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Vibratory communication in the jumping spider *Phidippus clarus*: polyandry, male courtship signals, and mating success

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The jumping spider *Phidippus clarus* uses signals that combine visual and substrate-borne vibrations, which predict the outcome of male–male competition and are important to copulation success. We investigated the function of males' substrate-borne vibrations by examining phenotypic correlates of vibratory signal traits and assessing whether these affect female mating and remating decisions. Virgin females were first paired with males, and females that copulated in first trials were then paired with a second male to determine whether females remate. We measured vibratory signals produced by males during these interactions to determine 1) correlations between substrate-borne signal traits and male phenotypes, 2) whether properties of substrate-borne signals predicted mating success in first and second copulations, and 3) whether females of different mating status have different acceptance thresholds for male characters. Courtship vibration rate was positively correlated with male leg size, and signaling rate significantly predicted mating success in all copulations. Some females were polyandrous; however, copulation with mated females occurred after longer courtship durations, and courtship duration was positively correlated with male size, demonstrating that mated females are less receptive to mates and suggesting that females may be trading up in subsequent matings. Our study shows that males invest significant effort in courtship and that sexual selection via female choice may play a nontrivial role in the mating system. These results are the first to show that honest information about male size is encoded by substrate vibrations, and these signals are important for male mating success in both virgin and mated females. *Key words:* female mating status, honest indicator, jumping spiders, mate choice, *Phidippus*, polyandry, sexual selection, substrate-borne vibrations. *[Behav Ecol 21:1308–1314 (2010)]*

Sexually selected signals generally fall into 1 of 2 categories 1) signals used in intrasexual displays (aggressive signals) or 2) signals used in intersexual displays (courtship signals) (Andersson 1982, 1994). In some cases, a single signal can be used for both competition and courtship. For example, in red deer (*Cervus elaphus*), male antlers have been shown to play a role as weapons during male fights and to advertise sperm production and quality to females (Malo et al. 2005). In other cases, the signals used in male–male competition differ from those used to attract females. For example, in the male field crickets (Orthoptera: Gryllidae), the acoustic signals produced during courtship are different from the signals produced during male–male aggressive contests (Alexander 1961; Gray 1997).

Theory predicts that for courtship signals to evolve, signals should relay honest information about male quality, be costly to produce, and be reliably detected and processed by female receivers (Iwasa and Pomiankowski 1991; Endler 1992, 1993; Maynard-Smith and Harper 2003). This has been empirically shown in a variety of systems. For example, courtship signals in frogs provide honest information about male quality as large high-quality males produce lower pitched signals relative to small poor-quality males (Ryan 1980; Bosch et al. 2000). Costs associated with signals can be in the form of energy consumption (Taigen and Wells 1985; Hack 1998; Kotiaho et al. 1998, 1999), reduced longevity (Mappes et al. 1996; Jennions et al. 2001; Hunt et al. 2004), and/or predation risks (Burk 1982; Zuk and Kolluru 1998; Godin and McDonough 2003; Lindstrom et al. 2006). Under a cost scenario, females prefer higher values of a trait, and higher quality males are better able to afford the costs associated with the production of these traits (Andersson 1994; Kotiaho et al. 1998; Kotiaho 2000 (but see Getty 2006).

Several studies have examined communication behavior in spiders (Uetz and Stratton 1982; Witt and Rovner 1982; Land 1985; Harland and Jackson 2000; Barth 2002; Uetz and Roberts 2002; Huber 2005; Nelson et al. 2005; Cross et al. 2007). In particular, work on vibratory communication has been a focus, as most spider groups use vibration as the primary sense guiding behavior (Baurecht and Barth 1992, 1993; Dierkes and Barth 1995, 2002; Elias et al. 2003, 2008; Elias, Hebets, and Hoy 2006; Elias, Lee, et al. 2006; Gibson and Uetz 2008; Hebets et al. 2008; Uetz et al. 2009). Although work in a range of species has shown that the presence of vibrations is important for mating success, few studies have directly assessed the information content in signals (but see Kotiaho et al. 1998; Rivero et al. 2000; Gibson and Uetz 2008; Hoefler et al. 2009; Shamble et al. 2009) and even fewer have

