High resource valuation fuels "desperado" fighting tactics in female jumping spiders

Damian O. Elias,[a] **Carlos A. Botero,**[b] **Maydianne C. B. Andrade,**[c] **Andrew C. Mason,**[c] **and Michael M. Kasumovic**[c,d]

[a]Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA 94720, USA, [b]National Evolutionary Synthesis Center, 2024 W. Main St. (Suite A200), Durham, NC 27705, USA, [c]Integrative Behaviour and Neuroscience Group, University of Toronto Scarborough, Toronto, Ontario, Canada M1C 1A4, and [d]Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, Sydney 2052 NSW, Australia

Opponent asymmetries often determine the probability of winning a fight in agonistic situations. In many animal systems, the asymmetries that drive the dynamics and outcome of male—male contests are related to resource holding potential (RHP) or territory ownership. However, recent studies have shown that this is not the case among females and suggest that resource valuation may be more important in that context. We studied contests between the female jumping spider, *Phidippus clarus*, and compared them with male–male contests in this same species. Our observations document several key differences between the sexes: Precontact and contact phases are longer in females, ritualized displays are rare in females but common among males, and female fights are more likely to end in injury or death. In sharp contrast with male contests, female weight and size do not correlate with signaling behavior, and the outcome of fights is predicted by differences in resource valuation rather than RHP. We interpret these differences in light of the different natural history of the sexes and discuss how the economics of fighting may lead to the evolution of ritualized displays in males and a "desperado effect" in females. *Key words:* divisive asymmetry, female—female competition, game theory, jumping spider, resource holding potential, resource potential value. *[Behav Ecol 21:868–875 (2010)]*

Theoretical investigations have proposed that opponent asymmetries determine the probability of winning a fight in agonistic situations (Parker 1974; Maynard Smith and Parker 1976; Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983, 1987, 1990; Riechert 1988; Leimar et al. 1991; Payne and Pagel 1996; Payne 1998). This deterministic relationship promotes the evolution of ritualized displays that help reduce the frequency of escalated fights with stronger (larger, older, etc.) opponents (reviewed by Bradbury and Vehrencamp 1998; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). In most animal systems, empirical work on male–male agonistic interactions has demonstrated that ritualized displays and contest dynamics are largely determined by the quality and condition of opponents (Koivula et al. 1993; Jennions and Backwell 1996; Taylor et al. 2001; Taylor and Elwood 2003; Jennings et al. 2004; Hsu et al. 2006; Prenter et al. 2006; Hoefler 2007; Arnott and Elwood 2008, 2009a; Brandt and Swallow 2009; Hsu et al. 2009). However, recent studies show that female–female fights in some of these same species tend to be less ritualized, riskier, and appear to be uncorrelated with resource holding potential, hereon RHP (Robinson 1985; Koivula et al. 1993; Dale and Slagsvold 1995; Draud et al. 2004; Fowler-Finn and Hebets 2006; Arnott and Elwood 2009b) (but see Rillich et al. 2009). For example, Draud et al. (2004) found that in Texas cichlids, male contest structure and outcome were decided on the basis of size asymmetries, whereas in female contests, it was not. In

convict cichlids, Arnott and Elwood (2009b) found that female fights involve more costly "bite" and "frontal display" behaviors than do male fights. One possible explanation for these intraspecific differences is that agonistic behavior in females is driven by differences in resource potential valuation, hereon RPV rather than RHP (Draud et al. 2004; Tibbetts 2008).

Theoretical work has suggested that RPV asymmetries may best predict contest success in situations where the costs of not fighting at all are even higher than those of losing against opponents with greater fighting ability (Grafen 1987). For example, whenever reproductive substrates are scarce, individuals may only be able to reproduce if they defend it against all rivals regardless of quality or condition ("desperado effect," Grafen 1987). This scenario is known as a "divisive asymmetry" (Grafen 1987) because weaker (or smaller, lighter, etc.) individuals would never reproduce if they respect RHP asymmetries. Divisive asymmetries promote the evolution of fights with higher risk of injury/death and little or no signaling. Although this scenario has been described theoretically, direct empirical support is scarce (but see Plaistow and Siva-Jothy 1996).

Jumping spiders have been the focus of several recent studies on male–male aggression (Jackson 1980; Wells 1988; Jackson and McNab 1989; Faber and Baylis 1993; Clark et al. 1999; Taylor and Jackson 1999; Taylor et al. 2000, 2001; Cross et al. 2006; Jackson et al. 2006; Cross et al. 2007; Hoefler 2007; Elias et al. 2008; Kasumovic et al. 2009b; Kasumovic et al. 2010). *Phidippus clarus* is a member of this group that routinely engages in highly aggressive acts toward conspecifics. Males of this species exchange ritualized vibratory and visual signals prior to contact and, in most cases, engage in direct contests consisting of leg fencing and grappling

(Hoefler 2007, 2008; Elias et al. 2008; Kasumovic et al. 2009b). In these contests, precontact bout duration is positively correlated with the number of vibrations emitted by the eventual winner, and the duration of the physical contact phase is determined by the weight of the loser and, to a lesser extent, the weight of the winner (Elias et al. 2008). As a general rule, heavier males that signal more are more likely to win a fight, suggesting that males engage in partial mutual assessment during these fights (see Hoefler 2007; Elias et al. 2008; Arnott and Elwood 2009a).

Here, we study female–female contests in adult nongravid *P. clarus* to determine 1) signaling behavior, 2) risk of injury, 3) contest dynamics, and 4) properties that determine the duration of the pre and postcontact phases in these interactions. First, we compare these contests with previous findings on male–male interactions and describe sex-specific differences in agonistic behaviors. In a follow-up experiment, we then test the hypothesis that contest dynamics in female–female interactions are driven by asymmetries in RPV rather than by relative RHP or ownership.

