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Tactical adjustment of signaling leads to increased mating success and survival

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Abstract

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 behavioral solutions exist for overcoming such environmental variability, including the adjustment of signaling behavior based upon receiver feedback. Few studies have directly examined the relationship between such tactical signaling 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 signaling on an effective signaling substrate (filter paper) while others decreased signaling 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 signaling adjustments and subsequent mating success. Males that adaptively adjusted their signaling (i.e. increased signaling 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 signaling and male fitness.

Keywords: communication, dialogue, experience, fitness, learning, plasticity

Sexual communication takes place in environments that are constantly changing, both temporally and spatially. The effective transmission of advertisement signals through this variable signaling 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 signaling behavior. Signalers have evolved many tactics to adjust their signaling with changes in the abiotic environment (e.g. Gordon & Uetz, 2012; McNett & Cocroft, 2010; Schwartz, Buchanan, & Gerhardt, 2002). Not only do signalers 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 behavior 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, & He-

bets, 2014). In all of these examples, it is predicted, although not tested, that signalers (typically males) that are more responsive to fluctuations in their signaling environments, including those in their intended receivers, will increase their chances of mating by enhancing the efficacy of their signaling.

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 non-duetting 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 signaling and, that by attending to such feedback and responding appropriately, males can increase their reproductive success. We propose that this responsiveness to female feedback is important in repro-

ductive communication across a wide range of taxonomic groups, especially in systems that communicate through heterogeneous signaling 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 behavior 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 signaling behavior (Sullivan-Beckers & Hebets, 2011). In support of this hypothesis, we found that males adjusted their use of signaling 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 signaled 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 signaling following female feedback is predictive of their future mating success. Given the challenges of mate attraction in heterogeneous signaling environments, we make two a priori predictions. Males that constructively modify their signaling behavior in response to female feedback cues, and therefore increase signaling on a more effective signaling 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, USA during 3–5 April 2011. Immature spiders were brought to the laboratory at the University of Nebraska, USA 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 molts 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 Signaling Adjustments

Our first objective was to characterize the range of signaling 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 signaling 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 signaling substrates, (2) a training trial in which males received feedback cues only when signaling 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 signaled 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 signaled 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 center 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 stim-

ulus within males. To collect silk, cotton wicks were placed in female housing containers for at least 12 h prior to their use.

The courtship signal of *S. rovneri* males consists of a body bounce, wherein the spider strikes the substrate with his whole body (Stratton & Uetz, 1981; Sullivan-Beckers & Hebets, 2011). This conspicuous movement produces a short broadband pulse of vibration and is easily quantified by visual observation. During each 5 min trial (pretraining, training, post-training), we counted the number of body bounces and the substrate (granite or filter paper) used by each male. The side of the arena with each substrate (filter paper versus granite) was alternated between the pre- and post-training trials to control for any side bias. The arenas were cleaned with a 70% ethanol solution before each trial to remove any pheromones and/or silk.

We quantified changes in substrate use by comparing the proportion of signals emitted on filter paper in the pretraining and post-training trials. Henceforth, we refer to this metric as the "signal modification score." It was calculated by quantifying the number of signals emitted on filter paper divided by the total number of signals emitted during the trial. As such, higher scores reflect an increase in the use of the filter paper substrate. The signal modification score was determined for 64 males after experiencing female feedback; nine males were excluded from analyses for failing to signal in at least one trial. To allow us enough time to compare the responses of a group of males to training, we haphazardly assigned each male to a group of eight, all of which were screened on the same day. We calculated signal modification scores for each male, then ranked males by their performance relative to others in the group. All statistical analyses from the mating trials combine males of each category (upper- and lower-quartile males, see below).

Quantifying Male Mating Success

Our second objective was to determine whether the variation we observed in signaling modification would be predictive of a male's mating success. To do this, we separated males by their signal modification scores and compared the mating success of (1) males that responded most constructively to female feedback (upper quartile) and (2) males that responded detrimentally to female feedback (lower quartile). These male groups encompassed 50% of the tested males, representing the two ends of the distribution.

