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Original Article

Visual mutual assessment of size in male *Lyssomanes viridis* jumping spider contests

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Numerous animals are known to assess the resource holding potential of their opponents using conventional signals and other correlates of resource holding potential. Although body and weapon size generally correlate with resource holding potential and are often presumed to be visually evaluated in animal contests, no one has demonstrated visual assessment of opponent size while controlling for all potential correlates of size. To this end, we presented male *Lyssomanes viridis* jumping spiders with computer-animated opponents 1) of 3 different overall sizes and 2) with different weapon and nonweapon appendages elongated by the amount that would normally accompany a 20% increase in body size. Male *L. viridis* have strikingly colored, exaggerated chelicerae and forelegs, which are used as weapons in contests, and the forelegs are waved during visual agonistic displays. We scored 4 levels of escalation in males' responses to animations. Using generalized linear mixed modeling, we assessed the relative predictive power of the following variables on escalation intensity: 1) focal male size, 2) animated opponent size, and 3) the difference in size between the focal male and his animated opponent. When we presented males with animations scaled to different sizes, we found that size difference was the best predictor of escalation intensity, followed by opponent size. The effect of opponent size disappeared when size difference was included in the same model. Focal male size did not significantly predict escalation intensity. This suggests that males employ a mutual assessment strategy. Surprisingly, males did not respond differently to animations with versus without elongated weaponry.

Key words: **assessment strategy, male–male competition, resource holding potential, Salticidae, size assessment, vision, weaponry.**

INTRODUCTION

An individual's capacity to take possession of and defend resources against competitors is termed resource holding potential or RHP (Parker 1974). The ability to assess the RHP of one's opponent, and to compare that to one's own RHP, is thought to be adaptive because it allows an individual to concede a contest it is unlikely to win without expending unnecessary energy in escalated combat (Parker 1974; Maynard Smith and Parker 1976). In line with this prediction, researchers have found numerous examples of animals assessing conventional signals and other correlates of their opponents' RHP, such as the fundamental frequency of growls and roars (Reby et al. 2005; Taylor et al. 2010), the rate of frequency modulation and range of frequencies (i.e., "vocal performance") in birdsong (Illes et al. 2006; DuBois et al. 2011), the color of plumage (Fugle et al. 1984; Rohwer 1985), and the temporal frequency of push-up displays in lizards (Van Dyk et al. 2007). Despite the wide range of evidence for the assessment of conventional signals, however, little is known as to whether or not animals directly assess the trait that is most often used by researchers as a proxy for RHP and is also likely the most reliable indicator of RHP, that is, body size. Whether or not animals assess weapon size is also poorly understood despite various empirical attempts to answer this question (reviewed by Clutton-Brock 1982).

Whether animals compare information about their opponents to information about themselves (i.e., use a "mutual assessment" strategy) is also not well understood. Studies prior to 2003 tended to presume that a negative correlation between contest duration and size disparity between opponents was evidence of mutual assessment. This has since been invalidated by models showing that a similar pattern can arise out of a self-assessment strategy, in which an individual only has access to information about its own RHP and competes until it hits an energetic ceiling (Taylor and Elwood 2003). In light of this, Elwood and colleagues put forward a new statistical technique for analyzing contests between live males to distinguish between mutual and self-assessment (Taylor and Elwood 2003; Arnott and Elwood 2009; Elwood and Arnott 2012). Since then, only a few studies have been able to find support for mutual assessment of RHP using this methodology (Pratt et al. 2003; Kemp et al. 2006; Keil and Watson 2010; Yasuda et al. 2012) despite the apparent evolutionary advantages of such a strategy. There is mounting evidence that more rudimentary assessment

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strategies, in particular, variants of self-assessment, are more common across the animal kingdom (Bridge et al. 2000; Taylor et al. 2001; Morrell et al. 2005; Kelly 2006; Prenter et al. 2006; Stuart-Fox 2006; Elias et al. 2008; Moore et al. 2008; Brandt and Swallow 2009; Kasumovic et al. 2011; Tsai et al. 2014). It has been theorized that this may be due to cognitive, perceptual, or energetic limitations associated with mutual assessment (Elwood and Arnott 2012; Mesterton-Gibbons and Heap 2014).

