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Special Issue: Communicative Complexity

Complex signals and comparative mate assessment in wolf spiders: results from multimodal playback studies

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Complex signals of animals involve multiple sensory modes and contain multiple structural components, and teasing apart how these modes and components interact in receiver decision making is an experimental challenge. Females of many species have ordered preferences for increased size or expression of male indicator traits. However, studies also suggest other species may exhibit comparative evaluation of mates rather than absolute preference hierarchies. We examined mate assessment by female wolf spiders, *Schizocosa ocreata*, using digital playback of video and vibratory/seismic signals in preference and choice tests of male trait differences. In playback experiments, female wolf spiders showed ordered preferences for male condition indicating traits (leg tuft size, vibration signal amplitude) in both individual sensory modes and multimodal (combined) signals. Tests with single modes and multimodal signals showed that trait expression in either signal mode affects outcome of mate choice. Females exhibited transitive preferences, consistently choosing males with larger tuft size or higher amplitude vibration in no-choice and two-choice tests. Thus, female *S. ocreata* do not necessarily need to compare mates to exhibit preferences for particular traits. Choice tests with multimodal playback showed that females made predicted choices when male traits covaried positively, but in 'cue-conflict' (negative trait covariance) choice tests, females showed a bias for visual signal trait expression (tuft size), displaying priority for visual signals over vibratory signals when in conflict. These studies demonstrate that under controlled experimental conditions, differences in behavioural responses to manipulation of digital video and vibration playback can provide valuable insights about recognition and interpretation of complex signals and their components.

Much current interest in complex animal signals is focused on signals used in mate choice, as effective communication affects reproductive decisions and individual fitness (Andersson, 1994; Bateson & Healy, 2005; Darwin, 1871; Phelps, Rand, & Ryan, 2006). Complex male courtship signals have often been explained by sexual selection, since they may increase conspicuousness of males to females and/or serve as indicators of male quality (Andersson, 1994; Johnstone, 1995). However, male signalling traits may differ in information provided to females, and females may simultaneously assess multiple traits and weight them differently (Candolin, 2003; Hebets & Papaj, 2005; Hebets & Uetz, 1999; Johnstone, 1996; Moller & Pomiankowski, 1993; Partan & Marler, 2005). Furthermore, females often encounter several males simultaneously or sequentially, allowing for comparative evaluation (Bakker & Milinski, 1991; Bateson & Healy, 2005; Janetos, 1980; Weigmann, Real, Capone, & Ellner, 1996). Complex signals of animals often involve multiple sensory modes (acoustic, chemical, electric, vibratory, visual, etc.) and contain multiple structural components (e.g. within the vibratory modality, components such as frequency, signal rate, amplitude can also vary; or within the visual modality, components such as decorations and colour patterns, as well as visual display behaviours may also vary). Consequently, teasing apart how these modes and components function and interact in receiver decision making is an experimental challenge (Bro-Jorgensen, 2010; Hebets & Papaj, 2005; Higham & Hebets, 2013; Partan & Marler, 2005; Rowe, 1999; Smith & Evans, 2013).

Female preference for male traits may vary directionally with increasing trait magnitude or signal strength, but may also depend on comparison of relative signal strength with other males (Bateson & Healy, 2005; Lea & Ryan, 2015). Theory predicts females should

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make rational mating decisions, such that females exhibit an ordered preference hierarchy for males based on the size or expression of quality-indicating traits (transitivity: if A > B > C, then A > C; Kirkpatrick, Rand, & Ryan, 2006; Ryan, Akre, & Kirkpatrick, 2009). Recent work suggests some species employ comparative rather than absolute evaluation of mates (Bateson & Healy, 2005; Gabel & Hennig, 2016), such that females assess males on a relative scale in comparison to other options (Shafir, 1994). Comparing available options might be less costly (e.g. time or neural investment) than assigning transitivity scores based on traits of males previously encountered (Bateson & Healy, 2005). However, in complex signals, where individual modes or components may reflect quality of different fitness-related traits (e.g. foraging history, immune function, territory defence ability, etc.), female preference for multiple male signalling traits may be differentially 'weighted'. Therefore, females might use absolute (transitivity) or comparative mate evaluation in one modality, but perhaps not in the other modality.