Twenty-four hours after the screening procedure, upper- and lower-quartile males were tested for mating success with a live female. As we did not know how long the effect of the change in substrate use would last after the experience in the previous day's training trial (Screening Procedure) and we were not interested in testing this separate question, we exposed each male to a second training trial (a 'repeat trial') before beginning the mating trial. The repeat trial was conducted in exactly the same manner as the training trial. Approximately 1 min after the conclusion of the repeat trial, the mating trial began.

We compared the mating success of the two groups of males by creating a heterogeneous signaling environment in the laboratory and allowing individual male–female pairs to interact freely. Mating trials consisted of one male and one female and lasted 60 min or until a mating occurred. We conducted a total of 30 mating trials, but we excluded five trials from analyses either because the female showed no pivoting display (four cases) or because the male failed to signal (one case). Individual male–female pairs interacted in a large rectangular (30 × 60 cm) mating arena, which was floored with filter paper on one half and granite on the other half, representing a heterogeneous environment. On each half of the arena, three rectangular barriers (65 mm wide × 75 mm long × 50 mm high, similar to playing cards folded in half) constructed

of filter paper or granite, matched to the substrate of the arena floor, were placed together to obstruct the view of the individuals inside the arena, thus adding visual heterogeneity (see Supplementary Fig. S1). A glass vial was placed in each corner of the arena and in the center of each long side of the arena (where the two substrates met) to keep spiders from climbing the walls and to interrupt their movement. (*Schizocosa* wolf spiders are thigmotactic and tend to continuously walk laps around the arena unless an object stops them.)

All females were introduced into the arena on the filter paper substrate behind a filter paper barrier, and males were introduced in the center of the arena straddling the two substrates. As in the screening trials, we placed males on a pheromone-laden cotton wick before the start of each trial to stimulate courtship. The silk used for each male was collected from the same female used in the screening procedure, which was a different female from the live female used in the mating trial. The cotton wick was placed in the center of the arena between the two substrates. Males were allowed to explore and sense the cotton wick indefinitely, but males typically dismounted the wick within 3 min and began courtship on one of the substrates in the arena. The trial began when the male moved off of the wick. Each individual was used only once in mating trials.

We recorded the presence or absence of copulation and the time of copulation in real time. Mating trials were videotaped and an observer, blind to the male's responsiveness group, scored signaling activity on each substrate, female receptivity displays and female attacks. Time spent signaling was measured as periods of continuous signaling, separated either by a 30 s gap of no signaling, or by the male's movement to a new location.

Previous studies with closely related species have demonstrated that at approximately 30 days postmaturation, females select conspecific males indiscriminately (Uetz & Norton, 2007; Wilgers & Hebets, 2012). As we were primarily interested in male behavior, we tested males and females around this age to minimize effects of female mate choice, although we note that female choice could still contribute to patterns of male mating success. Males averaged 31.09 ±1.48 days postmaturation and did not differ between upper- and lower-quartile groups (t test: $t_{23} = 0.541$, $P = 0.594$); females averaged 27.541 ±1.318 days postmaturation and did not differ between groups (t test: $t_{23} = 0.010$, $P = 0.992$).

Statistical Analyses

Using data from our responsiveness screening, we compared the signaling behavior of males in three groups: (1) upper-quartile males were those that had higher signal modification scores, thereby increasing their use of the filter paper substrate, and presumably responding most constructively, (2) lower-quartile males were those with lower signal modification scores, decreasing their use of the filter paper substrate, and presumably responding detrimentally, and (3) middle-quartile males were males that showed little to no change in substrate use. To assess differences between categories of males in the responsiveness screening trials, we used one-way ANOVA with post hoc Tukey tests to determine differences between each category in the distribution (upper, middle and lower quartile).

To investigate the use of signaling substrates during the mating trials, we compared the signal modification score to random chance (50%). We used a linear regression to examine the relationship between the proportion of signals produced on filter paper during the mating trial and the latency to mate. This regression pooled all males that mated ($N = 17$). All other comparisons were evaluated with t tests and Wilcoxon tests, depending on the

distribution of the data. Means are presented with standard errors of the mean. Effect sizes (*d* and *r*) were calculated using the *t* and *z* values provided by our Student's *t* and Wilcoxon tests (see Nakagawa & Cuthill, 2007). All effect size values were calculated with software from David B. Wilson <http://mason.gmu.edu/wdwilsonb/ma.html>.