Early in the breeding season, immature females inhabit silken retreats (hibernacula) that are built within rolled-up leaves (Hoefler and Jakob 2006; Elias et al. 2008). In the field, females prefer some nest sites over others (Elias DO, Kasumovic MM, personal observation) and return to these hibernacula with high fidelity (Hoefler and Jakob 2006). During reproduction, subadult females and hibernacula are defended by adult males (Hoefler and Jakob 2006; Hoefler 2007, 2008). Females must first molt to maturity before they are able to breed, and during this molting period, they are likely vulnerable to predation and other risks (see Soluk 1990; Witt and Dill 1996; Lucas et al. 2000; Patek 2001). Because molting takes place within the safety of the hibernacula (Hoefler 2007; Elias et al. 2008), immature females that are about to molt are expected to value nesting sites more highly than younger less vulnerable ones. We took advantage of this potential effect of latency to molt on resource valuation to test whether weight asymmetries (RHP), latency to molt asymmetries (RPV), or residency asymmetries (intruder vs. resident) predicted contest success in immature (penultimate) females.

METHODS

Experimental setup 1: nongravid adult females

We measured aggressive behavior and assessed contest dynamics by observing staged pairings between nongravid adult females (collected in 2008). Our contests mimicked natural interactions between females as adult females wander away from their nests in search of food after sexual maturation. Females were paired randomly with contestants (female weight range: 21.80–69.0 mg; 42.85 ± 11.44 mg, mean ± standard deviation [SD], $n = 88$ females; mean absolute size difference ± SD: 8.65 ± 7.50 mg, $n = 44$ pairings), and each female was only used once.

We used only females collected in their last juvenile instar (penultimate females) to ensure that all focal females were of the equivalent developmental stage and mating status. Maturity of females was monitored closely throughout the experiment. Adult females were considered nongravid if they were unmated ($= 61$) or had mated less than 4 days prior to the nongravid trials ($n = 27$). Preliminary work suggested that females become gravid after a minimum of 14 days following mating (Elias DO, Kasumovic MM, unpublished observations). At least 2 days prior to experiments, females were anesthetized with CO_2 and 2 dots of nontoxic paint (Luminous paint, BioQuip Products, Inc, Rancho Dominguez, CA) placed on the abdomen (opisthosoma) to allow individual identification during

contests. We ensured that females recovered from the anesthetic by verifying that they fed on prey after the procedure. This method has been used successfully in previous experiments on males (Elias et al. 2008; Kasumovic et al. 2009b).

Contest arenas were constructed by stretching nylon fabric on a circular 20-cm diameter needlepoint frame and placing a cylinder of clear acetate around the frame. Petroleum jelly was placed on the inside of the cylinder wall to prevent spiders from crawling out of the arena, and an opaque paper ring was placed around the outside of the cylinder to prevent unwanted visual distractions. Between trials, we cleaned the arena with ethanol to prevent the buildup 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 contests 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; Elias et al. 2008). A piece of reflective tape (ca. 1 mm^2) was placed on the center of the arena to serve as a measurement point for the LDV. 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).

Initially, a removable cardboard barrier was placed in the arena to divide it into 2 equal parts, and a single female was introduced into each side of the arena. The barrier ensured that each female had a period to acclimatize and removed any resident or ownership asymmetries from the interaction. The barrier was removed after 2 min. After experiments concluded, we weighed (Ohaus electronic balance) and digitally photographed (Nikon Digital Camera DXM 1200) all females using a Zeiss microscope (Stemi 2000C). We then measured cephalothorax (prosoma) width as a metric for body size from the digital photographs using ACT-1 measurement software (Nikon).

In all the interactions, the duration of precontact and postcontact escalation phases were recorded. Precontact phases were measured from the time both females oriented toward one another to the initiation of body contact or the retreat of one of the females. If females did not orient to each other ($n = 11/44$ trials), females were separated by the observers using light touches with a paint brush in order to limit the probability of death (as females often attack and eat unobservant opponents). Females were separated until both successfully orientated to each other. Interruption had no qualitative affects on contests, and all results were indistinguishable if only interrupted or noninterrupted contests were included (data not shown). Contact phases were measured from the initiation of body contact to the time the losing female turned away from the winning female. In addition, we recorded the number of substrate-borne signals produced by each female. Females produce vibratory signals using abdominal tremulations much the same way as males (Elias et al. 2008). These tremulations are visible to the naked eye and are evident in the videotaped recordings. All interactions were observed by 3 researchers. Two researchers recorded the occurrences of vibratory signals (each scored a different female), whereas the third researcher recorded overall contest properties. Observations were later verified using videotapes. From these videotapes, we also collected a sample of substrate-borne signals ($n = 27$) using Adobe Premiere Pro 2.0. The temporal and spectral properties of these signals were measured using Matlab (The Mathworks).

Statistical analyses (nongravid adult females)

Female weight and size were highly correlated ($r^2 = 0.504$, $P < 0.0001$). Because weight was the strongest predictor of contest

success in males (Elias et al. 2008; Kasumovic et al. 2009b), we only include this factor in all the statistical models described below to avoid multicollinearity. Our results are qualitatively identical if other morphometric traits are included or if morphometric traits are collapsed into a single principal component score (data not shown).

In order to determine which variables are the best predictors of success in female fights, we used a binary logistic regression with weight asymmetry (focal female weight minus opponent female weight), relative vibrations (focal female vibrations minus opponent female vibrations), mating status (virgin vs. mated), and all possible two-way interactions as independent factors. To avoid pseudoreplication, this model only included measurements of 1 focal individual per contest (chosen at random using a coin flip).

