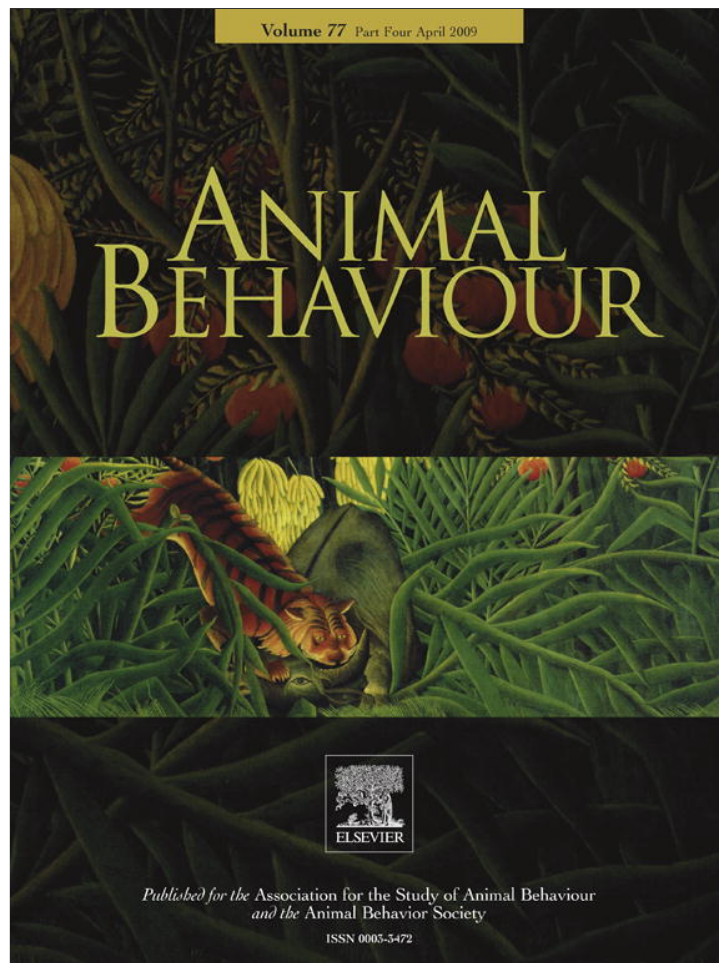


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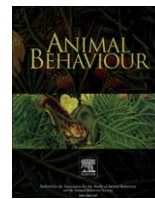
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Multimodal signalling: the relative importance of chemical and visual cues from females to the behaviour of male wolf spiders (Lycosidae)

Ann L. Rypstra^{a,b,*}, Ann M. Schlosser^{c,d,1}, Patrick L. Sutton^{c,d,2}, Matthew H. Persons^{e,3}

^a Center for Animal Behavior, Miami University, Hamilton, OH

^b Department of Zoology, Miami University, Hamilton, OH

^c Center for Animal Behavior, Miami University, Oxford, OH

^d Department of Zoology, Miami University, Oxford, OH

^e Department of Biology, Susquehanna University, Selinsgrove, PA

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Many animal signals, especially those important to finding and attracting mates, are multimodal, which means they involve two or more sensory modalities. Among other sensory modalities, the wolf spider, *Pardosa milvina* (Araneae, Lycosidae), uses a variety of chemical and visual information in reproductive activities. Here we report the results of four laboratory experiments in which we explored the effects of visual and chemical information on the behaviour of males. First we established that chemical cues enabled males to find females and that visual cues kept the males' attention focused in the area of the females. Subsequently, we examined the separate and combined effects of visual and chemical cues on the interactions between males competing for virgin or mated females. The behaviour of interacting males revealed that either chemical or visual information was sufficient for them to discriminate between mated and virgin females. Chemical cues elicited more courtship activity and more intense aggressive interactions between males than visual cues. When males were able to see live mated females but were in contact with chemical cues from virgins, aggression was lower and, conversely, when males were able to see live virgin females but were in contact with chemical cues from mated females, aggression increased. We conclude that chemical cues provided males with the most critical discriminatory information. Although the two types of signals are largely redundant, there are some circumstances where they enhance the response of the males and there is an intersignal interaction that allows males to adjust their behaviour when presented with a receptive female.

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For effective communication to occur, animals must receive and interpret specific signals against environmental background noise (Guilford & Dawkins 1991; Hebets & Papaj 2005). Although it is easier to explore the specific role of individual signals in isolation, the complexity of animal interactions will typically require information that engages several sensory modalities simultaneously or in sequence (Partan & Marler 1999, 2005; Uetz 2000; Uetz & Roberts 2002; Candolin 2003; Hebets & Papaj 2005). These

multimodal signals allow animals to communicate more information with higher signal range, more precise identification of locality, and higher levels of detection in heterogeneous environments where signals have to be filtered from a rich array of alternative sensory input or noise (Partan & Marler 1999, 2005; Hebets & Papaj 2005). Recent reviews discuss the diversity and versatility of multimodal communication and attempt to establish a unifying framework to guide the interpretation of research on this topic (Partan & Marler 1999, 2005; Uetz 2000; Uetz & Roberts 2002; Candolin 2003; Hebets & Papaj 2005).

Sexual displays often involve multimodal signalling presumably because of the complex information that must be exchanged in the two-way interaction between prospective mates that need to identify the viability and genetic quality of one another as potential partners (Candolin 2003; Hebets & Papaj 2005; Partan & Marler 2005). Much of the seminal work on multimodal communication has focused on elaborate male courtship displays that obviously include a variety of signal components (Candolin 2003; Hebets &

* Correspondence: A. L. Rypstra, Department of Zoology, 1601 Peck Blvd, Hamilton, OH 45011, U.S.A.

E-mail address: rypstral@muohio.edu (A.L. Rypstra).

¹ A. M. Schlosser is at the Center for Animal Behavior and Department of Zoology, Miami University, Oxford, OH 45056, U.S.A.

² P. L. Sutton is at the Department of Microbiology, University of Alabama at Birmingham, Birmingham, AL 35294, U.S.A.

³ M. H. Persons is at the Department of Biology, Susquehanna University, Selinsgrove, PA 17870, U.S.A.

Papaj 2005; Partan & Marler 2005 and references therein). For example, male whitethroats (*Sylvia communis*) perform visual flight displays, which are only successful in attracting females when they are accompanied by specific song elements (Balsby & Dabelsteen 2002). Male courtship in fruit flies (*Drosophila* spp.) involves visual, tactile and chemical signals along with wing vibrations that produce at least two distinct types of acoustic signals (Ewing 1983; Hall 1994; Rybak et al. 2002). Closely related species of wolf spiders in the genus *Schizocosa* differ in their use of unimodal versus multimodal displays (Hebets & Uetz 1999; Uetz 2000; Uetz & Roberts 2002; Hebets 2003; Hebets & Papaj 2005) and, in some species, males shift from emphasizing one sensory component to focusing on another as environmental circumstances change (Taylor et al. 2005a). Indeed, the comprehensive explorations of the male displays in *Schizocosa* spp. serve as models for the study of multimodal communication (Uetz 2000; Uetz & Roberts 2002; Hebets & Papaj 2005).

