

Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders (Araneae: Lycosidae)

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Abstract. Male wolf spiders, *Schizocosa ocreata*, possess tufts of bristles on the forelegs, which are used in visual courtship displays, but males of a closely related species, *S. rovneri*, lack tufted forelegs. In studies with live males, female *S. ocreata* showed receptivity more often to males with larger tufts than to males with smaller or shaved tufts. Male body size and/or shaving of tufts may affect male courtship behaviour, however, which could influence female receptivity. Manipulated video images of the same courting male were used to control for male behaviour and to test the hypothesis that these tufts influence female choice. Video images of *S. ocreata*, and images of *S. rovneri* males (control: without tufts; experimental: with tufts added) were shown to females of both species. Female *S. ocreata* showed lowered receptivity to a video of a male with tufts removed and equal receptivity to a video of a male with enhanced tufts compared to a control video of a conspecific male with typical tufts. Responses of female *S. ocreata* to heterospecific video male *S. rovneri* were significantly lower than to conspecifics. In contrast, female *S. rovneri* are more receptive to video images of conspecific males with tufts added and heterospecific male *S. ocreata* than to control images. Phylogenetic analyses suggest that tufts are apomorphic, and that *S. rovneri* is more basal within the clade than *S. ocreata*. Since female *S. rovneri* respond receptively to both conspecific and heterospecific males with tufts and/or active leg waving displays, these results may provide evidence of pre-existing bias and/or sexual selection for a novel trait.

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The mechanisms responsible for the evolution of exaggerated male secondary sexual characters, first proposed by Darwin (1871), have recently experienced a renaissance of interest (Bateson 1983; Bradbury & Anderson 1987; Harvey & Bradbury 1991; Andersson 1994). Currently, many of these ideas are being discussed within the context of signal-receiver evolution (Guilford & Dawkins 1991; Endler 1992b, 1993; Ryan & Rand 1993). Whether females respond to the intended male signal depends on several factors: (1) whether the signal was successfully generated, (2) whether the signal was successful at reaching the female through the environment, (3) whether

the signal was received by the female once it reached her, and (4) the 'decision' of the female to act on the perceived signal (Guilford & Dawkins 1991; Endler 1993). Factor 1 depends on the physiological, biophysical and biochemical state of the male generating the signal (Endler 1993; Löfstedt 1993). Factors 2 and 3 refer to what Guilford & Dawkins (1991) called the 'efficacy' of the signal, and may depend on characteristics of the microhabitat and female sensory system. Factor 4 depends on, among other things, the 'content' (Endler 1993) or 'strategy' (Guilford & Dawkins 1991) of the signal. For example, signals may contain information about male genetic quality (Zahavi 1975; Hamilton & Zuk 1982; Kodric-Brown & Brown 1984; Møller 1990; Thornhill 1992; Maynard-Smith 1994).

Endler (1992a) suggested that although many studies of sexual selection have focused on understanding what Guilford & Dawkins (1991) called

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'strategic' design in signal evolution (relating to the function of the signal; e.g. conveying male quality), fewer have addressed 'tactical design' (relating to the structure and efficacy of the signal, e.g., getting the attention of the female). In mating systems where the consequences for ineffective communication are severe, for example, cannibalism by potential mates, selection on tactical design may be strong, because in such cases an ineffective signal may be lethal.

Spiders are excellent model systems in which to study female choice and the evolution of signalling behaviour (Platnick 1971; Robinson & Robinson 1972; Witt & Rovner 1982; Uetz & Stratton 1983). Females are both potential predators and potential mates; hence selection for effective communication during courtship may be quite strong. Selection should favour males that evolve signals that clearly identify them as courting male spiders of the appropriate species rather than prey, and should favour signals that can be transmitted clearly in a given microhabitat. In addition, selection may favour males with courtship displays and secondary sexual characters that stimulate pre-existing sensory biases in females. Studies with spiders have demonstrated the importance of courtship communication in reproductive isolation (Stratton & Uetz 1981, 1983, 1986; Uetz & Stratton 1982) and in female assessment of males (Jackson 1977, 1982; Watson 1991, 1993; Clark & Uetz 1992).

This research concerns wolf spiders in the genus *Schizocosa* (Araneae: Lycosidae), in which a conspicuous male character (leg tufts) and courtship displays may function as signals for species recognition and female mate choice. We used a video imaging technique (Clark & Uetz 1990) to control for behavioural differences between males and to manipulate the presence of tufts. Because males of a closely related species, *S. rovneri*, do not possess tufts, this study also examined the pre-existing bias hypothesis. The pre-existing bias hypotheses (Endler & McLellan 1988; Ryan et al. 1990; Basolo 1990a, b, 1995a, b; Endler 1992a, b; Proctor 1992; Ryan 1994) predicts that female preferences precede male traits, and that male traits evolve as a means of exploiting these pre-existing female preferences. This study also provides a cladistic test of the pre-existing bias hypothesis. If the preference for tufts evolved prior to tufts themselves, female *S. rovneri* may prefer males with tufts over conspecific males.

METHODS

The Species

Schizocosa ocreata (Hentz) and *S. rovneri* Uetz and Dondale are wolf spiders common to the deciduous forests of the eastern United States. The two species are geographically sympatric, but generally occupy different microhabitats (Uetz & Denterlein 1979; Stratton & Uetz 1981). They are virtually identical with respect to body size, genital characters and colour (Dondale & Redner 1978; Uetz & Dondale 1979). One distinct morphological difference between the two species is the presence of a tuft of bristles on the first pair of legs in adult *S. ocreata* males. During courtship, males of both species produce species-specific substratum-coupled stridulation (Stratton & Uetz 1981, 1983, 1986). In addition, *S. ocreata* males perform a series of leg-waving displays using the first pair of legs which contain the conspicuous tufts, but *S. rovneri* males lack leg-waving displays during courtship (Stratton & Uetz 1981, 1983, 1986). The importance of courtship displays in these wolf spiders is supported by the fact that *S. ocreata* and *S. rovneri* are reproductively isolated by their courtship behaviour alone (Stratton & Uetz 1981, 1983, 1986). Although males of both species typically court females of either species, females only show sexual receptivity to conspecifics. Forced copulations between heterospecifics yield physiologically fertile offspring for F1 and F2 hybrids, but offspring remain behaviourally isolated from other hybrids and both parent species (Stratton & Uetz 1986).