Results

Tactical Courtship Signaling

To verify that, once pooled, the categories of male signal modification scores remained distinct, we statistically compared the average responses of each group. Males in our three groups (lower, middle and upper quartile) differed significantly in their change in substrate use after experiencing feedback (ANOVA: $F_{2,52} = 47.27$, $P < 0.0001$; Fig. 1a). Following experience with female feedback cues, upper-quartile males signaled on filter paper more frequently than expected by chance (Student's *t* test: $t_{11} = \_4.112$, $N = 15$, $P = 0.001$) while lower-quartile males signaled on filter paper less frequently than expected by chance ($t_{12} = 10.105$, $N = 15$, $P < 0.001$). The number of signals that a male produced determined the amount of feedback he would receive in the screening procedure (as each male's signal was followed by controlled female feedback). Importantly, males in these groups did not differ in the amount of signaling before and after experience with female feedback (ANOVA: $F_{2,52} = 5.147$, $P = 0.601$; Fig. 1b), demonstrating no difference in the amount of feedback received from females. This similarity in the amount of signaling between groups also suggests that males did not differ in their motivation to signal.

Male Mating Success

As we were interested in comparing the most and the least constructively responsive males, we compared the upper- and lower-quartile males from our responsiveness screening procedure. In support of our first prediction, males in the upper-quartile group (those responding constructively) were more likely to mate than males in the lower-quartile group (chi-square test: $\chi^2 = 6.515$, $P = 0.011$, $d = 1.187$; Fig. 2a). All but one mating occurred on the filter paper substrate. In support of our second prediction, males in the upper-quartile group achieved matings more quickly than males in the lower-quartile group (Wilcoxon signed-ranks test: $Z = 2.06$, $N = 25$, $P = 0.039$, $r = 0.504$; Fig. 3). For all mated males (regardless of their quartile), the difference in the time to mating was strongly correlated with male signaling behavior: males that focused their signaling efforts on the more effective signaling substrate (i.e. filter paper) mated more quickly ($r^2 = 0.36$, $P = 0.01$).

Trials in which a female did not perform a pivoting display and, therefore, did not provide the male any feedback cues (potentially indicating a lack of receptivity), were not included in analyses ($N = 4$). There were no differences between male groups or the females paired with them in terms of age or mass (all $P > 0.297$). Females paired with upper- and lower-quartile males did not differ in the average number of pivoting displays (i.e. feedback cues) per trial (lower quartile: $N = 13$, mean = 2.08 ±0.35; upper quartile: $N = 12$, mean = 1.83 ±0.42; Wilcoxon signed-ranks test: $Z = -0.822$, $P = 0.41$), and females performed pivots almost exclusively when situated on the filter paper substrate (92–95% on average). This pattern did not differ between male groups ($Z = 1.100$, $P = 0.271$). These analyses indicate that, during mating trials, live females were equally receptive to males in both groups and males were exposed to similar levels of female feedback in terms of number and successful transmission of cues produced by the pivoting display.

