

Article

Male courtship signal modality and female mate preference in the wolf spider *Schizocosa ocreata*: results of digital multimodal playback studies

Elizabeth C. KOZAK and George W. UETZ*

Department of Biological Sciences, University of Cincinnati, Cincinnati, OH, P.O. Box 260006, USA, 45221-0006

*Address correspondence to George W. Uetz. E-mail: george.uetz@uc.edu

Handling editor: Zhi-Yun Jia

Received on 15 December 2018; accepted on 7 May 2019

Abstract

Females must be able to perceive and assess male signals, especially when they occur simultaneously with those of other males. Previous studies show female *Schizocosa ocreata* wolf spiders display receptivity to isolated visual or vibratory courtship signals, but increased receptivity to multimodal courtship. It is unknown whether this is true when females are presented with a choice between simultaneous multimodal and isolated unimodal male courtship. We used digital playback to present females with a choice simulating simultaneous male courtship in different sensory modes without variation in information content: 1) isolated unimodal visual versus vibratory signals; 2) multimodal versus vibratory signals; and 3) multimodal versus visual signals. When choosing between isolated unimodal signals (visual or vibratory), there were no significant differences in orientation latency and number of orientations, approaches or receptive displays directed to either signal. When given a choice between multimodal versus vibratory-only male courtship signals, females were more likely to orient to the multimodal stimulus, and directed significantly more orients, approaches and receptivity behaviors to the multimodal signal. When presented with a choice between multimodal and visual-only signals, there were significantly more orients and approaches to the multimodal signal, but no significant difference in female receptivity. Results suggest that signal modes are redundant and equivalent in terms of qualitative responses, but when combined, multimodal signals quantitatively enhance detection and/or reception. This study confirms the value of testing preference behavior using a choice paradigm, as female preferences may depend on the context (e.g., environmental context and social context) in which they are presented with male signals.

Key words: mate choice, multimodal communication, *Schizocosa*, signaling, wolf spider

Female mate preferences may differ or change depending on the social or environmental context in which females perceive male courtship signals (Wagner 1998; Bateson and Healy 2005; Stafstrom and Hebets 2013; Hebets et al. 2016; Uetz et al. 2017). In particular, there are many species where females must respond to multiple males courting simultaneously (e.g., leks, choruses, skewed sex ratios, and high density populations). Animal communication,

especially in the context of courtship displays, often utilizes multiple sensory modalities (acoustic, visual, chemical, and vibratory). In social contexts in which there might be multiple males courting, a unimodal versus multimodal signal may be more or less easily detected or interpreted within a complex environment (Taylor and Ryan 2013), and mating decisions become even more complex when there is microhabitat variation that might affect the proper transmission

of multimodal signals (Uetz et al. 2013). For example, a female might be able to perceive a multimodal signal of 1 individual, yet receive a unimodal signal from another male due to the microhabitat blocking transmission of the full multimodal signal (Uetz et al. 2013).

Studies in the past 2 decades have used experimental techniques, including digital visual and acoustic playback, to examine the function and form of multimodal signals across animal taxa (anurans: Taylor et al. 2007; lizards: Woo et al. 2017, Gunderson et al. 2018; bowerbirds: Doucet and Montgomerie 2003; fish: Hankison and Morris 2003, Hiermes et al. 2016, Balzarini et al. 2017; spiders: Scheffer et al. 1996; Hebets and Uetz 1999, 2000; Elias et al. 2005, 2010; Uetz et al. 2009; Wilgers and Hebets 2011; Hebets et al. 2013). Since its earliest uses (Clark and Uetz 1990, 1992, 1993; Evans and Marler 1991; Evans et al. 1993), digital video playback has become a powerful and frequently used methodology in animal behavior research, and a number of reviews have raised cautions and added refinements to these methods (D'Eath 1998; Fleishman et al. 1998; Fleishman and Endler 2000; Oliviera et al. 2000; Uetz and Roberts 2002; McGregor 2013; Chouinard-Thuly et al. 2017; Witte et al. 2017). Previous experimental work with playback of multimodal male signals has either paired pre-recorded male visual signals with vibratory signals from live males (Hebets 2008) or has paired video with (unsynchronized) vibratory playback (Uetz and Roberts 2002). Some studies have presented females with male signals using a single presentation paradigm, which, while effective, raises the question whether female preferences for male signals would change in a different social or environmental context (Bro-Jorgensen 2010; Edward 2015; Dougherty and Shukar 2015; Hebets et al. 2016). In this case, 2-choice studies that investigate preferences for unimodal versus multimodal signals or unimodal signals of different modes might provide additional insight into the complex decision-making that females occasionally use in specific social contexts with constraints from the physical environment.

