AN EXAMINATION OF AGONISTIC INTERACTIONS IN THE WHIP SPIDER PHRYNUS MARGINEMACULATUS (ARACHNIDA, AMBLYPYGI)

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ABSTRACT.   Intraspecific interactions in adult whip spiders (*Phrynus marginemaculatus*) were investigated in a laboratory setting to quantify agonistic interactions and to determine predictors of contest outcome. Males were initially paired with size-symmetric or size-asymmetric opponents to assess the effect of size symmetry on contests. Three weeks later, the same males were paired with either the same opponent, or a different opponent to determine whether or not individuals remember earlier encounters. Finally, we quantified aspects of female-female contests. Agonistic encounters between males are characterized by varying degrees of pedipalpal opening, elevation displays, and rapid flicking ($\sim$ 29 Hz) of the antenniform leg. Duration of elevation displays was a predictor of contest outcome, with individuals being more likely to win if they held an elevated posture for longer than their opponent during the contest. Relative size influenced both contest duration and weight loss, with contests between size-symmetric males lasting longer and resulting in greater weight loss than size-asymmetric contests. In second contests, familiar encounters were both shorter in duration and involved fewer aggressive displays than unfamiliar second contests, suggesting that males were able to remember previous opponents. Females were less likely to exhibit aggressive displays than males, and female contests were shorter in duration than male contests. Overall, the results of our study suggest that agonistic interactions in *P. marginemaculatus* are extremely complex, varying with the sex and size-symmetry of individuals and involving elaborate signaling, and that there may be a large role for learning and memory.

Keywords: Agonistic interactions, amblypygid, intrasexual selection, intrasexual competition, learning and memory

Intrasexual competition is prevalent throughout the animal kingdom and is often manifest in agonistic encounters between males with examples ranging from frogs (Bee et al. 1999; Gerhardt 1994; Davies & Halliday 1978), to horned beetles (Emlen 1997; Rasmussen 1994), to jumping spiders (Faber & Baylis 1993; Taylor et al. 2001). Typically, agonistic interactions between males are driven by competition for access to mates, shelter and other limited resources (Andersson 1994; Huntingford & Turner 1987), with the winner of the contest often gaining first access to these resources (Huntingford & Turner 1987; horned beetles, Emlen 1997; and the copperhead snake *Agkistrodon contortrix*, Schuett 1997).

In order to avoid costly escalation and injury that could potentially lead to decreased fitness or death, males of many species may assess traits that are correlated with their opponent's quality through ritualized displays (Bee et al. 1999; Bradbury & Vehrencamp 1998). Male-male contests often select for this ritualized aggressive behavior in order to decrease risk during opponent assessment. These ritualized contests can involve displays of weaponry, postures that accentuate body size, and minor physical contact (such as pushing, touching or wrestling) (Huntingford & Turner 1987; cichlid fish, Neat et al. 1998). Ritualization of male-male contests often leads to exaggeration of male characters that correlate with size, strength or motivational state (e.g., hunger or ready access to a mate) (Andersson 1994), and as a result to sexual dimorphisms in body size and weaponry (Huntingford & Turner 1987; Andersson 1994).

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Most studies of agonistic behavior have focused on aggressive interactions between males; however, female-female contests are also observed in some taxa, for example in cichlids (Draud et al. 2004), whip spiders (Weygoldt 1969, 2000) and pied flycatchers (Dale & Slagsvold 1995). Because males and females employ different strategies to maximize reproductive success, it is not surprising that selection has acted differentially on the sexes to result in different agonistic behaviors between males and females (Draud et al. 2004).

Most studies of intrasexual contests have also focused on animals that rely predominantly on vision (e.g., cichlid fish (Neat et al. 1998; Barlow et al. 1986; Draud et al. 2004) jumping spiders (Faber & Baylis 1993; Taylor et al. 2001)) or their acoustic sense (e.g., territory defense in orthopterans (Greenfield & Minckley 1992), frogs (Bee et al. 1999; Davies & Halliday 1978)) in the early stages of a contest. In these systems, individuals begin displaying visually or acoustically from a distance and only progress to tactile displays and physical contact in prolonged or escalated contests (Faber & Baylis 1993; Neat et al. 1998; Davies & Halliday 1978). There are few studies of intraspecific contests in nonvisual specialists that do not rely on acoustic cues, stemming perhaps from difficulties associated with studies in other sensory modalities or observer biases toward the importance of vision and acoustics. Whip spiders (Arachnida, Amblypygi) represent such a group; in these animals, agonistic displays between males are prevalent (Weygoldt 2000), yet they do not use visual or long-range acoustic signals for communication, but instead rely on other sensory channels such as chemical, tactile, seismic or near field vibrations.

Whip spiders are strictly nocturnal and comprise one of the smaller arachnid orders about which surprisingly little is known (Harvey 2003). They walk on three pairs of legs, and are unique among arachnids in that their front pair of legs is extremely elongate and modified into sensory structures. These antenniform legs, or whips, function similarly to insect antennae and are able to detect airborne odors, contact chemicals and mechanical stimuli (Hebets & Chapman 2000; reviewed in Foelix & Hebets 2001). Due to the prevalence of sensory structures located on their antenniform legs, it is not surprising that whip spiders appear to use these structures to obtain sensory information about their surroundings in addition to using them for communication with other individuals (Weygoldt 2000; Foelix & Hebets 2001).

Despite the apparent ubiquity of male contests in whip spiders, quantitative behavioral studies are currently lacking. Here, we take a quantitative approach to exploring the agonistic encounters between male *Phrynus marginemaculatus* Koch 1841, and compare these male-male interactions to agonistic encounters between females. We provide a complete description of agonistic interactions in this species, evaluate determinants of contest outcomes, identify the influence of prior agonistic experience on fighting behavior and explore potential differences between the sexes.

METHODS

Specimens.—Adult male and female whip spiders (*Phrynus marginemaculatus*) were collected from Big Pine Key, Florida on November 6–9, 2002 and were housed individually in the laboratory in 10.5 × 8.5 × 8.5 cm clear plastic cages in a controlled reversed 12L:12D light cycle. We reversed their light cycle so activity coincided with normal daylight hours. In order to provide a constant source of water, holes were drilled in the bottom of each cage and cotton wicks were placed in the holes. Cages were arranged in water filled tubs (35 × 55 cm), and the cotton wicks were placed in the water, providing the animals with water ad libitum. Animals were fed 1–2 small crickets once a week. Each cage was provided with two pieces of wire screen taped to adjoining walls to serve as a surface upon which the animals could climb. All individuals were housed in the laboratory for at least 2 months prior to experiments.

