Vibratory Communication in the Jumping Spider *Phidippus clarus*: Substrate-borne Courtship Signals are Important for Male Mating Success

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Abstract

Recently, work has shown that multimodal communication is common throughout the animal kingdom but the function of multimodal signals is still poorly understood. *Phidippus clarus* are jumping spiders in which males produce multimodal (visual and vibrational) signals in both male–male (aggressive) and male–female (courtship) contexts. The *P. clarus* mating system is complex, with sex ratios and the level of male competition changing over the course of the breeding season. Vibrational signal components have been shown to function in male aggressive contests but their role in courtship has not been investigated. Here, we performed an experiment to test the role of vibrational signaling in courtship by observing mating success for males that were experimentally muted. We show that vibratory courtship signals, and in particular signaling rate, is an important component of mating success and potentially a target of female choice. While the ability to produce vibratory signals significantly increased mating success, some muted males were still able to successfully mate. In these trials, signaling rate also predicted mating success suggesting that redundant signal components may compensate for errors and perturbations in signal transmission or that vibratory signals function to enhance the efficacy of visual signals.

Introduction

Many animals, especially arthropods, use substrate-borne vibration signals in communication (Hill 2008, 2009). Substrate-borne vibrations have been demonstrated as an important mode of communication in bugs (Virant-Doberlet & Cokl 2004; Cocroft & Rodriguez 2005; Rodriguez et al. 2008), lacewings (Henry 1994; Henry et al. 2002), wolf spiders (Uetz & Roberts 2002; Hebets & Papaj 2005; Gibson & Uetz 2008; Hebets 2008; Shamble et al. 2009), wandering spiders (reviewed in Barth 2002), and jumping spiders (Elias et al. 2005, 2006a, 2008) but only in a few species. This has resulted in a relatively poor understanding of the general features and function of vibratory signals in communication.

Vibratory signals are often combined with other modalities, to produce complex, multimodal displays (Uetz & Roberts 2002; Hebets & Papaj 2005; Partan & Marler 2005). Much recent work has focused on the evolution and function of such complex signaling in courtship displays of certain spider groups (Hebets & Uetz 1999; Uetz & Roberts 2002; Elias et al. 2003, 2006a, 2008; Taylor et al. 2005; Delaney et al. 2007; Gibson & Uetz 2008; Uetz et al. 2009), but data across a variety of species is still scarce, and

little is known about the traits that females select in males (but see Gibson & Uetz 2008; Parri et al. 2002; Shamble et al. 2009).

In this paper, we examine the function of substrate-borne vibration signals in a jumping spider, *Phidippus clarus,* by correlating signaling rate with male mating success, and by examining the effect on mating success when preventing males from producing vibration signals. *P. clarus* is found in old fields throughout eastern North America (Edwards 2004). During aggressive intrasexual contests, *P. clarus* males use vibratory signals in combination with leg-waving (visual) displays; the number of vibration signals predicts contest success and certain contest dynamics (Elias et al. 2008). The shift in sex ratios from male to female biased during the breeding season suggests that female choice may become an important selective pressure during some point in the breeding season (Hoefler 2007). Males perform costly courtship displays to females (Hoefler 2008) and despite the presence of substrate-borne signals in multiple contexts, no studies have yet directly examined male courtship signals in this species.

Early in the season, in early to mid July, female *P. clarus* in their penultimate instar (one molt from maturity) build silken nests in rolled up leaves (hibernacula) and after foraging trips, return to them with high fidelity (Hoefler & Jakob 2006). Males mature first and seek out nests of penultimate females and build their own nests within or beside a female's hibernaculum (co-habitation) (Hoefler 2007). During this part of the season, sex ratios are heavily male biased (Hoefler 2007), and males aggressively defend nests against intruding males using multi-modal aggressive signals (visual and vibratory) and direct physical contests. Females become sexually mature virtually synchronously (Hoefler 2007, 2008) and during this part of the breeding season males begin to die off, resulting in sex ratios that shift from male biased to equal or slightly female biased (Hoefler 2007). Under these conditions, females are predicted to be the choosy sex, and males are predicted to court mates (Trivers 1972; Clutton-Brock & Vincent 1991; Andersson 1994). This has not yet been demonstrated in *P. clarus.*