Fewer studies have explored how males use multimodal communication as they search and possibly compete for receptive females. Males must gather information from females in order to identify and evaluate them as they decide how vigorously to court or fight with other males (Candolin 2003; Guerra & Mason 2005; Jackson et al. 2006). Research on crayfish (*Austropotamobius palipes*) suggests that males of that species require input to multiple sensory channels in order to recognize females (Acquistapace et al. 2002). Another example revealed that shore crab females (*Carcinus maenas*) release a pheromone that alone elicits mating and defensive behaviour in males, but the contests between males escalate much further when visual and tactile information are also present (Bamber & Naylor 1996; Sneddon et al. 2003). Clearly, multimodal signals from females are critical in guiding male behaviour in these invertebrate taxa. Further explorations of male responses to isolated and composite signals from females in a broader range of taxa will contribute to our understanding of the context, function and distribution of multimodal communication (Uetz 2000; Uetz & Roberts 2002; Hebets & Papaj 2005; Partan & Marler 2005).

The goal of this study was to examine how different types of female cues affect the behaviour of male wolf spiders (Lycosidae). Specifically, we manipulated male access to chemical and visual information from females to determine how it affected the ability of males to find females and influenced the interactions among males. In four experiments, we explored: (1) the relative roles of female visual and chemical cues on male search behaviour, (2) how visual cues from females that differed in mating status (virgin or mated) affected the interactions between two competing males, (3) how chemical cues from females that differed in mating status affected the interactions between two competing males, and (4) how visual and chemical cues work together to affect the interactions between two competing males using a cue conflict design (as recommended in Uetz & Roberts 2002). These experiments were designed to reveal how male wolf spiders use sensory information to find females and respond to male competitors for those same females. We predicted that, in the presence of the appropriate cues from attractive potential mates, males would approach females more quickly, remain in the vicinity of females longer, and fight more vigorously with other males.

To explore how males use multimodal signals from females, we used the wolf spider *Pardosa milvina* (Araneae, Lycosidae) (hereafter referred to as *Pardosa*), a common cursorial spider that is found in disturbed habitats such as agricultural fields in eastern North America (Marshall & Rypstra 1999; Marshall et al. 2002). Adult virgin females produce an airborne pheromone that alone is sufficient to attract males (Searcy et al. 1999). Male *Pardosa* commence a distinctive courtship display of double leg raises and

body shakes in the presence of substrate-borne chemical cues, which consist of silk and excreta that remain after females occupy an area (Montgomery 1903; Rypstra et al. 2003; Hoefler et al. 2008). The structure of the genitalia of wolf spiders suggests that they should have first-male sperm priority (Austad 1984), and *Pardosa* males show a distinct preference for virgin over mated females if the female has been allowed to deposit substrate-borne chemical cues in advance (Rypstra et al. 2003). Because this species is highly mobile, it is likely that a male will occasionally encounter chemical cues when he cannot see the female or will catch sight of a female with no chemical information in the vicinity. In addition, since chemical cues may persist after females have vacated, males may also receive visual and chemical information from different females simultaneously. This study examined the manner in which males use these two types of sensory input in their search for females and how that same sensory information from mated or virgin females affects the interactions between potentially competing males.

METHODS

General Laboratory Protocols

Male and female *Pardosa milvina* were collected from corn and soybean fields at Miami University's Ecology Research Center (Oxford, Butler County, OH, U.S.A.) between May and October 2002–2004. We assigned spiders sequential numbers during collection and later used those numbers to randomly assign them to treatments. Spiders collected as adults were maintained in the laboratory for a minimum of 3 weeks before participation in an experiment to acclimatize them and to eliminate differences in hunger. Spiders collected as subadults were held until they reached maturity and then maintained under standard laboratory conditions for an additional 3 weeks after the final moult. We did not attempt to control for the age or mating experience of males because mature males are active in the field throughout the season (Marshall et al. 2002) and so it is likely that males of all ages and levels of experience would be competing for the same females. However, because we knew that the mating status of females was a predictor of their desirability to males (Rypstra et al. 2003), we used it to manipulate female quality. All virgin females moulted to adulthood in the laboratory and were held in isolation from males until the beginning of an experiment. Mated females had produced at least one eggsac in the laboratory or were collected with an eggsac from the field. The eggsacs were gently removed from the spinnerets 1–2 days before the experiment. No spider died during an experimental trial, and after participation, they were either returned to the laboratory population or released into appropriate habitat in the field.

When not used in experiments, *Pardosa* were housed in translucent 150 ml containers (8 cm in diameter, 5 cm walls) with a layer of damp peat moss on the base to provide substrate and moisture. Containers were kept in an environmental chamber at 23 °C on a 13:11 h light:dark cycle. Twice a week, the peat moss was watered and the spiders were fed two crickets (*Acheta domesticus*), each approximately half the size of the spider, or six fruit flies (*Drosophila melanogaster*). Each spider participated in only one trial of one experiment.

Chemical cues were collected by releasing a female into a container with a clean piece of filter paper lining the bottom for a specified time period. As the female moved about the container, she deposited silk and excreta on the filter paper. We refer to these deposited substances as chemical cues, but other substances, such as airborne (olfactory) and substratum-borne chemicals (gustatory) along with tactile cues (thickness, type or density of silk fibres)

were also probably present on the filter paper. The paper used to deliver spider chemical cues was discarded after a single use. All other materials that came in contact with the spiders (arenas, vials, etc.) were washed with soapy water, rinsed, wiped with ethanol, and allowed to air dry before reuse.

We presented visual cues to males by sequestering a female under a clean, colourless glass vial large enough so that she could alter her posture and behaviour in response to the male's activity. Thus, unlike other video playback studies (e.g. see Uetz 2000; Uetz & Roberts 2002), we allowed the females to observe and respond to the male's activities and, in turn, for males to alter their behaviour in response to any changes in female behaviour. We do not know whether vibratory communication is important for *Pardosa* and it is possible that some information transfer occurred in these treatments seismically. We expect that the glass vial (23 ± 0.4 g) would have attenuated the signals such that information transfer would have been reduced and restricted to areas close to the vial. Nevertheless, what we refer to here as visual cues could also contain a vibratory component. In any case, the combination of signals we refer to as visual cues is a totally distinct subset of signals from those that we refer to as chemical cues.

Cue Use in Mate Location

The degree to which *Pardosa* males used chemical versus visual cues in their search for females was explored in rectangular plastic arenas, $30 \times 15 \times 7.75$ cm (L \times W \times H). The floor of each arena was covered with heavy white construction paper. We placed a disc of white filter paper (9 cm diameter) with a clear colourless glass vial (2.7 cm diameter, 5 cm tall) in the centre 4 cm from one end of the arena (Fig. 1). The filter paper was used to present female chemical cues when appropriate and the vial was inverted over a live virgin female for treatments with visual cues. This experiment included four treatments: no female cues, female chemical cues, female visual cues, and both visual and chemical cues (Table 1).