Individual observations.—To measure, mark and sex the animals, individuals were anesthetized with carbon dioxide. Animals were placed on top of a porous polyurethane sheet mounted on a plastic pipette box. Carbon dioxide was delivered into this apparatus from a tank, after being passed through a flask containing water to add moisture to the gas. Each animal was individually marked with two small colored dots of non-toxic paint using Deco Color paint pens. Ten colors of paint were assigned a number from 0–9 (for ex-

ample, red = 0, orange = 1) and were used to mark each individual with a two-digit ID number. Measurements of individuals were taken, including cephalothorax width (CW) and cephalothorax length (CL), total antenniform leg length (leg I), pedipalp femur length, pedipalp tibia length, and leg II femur length using a standard metric ruler under a compound dissecting scope (Leica WILD M3Z). As autotomization and the loss of appendages due to injury are common in nature, all quantitative comparisons using antenniform leg length measurements were made using the length of the longer appendage. The sex of every individual was confirmed. While anesthetized, whip spiders lift their genital operculum and evert their genitalia; females can be distinguished from males and juveniles by the presence of a pair of sclerotized claspers (orange in color) in their epigynum (Weygoldt 2000). Voucher specimens are deposited in a private collection (Hebets).

Experimental arena.—All contests were run in the dark and were viewed through the LCD screen of a Sony Nightshot camcorder. Contests were run in a circular (24.5 cm diameter) arena constructed of clear plastic mounted on poster board (0.16 cm thickness) with a glue gun. The arena floor consisted of removable paper inserts. The walls were cleaned with 70% ethanol and the floor was replaced between staged contests to remove any possible chemical residues from previous trials. All contests were videotaped (Sony Nightshot DCR-TRV25 Digital Handycams, 30 frames/s) simultaneously in two planes (top and side) with identical cameras, both using an infrared light source. The top view camera was positioned approximately 52 cm directly above the arena while the side view camera was positioned approximately 30 cm from the arena.

Behavioral observations.—Three sets of behavioral contests were run: size matched versus mismatched male-male contests, experienced male-male contests (males with laboratory fighting experience) and female-female contests (with no previous laboratory fighting experience).

For naïve male-male contests, we had 11 pairs of males separated into two treatments: size-symmetric contests ($n = 5$) and size-asymmetric contests ($n = 6$). Size-asymmetric individuals were animals with more than 10%

difference in cephalothorax width while size-symmetric males had less than 10% difference in cephalothorax width. Naïve contests were staged between 1–8 March 2003. Experienced male-male contests consisted of eleven contests involving all of the males from the naïve male-male contests (10 size-symmetric, 1 size-asymmetric). For experienced males, we were interested in the effect of prior experience on male performance and thus, our two treatment categories were: re-matches involving identical pairings as in the naïve male-male contests ($n = 5$, size-symmetric), and novel pairings in which males were paired with opponents with whom they had no previous experience ($n = 6$, 1 size-asymmetric, 5 size-symmetric). Experienced contests were staged between 27 March–17 April 2003. In the female-female contests, females were randomly assigned opponents resulting in 9 pairs (7 size-symmetric, 2 size-asymmetric. These contests were staged between 11 August–4 September 2003. Contests for all three groups were initiated at least 60 min after the beginning of the 12 hr dark cycle.

For all trials, opponents were introduced to opposite sides of the arena, each in a 2 cm diameter clear vial, within 5 sec of each other. The vials were flipped over onto the arena floor so that they entrapped the newly introduced animals. Since all trials were run in the dark and the introduction vials likely blocked any chemical stimuli, immediately upon introduction, the animals were likely unaware of each other's presence. Animals were allowed to acclimate for 2 min before the vials were simultaneously lifted to release the enclosed individuals and begin the trial. Individuals were allowed to freely interact and contests began when the individuals made first contact, and ended when one individual was deemed the loser. "Loser" was assigned to the individual in a contest that retreated to a distance of three body lengths or greater with continued progression away from the opponent. Immediately before and immediately after each contest, individuals were weighed (AE Mettler 100 Analytical scale) and weight loss was used as a proxy for energy expended by an individual for a given contest.

Analysis of behavior.—Video recording of contests was conducted using a Sony DVCAM digital video recorder. Videotapes were played back at 30 frames/second and

Table 1.—Behavioral ethogram for whip spider agonistic encounters.

Behavior	Description of behavior
Orient	Turning to face the opponent.
Approach	Moving toward the opponent to a distance of three body lengths or shorter.
1st contact	Initial contact by an individual's antenniform leg on the body and/or appendages of the opponent.
Inadvertent contact	Initial contact by both opponents without first orienting.
Contact	Both individuals touching each other with the antenniform legs (no antenniform leg flicking by either opponent).
Explore while other flicks	One individual touching the opponent with the antenniform legs while the opponent antenniform leg flicks.
Pedipalpal opening display	''Open palp,'' opening one or both pedipalps partially or fully: (asymmetric) partial pedipalp opening, (asymmetric) full pedipalp opening.
Partial pedipalp open	Both pedipalps open with the tips not touching and with the angle between the femur and tibia less than 90°.
Asymmetric partial pedipalp open	One pedipalp open the same angle as in 'partial pedipalp open.'
Full pedipalp open	Both pedipalps open with the angle between the femur and tibia greater than or equal to 90°.
Asymmetric full pedipalp open	One pedipalp open with the angle between the femur and tibia greater than or equal to 90°.
Pedipalpal contact	Opponents fully open their pedipalps, elevate themselves, lock pedipalps and attempt to push their opponent over or away.
Antenniform leg flick	''Flick,'' rapid back and forth movement of the antenniform leg directed at various parts of an opponent's body and/or appendages.
Retreat	Moving away from the opponent to a distance of three body lengths or greater with continued progression away from the opponent.

frame-by-frame for detailed analysis. For the video analysis, we noted when each individual started and ended various behaviors (see Table 1 for behaviors and descriptions of behaviors analyzed). Total duration of each behavior performed by an individual in a given contest was calculated, as was the proportion of total contest time an individual performed each behavior. Contests and video analysis started as soon as initial contact between two individuals occurred. Analysis ended as soon as a retreat by an individual was observed.