The brush-legged wolf spider *Schizocosa ocreata* (Hentz) (Lycosidae) is a well-studied model for questions of multimodal communication. Males court females using multimodal courtship displays, which consist of visual signals (tufts of bristles on the forelegs; leg displays including tapping, double tapping and raising, and extending the first pair of legs in a “wave and arch”), accompanied by vibratory signals (substratum-borne vibration produced by pulses of stridulation and percussion) (Stratton and Uetz 1981, 1983, 1986; McClintock and Uetz 1996; Uetz 2000). In single-presentation studies with live spiders, females showed equal receptivity to isolated visual and vibratory signals, but greater responses to multimodal courtship (Scheffer et al. 1996; Hebets and Uetz 1999; Uetz et al. 2009). In other studies, it was found that females preferred males with larger tufts more than smaller tufts in the isolated visual modality (McClintock and Uetz 1996; Uetz and Norton 2007; Uetz et al. 2017), and preferred higher peak amplitudes and peak frequencies in the isolated vibratory signal modality (Gibson and Uetz 2008). In recent studies using multimodal playback experiments (Stoffer and Uetz 2016a, 2016b; Uetz et al. 2017), female *S. ocreata* showed preferences for increased magnitude of male condition-indicating traits (larger leg tufts, greater amplitude vibration signals) in both isolated sensory modes and multimodal signals. Choice tests showed that with respect to information content of signals, females made expected choices between higher/lower quality multimodal signals when male traits covaried positively, but preferred video/vibratory stimuli with larger tuft size when they covaried negatively. These results suggest a previously unseen level

of nuance acting on mate choice in this species, that is, preference for 1 signal mode more than another when the information content of multiple sensory modes is different.

In this study, we use simultaneous digital multimodal playback in choice experiments to investigate further whether female preferences for unimodal and multimodal courtship signals vary in this specific social context and the manner in which signals are presented. In the set of experiments presented here, we provide signals with controlled information content (i.e., identical male quality in visual [tuft size, vigor] and vibratory [amplitude] components) but varied sensory modality (multimodal or isolated vibratory or visual signals). In a 2-choice design, we simulate a possible scenario likely to occur in nature where females perceive 2 males courting simultaneously but for 1 male, one of the signal components is absent (e.g., visual occlusion, discontinuous substrates, and leaves not in contact). In this way, we attempt to tease apart the different and possibly interacting aspects of multimodal signals in their social and environmental contexts.

Materials and Methods

Study species

The brush-legged wolf spider *S. ocreata* is a sexually dimorphic species found in deciduous leaf-litter habitat throughout the eastern USA (Stratton 2005). Immature *S. ocreata* spiders were collected in the field from the Cincinnati Nature Center Rowe Woods, Clermont County, OH (39°7'31.15"N; 84°15'4.29"W) in the fall of 2011 and reared in simulated springtime conditions until maturity. Laboratory conditions were maintained at 23°C–25°C and relative humidity of 65–75%, and a 13:11 h light:dark cycle to simulate late spring, when spiders mature. Spiders were maintained in the laboratory in individual cylindrical plastic deli containers with lids (9 cm diameter × 5 cm ht.) that visually isolated spiders. Spiders were fed twice each week with 3–5 small crickets *Acheta domesticus*, and water was provided *ad libitum*. Female *S. ocreata* were tested ~3 weeks after reaching maturity, when they are at peak receptivity (Norton and Uetz 2005; Uetz and Norton 2007).

Experimental apparatus

Video playback has been demonstrated as an effective method for presenting some spiders with visual stimuli, since wolf spiders (Lycosidae) and jumping spiders (Salticidae) perceive and react to video images as though they are real (Clark and Uetz 1990, 1993; McClintock and Uetz 1996; Uetz and Roberts 2002; Bednarski et al. 2012; Uetz and Clark 2014; Uetz et al. 2016; Jakob et al. 2018). Several methods have been employed to present spiders with vibratory signals (live spiders: Hebets and Uetz 1999; Gibson and Uetz 2008, Uetz et al. 2009; playback methods: Uetz and Roberts 2002; Uetz et al. 2016), with each method successfully meeting the needs for which it was designed. However, digital multimodal playback, especially in a choice paradigm, requires a method for vibratory playback that is appropriately scalable to video playback, small in size (i.e., 2 devices would need to fit in a 20-cm-diameter arena and provide a directional vibratory signal), and able to reliably transmit the same vibratory signal for multiple trials.