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demonstrated that variation in signal content correlates with mating success (but see Kotiaho et al. 1996; Gibson and Uetz 2008; Shamble et al. 2009). A seminal set of studies investigating vibratory communication in *Hygrolycosa rubrofasciata* wolf spiders found that females prefer males that drum at high rates (Parri et al. 1997) (also see *Schizocosa ocreata*; Delaney et al. 2007). As high drumming rate is energetically costly (Mappes et al. 1996; Kotiaho et al. 1998) and high drumming rates are correlated with increased male viability (Kotiaho et al. 1996; Mappes et al. 1996) and offspring survival (Alatalo et al. 1998), drumming is apparently a sexually-selected trait indicating male genetic quality. In contrast, in *Stegodyphus lineatus*, the presence of male vibrations was shown to stimulate females to mate, but no other function (i.e., mate recognition and indication of mate quality) was attributed to these vibrations (Maklakov et al. 2003).

In this study, we examine courtship signaling of the jumping spider, *Phidippus clarus*, and our primary goal was to test the hypothesis that vibratory courtship signals carry information about male size and that females choose males based on properties of vibratory courtship behavior. *Phidippus clarus* are found throughout Eastern North America (Edwards 2004; Hoefler 2007; Elias et al. 2008) where males and females build and live in silken nests (hibernacula) in rolled up leaves (Hoefler and Jakob 2006; Hoefler 2007; Hoefler 2008). *Phidippus clarus* have a temporally restricted breeding season, mating in early to mid-July, and laying eggs in mid- to late August (Hoefler 2007; Elias et al. 2008). During the early part of the breeding season, adult males wander in search of hibernacula-dwelling immature females. Males cohabit with these females, defending them against intruding males, and then attempt to mate with the females after they mature (Hoefler 2007; Elias et al. 2008; Kasumovic et al. 2009). In the latter part of the season, when most females have mated at least once, males wander and may encounter further mating opportunities outside of hibernacula. Like other jumping spiders, *P. clarus* produce substrate-borne vibrations (Gwynne and Dadour 1985; Maddison and Stratton 1988a, 1988b; Elias et al. 2003, 2008; Elias, Hebets, and Hoy 2006; Elias, Hebets, Hoy, Maddison, et al. 2006), many of which are produced along with visual signals (multimodal signaling).

Substrate-borne aggressive vibrations predict success in male–male contests with heavier males that signal more being more likely to win contests (Elias et al. 2008). When interacting with females, males produce a distinct set of courtship vibrations that are crucial to mating success outside of cohabitation context (Elias et al. 2010), and courtship behavior significantly reduces longevity of males regardless of whether males successfully copulate (Hoefler 2008). In male–male contests, it is likely that aggressive substrate-borne vibrations relay information about aggressive motivation and willingness to escalate intermale contests (Elias et al. 2008). However, whether information about males is transmitted to females via the costly courtship signals is unclear. Moreover, it is not known whether females discriminate among potential mates based on variation in these signals.

A secondary goal of our study is to examine polyandry in *P. clarus* as it is currently unknown whether females remate during the late stages of the breeding season. It has been suggested that multiple mating in *P. clarus* is unlikely (Hoefler 2007) due to the brief mating season and possible first male sperm precedence predicted by the morphology of the sperm storage organs (Eberhard et al. 1993; Hoefler 2007) and the fact that males of a congener leave sperm plugs in females (Jackson 1980). First male sperm precedence is also consistent with the intense contests that occur between males over access to virgin females (Hoefler 2007; Elias et al. 2008; Kasumovic et al. 2009). However, at the end of the breeding season, wandering males may encounter mated females, and because sperm precedence is rarely absolute (Elgar 1998; Simmons and Siva-Jothy 1998; Eberhard 2004), males may increase their fitness through additional copulations if females will accept them. Thus, our second goal is to examine whether *P. clarus* females remate and whether this is mediated by vibratory signals.

