

Assessment during aggressive contests between male jumping spiders

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Assessment strategies are an important component in game theoretical models of contests. Strategies can be either based on one's own abilities (self-assessment) or on the relative abilities of two opponents (mutual assessment). Using statistical methodology that allows discrimination between assessment types, we examined contests in the jumping spider *Phidippus clarus*. In this species, aggressive interactions can be divided into 'precontact' and 'contact' phases. Precontact phases consist of bouts of visual and vibratory signalling. Contact phases follow where males physically contact each other (leg fencing). Both weight and vibratory signalling differences predicted winners, with heavier and more actively signalling males winning more contests. Vibratory behaviour predicted precontact phase duration, with higher signalling rates and larger differences between contestants leading to longer precontact interaction times. Contact phase duration was predicted most strongly by the weight of losing males relative to that of winning males, suggesting that *P. clarus* males use self-assessment in determining contest duration. While a self-assessment strategy was supported, our results suggest a secondary role for mutual assessment ('partial mutual assessment'). After initial contest bouts, male competitors changed their behaviour. Precontact and contact phase durations were reduced while vibratory signalling behaviour in winners was unchanged. In addition, only vibratory signalling differences predicted winners in subsequent bouts, suggesting a role of experience in determining contest outcomes. We suggest that the rules and assessment strategies that males use can change depending on experience and that assessment strategies are probably a continuum between self-assessment and mutual assessment.

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Many game theoretical models have been developed to examine how animal contests are resolved. These models fall into one of two main categories based on the type of assessment that occurs during the contest: mutual assessment or self-assessment. In mutual assessment models, individuals assess their own resource holding potential (RHP) relative to their opponent. The assessment of RHP can occur based on characters that correlate with fighting ability (reviewed in Hsu et al. 2006), including body size,

weight, energy reserves, weaponry and acoustic signals (Mason 1996; Bridge et al. 2000; Briffa & Elwood 2000; Morrell et al. 2005; Garland & Kelly 2006; Hoefler 2007). In mutual assessment models, contest duration is predicted to be negatively correlated with the relative RHP of contestants, as closely matched contestants take longer to perceive RHP differences (Enquist & Leimer 1983, 1987, 1990). The ability to assess differences in RHP has been incorporated into several game theory models of animal conflicts (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Enquist & Leimer 1983; Leimar et al. 1991; Mesterton-Gibbons et al. 1996). Empirical studies have supported several of these models (Enquist & Jakobsson 1986; Enquist & Leimer

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1990; Jennions & Backwell 1996; Jensen & Yngvesson 1998; Bridge et al. 2000; Stuart-Fox 2006; Kokko & López-Sepulcre 2007; but see Leimar et al. 1991; Keeley & Grant 1993; Taylor et al. 2001; Draud et al. 2004).

In contrast, in self-assessment models, individuals do not assess the quality of their rivals, but instead males set a threshold based on their own ability and decisions are made solely on a male's own ability/reserves. Individuals with relatively smaller RHP reach their threshold first and essentially 'give up' sooner than their opponents, independent of their opponents' RHP. As in mutual assessment models, in self-assessment models, contest duration is negatively correlated with the RHP difference between the contestants (Mesterton-Gibbons et al. 1996; Payne 1998; Taylor et al. 2001). Several recent empirical studies have supported the self-assessment hypothesis (Bridge et al. 2000; Taylor et al. 2001; Jennings et al. 2004; Morrell et al. 2005; Garland & Kelly 2006; Prenter et al. 2006).

As both self-assessment and mutual assessment models predict a negative relationship between contest duration and RHP asymmetry (Taylor et al. 2001), distinguishing between the two models requires careful examination of contest dynamics (Taylor et al. 2001; Gammell & Hardy 2003; Morrell et al. 2005; Prenter et al. 2006). Using a simulation model, Taylor & Elwood (2003) outlined how to distinguish between self-assessment and mutual assessment mechanisms by comparing the direction of the correlation coefficients between the RHP of winners and losers (or larger and smaller rivals). In both assessment models, loser RHP should correlate positively with duration. In self-assessment models, winner RHP should also correlate positively with duration but more weakly than the positive correlation between loser RHP and duration (Taylor et al. 2001). In contrast, in mutual assessment models, winner RHP should be negatively correlated with contest duration, with approximately the same strength as the positive correlation between loser RHP and duration (Taylor et al. 2001).

In later studies, Prenter et al. (2006) and Morrell et al. (2005) modified predictions associated with both mutual and self-assessment models to include situations of 'partial mutual assessment'. In these cases, contest duration is driven most strongly by self-assessment mechanisms, but animals are able to gather information about opponents and use this information to modify their decisions (Prenter et al. 2006). As more information becomes available, the relationship between winner RHP and duration is predicted to shift from slightly positive to negative values (Prenter et al. 2006). Alternatively, Morrell et al. (2005) proposed that cumulative assessment games (Payne 1998) best fit some situations suggestive of 'partial mutual assessment'. Cumulative assessment games are similar to individual threshold models as individuals have a threshold of costs that they are willing to pay, but differ from these models in that contestants with greater RHP inflict higher costs and/or those with lower RHP amass costs more quickly than their opponents (Payne 1998; Briffa & Elwood 2000; Taylor et al. 2001; Morrell et al. 2005; Prenter et al. 2006). Morrell et al. (2005) went on to suggest that by examining the direction of the standardized

partial regression (β) coefficients in a multiple regression model, one could detect the presence of cumulative assessment mechanisms (Taylor et al. 2001; Morrell et al. 2005).