Piezoelectric actuators, or disc benders, contain a piezoelectric crystal between a copper and a porcelain disc that vibrates when voltage is applied across it—in this case, the voltage resulting from an audio signal being played through the crystal—fit all 3 above

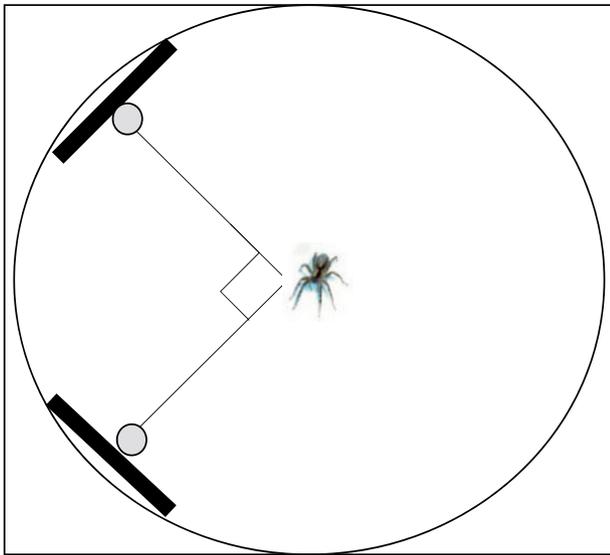


Figure 1. Experimental arena for female choice trials. Black rectangles signify iPod Classics®, gray circles represent disc benders.

criteria. Male vibratory signals were transmitted via piezoelectric disc benders (APC International, Ltd. #20-1205) affixed flush with the poster board substrate of the trial arena using clear adhesive tape, and placed in the center-front of each iPod® Classic (Figure 1). We used a 12-mm diameter circular disc bender, as it was 0.23 mm thick, and could therefore be placed in front of a video iPod®—to effectively pair its vibratory signal with the iPod®’s video signal—and easily laid beneath a piece of paper, through which vibratory signals could be transmitted. Copy paper was placed over the entire area of the arena, on top of the disc benders but under the polycarbonate arena wall, such that spiders could perceive vibration from disc benders via the copy paper throughout the arena. Vibration signals from pre-recorded male *S. ocreata* courtship signals were delivered to the disc benders from an iPod® Classic via an amplifier (Pyle model PTA2). Disc bender output was calibrated using a Laser Doppler Vibrometer (LDV, Polytec model PDV-100) and Raven (Cornell laboratory of Ornithology, version 1.3 Build 23) software to closely match the playback amplitude and frequency to original recordings from live male *S. ocreata* courtship, and to ensure that vibratory signals from each disc bender propagated throughout the area of the arena. Importantly, iPod® and disc benders were placed at a 90° angle from each other, so that spiders would be able to perceive signals simultaneously coming from separate individuals (Kozak and Uetz 2016). Otherwise, in an arena design with 180° separation, spiders might see only the screen they initially face, which could create a preference bias based on first perceived movement (Clark and Uetz 1992; Scheffer et al. 1996; Stoffer et al. 2016). In addition, disc bender output was also measured over distance across the parchment paper surface with the LDV and matched to natural levels to allow spiders to determine direction from attenuation patterns (Uetz et al. 2013; Kozak and Uetz 2016).

Trials were conducted in a 20-cm-diameter, clear plastic polycarbonate, circular arena placed on a 0.092 m² (1 ft²) piece of poster board that rested on four 18 cm high granite “feet,” all of which was situated in an anechoic chamber, effectively isolating the arena—and therefore female spiders—from extraneous environmental vibrations. Male visual courtship signals were presented using 2 iPod Classics® inserted into slots cut into the poster board at 90° to each other such that the bottom of screens were flush with the arena

substrate, and male video exemplars would be within females’ line-of-sight. Video male exemplars represented the population mean for body size, leg tuft size, and courtship vigor as in many previous studies (McClintock and Uetz 1996; Uetz and Roberts 2002; Uetz and Norton 2007; Roberts et al. 2007; Roberts and Uetz 2008; Uetz et al. 2011; Clark et al. 2012), and their vibratory signals were synchronized when both signal modalities were presented together. Vibratory signals accompanying each exemplar were previously recorded on the video soundtrack (16 bit; 48 kHz) by a PCB Piezotronics ICP® accelerometer (PCB-352C23) via an amplifying signal conditioner (PCB-480). To minimize background noise, recordings were made in a sound-attenuating room.