To address these questions, we measured vibratory courtship and mating behavior in laboratory-staged pairings and tested to see whether signal properties were correlated with male traits. We also tested for correlations between male traits and mating success. For those virgin females that mated, we ran a subsequent mating trial with a randomly paired male to determine the frequency of multiple mating.

MATERIALS AND METHODS

Collection and animal maintenance

Adult male and penultimate instar female *P. clarus* were collected from the Koffler Scientific Reserve at Jokers Hill, King City, Ontario, Canada, during mid-June to mid-July 2008. All spiders were housed individually in cages and were kept in visual isolation. All spiders were kept on a 12:12 h light:dark cycle and fed small crickets (*Acheta domesticus*) and/or several flies (*Drosophila hydeii*) twice a week. All individuals were weighed and photographed at the end of trials. Photographs were taken using a Nikon Digital Camera (DXM1200) attached to a dissecting microscope (Zeiss Stemi 2000-C) and captured using Nikon ACT-I (v2.63) software. We measured male and female cephalothorax width and male femur, tibia–patella, and tarsus length (averaged between the 2 front legs). All measurements were taken using Image Tool (Image Tool for Windows, v3.0, University of Texas Health Science Center in San Antonio).

Mating trials

Mating trials were conducted in a custom-made circular arena (11 cm in diameter and 1 cm in height), which consisted of a piece of nylon fabric stretched on a circular wooden needlepoint frame. A transparent acetate sheet served as the wall of the arena. Petroleum jelly was placed on the inside of the arena walls to prevent spiders from climbing the walls. A sheet of white paper on the outside of the arena was used to prevent visual distractions (Elias et al. 2008). All mating trials were videotaped from above (Navitar Zoom 7000 lens, JAI CV-S3200 CCD camera, Sony DVCAM DSR-20 digital VCR, and 44.1 kHz audio sampling rate) and illuminated using a Frezzi Minifill light. Substrate-borne vibrations were recorded using a Laser Doppler Vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head) attached to a translation stage (Newport model 421). Three small pieces of reflective tape (1 mm^2) were placed at the center of the arena in a circular fashion to serve as measurement points for the LDV. The nylon was cleaned with ethanol after each trial to prevent transfer of any chemical signals or cues between trials.

Only females that were collected in their last juvenile instar (penultimate females) and matured in the laboratory were used to ensure that all females were similarly aged virgins. At the start of a trial, a virgin female (within 1–5 days after maturing in the laboratory) was placed into the arena and allowed 30 s to habituate. A random male was then introduced and allowed to court freely. Only adult males were used as they are likely to court mature females, and it is not known whether subadult males court females. Trials were run for 10 min, and males that did not successfully copulate within 10 min were scored as unsuccessful. If males did not court or interact with the female, both the male and the female were removed from any analyses. Females that mated in the first experiment were randomly paired with a second male after 4–7 days. In total, 30 once-mated females were used in these "mated" trials. All procedures for the trials with mated females were the same as for the trials with virgin females.

Courtship began when the male and female oriented toward each other and ended when copulation began or the 10-min trial period ended. Almost immediately after both spiders oriented toward one another, the male would perform both visual and vibratory signals while moving from side to side ("zigzag" display). The visual signals consisted of extending forelegs horizontally and waving them vertically. These signals were produced simultaneously with vibratory signals produced by abdominal tremulations (Elias et al. 2010). Vibratory signals consisted of a single pulse produced simultaneously with the downward motion of the leg; we considered each pulse as a separate vibration signal. Males produced several vibrations throughout the duration of the courtship period.