Behavioural Tests

Subjects and housing

We collected immature spiders at two sites in southwestern Ohio during November 1992, and May and November 1993. *Schizocosa ocreata* were collected at the Cincinnati Nature Center, Clermont County, and *S. rovneri* were collected from Burnet Woods Park in the city of Cincinnati, Hamilton County. Spiders were raised to maturity in individual opaque plastic containers measuring 12 cm in diameter, 4 cm high and with a moistened plaster of Paris substrate to maintain humidity. Spiders received a diet of first or second instar crickets every two days (and on the day before testing) and water ad libitum, and were

kept at approximately 25°C under a 13:11 h light:dark photoperiod. We selected mature females (*S. ocreata*: $N=24$, *S. rovneri*: $N=20$) at random from the field-collected, laboratory-reared spiders. Testing began between 21 and 35 days after their final moult, and finished 12 days later.

Preparation and presentation of video stimuli

We videotaped courting male spiders with a JVC GX-N8 camera and JVC HRS-101 VHS video recorder. Images were digitized on to an AMIGA 2000HD computer using a Frame Grabber-Real Time Video Image Digitizer (Progressive Peripherals and Software). We used a digital paint and animation program (Deluxe Paint III; Electronic Arts) to manipulate images of male spiders. We manipulated the presence or absence of tufts and tuft size using this computer animation technique, while holding the behaviour of the 'video male' constant (see Clark & Uetz 1990, 1992, 1993). We used the following five male video stimuli: (1) control *S. ocreata* male, (2) *S. ocreata* male with tufts removed, (3) *S. ocreata* male with tuft area enlarged by approximately 25% from the control *S. ocreata* male, (4) control *S. rovneri* male and (5) *S. rovneri* male with tufts typical of *S. ocreata* added. In addition, we used a blank screen stimulus as a control to rule out the possibility that females were responding to the video monitor alone. Blank screen stimuli showed the same light grey background used for video male stimuli.

Female spiders were presented with video stimuli in an experimental apparatus consisting of a transparent plastic arena attached to a Sony Watchman (Model FDL-310) LCD microscreen television (5-cm diagonal screen) so that the television was level with the bottom of the arena. This clear plastic arena (15.5 cm diameter, 6.5 cm high) enclosed a circular area covered with filter paper upon which the female moved about freely. The entire apparatus was placed on foam blocks upon a 70 cm high table to reduce incidental vibratory stimuli. Evidence suggests that females respond to video males and live males with the same frequency (G. W. Uetz, unpublished data).

We placed females in the experimental apparatus and allowed them to acclimate for 2 min. This acclimation period sufficiently reduced female agitation due to transfer to the experimen-

tal apparatus. An opaque barrier was raised, exposing the Watchman screen, which displayed a video of a courting male spider. Trials lasted 6 min, during which we videotaped the female's behaviour so that we could analyse female sexual receptivity in response to the video stimulus in greater detail. Females were videotaped with a JVC GX-N8 camera and JVC HRS-101 VHS video recorder, and tapes were viewed on a Sony Trinitron 33 cm TV monitor. We removed the filter paper and cleaned the arena with alcohol and a cotton swab between each trial to remove any silk and/or pheromones left from the previous test subject. All females were shown each of the six video stimuli in a randomized order.

Tests for habituation/priming in response of females to video stimuli

Repeated presentation of video stimuli to females over time may contribute to an increased or decreased level of response. If females habituated over time in response to video stimuli, we expected the proportion of receptive females to decrease over time. On the other hand, if female receptivity was primed in response to repeated viewing of video stimuli, we expected the proportion of receptive females to increase over time. The randomized presentation of videos controlled for any habituation or priming effect that females may have shown in response to stimuli over the 12-day test period.

To test directly whether females showed habituation or priming, we showed an independent set of *S. ocreata* females ($N=17$) the same *S. ocreata* control male video stimulus over a 4-day period. Trials lasted 10 min, during which we videotaped the behaviour of the female for future analysis.

Tests with live males with varying tuft size

To examine the effects of tuft size on female receptivity, we divided male *S. ocreata* into three groups based on small ($<3.3 \text{ mm}^2$, $N=14$), medium ($3.4\text{--}3.8 \text{ mm}^2$, $N=10$) or large ($>3.9 \text{ mm}^2$, $N=10$) size tufts. Tuft sizes were arbitrarily divided based on total tuft area (tuft height \times length of the tibia). Males were placed in a rectangular box ($12 \times 6 \times 6 \text{ cm}$) made of clear acetate. Female *S. ocreata* were placed in an identical rectangular box situated adjacent to the box housing the male. The boxes housing the male

and female were mounted on separate 10-cm stacks of foam rubber spaced approximately 5 mm apart to prevent the transmission of vibratory signals between spiders. Trials lasted 6 min, during which the female was videotaped for subsequent analysis of receptivity behaviours.

Description of behavioural parameters

We measured three female response variables for each trial: (1) presence or absence of receptivity shown by the female (in trials using live males, this was the only parameter measured), (2) a scored response based on recognition, aggression and receptivity behaviours, and (3) the latency of response based on time elapsed after initial orientation to the stimulus (indicated by swivel or movement towards the screen) until receptivity behaviours were seen. The receptivity displays for females of both species are identical and clearly distinct from other visually-mediated behaviours, and are only seen in response to conspecific males (Stratton & Uetz 1981, 1983, 1986).

We considered females to be sexually receptive and scored them as positive only if they displayed one of the following sexual receptivity displays (Montgomery 1903; Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983): (1) slow turn: turn 90° to 180°, (2) settle: lower abdomen and cephalothorax to the substratum, (3) lower cephalothorax/raise abdomen, (4) leg extend: extend forelegs. Female receptivity behaviours may be given in sequence (Stratton & Uetz 1983) or individually (Scheffer et al. 1996), either of which can lead to the male mounting the female. Moreover, females usually will not mate until they show such behaviour patterns (Scheffer et al. 1996). When displayed, receptivity is usually seen within 3–4 minutes; mounting by the male follows immediately.