In *P. clarus* as well as a closely related congener (*Phidippus johnsoni*), males can detect female size and age based on chemical or pheromone signals/cues deposited in the female's silk (Jackson 1986; Hoefler 2007), and *P. clarus* males use this information to choose mates (Hoefler 2007). Males prefer to co-habit with large females (Hoefler 2007), which mature more quickly and have more offspring than smaller females (Hoefler 2008). Male mate choice for larger females combined with a large male weight advantage in aggressive contests is suggested to explain the pattern of size assortative pairing of co-habiting spiders in the field (Hoefler 2007). While male mate choice has been demonstrated, it is not clear what role female choice has in the mating system of *P. clarus*. Males that locate females engage in courtship behavior consisting of leg waving and abdominal tremulations (this study; Hoefler 2008). Males will readily court immature (Hoefler 2008), as well as adult virgin and mated females (this study; Sivalinghem et al. in revision). Courtship can be extremely costly as laboratory raised males with courtship experience have significantly reduced longevity compared to naïve laboratory raised males (Hoefler 2008). The cost of courtship and the observation that males actively initiate courtship behavior suggest a female choice component to the mating system of *P. clarus*.

Substrate-borne signaling has already been shown to occur in other *Phidippus* species but its exact role is so far unclear (Jackson 1977, 1980, 1982; Edwards 1981). The goal of this study is to examine courtship behavior, and in particular, female responses to substrate-borne male signals. In this study, we (1) characterize male substrate-borne courtship signals, (2) empirically test whether substrate-borne signals are important to mating success by experimentally muting males, and (3) test for correlations between substrate-borne signaling rates and mating success.

Methods

Spiders

We collected adult male and juvenile female *P. clarus* from Koeffler Scientific Reserve at Joker's Hill, King, Ontario, Canada (44° 03′ N, 79° 29′ W) in July 2008 and 2009. All individuals were housed in separate $3 \times 3 \times 5$ cm^3 clear plastic cages on a 12:12 light:-dark cycle and were fed small *Acheta domesticus* twice weekly. Since jumping spiders are known to possess well-developed vision (Land & Nilsson 2002), we ensured that cages were divided by opaque barriers to minimize the potential effects of prior visual interactions. All individuals were housed in this manner for at least 3 d to allow them to acclimate to laboratory conditions. Only, females collected in their last juvenile instar (penultimate females) were used to ensure female mating status and age was known. Maturity of females was monitored, and mature virgin females were used within 4 d following

maturation. All male and female spiders were fed 1–2 d prior to experiments.

Vibratory Signal Recordings

In 2008, forty mating interactions were videotaped from above (Zoom 7000 lens, Navitar, Rochester, NY; CV-S3200 CCD camera, JAI Inc., San Jose, CA) and substrate-borne vibrations measured using a laser Doppler vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head, Polytec, Waldbronn, Germany). Video and vibrations were recorded on a digital VCR (Sony DVCAM DSR-20 digital VCR, 48,100 kHz sampling rate, Sony, New York, NY). Three courtship vibration signals from each of the forty males were analyzed. For every individual (N = 40), we averaged the three vibratory signals. Each recording was conducted using a different female. Only males that courted within a 10 -min period were used. Mating recordings were conducted in a custom made arena. The arena consisted of a piece of nylon fabric stretched on a circular wooden needlepoint frame (Approx. 1.0 cm in height and Approx. 10.9 cm in diameter) similar to previous studies (Elias et al. 2008). A transparent acetate sheet served as the wall of the arena (Approx. 30 cm in length and Approx. 11.3 cm in width). A sheet of white paper on the outside of the arena was used to prevent visual distractions. Small pieces of reflective tape (Approx. 1 mm^2) were placed at the center of the arena to serve as measurement points for the LDV. Petroleum jelly was placed on the inside of the arena walls to prevent spiders from climbing out of the arena. Females were first placed into the arena and allowed 30 s to habituate. We then introduced males and allowed them to court freely. If males did not interact with females within 10 min, they were removed from the arena, and a new male was introduced. Arenas were cleaned with 75% ethanol between trials. All signal analyses were carried out using custom written Matlab scripts v7.0 (The Mathworks Inc., Natick, MA, USA).