During our trials, males vibrated while approaching females. In the later stages of courtship, the male repeatedly moved toward and away from the female; during each sequence, he extended his first pair of legs forward while attempting to contact the female (Elias et al. 2010). This contact behavior was also coupled with vibrations. Successful males proceeded to mount the female and copulation began when the male lifted the female's abdomen and inserted his pedipalp (copulatory organ) into the female's genital opening (epigynum—located on the ventral surface of the abdomen).

In addition to the main courtship vibratory signals, males also produced a second set of short vibratory signals (occurring as pairs or triplets) that were not always matched with leg waving. These signals were categorized as "aggressive courtship vibrations" due to their auditory resemblance to male aggressive vibratory signals during male–male competition (see Elias et al. 2008), and in some cases, it was in response to female aggression or unresponsive females (data not shown).

Statistical analysis

Courtship behavior was scored using JWatcher (JWatcher, version 1.0, Macquarie University and University of California–Los Angeles). The frequency and duration of 3 randomly selected courtship vibration signals were averaged for each of 58 randomly selected males (36 males that courted virgin females and 22 that courted mated females). In addition, the frequency and duration of 3 randomly selected aggressive courtship vibrations were also averaged for each of 14 randomly selected males (6 that courted virgins and 8 that courted mated females). All signal analysis was done using custom-written Matlab scripts (Mathworks Inc., v7.0).

Vibration rates were calculated by dividing the absolute number of vibrations by the latency to copulate in trials in which copulation occurred or by courtship duration (10 min) in trials with no copulation. A cube root transformation was performed on the courtship vibration rates and courtship duration to normalize the data. For aggressive courtship vibrations, due to the high variability in the occurrence and timing of these signals, rates were highly skewed, and it was not possible to normalize the data. We therefore used nonparametric analyses for these data. As all male measurements were highly correlated, we first standardized each trait (weight, femur, tibia–patella, and tarsus length and cephalothorax width) and then used a principal components (PC) analysis (on correlations) to create 5 new uncorrelated axes that explained all the variation in phenotypic traits (Table 1). The first axis (PC 1) described overall size with all traits loading approximately equally (Table 1). As the loadings of each of the 5 traits varied for the remaining 5 axes (PC 2–PC 5), these axes described variation in shape.

Table 1

Loadings of the 5 traits on each of the principal component axes

	PC 1	PC 2	PC 3	PC 4	PC 5
Male weight	0.42938	−0.20483	0.87919	−0.00384	−0.02625
Femur	0.46715	−0.18919	−0.25649	−0.55689	0.60833
Patella–tibia	0.47155	−0.11297	−0.28107	−0.28573	−0.77733
Tarsus	0.40723	0.90423	0.01438	0.10589	0.07150
Cephalothorax width	0.45740	−0.30308	−0.28641	0.77266	0.14107

We performed the same analysis on female traits (weight and cephalothorax width), where the first axes explained overall size with both weight (0.71) and size (0.71) loading equally. Weight loaded positively (0.71) and cephalothorax width loaded negatively (-0.71) on the second axes, therefore describing heavier females for their size.

We used backward stepwise regressions to examine predictors of mating success in virgin and mated trials. We used a 2-way analysis of variance to examine whether courtship duration and courtship vibration rates differed between virgin and mated trials and between successful and unsuccessful males. The proportion of males that produced aggressive courtship vibrations in each type of trial was analyzed using a χ^2 test for independence. We used SPSS (v 13.0) for all analyses.