Females were given a score of 0–3, representing levels of increased receptivity (Table I). We did not use this score for the independent set of female *S. ocreata* used to test for a habituation/priming response; rather, we determined sexual receptivity in these females strictly based on the presence or absence of any of the four receptivity behaviours.

We determined latency of response for females in response to video stimuli (but not for live males). Latency was determined as the time between the first orientation to the video stimulus and the time we observed the first receptivity

Table I. Behaviour patterns of female *S. ocreata* in response to male courtship (after first orientation)

Behaviour pattern	Score
No response	0
Lunge at male (predation)	0
Tandem leg raise (aggressive display)	0
Orient toward male	1
Approach male	1
Follow male	1
Leg touch/tap	2
Stagger walk	2
Slow turn	3*
Settle	3*
Leg extend	3*
Lower cephalothorax/raise abdomen	3*

*Copulation usually occurs only after one of the 'level 3' behaviour patterns is shown (Montgomery 1903; Uetz & Denterlein 1979; Scheffer et al. 1996).

display. For the analysis of latency of response, we only used females that displayed receptivity within the 6-min trial period were used.

Phylogenetic Test

The test presented here examined a hypothetical phylogenetic relationship between wolf spiders within the genus *Schizocosa*. In particular, we focused on the *ocreata* group, thought to be the most basal clade within the genus *Schizocosa* (G. E. Stratton, personal communication) to which both *S. ocreata* and *S. rovneri* belong. The presence or absence of tufts was mapped onto the resulting cladogram to determine polarity for that character.

Choice of taxa

The genus *Schizocosa* consists of more than 20 species (Dondale & Redner 1978), characterized by their medium to large body size and strong legs. *Schizocosa ocreata* and *S. rovneri* are found within the *ocreata* group, which is characterized by a long distal process on the palpa of the male palp. The six species described and included in this analysis were *S. ocreata* (Hentz), *S. rovneri* Uetz and Dondale, *S. crassipes* Walckenaer, *S. floridana* Bryant, *S. stridulans* Stratton, and *S. sp. 'a'* (G. E. Stratton, personal communication). In addition, we chose *Pardosa milvina* for the outgroup to polarize characters used to

Table II. Morphological characters used to construct cladogram

Adult male characters

- 1 Lines on chelicerae: present: 1; absent: 0.
- 2 Submarginal band on carapace present: 1, absent: 0.
- 3 Colour of sternum: yellow-brown: 2; yellow: 1; orange-red: 0.
- 4 Brush (tuft) on femur of leg I: brush: 1; no brush: 0.*
- 5 Cardiac mark on dorsal abdomen: present: 1, absent: 0.
- 6 Chevrons on dorsal abdomen: present: 1, absent: 0.
- 7 Spots on ventral abdomen: present: 1, absent: 0.
- 8 Terminal macrosetae on cymbium of palpus: present: 1, absent: 0.
- 9 Embolus concealed: yes: 1; no: 0.
- 10 Colour on femurs II–IV: yellow: 0; light brown: 1; dark brown: 2.
- 11 Pigment on femur I: none: 0; half leg—wash: 1; whole leg—variable: 2; whole leg—wash: 3.
- 12 Annulations on femur I: present: 1, absent: 0.
- 13 Colour on femur I: yellow: 0; light brown: 1; dark brown: 2.

Adult female characters

- 14 Atrium of epigynum deep: yes: 1; no: 0.
- 15 Epigynum transverse piece with excavations meeting at the midline: yes: 2; almost: 1; no: 0.
- 16 Spermathecae with blunt prominence: yes: 1; no: 0.

*Character omitted from phylogenetic analysis and later mapped onto the resulting tree.

Table III. Character state matrix for characters described in Table II

Taxon	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>S. ocreata</i>	1	0	0	1	1	0	1	1	1	2	3	0	2	0	2	1
<i>S. crassipes</i>	1	1	1	1	0	1	1	1	0	1	3	1	1	1	0	1
<i>S. floridana</i>	1	1	1	0	1	1	1	0	0	2	0	1	2	0	1	1
<i>S. rovneri</i>	0	1	0	0	0	0	0	1	1	0	0	1	0	0	2	0
<i>S. stridulans</i>	0	1	2	0	1	0	0	0	1	0	3	0	0	1	2	0
<i>S. sp. 'a'</i>	1	1	2	0	1	0	1	1	0	0	1	1	0	1	2	?
<i>P. milvina</i>	0*	0*	1	0	0	0	1	0	0	0	?	0	0	0	1*	0

*Indicates when character was confirmed by personal observation.

construct the cladogram. Both *Pardosa* and *Schizocosa* belong to the family Lycosidae, with *Pardosa* appearing basal to *Schizocosa* (Dondale 1986). Because this sample does not include all of the species in the clade, or the genus itself, this should not be considered the definitive phylogeny but rather a preliminary analysis of the evolutionary relationships between these species.

Choice of characters

We took 16 morphological characters of adult spiders (Table II) from published descriptions of the above species (Dondale & Redner 1978, 1984; Uetz & Dondale 1979; Stratton 1991). We

confirmed some characters for *P. milvina* by direct observation (Table III) of specimens collected in Burnet Woods Park, Hamilton County, in southwestern Ohio during spring 1994. To avoid circularity, we omitted the characters of interest (tufts) from cladistic analysis (e.g. Proctor 1992) and only used them for mapping once the cladistic analysis was complete.

