

Mutual Mate Assessment in Wolf Spiders: Differences in the Cues Used by Males and Females

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Abstract

When males engage in conspicuous courtship displays, it seems obvious that females would use characteristics of that display in mating decisions. However, males must also have a way to identify and evaluate females prior to engaging in what might be a costly mating ritual. Although it was known that female wolf spiders of the species *Pardosa milvina* (Araneae; Lycosidae) attract males using volatile chemical cues, the nature of the cues used by males and females in mate selection had not been investigated. Specifically we determined whether males could detect the mating status of the female and if chemotactile cues from the female played a role in that process. In addition, we quantified conspicuous aspects of the male courtship (leg raises and body shakes) to determine if courtship intensity was related to female choice. Although repeated mating occurred in our studies, males were more likely to court and mate with virgin females. Males used substrate-borne cues deposited by females to discriminate between mated and virgin females. Females used the conspicuous behaviors of males during courtship, body shakes and leg raises, in mate selection. Thus males and females use different kinds of information and different sensory modalities to assess the suitability of a potential mate.

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Introduction

Darwin (1871) originally proposed that males typically invest relatively little in parental care and so they should be selected to acquire many mates whereas females typically invest heavily in egg production and parental care and so they should be more selective of their mates (Darwin 1871; Trivers 1972;

Andersson 1994). However, when there are costs associated with courtship and mating, males must also make decisions regarding the acceptability of prospective mates (Johnstone 1997a; Bonduriansky 2001). For example, if first male sperm precedence is high and/or males engage in potentially expensive activities to find and attract females, selection should favor some mechanism by which males can accurately assess the mating status of females (Dewsbury 1982; Simmons et al. 1994; Bonduriansky 2001). In addition, females may damage or kill males during courtship or mating and eliminate any further reproductive potential (Elgar 1992; Schneider et al. 2001), a situation which puts even more pressure on males to make a careful choice. Recent mate-choice models have made a more explicit effort to take into account male mate choice and have incorporated mutual assessment by the sexes (Owens & Thompson 1994; Johnstone 1997b; Bonduriansky 2001). Critical to mate choice by either sex is the evolution of clear detectable cues that accurately reveal relevant properties, including the species identity and overall quality of the individuals involved (Guilford & Dawkins 1991; Johnstone 1997b; Uetz 1999). As males and females are selected to maximize different aspects of reproduction, they might be expected to use different criteria to evaluate potential mates and thus might be expected to use different cues and/or different sensory modalities in selecting a mate.

Male wolf spiders (Lycosidae) are known to engage in visually and vibratory conspicuous courtship displays that are important in species recognition and sexual selection (Kaston 1936; Stratton & Uetz 1986; Uetz 1999). As females produce large egg sacs and are the sole providers of parental care (Foelix 1996), wolf spiders fit into the female choice paradigm as proposed by Darwin (1871) (Trivers 1972; Andersson 1994). However, the structure of the female genitalia in wolf spiders suggests that the sperm of the first male to copulate should have fertilization priority (Austad 1984) and, if so, selection should favor males that can detect virginity in females.

We studied courtship behavior and how it affects sexual selection in the wolf spider, *Pardosa milvina* (Araneae; Lycosidae) with particular emphasis on the cues used by males and females to detect and evaluate one another. This wolf spider is a small, active species that prefers to be associated with patches of plant debris on barren soil surface in disturbed habitats such as agricultural fields (Marshall & Rypstra 1999; Walker et al. 1999). Although most spider pheromones are attached to silk and are only detected on contact (Tietjen & Rovner 1982; Roland 1983), females of this species also emit an airborne pheromone that attracts males from long distances (Searcy et al. 1999). Upon contact with females, males engage in vigorous courtship consisting of two distinct behaviors, leg raises and body shakes (see Montgomery 1903; Kaston 1936 for complete descriptions). The goals of this study were: (1) to determine if *P. milvina* males and females mate more than once and, if so, to further characterize the mating interactions by determining; (2) if male courtship of virgin females differed from courtship of mated females; (3) if the frequency of the obvious courtship behaviors were related to female mate choice, and (4) if courtship and other mating behaviors

were altered when females were not given the opportunity to deposit pheromonal cues in the mating arena prior to the introduction of the male.