RESULTS

Substrate-borne vibrations

Most males, courting virgin or mated females, produced vibratory signals during courtship of 2 distinct types (Figure 1). Courtship vibrations were the more common signals (61/68 males; 2 tailed: $\chi^2 = 31.57$, $P < 0.0001$), but males also produced aggressive courtship vibrations (29/68 males; so called because they are comparable to those described during intermale contests) (Elias et al. 2008). A single courtship vibration was relatively long in duration (468.27 ms, *standard error* [SE] = ±17.58 ms, $N = 58$) and low in frequency (69.05 Hz, SE = ±1.28 Hz, $N = 58$). This signal was produced by all males that successfully copulated regardless of female mating status. Courtship vibration rate (No. of vibrations/total courtship duration) was significantly correlated with male femur length ($\beta^2 = 1.69$, $F_{1,68} = 5.23$, $P = 0.03$) and male cephalothorax width ($\beta^2 = -1.90$, $P = 0.01$) (final model $r^2 = 0.09$, $F = 3.23$, $P = 0.05$). In comparison, aggressive courtship vibrations were much shorter in average duration (88.26 ms, SE = ±0.005 ms, $N = 6$) and relatively higher in frequency (112.58 Hz, SE = ±3.14 Hz, $N = 6$). These vibrations occurred either as single pulses or in bouts of pairs or triplets (Figure 1). The proportion of males that produced aggressive courtship vibrations was significantly higher in pairings with mated females (60%, 15/25 males) compared with virgin females (32.6%, 14/43 males) ($\chi^2 = 4.87$, $P = 0.03$). However, because aggressive courtship vibrations were sporadic, all remaining analyses focus on the more common courtship vibrations.

Mating trials

Of 50 virgin females, 33 (66%) copulated during our "virgin" trials. Three of the mated females died shortly after, and as a result, our mated female trials are based on the 30 surviving females of which 16 copulated a second time (53%). Due to problems in vibration recordings from 4 virgin trials and 5 mated trials, we report signal analysis from 43 virgin and 25 mated ($n = 68$) trials.

We first examined whether any factors predicted overall mating success regardless of female mating status ($n = 68$). We

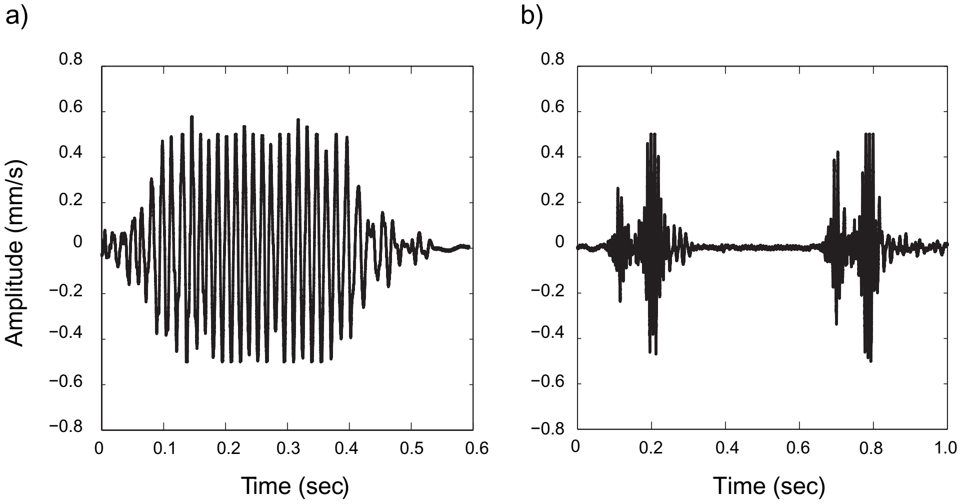

Figure 1
Oscillogram of a male *Phidippus clarus* (a) courtship vibration and (b) aggressive courtship vibration signal. Male courtship vibrations are relatively longer in duration compared with male aggressive courtship vibrations.

placed the 2 female PC axes as well as male courtship vibration rate and male PC axes in a backward stepwise binary logistic regression model. In the final model, higher courtship vibration rates ($\beta = 5.260$, Wald = 13.366, degrees of freedom [df] = 1, 61, $P = 0.00003$) and both female PC axes (PC 1 coefficient matrix: female weight = 0.887, female cephalothorax size = 0.887; factor 1 model: $\beta = 1.016$, Wald = 4.521, df = 1, $P = 0.03$ and PC 2: $\beta = -1.144$, Wald = 5.527, df = 1, $P = 0.02$) predicted mating success.

