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Tactical adjustment of signalling leads to increased mating success and survival☆

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Most sexually reproducing animals overcome the challenge of searching for and attracting mates by utilizing signals that are broadcast through a spatially and temporally varying environment. A diverse suite of behavioural solutions exist for overcoming such environmental variability, including the adjustment of signalling behaviour based upon receiver feedback. Few studies have directly examined the relationship between such tactical signalling adjustments and proxies of male fitness; the few that have, failed to find a relationship. Using the wolf spider, *Schizocosa rovneri*, we set out to first quantify among-male variation in the form and degree of responsiveness to female feedback. Following exposure to female receptivity cues, some males increased their signalling on an effective signalling substrate (filter paper) while others decreased signalling on the effective substrate. These groups of males were then run through mating trials, conducted in a heterogeneous environment, to examine the relationship between male signalling adjustments and subsequent mating success. Males that adaptively adjusted their signalling (i.e. increased signalling on a more effective substrate) were (1) more likely to copulate, (2) achieved a copulation more quickly and (3) were less likely to be attacked; thus establishing a positive relationship between tactical adjustments of courtship signalling and male fitness.

Sexual communication takes place in environments that are constantly changing, both temporally and spatially. The effective transmission of advertisement signals through this variable signalling environment is often essential to bring the sexes together for mate choice and reproduction, and therefore, is a potent evolutionary force. Successful communication frequently requires environment-dependent modifications of signalling behaviour. Signallers have evolved many tactics to adjust their signalling with changes in the abiotic environment (e.g. Gordon & Uetz, 2012; McNett & Cocroft, 2010; Schwartz, Buchanan, & Gerhardt, 2002). Not only do signallers often adjust signals to changes in the abiotic environment, but males of many species also modify courtship effort based on the perceived quality of potential mates (e.g. coloration: Amundsen & Forsgren, 2001; body size: Bateman & Fleming, 2006; and cues to a female's reproductive state: Gaskett, Herberstein, Downes, & Elgar, 2004), and show plasticity in courtship behaviour associated with additional environmental variability or cues, such as those indicating a risk of predation (e.g. Fowler-Finn & Hebets, 2011; Wilgers & Hebets, 2011; and Wilgers, Wickwire, & Hebets, 2014). In all of these examples, it is predicted, although not tested, that signallers (typically males) that are more responsive to fluctuations in their signalling environments, including those in their intended receivers, will increase their chances of mating by enhancing the efficacy of their signalling.

Examples of male courtship plasticity in response to environmental noise are not uncommon, but relatively few studies have assessed how, or if, males respond to dynamic feedback from potential mates (i.e. females). Even fewer studies have explored the relationship between male responsiveness to female cues and subsequent mating success. None the less, in many animals, including nonduetting species, females actively provide courting males with real-time feedback, often using stereotyped displays (e.g. Patricelli, Uy, & Borgia, 2003; Rodriguez, Haen, Cocroft, & Fowler-Finn, 2012; Swierk, Myers, & Langkilde, 2013). We hypothesize that such female feedback can facilitate the efficacy of male signalling and, that by attending to such feedback and responding appropriately, males can increase their reproductive success. We

☆ Dedicated to Mari Pesek, a bright star with a fantastic future sadly cut short. She was a wonderfully inimitable member of the lab and a tireless student of biology.

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propose that this responsiveness to female feedback is important in reproductive communication across a wide range of taxonomic groups, especially in systems that communicate through heterogeneous signalling environments.

A pioneering study that highlighted the importance of male responsiveness to female feedback used robotic female bowerbirds whose feedback could be manipulated and controlled to establish that males reduce the intensity of their courtship in response to female startling, which is presumably followed by a female flying away from the male (Patricelli, Uy, Walsh, & Borgia, 2002). Importantly, results of this study also demonstrated that males that startled females less had a higher probability of copulation, suggesting that more responsive males receive fitness payoffs (Patricelli et al., 2002). A follow-up study, however, failed to find the predicted relationship between male responsiveness to female startling (again, using robotic females) and natural mating success (Patricelli, Coleman, & Borgia, 2006). Similarly, in a different system involving a copulatory dialogue between male and female spiders, males that responded to female feedback were shown to obtain greater paternity, but the degree of responsiveness had no influence (Peretti, Eberhard, & Briceno, 2006). Ultimately, only a handful of studies have documented plasticity in male courtship or copulatory behaviour in response to female cues (Patricelli et al., 2002, 2006; Patricelli & Krakauer, 2009; Peretti et al., 2006; Rodriguez et al., 2012; Sullivan-Beckers & Hebets, 2011), and the few that have directly examined the relationship between the degree of male responsiveness and measured proxies of fitness failed to find a relationship (Peretti et al., 2006).