We analyzed substrate-borne signaling (i.e., number of vibrations produced by the focal individual) using a multiple regression model that included focal female weight, number of opponent vibrations, and focal weight $\times$ opponent vibration interaction as independent variables. All tests reported here are two-tailed, and summary statistics are presented as mean $\pm$ standard error unless otherwise noted. We report standardized coefficients for β and adjusted r^2 values. Statistical analyses were performed using JMP 7.0 (SAS Institute Inc., Cary, NC).

Experimental setup 2: penultimate residents and intruders

We examined how RHP, RPV, and ownership affect contest outcomes by staging trials between pairs of penultimate instar females, where 1 female was established before the trial as the resident in an artificial hibernaculum. In 2009, we placed penultimate instar field-collected females in a $10 \times 10 \times 3$ cm plastic arena with a small translucent vinyl tube (1.5 cm in diameter and 4-cm long) secured at the center of arena using blue tack. Penultimate females in the field and in the laboratory will build hibernacula within these vinyl tubes (Hoefler and Jakob 2006). Container walls were covered with petroleum jelly to prevent individuals from climbing. Females were allowed to acclimate to their new surroundings for at least 1 day. To start each contest, we dislodged one randomly chosen female (intruder) from a hibernaculum and placed her into the container of another resident female. The contest started once the intruding female approached and contacted the entrance to the resident's hibernaculum. Contests lasted until the losing female turned and ran from the winner, and the winner settled within the tube. We timed all contests using a stopwatch, noting the time the individuals first observed one another, the time of first contact, the length of each bout, as well as the winner. After the contest concluded, we removed each individual, weighed them, and placed them back into their individual cages. We monitored females twice daily to note the time when penultimate females matured. Latency to molt was recorded as the number of days between the trial and maturation and serves as a proxy for RPV (females with the shortest latencies should value the hibernaculum most highly).

Statistical analyses (penultimate females)

As in the previous experiment, we randomly selected a focal individual from each contest using a coin flip. For each focal individual, we noted weight asymmetry (focal weight − competitor weight), molt asymmetry (focal latency to molt − competitor latency to molt), and residency status (resident vs. intruder) as well as whether the focal individual won or lost the contest. We used a binary logistic regression to determine the effects of latency-to-molt asymmetry, weight asymmetry,

and resident status on contest outcome. Statistical analyses were performed using JMP 7.0 (SAS Institute Inc.).

RESULTS

Experiment 1: nongravid adult females

Precontact phase
Females often "stalked" unsuspecting opponents in a manner that is typical of predatory behavior in jumping spiders. In contrast, males do not stalk opponents and instead display at a distance until their opponents orient toward them (Elias et al. 2008). When both females in our trials became aware of each other's presence, they oriented toward each other, stopped abruptly, and remained stationary for some time. After this initial "staring" period, some females retreated immediately ($n = 18/44$ trials), whereas others approached their opponents with the forelegs outstretched ($n = 26/44$ trials). These approaches were direct and unlike the typical "zigzag" approaches observed in males (Elias et al. 2008). In a multiple stepwise regression, no weight or signaling asymmetries significantly predicted whether contests escalated to direct physical contact (final model: $\chi^2 = -0.39$, degrees of freedom [df] = 1, $P = 0.53$, $n = 44$).

Precontact staring phases lasted 98.2 ± 15.5 s, which is twice the duration of precontact bouts in males (41.85 ± 3.85s in males; Elias et al. 2008; $F_{1,106} = 16.448$, $P < 0.01$). Winner weight, loser weight, and the number of vibrations of both winners and losers were not significant predictors of precontact phase duration in females (multiple stepwise regression: $P > 0.05$). In contrast, the number of vibrations performed by the winner predicts the duration of the precontact phase in male trials (Elias et al. 2008).

In spite of having longer precontact phases, females used visual and vibratory signals much less often than males ($n = 29/88$ females, this experiment, vs. 108/112 males, unpublished data from Elias et al. 2008). Furthermore, when opponents signaled, the number of signals produced by females was smaller than that produced by males (male vibrations: 7.36 ± 0.63; female vibrations: 3.24 ± 0.71; $F_{1,198} = 18.9373$, $P < 0.01$; male leg waves: 7.36 ± 0.47; female leg waves: 0.49 ± 0.47; $F_{1,198} = 94.2951$, $P < 0.01$). Female vibratory signals were produced in bouts consisting of a single vibration (Figure 1A). Although these vibrations were similar in frequency to those produced by males (143.4 ± 1.4 Hz, $n = 18$ females vs. 155.4 ± 8.4 Hz in males; Elias et al. 2008), female vibrations lasted much longer (399.0 ± 49.74 ms, $n = 17$ females vs. 64.69 ± 2.06 ms males; Elias et al. 2008).

Relative weight differences did not predict the tendency to emit aggressive vibratory signals in females (binary logistic regression: $P > 0.05$). Nevertheless, in the subset of cases in which females vibrated, opponent vibrations (multiple stepwise regression, $r^2 = 0.1838$: $\beta = 0.27$, $F_{2,84} = 10.49$, $P < 0.01$; Figure 1B), focal weight ($\beta = 0.08$, $F_{2,84} = 4.05$, $P = 0.03$), and the interaction between focal female weight $\times$ opponent vibration ($\beta = 0.02$, $F_{1,84} = 6.39$, $P = 0.01$) were significant predictors of the number of vibrations produced by the focal individual. In males, only size ($r^2 = 0.09$, $\beta = 0.32$, $P < 0.01$, $n = 112$) and opponent vibrations ($r^2 = 0.27$, $\beta = 0.52$, $P < 0.01$, $n = 112$) predict the number of vibrations produced (Elias et al. 2008).