We then performed separate stepwise regressions to examine the factors that predicted mating success within virgin ($n = 43$) and mated ($n = 25$) females. In the virgin trials, increased courtship vibration rates ($\beta = 4.130$, Wald = 9.675, df = 1, $P = 0.001$) significantly predicted mating success, whereas there was a trend for female PC 1 to predict mating success ($\beta = 0.969$, Wald = 3.492, df = 1, $P = 0.062$). In the mated trials, higher courtship vibration rates ($\beta = 8.608$, Wald = 4.095, df = 1, $P = 0.04$) and female size/weight (PC 1: $\beta = 1.816$, Wald = 3.316, $P = 0.07$ and factor 2: $\beta = -2.335$, Wald = 4.115, df = 1, $P = 0.04$) predicted mating success.

We examined whether courtship vibration rates differed between males mating with females of different mating status. There was no difference between the courtship vibration rates of males that courted virgin or mated females (5.50 ± 0.63 and 3.06 ± 0.82, respectively; $t = 1.52$, df = 66, $P = 0.13$). Males that successfully courted virgin females ($N = 29$), however, had significantly higher courtship vibration rates than those that successfully courted mated females ($N = 15$) ($t = 6.93$, df = 41, $P < 0.0001$) (Figure 2). Furthermore, males that successfully courted mated females courted for almost twice as long compared with successful males courting virgin females (8.95 ± 0.94 and 4.74 ± 0.68 min, respectively; $t = 33.37$, df = 42, $P = 0.0009$).

We next used separate stepwise regressions to examine whether any of the measured traits were correlated with courtship rate and courtship duration. Male courtship vibration rate was significantly correlated (final model: $F = 6.381$, df = 1, $P < 0.01$) with the male PC 4 ($\beta = -0.297$, $t = -2.526$, $P < 0.01$), which is explained predominantly by cephalothorax width and femur length (Table 1). In addition, courtship duration was negatively correlated with male weight ($\beta = -0.01$, df = 1,66, $P = 0.04$). In addition, there was a trend (final model $r^2 = 0.042$, $F = 2.887$, $N = 68$, $P = 0.094$) for courtship duration to be correlated with male femur length and cephalothorax width (PC 4) ($\beta^2 = 0.205$, $P = 0.094$).

DISCUSSION

We examined the importance of male courtship and female mating status in mating success in the jumping spider *P. clarus*. We demonstrate that mating success in *P. clarus* (both virgin and mated females) is dependent on high courtship vibration rates and that vibration rate is correlated with male size. Thus, both virgin and mated females may be indirectly assessing male size through courtship vibration rates. Size is likely an important predictor of fitness in this species as larger heavier males are more successful in male–male competitive contexts (Hoefler 2007; Elias et al. 2008; Kasumovic et al. 2009). We also show that female *P. clarus* mate multiply throughout the

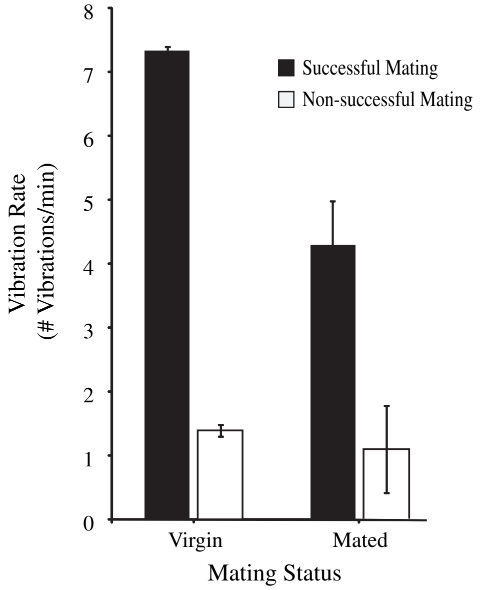

Figure 2
Average courtship vibration rates of males that mated successfully and males that did not mate with virgin and mated females. Successful mating in both virgin and mated females was dependent on high courtship vibration rates. Males that successfully mated with virgin females had a higher courtship vibration rate than those that successfully copulated with mated females. Courtship vibration rates were measured by counting the absolute number of vibrations and dividing it by the total duration of courtship (minutes).