Upper-quartile males spent a greater proportion of the trials signaling to females than did lower-quartile males (48% versus 33%; Student's *t* test: $t_{23} = 3.09$, $P = 0.005$, $d = 1.237$; Fig. 4a). This difference was likely driven, at least in part, by the difference in total trial length between the two groups, as trials were significantly shorter for upper-quartile males, which mated more quickly than lower-quartile males (mean ±SE: upper quartile: 18.91 ±5.40 min; lower quartile: 46.67 ±5.09 min; Wilcoxon signed-ranks test: $Z = -2.69$, $N = 25$, $P = 0.007$). Shorter trial durations (<10 min) are more easily filled with continuous signaling. Longer trials will have periods of time in which the male is not signaling, presumably because males must rest in between signaling bouts. As such, males that achieve a mating more quickly may also spend a great proportion of the (shorter) trial signaling. Upper-quartile males signaled more often on the filter paper substrate (average of 78% of signals; Student's *t* test: $t_{11} = 3.22$, $P = 0.008$; Fig. 4b), whereas males in the
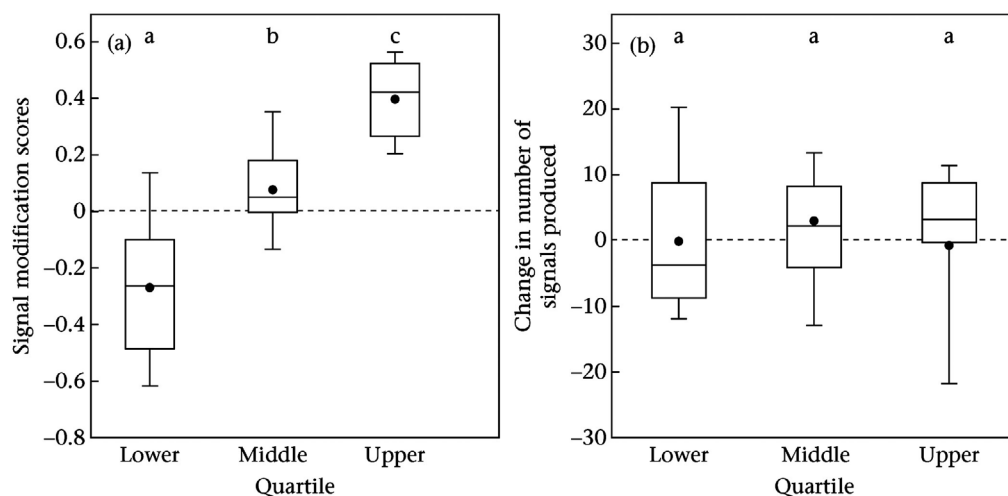

Figure 1. (a) Signal modification scores of male wolf spiders in each quartile after experiencing female feedback cues. The proportion of signals emitted on filter paper substrate either increased (upper-quartile males), decreased (lower-quartile males) or showed little to no change (medium-quartile males). (b) Change in the number of signals produced by males in each quartile before and after experiencing feedback. Boxes indicate the lower and upper quartiles for males in each category; horizontal lines within boxes indicate the median, circles indicate the mean, and whiskers extend to the 1.5 interquartile range from the box. Different letters indicate significant differences between categories ($N = 55$ males screened).
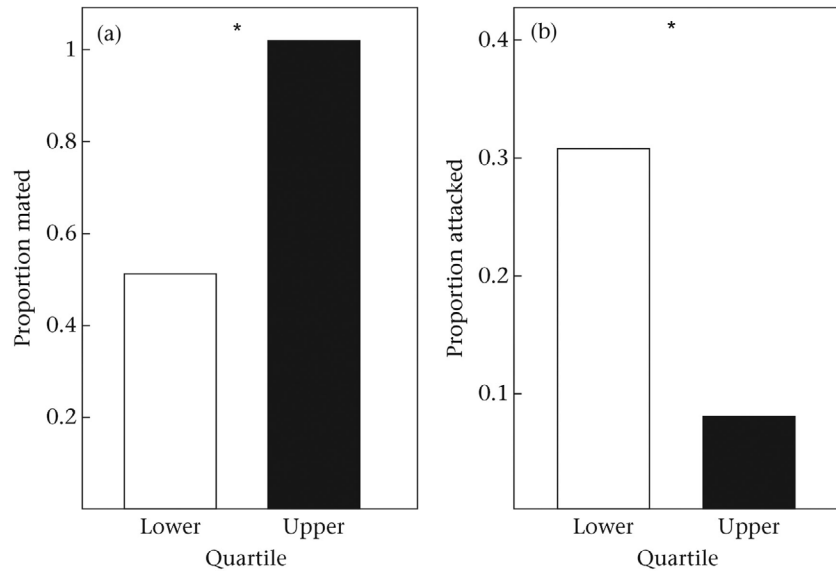
Figure 2. Proportions of upper- and lower-quartile male wolf spiders that (a) successfully mated and (b) were attacked by females. Asterisks denote significant differences between categories (N_{lower} = 13, N_{upper} = 12). Note different Y-axis scales.

lower-quartile group signaled indiscriminately with regard to substrate, not differing from random chance (or 50%; t_{12} = 0.684, P = 0.507). Upper- and lower-quartile males did not differ in latency to initiate courtship signaling (mean ±SE: upper quartile: 277.67 ±78.63 s; lower quartile: 394.69 ±116.36 s; Wilcoxon signed-ranks test: Z = 0.027, N = 25, P = 0.978).