Experimental Trials

In 2009, we assigned mature males to one of two treatments: (1) muted (N = 39) or (2) control (non-muted) (N = 37). Two days prior to the experiments, we anesthetized males with CO_2 and placed a mixture of dental and bee's wax either (1) between the prosoma and opisthosoma (the first and second body regions), connecting the two and inhibiting their relative movement (muted treatment), or (2) on top of the prosoma not connected to any other body part (control). As male *P. clarus* produce vibration signals by tremulation of the abdomen, this method of fixing the prosoma to the opisthosoma eliminates all substrate-borne signals as shown in other spider species that produce vibrations via tremulations (Elias et al. 2005, 2006d). Using laser Doppler vibrometry, we verified that the 'muted' procedure eliminated all substrate-borne signals (data not shown). Placing wax only on the prosoma does not affect any visual or substrate-borne signals (Elias et al. 2005). We used approximately the same amount of wax for both treatments. To ensure that these treatments did not affect normal locomotory activities, we observed whether or not waxed spiders were able to successfully capture prey during the 2 d following these manipulations and prior to experiments. Approximately, equal numbers of each treatment were run for the duration of the experiment.

Each male was randomly paired with a virgin female, and females and males were only used once. Trials were conducted in $10 \times 10 \times 3$ cm^3 plastic containers. All four walls were covered with petroleum jelly to prevent individuals from climbing the walls. Females were allowed to acclimate to their new surroundings for 30 s after which we randomly placed a male within the container. Trials lasted 15 min and only males that interacted with females during this time were included in the analysis. The floor of the container was cleaned with 75% ethanol after every trial to eliminate potential chemical cues left by the previous trials.