In keeping with the first question addressed in this special issue, i.e. 'Which methods have been used and which methods will play a crucial rule in future studies of communicative complexity?' we discuss general approaches in which video and vibratory playback techniques have been used to improve the study of animal communication. A typical approach for investigating absolute preference order and comparative mate evaluation is to examine female preferences for live animal trials with natural variation in trait magnitude, often comparing results from single-presentation (i.e. presenting a female with a single male at a time) and/or choice (i.e. presenting a female with two or more males at a time) tests (see Dougherty & Shuker, 2015 and citations within). If females demonstrate a preference in two-choice, but not no-choice trials, then females only exhibit preferences when they are able to compare available mating options. If female preferences follow identical patterns in no-choice and two-choice experiments, however, either possibility (absolute or comparative evaluation) could occur and further tests need to be conducted (as tested in Lea & Ryan, 2015; Gabel & Hennig, 2016). Assessment of female preferences and comparative mate evaluation based on complex signals may therefore require different approaches, because complex signals often exhibit covariance among signal components, making it difficult to determine whether each of these contributes equally or disproportionately. Consequently, playback studies of various types (audio, video, multiple stimuli) have been used to examine mating behaviours in amphibians (Bernal, Akre, Baugh, Rand, & Ryan, 2009; Gerhardt, 1991; Gerhardt, Tanner, Corrigan, & Walton, 2000; Wilczynski, Rand, & Ryan, 1999), birds (Ophir & Galef, 2003; Partan, Yelda, Price, & Shimizu, 2005), crustaceans (Aizawa, 1998; Burford, McGregor, & Oliveira, 2000), fish (Allen & Nicoletto, 1997; Kodric-Brown & Nicoletto, 1997, 2001; Nicoletto & Kodric-Brown, 1999; Rosenthal & Evans, 1998; Rosenthal, Evans, & Miller, 1996; Rowland, Bolyard, & Halpern, 1995; Rowland, Bolyard, Jenkins, & Fowler, 1995), insects (Gray, 1997; Hedrick, 1986; Rodríguez, Ramaswamy, & Cocroft, 2006; Shaw & Herlihy, 2000; Stoffer & Walker, 2012) and spiders (Clark & Uetz, 1990, 1992, 1993; McClintock & Uetz, 1996; Stoffer & Uetz, 2015, 2016a, 2016b, 2017; Stoffer, Williams, & Uetz, 2016), for example. However, questions regarding complex signals, comparative mate evaluation and absolute preference hierarchies not only require techniques for experimental manipulation of different modalities and multimodal playback techniques, but also require study organisms in which individuals respond to both unimodal and multimodal signals.

To address the second question raised by papers in this special issue, 'Are model systems used in contemporary studies sufficient to understand the evolution and variety of communicative complexity?', we introduce readers to wolf spiders of the genus *Schizocosa*, an emerging model for the study of complex signals in courtship communication and mate choice. Complex signals used in courtship communication of *Schizocosa* wolf spiders have offered many research opportunities for the study of mechanisms of female mate choice (Hebets & Uetz, 1999, 2000; Hebets & Vink, 2007; Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013; Stratton, 2005; Uetz, 2000; Uetz & Roberts, 2002). One species, the brush-legged wolf spider *Schizocosa ocreata*, has an extensive research background, allowing for deeper questions regarding mating decisions to be posed (see reviews in Uetz, 2000; Uetz & Clark, 2014; Uetz, Clark, & Roberts, 2016; Uetz & Roberts, 2002). Upon detection of chemical cues in female dragline silk (Moskalik & Uetz, 2011; Roberts & Uetz, 2004, 2005), males exhibit elaborate, multimodal courtship in which signals are transmitted to females via visual leg-waving displays and substratum-borne vibratory signals (Scheffer, Uetz, & Stratton, 1996; Stratton & Uetz, 1981, 1983, 1986). Vibratory communication in male courtship consists of both substrate-borne stridulation produced in the tibio-tarsal joint and percussion of the abdomen and chelicerae against the substrate (Gibson & Uetz, 2008, 2012; Stratton & Uetz, 1981, 1983). Visual communication consists of active leg-waving displays of the first pair of legs, the tibiae of which are ornamented with tufts of bristles that tend to increase male mating success (Hebets & Uetz, 2000; McClintock & Uetz, 1996; Persons & Uetz, 2005; Scheffer et al., 1996; Stoffer & Uetz, 2016a, 2016b; Uetz, 2000; Uetz, Clark, Roberts, & Rector, 2011; Uetz & Roberts, 2002). These secondary sexual characters are influenced by nutrition during the juvenile stage, and serve as 'honest' indicators of male quality (Gilbert, Karp, & Uetz, 2016; Gilbert & Uetz, 2016; Uetz, Papke, & Kilinc, 2002; Zahavi, 1975, 1977). Likewise, several measures of vibratory signals reflect adult body condition, and increased mating success is associated with vibratory signal amplitude (Gibson & Uetz, 2008, 2012). In addition, the vigorous courtship of *S. ocreata* is energetically expensive (Cady, Delaney, & Uetz, 2011) and the rate of display is also associated with mating success (Delaney, Roberts, & Uetz, 2007).

In this paper, we present a set of studies on female preferences of *S. ocreata* wolf spiders for male traits in two different signal modes (visual: leg tuft size; vibratory: signal amplitude), which were assessed in several ways using playback techniques. First, we investigated mate preferences of female *S. ocreata* in response to unimodal visual signals and (separately) unimodal vibratory signals on continuous scales in order to construct preference functions for each isolated courtship modality. By constructing preference functions (i.e. the function of the relationship between male traits and female preferences), we could identify possible thresholds in preferences for male traits, visualize the shape of the preference functions on a continuous scale, and begin to consider how unimodal preference functions may interact in multimodal preference functions (Wagner, 1998). Second, we measured female preferences of *S. ocreata* for unimodal courtship signals in single-presentation or no-choice trials, as well as two-choice trials. The visual preference studies aimed to confirm previous results that females prefer large-tufted males, while vibratory preference studies used vibratory playback to examine female mate preferences for low- and high-amplitude signals. Conducting both preference studies in no-choice and two-choice designs allowed us to determine whether female preferences were dependent upon their ability to compare male traits. Third, we examined preferences in choice tests with variation in relative trait magnitude of individual male quality-indicating traits within a multimodal signal (varying visual or vibratory). These studies informed us whether female *S. ocreata* only respond to increasing trait magnitude in isolation, or whether they still increase their preferences for these traits when combined as a multimodal signal. Finally, we measured female preferences