Females were more likely to attack males from the lower-quartile group (chi-square test: χ^2_1 = 4.82, P = 0.028, d = 0.977; Fig. 2b), and attacked many of them repeatedly (67%) despite tightly controlled feeding regimes implemented to equilibrate female hunger levels.
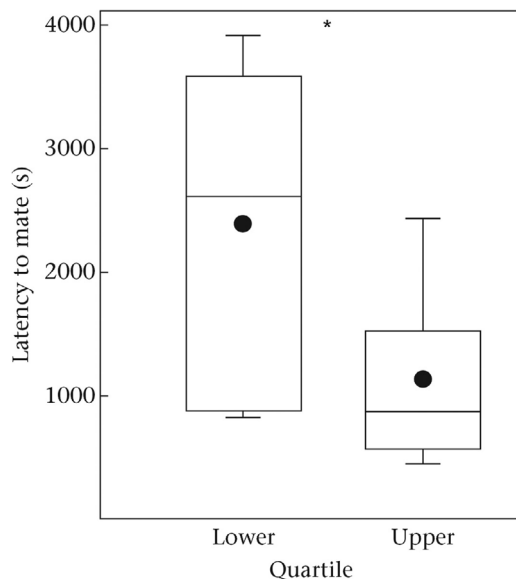

Figure 3. Variation in the latency to mate for male wolf spiders in the lower and upper quartiles. Boxes indicate the lower and upper quartiles for males in each category; horizontal lines within boxes indicate the median, circles indicate the mean, and whiskers extend to the 1.5 interquartile range from the box. Asterisk denotes a significant difference between categories. Note: only the subset of males that mated are included in this analysis (N_{lower} = 6, N_{upper} = 11).

Discussion

Male *S. rovneri* wolf spiders differed in the form and degree to which they modified their signaling behavior following the perception of female feedback cues, and this modification was predictive of male mating success. In the responsiveness screening trials, males ranged from a seemingly constructive response of increasing their use of the substrate upon which they received receptivity cues (filter paper) to a seemingly detrimental response of decreasing their use of this substrate. We predicted that males that responded constructively (those with higher signal modification scores) would experience increased mating success, a prediction confirmed in our mating trials. Males that initially modified their behavior to focus signaling efforts on a more effective substrate continued to use the filter paper substrate preferentially in subsequent mating trials. In contrast, males that initially adjusted their signaling in a seemingly detrimental manner (i.e. signaling more frequently on granite) signaled indiscriminately with regard to substrate in the live mating trials. In the heterogeneous mating trial environment, males with higher signal modification scores (1) were more likely to mate and (2) achieved a mating more quickly than the detrimentally responsive males. In addition, the males with lower signal modification scores were more likely to be attacked by females in the live mating trials. Thus, a tactical adjustment of signaling behavior by males in response to female feedback cues led not only to an increased likelihood to mate and a faster time to mating, but also to a decreased likelihood of attack by a female, all of which have important fitness consequences.