Male courtship in *P. clarus* begins when males orient toward females. Males extend their forelegs horizontally and approach the female in a typical jumping spider 'zig–zag' visual display (Forster 1982). During zig–zag movements, males wave their legs vertically up and down (leg waves). Vibratory signals are produced concurrently with leg waves (data not shown). Courtship displays are often interrupted by directed female aggression or females running away. Courtship usually resumes when females reorient toward males. When males are within half a body length of females, males outstretch their legs toward the female and wave them rapidly up and down, contacting females with their forelegs. Contacts are produced concurrently with vibratory signals that are similar to pre-contact courtship vibrations (data not shown). After contact behavior, if the female is still receptive, males proceed to climb onto the female's dorsum (mount, Fig. 1a). Vibrations during mounting are longer than courtship
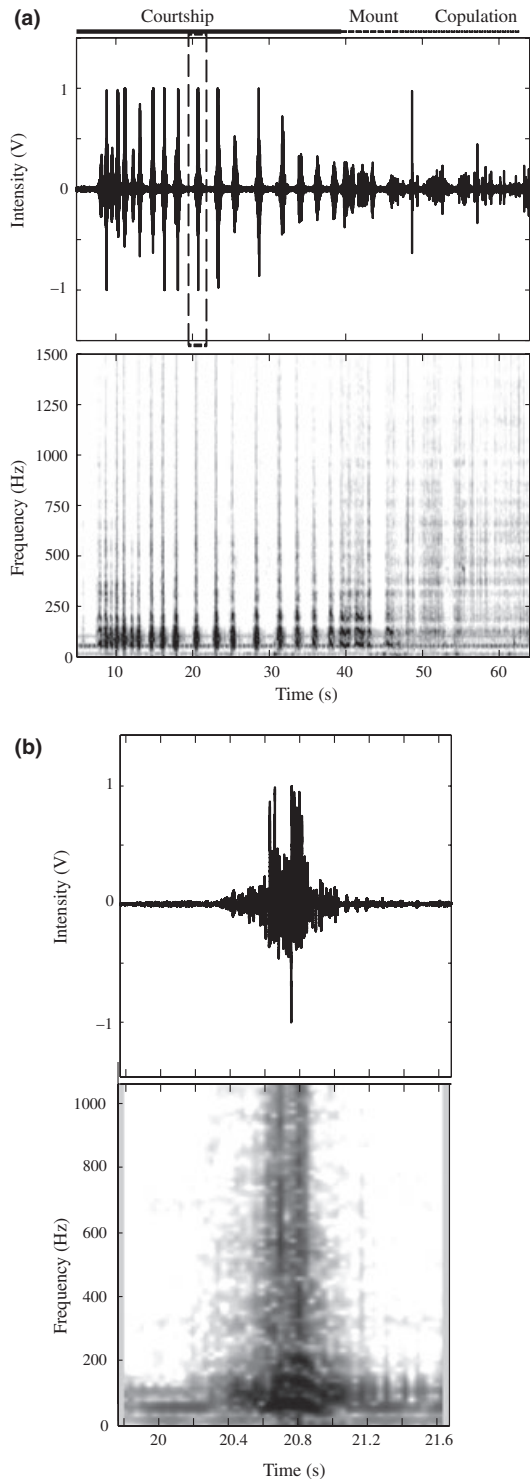
(a)

(b)

Fig. 1: Substrate-borne vibrations during mating behavior in *Phidippus clarus*. (a) Oscillogram and spectrogram of a complete courtship display of *P. clarus*. Mating behavior can be divided into three general categories, courtship, mounting, and copulation. Substrate-borne vibrations occur predominantly during courtship but may also occur in other phases. (b) Oscillogram and spectrogram of a single substrate-borne courtship display from 1a.

vibrations (data now shown). Copulation often follows a mount when a male lifts the female's abdomen and inserts his pedipalp (copulatory organ) into the female's genital opening (located on the ventral surface of the abdomen).

We measured several parameters of courtship behavior. First, we measured courtship duration by recording the time males spent actively courting the female. Different bouts of uninterrupted courtship behavior were added together to calculate total courtship duration (in seconds). In addition, we calculated the number of male multimodal displays by counting leg waves and contacts. Although leg waves and substrate-borne vibrations are emitted concurrently, they are produced independently by the legs and abdomen, respectively. For the purposes of this study, we assumed that signaling rates were equivalent between leg waves and vibrations. Courtship display rate was calculated by dividing the number of displays by courtship duration (displays/second). To get a measure of copulation success, we measured presence/absence of copulation. We weighed both the male and female after each trial (Ohaus electronic balance).

Courtship duration for both treatments was compared using a Student's *t*-test. The proportion of males that copulated in each treatment was compared using a Pearson Chi-Square test. In addition, we examined the traits that predict mating success using a multiple backwards logistic regression with mating outcome as the independent variable and male weight, female weight, male × female weight interaction, the total number of displays, courtship duration, and courtship rate as the dependent variables. Statistical tests were conducted using SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and JMP 7.0 (SAS Institute Inc., Cary, NC, USA). All data are presented as mean ± SE unless otherwise indicated.