Construction of cladograms

Characters from Table II were analysed using PAUP 3.1 (Swofford 1991). We gave all characters equal weight, and all characters except character 15 were unordered. Once the most parsimonious tree had been identified from an exhaustive

Table IV. Analysis of variance of female *Schizocosa* response to video stimuli (based on 0–3 score)

Test	Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
1	Species	1	0.092	0.07	>0.05
	Stimulus	5	26.906	25.35	<0.001
	Species*stimulus	5	0.755	0.72	>0.50
	Individual (Species)	42	1.295	Cannot test	—
	Individual*stimulus (Species)	210	1.045	Cannot test	—
2	Stimulus	5	16.313	15.26	<0.001
	Error	115	1.069		
3	Stimulus	5	11.748	11.58	<0.001
	Error	95	1.015		

Test 1: Three-way mixed model nested ANOVA of female *Schizocosa* response.

Test 2: One-way repeated measures ANOVA of female *S. ocreata* response.

Test 3: One-way repeated measures ANOVA of female *S. rovnneri* response.

search, we used MacClade (Maddison & Maddison 1992) for mapping the character of interest (tufts) onto the resultant tree.

The amount of homoplasy is reflected in the consistency index, which is a ratio of the minimum possible number of steps on a given tree to the actual number of steps. If the consistency index is equal to 1.0, there is no homoplasy. The further the consistency index is from 1.0, the greater the number of parallelisms and reversals.

The phylogeny presented here uses morphological data to illustrate hypothetical phylogenetic relationships between the spiders in the *ocreata* group. Many of the characters used are variable within species, however, as is common for many morphological characters in spiders (Dondale & Redner 1978). Therefore, this preliminary cladogram should be used with caution when interpreting the order in which tufts and preferences evolved. Currently, a phylogeny based on mitochondrial DNA sequences of spiders in the *ocreata* clade is being constructed. Molecular data of this type has been particularly useful in testing hypotheses of sensory bias in recent studies (Ryan & Rand 1993).

RESULTS

Habituation/Priming Behaviour

Females did not appear to show habituation or priming in their response to video stimuli. When the same *S. ocreata* control male video stimulus was shown to *S. ocreata* females ($N=17$) once a

day over a 4-day period, the proportion of females displaying sexual receptivity ranged from 0.50 to 0.70, and was not significantly different from day to day (Cochran's Q -test, $Q=1.71$, $df=3$; $P>0.50$). Therefore, a female's response to a video stimulus is independent of the number of stimuli she has viewed previously.

Species Differences in Response

We used a three-way mixed model nested ANOVA to analyse the level of female *S. ocreata* and *S. rovnneri* receptivity in response to male video stimuli. We tested the primary parameter, receptivity level (score), using species (fixed), individual (random, nested within species) and male video stimulus (fixed) as categorical variables. F -values were calculated using the appropriate three-way mixed model nested design (Scheffé 1959). Results from the three-way mixed model nested ANOVA indicate a significant effect of video stimuli on female response ($F_{5,210}=25.35$, $P<0.001$) but no significant difference between species in responses to video stimuli ($F_{1,42}=0.0711$, $P>0.50$; Table IV). Because individual female spiders were shown all six video stimuli one time each in random order, individual effects could not be tested due to a lack of replication. Post-hoc analyses could not be performed due to the nature of the repeated measures ANOVAs, so we analysed differences in response across video stimuli within each species. We used two separate one-way repeated measures ANOVAs for female *S. ocreata* and *S. rovnneri* where the level of receptivity was the primary parameter and video

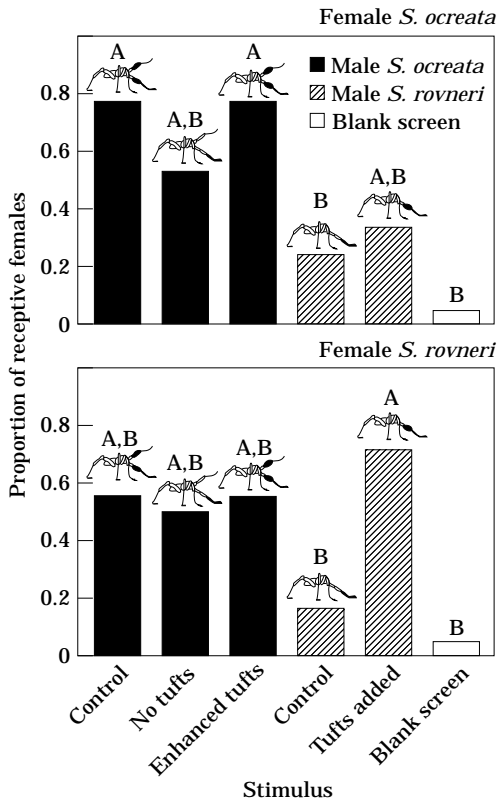


Figure 1. Proportion of female *Schizocosa ocreata* ($N=21$) and *S. rovneri* ($N=18$) displaying sexual receptivity in response to male video stimuli. Shared letters indicate no significant difference between stimuli.

stimulus was the categorical variable. Results are reported separately below.

Female *S. ocreata* Response

Receptivity of female *S. ocreata* measured as the presence or absence of one of the four level-3 sexual receptivity displays (Table I), was not independent of video stimulus (Cochran’s Q -test, $Q=32.7$, $df=5$; $P<0.05$). The proportion of females ($N=21$) displaying receptivity varied significantly across video stimuli (Fig. 1). A high proportion (76.2%) of females showed sexual receptivity to *S. ocreata* control males and *S. ocreata* males with enhanced tufts. Pair-wise comparisons between stimuli (Marascuilo & McSweeney 1967) showed that the proportion of females that displayed receptivity was significantly higher with the *S. ocreata* control male than with

the *S. rovneri* control male ($S=3.28$, $P<0.05$) and the blank screen ($S=4.48$, $P<0.01$; Fig. 1). Additional pair-wise comparisons showed that female *S. ocreata* responses to other stimuli were intermediate, however, and not significantly different from either extreme; i.e., receptivity range differences overlapped between control *S. ocreata* male, the *S. ocreata* male with tufts removed, and the *S. rovneri* male with tufts added. These data suggest a trend (Fig. 1): female *S. ocreata* displayed sexual receptivity most often to males with tufts and species-typical leg waving displays (control conspecific males and conspecific males with enhanced tufts), less often to males with species-typical displays but without tufts (male *S. ocreata* with tufts removed) or males with tufts but lacking species-typical leg waving displays, and least often to males without tufts or species-typical leg waving displays (control heterospecific males).