Female feedback cues likely encompass signals that have evolved to facilitate pair formation, including a decrease in courtship and assessment time. A reduction in the time to mating has numerous potential advantages for males, including a presumed decrease in energy expenditure (Cady, Delaney, & Uetz, 2011) and a decrease in the likelihood of being attacked by predatory eavesdroppers. Eavesdropping on male courtship displays by predators is known to increase a male's risk of predation in *Schizocosa* wolf spiders (Pruden & Uetz, 2004; Roberts, Taylor, & Uetz, 2006), and increased time spent courting results in an increased potential for eavesdropping. When females are approached by a displaying
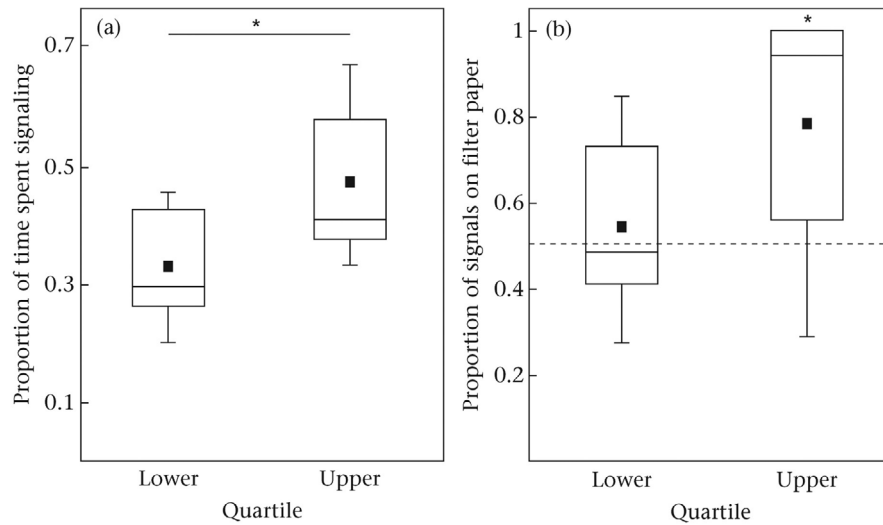
Figure 4. Variation in (a) the proportion of the mating trial that male wolf spiders spent signaling regardless of substrate type and (b) the proportion of signals that males produced on the filter paper substrate. Boxes indicate the lower and upper quartiles for males in each category; horizontal lines within boxes indicate the median, solid squares indicate the mean, and whiskers extend to the 1.5 interquartile range from the box. In (a), an asterisk denotes a significant difference between male categories ($N_{lower} = 13$, $N_{upper} = 12$). In (b), variation was tested against a null expectation of 0.5, indicated by the dashed line (*$P < 0.05$).

male, they may also be at an increased risk of predation due to the conspicuousness of male courtship (e.g. Martin & Wagner, 2010; Pocklington & Dill, 1995). We expect that the facilitation of faster pair formation due to a two-way dialogue between males and females is especially important in heterogeneous signaling environments, and we predict the occurrence of distinct female receptivity displays and male attention to female receptivity displays in such environments.

In potentially cannibalistic animal taxa, appropriate responses to female feedback may not only reduce courtship time, but could also reduce the likelihood of sexual cannibalism. In our study, males that displayed tactical adjustments in signaling also experienced a decreased likelihood of being attacked, which is presumably correlated with a decreased likelihood of being killed. Sexual cannibalism is common among *Schizocosa* wolf spiders (Persons & Uetz, 2005) and is prevalent in laboratories trials with *S. rovneri* (Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013). We hypothesize that these males are attending more closely to subtle female cues and adjusting their behavior accordingly, thus avoiding the elicitation of female aggression. A similar dialogue is observed in satin bowerbirds, *Ptilonorhynchus violaceus*, where males adjust the intensity of their courtship behavior according to a female's startle response (Patricelli et al., 2006). The difference we observed in the frequency of attacks between males that varied in their responsiveness underscores the importance of attending to a potential mate in the two-way exchange of sexual communication, particularly in cannibalistic species.

Constructively responsive males not only signaled more on filter paper during the mating trials, but they also spent a greater proportion of the mating trial signaling. This could indicate a higher motivation to mate, which would potentially provide an additional explanation to our results. However, we see this as a less likely explanation. First, all males were virgins and of similar age. More importantly, during screening trials, all males signaled in equal amounts, and during the mating trials, we observed no difference in the time to initiate courtship among male groups (an established proxy of motivation used in other mating trials with *Schizocosa*; Rundus, Sullivan-Beckers, Wilgers, & Hebets, 2011). Instead, as these constructively responsive males were also signaling on a more effective substrate, their signaling

effectiveness probably led to the shorter trial durations we observed and, thus, an observed increase in the proportion of time spent signaling.

The differences that we observed in signaling behavior, mating success and attack frequency between constructively responsive males and detrimentally responsive males could result either (1) from continued modification of behavior from previous experience (i.e. feedback experienced during screening procedure) and/or (2) from real-time adjustment of behavior in response to current feedback (i.e. feedback experienced during mating trial). We note that these are not mutually exclusive alternatives. While we were unable to tease apart whether differences in signaling behavior and mating success arise from previous or current experience with female feedback, it is clear that males can increase their odds of mating and decrease their odds of attack by responding adaptively to cues from their potential mates, and these results are most likely driven by differences in how males respond to female feedback. All females included in the analyses displayed receptivity to males, and we intentionally elected to use older females, which are potentially less choosy (Uetz & Norton, 2007; Wilgers & Hebets, 2012), making it less likely, although not impossible, that our results were driven by differences in female preferences. Instead, we suggest that the differences in male mating success were primarily driven by differences in male behavior.