Jumping spiders have been used in several studies examining male contests (Pollard et al. 1987; Wells 1988; Faber & Baylis 1993; Taylor et al. 2001; Cross et al. 2006, 2007; Hoefler 2007). When two males meet, they usually enter into stereotyped displays consisting of visual and tactile signals (Pollard et al. 1987; Taylor et al. 2001). In addition to visual displays, some jumping spiders have been described as producing substrate-borne (vibratory) signals (Gwynne & Dadour 1985; Pollard et al. 1987; Taylor et al. 2001; Wynne-Edwards 2001; Elias et al. 2003, 2005, 2006). It is yet unknown whether substrate-borne signals are important in aggressive contexts.

Phidippus clarus is a common jumping spider in mid-successional fields throughout North America and has a very restricted breeding season, mating in mid-July and ovipositing in August (Roach 1988; Hoefler 2007). Individuals build silken nests (retreats) in rolled-up leaves on plants and return to the same nests throughout their lifetime (Hoefler 2007). During the breeding season, adult male *P. clarus* visit and guard immature female nests over a period of several weeks (Hoefler 2007; D. O. Elias, M. M. Kasumovic & D. Punzalan, personal observation). During this time, males engage in repeated contests with numerous rivals for access to female's nests. Because of the short life span of males (Hoefler 2007; D. O. Elias, personal observation), successful mate guarding is of critical importance in ensuring reproductive success. Males prefer larger females, and larger males are more likely to win contests, leading to size-assortative pairing (Hoefler 2007).

The aim of this study was to determine (1) the presence and importance of substrate-borne signals in male contests, (2) the assessment mechanisms used in contests and (3) the factors that decide contest outcomes.

METHODS

Spiders

We collected adult and penultimate (one moult from maturity) male and female *P. clarus* from the Koffler Scientific Reserve at Jokers Hill, King City, Ontario, Canada in June and July 2006. Each spider was held in the laboratory individually in $2 \times 2 \times 3$ cm cages on a 12:12 h light:dark cycle and kept in visual isolation from one another. We cut the bottom off a 1.5 ml plastic Eppendorf tube and placed a tube in each container to give spiders a substrate to build nests. Spiders were fed several small crickets (*Acheta domesticus*) and flies (*Drosophila hydei*) approximately twice each week. We housed individuals for at least 4 days in the laboratory before using them in any experiments to allow them to acclimate to the laboratory conditions.

Experimental Setup

At least 4 days prior to experiments, males were weighed and numbered. Males were then anaesthetized with CO₂ and two dots of nontoxic paint (Luminous paint, BioQuip

Products, Inc., Rancho Dominguez, CA, U.S.A.) were placed on each male's abdomen (opisthosoma) to allow individual identification of males during contests (both live and in videotapes). We ensured that males recovered from the anaesthetic by verifying that males fed on prey after the procedure.

A plastic cylinder (12 cm in diameter, 9 cm high) was used as the experimental arena. We placed petroleum jelly on the inside of the cylinder wall to prevent spiders from crawling out of the arena and placed an opaque paper ring around the outside of the cylinder to prevent unwanted visual distractions. A piece of graph paper, cut to fit inside the cylinder, was used as the arena floor. We replaced the graph paper every two trials to prevent the build up of any chemical cues. A Frezzi Minifill light was used to illuminate the arena as we videotaped the contest from above (Navitar Zoom 7000 lens, JAI CV-S3200 CCD camera, Sony DVCAM DSR-20 digital VCR). We recorded substrate vibrations produced during interactions using a laser doppler vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head) attached to a translation stage (Newport Model 421) (Michelsen et al. 1982; Elias et al. 2003). Pieces of reflective tape (approximately 1 mm²) were placed at 10 mm increments on the arena floor to serve as measurement points for the LDV. The laser was positioned at the closest point possible to the spiders at the start of each interaction. The LDV signal was synchronized and recorded along with the video taping of contests (Sony DVCAM DSR-20 digital VCR, 44.1 kHz audio sampling rate).

An Eppendorf tube containing an empty female nest was placed at the centre of the arena. Initially, a removable opaque barrier was also placed in the arena to divide it into two equal parts, and a single male was introduced into each side of the arena. After a 5 min acclimation period, we removed the barrier. Initial placement of the barrier ensured that each male had time to acclimate and it also removed any resident or ownership effects from the interaction. Contest observation was terminated after three bouts were completed (see below). Most males were only used once ($N = 108$), except for four males that were used twice (against different opponents). A minimum of 7 days elapsed between the contests of males used more than once. Males were paired randomly with contestants (male weight range 17.30–69.90 mg; mean \pm SE = 45.11 ± 1.02 mg, $N = 108$ males; mean absolute size difference \pm SD: 9.59 ± 7.40 mg, $N = 56$ pairings).

After experiments were concluded, we weighed (Ohaus electronic balance) and digitally photographed (Nikon Digital Camera DXM 1200) all males using a Zeiss microscope (Stemi 2000C). We then measured two metrics for body size from the digital photographs using ACT-1 measurement software: cephalothorax (prosoma) width and patella–tibia length (an average of both front legs). As cephalothorax width was correlated strongly with male patella–tibia length ($r^2 = 0.52$, $N = 112$, $P < 0.0001$), we only used cephalothorax width as a measurement of male size in our analyses.