Methods

All spiders were collected from within and between soybean fields at Miami University's Ecology Research Center (Oxford, Butler County, OH, USA) between June and December 1999. Spiders were maintained in individual translucent plastic containers 8 cm in diameter and 5 cm tall with 1–2 cm of moist peat moss substrate on the bottom to provide moisture. Spiders were housed in an environmental chamber on a 14:10 L:D cycle at 25°C. Every 3–4 d, each spider was provided with a combination of fruit flies (*Drosophila melanogaster*) and/or crickets (*Acheta domesticus*). Spiders were separated by sex at the penultimate instar and used in experiments only after molting to adulthood. All females used in experiments had gone through this final molt in the laboratory so that their mating histories were known. We were unable to collect sufficient numbers of immature males to ensure that all were inexperienced. As we had to assume that field-caught males had mating experience, we mated all males at least 48 h before experimentation. Each spider was assigned to a treatment randomly and was used in only one experimental trial. Females were either virgin or had been mated 48–72 h (with a male otherwise not involved in this experiment) before they were paired with a male for this experiment. We selected the 48–72-h time frame so as to be sure that any physiological changes that occur after mating would have begun but no female would have had sufficient time to produce an egg sac.

Mating behavior was videotaped in a circular plastic arena (20 cm in diameter; 7.5 cm high). Behaviors were taped from a remote location so that the presence of an observer did not interfere with the spider's activities. White filter paper covered the bottom of the container to provide a substrate suitable for spider locomotion, to collect chemical cues or pheromones the spiders deposited, and to improve contrast during videotaping. Between experimental runs, the arenas were swabbed with alcohol, allowed to dry, and the filter paper was replaced. In each run, a male and a female were placed in the experimental arena and videotaped for 2 h or until copulation was complete. Previous experiments revealed that any male would commence courtship within 30 min of containment with a female (if it were to commence) and that the whole process of courtship and copulation never took more than 1 h.

In two treatments, either a virgin female or a female that had been mated just 48–72 h earlier were released into the arena and allowed to acclimate for 30 min during which time we presume they deposited silk draglines, pheromones, and other chemical cues. After that half hour, a male was introduced into the arena under a clear plastic vial, 1.5 cm in diameter. After 2 min, the vial was lifted and videotaping began. In two additional treatments, we introduced either a virgin female or female that had mated 72 h earlier at the same time as the male so that there was no opportunity for pheromonal deposition. Both were held under

separate vials for 2 min and then released. Videotaping of courtship and mating behaviors began immediately and continued for 2 h as described above.

Preliminary screening of the videotapes revealed whether copulation had occurred or not. If it occurred, we recorded the number of leg raises and body shakes the males performed in the 5 min just prior to copulation, which is the period during which the male courts most intensively. In addition, we recorded the total time the pair remained in copula. If copulation did not occur, we selected the 5 min period in which we observed the most vigorous courtship (the highest frequency of body shakes and leg raises) and recorded the frequency of body shakes and leg raises during that time.

We compared the frequency of courtship and the frequency of copulation events across treatments using log linear analyses of $2 \times 2 \times 2$ contingency tables. Total courtship time, the frequency of leg raises, the frequency of body shakes, and total copulation time were compared in two-way ANOVAS with the mating status of the female and whether or not cues had been deposited before the introduction of the male as factors. Pairwise comparisons of different treatments were made using Fisher's protected least significant difference (PSLD). The ability of body shakes or leg raises to predict whether copulation occurred was tested using logistic regression with treatment (mating status and cue presence or absence) as covariates. Fisher's PSLD was used to make pairwise comparisons of the frequency of courtship behaviors performed across treatments and outcome (i.e. whether courtship occurred or not).

Results

Males were not equally likely to court females in all treatments (Tables 1 and 2). Courtship occurred much more frequently when males were paired with females that deposited cues in the arena before the male was released regardless of the mating status of the female (Tables 1 and 2). The fact that there was an interaction between female mating status, the presence of cues, and the frequency of courtship suggested that the cues deposited by females influenced male courtship (Tables 1 and 2). Specifically, when cues were present, all but one of the