The ability of the *S. rovneri* males to acquire information from female receivers and alter their behavior accordingly, whether in real-time or based upon prior experience (or both), may itself be under selection. Our results clearly show reproductive benefits to males that respond effectively to female feedback. In addition, we would argue that females may also benefit (directly and/or indirectly) from choosing such males. By selecting a male that responds quickly and constructively to her feedback, a female could decrease her risk of predation as well as reduce the energy invested in mate assessment. Furthermore, if the male's ability to respond effectively to female feedback has a heritable basis, a question still to be addressed, then a female that chooses such a male could benefit indirectly by passing this ability onto her offspring. Such males may also be more responsive to cues from potential predators or prey. We suggest that selection for responsiveness per se is worthy of future study.

In summary, plasticity in male courtship behavior has been documented in a number of animal taxa (e.g. Balsby & Dabelsteen, 2003; Moskalik & Uetz, 2011; Patricelli et al., 2002), including *S. rovneri* wolf spiders (Sullivan-Beckers & Hebets, 2011), but the majority of such studies have not measured the (assumed) fitness benefits of such behavioral adjustments (but see Patricelli et al., 2002, 2006; Patricelli & Krakauer, 2009; Peretti et al., 2006). In the few studies that have, the degree of male responsiveness was not correlated with measured proxies of fitness (Patricelli et al., 2006; Peretti et al., 2006), whereas our study demonstrates a clear relationship between tactical adjustments in male signaling following female feedback and not only subsequent male mating success, but also presumed survival. Our results demonstrate that the form of responsiveness of males can influence male fitness, suggesting that selection may act on "responsiveness" itself. The dialogue between males and females is often an overlooked feature of reproductive communication, and we suggest that in heterogeneous signaling environments that make finding a mate difficult and/or in systems where prolonged courtship is costly to females, there will be selection for stereotyped female receptivity responses.

Supplementary Material appears following the **References**.

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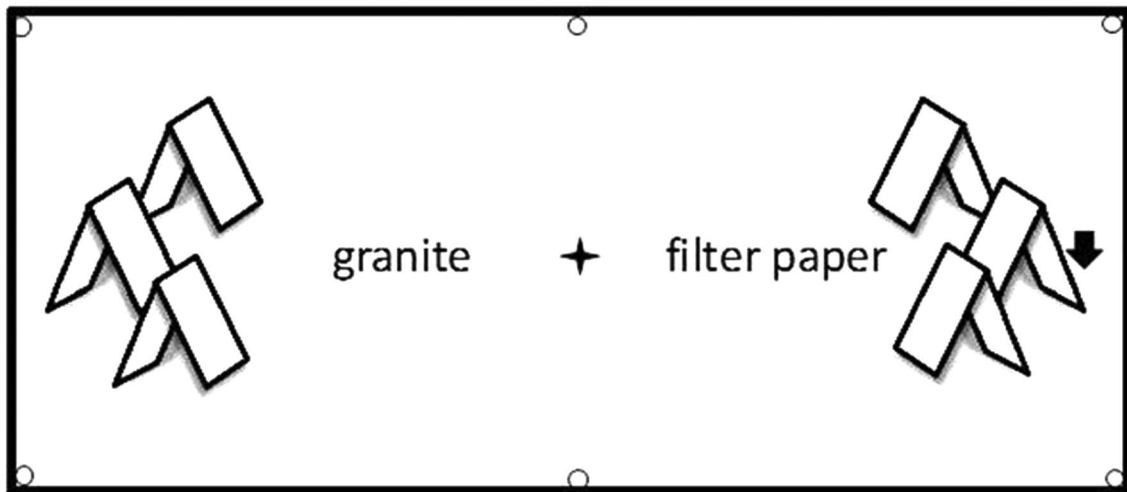
Figure S1. Graphic depicts the mating arena used in trials with a live female. The star in the centre of the arena indicates the release point of each male. The female's release point is shown by the arrow. The open circles around the arena represent the clear glass vials used to interrupt the thigmotactic movement of individuals. See Methods for further details.