Male Behaviour

Males perform a series of stereotyped behaviours during aggressive interactions. Broadly, these behaviours can be

divided into two phases: (1) a precontact phase prior to male–male contact and (2) a contact phase where males physically contact each other. The precontact phase begins when the two spiders orient towards one another and adopt a hunched posture with the body raised above the substrate, the front pair of legs curled in front of the body and the abdomen curled underneath the body. Males then approach or retreat from one another with their front legs outstretched horizontally. During these displays, males produce a series of substrate-borne vibrations (see below). These substrate-borne signals usually precede movements towards rivals and rarely precede retreats. The contact phase begins when the two spiders are close to each other and begin to 'leg fence' ('embracing' in Pollard et al. 1987). Leg-fencing behaviour occurs as males attempt to push each other backwards with their front legs. A subset of these interactions escalate further to 'grappling'. Grappling behaviour occurs when two males lock legs and chelicerae (jaws). We considered a male to have won a bout when the rival male turned away and retreated for more than two body lengths. Often fights occurred at the wall of the arena where losing males were not able to escape readily. In this case, we assessed winners when losers turned away and continually tried to climb the petroleum jelly coated wall for more than 2 s.

In all the interactions, the duration of precontact and contact phases were measured using Observer event recorder software (Observer Video PRO 5.0, Noldus Information Technology, Wageningen, The Netherlands). Precontact phases were measured from the time that both males oriented towards one another to the initiation of body contact. Contact phases were measured from the initiation of body contact to the time that the losing male turned away from the winning male. In addition, we recorded the number of substrate-borne signals produced by each male. Males produce signals using abdominal tremulations (D. O. Elias & A. C. Mason, unpublished data) similar to other jumping spiders (Elias et al. 2003). These tremulations are visible to the naked eye and were evident in the videotaped recordings. In addition, we noted the occurrence of vibratory signals from each male during the recording procedure. All measurements were recorded for each contest bout.

Statistical Analyses

To measure the properties of substrate-borne signals, we acquired a subset of signals ($N = 112$) from videotapes using Adobe Premiere Pro 2.0. The temporal and spectral properties of signals were measured using Matlab (Mathworks, Natick, MA, U.S.A.).

We tested for relationships in the first bout between substrate-borne signals and different male measurements using simple and stepwise backward multiple regression models. For the analysis of contest duration for each phase, we used the framework suggested by Taylor & Elwood (2003) and Morrell et al. (2005). For the first contest bout, we investigated winner and loser traits as distinct explanatory variables in simple and backward multiple regression models with contest phase duration

as the dependent variable. In addition, we modified some of these analyses. Taylor & Elwood (2003) correctly noted that strict reliance on composite measures based on RHP of both contestants (e.g. the absolute RHP difference between winner and loser) fails to distinguish between alternative mechanisms underlying the (frequently observed) inverse relationship between contest duration and RHP differences. Taylor & Elwood (2003) offer some useful suggestions for analysis, including the use of winner and loser RHP as independent variables in a multiple regression combined with graphical examination of simple linear regressions of contest duration on winner and loser RHPs separately. However, one drawback of their approach is that it does not allow assessment of the effect of RHP differences between contestants, independent of each contestant's absolute RHP. Comparing slopes derived from a simple (univariate) regression of duration on RHP for winners and losers separately is susceptible to effects of correlations between winner and loser RHPs that may result by chance even when contestants are paired randomly. For example, if pairs frequently consisted of contestants of very similar or dissimilar RHP, then these (positive or negative) correlations between winner and loser RHPs could generate a spurious relationship between duration and RHP when considering winners and losers separately (i.e. in simple linear regressions). As contests are inherently an interaction, contest duration might be expected to depend critically on the relative properties of contestants. In our analyses, we therefore included the cross-product term of (winner trait \times loser trait) as a predictor variable in addition to winner and loser traits themselves. This provides an easily interpretable and statistically valid means to evaluate the effects of all three variables potentially influencing contest duration, without the statistical problems associated with the use of composite measures of RHP differences. Our approach has the added benefit of providing a means to quantify the difference in partial effects (i.e. standardized partial regression coefficients) of winner and loser RHPs analogous to the qualitative slope differences that Taylor & Elwood (2003) suggest to be diagnostic of assessment mechanisms governing contest dynamics.

For our examination of factors determining contact phase duration we excluded contests that escalated to grapples because these occurred infrequently and were distinctly different behaviours from leg fences (see below). The result of the analysis, however, was similar when grapples were included (data not shown).