Although Elwood and colleagues' methodology is able to distinguish between different assessment strategies, it is not designed to identify which physical traits competitors actually evaluate in the case of mutual assessment. In the present study, we attempted to unite their multiple regression testing approach (Taylor and Elwood 2003) with an approach using virtual opponents in order to determine which, if any, size-related traits contestants visually evaluate in their opponents and whether or not they compare their opponents' size to their own (i.e., use a mutual assessment strategy). To accomplish this, we challenged males of the jumping spider *Lyssomanes viridis* (Walckenaer 1827) with virtual opponents with manipulated size traits and assessed the relative predictive powers of 1) an individual's own size, 2) the size of his animated opponent, and 3) an individual's size relative to his animated opponent, as to the level to which that individual would escalate a contest.

We selected *L. viridis* as our study species because it responds to computer-animated images as if they were real (Tedore and Johnsen 2013) and is a visually oriented animal with obvious visual agonistic displays and exaggerated weaponry. Previous work has shown that the lengths of males' strikingly colored weapons (the chelicerae and forelegs) exhibit strong positive allometry with body size (Tedore and Johnsen 2012). This is in contrast to females' corresponding appendages, which are cryptically colored and have significantly lower allometric slopes than males' corresponding appendages. When males encounter each other, they typically wave their forelegs and often approach one another until one of them retreats or, if neither of them retreats, they escalate to a physical fight. When fighting, males press their chelicerae and forelegs against each other and push until one of them gives way and retreats. Within a confined arena in the laboratory, about 25% of male–male pairings escalate to such pushing contests. It is unknown how this frequency compares to that in nature. The larger of the 2 males tends to win contests (Tedore and Johnsen 2012). The colorfulness and utility of the male weapons in escalated contests, and the fact that males wave their forelegs during visual agonistic displays, led us to hypothesize that the weapons may have been evolutionarily co-opted as visual signals of RHP.

Previous studies of assessment strategies in jumping spiders, using Elwood and colleagues' statistical methodology, have found good support for self-assessment only (Taylor et al. 2001; Elias et al. 2008; Kasumovic et al. 2011). However, Drees (1952), using drawings and dummies, was able to show that the jumping spider *Epiblemum scenicum* distinguishes between different sizes of prey and mates, preferring smaller prey and larger females. So it would seem that jumping spiders possess the sensory and cognitive machinery to assess another spider's size at a distance, and thus, without the costs of physical combat. This apparent contradiction between jumping spiders' abilities, and the assessment strategies they actually use, would make a demonstration of opponent assessment, and in particular, mutual assessment, especially compelling. To determine whether males assess some component of each other's size, and use visual cues to do so, we presented males with animated images of a male competitor scaled to 3 different sizes. Then, to determine if males specifically home in on and evaluate weapon size, we presented a separate set of males with a control, a secondary control, and 2 experimental animated spiders. The secondary control had elongated nonweapon appendages, and the 2 experimental animations had elongated weapon appendages. In all 3 of these animations, the relevant appendages were elongated by the amount that would normally accompany a standard increase in prosoma (i.e., "cephalothorax") diameter in live males. This resulted in isometric elongation in the secondary control animation and allometric elongation in the experimental animations. We expected the nonweapon appendages in the secondary control not to be evaluated because they do not function as weapons and scale isometrically with body size, which suggests that their length is not under positive selection.

METHODS

Subjects and housing

Immature *L. viridis* (70 males and 70 females) were collected by beating American holly trees (*Ilex opaca*) (Aiton 1789) along the Black Creek Greenway (35°49.3′N, 78°47.1′W) in Wake County, NC, USA, in late March 2010 and in the Cole Mill Access section of Eno River State Park (36°3.39′N, 78°58.80′W), in an area spanning Durham and Orange Counties, NC, USA, in early April 2013. All spiders had molted to sexual maturity prior to being run in experimental trials.

Spiders were individually housed in $10 \times 10 \times 10$ cm clear plastic boxes, which were visually isolated from one another by white paperboard barriers. Boxes were illuminated by 2 full-spectrum (including UV) fluorescent mercury vapor tubes (T8, 32 W, 48 in., Duro-Test Lighting's Vita-Brite, Philadelphia, PA). The light cycle mimicked daily changes in the outdoor diurnal light cycle, and the room temperature was held constant at 24 °C. To serve as artificial leaves, an 8×10 cm piece of green paper was placed on top of each box, and a 6×14 cm piece of green paper was folded and placed inside each box. During the weeks leading up to experiments, spiders were fed 8 *Drosophila* 2 times per week. Four days before behavioral trials began, we increased feeding frequency, providing each spider with 4 *Drosophila* daily, and continued this feeding regime until all behavioral trials were finished. Spiders were always fed after all behavioral trials for the day had been completed and at least an hour before their lights turned off. Each feeding was accompanied by a light misting of filtered water. All animal housing and experimental procedures were in accord with animal welfare regulations in the United States.