An ethogram of male contest behaviors was constructed by defining repeated behaviors that appeared to play major roles in the contests (Table 1). Next, a descriptive behavioral transition diagram was constructed from analyzing the 11 naïve male contests (Experiment 1; Fig. 1). Behavioral transitions between defined behaviors occurring after the first initial contact of two individuals were noted for winning and losing individuals in all contests. Transitions for winners and losers were calculated separately. We were interested in the order of behavioral transitions, e.g., how likely is it that a double pedipalp open display will follow a flick display as compared to an asymmetric pedipalp open display. To address this, we calculated the proportion of time a given behavior followed a focal behavior by taking the total number of behavioral transitions involving the focal behavior, and dividing it by the number of times it was followed by a given behavior. We then used these proportions to construct a transition diagram with the focal behavior expressed as the first behavior at the foot of the arrow and the given behavior at the arrowhead (Fig. 1). The widths of the arrows represent the proportion of times these behaviors occurred in the given order.

High-speed video analysis.—We captured high-speed video of antenniform leg flicking
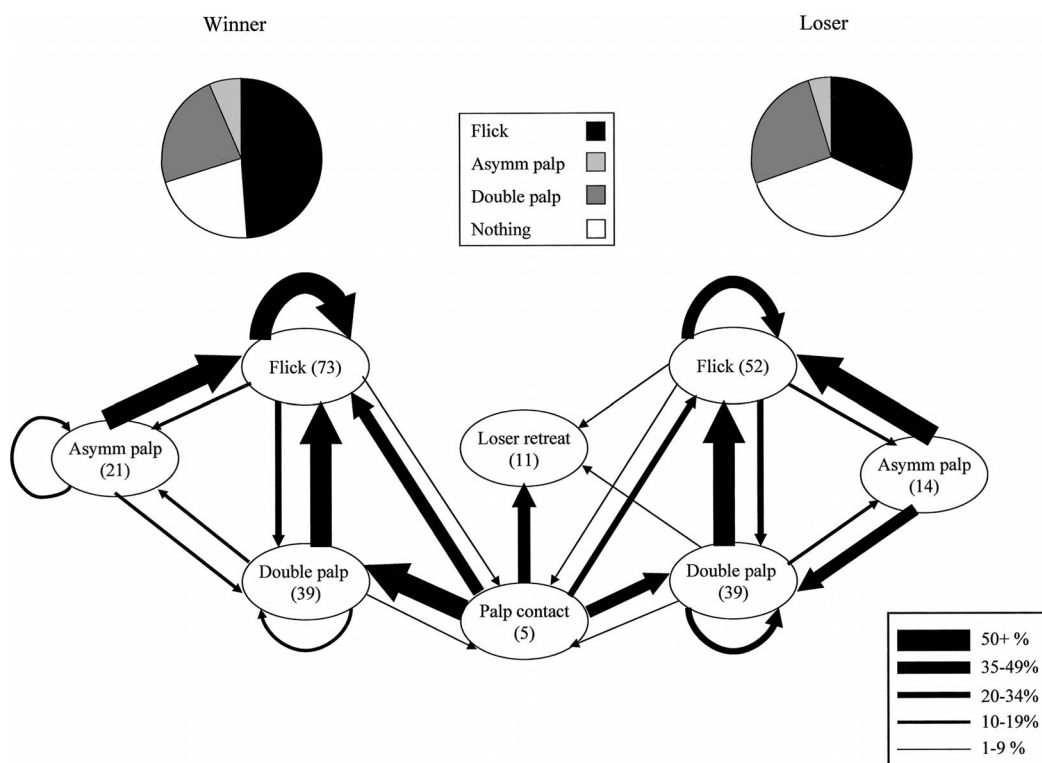
Figure 1.—A behavioral transition diagram that shows the flow of behaviors for male-male agonistic behavior in *P. marginemaculatus* ($n = 11$). The widths of the arrows represent the proportion of times the behavior at the arrowhead followed the behavior at the foot of the arrow. The pie charts above show the fractions of contest duration that winners versus losers flick and perform displays of asymmetric and double pedipalp opening.

to calculate flicking rate and to more closely examine the biomechanics of antenniform leg flicking. Because the light level necessary to capture high-speed video can disturb the animals and possibly influence contest outcome, three contests independent of the those used for previous analyses were staged between randomly chosen males after the completion of the other contests. High-speed video was captured using a motion scope high-speed video camera at 1000 frames/s and then transferred over to digital video (SONY DVCAM digital videocassette recorder). Video clips were analyzed by measuring the flicking frequency of antenniform legs and by characterizing the rapid flicking motion of the antenniform legs.

Statistical analyses.—Contest durations and body size measurements are reported as the mean ± standard deviation. Comparisons of contest duration and contest characteristics

were made using a one-way ANOVA. Comparisons of contest durations of size-asymmetric versus size-symmetric male contests and of first and second trials between familiar males were made using a one-tailed t-test. Likelihood measures for behaviors associated with either male or female contests were done using Fisher's exact probability test. Logistic regression is an appropriate model to use in identifying predictors of outcomes of animal contests (Hardy & Field 1998), and predictors of contest outcome were evaluated using binomial logistic regression analysis. Correlation analyses, t-test analysis, and ANOVA were run using JMP IN 4.0.4 software. Differences in means for variables entered in the logistic regression analysis were calculated using a one-tailed, one-way ANOVA using STATA. Logistic regression, and prediction calculations were made using STATA.

RESULTS

Contest description.—Male contests of *P. marginemaculatus* are characterized by an exploratory period when the opponents first approach one another and make contact. This involves contact of the antenniform legs by one contestant onto various parts of the opponent's body (e.g., contact on the cephalothorax, the pedipalps, the legs or the opisthosoma). This exploratory period can be followed by the retreat of one individual, but more commonly progresses to aggressive displays (naïve males, 100%, $n = 11$; experienced males, 82%, $n = 11$). Aggressive displays are characterized by rapid antenniform leg flicking and pedipalpal opening displays (see Table 1) and in a given contest are often performed by both opponents (in naïve male contests, 91%, $n = 11$; in experienced male contests, 64%, $n = 11$). In a typical contest, animals vary their body position relative to the ground and relative to each other. Starting with the initial contact, individuals elevate themselves above their normal resting posture in an elevation display and they continue to vary their height off the ground throughout the contest. In escalated contests, during a bout of antenniform leg flicking, opponents often push forward then retreat back slightly, giving the general impression of a fencing tournament. Individuals frequently take an asymmetric stance in which they flick one antenniform leg at their opponent, and position that side of their body closer to their opponent while maintaining a distance of about 2–3 body lengths (Fig. 2). The pedipalp that is furthest away from the opponent is often open fully while the pedipalp closest to the opponent is often mostly closed. During these asymmetric stances, the opisthosoma is also directed away from the opponent in a posture previously described by Weygoldt (1969) and characteristic of whip spider agonistic encounters (Weygoldt 2000; also described in Alexander 1962).