The level of receptivity of female *S. ocreata* assessed on the basis of scores, also varied significantly across video stimuli (one-way ANOVA $F_{5,138}=15.121$, $P<0.0001$) (Table V). In post-hoc analysis of receptivity score data (Tukey post-hoc comparison of means test), receptivity of female *S. ocreata* in response to all conspecific male stimuli was significantly higher than to the heterospecific male control. Responses of female *S. ocreata* to video *S. rovneri* males with tufts added were intermediate, however, and not significantly different from the others (Fig. 2). Differences between the responses of females to all video stimuli versus the blank screen were significant ($P<0.001$; Fig. 2, Table V).

Female receptivity in response to live males (with small, medium and large size tufts) was not independent of tuft size ($\chi^2=11.76$, $P<0.01$). Subsequent testing revealed that the proportion of female *S. ocreata* ($N=31$) that displayed sexual receptivity to male *S. ocreata* with small tufts (42%) was significantly less than the proportion that displayed receptivity to males in the other categories (medium tufts=90%, large tufts=100%) which were not significantly different from each other. These data suggest that tuft size may be important in female mate choice as well as species recognition.

In contrast to the other response variables measured, the latency of the receptivity response for female *S. ocreata* did not vary significantly across video stimuli ($F_{5,51}=0.668$, $P=0.649$;

Table V. One-way analysis of variance of female response to male video stimuli based on 0–3 score and latency of response

Dependent variable	Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Female <i>S. ocreata</i>					
0–3 score	Stimulus	5	16.31	15.121	<0.001
	Error	138	1.08		
Latency of response	Stimulus	5	7569	0.668	0.649
	Error	51	11 326		
Female <i>S. rovneri</i>					
0–3 score	Stimulus	5	11.348	10.4	<0.001
	Error	114	1.095		
Latency of response	Stimulus	5	6264	1.1	0.396
	Error	42	5905		

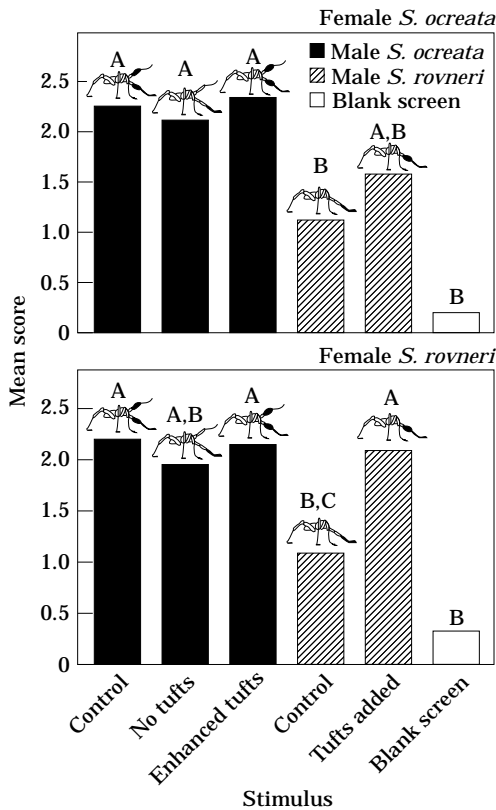
**Figure 2.** Mean sexual receptivity level (score) in female *S. ocreata* ($N=24$) and *S. rovneri* ($N=20$) in response to male video stimuli. Shared letters indicate no significant difference between stimuli.

Table V, Fig. 3). Latency was not measured in trials with live males, as it had previously been determined this was an uninformative measure.

Female *S. rovneri* Response

Receptivity of female *S. rovneri* ($N=18$), based on the presence or absence of one of the four sexual receptivity displays, was not independent of video stimulus (Cochran's Q -test: $Q=24.167$, $df=5$, $P<0.01$; Fig. 1). Pair-wise comparisons between stimuli showed that the proportion of females that displayed receptivity was significantly higher to the *S. rovneri* male with tufts added than to the *S. rovneri* control male and the blank screen. Females oriented to these video images with equal frequency, indicating that movements of the stationary *S. rovneri* male were detected, but receptivity displays were given more often in response to male *S. rovneri* with tufts added. Additional pair-wise comparisons showed that female *S. rovneri* responses to heterospecific male stimuli (male *S. ocreata* with tufts removed; control male *S. ocreata*; male *S. ocreata* with enhanced tufts) were intermediate, but not significantly different from the other stimuli.

Results from the one-way ANOVA indicate that female *S. rovneri* receptivity level (score) varied significantly across video stimuli (Table V). Results of post-hoc analyses (Tukey post-hoc comparison of means test) suggest a trend, but are difficult to interpret. Response scores for the *S. rovneri* male with tufts added were significantly higher than those for the *S. rovneri* control ($P<0.01$). In addition, significant differences in response ($P<0.05$) were found between the *S. rovneri* control male and two of the heterospecific male stimuli (both the *S. ocreata* control and the male *S. ocreata* with enhanced tufts elicited a higher level of receptivity). Significance levels overlapped, however, between the *S. rovneri*