To test which variables predicted grappling behaviour and overall contest outcome in the first contest bout, we used a backward multiple logistic regression model. To avoid pseudoreplication, we randomly selected a focal individual from each contest using a coin flip. Only measurements on this focal individual were included in the statistical model. To examine differences in signalling behaviour between contest bouts, we used a repeated measures ANOVA procedure. We also used a backward multiple logistic regression model to test which variables predicted overall contest outcomes in subsequent contest bouts. All tests were two tailed and summary statistics are presented as mean \pm SE unless otherwise noted. We report

standardized coefficients for β and adjusted r^2 values. Statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Substrate-borne Signals

Most males produced substrate-borne vibrations. Substrate-borne signals were produced in a series of bouts consisting of two to seven vibrations (Fig. 1a). Bouts occurred at a frequency of 10.96 ± 0.32 Hz ($N = 15$) (Fig. 1a). Single vibrations were of short duration (64.69 ± 2.06 ms, $N = 112$) and had narrowband frequency characteristics centred at 155.4 ± 8.4 Hz ($N = 112$). To determine whether any measured variables correlated with signalling, we entered weight (mg), size (cephalothorax width) and the number of opponent vibrations in a multiple stepwise regression model (final model: $r^2 = 0.342$, $F_{2,108} = 29.534$, $P < 0.0001$). In the final model, both the size of the signalling individual ($\beta_2 = 0.284$, $P < 0.0001$; Fig. 1b) and the number of vibrations by the opponent ($\beta_2 = 0.507$, $P < 0.0001$; Fig. 1c) significantly predicted the number of vibrations produced by an individual.

Precontact Phase

The precontact phase lasted 41.85 ± 3.85 s ($N = 56$). The absolute size difference between males significantly predicted precontact phase duration ($r^2 = 0.305$, $\beta = 0.564$, $N = 56$, $P < 0.0001$; Fig. 1d). Following the procedures highlighted by Taylor & Elwood (2003), we examined the variables that predicted precontact phase duration. We entered weight, size and the number of vibrations of both the winner and loser in a multiple backward stepwise regression model (final model: $r^2 = 0.642$, $F_{1,54} = 99.452$, $P < 0.0001$). In the final model, winner vibrations ($\beta_2 = 0.805$, $P < 0.0001$) significantly predicted precontact phase duration (Fig. 1e). In addition, when a vibration interaction term (winner vibrations \times loser vibrations) was included in the multiple regression model (final model: $r^2 = 0.648$, $F_{1,54} = 99.453$, $P < 0.0001$) only winner vibrations ($\beta_2 = 0.805$, $P < 0.0001$) significantly predicted precontact phase duration. In simple linear regressions, both loser vibrations ($r^2 = 0.384$, $F_{1,54} = 35.328$, $\beta = 0.629$, $P < 0.0001$) and winner vibrations ($r^2 = 0.642$, $F_{1,54} = 99.453$, $\beta = 0.805$, $P < 0.0001$; Fig. 1e) predicted precontact phase duration. This pattern is best explained by our observation that *P. clarus* males vibrated as they approached opponents and did not vibrate as they retreated. Opponents of bigger males retreated more often than those of smaller males, and bigger males were more likely to win. This pattern led to higher numbers of vibrations for larger winning males. In addition, small vibratory signalling differences (Fig. 1d) led to shorter precontact durations, because when males vibrated at similar rates, they were more likely to contact each other sooner. Large differences in precontact duration resulted from one male vibrating as its opponent silently retreated.