All females were fed two crickets four times per week for 3 weeks before testing. To standardize female condition across treatments, we provided each female with five crickets 24 h before their trial. Females assigned to chemical cues were allowed to feed on those crickets for 90 min, then transferred to cylindrical containers (9.5 cm diameter, 4 cm walls) with a 9 cm filter paper

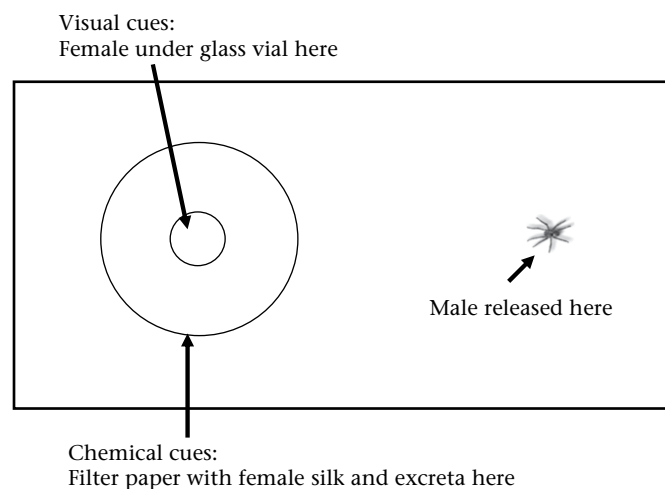


Figure 1. Schematic of the arena used to explore the cues used in mate location by wolf spiders. Chemical cues were presented on the circular piece of filter paper; visual cues were presented by a female under a vial in the centre of that filter paper and the male was released at the opposite end of the arena.

Table 1

Summary of treatments and results for the experiment exploring cue use in mate location

Treatment	N	Number finding filter paper (%)	Mean \pm SE time (s) on filter paper*	Number courting (%)
No cues	23	17 (73.9%)	629 \pm 297 A	0 (0.0%)
Chemical cues	20	18 (90.0%)	1856 \pm 453 A, B	11 (55.0%)
Visual cues	21	16 (76.1%)	2436 \pm 675 B	8 (38.0%)
Chemical and visual cues combined	21	18 (85.7%)	4029 \pm 647 B	13 (61.9%)
Total for all treatments	85	69 (82.2%)	2245 \pm 721	32 (37.6%)

* Values with different letters denote a significant difference (post hoc Kruskal–Wallis test: $P < 0.05$).

disc on the bottom for 24 h. Females to be used as sources for visual stimuli were allowed to feed on the five crickets for the entire 24 h period before they were placed under the glass vial in the arena at the beginning of a trial.

Males were randomly assigned to treatments and maintained in the laboratory for a minimum of 3 weeks before experimentation (see Table 1 for complete list of treatments and sample sizes). Twenty-four hours after a feeding, we placed the male under a glass vial, rendered opaque with black electrical tape, at the opposite end of the arena from the female cues (Fig. 1). After a 1 min acclimation period, we released the males and observed them for 3 h. We recorded whether and when the male reached the filter paper disc, how much time he spent on the disc, and if he engaged in any courtship activity, as evidenced by distinctive double leg lifts, during the trial.

The number of males reaching the filter paper disc surrounding the vial and the number that engaged in courtship were compared across female sensory cue treatments using Fisher exact tests. Not all of the spiders found the filter paper during the trials and so we used survival regression analysis that takes this right-censored data into account (Muenchow 1986; Fox 1993; Moya-Laraño & Wise 2000; Lehmann et al. 2004). To compare the time it took males to find the filter paper disc across all treatments, we used a two-factor proportional hazard survival model (Cox 1972). We compared the time that the males spent on the filter paper disc using the one-way Kruskal–Wallis ANOVA because we were unable to transform the data to meet the assumption of normality for parametric analyses.

Cue Effects on Male–Male Competition

Three additional experiments were conducted to quantify the behavioural interactions between *Pardosa* males in the presence of visual and/or chemical cues from females. First, the reactions of two males to either visual or chemical cues from mated and virgin females were explored. Later, we documented the reactions and interactions of two competing males by independently manipulating chemical and visual cues of mated and virgin females in a full factorial design.

The day before the experiment, we assigned males a treatment (Table 2), categorized them by size, and arbitrarily paired each with a similarly sized male to control for potential effects of size asymmetry on males' interactions. One member of each pair was marked with a dot of nontoxic white paint on the dorsal surface of the abdomen so that we could identify individuals during the trial. Individual males were then fed two crickets and left for 24 h. Just before the experiment, we measured the carapace width of each male to the nearest 0.1 mm using an ocular micrometer on a Wild M5 Heerbrugg stereomicroscope.

Experimental trials were conducted in cylindrical plastic arenas (20 cm diameter, 8 cm walls), with a filter paper disc covering the entire bottom of the container. The two males were introduced under separate vials (2.67 cm diameter), rendered opaque by

Table 2
Summary of treatments for experiments exploring cue effects on male–male competition along with the number and percentage of trials with aggression, the number and percentage of trials with courtship, and the mean distance between the two males during trials

Experiment and treatment		N	Trials with aggression	% Trials with aggression	Trials with one male courting	Trials with both males courting	% Trials with courtship	Mean±SE distance (cm) apart during trial*
Chemical cues	Visual cues							
Visual cues only								
—	None	20	15	75.0	0	0	0.0	14.1±1.3 A
—	Virgin female	22	16	72.7	7	5	54.5	14.1±1.6 A
—	Mated female	23	8	34.8	4	5	39.1	14.5±1.7 A
Chemical cues only								
None	—	20	10	50.0	0	0	0.0	16.2±1.5 A, B
Virgin female	—	25	22	88.0	7	18	100.0	18.5±1.6 A
Mated female	—	25	12	48.0	5	15	80.0	14.8±1.9 B
Cue conflict: chemical and visual cues								
None	None	35	22	62.9	0	0	0.0	16.0±2.2 B, C
Virgin female	None	28	25	89.3	10	18	100.0	19.6±1.5 A
None	Virgin female	28	21	75.0	10	6	57.1	14.0±1.9 D, C
Virgin female	Virgin female	26	23	88.5	0	26	100.0	13.7±2.1 D
Virgin female	Mated female	23	22	95.7	1	22	100.0	10.1±1.8 E
Mated female	None	31	16	51.6	12	6	58.1	15.0±1.8 B, C
None	Mated female	30	10	33.3	6	1	23.3	14.4±1.9 C, D
Mated female	Mated female	28	25	89.3	8	9	60.7	14.3±1.7 D
Mated female	Virgin female	22	19	86.4	9	12	95.5	12.7±2.0 D, E

* Values with different letters for a given experiment denote a significant difference (Tukey HSD pairwise comparisons: $P < 0.05$).

wrapping them with black electrical tape, on either side of the arena and allowed to acclimate for 1 min before they were released. We recorded the behaviour of the males for 15 min using a video camera (Sony CCD-V101) connected to a recorder (Panasonic AG1970) that was located in an adjacent room. Upon review of the videotape, we recorded the number of times that each male touched the other male with the legs and the number of times the males attacked one another. Attacks are easy to differentiate from touches because males lunge forcefully towards one another during attacks, then grapple and make carapace and/or abdomen contact. We also measured the distance between the two males at each 1 min interval and calculated the mean for each trial. Finally, we documented whether one or both males engaged in courtship activity as defined by the characteristic double leg lift.