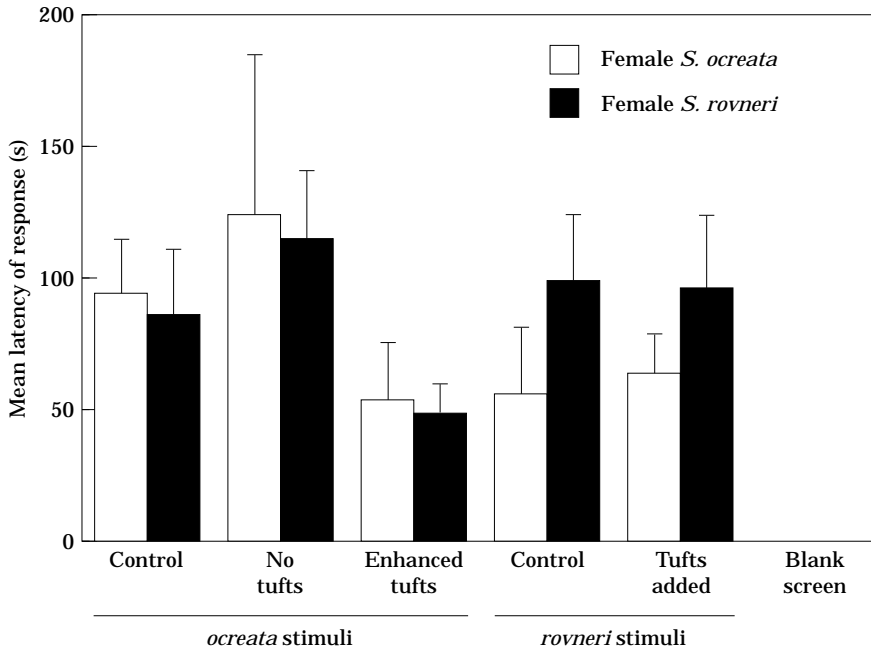


Figure 3. Mean \pm SE latency of response to male video stimuli for female *S. ocreata* ($F_{5,51}=0.668$, $P=0.649$) and female *S. rovneri* ($F_{5,42}=1.061$, $P=0.396$).

control male and the *S. ocreata* male with tufts removed, as well as between the *S. rovneri* control male and the blank screen (Fig. 2). Despite these overlapping ranges, the data suggest a trend towards a higher level of response in female *S. rovneri* when the male stimulus includes a more obvious visual signal (either tufts or heterospecific active leg waving display).

As with female *S. ocreata*, the latency of receptivity response for female *S. rovneri* did not vary significantly across video stimuli ($F_{5,42}=1.061$, $P=0.396$; Table V, Fig. 3).

Phylogenetic Tests

Analysis yielded five equally parsimonious trees with a total length of 34 and a consistency index of 0.588, suggesting that some homoplasies exist. These trees were used to calculate a strict consensus tree (Sokal & Rohlf 1981) containing only those monophyletic groups common to all trees (Fig. 4). In all of these trees, the phylogenetic position of *S. rovneri* is basal to *S. ocreata*. Mapping the character 'tufts' onto the consensus tree (Fig. 4) suggests that tufts are a derived character in the *ocreata* clade. The results are equivocal

however; the number of times that tufts have evolved is uncertain. Tufts may have evolved twice independently within the *ocreata* clade: once in *S. crassipes* and again in *S. ocreata* (Fig. 4a). On the other hand, tufts may have evolved only once in the ancestor common to *S. ocreata* and *S. crassipes* (Fig. 4b), and were secondarily lost in *S. floridana*.

DISCUSSION

Results of these studies show that female wolf spiders respond differently to various manipulated video images of males. It is not surprising that *S. ocreata* females show receptivity more frequently to conspecifics (with species-typical appearance and behaviour) and far less to heterospecifics. Even though the visual signal most likely to elicit receptivity is one that incorporates tufts and species-typical leg waving displays together (i.e., a conspecific), however, manipulation of a single component (the tufts) may change the level of female response. The reduced (although overlapping in statistical significance) levels of response seen in female *S. ocreata* shown altered

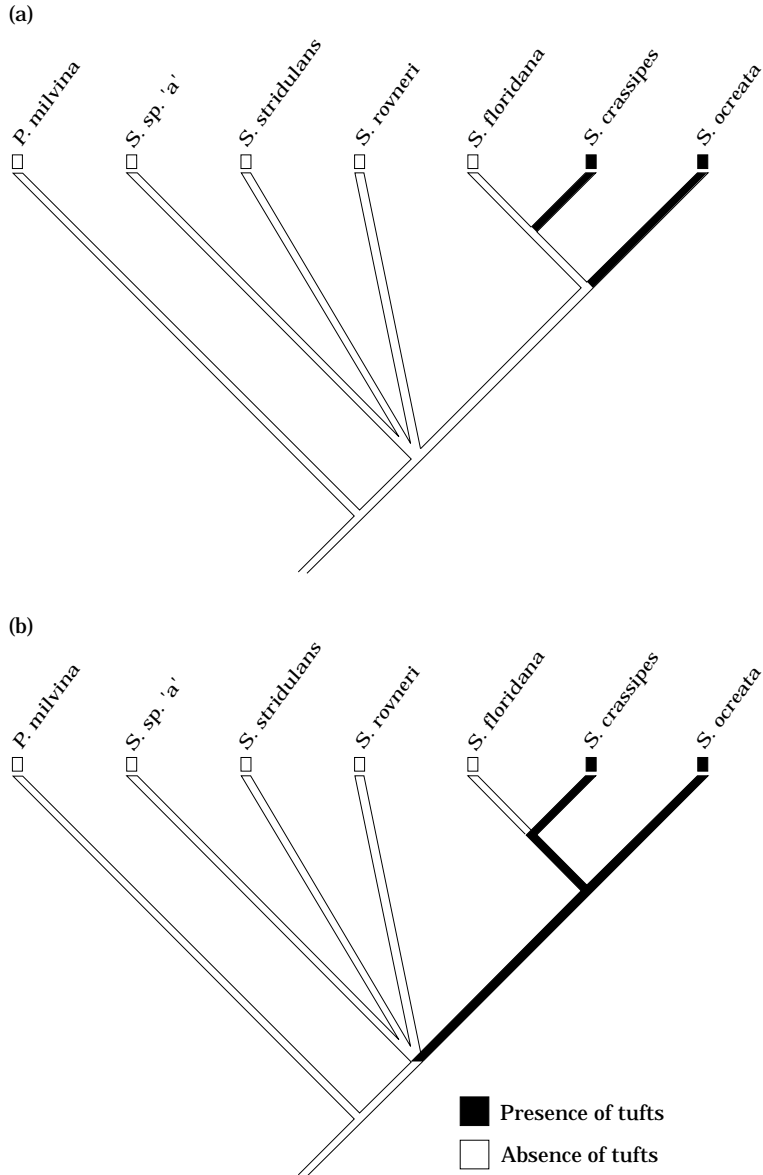


Figure 4. Cladogram of the consensus tree derived from five equally parsimonious trees (length: 31; consistency index: 0.581). The morphological character state for 'tufts' is overlaid on the cladogram. Tufts may have evolved twice independently (a) or may have evolved once and been subsequently lost in *S. floridana* (b).