Experimental trials

Females ($N = 81$) were presented with 1 of 3 experimental treatments in which they had a choice between isolated unimodal signals (visual alone vs. vibratory alone, $N = 17$), between a multimodal (visual + vibratory) and visual-alone signal ($N = 38$), or between a multimodal and a vibratory-alone signal ($N = 26$). Signal origin (left or right iPod®) was varied at random between females to control for any side biases. All trials were conducted with females that were between 15 and 25 days mature, when females are at peak receptivity (Uetz and Norton 2007). Female hunger was controlled by feeding all females one 10-day-old cricket 12–24 h before trials were conducted. Each female was placed in the center of the experimental arena under a translucent plastic vial and allowed to acclimate for 1–2 min; during this time, there was no playback of visual or vibratory signals. Trials commenced with the start of playback and the careful removal of the vial so as not to disturb the female; trials lasted 10 min and were video recorded and later scored for female orientation and approach behaviors as well as receptivity displays (settle, tandem leg extend, and slow turn/pivot) to each screen. These behavioral displays were used as a proxy for actual mating in this case, because copulation will usually not occur unless one or more of them is displayed (Montgomery 1903; Uetz and Denterlein 1979; Stratton and Uetz 1981, 1983; Scheffer et al. 1996; Norton and Uetz 2005; Delaney et al. 2007; Johns et al. 2009). In addition, the sum of receptivity displays was used as a comprehensive index of receptivity (Uetz and Roberts 2002; Uetz and Norton 2007; Rutledge and Uetz 2014).

Statistical analyses

All statistical analyses were performed using JMP version 10 (SAS Institute, Cary, NC, USA). Several response variables (orientation [Y/N], latency to orient, number of orientations, number of approaches, comprehensive receptivity score) representing spider behavior toward each iPod® screen in choice tests were analyzed using matched-pairs analysis. The comprehensive receptivity score was computed as a sum of the total number of receptive behaviors (tandem leg extend, slow turn/pivot, and settle) the female exhibited toward each screen.

Ethical note

Spiders are invertebrate animals, and there are no regulations and/or Institutional Animal Care and Use Committee (IACUC) requirements of the University of Cincinnati, the State of Ohio, and the USA regarding their care and maintenance. Our study species, *S. ocreata*, is not an endangered or threatened species. We have made every effort to comply with the “Guidelines for the treatment of animals in behavioural research and teaching,” published by the