The present study explores courtship plasticity in the wolf spider, *Schizocosa rovneri*, by first quantifying among-male variation in responsiveness to female feedback and subsequently comparing mating success between males showing distinct responses. Male *S. rovneri* use a vibrational signal transmitted through a diversity of substrates on the forest floor (e.g. fallen leaves, logs and exposed soil) to attract females for mating. Females, if receptive, respond to a male signal with a multimodal pivoting display of their own that combines vibrational and visual cues (Stratton & Uetz, 1981; Uetz & Denterlein, 1979). Previously, we tested the hypothesis that males use feedback from stereotyped female receptivity displays to adjust subsequent signalling behaviour (Sullivan-Beckers & Hebets, 2011). In support of this hypothesis, we found that males adjusted their use of signalling substrates, which differed in transmission properties (e.g. filter paper: more effective transmission; granite: less effective transmission; Elias & Mason, 2011) following female feedback. Specifically, males signalled more on the more effective substrate after experiencing vibratory feedback cues, presumably resulting in increased effectiveness of vibratory signal transmission (Sullivan-Beckers & Hebets, 2011). Despite the significant pattern of tactical adjustments observed in this prior study, however, individual males varied in their responsiveness to female feedback cues (Sullivan-Beckers & Hebets, 2011).

This study tests the hypothesis that variation observed among males in their modification of signalling following female feedback is predictive of their future mating success. Given the challenges of mate attraction in heterogeneous signalling environments, we make two a priori predictions. Males that constructively modify their signalling behaviour in response to female feedback cues, and therefore increase signalling on a more effective signalling substrate, should experience (1) increased mating success and (2) decreased time to mating. We test these predictions in the wolf spider *S. rovneri*. Males of this species attempt to obtain as many mates as possible in their single breeding season, resulting in a close relationship between mating success and fitness.

METHODS

Spiders

We collected approximately 400 spiders as juveniles (to ensure that all spiders were unmated and naïve to mature individuals of the opposite sex at the time of testing) from two public use areas (Clear Creek Landing and Moccasin Point) located on opposite sides of Sardis Lake, separated by 7 km, near Oxford, MS, U.S.A. during 3–5 April 2011. Immature spiders were brought to the laboratory at the University of Nebraska, U.S.A. and kept on a diet of two crickets (size-matched to the individual's body) twice weekly and provided water ad libitum. Spiders were housed in individual containers (plastic deli dishes) on a 12:12 h light:dark cycle at 23 ± 2 °C. Visual barriers around each container prevented (adult) experience with conspecifics until testing. At each feeding, individual cages were checked for moults and the date of maturation was recorded. Males and females were fed one small cricket the evening before trials to standardize hunger levels and minimize the risk of presexual cannibalism.

Quantifying Male Signalling Adjustments

Our first objective was to characterize the range of signalling modification observed among males after experiencing simulated female feedback cues. We achieved this by screening individuals following previously established methods (Sullivan-Beckers & Hebets, 2011). The responsiveness screening procedure allowed us to sort males relative to each other in terms of their change in use of signalling substrates. The methods were nearly identical to those of Sullivan-Beckers and Hebets (2011) with the exception that all males were provided vibrational plus visual feedback cues, as all were trained to signal on a filter paper substrate.

Briefly, each trial was performed in an arena floored with two substrates representing environmental heterogeneity; one that transmitted the vibrational signal (filter paper) and one that did not transmit the vibrational signal (granite). Individual males were run through three 5 min trials: (1) a pretraining trial to establish a male's baseline use of two signalling substrates, (2) a training trial in which males received feedback cues only when signalling on filter paper and (3) a post-training trial in which we examined a male's subsequent use of substrates in the absence of female feedback. In the pre- and post-training trial, males did not receive female feedback. In the training trial, a puppet female provided feedback to the males only when they signalled on the filter paper substrate.

Pre- and post-training trials were performed in a plastic circular arena (13 cm in diameter with walls 6 cm high). The training trial was performed in a rectangular arena (15 × 23 cm with walls 8 cm high). The training arena was raised on a platform to allow the experimenter to manipulate the puppet female from below. Puppet females used to provide feedback to males during the training trials were constructed from dead *S. rovneri* females affixed to a dowel rod. When a male signalled on the filter paper substrate, the puppet female was rotated approximately 180° (turned by hand from beneath the arena) to mimic the natural female receptivity cues associated with this display.

Schizocosa rovneri males will signal in the absence of a live female after sensing pheromones contained in female silk. To stimulate males to begin courtship, we placed a cotton wick covered with silk from a mature virgin female in the centre of the arena. Test males were placed directly on the wick, and the 5 min trial began when the male moved off of the wick and the wick was removed from the arena. Silk cues were different for each male, but consistent within a male across trials to provide a controlled stimulus