Contact phase
When females were in close proximity (i.e., less than one body length away), they lunged at each other repeatedly with frontally extended forelegs and attempted to bite each other. Although a small proportion of females ($n = 4/44$ trials) pushed their opponents backward, similar to "fencing" behavior in males
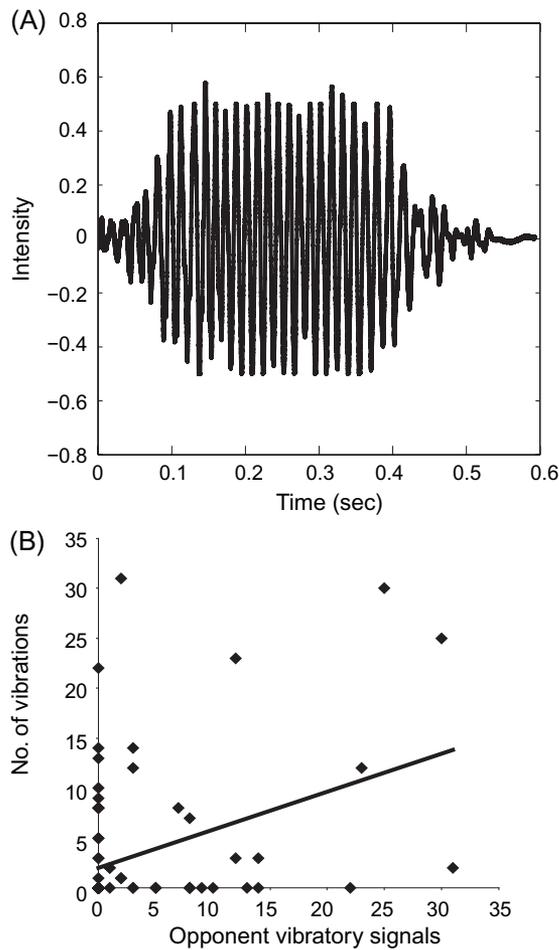
Figure 1
Aggressive vibratory signaling in female *P. clarus*. (A) Oscilligram of vibrational signal. (B) The relationship between an individual's own vibrations and the vibration of her opponent. Most females did not produce vibratory signals (59/88 individuals).

(Elias et al. 2008), all females reverted to lunge/bite attacks. Female fights were more aggressive than male fights and led to a significantly higher mortality rate (7/44 attacks ended in death in females, this experiment, whereas 0/56 attacks ended in death in males; unpublished data from Elias et al. 2008; likelihood ratio test: $\chi^2 = 10.31$, df = 1, $P < 0.01$). In addition, bleeding as a direct result of contests was evident in many surviving females but rare in males.

On average, the contact phase was almost 10 times longer in females (29.5 ± 5.95 s) than in males (3.52 ± 3.23 s; Elias et al. 2008; male vs. female duration: $F_{1,78} = 37.41$, $P < 0.01$). Only loser weight significantly predicted the duration of this phase (multiple stepwise regression, $r^2 = 0.21$: β = 1.61, $F_{1,39} = 9.94$, $P < 0.01$; Figure 2). The lack of an effect of winner weight (β = 0.49, $P = 0.50$) on postcontact duration is consistent with a pure self-assessment strategy in females (Arnott and Elwood 2009a).

Contest outcome
No observed asymmetries or potential interactions significantly predicted contest outcome in females if all nongravid females were lumped (binary logistic regression: $P > 0.05$; Figure 3). In contrast, weight and signaling asymmetries strongly predict contest outcome in male contests (Elias et al. 2008). If contest outcome was analyzed separately for adult virgins ($n = 61$) or mated females ($n = 27$), no asymmetry or potential interaction significantly predicted outcome (binary logistic regres-

sion: $P > 0.05$). In addition, no measured asymmetries predicted winners if only escalated contests (contests with contact phases; binary logistic regression: $P > 0.05$, $n = 29/44$ trials) or non–escalated contests (binary logistic regression: $P > 0.05$, $n = 15/44$ trials) were analyzed.

Experiment 2: penultimate resident and intruder behavior

In penultimate female trials, residents noticed intruders first in 26 of 27 trials. In all instances, residents stayed in their own hibernacula but continuously tracked movements of intruders. Once intruders found a hibernaculum, we observed 1 of 3 outcomes: 1) In 11 of 27 trials, intruders approached and attempted to enter the hibernaculum, whereas residents attempted to close the silken entrance by pinching it with their forelegs. Residents then exited through the opposite entrance (experimental hibernacula, as those observed in natural settings, had 2 entrances). Intruders won all these interactions. 2) In 8 out of 27 trials, intruders approached the entrance of the hibernacula and the resident emerged immediately. In these cases, intruders often displayed briefly before retreating without any physical contact. Residents won all these interactions. 3) In the remaining 8 trials, both intruders and residents proceeded to display and sometimes to lunge at each other (as in the contests between nongravid adult females, see above). The postcontact phases in these trials were slightly shorter (16.5 ± 13.66 s, $n = 8$) and less intense than those observed in adult female contests ($F_{1,42} = 3.6892$, $P = 0.06$). We did not record substrate-borne vibrations in these trials but observed vibrations occurring in some contests (9 of 27 contests).

Contest outcome
We used a binary logistic regression to look at the conditions that predict contest outcomes in penultimate females. In the final model ($\chi^2 = 34.22$, df = 14, $P < 0.01$, $n = 27$), latency to molt differences ($\chi^2 = 18.25$, df = 2, $P < 0.01$; Figure 4) and a residency × weight difference interaction (residency: β = 5.24, $\chi^2 = 1.67$, df = 2, $P = 0.43$; weight difference: β = –3.48, $\chi^2 = 2.20$, df = 2, $P = 0.33$; residency × weight difference: $\chi^2 = 14.98$, df = 2, $P < 0.01$) predicted contest outcome and not weight difference ($\chi^2 = 2.20$, df = 1, $P > 0.05$) or residency status alone ($\chi^2 = 1.67$, df = 2, $P > 0.05$). Females with shorter latency to molt were more likely to win contests.