Results

Vibratory Signals

All males that interacted with females produced vibratory signals during courtship. Courtship signals are low in dominant frequency (67.95 ± 9.19 Hz, mean ± SD, range: 53.60–92.59 ms, N = 40) (Fig. 1b) with a duration of 468.27 ± 111.19 ms (mean ± SD, range: 198.00–734.00 ms, N = 40; Fig. 1b). Courtship signals also include energy in higher harmonics (Fig. 1b). During our experimental trials (see below), males on average courted for 174.32

± 32.62 s (range: 13.10–777.00 s, N = 39), produced 28.7 ± 2.64 vibratory signals (range: 1–109 signals, N = 39, Fig. 1a) during the entire courtship display, and had an overall courtship rate of 0.276 ± 0.02 signals/s (range: 0.01–0.69 signals/s, N = 39).

Experimental Trials

Virgin females copulated more frequently with control (unmuted) males than muted males (X^2 = 4.21, p = 0.04, N = 76, Fig. 2). Of all the variables added to the logistic regression analysis (Final Model: X^2 = 23.01, df = 1, p < 0.0001), only courtship rate significantly predicted copulation (β = 9.18, Wald = 2.40, df = 1, p < 0.0001, Fig. 3). This was true if all the data were included or if the data were separated by treatment (control: Final Model: X^2 = 11.94, df = 1, p < 0.0001; courtship rate: β = 11.40, Wald = 7.17, df = 1, p = 0.007; muted treatment: Final Model: X^2 = 9.39, df = 1, p = 0.002; courtship rate: β = 6.79, Wald = 6.37, df = 1, p = 0.01).

Experimental manipulations did not affect any male courtship behaviors including courtship duration (control males: 169.46 ± 33.14 s, N = 37; muted males: 197.34 ± 36.24 s, N = 39; t_{73} = −0.567, p = 0.572), number of displays (mean ± SD, control males: 29.32 ± 2.97 displays, N = 37; muted males: 28.15 ± 3.99 displays, N = 38; t_{74} = 0.233, p = 0.816), and courtship rate (control males: 0.27 ± 0.03 displays/s, N = 35; muted males: 0.22 ± 0.03 displays/s, N = 37; t_{70} = 1.430, p = 0.157).
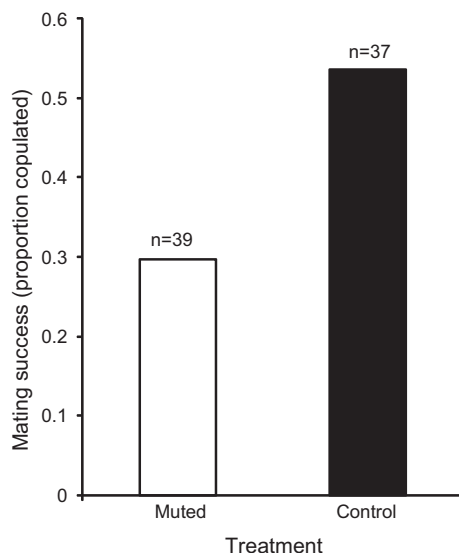

Fig. 2: The proportion of muted and control males that successfully copulated with females. Copulation proportions were compared using a Pearson chi-square test (p < 0.05).

Discussion

This study demonstrates that female *P. clarus* can use substrate-borne vibrations in their mating decisions. There was no difference in signaling behavior or courtship duration between muted and control (unmuted) males suggesting that males expended the same effort to court females. The decreased mating success of muted males was thus dependent on female responses to substrate-borne signals. This study provides further evidence that female mating decisions are influenced by substrate-borne vibration signals (Edwards 1981; Gwynne & Dadour 1985; Maddison & Stratton 1988; Elias et al. 2003, 2005, 2006b). This study is one of the first to provide evidence that jumping spider females can choose males based on properties of substrate-borne signals, namely courtship rate. Courtship rate, in other spider species, has been demonstrated to be important and honestly reflect different aspects of male quality (Parri et al. 1997, 2002; Kotiaho et al. 1998, 1999; Ahtiainen et al. 2005; Lindstrom et al. 2006; Gibson & Uetz 2008; Hoefler et al. 2009; Shamble et al. 2009). Male courtship is costly in *P. clarus* (Hoefler 2008) and rate may thus be a good indicator of male quality and/or condition, and advantageous as a signal for female choice. It is unknown what aspects of male quality, if any, are correlated to courtship rate. Courtship rate predicted mating success even among muted males, suggesting that females are also able to assess other sources of information linked with desirable traits.