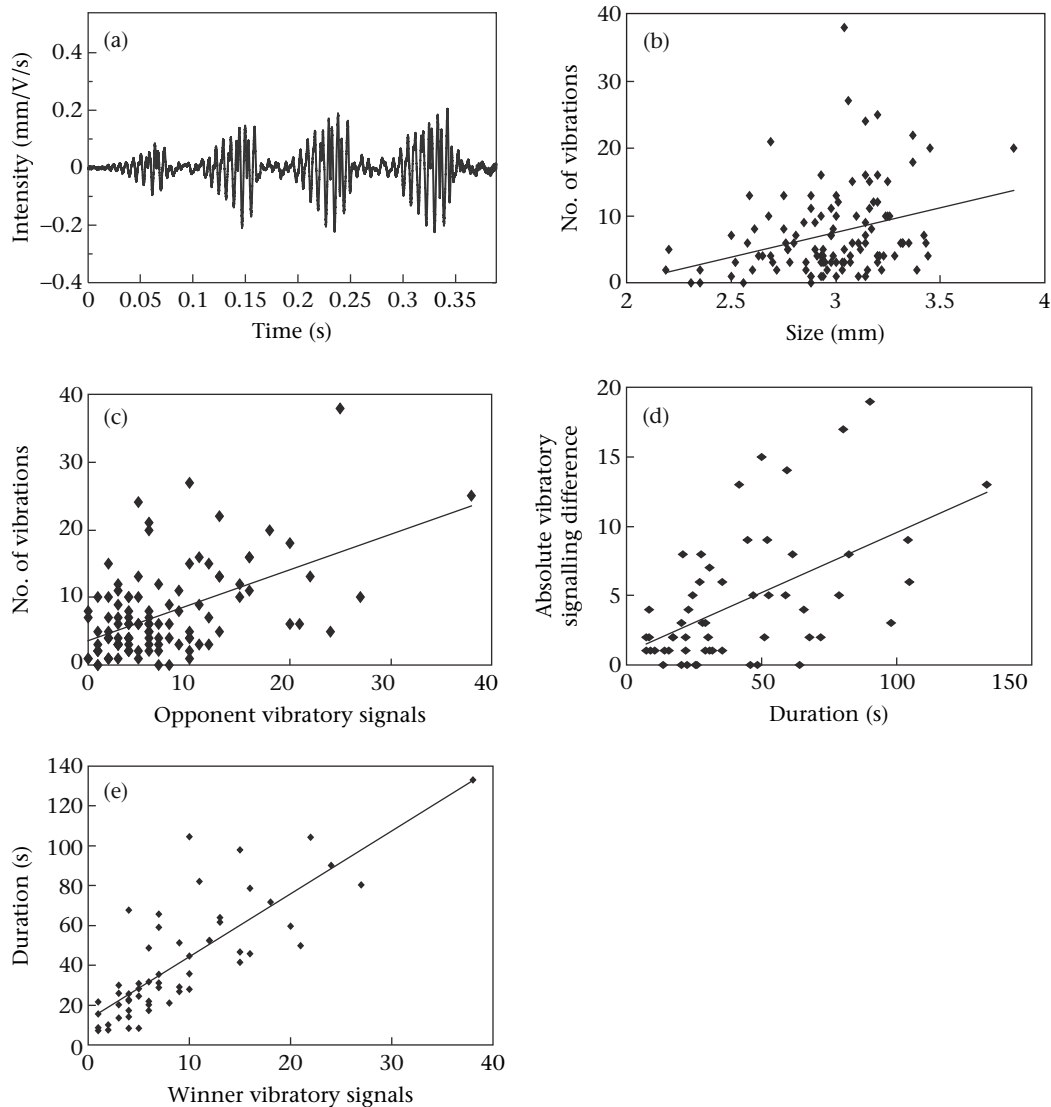


Figure 1. Precontact phase in *Phidippus clarus*. (a) Oscillogram of a bout of vibrational signalling. (b) The relationship between the number of vibration signals produced and size (cephalothorax width). (c) The relationship between an individual's own vibrations and vibrations produced by opponents. (d) The relationship between vibration signalling differences and the duration of the precontact phase (e) The relationship between winner vibration and the duration of the precontact phase.

Contact Phase

Contact phases can be divided into relatively short 'fencing' escalations (3.52 ± 3.23 s, $N = 48$) and relatively long 'grappling' escalations (146.18 ± 91.59 s, $N = 8$). The absolute weight difference between males was inversely related to contact phase duration ($r^2 = 0.213$, $\beta = -0.479$, $N = 56$, $P < 0.001$). Following the procedures described by Taylor & Elwood (2003), we examined the variables that predicted fencing escalation duration. We again entered weight, size and the number of vibrations, for both winners and losers in a multiple backward stepwise regression model (final model: $r^2 = 0.154$, $F_{2,45} = 5.269$, $P < 0.009$). Both winner weight ($\beta_4 = -0.407$, $P = 0.017$; Fig. 2a) and loser weight ($\beta_4 = 0.517$, $P = 0.003$; Fig. 2b) significantly predicted contact phase duration. When a weight interaction term

(winner weight \times loser weight) was included in the multiple regression model (final model: $r^2 = 0.166$, $F_{2,45} = 5.686$, $P < 0.006$) both loser weight ($\beta_2 = 1.028$, $P = 0.002$) and the interaction term ($\beta_2 = -0.824$, $P = 0.012$) significantly predicted contact phase duration, while winner weight did not ($\beta_1 = -0.060$, $P = 0.895$). In simple linear regressions, loser weight ($r^2 = 0.060$, $F_{1,46} = 3.980$, $\beta = 0.282$, $P = 0.05$; Fig. 2b) but not winner weight ($r^2 = -0.10$, $F_{1,46} = 0.541$, $\beta = -0.108$, $P = 0.466$; Fig. 2a) significantly predicted contact phase duration.

Using backward multiple logistic regression, we examined conditions that predicted whether fencing escalated to grappling. We entered the absolute differences in weight, size and vibration signalling into the model. In the final model, only size difference ($\beta_3 = -8.765$, $P < 0.0001$, Nagelkerke $R^2 = 0.218$) significantly predicted the occurrence of grappling, with similarly sized males

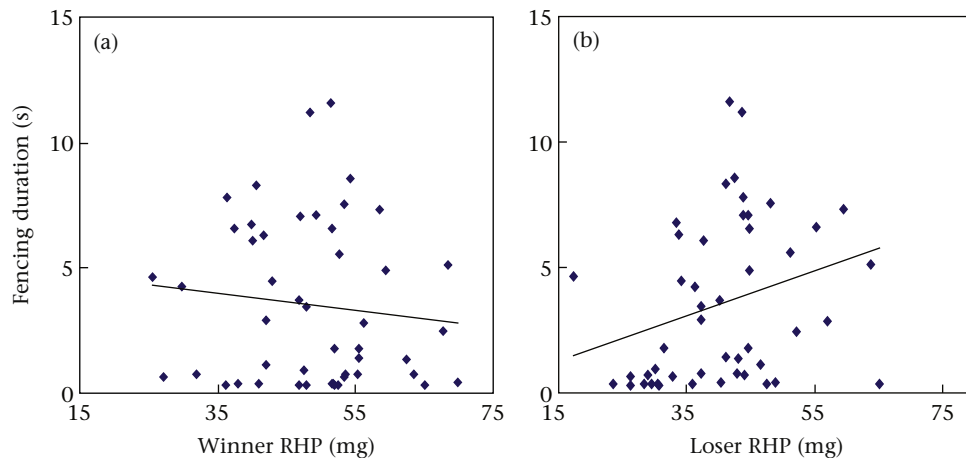


Figure 2. Fencing escalations in the contact phase in *Phidippus clarus*. The relationship between fencing duration and (a) winner RHP (weight) and (b) loser RHP (weight).

more likely to engage in grapples (Fig. 3). We also performed a multiple backward stepwise regression to see whether any variables predicted grappling duration. The final model was not significant (final model: $r^2 = 0.355$, $F_{1,6} = 4.857$, $P = 0.070$), but there was a trend for the duration of grappling to be predominantly driven by loser weight ($\beta_6 = 0.669$, $P = 0.070$) but not winner weight ($\beta_6 = 0.435$, $P = 0.640$). The final model had low power brought about by the small sample of grapples ($N = 8$).