DISCUSSION

Agonistic interactions in *P. clarus* show strong sexual differences in every way measured in this study. Most strikingly, female–female contests are less ritualized than those of males and result in higher rates of injury and death. These costs are likely to be higher in natural conditions because wandering females can carry out surprise attacks (note that in our trials, females were prevented from stalking their opponents). Female–female contests also have a substantially longer precontact phase than those between males and fewer ritualized displays (both in terms of visual and vibratory signals). Furthermore, our data indicate that during same-sex interactions, females rely mainly on self-assessment (although stalking and precontact staring suggest at least a crude form of rival assessment), whereas males appear to modify individual thresholds depending on their opponent's relative quality (partial mutual assessment; Elias et al. 2008). Finally, winners in male–male contests are determined by RHP (Hoefler 2007; Elias et al. 2008; Kasumovic et al. 2009b) and residency status (Kasumovic MM, Elias DO, unpublished data), whereas in female–female contests, they were not. Instead, we suggest that they are determined by differences in RPV (as shown in experiment 2).

Figure 2
Contact phase in female *P. clarus.* The relationship between contact phase duration and (A) winner RHP (weight) and (B) loser RHP (weight). Results of both linear and multiple regressions support a scenario of pure self-assessment.
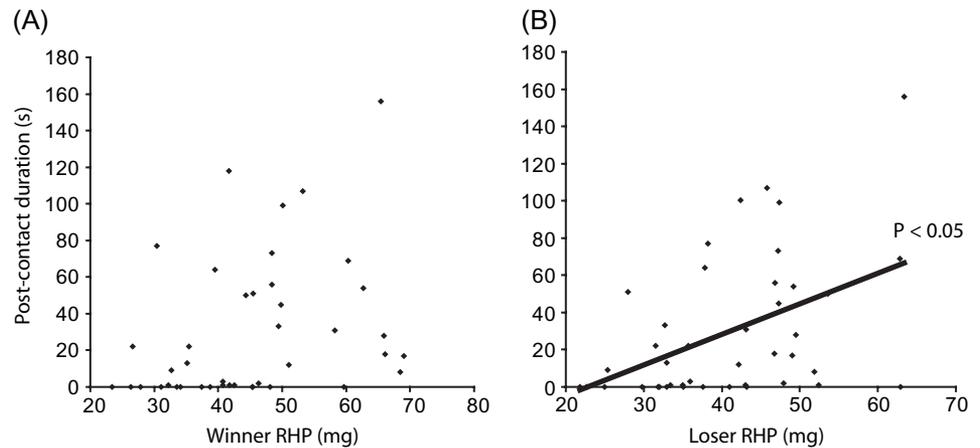
Differences in natural history may explain the observed differences in agonistic behavior between the sexes of *P. clarus.* Males mature quickly and die shortly after the end of the breeding season (Hoefler 2007, 2008). They are highly mobile and encounter each other at a high rate, primarily in the context of competition for receptive females. Each male may defend multiple females throughout its lifetime. Those who succeed at finding and defending a partner will mate and potentially move on to seek another one, whereas those that do not can potentially locate a new partner. As a result, the benefit of winning a single fight is relatively small because the losers are very likely to be able to reproduce elsewhere. Thus, the steep cost/benefit ratio of male–male encounters may explain why males have evolved ritualized displays in this species and do not fight to the death (see Grafen 1987).
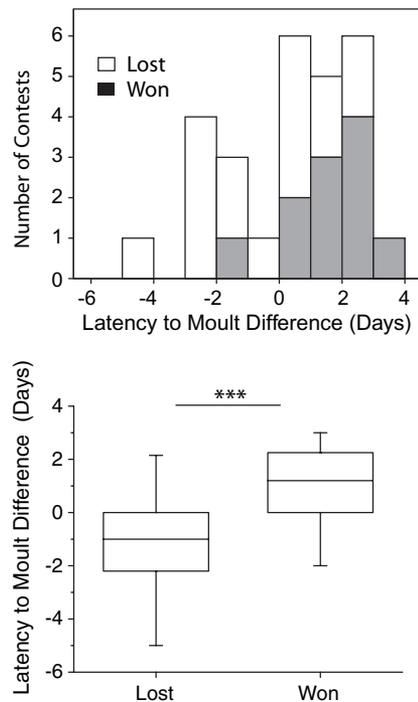

Figure 3
Outcome of contests between adult nongravid female *P. clarus.* (a) Stacked histogram chart of the distribution of winners (black) and losers (white) as a function of weight asymmetry. (b) Box plots of winners and losers as a function of weight asymmetry. No observed RHP measure predicts contest winner.

In sharp contrast, female jumping spiders mature more slowly and spend most of their adult life close to their hibernacula (Hoefler and Jakob 2006). These nests are not only important for safety during molting but also necessary for reproduction. Field observations indicate that suitable sites for hibernacula are limiting. *P. clarus* is found in early succession fields consisting mainly of grasses, goldenrod, and milkweed. When plastic tubes are provided, females prefer to nest on these artificial substrates rather than on natural ones, suggesting that high-quality nest sites are limited (Hoefler and Jakob 2006). Furthermore, in the absence of artificial nests, females prefer to occupy young nonflowering milkweed plants over other more abundant substrates, such as flowering milkweeds, goldenrods, or other plants (Elias DO, Kasumovic MM, unpublished observation). Given that females stay close to their nests once they have found one, it is likely that females encounter each other primarily when one or both of them are searching for a nest site. As a result, there is a high premium for winning female–female fights because losers are unlikely to find other suitable nest sites or to be able to reproduce elsewhere. In the case of penultimate females (experiment 2), the premium of winning fights is highest for females closer to molting. These conditions set the stage for a divisive asymmetry and the subsequent desperado effect (sensu Grafen 1987), where females are unwilling to respect RHP or ownership asymmetries and are more likely to engage in injurious or fatal fighting.