video images of conspecific and hetero-specific males (i.e. removal of foreleg tufts from a conspecific male and/or addition to a hetero-specific male) suggests that the presence or absence of either tufts or species-typical leg waving displays affects mate recognition. In contrast, responses of female *S. rovnerei* to male video

stimuli suggest that the visual stimuli most likely to elicit a receptive response were conspecific males with (heterospecific) tufts added, or hetero-specific males (with tufts and active leg-waving displays). These results raise several questions about the evolution of decorative foreleg tufts and their role in mate recognition and female choice:

have tufts evolved as a means of increasing signal efficacy (Guilford & Dawkins 1991)? Is this a case of pre-existing bias (Basolo 1990, 1995b) for a conspicuous visual character? What role do tufts play in female mate choice?

Signal Efficacy

Signal efficacy, or the 'tactical design' of signals (Guilford & Dawkins 1991) depends on signal structure. Signals that are more effectively transmitted and received within the constraints of the natural microhabitat will have a natural selective advantage over those signals that are not. If natural selection influences courtship displays, we would expect differences in courtship signals of male *S. ocreata* and *S. rovneri* to reflect differences in habitats, microhabitat structure, or some other factor which influences signal transmission and/or detection.

The modes of communication most commonly used by lycosid spiders during courtship include visual and vibratory signals. Males use percussion or stridulation to produce substratum-coupled vibrations (Rovner 1967, 1975; Uetz & Stratton 1982). Females detect these vibrations via slit sensillae, vibration-sensitive receptors located on the metatarsal and pretarsal portions of the leg (Barth 1982). The visual system of lycosid spiders is also fairly acute (Land 1985), and visual signals are common in the courtship behaviour of many species (Hollander & Dijkstra 1974). Scheffer et al. (1996) demonstrated differences between these two *Schizocosa* species in the relative importance of visual and vibratory cues during courtship. They found in female *S. ocreata* that male visual or vibratory cues were each alone sufficient to elicit receptivity, but only vibratory cues from males (alone or in combination with visual cues) elicited receptivity in *S. rovneri*.

Differences between these species' courtship displays (Stratton & Uetz 1981, 1983, 1986) correspond to differences in microhabitat structure, and may reflect evolution of communication mechanisms under different environmental constraints (Uetz 1991; Scheffer et al. 1996). *S. ocreata* is found in areas with complex deciduous litter, which attenuates substratum-borne vibrations so rapidly that male vibrations could not be detected beyond the leaf upon which the spider was courting (Scheffer et al. 1996). In contrast, *S. rovneri* are found in the compressed

leaf litter microhabitat of floodplain forests, which does not attenuate vibration as much as complex litter (Uetz 1991; Scheffer et al. 1996). Moreover, when tested in this microhabitat, the somewhat louder vibratory courtship signals of male *S. rovneri* could be detected at a significantly greater distance (50 cm) than the vibratory signals of male *S. ocreata* (<20 cm; Scheffer et al. 1996).

The results cited above suggest that in the field, male *S. ocreata* vibratory courtship signals attenuate more rapidly than *S. rovneri* signals, due to the nature of the signal itself and the microhabitat in which it is generated. Since the visual range for female *S. ocreata* (35–40 cm) exceeds the distance which vibrations can travel in their normal microhabitat, males can be seen at a distance greater than they can be heard (Rennecker, Valerius & G. W. Uetz, unpublished data). Because males are potentially subject to cannibalism by females, natural selection will favour males that can signal their identity and intent to mate at a distance, thereby reducing their chances of being consumed as prey. In a sound-dampening environment like that of *S. ocreata* visual signals may be more likely to reach the receiver, and therefore will be selectively advantageous. A display incorporating the waving of conspicuously decorated forelegs may increase detectability of the male by the female and enhance species recognition. Scheffer et al. (1996) found that in the absence of vibratory communication, female *S. ocreata* showed less sexual receptivity to shaved males (tufts removed) than to intact males, suggesting that tufts represent a visual signal that may be important in species recognition and/or female choice. Although the authors found no behavioural differences between shaved and intact males, however, slight differences in behaviour patterns of males as a result of the experimental procedure may have contributed to lowered female receptivity.

Use of video stimuli allows further testing of the hypothesis that tufts have evolved as a means of increasing the efficacy of the highly visual leg waving display in male *S. ocreata* courtship, by altering components of visual displays while controlling for behaviour. Because female *S. ocreata* respond maximally to video male stimuli of conspecifics with tufts, and response decreases when tufts are removed (in live spiders or video stimuli) or when species-typical leg waving displays are absent (in heterospecific males), both leg-waving

displays and tufts together appear essential for species recognition. The addition of tufts to the male *S. rovneri* stimulus, however, is not enough to elicit more receptivity from female *S. ocreata* than does the heterospecific control male (which lacks tufts and leg-waving displays). Likewise, female *S. ocreata* receptivity levels decrease when tufts are removed from the conspecific male stimulus (which has leg-waving displays). Therefore, tufts alone are not a necessary species recognition cue, and must be considered an amplifier (Hasson 1991) that increases efficacy of the species-typical leg waving display.

Female Choice

Although female *S. ocreata* prefer males with tufts over those without, results are less clear with respect to the role of the tufts in female mate choice. In experiments with live males, female *S. ocreata* receptivity varies significantly with tuft size, but this result is largely due to reduced receptivity to males with small tufts. Responses to video males with enhanced tufts are not significantly greater (Figs 2, 3), which suggests that larger male tuft size may not be important in female choice. If females are receptive less often to males with small tufts, the same might be expected for video males with reduced tuft size. We created all video stimuli from the same male, however, and made no attempt to test the effect of reduced tuft size on female choice. Because natural variation in tuft size and other characteristics may influence female choice, selection of the template male may have biased the results of video playback experiments (Kroodsma 1989). Another possibility is that female preferences may be influenced by display rates, which are controlled in the video image studies, but not in studies with live males (display rate and tuft size may be correlated). To test for the influence of these factors, one needs to show females video images of several males that display at different rates with digitally reduced or enhanced tufts and measure their response. Such a test may provide a more accurate assessment of the role of tufts in female choice.