Aggressive displays escalated to pedipalpal contact in 27% ($n = 11$) of contests between naïve males and 9% of contests between experienced males ($n = 11$). Pedipalpal contact is characterized by the appearance from above that the open pedipalps of opponents are pressed together. From the side view, it appears as though the more important contact is
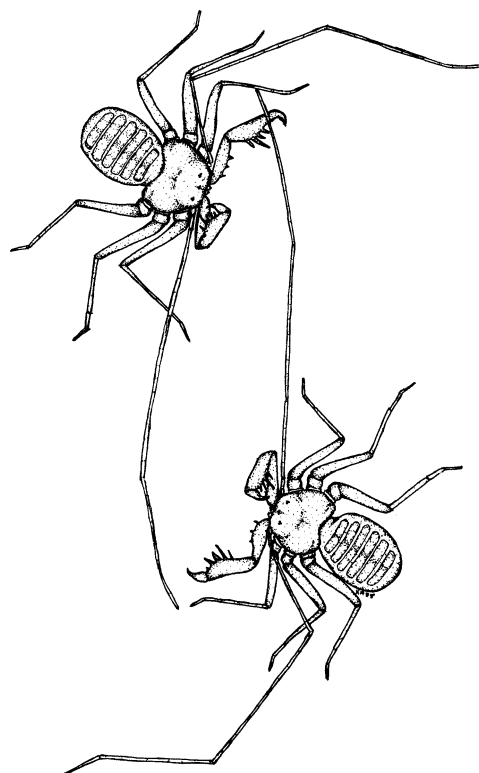

Figure 2.—Typical asymmetric stance in a contest of *P. marginemaculatus*. Individuals are approximately 1.5 cm in length from the front of the carapace to the tip of the abdomen.

cheliceral contact between opponents, but with our recording devices we were unable to confirm this. During pedipalpal contact both individuals approach slowly, elevate themselves off the ground and fully open their pedipalps. Contact between individuals is brief and the front pair of walking legs sometimes loses contact with the ground as the animals quickly attempt to push their opponent away or over. This was always followed by the retreat of one individual in this study. No cases were observed in which injury or death were inflicted. In all cases involving pedipalpal contact, opponents were of similar size, and in the case involving experienced males, the males had not been previously paired with one another. On average, males lost 1.06 ± 1.43 mg ($n = 34$) of body weight through the duration of a contest.

Size-symmetric vs size-asymmetric contests.—Since there were no detectable differences between first and second contests as

Table 2.—Laboratory contests of *P. marginemaculatus*. * $P < 0.05$.

	Total # of individuals	Individuals flicking	Individuals opening the pedipalps	Contests escalated to pedipalpal contact
Size-symmetric males	20	90%	95%	30%
Size-asymmetric males	14	93%	79%	14%
Males	34	91%*	88%*	24%
Females	18	50%*	50%*	33%
Familiar males 1st contest	10	100%*	100%*	20%
Familiar males 2nd contest	10	60%*	60%*	0%
Unfamiliar males 1st contest	12	92%	83%	17%
Unfamiliar males 2nd contest	12	83%	83%	33%

long as both contests involved unfamiliar individuals (see effects of experience below), we included in these analyses all size-symmetric and size-asymmetric trials from an individual's second contest as long as it was with an unfamiliar individual (size-symmetric $n = 10$, size-asymmetric, $n = 7$). Aggressive displays of antenniform leg flicking and pedipalpal opening were no more/less likely to be observed in size-symmetric male contests versus in size-asymmetric male contests (antenniform leg flicking, Fisher's exact $P =$ 1.00, two-tailed; pedipalpal opening, Fisher's exact $P = 0.28$, two-tailed; Table 2). Size-symmetric male contests were longer in duration than size-asymmetric contests (size-symmetric male contest duration = 745.1 ± 378.7 s, $n = 10$; size-asymmetric male contest duration = 447.0 ± 255.0 s, $n = 7$; $t_{15} = 2.06$, $P = 0.05$; Fig. 3). Also, males paired with males of similar size lost more weight during the contest than males paired with males of a different size (Welch's ANOVA: size-symmetric weight loss = 1.46 ± 1.75 mg, $n =$
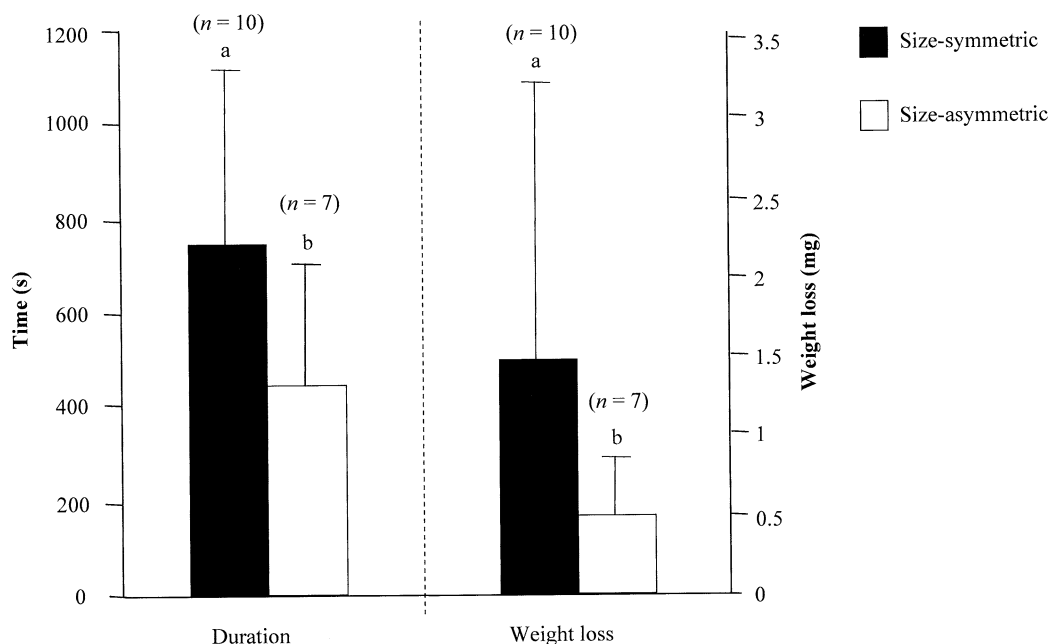