Our results may be a reflection of a much broader phenomenon and, thus, could also help explain some differences in fighting behavior across species (see Grafen 1987). In general, evolutionary incentives for developing ritualized agonistic displays can be expected to be small in systems with divisive asymmetries because opponents gain little or no benefits from attending to signals (see Grafen 1987, Enquist and Leimar 1990). Thus, a detailed knowledge of the contested resources and how they affect lifetime reproductive success may provide important clues as to why ritualization is present in some species but poorly developed or lacking in others (e.g., gladiator frog; Martins et al. 1998).

Excluding systems with sex-role reversal (see Balshine-Earn and McAndrew 1995) or with mutual territorial defense (Arnott and Elwood 2009b), it appears that a correlation between RHP asymmetry and contest success in males but not in females may be common to many different species (Koivula et al. 1993; Dale and Slagsvold 1995; Draud et al. 2004; Arnott and Elwood 2009b) (but see Pie 1998). Recently, Draud et al. (2004) interpreted these differences in Texas cichlids (*Herichthys cyanoguttatum*) as an indication that female contests might be decided on the basis of differences in RPV rather than in
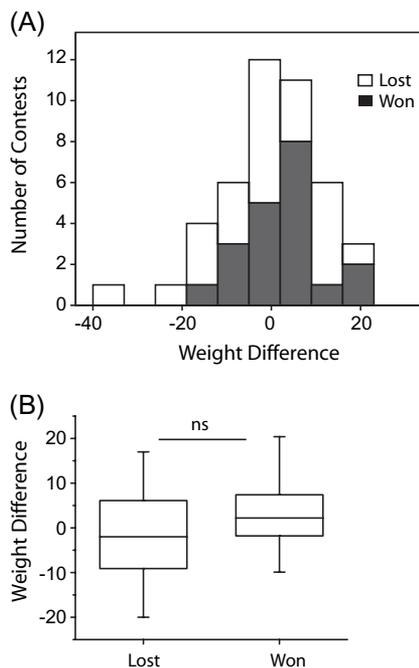
Figure 4
Outcome of immature resident and intruder female *P. clarus* contests. (a) Stacked histogram chart of the distribution of winners (black) and losers (white) as a function of age asymmetry. (b) Box plots of winners and losers as a function of age asymmetry. RPV (latency to molt) asymmetry predicts contest winner in immature females. ***$P < 0.0001$.

RHP. Our data provide the first experimental support for this hypothesis. In our system, it is noteworthy that female vibratory signals appear to provide little information about the sender's quality or ability to win a contest, yet elicited significant responses in opponents. One possible explanation for this result is that female vibratory signals provide information about resource valuation or individual motivation rather than about fighting ability. Alternatively, female vibratory signals may be used to deter stalking rivals from launching a surprise attack by alerting them that they have been detected. A third possibility is that signals in female–female fights are nonadaptive correlates of signaling behavior that occurs in contexts outside of the scope of this study. For example, similar vibratory signals have been observed in male–female interactions where unreceptive females vibrate aggressively toward courting males (Sivilinghem S, Elias DO, Kasumovic MM, unpublished data).

Our interpretation of the results for experiments 1 and 2 relies on the assumption that differences in RHP between females are properly measured by weight/size asymmetries. It could be argued that other variables not measured in this study (e.g., energy reserves) could also influence RHP and, thus, that agonistic behavior may still be ultimately determined by RHP. Additionally, latency to molt could be a proxy for RHP instead of RPV if, for example, molting hormone titers are related to fighting ability. However, these alternative scenarios are unlikely because size and weight are the main correlates of fighting ability in most systems (Enquist et al. 1990; Jennings et al. 2004; Morrell et al. 2005; Hsu et al. 2006; Arnott and Elwood 2009a), including the case of male–male contests in *P. clarus* (Hoefler 2007; Elias et al. 2008; Kasumovic et al. 2009a). Furthermore, it is highly unlikely that fighting ability would be enhanced as females approach the final molt.

In general, spiders show a decrease in activity at this time; and *P. clarus* females close to molting spend the majority of time in their nests, avoid interactions with other conspecifics, and even cease capturing prey (Elias DO, personal observation). Future work is needed to test these assumptions.

There is an additional alternative explanation for the results in experiment 2, which is that success in aggressive contests may trigger faster maturation in winning penultimate females. Many animals have shown developmental plasticity in response to competitive contexts (see Kasumovic and Andrade 2006, 2009a, 2009b), and it is possible that after competitive interactions, winners speed-up development and losers slow-down development. Although our experimental design cannot distinguish whether winning contests triggers maturation or whether developmental state influences winning, males choose females closer to maturation based purely on silk cues (Hoefler 2007), suggesting that female developmental state is detectable by rivals/potential mates. This indirect line of evidence suggests that developmental states are set in the time frames examined in this study. Future work will pursue the possibility that external effects such as male cohabitation, male experience, and female competitive success shifts developmental trajectories.