We tested the effects of visual cues (and possibly vibratory information) from females that differed in mating status on male–male competition by sequestering either a mated or virgin female under a transparent colourless glass vial (2.67 cm diameter) in the centre of the arena. We tested the effects of chemical cues from mated and virgin females on interactions between the males. To gather the chemical cues, we placed the female into the arena with access to water but no additional food and left her to deposit chemical cues on the filter paper for 24 h. At this time, the female was removed and the trial commenced. After we conducted experiments in which visual and chemical cues were manipulated separately, we executed an expanded experiment in which we manipulated visual and chemical cues from virgin and mated females in a complete factorial design (see Table 2 for treatments and sample sizes).

Because the three experiments did not completely overlap in time, we analysed each of them separately. To verify that the size difference between competing males did not drive treatment effects, we took the absolute value of the difference between the carapace widths of the two males in each treatment and compared it across treatments in an ANOVA. We transformed the number of touches and number of attacks using the square root of each, which succeeded in normalizing the data. The square root of the number of touches and attacks as well as the mean distance between males were compared using ANOVAs with Tukey HSD pairwise comparisons. Two-way ANOVAs allowed exploration of the interaction

between cue type and female quality in the cue conflict experiment. The probability of an aggressive encounter and the probability of one or both males engaging in courtship across all treatments were assessed using logistic regression. We used a Fisher exact test to determine whether the frequency of courtship activity by one or both males was influenced by cue treatments.

RESULTS

Cue Use in Mate Location

Neither the presence of the female under a glass vial, nor her chemical cues affected the total number of males that found the filter paper disc surrounding the vial in the 3 h time frame of this experiment (Fisher exact test: $P = 0.55$; Table 1). However, the time that it took males to find the filter paper was influenced by the cues present (proportional hazard analysis, whole model: $\chi^2_3 = 12.1$, $P = 0.007$; Fig. 2). Specifically, chemical cues on the filter paper enabled males to find the disc more quickly ($\chi^2_3 = 10.9$, $P = 0.0009$), whereas the presence of the female had no effect ($\chi^2_3 = 0.14$, $P = 0.71$) and there was no interaction between chemical and visual cues ($\chi^2_3 = 1.25$, $P = 0.26$). Males spent the longest time on the filter paper when visual cues and chemical cues were combined and significantly less time when no cues were present (Kruskal–Wallis test: $\chi^2_3 = 18.90$, $P = 0.001$; Table 1). Although pairwise comparisons did not reveal significant differences, there was a suggestion of a gradation where males spent somewhat more time on the filter paper when the female was present under glass than in treatments where she was absent (Table 1). No males courted in controls where no female information was present. Excluding the control treatment, there were no significant effects of visual or chemical cues on the number of males that courted (Fisher exact test: $P = 0.46$; Table 1).

Cue Effects on Male–Male Competition

The difference in carapace width between the two males was not significantly different across treatments in any of the three experiments (Table 3). This result verified that the experiments were not unduly affected by an excessive size asymmetry between the paired males in any particular treatment.

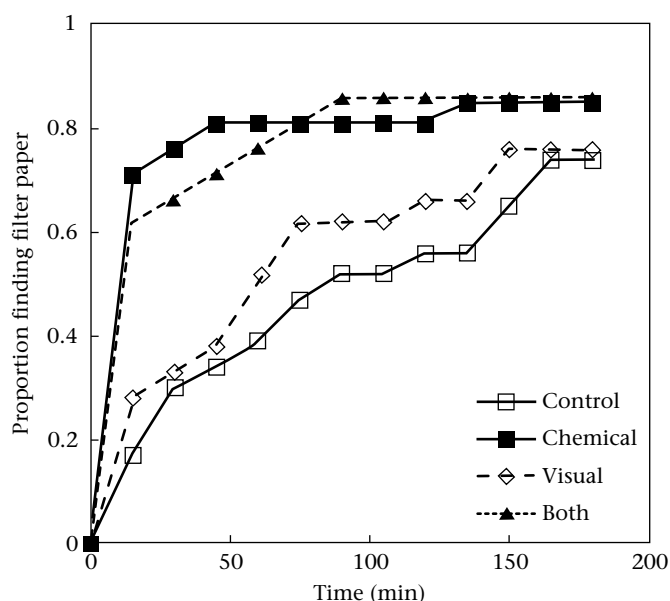


Figure 2. Proportion of males that arrived at the filter paper over the duration of the experiment categorized by the female cues that were presented there.

The presence of a virgin or mated female in the arena had no effect on the average distance between the two males during these 15 min trials (Tables 2, 3) but did influence the frequency with which males approached and touched one another (Table 3, Fig. 3). Males engaged in this nonaggressive contact more than 20 times in the 15 min interval when a virgin female was present, which was significantly more than the number observed in controls when no female was present (Table 3, Fig. 3). The mating status and presence of the female was related to the probability that an aggressive attack occurred during a trial (logistic regression: $\chi^2_2 = 9.50$, $P = 0.009$; Table 2). We observed aggression in only 35% of the control trials, whereas aggression occurred in more than 70% of the trials when a female was sequestered under glass in the arena (Table 2). Despite this difference, there were no treatment effects on the mean number of aggressive encounters observed during

a trial (Table 3, Fig. 4). The likelihood that one or both males initiated courtship was also related to the presence and status of the female (logistic regression: $\chi^2_2 = 20.25$, $P < 0.0001$; Table 2). Not surprisingly, courtship was most likely to occur when a virgin female was present and did not occur in trials without females (Table 2). Female mating status had no effect on whether one or both males engaged in courtship (Fisher exact test: $P = 0.49$; Table 2).