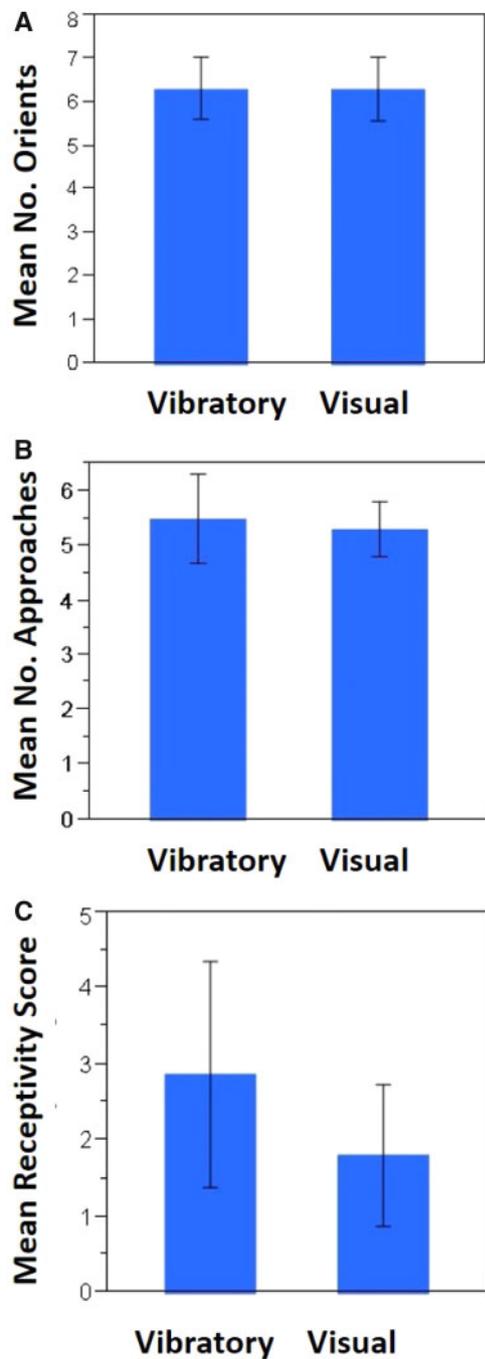


Figure 2. Mean number of female behavioral responses (\pm SE) directed to isolated visual and vibratory male courtship signals: (A) orientations; (B) approaches; (C) receptivity displays.

Animal Behavior Society (*Animal Behaviour* 85 (2013) 287–295). At the end of the study, spiders were humanely euthanized with CO₂ anesthetization and freezing, then placed in 70% ethanol.

Results

Initial analyses of orientation to isolated visual versus vibratory stimuli found equal probability of orientation to each ($\chi^2 = 0.5$; $df = 1$; $P = 0.479$). There were no significant differences in latency to orient to either stimulus, and no significant differences for any

Table 1. Matched-pairs analysis of mean orient, approach, and comprehensive receptivity behaviors exhibited by females with a choice between multimodal and vibratory-only (vis/vib vs. vib), multimodal and visual-only (vis/vib vs. vis), or vibratory-only and visual-only (vis vs. vib) male courtship signals

Treatment	Response	Paired <i>t</i>	<i>df</i>	<i>P</i>
Vib versus vis	Orientation latency	0.509	16	0.673
	No. of orientation	0	16	1
	No. of approach	0.33282	16	0.7436
Vis/vib versus vib	Receptivity	0.43295	16	0.6708
	Orient latency	0.939	22	0.362
	No. of orientation	3.21996	22	0.0039
Vis/vib versus vis	No. of approach	1.89929	22	0.0354
	Receptivity	2.62681	22	0.0154
	Orientation latency	0.987	34	0.343
Vis/vib versus vis	No. of orientation	3.36844	34	0.0019
	No. of approach	3.2432	33	0.0027
	Receptivity	1.103569	32	0.278

Significant *P*-values in bold.

female behaviors directed to either unimodal signal (Table 1; Figure 2).

Orientation of females toward isolated vibratory versus multimodal stimuli showed higher probability of orientation to the multimodal stimulus ($\chi^2 = 4.26$; $df = 1$; $P = 0.039$), but no significant differences in latency to orient to either stimulus (Table 1). Matched-pairs analyses yielded significant differences in mean number of orient, approach, and receptivity behaviors for treatments presenting multimodal male courtship signals against unimodal vibratory male courtship signals (Table 1; Figure 3). Females that initially oriented to the multimodal stimulus were more likely to approach and show receptivity to that stimulus ($\chi^2 = 8.556$; $df = 1$; $P = 0.0034$).

Female spiders responding to isolated visual versus multimodal stimuli exhibited equal probability of orientation to each ($\chi^2 = 0.00$; $df = 1$; $P = 0.100$), and no significant difference in latency to orient to either stimulus (Table 1). Females oriented to and approached multimodal male courtship signals significantly more often than they did unimodal visual male courtship signals, although differences in receptivity to multimodal signals versus isolated visual-only signals were not significant (Table 1; Figure 4). Females that initially oriented to the multimodal stimulus were more likely to approach and show receptivity to that stimulus ($\chi^2 = 7.879$; $df = 1$; $P = 0.005$).

Discussion

In social contexts where multiple males are courting at the same time, detection or interpretation of unimodal versus multimodal signals may vary (Taylor and Ryan 2013), and mating decisions become more complex, especially if there is microhabitat variation that might affect the full transmission of signals (Uetz et al. 2013). This study investigated the effect of unimodal versus multimodal courtship signals of male *S. ocreata* wolf spiders in a choice paradigm used successfully in other studies (Stoffer and Uetz 2017; Uetz et al. 2017). In particular, we used simultaneous presentation of synchronized digital multimodal playback, while controlling for differences in male quality information. In this way, we tested the relative importance of signal modes by simulating conditions a female might encounter in the field—for example, a multimodal signal from 1 individual versus a unimodal signal from another constrained by microhabitat transmission properties (Uetz et al. 2013). Results

