follow any type of line (proportion of following: 0.79 for adults, 0.50 for penultimate males; z test with Yates' correction: $z = 2.219$, $P = 0.027$).

Adult Female *Xysticus* Lines

Adult males strongly preferred to follow the lines of adult female conspecifics over those of adult *Xysticus* (two-tailed binomial test: $N = 16$, $P < 0.001$; Fig. 3a), and rates of line following were high (only two males did not follow either line). When presented with a choice between three lines (those of adult female *M. vatia*, adult female *Xysticus* and their own line), adult males again showed clear preferences (G test with Yates' correction: $G_2 = 16.72$, $N = 13$, $P < 0.001$; Fig. 3b). Of the 14 subjects, nine followed female *M. vatia* line, three followed their own line and two did not cross any of the lines (none followed the *Xysticus* line).

Juvenile Female Lines

When presented with a choice between adult male lines and lines from juvenile females, adult males crossed the juvenile female lines more frequently than predicted by chance (two-tailed binomial test: $N = 35$, $P < 0.05$; Fig. 4a). This pattern closely resembled that of their responses to adult female lines (Fig. 2a). Penultimate males'

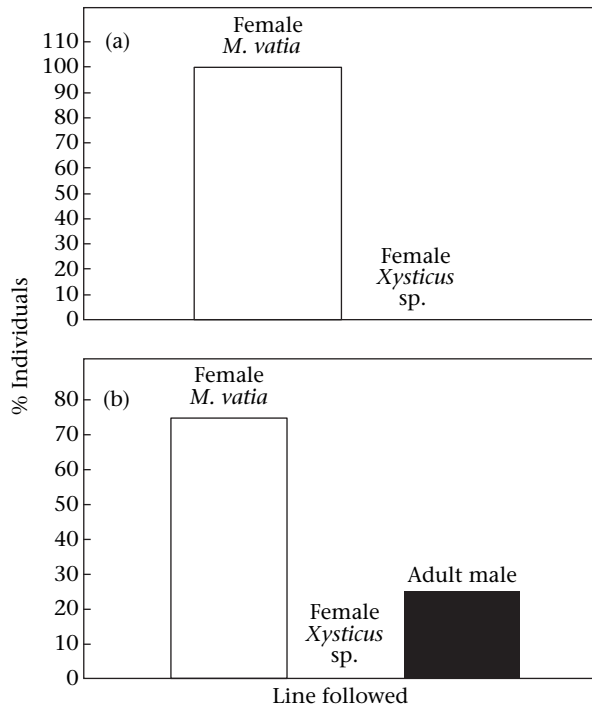


Figure 3. Responses of adult males to a choice between (a) adult female *M. vatia* and male draglines and (b) a three-way choice between adult female *M. vatia*, *Xysticus* sp. and male draglines.

responses to lines of juvenile females also resembled their responses to adult females; they showed no preferences between the two types of lines ($N = 17$, $P = 1.0$, power = 0.055; Fig. 4b). Adult males followed lines more

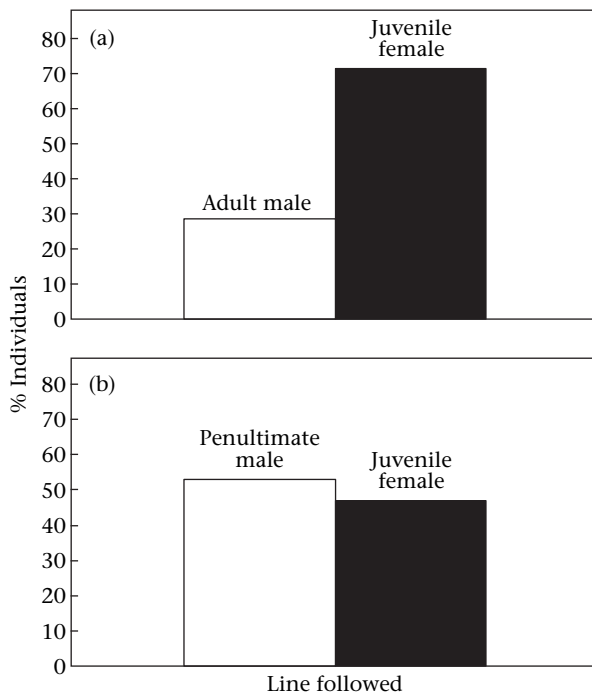


Figure 4. Responses of (a) adult and (b) penultimate males to a choice between male and juvenile female draglines.

than did penultimates, but rates of overall line following between penultimate males and adult males did not differ significantly (proportion of line following: adults: 0.88 penultimates: 0.68; z test with Yates correction: $z = 1.652$, $P = 0.099$).