The presence of chemical information from mated and virgin females strongly affected all aspects of the interactions between the males in these 15 min trials (Table 3). In the presence of chemical cues from a virgin female, males tended to position themselves at opposite sides of the arena and as far away from one another as possible, whereas in the presence of chemical cues from a mated female, males stayed significantly closer together (Tables 2, 3). Even though males were generally further apart when chemical cues from a virgin female were present, they approached and touched one another more often, and even though they were generally closer together in the presence of chemical cues from a mated female, they touched one another the least (Table 3, Fig. 3). The likelihood of an aggressive attack occurring in a trial was related to the presence of the female chemical cues and the mating status of the female (logistic regression: $\chi^2_2 = 11.67$, $P = 0.003$; Table 2). Attacks were most likely to occur when chemical cues from a virgin female were present (Table 2). Additionally, the number of attacks observed per trial was higher with virgin chemical cues than in the other treatments (Table 3, Fig. 4). Female chemical cues also influenced the initiation of courtship (logistic regression: $\chi^2_2 = 60.42$, $P < 0.0001$; Table 2). At least one male started courting in all of the trials with chemical cues from virgin females and in 80% of the trials with mated female cues (Table 2).

All of the behaviours that we quantified were affected by cue treatments in the cue conflict experiments. Consistent with the results reported above, visual cues did not affect the average distance between the two males (Tables 2, 3), but cue type and mating status of the female producing the cues had significant effects on all other behaviours that we quantified and all of the interactions in the analyses of those behaviours were significant as well (Table 3).

Males maintained the greatest distance when chemical cues from a virgin female were present (Table 2). The distances

Table 3
Results of ANOVAs for experiments exploring cue effects on male–male competition

Experiment	Variable	df	Sum of square	F ratio	P	
Visual only	Carapace difference	2	0.001	0.396	0.6747	
	Touches	2	750.69	4.45	0.0157	
	Attacks	2	9.16	0.961	0.3880	
	Distance	2	1.58	1.22	0.2960	
Chemical only	Carapace difference	2	0.001	0.372	0.691	
	Touches	2	1177.69	9.60	0.0002	
	Attacks	2	244.38	8.15	0.0007	
	Distance	2	21.92	5.71	0.0051	
Cue conflict: chemical and visual	Carapace difference	8	0.006	0.48	0.873	
	Touches	Visual cues	2	3149.91	22.41	<0.0001
		Chemical cues	2	1387.77	9.87	<0.0001
Interaction		4	975.13	3.47	0.0088	
Attacks	Visual cues	2	809.97	29.61	<0.0001	
	Chemical cues	2	198.30	7.25	0.0009	
	Interaction	4	149.37	2.73	0.0297	
Distance	Visual cues	2	0.577	0.16	0.890	
	Chemical cues	2	358.23	96.59	<0.0001	
	Interaction	4	110.86	14.95	<0.0001	

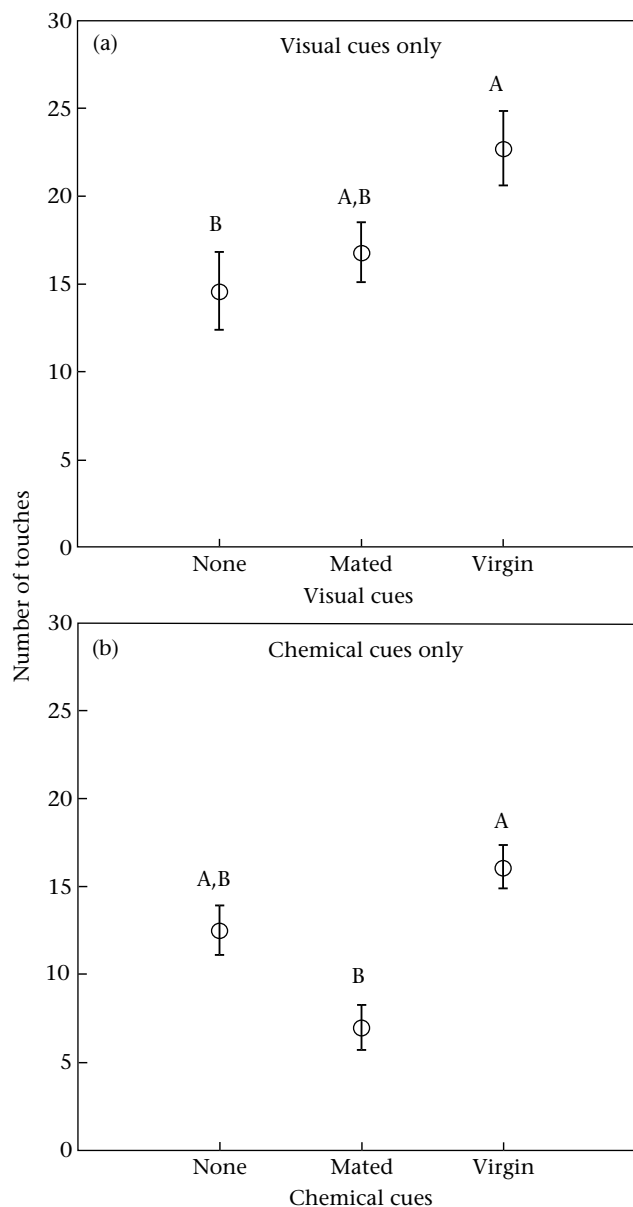


Figure 3. Mean \pm SE number of times that competing males touched one another in experiments in which only (a) visual cues or (b) chemical cues were manipulated. Different letters denote significant differences between means (Tukey HSD comparison: $P < 0.05$).

maintained between the two males in controls with no cues and those in the presence of chemical cues from mated females were not significantly different and, in general, tended to be greater than those in other treatments (Tables 2, 3). Males seemed to approach each other more closely when they had conflicting chemical and visual information (Table 2). In the presence of chemical cues from a virgin female and visual cues from a mated female, the males stayed the closest to one another (Table 2) and that distance was not significantly different from the other treatment where they had contradictory information regarding the status of the female (virgin visual and mated chemical) (Tables 2, 3).

Overall, males most frequently touched one another non-aggressively in the presence of visual cues from a virgin female (Fig. 5). The number of times that males touched one another was slightly lower when they could see a virgin female but sense chemical cues from a mated female, but the number of touches by males did not differ significantly from trials with chemical cues

from a virgin alone or from treatments with visual cues from mated females (Fig. 5). Males were least likely to contact one another when they only had access to chemical cues from a mated female and this number was not significantly different from that observed in trials with no cues, concordant chemical and visual cues from a mated female, and when chemical cues from a virgin were paired with visual cues of a mated female (Fig. 5).