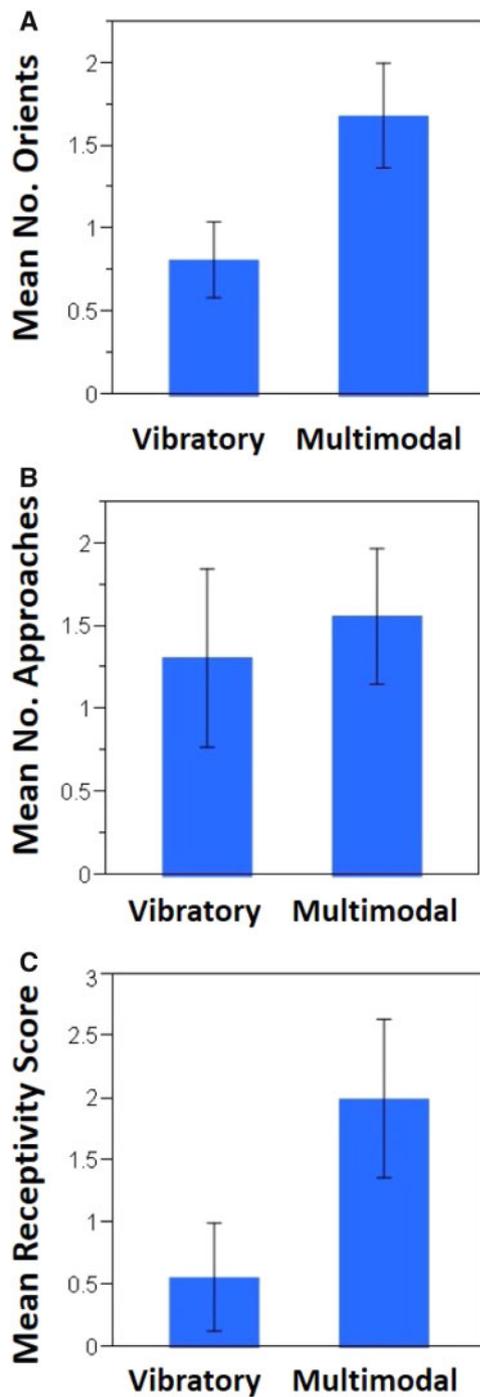


Figure 3. Mean number of female behavioral responses (\pm SE) to multimodal and to vibratory male courtship signals: (A) orientations; (B) approaches; (C) receptivity displays.

indicate that female *S. ocreata* preferences for male courtship signal modality may be dependent on the context in which they are perceived. When presented with a choice between male courtship signals, females displayed no preference for either individual signal mode in isolation, but significantly preferred multimodal courtship signals over isolated vibratory male signals, and tended to prefer multimodal signals over isolated visual signals. In one experiment, females displayed more orientation, approach, and receptivity to multimodal signals more than isolated vibratory signals. However,