Table 1: Frequency and duration (mean \pm SE) of courtship and copulation

	Virgin females with cues	Mated females with cues	Virgin females no cues	Mated females no cues
Number tested	35	36	20	20
Number of males that courted (%)	34 (97%)	29 (81%)	12 (60%)	13 (65%)
Courtship time (min)	17.0 \pm 2.1	16.4 \pm 2.4	14.8 \pm 1.8	16.2 \pm 1.7
Number that copulated (percentage of those courted)	25 (74%)	5 (17%)	7 (58%)	4 (31%)
Copulation time (min)	11.2 \pm 1.3	9.6 \pm 2.0	7.8 \pm 1.5	10.1 \pm 2.0

Table 2: Results of log-linear analysis of the frequency of courtship or frequency of copulation when courtship occurred in relationship to the mating status of the female and whether or not she was able to deposit pheromonal cues in the area prior to testing

Interaction	G ²	Degrees of freedom	p-Value
Frequency of courtship			
Status * Cues	0	1	1.000
Cues * Courtship	10.36	1	0.0013
Status * Courtship	1.28	1	0.2579
Status * Cues * Courtship	15.92	4	0.0031
Frequency of copulation			
Status * Cues	0.26	1	0.6101
Cues * Copulation	0.10	1	0.7518
Status * Copulation	21.41	1	0.0001
Status * Cues * Copulation	23.56	4	0.0001

males paired with virgin females courted (97%) but only 81% of those paired with mated females courted. On the other hand, in the absence of cues, males courted 60% of the virgins and 65% of the mated females (Table 1). There was no difference in the total courtship time across treatments (Tables 1 and 3).

The frequency with which a particular pairing concluded in copulation also varied across treatments (Tables 1 and 2). Pairings of males with virgin females were more likely to end in copulation regardless of whether cues were present or not (Tables 1 and 2). However, the three-way interaction between female mating status, cues and the frequency of copulation suggested that both the presence of cues and female mating status played a role in determining whether copulation occurred (Tables 1 and 2). Specifically the difference in the frequency of copulation between mated and virgin treatments was much greater in the presence of cues than when females were not provided the opportunity to deposit cues (Table 1). There was no difference in copulation time across treatments (Tables 1 and 3).

Mating status of the female had a significant effect on both the number of leg raises and the number of body shakes males performed during courtship (Fig. 1; Table 3). Males performed these courtship behaviors at the highest frequencies when paired with a virgin female who had deposited cues in the arena (Fig. 1; Table 3). The importance of pheromones was revealed in the significant interaction between mating status and cue deposition evident in the analyses of both leg raises and body shakes (Fig. 1; Table 3). When pheromones were present, males performed both behaviors at a higher frequency when courting virgin females than when courting mated females but, in the absence of pheromones, there was no difference in the rate at which these activities were performed for virgin or mated females (Fig. 1).

The likelihood of a courtship ending in copulation across all treatments was significantly related to the frequency of both leg raises and body shakes

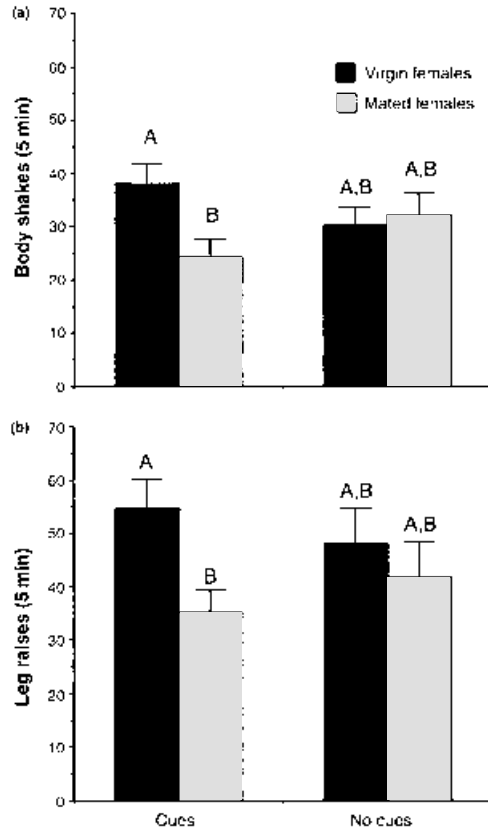


Fig. 1: The frequency of body shakes (a) and leg raises (b) performed by courting males separated by the mating status of the female, whether she had the opportunity to deposit cues in the arena before the male was introduced. The groups indicated with different letters are significantly different from others according to Fisher's PSLD ($p < 0.05$)

during courtship (leg raises $R^2 = 0.272$; $p < 0.0001$; body shakes $R^2 = 0.499$; $p < 0.0001$) (Fig. 2). However, as judged by the R^2 values and pairwise comparisons, the number of body shakes was a better predictor of copulation than leg raises (Fig. 2).