There has been much interest in the function of multimodal signals and in particular the content of multimodal signals (Moller & Pomiankowski 1993; Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994; Johnstone 1996; Partan & Marler 1999, 2005; Rowe 1999; Rowe & Guilford 1999; Uetz & Roberts 2002; Candolin 2003; Hebets & Papaj 2005; Bro-Jørgensen 2010). Three main categories of functional hypotheses for multimodal signals have been identified: (1) redundant signals (multiple signals carry the same information), (2) multiple messages (multiple signals carry different information), and (3) unreliable signals (one signal carries information while the other is unreliable). The close association between leg waves and substrate-borne vibrations in courtship signals suggests that different signal components carry the same information (redundant signal) similar to work in the jumping spider genus *Habronattus* (Elias et al. 2003, 2006c). The trait that mediates female choice (courtship rate) could presumably be assessed using leg waves or substrate-borne
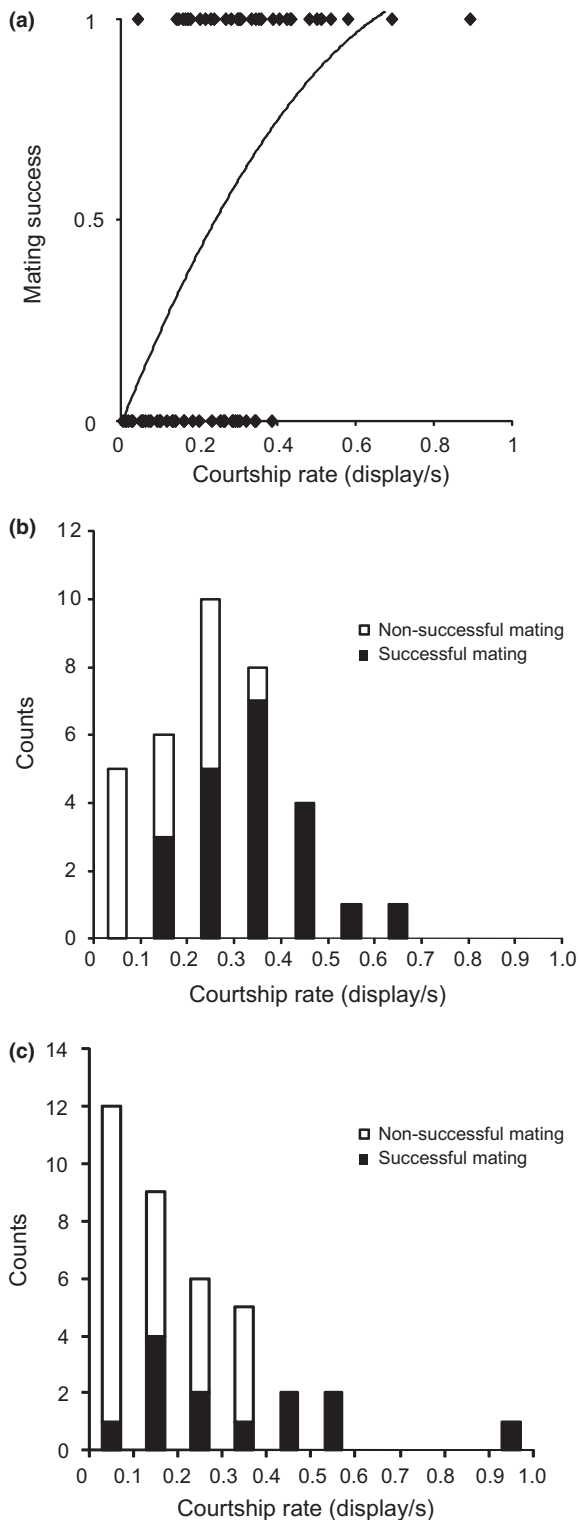
Fig. 3: Copulation outcome of *Phidippus clarus* mating trials. (a) Logistic function of the likelihood of mating as a function of courtship rate (# of displays/s). (b) Histogram of courtship rates for successful and non-successful control males. (c) Histogram of courtship rates for successful and non-successful muted males.