In conclusion, differences in the dynamics of male and female same-sex contests are potentially based on differences in encounter rates with rivals, fighting costs, resource value, and expected future reproductive success. Throughout a lifetime, males not only encounter more rivals but also have more reproductive opportunities. These conditions may have promoted the evolution of ritualized displays by increasing the fitness costs of fighting and decreasing the value of wining each fight (Grafen 1987). In contrast, females rarely encounter other females and when they do, it is likely that one or both of them is seeking a nest and/or territory. The need to obtain nests in order to accrue any fitness suggests a high valuation of winning fights that may lead to a desperado effect (Grafen 1987) and may promote the evolution of signals that are used only rarely and contain little information about the sender's quality or motivation.

Although our current knowledge of female–female interactions is much more limited than that of male–male interactions, the available studies suggest that intraspecific sexual differences in same-sex agonistic behavior may be the norm. New studies comparing male and female behavior will allow us to examine this pattern and may reveal some of the evolutionary underpinnings behind the evolution of contest resolution strategies and agonistic communication.

REFERENCES

Arnott G, Elwood RW. 2008. Information gathering and decision making about resource value in animal contests. Anim Behav. 76: 529–542.

Arnott G, Elwood RW. 2009a. Assessment of fighting ability in animal contests. Anim Behav. 77:991–1004.

Arnott G, Elwood RW. 2009b. Gender differences in aggressive behaviour in convict cichlids. Anim Behav. 78:1221–1227.

Balshine-Earn S, McAndrew BJ. 1995. Sex-role reversal in the black-chinned tilapia, *Sarotherodon melanotheron* (Ruppel) (Cichlidae). Behaviour. 132:861–874.

Bradbury JW, Vehrencamp SL. 1998. The principles of animal communication. Sunderland (MA): Sinauer Associates.

Brandt Y, Swallow JG. 2009. Do the elongated eye stalks of diopsid flies facilitate rival assessment? Behav Ecol Sociobiol. 63:1243–1246.

Clark RJ, Jackson RR, Waas JR. 1999. Draglines and assessment of fighting ability in cannibalistic jumping spiders. J Insect Behav. 12:753–766.

Cross FR, Jackson RR, Pollard SD, Walker MW. 2006. Influence of optical cues from conspecific females on escalation decisions during male-male interactions of jumping spiders. Behav Processes. 73:136–141.

Cross FR, Jackson RR, Pollard SD, Walker MW. 2007. Cross-modality effects during male-male interactions of jumping spiders. Behav Processes. 75:290–296.

Dale S, Slagsvold T. 1995. Female contests for nest sites and mates in the pied flycatcher *Ficedula hypoleuca*. Ethology. 99:209–222.

Draud M, Macias-Ordonez R, Verga J, Itzkowitz M. 2004. Female and male Texas cichlids (*Herichthys cyanoguttatum*) do not fight by the same rules. Behav Ecol. 2004:102–108.

Elias DO, Kasumovic MM, Punzalan D, Andrade MCB, Mason AC. 2008. Assessment during aggressive contests between male jumping spiders. Anim Behav. 76:901–910.

Elias DO, Mason AC, Maddison WP, Hoy RR. 2003. Seismic signals in a courting male jumping spider (Araneae: Salticidae). J Exp Biol. 206:4029–4039.

Enquist M, Leimar O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. J Theor Biol. 102: 387–410.

Enquist M, Leimar O. 1987. Evolution of fighting behaviour: the effect of variation in resource value. J Theor Biol. 127:187–205.

Enquist M, Leimar O. 1990. The evolution of fatal fighting. Anim Behav. 39:1–9.

Enquist M, Leimar O, Ljungberg T, Mallner Y, Segerdahl N. 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. Anim Behav. 40:1–14.

Faber DB, Baylis JR. 1993. Effects of body size on agonistic encounters between male jumping spiders (Araneae: Salticidae). Anim Behav. 45:289–299.

Fowler-Finn KD, Hebets EA. 2006. An examination of agonistic interactions in the whip spider Phrynus marginemaculatus (Arachnida, Amblypygi). J Arachnol. 34:62–76.

Grafen A. 1987. The logic of divisively asymmetric contests—respect of ownership and the desperado effect. Anim Behav. 35:462–467.

Hammerstein P, Parker GA. 1982. The asymmetric war of attrition. J Theor Biol. 96:647–682.

Hoefler CD. 2007. Male mate choice and size-assortative pairing in a jumping spider, Phidippus clarus. Anim Behav. 73:943–954.

Hoefler CD. 2008. The costs of male courtship and the potential benefits of male choice for large mates in Phidippus clarus (Araneae, Salticidae). J Arachnol. 36:210–212.

Hoefler CD, Jakob EM. 2006. Jumping spiders in space: movement patterns, nest site fidelity and the use of beacons. Anim Behav. 71:109–116.

Hsu Y, Lee IH, Lu C-K. 2009. Prior contest information: mechanisms underlying winner and loser effects. Behav Ecol Sociobiol. 63: 1247–1257.

Hsu YY, Earley RL, Wolf LL. 2006. Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biol Rev. 81:33–74.

Jackson RR. 1980. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae). J Arachnol. 8:241–249.

Jackson RR, McNab AM. 1989. Display, mating and predatory behaviour of the jumping spider *Plexippus paykulli* (Araneae: Salticidae). N Z J Zool. 16:151–168.

Jackson RR, Walker MW, Pollard SD, Cross FR. 2006. Influence of seeing a female on the male-male interactions of a jumping spider, Hypoblemum albovittatum. J Ethol. 24:231–238.

Jennings DJ, Gammell MP, Carlin CM, Hayden TJ. 2004. Effect of body weight, antler length, resource value and experience on fight duration and intensity in fallow deer. Anim Behav. 68:213–221.