breeding season. Remating occurred, but with longer latencies, as courtship duration almost doubled in cases where females mated a second time, suggesting that mated females were not as willing to mate as virgin females, which may be an indication of mated females becoming "choosier." Although several studies demonstrate that substrate-borne vibrations are necessary for successful copulation in spiders (Scheffer et al. 1996; Parri et al. 1997; Hebets and Uetz 1999; Parri et al. 2002; Elias et al. 2005; Elias, Hebets, and Hoy 2006; Hebets 2008; Uetz et al. 2009), this is one of only a few that shows that information about male phenotype is encoded by the vibratory signals and that variation in signal rate is linked to mating success (Shamble et al. 2009; Rundus et al. 2010).

High courtship vibration rates were correlated with larger femur length and with smaller cephalothorax width. It is unclear why larger femurs and smaller cephalothorax widths would be preferred by females, but foreleg femurs are flattened and used in both courtship and aggressive contexts. In male contests, the flattened femurs are used directly in physical leg grappling and leg fencing interactions (Elias et al. 2008).

Our data suggest that males convey honest information about size to females through vibration rates. Signal honesty is typically maintained through costs of signal production, with higher quality males able to maintain higher signaling levels (Andersson 1994; Kotiaho et al. 1996; Kotiaho 2000; but see Kotiaho 2001). Furthermore, Ryan (1988) suggested that a preference for a higher calling rate can be interpreted as a preference for higher energetic output. As a result, females that prefer high courtship vibration rates may be assessing the energetic output of the male and indirectly assessing male qualities, such as size, weight, and/or energetic reserves (vigor) (see Byers et al. 2010). Preference for higher courtship vibration rate has also been shown in wolf spiders. For example, in *Schizocosa ocreata*, females prefer males with higher courtship signaling rates and longer durations (Delaney et al. 2007; Gibson and Uetz 2008). In *P. clarus*, males producing courtship vibrations are at more risk of predation and have reduced longevity (Hoefler 2008), further indicating the costs of vibratory signals in this system. Although honest signaling of male quality has been shown in a wolf spider (Kotiaho et al. 1998) and the importance of vibrations has been demonstrated in some jumping spider species (Jackson 1977; Elias et al. 2005, 2008), this is the first study to show that vibratory signals carry information about male phenotypic quality in jumping spiders.

Previous research has suggested that most of a male's reproductive effort in *P. clarus* focuses on guarding subadult females early in the breeding season (Hoefler 2007; Elias et al. 2008; Hoefler 2008; Kasumovic et al. 2009). Here, we demonstrate that males also invest resources in courting females found outside of this context (Jackson 1978, 1980). Males readily court both virgin and mated females, and although successful males that courted virgin females had higher courtship vibration rates, males courting mated females persisted for relatively long periods and often included aggressive-like vibratory signals. Despite the high costs associated with courtship vibrations, males may gain benefits from high courtship vibration rates when courting virgin females due to possible first-male sperm precedence given that females mate multiply (shown in this study).