Visual stimuli

The same male *L. viridis* photograph that was used to construct animations in Tedore and Johnsen (2013) was animated to wave its forelegs in a threat display. Display movements were based on our own behavioral observations of male–male contests and were similar to those described in Tedore and Johnsen (2012) and Jackson and Macnab (1991). The forelegs of the animated spider were extended roughly 55° above horizontal and animated to quickly dip down 20° and then back up again (bending at the patellofemoral joint) once every 7.5 s. The entire animation moved alternately to the left or right a few millimeters every 15 s, in synchrony with every second foreleg wave. These back-and-forth movements scaled with body size, such that larger animated spiders moved the same distance, relative to their body size, as smaller animated spiders

did. This seemed the most appropriate way to scale the quick side-step that males often make as they display because step size should scale with leg length. The temporal properties of the movements remained the same across all animations, regardless of size.

For the first experiment, which we called the Overall Size Experiment, we created 3 different sizes of the same animation: small, medium, and large. The small animation was the medium-sized animation scaled by a factor of 0.6, and the large animation was the medium-sized animation scaled by a factor of 1.4. The actual size of the medium-sized animation, as displayed on the Fujitsu screen, was scaled so that the length of the right chelicera matched what we estimated to be the average cheliceral length of our sample in the Overall Size Experiment (i.e., before we were able to sacrifice and measure our subjects to get precise measurements) (cheliceral length of animation = 2.30 mm; average cheliceral length of male subjects = 2.20 mm).

For the second experiment, which we called the Weapon Size Experiment, we created a control, a secondary control, and 2 experimental animations. For the control animation, we started with the same animation as the one used in the Overall Size Experiment but manipulated the pedipalps to be in a more neutral position so as not to obscure the chelicerae in the elongated-chelicerae animation. In the Overall Size Experiment, the pedipalps had been unmodified from the original photograph, in which the male was not displaying, but was standing still and moving his pedipalps in search of, or in response to, chemosensory cues. Males typically do not wave their palps when engaged in a visual agonistic display. To make the chelicerae more symmetrical in the Weapon Size Experiment, we mirrored the right chelicera to the left side. We then scaled the entire animation such that the length of the chelicerae fell midway between the cheliceral length of the small and medium animations of the Overall Size Experiment (=1.80 mm). This constituted our control animation. We then used this animation as a base for constructing the secondary control and the 2 experimental animations.

The secondary control and each of the experimental animations consisted of the control animation with different body parts elongated by the amount that would normally accompany a 20% increase in prosoma (i.e., "cephalothorax") diameter in live males. We chose the number 20% because it covered a large portion of the natural variation in males but did not result in animations that were among the tiniest or largest of all spiders (see Results) (Figure 2). For the secondary control, we chose to elongate legs that are not used as weapons and scale roughly isometrically with prosoma diameter. We suspected that legs 2–4 would meet these requirements, and verified this by thawing and measuring frozen subjects from Tedore and Johnsen (2012), using the methods described therein. We used reduced major axis regression to fit a line to the relationship between the length of the second pair of legs and prosoma diameter. From this regression line, we calculated that a theoretical average-sized male experiencing a 20% increase in prosoma diameter should experience a 21% increase in the length of the second pair of legs. We assumed that legs 3 and 4 would scale similarly to the second pair of legs because we observed that they were of similar length to the second pair of legs. Thus, the secondary control animation had its legs 2–4 lengthened by a factor of 1.21 (21% increase). The experimental animations included 1) a male with its chelicerae lengthened by a factor of 1.55 (i.e., a 55% increase) and 2) a male with its forelegs lengthened by a factor of 1.25 (25% increase). The scaling factors for the 2 experimental animations were calculated from similar linear regressions of weapon length versus prosoma diameter taken from Tedore and Johnsen (2012).

All manipulations of size were done using Photoshop CS4 and CS5, and images were animated using Adobe Flash CS4 and CS5 (Adobe, San Jose, CA). Animations were displayed on a high pixel–density (10.6 pixels per mm) computer screen (Fujitsu Lifebook U820, Tokyo, Japan). The high-resolution master image was downsampled using Adobe Photoshop's bicubic interpolation algorithm to match the native resolution of the display device and scale at which each animation was displayed. At no point was an image upsampled. All animations were equally sharp and contained equal amounts of visual information per unit area. The relative sizes of the animations to one another can be seen in Figure 1 and their movements in Supplementary Video 1.