Jennions MD, Backwell PRY. 1996. Residency and size affect fight duration and outcome in the fiddler crabUca annulipes. Biol J Linn Soc. 57:293–306.

Kasumovic MM, Andrade MCB. 2006. Male development tracks rapidly shifting sexual versus natural selection pressures. Curr Biol. 16:R242–R243.

Kasumovic MM, Andrade MCB. 2009a. A change in competitive context reverses sexual selection on male size. J Evol Biol. 22:324–333.

Kasumovic MM, Andrade MCB. 2009b. Plasticity in response to demographic variation may help explain continuous phenotypic variation in nature. Ecology. 90:2287–2296.

Kasumovic MM, Elias DO, Punzalan D, Mason AC, Andrade MCB. 2009a. Experience affects the outcome of agonistic contests without affecting the selective advantage of size. Anim Behav. 77:1533–1538.

Kasumovic MM, Elias DO, Punzalan D, Mason AC, Andrade MCB. 2009b. The role of multiple experiences on contest outcome and patterns of selection in a jumping spider. Anim Behav. 77:1533–1538.

Kasumovic MM, Elias DO, Sivalinghem S, Mason AC, Andrade MCB. 2010. Examination of prior contest experience and the retention of winner and loser effects. Behav Ecol. 21:404–409.

Koivula K, Lahti K, Orell M, Rytkonen S. 1993. Prior residency as a key determinant of social dominance in the willow tit (*Parus montanus*). Behav Ecol Sociobiol. 33:283–287.

Leimar O, Austad SN, Enquist M. 1991. A test of the sequential assessment game—fighting in the bowl and doily spider *Frontinella pyramitela*. Evolution. 45:862–874.

Lucas E, Coderre D, Brodeur J. 2000. Selection of molting and pupation sites by Coleomegilla maculata (Coleoptera: Coccinellidae): avoidance of intraguild predation. Environ Entomol. 29:454–459.

Martins M, Pombal JP, Haddad CFB. 1998. Escalated aggressive behaviour and facultative parental care in the nest building gladiator frog, Hyla faber. Amphib Reptil. 19:65–73.

Maynard Smith J, Harper D. 2003. Animal signals. Oxford: Oxford University Press.

Maynard Smith J, Parker GA. 1976. The logic of asymmetric contests. Anim Behav. 24:159–175.

Michelsen A, Fink F, Gogala M, Traue D. 1982. Plants as transmission channels for insect vibrational songs. Behav Ecol Sociobiol. 11: 269–281.

Morrell LJ, Backwell PRY, Metcalfe NB. 2005. Fighting in fiddler crabs Uca mjoebergi: what determines duration? Anim Behav. 70: 653–662.

Parker GA. 1974. Assessment strategy and the evolution of fighting behaviour. J Theor Biol. 47:223–243.

Parker GA, Rubenstein DI. 1981. Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Anim Behav. 29:221–240.

Patek SN. 2001. Spiny lobsters stick and slip to make sound. Nature. 411:153–154.

Payne RJH. 1998. Gradually escalating fights and displays: the cumulative assessment model. Anim Behav. 56:651–662.

Payne RJH, Pagel M. 1996. Escalation and time costs in displays of endurance. J Theor Biol. 183:185–193.

Pie MR. 1998. Lek behavior as the mating strategy of Setellia sp (Diptera: Richardiidae). J Insect Behav. 11:823–832.

Plaistow S, Siva-Jothy MT. 1996. Energetic constraints and male mate-securing tactics in the damselfly calopteryx splendens xanthostoma (Charpentier). Proc R Soc Lond B Biol Sci. 263:1233–1239.

Prenter J, Elwood RW, Taylor PW. 2006. Self-assessment by males during energetically costly contests over precopula females in amphipods. Anim Behav. 72:861–868.

Riechert SE. 1988. Game theory and animal conflict. In: Dugatkin LA, Reeve HK, editors. Game theory and animal behavior. New York: Oxford University Press. p. 64–93.

Rillich J, Buhl E, Schildberger K, Stevenson PA. 2009. Female crickets are driven to fight by the male courting and calling songs. Anim Behav. 77:737–742.

Robinson SK. 1985. Fighting and assessment in the yellow-rumped cacique (*Cacicus cela*). Behav Ecol Sociobiol. 18:39–44.

Searcy WA, Nowicki S. 2005. The evolution of animal communication. Reliability and deception in signaling systems. Princeton (NJ): Princeton University Press.

Soluk DA. 1990. Postmolt susceptibiligy of *Ephemerella* larvae to preda-
tory stonefiles—constraints on defensive armor. Oikos. 58:336–342.

Taylor PW, Elwood RW. 2003. The mismeasure of animal contests.
Anim Behav. 65:1195–1202.

Taylor PW, Hasson O, Clark DL. 2000. Body postures and patterns as
amplifiers of physical condition. Proc R Soc Lond B Biol Sci.
267:917–922.

Taylor PW, Hasson O, Clark DL. 2001. Initiation and resolution of
jumping spider contests: roles for size, proximity, and early detec-
tion of rivals. Behav Ecol Sociobiol. 50:403–413.

Taylor PW, Jackson RR. 1999. Habitat adapted communication in *Trite
planiceps*, a New Zealand jumping spider (Araneae, Salticidae). N Z J
Zool. 26:127–154.

Tibbetts EA. 2008. Resource value and the context dependence of
receiver behaviour. Proc R Soc B Biol Sci. 275:2201–2206.

Wells MS. 1988. Effects of body size and resource value on fighting
behaviour in a jumping spider. Anim Behav. 36:321–326.

Witt DL, Dill LM. 1996. Springtail postmolt vulnerability to pseudo-
scorpion predation: mechanisms and implications. J Insect Behav.
9:395–406.