vibrations, but we show here that the presence of vibrations significantly improve a male's likelihood to mate. This may be because of an interaction effect where the presence of vibrations enhances a female's ability to assess courtship rate. In a recent study on wolf spiders, multimodal signals (visual plus substrate-borne vibration) facilitated detection even in species where mating decisions were made predominantly using information relayed by substrate-borne signals (Hebets 2005; Uetz et al. 2009). In this study, visual signals alone are able to at least partially compensate for deficiencies in substrate-borne signaling, because courtship rate predicted mating success in all treatments including when only muted males were used. It is yet unknown how females would behave in situations where only vibratory signals are available. Jumping spiders, however, are strictly diurnal and are unlikely to court in situations where no light is available (Forster 1982). Future work will investigate this topic.

The picture that is starting to emerge on *P. clarus* is complex but one that may illuminate the roles of male mate choice, male–male competition, female mate choice, and male courtship in driving mating system evolution. Our data support the role of substrate-borne vibratory signals in female choice but this may only be important in later periods in the mating season. Early in the season, the sex ratio is heavily male biased, as the majority of females are not receptive (Hoefler 2007). Theory predicts that mate guarding should evolve when there are male-biased sex ratios and short, intense breeding seasons (Grafen & Ridley 1983; Ridley 1983); factors that are present in *P. clarus*. In later stages of the breeding season, as females mature, the sex ratio shifts from male biased to equal/female biased as females become reproductively mature and males die off (Hoefler 2007). Under these 'typical' conditions, females are predicted to be the choosy sex, and males are predicted to compete for mates (Trivers 1972; Clutton-Brock & Vincent 1991; Andersson 1994). It is during this period in the breeding season that females may choose mates based on courtship rate. We suggest that in *P. clarus,* a 'male–male competition' mating system shifts to a 'female choice' mating system as selective pressures based on shifting sex ratios change.

Many crucial questions remain on the *P. clarus* mating system namely, whether females mate multiply, and whether males switch their behavior based on shifts in the sex ratio. In studies of a closely related congener, *P. johnsoni*, it was shown that females mate multiply in some instances (Jackson

1980, 1981, 1982), and preliminary data suggest that such a pattern is also seen in *P. clarus* (Sivalinghem et al., in revision). In addition, it is not known whether males will adaptively switch strategies depending on local sex ratios. Males, however, are able to detect female age from silk cues (Hoefler 2007) and as males will actively court females of any age and mating status, mating system shifts may be opportunistic as males will co-habit when they find immature female nests and court any female they find when wandering.

Phidippus clarus seems an ideal system to test for the interplay between shifting selective pressures, mate choice mechanisms, and sexual selection. The fact that males have suites of signals that are unique to male–male competition (Elias et al. 2008), and signals that are unique to courtship (this study) suggest that two distinct selective pressures have shaped the overall *P. clarus* mating system. Trade-offs between selection for arriving first to immature females (faster development) vs. selection for high quality (larger size, better condition, etc) may lead to patterns of rapidly divergent selective pressures in early and late breeding season (Kasumovic & Andrade 2009a,b). Our study highlights the necessity in understanding shifts in mating behavior as this is likely determined by fluctuation in selection throughout a breeding season (Kasumovic & Andrade 2006, 2009b; Kasumovic et al. 2008; Bro-Jørgensen 2010). Understanding the various types of selection males can encounter throughout their lifetime will provide a better view of phenotype-fitness relationships and how 'total selection' shapes the evolution of male traits and mating systems (Hunt et al. 2009).

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