Xysticus Lines

We also observed a reticence to follow *Xysticus* draglines when we presented male subjects with a single *Xysticus* line. Given only the option to cross a *Xysticus* line or remain on their grass stem, most subjects did not cross the line (two-tailed binomial test: $N = 20$, $P < 0.05$; Fig. 5a). After completion of that 20-min trial, we gently prodded each of the 17 nonfollowers with a brush. Only three of them eventually started out across the line, but only one continued to the other stem. This avoidance of *Xysticus* cues did not, however, translate into an avoidance of surfaces recently occupied by *Xysticus*. When presented with two substrates, one recently occupied by a female *Xysticus*, males did not differentially associate with either part of the petri dish (two-tailed Wilcoxon matched-pairs signed-ranks test: $T = 121$, $N = 20$, $P < 0.6818$; Fig. 5b).

DISCUSSION

In their search for cryptic mates, male *M. vatia* move through field environments containing the draglines of various species, sexes and ages of spiders. Considering the fitness payoffs of locating adult females by detecting signs of their presence, we hypothesized that males have the

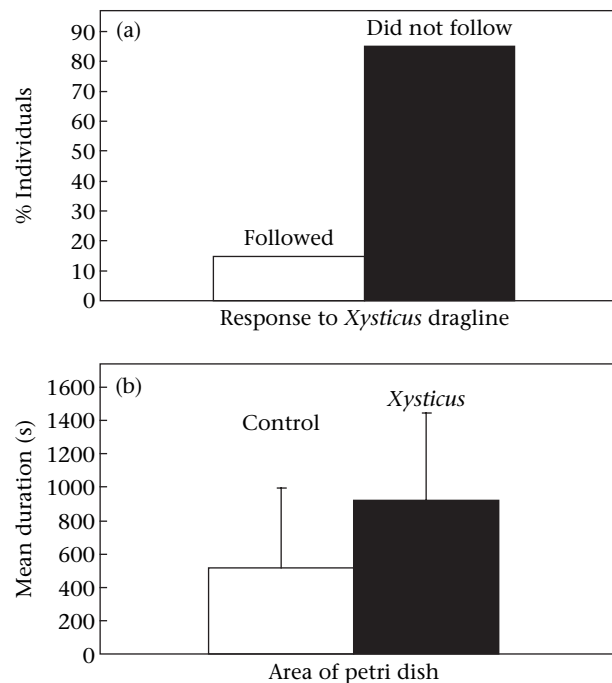


Figure 5. Responses of adult males to (a) an adult female *Xysticus* dragline and (b) petri dish, half of which contained filter paper recently occupied by an adult female *Xysticus* and half of which was unaltered ('Control').

capacity to recognize the lines of sexually mature conspecific females.

Line Following as a Reproductive Behaviour

Male preferences for following female line clearly suggest that draglines could be of use to males engaged in competitive search for females. We reasoned that if line following is associated with the search for mates, it should be most prevalent and most female biased among adult males. Although the low power of our binomial test prevents us from concluding that penultimate males lack a preference for female lines, the raw data point in this direction, and we observed lower rates of dragline following among penultimate males than adult males. Among *M. vatia*, these differences between penultimate and adult line-following behaviour correlate with the transition from a relatively sedentary penultimate lifestyle to an adult stage characterized by the active search for mates (LeGrand & Morse 2000; Anderson & Morse 2001). This developmental divide mirrors an age-based difference in response to sensory cues reported in other spider species (reviewed in Krafft 1982). Among lycosids, for example, Tietjen & Rovner (1980) found a similar lack of dragline-following behaviour among penultimate males and Persons & Uetz (1999) demonstrated that adult and juvenile wolf spiders, *Schizocosa rovnieri*, make use of different types of sensory information to determine patch residence times.

Interspecific Discrimination

When we presented male subjects with a choice between lines of adult female *M. vatia* and of similarly sized adult female *Xysticus*, crab spiders that inhabit the same fields as *M. vatia*, adult males unequivocally preferred to follow the line of conspecifics. This preference for *M. vatia* line over *Xysticus* line was replicated in a second trial in which adult male subjects were presented with three line options (female *M. vatia*, female *Xysticus* and their own lines).

We have also observed this reticence to follow *Xysticus* in a no-choice trial. These results are in sharp contrast to the general propensity of adult males to follow the lines of adult female *M. vatia*. In a similar no-choice trial, Anderson & Morse (2001) found that 10 of 15 males followed single adult female *M. vatia* lines, and in our trials, we found equivalently high rates of conspecific female line following. Our finding that males did not avoid substrates recently associated with female *Xysticus* suggests that, whatever the cue that promotes avoidance among adult males, this cue is restricted to or amplified by the presence of draglines.

What are the Cues Involved?