The nature of the information available to the males affected whether aggression occurred in a trial (logistic regression: $\chi^2_8 = 52.28$, $P < 0.0001$; Table 2). In this model, although chemical cues were determinants of aggression ($\chi^2_2 = 20.59$, $P < 0.0001$) whereas visual cues were not ($\chi^2_2 = 3.85$, $P = 0.15$), there was a significant interaction between chemical and visual information ($\chi^2_4 = 16.92$, $P < 0.002$). This interaction was due to low levels of aggression when either visual or chemical cues from a mated female were presented alone (33% and 52% respectively) but higher levels of aggression in controls (63%) and when mated cues were

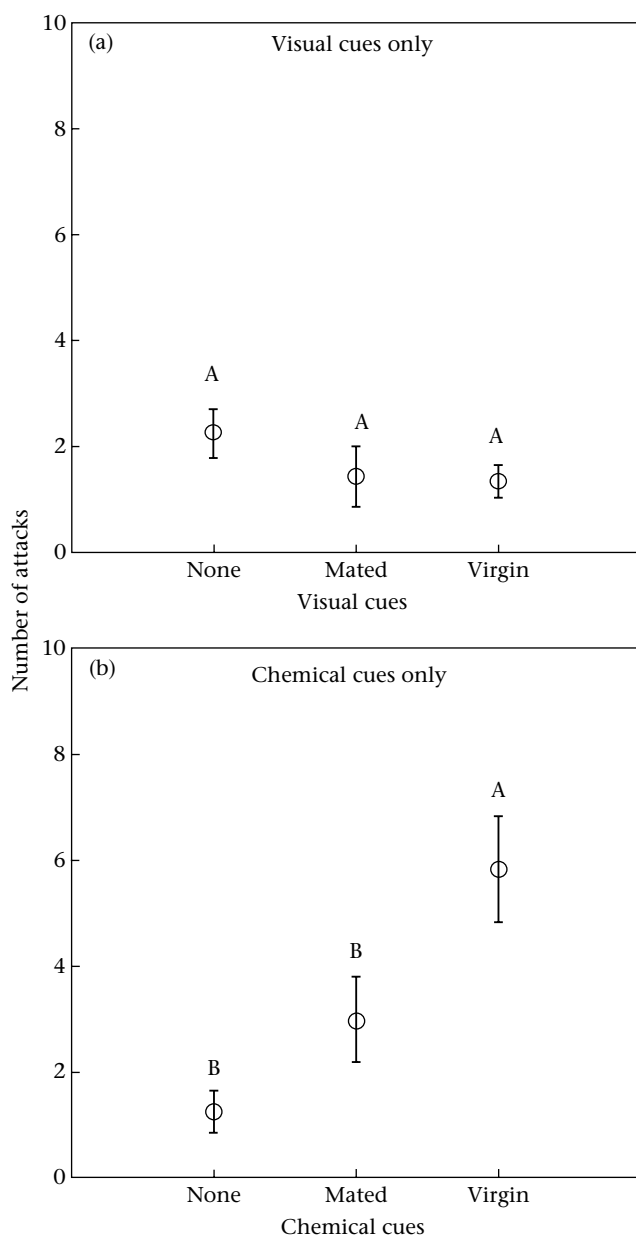


Figure 4. Mean \pm SE number of times that competing males attacked one another in experiments in which only (a) visual cues or (b) chemical cues were manipulated. Different letters denote significant differences between means (Tukey HSD comparison: $P < 0.05$).

combined with other information (all over 85%) (Table 2). The number of attacks per 15 min trial was highest when males had access to both chemical and visual information from virgins (Fig. 6), however, the number of male–male attacks was nearly as frequent when they just had chemical cues from a virgin (Fig. 6) and when a virgin was presented under glass surrounded by chemical cues from a mated female (Fig. 6). Males engaged in the fewest aggressive interactions in treatments that included no chemical information from a female (Fig. 6).

Female information affected the probability that males would commence courtship (logistic regression: $\chi^2_8 = 214.73$, $P < 0.0001$; Table 2). Both chemical ($\chi^2_2 = 9.33$, $P = 0.009$) and visual ($\chi^2_2 = 10.97$, $P = 0.004$) cues were related to the occurrence of courtship, and there was no interaction between the two ($\chi^2_4 = 0.90$, $P = 0.92$). Chemical cues were more likely to elicit

courtship in general, particularly when they came from a virgin female (Table 2). Courtship occurred in all the trials in treatments that included chemical cues from virgin females, and both males courted in all but one of the trials where they had chemical cues from a virgin and some visual cues (either a mated or virgin female sequestered under glass) (Table 2). However, visual signalling from a virgin was also important to the initiation of courtship, because we observed courtship in 95% of the trials in the treatment that included a virgin female under glass surrounded with chemical information from a mated female (Table 2). Males were least likely to commence courtship when the mated female was present with no chemical information (only 23% of trials) (Table 2).

DISCUSSION

Male *Pardosa milvina* integrate information from multiple sensory inputs in their search for females. In these experiments, the different sets of cues interacted to determine male behaviour once they found a female, including the degree to which they invested in competition with other males. Not only were chemical cues critical to the search for females, but they also provided males with evidence of the mating status or receptivity of the female. Since chemical cues collected in this manner provide information to *Pardosa* regarding the diet and hunger level of other species of predatory spiders (e.g. Persons et al. 2001; Bell et al. 2006), it is not surprising that *Pardosa* males can glean complex information from them about the mating status of the females. Here, substrate-borne chemical information from virgin females always elicited male courtship and led to increased levels of aggression between competing males. The presence of females, in this case sequestered under glass, helped males to localize their activity and further escalate or moderate their interactions with other males based on their assessment of females. For example, although the presence of chemical cues from females was likely to evoke some level of aggression between competing males, the highest frequency of aggression occurred in the presence of chemical information from virgins (Figs 4, 6). However, in cue conflict treatments in which pairs of males encountered chemical cues from virgins but were confronted with mated females under glass, they attacked one another less frequently (Fig. 6). In contrast, when exposed to chemical cues from mated females and visual cues from virgins, attack rates of males were higher than in trials with no visual information (Fig. 6). These shifts suggest that something about the visual presentation of females revealed their quality and allowed males to assess whether they were worth fighting over. Thus, input to multiple sensory modalities guides the behaviour of males in courtship and competition.

The communication ability of an animal has consequences for its reproductive success and, as such, must function effectively within its habitat and shape its interactions with other organisms (Endler 1992; Persons et al. 1999; Partan & Marler 2002). *Pardosa milvina* densities are quite high on the soil surface of agricultural fields where they collect in patches of plant debris and dirt clods (Marshall & Rypstra 1999; Marshall et al. 2000). The airborne pheromone produced by virgin females is spread broadly and serves to attract males into localized aggregations (Searcy et al. 1999). Here we show that substrate-borne chemical information initiated more directed search behaviour and stimulated courtship by males. The three-dimensional complexity of the environment makes it likely that, in nature, females may sometimes observe courtship and interactions among multiple males from hiding places where the males cannot see them. Female *Pardosa milvina* base their mate choice decisions on the intensity of the visual courtship display of the males (Rypstra et al. 2003; Taylor et al. 2005b). Although not tested in *Pardosa*, female mate choice is