Although female *S. ocreata* receptivity may be strongest in response to males with both tufts and leg-waving displays, further testing is needed before any strong conclusions are drawn regarding the importance of these cues in female choice.

For example, a more direct test of female response to these characters would be to present female *S. ocreata* with conspecific males without tufts and leg waving, and a heterospecific male with both tufts and leg waving. Indeed, female *S. ocreata* showed significantly less sexual receptivity to heterospecific males which lack both tufts and leg waving (Figs 1, 2) but this decrease in receptivity may be due in part to other aspects of the display not considered (e.g. the spider's gait while walking).

Have Tufts Evolved via a Pre-existing Bias?

Perhaps the most striking finding of this research is that a high proportion of female *S. rovneri* show receptivity to conspecific males with tufts added, and to heterospecific males with or without tufts (but with species-specific active leg waving displays), even though these tufts are lacking in conspecific males. Could this finding be evidence of a pre-existing bias for a visual character? Pre-existing bias models suggest that male courtship displays and secondary sexual characters may evolve to maximally stimulate pre-existing female sensory and/or cognitive systems (Endler & McLellan 1988; Ryan et al. 1990; Basolo 1990a, b, 1995a, b; Endler 1992b; Proctor 1992; Ryan 1994). Several recent studies have demonstrated the existence of a preference for a male morphological or behavioural character in species lacking such characters (e.g. the sword in swordtails: Basolo 1990a, b, or male vibrating displays in water mites; Proctor 1992). If tufts in *S. ocreata* are a derived character and their absence in *S. rovneri* is typical of the ancestral condition, then a case could be made for their evolution on the basis of a pre-existing bias.

The preliminary phylogenetic analysis provided here suggests that tufts are a derived character in the *ocreata* clade that has either evolved once and has been secondarily lost in *S. floridana* (Fig. 4b), or has evolved independently twice in *S. ocreata* and *S. crassipes* (Fig. 4a). In either case, *S. rovneri* is in a position basal to the species with tufts. This phylogeny must be interpreted with caution, because it is a strict consensus tree derived from five equally parsimonious trees (but in all of these equally parsimonious trees, *S. rovneri* is basal to *S. ocreata*). Since female *S. rovneri* prefer males with tufts, the female preference for tufts appears to be the ancestral state. It is uncertain, however,

whether female preference has evolved because tufts (1) are novel, (2) stimulate more photoreceptors and therefore are perceived as a stronger stimulus and/or (3) stimulate a specific pre-existing bias for tufts. This issue may be resolved by determining the relative likelihood of two independent gains of tufts (Fig. 4a) versus a single gain and a single subsequent loss (Fig. 4b). The Dollo parsimony model (Farris 1977) suggests that a single gain and subsequent loss of a given character is more likely than two independent gains because losses are 'easier' than gains. Under this model, the order of character evolution in Fig. 4b is more likely; tufts evolved once and were subsequently lost in *S. floridana*. The preference for tufted males in female *S. rovneri* may therefore be a preference for a novel trait, rather than a pre-existing bias. On the other hand, the Fitch and Wagner parsimony models (Swofford & Olson 1990) assume that two independent gains are equally likely to occur as are a single gain and independent loss. Under this model, the order of character evolution in either Fig. 4a or b is equally likely. Female *S. rovneri* preference may be directionally biased and/or simply a response to novelty. To answer the question of pre-existing bias or preference for novelty, additional phylogenetic analysis of more species is required.

At first, these data may appear to conflict with earlier studies (Stratton & Uetz 1981, 1983, 1986) which show that female *S. rovneri* show sexual receptivity to conspecific males only, and that visual cues are unimportant (Scheffer et al. 1996). In these studies, however, all heterospecific pairings were conducted in arenas which permitted transmission of vibratory information. The present study was conducted in the absence of sound, so female response was based on the visual cues alone. This difference suggests that in the absence of sound, female *S. rovneri* may be prone to making a reproductive mistake by mating with a heterospecific male with the preferred visual stimulus including tufts and leg waving. Given these results, we might expect to find hybrid zones where both species are in typical *S. ocreata* (e.g. sound-dampening) environments, but such hybrid zones have not been found. Moreover, in circumstances where sound transmission is permitted, as in typical *S. rovneri* microhabitat, only males with the appropriate species-specific vibratory signal will elicit female receptivity (Stratton & Uetz 1983). Given that female *S. rovneri* respond to

males with tufts and/or leg waving displays, why don't male *S. rovneri* possess such characters? If the microhabitat of *S. rovneri* transmits vibrations over relatively long distances (Scheffer et al. 1996), then selection would favour males with loud stridulation rather than visual displays that might attract predators. In addition, males would not be expected to evolve alternatives to vibratory displays unless vibratory displays were ineffective.

Conclusions

This study suggests that mate recognition and female choice in *S. ocreata* depends on the presence of tufts and leg-waving displays in males. The several models proposed here (species recognition, female choice, signal efficacy and pre-existing bias) are not mutually exclusive, nor are they easy to refute completely. At the very least, we suggest that there is strong evidence that tufts have evolved as a means of amplifying or increasing the efficacy of male courtship display in an environment that constrains vibratory communication. This is consistent with current hypotheses based on signal-receiver psychology (Guilford & Dawkins 1992; Endler 1993; Hasson 1993). Tufted males with leg waving displays (in the case of *S. ocreata*) and/or without leg waving displays (in the case of *S. rovneri*) may incur a mating advantage if courting in microhabitats which dampen vibratory communication. However, it is also possible that female preference for tufts may have evolved prior to the tufts themselves, because female *S. rovneri* a primitive species within the *ocreated* group, prefer males with tufts. Further research will be required before a definitive mechanism for evolution of decorative leg tufts and leg-waving displays can be accepted.

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