Discussion

Mate selection in *P. milvina* clearly involved mutual mate assessment with males and females using different sensory information. Males used female chemical cues to garner information on the reproductive status of females, whereas females used visual displays performed by males to garner information about males, presumably related to their stamina or condition. Such an asymmetry in focus is consistent with sexual selection theory, which suggests

Table 3: Results of two-way ANOVAs of total courtship time, and copulation time as well as the frequency of body shakes and leg raises performed during a 5 min period of male courtship. Mating status of the female and whether or not the female was able to deposit pheromonal cues before the male was introduced into the arena were entered as factors in the analyses

	Sum of squares	Mean square	F-value	Degrees of freedom	p-Value
Copulation time					
Female status	12.70	12.70	0.79	1	0.380
Cues	0.89	0.89	0.06	1	0.816
Interaction	24.56	24.56	1.53	1	0.225
Residual	595.36	16.10		37	
Courtship time					
Female status	25.26	25.26	0.60	1	0.443
Cues	1.86	1.86	0.04	1	0.835
Interaction	17.61	17.61	0.42	1	0.521
Residual	3564.47	42.43		84	
Body shakes					
Female status	1885.19	1885.19	5.55	1	0.021
Cues	26.34	26.34	0.08	1	0.781
Interaction	1531.96	1531.96	4.51	1	0.037
Residual	28 511.81	339.43		84	
Leg raises					
Female status	3559.89	3559.89	5.99	1	0.017
Cues	0.02	0.02	0.00	1	0.996
Interaction	3133.99	3133.99	5.27	1	0.024
Residual	49 955.24	594.71		84	

that male preferences should focus on the impact of expected fertilization success and females should focus on male quality (Andersson 1994; Ryan 1997). In *P. milvina*, the fertilization rate of males should be lower with mated females than with virgins if they have first-male sperm priority. However, in an active cursorial spider such as *P. milvina*, the ability to engage in a vigorous display may be an indication of male stamina and vigor.

Few studies have looked for evidence of male mate recognition in cursorial spiders and the kinds of cues that they might use to assess females. In groups with high visual acuity (e.g. Salticidae and Lycosidae), the onus is on males to perform specific courtship rituals so that females do not treat them as prey (Uetz 1999) and there is considerable evidence that selection has operated on the morphology and behavior of males to be visibly recognizable from a distance (Clark & Uetz 1992; Miller et al. 1998; Hebets & Uetz 2000). However, females of these same species tend to be quite monomorphic. This observation raises the question as to how males recognize females in the first place. The conspicuous displays of males attempting to attract females without eliciting a predatory response may also serve to attract other predators. Thus, we would expect

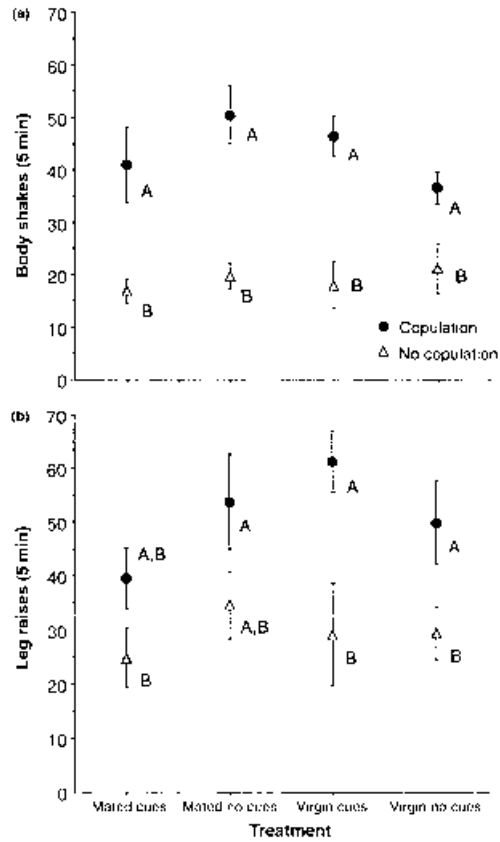


Fig. 2: The frequency of body shakes (a) and leg raises (b) performed by courting males separated by the mating status of the female, whether she had the opportunity to deposit cues in the arena before the male was introduced, and whether or not the interaction ended in copulation. The groups indicated with different letters are significantly different from others according to Fisher's PSLD ($p < 0.05$)