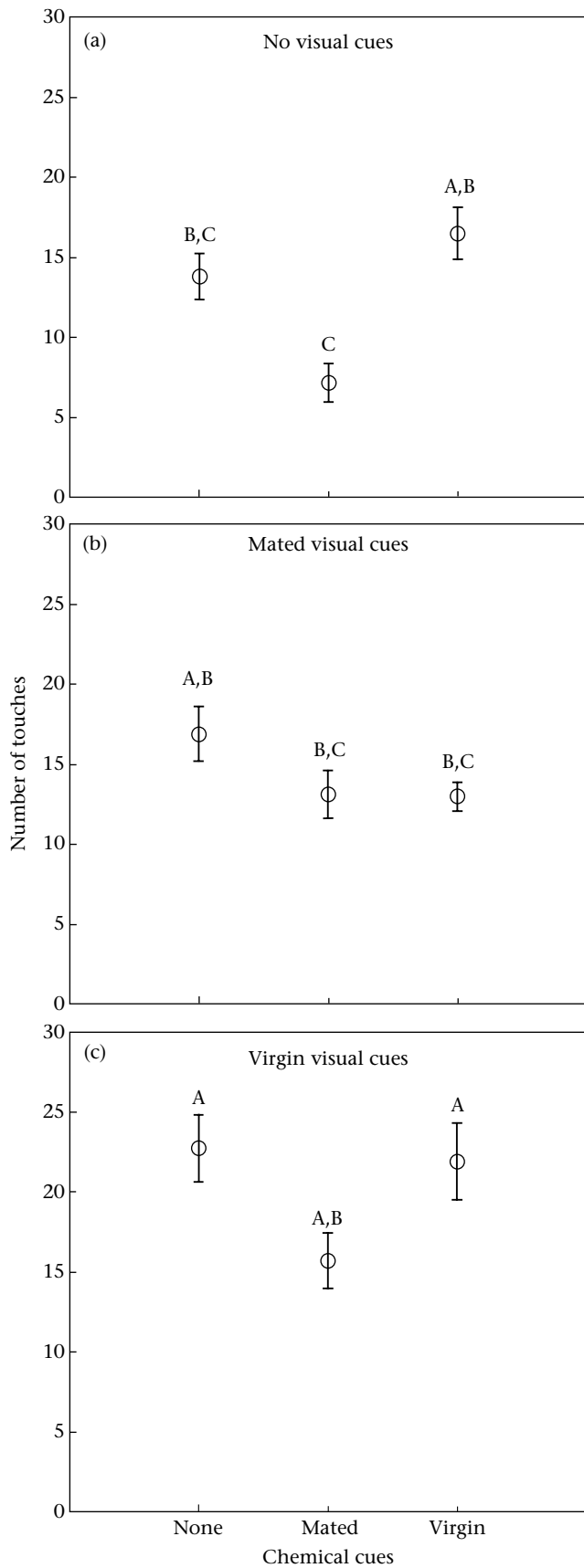


Figure 5. Mean \pm SE number of times that males touched one another in cue conflict experiments where both visual and chemical information were manipulated in a full factorial design. Different letters denote significant differences between means (Tukey HSD comparison: $P < 0.05$).

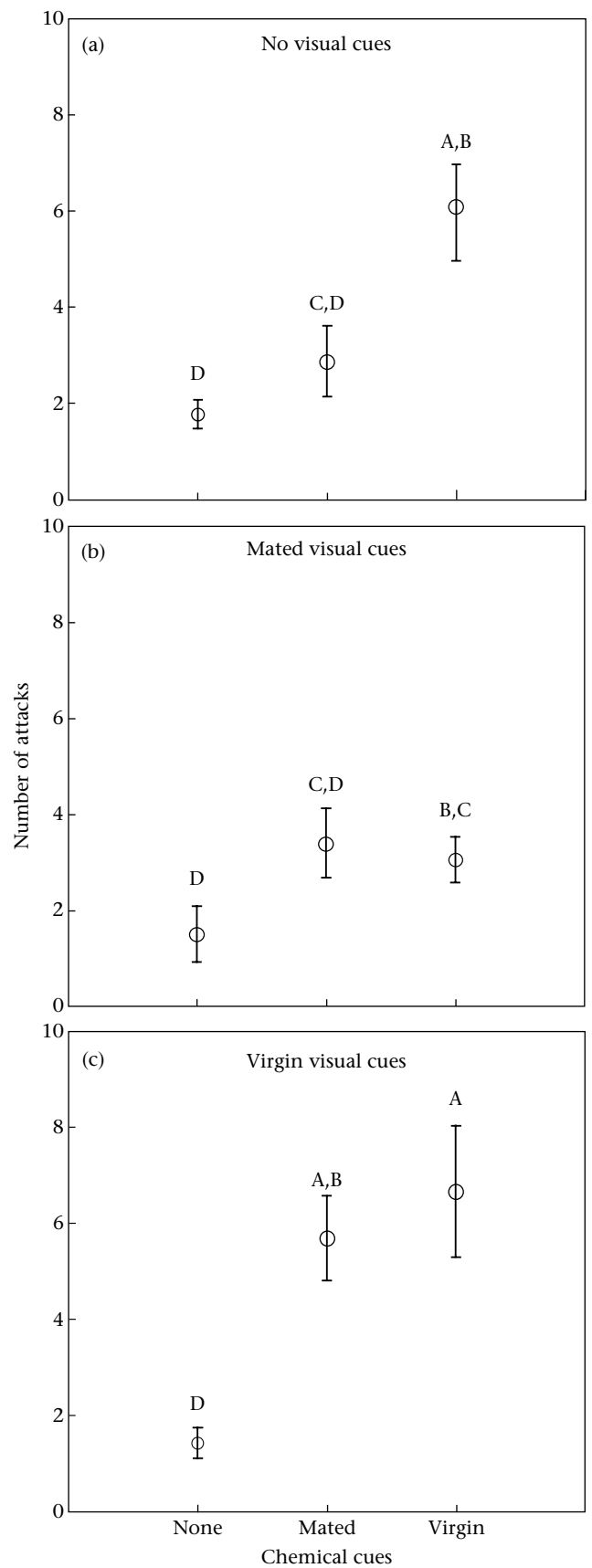


Figure 6. Mean \pm SE number of times that males attacked one another in cue conflict experiments where both visual and chemical information were manipulated in a full factorial design. Different letters denote significant differences between means (Tukey HSD comparison: $P < 0.05$).

influenced by observations of male fighting behaviour or dominance in a variety of other species including Japanese quail, *Coturnix japonica* (Ophir & Galef 2003), fighting fish (Doutrelant & MacGregor 2000) and the jumping spider, *Thiania bhamoensis* (Chan et al. 2008). Thus, male *Pardosa*, confronted with the high concentration of female silk and other excreta such as that which we provided here, should benefit from performing courtship and competing with other males even without confirmatory visual evidence that females are present. Indeed, females may not emerge from their observation site or retreat until the activities of the males have convinced them that one or both of the males are of sufficiently high quality. On the other hand, the conspicuousness of courtship displays increases the male's vulnerability to cannibalism or predation (Persons et al. 2001; Lynam et al. 2006; Hoefler et al. 2008). Hence, they should be very aware of and sensitive to other sensory input that will alert them to the presence of potential predators, help them identify females, and provide more specific information as to whether the females are risky or receptive (e.g. Jackson et al. 2006). In essence, chemical cues from females seem to serve to prime males to be more attentive to visual cues in their search for potential mates.