Contest Outcome

In the majority of contests (53 of 56), males that won the first bout won all three bouts. Using a backward multiple logistic regression for the first bout, we examined conditions that predicted whether individuals won contests. We entered weight, size and vibration signalling

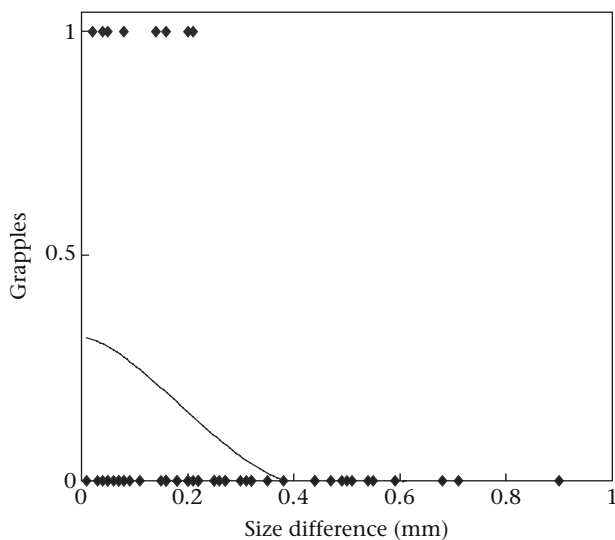


Figure 3. Grappling escalations in the contact phase *Phidippus clarus*. Logistic function of the likelihood of grapple escalation and differences in overall size (cephalothorax width).

differences into the model. In the final model ($P < 0.0001$, Nagelkerke $R^2 = 0.734$), both weight difference ($\beta_2 = 0.241$, $P = 0.003$) and vibration signalling differences ($\beta_2 = 0.350$, $P = 0.008$) significantly predicted contest outcome, with heavier and more actively signalling males winning more contests (Fig. 4).

Second and Third Bouts

After the initial contest was concluded, we recorded detailed behaviours on two more contest bouts. In the second and third contest bouts, males spent significantly less time in precontact phases (repeated measures ANOVA: $F_{1,54} = 41.218$, $P < 0.0001$; bout 1: 41.845 ± 3.851 s; bout 2: 18.988 ± 1.380 s; bout 3: 13.946 ± 1.665 s). There were significant differences in precontact duration between bout 1 and bout 2 (Tukey post hoc: $P < 0.0001$), between bout 1 and bout 3 ($P < 0.0001$) and between bouts 2 and 3 ($P = 0.02$; Fig. 5a). In the second and third contest bouts, males also spent significantly less time in contact phases (repeated measures ANOVA: $F_{1,54} = 8.083$, $P < 0.001$; bout 1: 23.913 ± 8.033 s (with grapples included, $N = 56$), 3.535 ± 0.466 s (without grapples, $N = 48$); bout 2: 1.765 ± 0.315 s, $N = 56$; bout 3: 1.020 ± 0.315 s, $N = 56$). Whether or not escalation included grapples, there were differences between bout 1 and bout 2 (Tukey post hoc: $P < 0.001$), between bout 1 and bout 3 ($P < 0.001$) and between bouts 2 and 3 ($P < 0.001$). No grapples occurred in bouts 2 or 3 (Fig. 5a).

Changes in vibratory behaviour after the initial bout depended on contest outcome. The number of vibrations produced by the winner did not significantly change from bout to bout (repeated measures ANOVA: $F_{1,55} = 3.611$, $P > 0.05$; Fig. 5b). The number of vibrations produced by the loser, however, significantly changed between bouts ($F_{1,55} = 54.582$, $P < 0.0001$; Fig. 5) and differences were observed between bouts 1 and 2 (Tukey post hoc: $P < 0.0001$), and bouts 1 and 3 ($P < 0.0001$) but not between bouts 2 and 3 ($P > 0.05$; Fig. 5b).

In bouts 2 and 3, contest winners were significantly predicted by differences in vibratory signalling ($\beta_3 = 10.661$,

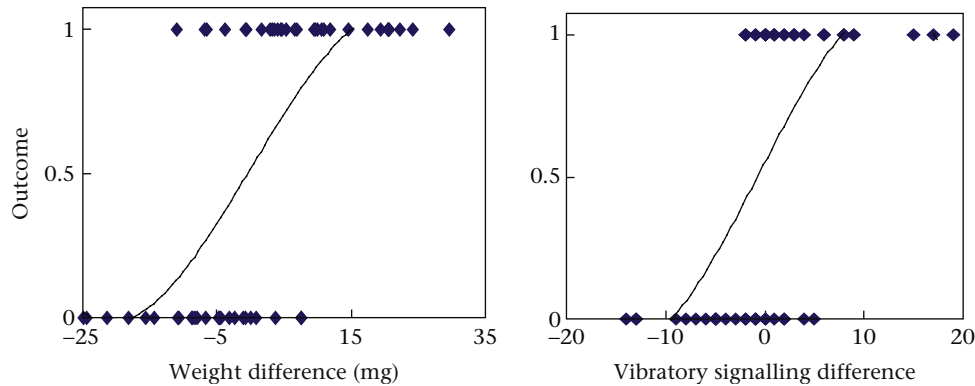


Figure 4. Outcome of *Phidippus clarus* contests. Logistic function of the likelihood of winning and losing as a function of (a) weight differences between rivals and (b) signalling differences between rivals.