selection to favor males that could detect and identify appropriate females from cues left in the environment so that they do not display indiscriminately and expose themselves to unnecessary risk. In *P. milvina*, chemical or tactile cues deposited by females clearly influenced male courtship behavior (Fig. 1). In the absence of these cues, males were less likely to court overall and they courted mated and virgin females with similar intensity, which suggests that they could not identify the reproductive status of females (Table 1; Fig. 1). There are only a few other studies of male assessment of females and the results are not consistent across species. Males of the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae), and the web spider, *Agelenopsis aperta* (Araneae; Agelenidae), both use pheromones to discriminate between mated and unmated females (Jackson 1981, 1982; Riechert & Singer 1995; Papke et al. 2001). However, males of two *Schizocosa* and two other *Pardosa* species (not

P. milvina) responded identically to contact pheromones from mated and unmated females (Hegdekar & Dondale 1969).

When *P. milvina* females were not allowed to deposit cues in the arena, there was no difference in male courtship behavior in the presence of mated or unmated females (Fig. 1). This observation suggests that, although males were able to identify the presence of females, they were not able to accurately determine mating status. Thus, in the presence of ambiguous information regarding female mating status, the default strategy for the male is some intermediate level of courtship. As it may be difficult to find females in a complex environment, selection might favor the strategy of attempting to mate with all females, especially when her mating status cannot be detected. In addition, courtship behavior itself may offer some protection from cannibalism by females and give males time to assess receptivity and escape if necessary.

The importance of visual and vibratory signals in female mate choice has been well documented, particularly for members of the genus *Schizocosa* (Uetz 1999 and references therein). Thus, the finding that *P. milvina* females use the obvious behaviors performed by males during courtship to make their selection is not surprising. Although courtship intensity was highly variable from male to male, females were consistent in their selection criteria across all treatments (Fig. 2). This result raises the question as to what factors generate the variability in male courtship behavior. As a part of the experimental protocol, we attempted to make the males as similar as possible. They were all well fed and had mating experience prior to our observations. If there is a marginal fitness gain to additional copulations and an inherent cost associated with continuing to search for females, the prediction would be that males should court all females as vigorously as possible. The most likely reason for this male selectivity is that there is an exchange of signals between males and females during the courtship process that causes males to intensify courtship upon receiving information that females were receptive (Johnstone 1997b). In addition, there may be differential costs to courtship relating to such things as relative size and age that factor into the behavior of males in this situation.

The fact that females communicated their reproductive status to males suggests that repeated mating is costly and/or risky for them. Presumably the conspicuous courtship behavior of the male can attract the attention of predators. Likewise the time spent by the female observing courtship and copulating might better be spent in the search for food, which may directly lead to an increase in clutch size (Wise 1979; Uetz 1992). Thus, unless the female has information that the sperm she has is insufficient or inferior and/or that the male in front of her is clearly superior in some way to other males, there is no real reason for her to attempt to attract additional males or engage in additional matings. The differential use of pheromones by mated and unmated females to attract males might suggest that females manipulate male courtship and, thus that the system was ultimately governed by female choice. Our data suggest that any male that ignored her signals and courted intensively would be able to mate and presumably increase his fitness. On the other hand, a high level of activity

in front of a non-receptive female could merely serve to make him a conspicuous prey item. Clearly other subtle signals pass between males and females during courtship to indicate receptivity and reinforce the selection process as courtship proceeds. For example, occasionally *P. milvina* females tap one or more legs in an arc during male courtship, a behavior that may signal their receptivity to males (Kaston 1936).

A complex combination of signals is involved in the process of finding mates and the mutual assessment of their suitability in *P. milvina*. These results suggest that chemical and tactile cues take precedence in the detection and assessment of females by males whereas visual (and possibly vibratory) stimuli are important to the detection and assessment of males by females. Future research should address the costs and benefits of the use of various sensory modalities in interactions between males and females and their evolutionary context.

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