The apparent absence of chemical cues on *M. vatia* lines (Anderson & Morse 2001), combined with the responses to lines in the experimental presentations, suggests that

adult male *M. vatia* use structural cues from dragline silk to make decisions about whether to follow the lines of other individuals. Adult males showed similar preferences for the lines of both adult and juvenile females, even though draglines of these age classes vary widely in their thickness (juvenile female and male draglines are similar and are dwarfed by the much thicker lines of adult females). This result suggests that while size may be an important cue for males deciding whether to follow a foreign line, it is probably not the only factor involved. Multiple characteristics probably influence line preference, since an indiscriminant preference for thick lines would concentrate males on the lines of larger, probably predatory, spiders. Furthermore, size in its own right may not separate *M. vatia* lines from those of *Xysticus*, or those of many other species, because the microscopic structure of silk differs between species (Foelix 1996; Madsen et al. 1999). It is not known, however, whether the individuals that encounter these differences use them in species identification.

The Information Content of Draglines

Spiders' response to conspecific and interspecific draglines is emerging as a nexus of insight into sensory ecology (Persons et al. 2002; Lehmann et al. 2004), the origin of sociality (Evans & Main 1993; Jeanson et al. 2004), and the evolution of communicative systems (Krafft 1982; Uetz & Roberts 2002). Recent discoveries among lycosid species, for example, suggest that predator draglines may provide prey species of wolf spiders with information about the producer's sex, feeding status, size and recency of line deposition (reviewed in Lehmann et al. 2004). In a similar vein, recent work on lycosids' intraspecific interactions suggests that chemical cues may allow males to identify the species, age and sexual receptivity of female spiders (Roberts & Uetz 2004; J. A. Roberts & G. W. Uetz, unpublished data). Researchers in these systems are able to pinpoint the specific cues used with greater degrees of precision and understand a particular complex communicative interaction with increasing depth; it is therefore worthwhile to highlight systems that seem to depart from this well-known example of dragline-mediated interactions. Through such intertaxal comparison, general patterns may emerge that establish how these dragline-mediated interactions reflect particular ecological conditions, phylogenetic factors, sensory abilities and developmental histories.

To this end, we have described a system in which males do not appear to gain the same sort of information from conspecific draglines as do their lycosid counterparts. To date, evidence suggests that male *M. vatia*'s response to female draglines may effectively bias their search for females in subtle ways: away from heterospecific females, towards conspecific females, but interestingly, not towards the expected 'appropriate' age class of females. Dragline following and mate guarding of penultimate females is not uncommon in *M. vatia* (Holdsworth & Morse 2000; Anderson & Morse 2001). However, we have never observed males in the field guarding the third- and

fourth-instar females used in this study. Since guarding these females until maturity would require a commitment of several weeks, the lack of such guarding behaviour is perhaps understandable; however, further experiments are necessary to establish whether males will guard these young females. Although this study was not designed to examine or identify all potential cues that males use in recognizing female dragline as such, it seems clear that the cue or combination of cues that males rely upon is present in female dragline long (2–3 moults) before the advent of sexual maturity.

By-product Cues May Facilitate Mate Location

Silken draglines are excellent examples of how by-product cues may contribute to mate location. They are produced routinely by receptive females, they persist in the environment and they probably have structural (or chemical) characteristics typical of their producer's species and sex. Although female *M. vatia* do not appear to use visual or chemical signals advertising their presence to males, we found that males discriminated among the various types of lines encountered in their search. This preference for following lines of female conspecifics suggests that, even if females do not produce advertisement signals obvious to the observer, searching male spiders can still discover the characteristic signs of their presence.

Could draglines in this system also be viewed as signals rather than 'inadvertent stimuli'? Among *M. vatia*, draglines may certainly function as a signal to male receivers, however our receiver-oriented study was not designed to directly address the evolutionary hypothesis that the female production of draglines has undergone specialization for its current role in mate search. The draglines of *M. vatia* lack pheromones used by the males, and they direct males towards a broad age range of conspecific females, so any selection on female senders to modify draglines for their role in mate search has not yielded a highly specialized signal. As potential senders, females are probably constrained by two major selective pressures: remaining cryptic to predators/prey while locatable by searching males. Future research that adopts the 'signal evolution' perspective has the potential, therefore, to explore how dragline production has been influenced by both intraspecific (sender–receiver) and interspecific (predator–prey) coevolution.

Previous studies have often focused on the extreme ends of the spectrum of mate location systems (i.e. on specific advertisement signals produced by the opposite sex or general search strategies that increase the odds of finding sites with females; Thornhill & Alcock 1983; Andersson 1994). We have presented evidence that searching males can respond to cues that seem to be neither explicitly advertisement signals nor environmental characteristics, but that are produced by the sought-after sex as part of its normal activity in a nonmating context. Although mate location is likely to be a complex process based upon responses to a variety of proximate cues, these results have important implications for how sensory morphology,

antipredator behaviour and decision-making capacity have synchronously evolved in searchers. Study of species that lack the usually encountered elements of a communication system may thus reveal important interactions between selective forces acting simultaneously on both the searching and sought-after sex.

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