$P < 0.0001$, Nagelkerke $R^2 = 1.0$) and not by differences in weight. Vibratory signalling differences in the model almost perfectly predicted winners in bouts 2 and 3 since losing males virtually stopped vibrating. Since vibratory signalling almost perfectly predicted contest outcome and explained all the variance in the data, weight differences were not significant in the final logistic model for bouts 2 and 3.

DISCUSSION

Our results reveal that male jumping spiders use multimodal signals (visual and substrate borne) during aggressive interactions. In particular substrate-borne vibratory signals appear to be of special importance as the number of vibratory signals accurately predicted contest outcome for repeated bouts against the same opponent. Furthermore, the duration of precontact phases was based on differences in vibration behaviour between males. Bigger males were more willing to escalate towards contact phases even though the outcome of escalated fights was based more on weight than on size. The upper limit of a male's weight depends on his size (larger males are heavier), so overall size is set, whereas weight depends on the animal's current feeding history. Thus, size is ultimately an unreliable cue of fighting ability because male weight can vary greatly within size classes (D. O. Elias & M. M. Kasumovic, personal observation). This may explain why males always escalated to leg fencing in the first contest bout. Once males have additional information regarding the true fighting ability (weight) of opponents, contest outcome in subsequent bouts is based on vibratory signals. Escalation in early bouts may therefore be a way to ensure honest signalling behaviour. Alternatively, the presence of a valuable resource (female nest) may explain escalation, because pheromones can increase the likelihood of escalation in some jumping spider species (Cross et al. 2007).

Experience effects are extremely important in many animal contests (reviewed in Hsu et al. 2006), and our results suggest that this is also the case for multiple contests with the same opponent in *P. clarus*. First, contest experience affected a male's signalling rate; although winners

signalled repeatedly at the same rate, losers significantly decreased their signalling rate after losing the first bout. Second, experience appeared to influence the importance of vibratory signalling behaviour in predicting contest outcome. Lastly, experience affected the time that males spent in escalated fights, with subsequent bouts being significantly briefer than the first bout. It is unknown how long these experience effects last and whether or not this effect would transfer to new opponents. It is possible that these experience effects could be attributed to a switch of the 'rules' that govern contest outcomes. In initial contests, winners were decided by directly measuring fighting ability, whereas in subsequent contests, males used information from multimodal signals. In the field, males may very likely escape after losing a single contest, so repeated bouts with the same individual may be rare. However, our results are still valuable because they reveal that experience (particularly losing experience) can have substantial effects on subsequent behaviours. Future work will assess experience-dependent effects of *P. clarus* contests.

Our study suggests that contest duration, particularly when males are physically competing against each other, are based predominantly on individual thresholds (self-assessment) and to a lesser extent on opponent assessment (mutual assessment). When loser and winner weights were considered separately, loser weight was significantly positively related to contact duration and winner weight showed a tendency to be negatively related to contact phase duration. These results match the predictions of self-assessment, since 'true' mutual assessment mechanism should show an equal but opposite relationship between losers and winners (Taylor & Elwood 2003).

While supporting self-assessment, our results also suggest that rival assessment may play a secondary role. In partial mutual assessment cases, one would predict that as more rival assessment occurs, a negative relationship will develop between winner weight and contest duration (Prenter et al. 2006). We found a nonsignificant negative trend between winner weight and contest duration, consistent with a scenario of partial mutual assessment. More definitively, in our multiple regression model that included both winner and loser weights, both showed