Figure 3.—Size-symmetric versus size-asymmetric contest duration and weight loss. Size-symmetric contests were significantly longer in duration than size-asymmetric contests and the mean weight loss in size-symmetric contests was greater than in size-asymmetric contests. Different letters indicate significant differences at $P < 0.05$.
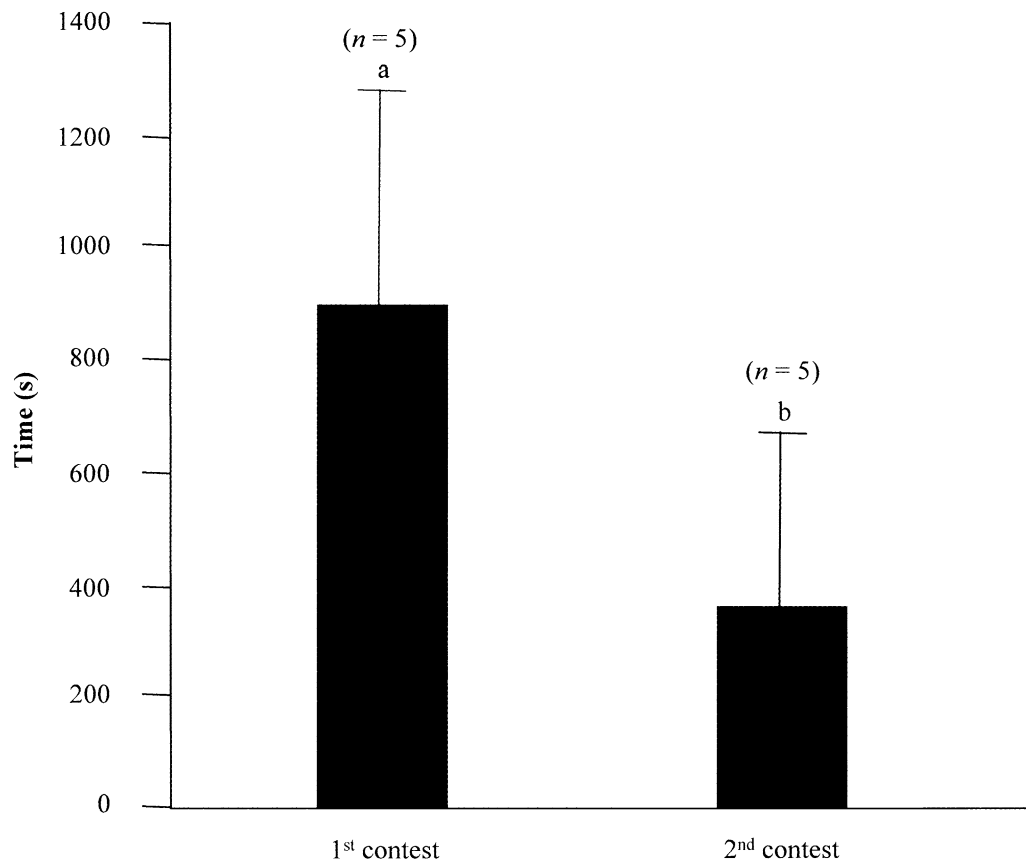
Figure 4.—The effect of experience on subsequent encounters. The contest duration for males in their first contest was longer than the contest duration for the same (familiar) pairs in their second contest. Different letters indicate a significant difference at $P < 0.05$.

20; size-asymmetric weight loss $= 0.49 \pm 0.36$ mg, $n = 14$; df $= 21$, F $= 5.8$, $P = 0.03$; Fig. 3).

Experienced male-male contests.—We looked at the effects of experience on contest duration, likelihood of pedipalpal opening displays, and likelihood of antenniform leg-flicking displays in two groups of male-male contests: those between males paired with a familiar opponent and those between males paired with an unfamiliar opponent.

Contests between familiar males were significantly shorter in their second contest encounter as compared to their first contest encounter (familiar male second contest duration $= 374.0 \pm 320.5$ s; first male contest duration $= 902.0 \pm 356.0$ s; $t_8 = 2.05$, $P = 0.02$; Fig. 4). Males re-paired with a familiar opponent were also less likely to perform aggressive displays of pedipalpal opening and antenni-

form leg flicking in the second contest against a given opponent (pedipalpal opening: Fisher's exact, $P = 0.04$, one-tailed; antenniform leg-flicking: Fisher's exact, $P = 0.04$, one-tailed; Table 2), and there were no cases of pedipalpal contact in the second contest.

In comparing contests between the first laboratory encounters for males and contests between males re-paired with an unfamiliar opponent, we found no statistical difference between contest durations (naïve male contest duration $= 650.2 \pm 384.2$ s, $n = 11$; experienced unfamiliar male contest duration $= 571.2 \pm 330.6$ s, $n = 6$, $F_{1,15} = 0.18$, $P = 0.68$). Furthermore, males were no less likely to perform aggressive displays of pedipalpal opening and antenniform leg-flicking in their second contest paired with a different opponent than in their first contest (pedipalpal opening: Fisher's exact, $P = 0.705$, one-tailed;
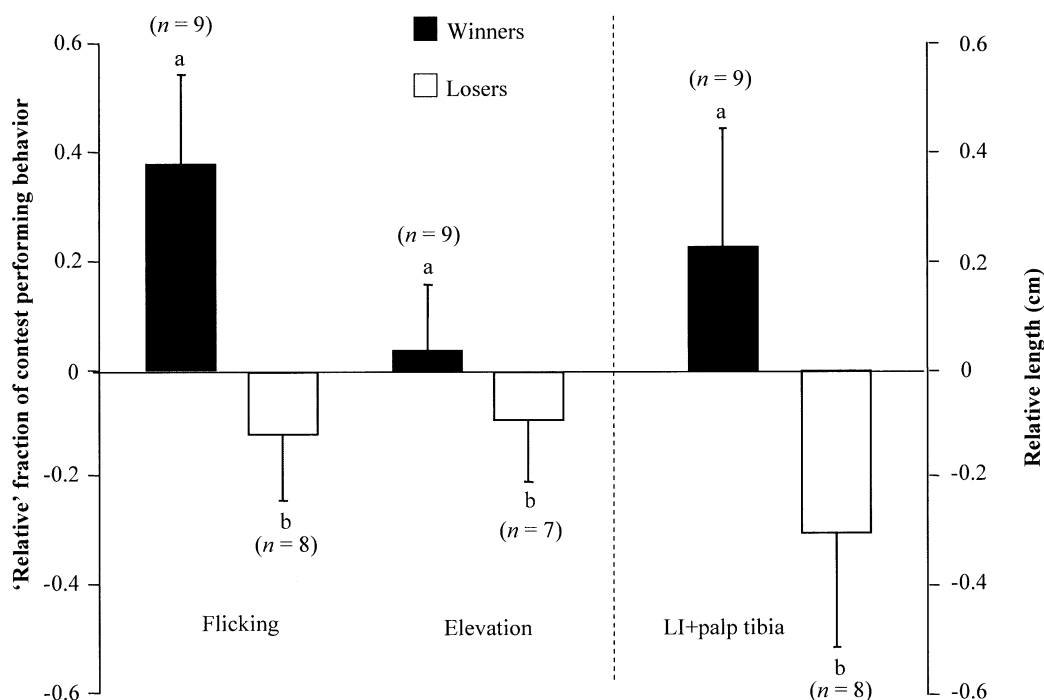
Figure 5.—A comparison of winners versus losers for 'relative' proportion of contest duration spent antenniform flicking and spent elevated higher than the opponent as well as a comparison of winner's and loser's weaponry size (tibia of pedipalp plus antenniform leg). There were significant differences between winners and losers in 'relative' flicking and elevation as well as weapon size using one-tailed ANOVA, but these characters were not statistically significantly correlated with contest outcome in our logistic regression models (see Table 3). Different letters indicate a significant difference at $P < 0.05$.

antenniform leg-flicking: Fisher's exact, $P = 0.50$).