Our results that a significant proportion of *P. clarus* females (53%) will mate multiply are surprising as it was previously thought that the mating system was primarily driven by male–male competition and that males only gained fitness through guarding females (Hoefler 2007, but see Jackson 1981). Studies have shown that despite the high cost of polyandry (Pomiankowski 1987), females of many species engage in multiple mating (Arnqvist and Nilsson 2000; Jennions and Petrie 2000). In mating systems like in *P. clarus* where the female can only assess mates sequentially, females can increase the genetic quality of their offspring by remating if a subsequent male proves to be superior to her first (the "trade-up hypothesis"; Halliday 1983; Gabor and Halliday 1997; Pitcher et al. 2003). The trade-up hypothesis suggests that virgin females should be relatively indiscriminant in order to ensure fertilization, but once sperm is obtained and stored, they can choose to mate with higher quality males (Halliday 1983; Jennions and Petrie 2000; Pitcher et al. 2003). For example, in guppies, *Poecilia reticulate*, Pitcher et al. (2003) showed that mated females were more responsive to second males with greater ornamentation than the first male and that these males were more likely to sire a greater proportion of offspring. Multiple mating can also ensure that her eggs are fertilized by high-quality sperm through postcopulation sperm competition.

In *P. clarus*, virgin females might be less discriminating because of the brief mating season (Hoefler 2007; Elias et al. 2008; Kasumovic et al. 2009) and the highly female-biased sex ratio (Hoefler 2007; Hoefler 2008) because being too choosy might entail the risk of failure to reproduce. Once a female has obtained her first mate and has secured sperm, however, the disadvantages of discriminatory behavior may be lost, and mated females are expected to be more reluctant to mate. Our study shows that mated females had a longer latency to copulate than virgins, which indicates a reluctance to remate. Longer latency to copulation may also indicate increased choosiness. This shift in behavior suggests that mated females require subsequent males to meet a higher courtship threshold to successfully copulate. Furthermore, mating success in mated trials was also correlated with female weight, suggesting that larger females were more likely to remate. Larger females were shown to be more fecund (Hoefler 2008), and it is possible that larger females possess more eggs and need to remate to ensure that all their eggs are fertilized.

Like many other spider species (Gaskett 2007), male *P. clarus* can distinguish between virgin and mated females (Hoefler 2007), and given that females are more discerning after mating, it is not surprising that males courting mated females became more aggressive toward mated than virgin females during courtship. Aggressive courtship vibrations might function to suppress female aggression and indicate vigor. Alternatively, these signals might also be used to ward off potential eavesdropping competitors (Morris et al. 2007). A shift of male signaling effort to aggressive courtship vibrations with mated females could also account for the lower courtship vibration rates than those of males successfully courting virgin females. However, the function of male aggressive courtship vibrations remains unknown, and further studies looking at changes in male courtship behavior when courting virgin versus mated females are needed.

The mating system of *P. clarus* is highly complex and provides an opportunity to study the importance of signals during different phases of the mating period. Elias et al. (2010) have suggested that in *P. clarus*, there is a shift in the mating system from "male–male competition" and "male mate choice" to "female mate choice" due to changes in the sex ratio throughout the breeding season. During the early part of the mating season, when the sex ratio is male biased, male mating success is determined by male–male competition, where larger and heavier males that signaled more were more likely to win contests and mate with larger, early maturing, and highly fecund females (Elias et al. 2008; Hoefler 2008; Kasumovic et al. 2009). During mid-season, when the sex ratio becomes even or female biased, male mating success is determined by female choice, where males that have higher signaling rates (indicating male phenotypic quality) successfully copulate with both virgin and mated females (shown in this study). Furthermore, changes in female mating status is correlated with those in female threshold (indicated by increased latency to copulate), and we suggest that males might be responding to this behavioral shift by changing their signaling behavior as male courtship signaling rates and aggressive courtship vibration proportions varied between virgin and mated females (shown here). In addition, Elias et al. (2010) have demonstrated that male *P. clarus* prevented from producing substrate vibrations can also achieve matings and suggest the importance of visual signals during courtship. The importance of vibratory signals has only recently been appreciated (Virant-Doberlet and Cokl 2004; Cocroft and Rodriguez 2005; Hill 2008), and the ubiquity of vibratory communication makes it essential to understand the form, function, and processing of vibratory information.

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