Males were able to discriminate between virgin and mated females without chemical information even though the glass vials restricted the activity range of females. Although chemical cues are important to the interactions between male and female wolf spiders, at some point, the immediacy of mating assessment requires the two-way exchange of signals. We presume that males could not detect the mating status of females by their gross appearance alone but rather that males responded to the stance or posture that the females assumed upon viewing the courtship or fights performed by males in the arena. Many female wolf spiders adopt receptivity postures that signal their willingness to mate (Montgomery 1903; Kaston 1936) and, for most, this is a stereotyped response involving lowering of the cephalothorax, raising of the abdomen, and placing at least the first two pairs of legs in an extreme prostrate posture (Stratton & Uetz 1983; McClintock & Uetz 1996; Hebets & Uetz 2000). Female *Pardosa* will also tap their first pair of legs in the direction of courting males to signify receptivity (Brautigam & Persons 2003). Although our set-up did not allow us to quantify female behaviour, we presume that their visual (and perhaps accompanying seismic) signals were what influenced the response of males. Thus, we believe that virgin females are more likely to signal receptivity and that males, in treatments with visual cues, were probably responding to female behaviour as opposed to detecting and responding to female mating status per se. In natural situations, the male's behaviour reflects an integration of all chemical information that the male receives that can clearly tell him the mating status of a female, moderated by evidence from the visual cues that the female is or is not receptive.

Male courtship in wolf spiders is generally thought to be important to species recognition as the first step to female evaluation and mate selection (Uetz 2000). This assumption raises the obvious question as to how males might come to recognize females, although evidence for the primary role of chemical stimuli is mounting (Roberts & Uetz 2005; this study). However, if several spiders are aggregated in a small area and the available chemical cues are either insufficient or ambiguous, males need to gather more information in order to discriminate competitors and predators from potential mates. Obviously, if the female is in sight, her behaviour and posture will provide critical information, but females may not be visible. In our observations, we were surprised by the frequency with which males approached and touched the legs of other males in a nonaggressive way, often following this action with a quick retreat. The frequency of these touches was

generally higher when there were no chemical cues present, but they were also fairly frequent when the chemical information was from virgin females. We suspect that this was a type of sampling behaviour by which males, through tactile signals or some contact pheromone, sought to identify the sex or status of other spiders in the area. If assessment is a function of touches, it suggests that males may not be able to accurately determine the identity of another spider from visual cues alone, or at least that they question their identification when confronted with high concentrations of chemical information suggesting a female must be present. Other species of wolf spider are unable to detect and localize potential mates unless they are moving (Rovner 1991, 1993). Since males courted females held under vials in the visual only treatments and did not court when no female information was available (Table 2), the small degree of movement possible within the confines of the glass vials holding females must have been sufficient for *Pardosa* males to determine that females were present. However, the high degree of movement by their male partner may have distracted males from sequestered females and caused them to approach. Interestingly, the number of touches seems also to be loosely related to the spacing of the two males relative to one another, especially in trials where no female was in the arena (Table 1, Fig. 5). Possibly out of surprise or to avoid aggression, after coming in contact, the two males typically retreated quickly to opposite sides of the arena, only to approach again in an attempt to find a female.

One concern with our presentation of visual cues was that the airborne pheromone produced by virgins might escape to influence the behaviour of the males by dissolving into the filter paper and diffusing under the vial. If this were occurring, we would have expected it to be most evident in the mate location experiment in which the response of males was observed over the relatively long 3 h time period. However, there was no difference in either the number of males that approached or the time that it took them to approach empty vials and vials holding virgin females (Table 1, Fig. 2). Thus, it seems unlikely that volatile cues were escaping in sufficiently high concentrations to alter the reactions of the interacting males in the competition experiments, which were only 15 min long.

The structure of the genitalia of wolf spiders suggests that there should be first-male sperm priority (Austad 1984), and at least one other species is considered monandrous (Norton & Uetz 2005), even though in laboratory studies remating can be as high as 14% (Persons & Uetz 2005). Previous studies with *Pardosa* (*P. milvina* and other species within the genus) reveal that mated females will accept additional mates (Rypstra et al. 2003; Szirányi et al. 2005); however, no genetic studies have been conducted to determine how reproductive success might be partitioned among sequential mates. Nevertheless, the differential reaction of males to mated and virgin females in the presence of either type of cue verifies that *Pardosa* males can discriminate mating status of females. Given that courtship is risky for *Pardosa* males (Hoefler et al. 2008) and that males readily courted when presented with cues from mated females, it seems that males must achieve some fitness gains from securing copulation with mated females. Szirányi et al. (2005) suggested that, in *Pardosa agrestis*, males transfer some substance that enhances sperm competition in copulatory bouts with multiply mated females. Our experimental design may have increased the attractiveness of the mated females because all the females that we included in these experiments were quite well fed. Evidence suggests that spiders are food limited in nature and egg production is strongly linked to food consumption by females (Wise 2006). Consequently, the mated females that we used in trials may have been much more attractive than the ordinary mated female in a field situation because, if they lived long enough, they should be able to produce several large eggsacs. As such, these

second or third males may gain some reproductive success even if the sperm of the first male is prioritized. It would be interesting to explore the interaction between mating experience and hunger level to determine how males weigh the various attributes of a prospective mate, given that females can and do mate multiple times.

Recently, several reviews have proposed classification schemes for multimodal signalling in animals (Hebets & Papaj 2005; Partan & Marler 2005). A preponderance of the studies in these reviews focus their exploration of cues on the signal display of the males aimed to attract a female. Thus, one critical result of our study, even though it should not be surprising, is that male detection and evaluation of females also requires multiple sensory modalities. In *Pardosa*, the chemical and visual cues that males use are largely redundant (sensu Partan & Marler 2005), as they both allowed males to locate and determine the mating status of the female; however, the specific behavioural responses that each cue type elicited from the males were different. Chemical cues provided the richest information regarding the female except, of course, her exact location and receptivity, which males discerned from observation of a female sequestered under glass. Consequently, we suggest that these signals conform with the intersignal interaction hypothesis as proposed by Hebets & Papaj (2005); specifically, when we add visual cues to chemical information, we see increased detection and discrimination as evidenced by an alteration in the response of the receiver. Further experiments need to uncouple the chemical signals that we used in these experiments (i.e. to separate olfactory, gustatory and tactile components) and to specifically explore the separate and combined importance of visual and vibratory information in this species. Nevertheless this study represents an important step in understanding the relative roles of two distinct classes of sensory cues in an evolving exchange of information between males and females as they assess one another as potential mates.

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