Predictors of contest outcome.—In testing for predictors of contest outcome, we chose to examine four characters: fraction of contest duration in which an individual flicked his antenniform leg(s) as a measure of display intensity, the length of the tibia of the pedipalp plus the length of the antenniform leg as a measure of weapon size (these are the two appendages most heavily used during agonistic displays), cephalothorax width as a measure of body size, and the fraction of contest duration during which one individual held his elevation display higher than his opponent as a potential measure of both body size and motivation. Instead of using the raw values for each of the characters described above, we used the values relative to an individual's opponent. Thus, for each character, we calculated the 'relative' value by subtracting the value for one individual minus that of his opponent. We calculated a relative value for only one individual from each pair so as to not replicate the data ('winners' values are 'losers' values multiplied by negative one). For these analyses, we included all naïve male trials as well as all experienced male trials involving unfamiliar opponents.

Using a one-tailed ANOVA to compare the group means, we found that winners averaged statistically significantly greater 'relative' values for the elevation display, antenniform leg flicking, and weapon length (reported as mean $\pm$ S.E; flicking: winners $= 0.370 \pm 0.169$, $n = 9$; losers $=-0.122 \pm 0.115$, $n = 8$, difference $=-0.492 \pm 0.205$, approx df $= 13.8$, $P = 0.02$; weapon size: winners $= 0.219 \pm 0.223$, $n = 9$, losers $=-0.305 \pm 0.210$, $n = 8$, difference $=-0.524 \pm 0.306$, df $= 15$, $P = 0.05$; elevation: winners $= 0.0288 \pm 0.125$, $n = 9$, losers $=-0.094 \pm 0.112$, $n = 7$, difference $=-0.382 \pm 0.168$, df $= 14$, $P = 0.02$; Fig. 5) and there was a trend for greater 'relative' cephalothorax width in winners (reported with mean $\pm$ S.E; CW: winners $=$

Table 3.—Logistic models predicting contest outcome. Relative elevation above the opponent is the best predictor of outcome.

Model variables	Logistic coef	Estimated s.e.	z-test	p-value
1. Relative elevation	3.5	1.9	1.83	0.067
2. Relative flick	4.6	2.8	1.63	0.104
3. Relative CW	1.0	0.7	1.44	0.150
4. Relative LI + palp	1.4	0.9	1.52	0.128
5. Relative flick	4.2	3.4	1.26	0.207
Relative elevation	2.3	2.0	1.11	0.267
6. Relative flick	4.2	3.4	1.21	0.226
Relative LI + palp	2.2	2.8	0.77	0.444
Relative CW	−0.8	1.9	−0.44	0.660
Relative elevation	1.2	2.6	0.47	0.641

0.394 ± 0.271, $n = 9$, losers $= -0.225 \pm 0.284$, $n = 8$, difference $= -0.619 \pm 0.393$, df $= 15$, $P = 0.07$). Even with differences between winners and losers, we lack enough information to have discriminatory power for predicting outcome using logistic regression. Furthermore, because the 'relative' variables entered into the logistic models are strongly correlated ('relative' elevation and 'relative' flicking, Coef $= 0.593$, $P = 0.02$; 'relative' elevation and 'relative' CW, Coef $= 0.521$, $P = 0.04$), we ran into problems building a statistically significant model with multiple variables. We ran logistic regression analyses using the following combinations: all four 'relative' variables together, each 'relative' variable separately, and both 'relative' antenniform leg flicking and 'relative' elevation together (see Table 3). Our best model uses the 'relative' elevation as a predictor of outcome (Coef $= 3.50$, SE Coef $= 1.91$, $P = 0.07$), followed by 'relative' antenniform leg flicking (Coef $= 4.63$, SE Coef $= 2.85$, $P = 0.10$). Predictive ability for the elevation model and flicking model are summarized in Table 4.

Examining all individuals in all 17 contests,

Table 4.—Using the relative elevation and flicking logistic models for predicting contest outcome, predictions for winners can be made.

Model and cutoff probability	Actual won/lost	Prediction	
		Won	Lost
Elevation, 50%	won = 9	7	2
	lost = 7	2	5
Flicking, 50%	won = 9	6	3
	lost = 8	4	4

we found that all characters analyzed were strongly correlated with the fraction of total contest time one individual was higher than his opponent (flick fraction versus fraction higher elevation: Coef $= 0.4836$, $P = 0.005$; CW versus fraction higher elevation: Coef $= 0.4218$, $P = 0.02$; LI + palp tibia length: Coef $= 0.3487$, $P = 0.05$), and also LI + palp tibia length was highly correlated with CW (Coef $= 0.9443$, $P \leq 0.0001$).

Initial contact was made by four males that subsequently lost the contest, four males that subsequently won the contest, and two initial contacts appeared inadvert ent. The behavioral transition diagram (Fig. 1) shows the progression of behaviors by winning and losing males during a male-male contest. A total of 138 behavioral transitions were observed in winning males and 113 behavioral transitions in losing males.