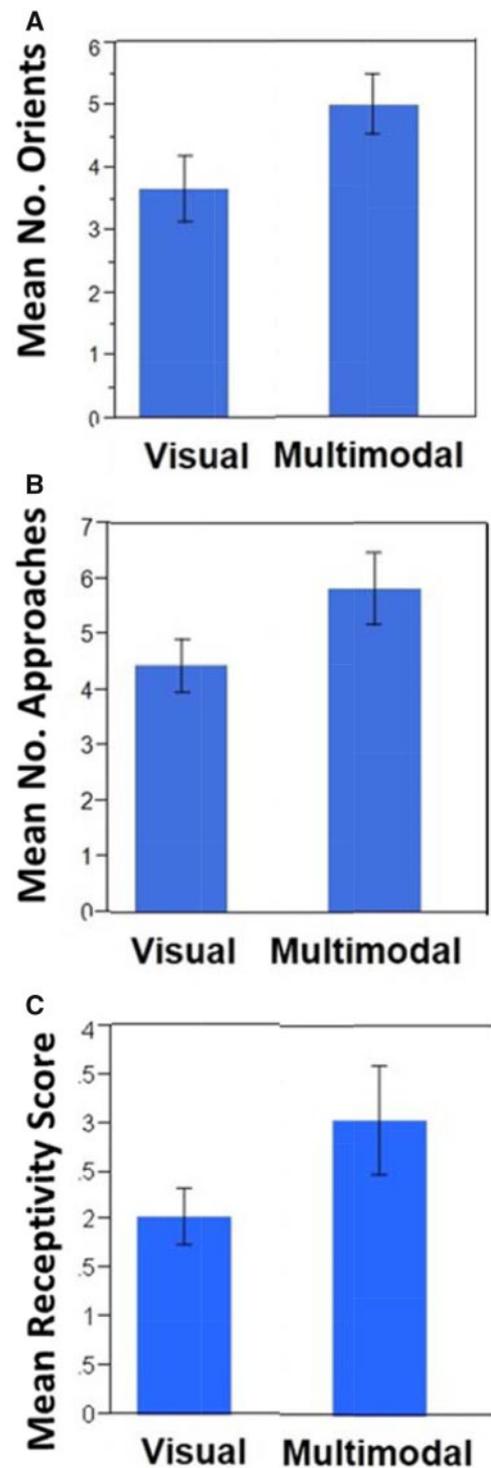


Figure 4. Mean number of female behavioral responses (\pm SE) directed to multimodal and to visual male courtship signals: (A) orientations; (B) approaches; (C) receptivity displays.

when presented with a choice between multimodal signals and isolated visual signals, this strong preference relaxed, perhaps because a visual signal was present in both choices. These results indicate the possibility of a hierarchy of preference among sensory modes, with multimodal signals as most preferred, followed in order by visual signals and vibratory signals (Uetz et al. 2017).

A number of studies have raised the question whether female preferences would change when presented with options to choose from when selecting a mate (Wagner 1998; Bateson and Healy 2005; Dougherty and Shukar 2015; Hebets et al. 2016; Uetz et al. 2017). Earlier work on this species and others has tested female preferences for multimodal versus isolated modes of male courtship signals without giving females a choice between those signals (McClintock and Uetz 1996; Scheffer et al. 1996; Uetz et al. 2009), although recent studies have used choice designs (Stoffer and Uetz 2015, 2016a, 2016b; Uetz et al. 2017). Because information content of paired signals (male quality-indicating traits) was held constant in this case, these results support the hypothesis of redundancy of signal modes *sensu* Partan and Marler (1999, 2005), as females demonstrated the same qualitative response (i.e., display receptivity) to both unimodal signals. Unimodal signals could be further classified as “equivalent,” because responses (receptivity scores) were equal to both modes. However, while females’ preferences for multimodal male signals varied depending on the signal modality it was paired with (visual or vibratory), receptivity responses for multimodal signals tended to be stronger than either of the others, suggesting enhancement more than equality of multimodal signals (Partan and Marler (1999, 2005)). Although slightly different from results of earlier preference studies, which found equivalence or redundancy of the visual and vibratory modes in multimodal signals when females make single-choice mating decisions (Gibson and Uetz 2008; Uetz et al. 2009; Gordon and Uetz 2011), current data more closely match recent findings from direct tests of context dependence (Uetz et al. 2017).

These results demonstrate the importance of testing for female preferences under different contexts, for example, when females are offered a choice versus no-choice paradigm (Wagner 1998; Dougherty and Shukar 2015). It is possible that female responses may be different in a choice paradigm that more closely mimics conditions in the field than when females are not given a choice of stimuli to respond to. This is especially true for high density populations of with male scramble competition, or lek mating systems, where multiple males court females simultaneously (Patricelli et al. 2002; Coleman et al. 2004; Patricelli et al. 2006; Stoffer and Uetz 2015; Patricelli et al. 2016). Ultimately, these results demonstrate the importance of taking multiple approaches when investigating female preferences for male sexual characters, especially with multiple signaling modes (Dougherty and Shukar 2015; Uetz et al. 2017).

Acknowledgments

This work represents a portion of a thesis submitted by E.C.K. in partial fulfillment of the requirements for the M.S. degree from the Department of Biological Sciences at the University of Cincinnati. This research was supported by grant IOS-1026995 from the National Science Foundation (to G.W.U.) and the UC Biological Sciences Wieman/Wendell/Benedict Student Research Fund (to E.C.K.). The authors thank the Cincinnati Nature Center for permitting them to collect spiders on their property, and Granite Concepts for providing the materials and fabrication of the arena. Additional thanks to R. Gilbert, A. Sweger, B. Stoffer, A. Kluckman, R. Wilson, M. Williams, and M. Lallo for various assistance on this project. Thanks as well to E. Maurer and J. Layne for feedback on the research and especially to B. Stoffer and M. Lallo for their review of this article.

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