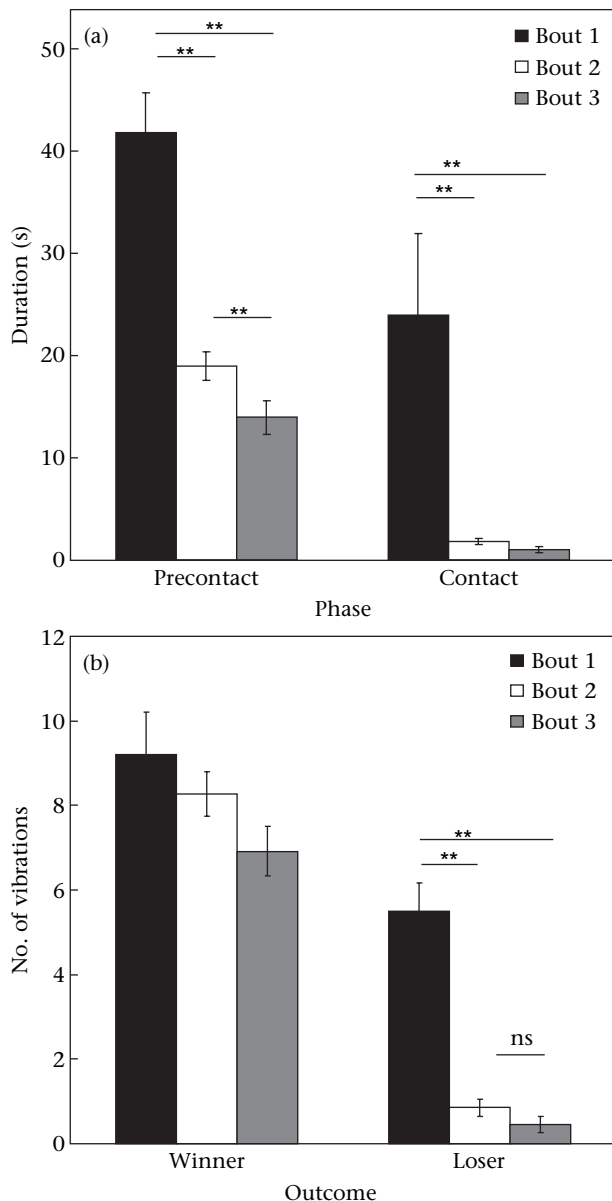


Figure 5. Effect of experience on contests. (a) Differences between contest phase duration in different bouts. Both precontact and contact phase duration were significantly reduced after initial contests. (b) Difference between vibrational signalling between different contest bouts. $**P < 0.001$.

a significant but opposite relationship with duration, once again suggesting the contribution of mutual assessment mechanisms. When the covariance between both opponents (winner weight \times loser weight) was accounted for, both loser weight and the interaction term were significant, once again suggesting a primary role for self-assessment and a secondary role for mutual assessment. Mutual assessment and self-assessment mechanisms may thus be part of continuum of assessment strategies, and males may shift between self-assessment and mutual assessment as more information becomes available or as information becomes more reliable (Prenter et al. 2006).

Using individual thresholds (self-assessment) to determine contest duration may be an economical way to

accurately determine the degree of escalation, and ultimately, contest outcome while avoiding the costs associated with accurate rival assessment. The energetic demands needed to detect and process a rival's cues and signals as well as the time needed to process the information for accurate decisions could be substantial. These costs would be even more extreme if cues and/or signals are unreliable indicators of actual fighting ability. Using individual-based thresholds to decide contests, therefore, allows males to pay only the costs that they are willing to pay, while retaining a high likelihood of winning contests against inferior rivals. The growing number of studies showing the importance of self-assessment mechanisms suggests that this mechanism could be common throughout the animal kingdom (Bridge et al. 2000; Taylor et al. 2001; Jennings et al. 2004; Morrell et al. 2005; Garland & Kelly 2006; Prenter et al. 2006).

In a previous study, Morrell et al. (2005) observed similar results and proposed that a cumulative assessment game theory model (Payne 1998) may explain their results. In such scenarios, no actual opponent assessment is necessary and male contest duration is based on individual thresholds (self-assessment), but a form of rival 'assessment' results from rival dependent cost accumulation (Payne 1998; Morrell et al. 2005). Cumulative assessment games also predict that individuals of higher quality (i.e. bigger males) begin contests at higher intensity (Payne 1998), a prediction met in our study of *P. clarus*, as bigger males vibrated more at the initial stages of contests. In addition, cumulative assessment games predict that as contests proceed, both contestants escalate to maintain the optimum balance between damage and energetic costs (Payne 1998). This prediction was also met in *P. clarus* in the ordered escalation of behaviours from multimodal displays to fencing and grappling. While cumulative assessment is a distinct possibility in *P. clarus*, the existence of multiple signals in aggressive displays as well as the increased importance of vibratory signals with contest experience suggest that mutual assessment mechanisms (i.e. sequential assessment games; Enquist & Leimer 1983, 1987, 1990) also have a significant effect on contests. Our results thus suggest the possibility that contests may switch from cumulative assessment rules to sequential assessment rules as the predictive accuracy of behavioural elements increases (Enquist & Leimer 1983, 1987, 1990; Payne 1998; Stuart-Fox 2006).

Our study also has implications for understanding the evolution of communication in the context of intermale contests. In our trials, males relayed information about size (both foreleg waving and vibration signals), even though size did not predict contest outcome. Thus, our work shows that multiple signals can persist even if they are unreliable indicators of a male's actual fighting ability (Bridge et al. 2000). Theoretical work has suggested that unreliable signals can evolve when costs of producing signals are relatively low, and thus, may offer some small Fisherian benefit (Pomiankowski & Iwasa 1993, 1998; Iwasa & Pomiankowski 1994). Our results suggest that initially unreliable signals (e.g. visual or vibratory signalling) may be ignored by the receiver, but as the information

value of these signals increases during assessment of another male cue (i.e. male fighting ability), the initially unreliable signal can become informative and processed so the receiver can make appropriate choices in subsequent decisions. Such composite effects of different signals may be important in the evolution of multiple signals (Rowe 1999; Hebets & Papaj 2005; Partan & Marler 2005).

In summary, our results show that in the jumping spider *P. clarus*, even though males used multimodal signals in aggressive contests, contests were determined predominantly by a male's assessment of his own fighting ability. However, our statistical examination of covariances between traits of rivals also suggests that mutual assessment plays a secondary role in determining contests. We conclude that the importance of mutual assessment may increase based on the reliability of information available to males as well as their previous fighting experience. Future studies are necessary to examine the role of experience in future contests against new rivals, and whether males follow the same set of rules of assessment when multiple rivals are encountered.

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