Female-female contests.—Contests between *P. marginemaculatus* females appeared qualitatively similar to those between males, however, there were significant differences in some aspects of the contests. Again, because no differences were found between males repaired with an unfamiliar male in their second contest and males in their first contest, we compiled data from naïve male contests and experienced male contests between males repaired with unfamiliar opponents. Females were less likely to exhibit antenniform leg flicking than were males (females, 50%, $n = 18$; male, 91%, $n = 34$; Fisher's exact, $P = 0.001$, one-tailed; Table 2). Females were less likely to exhibit aggressive displays of pedipalpal opening than were males (females, 50%, $n = 18$; males, 88%, $n = 34$; Fisher's
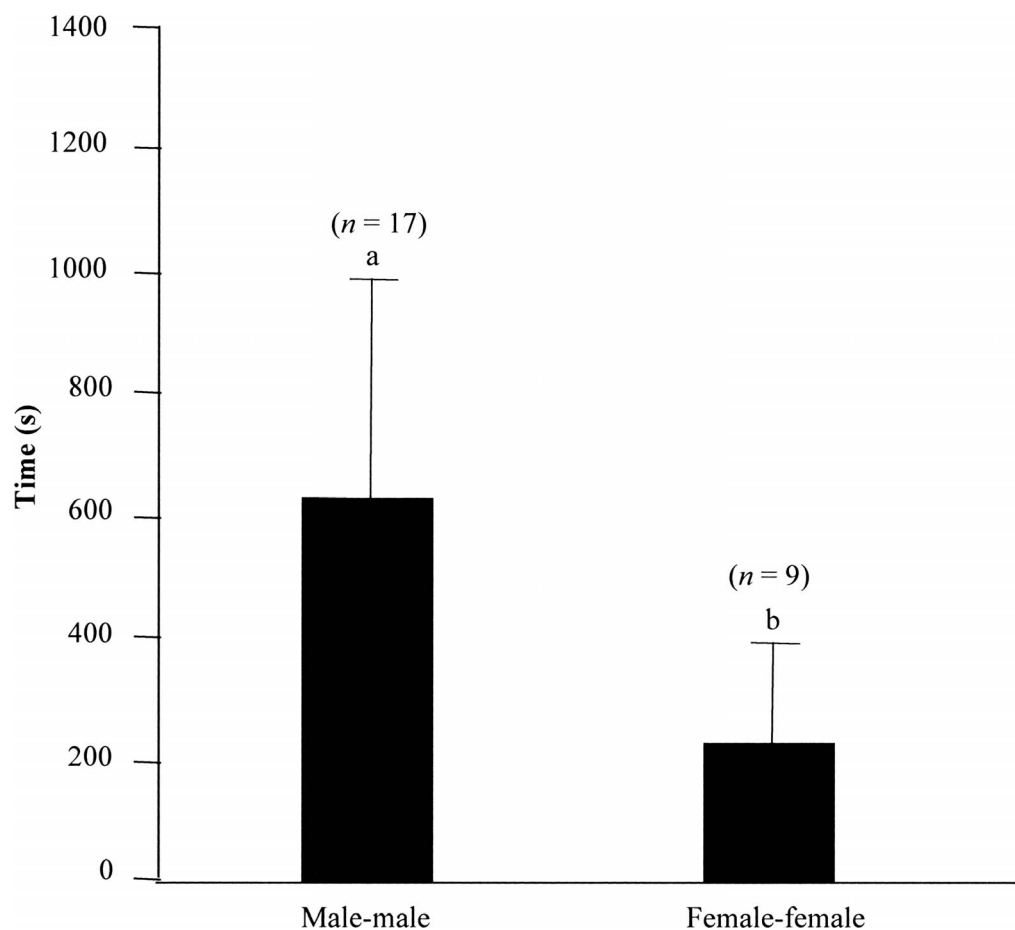
Figure 6.—Female-female versus male-male contest duration. Female contest duration was significantly shorter that male contest duration. Different letters indicate a significant difference for $P < 0.05$.

exact, $P = 0.004$, one-tailed; Table 2). Female contests were significantly shorter in duration than male contests (female contest duration = 225.6 ± 160.7 s, $n = 9$; male contest duration = 622.3 ± 357.7 s, $n = 17$; $F_{1,24} = 9.9$, $P = 0.004$; Fig. 6). In three of the nine female-female contests, individuals escalated to pedipalpal contact (one size-symmetric contest, two size-asymmetric contests). While not statistically significant, females lost almost half the weight that males lost during a contest (male weight loss = 1.46 ± 1.75 mg, $n = 20$; female weight loss = 0.54 ± 0.58 mg, $n = 12$; $F_{1,30} = 3.0695$, $P = 0.09$).

High-speed video.—Of the three male-male contests we recorded under high speed video, we observed antenniform leg flicking in only two of the pairs. In one contest, one individual flicked at a rate of 29.5 Hz and his

opponent did not flick. In another contest, one individual flicked at a maximum of 27 Hz and his opponent flicked at a maximum of 28 Hz.

An animal normally flicks the antenniform leg across the body of his opponent, directing contact back and forth between the walking legs and the pedipalps. However, sometimes antenniform leg flicking does not result in contact with the opponent, but rather occurs next to the opponent. When antenniform leg flicking is viewed at a slower speed (1000 frames/sec), it is much easier to discern the particular pattern of antenniform leg movement. The following description of this movement is qualitative, as quantitative characterization of the motion was not performed. A back-and-forth movement originates from the base of the femur and the two-thirds of the antenniform leg closest to the body of an an-

imal stay relatively stiff. The outer third of the antenniform leg is held out straight along the axis of the leg, but appears slightly limp and its movement is slightly out of phase with the inner part of the leg.

DISCUSSION

Male-male contests.—This study demonstrates that intraspecific contests in *Phrynus marginemaculatus* are ritualized and have a natural progression from an exploratory period of light contact to more aggressive displays of antenniform leg flicking and pedipalpal opening. No contests resulted in injury or death, and escalation to pedipalpal contact was observed in only four of twenty-two male-male contests and three of nine female-female contests. Theory predicts that when opponents in an agonistic interaction are similar in size, escalation is more likely to occur (Parker 1974). This is consistent with our results in that all four cases where pedipalpal contact occurred were between males of similar size. However, only one of the three cases where pedipalpal contact occurred between females was between females of similar size.

The results of this study are similar to Weygoldt's (1969) study of *P. marginemaculatus*, but differ in some basic descriptive aspects as well as in the comparison of male and female contests. Weygoldt (1969) recounts that opposing animals try to flick the antenniform leg underneath the opponent. While we found that this behavior varied greatly between contests, we saw no evidence that animals were attempting to flick under the opponent as opposed to on top of them. Weygoldt (1969) also describes the female contests as being much more "spectacular." Data analysis revealed that female contests are shorter in duration with less displaying of aggression (potentially due to their shortened duration), but have a higher likelihood to escalate. Weygoldt (1969) further reports that females flick their antenniform legs extremely rapidly and that males flick their legs much more slowly and in a biomechanically different manner. In this study, in both initial observations and examination of videotapes, no apparent differences were discovered between male and female antenniform leg flicking, and males as well as females flicked their antenniform legs at a rate too fast to be determined using regular speed video recordings. However, we did not observe any female-female contest with high-speed video and therefore, we cannot adequately address the relative rates of antenniform leg flicking between males and females.

The results in the behavioral transition diagram show that antenniform leg flicking composed a large proportion of the originating behaviors for both winning males and losing males. Winning males tended to flick their antenniform legs more often than losing males. Antenniform leg flicking is clearly important in determining contest outcomes. Unfortunately, this study only addresses durations and numbers of behaviors, and does not quantify the speed with which the antenniform leg is moved. Antenniform leg flicking could demonstrate an individual's motivation level, or if it is energetically expensive, it could demonstrate the current fitness of a male. Future studies are needed to explore these possibilities.

Predictors of contest outcome.—Animals in conflict have been shown to assess asymmetries between themselves and their opponent which can be used in resolving agonistic encounters. These characters can include body size (Taylor & Jackson 2003) and call frequency (Bee et al. 1999; Davies & Halliday 1978) or weapon size (Weygoldt 2000; Sneddon et al. 1997), and can influence contest outcome (Maynard Smith & Parker 1976). In this study, the best logistic regression model shows that a longer relative amount of time spent at a height higher than an opponent best predicts outcomes of male-male contests. Using this model at a cutoff of 50% probability of winning, we can predict contest outcome fairly well. Whip spiders normally spend their time flat against the substrate but perform an elevation display during agonistic encounters. Elevation displays may signal motivation or likelihood of escalation. If there is a discrepancy in motivation between two opponents, the less motivated opponent may give up more easily. Elevation displays could also provide information on body size or weapon size since both these characters are highly correlated with time elevated higher than an opponent. Larger individuals will have longer legs and subsequently be able to push up higher than a smaller opponent. Body size is likely to influence contest outcome as it is a good indicator

of age and fighting ability in other animals (Olsson & Shine 2000).

Theory predicts that when opponents in an agonistic interaction are similar in size, escalation is more likely to occur (Parker 1974). Aggressive displays of antenniform leg flicking and pedipalpal opening did not occur more often in contests between males of similar size than in males of different size. Fight duration is also predicted to be longest between individuals of similar size, and shortest with a large body-size asymmetry (Parker 1974). This prediction has been supported in studies of bowl and doily spiders (Leimar et al. 1991) and jumping spiders (Faber & Baylis 1993), and our study further supports the prediction with longer contests between size-symmetric males versus size-asymmetric males. Furthermore, males lost more weight in contests against opponents of similar size. This increased weight loss is potentially related to contest duration.

Effects of experience.—We observed effects of prior contest experience on later contests. In contests where males were subsequently re-paired with the same opponent, in the second contest, males were less likely to exhibit aggressive displays and contest durations were significantly shorter. However, when males were re-paired with a different opponent, the likelihood of exhibiting aggressive displays was no different, and the contest duration was no different. This finding suggests that the males were able to remember previous opponents over the three-week time period that elapsed in between trials and retained effects of earlier contest experience.

Female-female contests.—Female-female contests were similar to male-male contests, suggesting that ritualized agonistic encounters in *P. marginemaculatus* have experienced similar selection pressures in males and females. Weygoldt (1969) suggests that the contests lower the density of individuals in an area. While the contests were similar in general progression, there were subtle behavioral differences between female and male contests. Females were less likely to display the aggressive behaviors of antenniform leg flicking and pedipalpal opening than males, and female-female contests were shorter in duration than male-male contests. These behavioral differences may be due to sexual selection pressure also acting on the male contests, es-

pecially if fighting behavior plays a role in a male's ability to find mates successfully. In crab spiders (Hoefler 2002) and jumping spiders (Faber & Baylis 1993), contest duration and escalation increase when contestants were in the presence of a female. In the field, male-male contests may predominantly occur when there is ready access to a female. Thus, the longer and more aggressive contests by male *P. marginemaculatus* seen in the laboratory may reflect typical battles in the field. Males may have more at stake than females: a potential mating in addition to territory defense, as territory defense is a likely context for agonistic behavior in whip spiders (Weygoldt 2000).

Potential role of agonistic interactions.—In spiders, male-male agonistic behaviors have been described in the context of competition for mate access (Schmitt et al. 1990). Winning males often mate with females (Huntingford & Turner 1987). A study examining the ecology and behavior of a whip spider closely related to *Phrynus marginemaculatus*, *P. parvulus* (Hebets 2002), suggests that males wander in search of mates while females remain in a home crevice over extended periods of time (Hebets 2002). When males encounter other males while wandering, they engage in agonistic behavior (Hebets pers. obs.). In *P. marginemaculatus*, males may be more mobile than females, and therefore may encounter each other more in the field. If this is the case, then there would be stronger selection on ritualization of male contests versus female contests, and this could explain the tendency for females to escalate to pedipalpal contact faster and for female contest duration to be shorter. The agonistic behaviors observed in *P. parvulus* likely reflect competition for mates in addition to territory defense (Weygoldt 2000). Whether or not male fighting behavior in *P. marginemaculatus* is associated with mate access has not yet been studied. Although sexual selection may be a selective force behind the fighting behavior of *P. marginemaculatus*, it cannot be the exclusive selective force shaping agonistic behavior since females demonstrate fighting behaviors similar to male fighting behaviors. Individuals of *P. marginemaculatus* are typically found individually under limestone rocks on the Florida Keys and part of their agonistic interactions may reflect territoriality, with in-

dividuals defending their home rock. Extensive field studies exploring their natural history and behavior are necessary to draw a more conclusive picture of the selective forces acting on contests in *P. marginemaculatus*.

Most studies of intraspecific competition have focused on visual or auditory animals (Barlow et al. 1986; Faber & Baylis 1993; Taylor & Jackson 2003). However, whip spiders are unique in that they most likely do not rely on sight or sound for communication. They provide a novel system for studying communication in a non-visual animal. In order to better determine what cues individuals use to assess their opponent, further studies with larger sample sizes need to be conducted. Also, further investigation of the natural history of *P. marginemaculatus* would provide a good framework within which their complex ritualized fighting behavior can be studied. As this study has shown, the antenniform leg is heavily utilized in intraspecific contests and tactile cues likely play a large role in intraspecific contests in *P. marginemaculatus*.

Conclusions.—This study characterizes male-male contests in the whip spider *P. marginemaculatus*, investigates effects of experience on male fighting behavior, and compares male contests with female contests. Elevation displays potentially play an important role in intraspecific contests, and can be used to predict contest outcome with some accuracy. Our results indicate that males retain effects of previous contest experience and remember previous opponents for at least three weeks. We found that female contests were shorter in duration and more intense than male contests, suggesting stronger selection pressure on male-male fighting behavior. This study suggests that whip spiders have complex behaviors in which learning and memory may play a large role.

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