Experimental arena

Arenas were 10 × 10 × 10 cm clear plastic boxes whose floor and walls were surrounded by white paperboard. The arena's ceiling was covered by white translucent vellum to diffuse the room's ambient lighting. A webcam (Logitech QuickCam Pro for Notebooks; Logitech Inc., Newark, CA), pointed through a small opening in one of the paperboard walls, was used to monitor the spider's behavior. A portion of the opposing wall was open so that an animation, displayed on the Fujitsu screen, could be slid into the spider's view.

Experimental procedure

An experimentally naive set of subjects (35 males and 35 females) was used in the Overall Size Experiment. A separate experimentally naive set of subjects (35 males and 35 females) was used in the Weapon Size Experiment. Experimentally naive spiders had not been used in any previous experiments. To minimize any possible effects of previous mating or fighting history on motivation, all subjects were virgins and had not encountered an adult *L. viridis* for several months, when they were several molts away from maturity, if they had encountered one at all.

Dragline silk from virgin females, which is known to contain pheromones (Nelson et al. 2012; Tedore and Johnsen 2013) and to prime males for competition (Tedore and Johnsen 2013), was introduced into the experimental arena in the same way as described in Tedore and Johnsen (2013): by enclosing the arena with a lid taken from a female's home enclosure. Each male was exposed to the same individual female's silk in each of his consecutive behavioral trials, and each individual male was exposed to silk from a unique female. Males were placed on the silk-covered arena lid such that they were oriented in the same viewing plane as the computer-animated spider. When used to enclose the arena, each lid was oriented such that the male was in the rear half of the experimental arena, between 6 and 10 cm away from the computer screen. When placed in the arena, males typically stood still for several seconds before beginning to move about and explore the female silk with their pedipalps. A male was considered habituated to the arena when he began moving about. At this point, the Fujitsu screen, displaying one of the animated images described above, was slid into view. Males typically oriented to the movement of the animation and examined it for awhile before deciding whether or not to direct a threat display toward it.

We scored 4 levels of escalation: 1) turning and walking away, 2) threat display, 3) threat display with advancement toward the computer screen, and 4) threat display with advancement toward computer screen, culminating in touching, climbing, or jumping onto the computer screen. If a male did not threaten the animation

Figure 1
Animated images with their sizes relative to one another preserved for comparison. Top row: Overall Size Experiment (from left to right: small, medium, and large). Bottom row: Weapon Size Experiment (from left to right: control, legs 2–4 elongated by 21%, chelicerae elongated by 55%, and forelegs elongated by 25%).

after examining it for the first time, he was allowed to reorient toward and examine the animation a second time before the trial ended. If, after one of these orientations, a male, while inspecting the animation, was positioned in such a way that his face was oriented anywhere from perpendicular to upside down relative to the face of the animation, and he did not respond with a threat display, then he was allowed to reorient toward and examine the animation once again, this time with his face in the same orientation as the animation's face. The reason we did this was because other studies have indicated that males have more difficulty recognizing conspecifics when they are not oriented in the same image plane (Drees 1952; Tedore and Johnsen 2013). In both the Overall Size and Weapon Size Experiments, each male saw each animation used in a given experiment, presented in random order, 1 animation per day, on consecutive days. All males were between 5 and 50 days past their terminal molt.

When behavioral experiments were complete, spiders were sacrificed via overanesthesia with nitrogen gas. The length of each spider's right chelicera was then measured using the procedure described in Tedore and Johnsen (2012).

Statistical analyses

For the Overall Size Experiment, we used cheliceral length as a proxy for overall size. To determine the relative effects of 1) focal male size, 2) animated opponent size, and 3) the difference in size between the focal male and his animated opponent, as to the level to which a male would escalate a contest, we ran ordinal generalized linear mixed models with the above 3 factors as fixed effects and male identity as a random effect. We also tested trial order as a fixed effect. All models allowed random intercepts but not random slopes because likelihood ratio tests indicated a better fit for models allowing intercepts, but not slopes, to vary across subjects. We used a cumulative logistic link function and adaptive quadrature as an optimization method. For each combination of fixed effect and outcome variable, we used a likelihood ratio test to test the proportional odds assumption, which is the assumption that the effect of an independent variable is of equal magnitude across successive steps of an ordered categorical outcome variable. This assumption is often violated in ordinal models and was violated for the effect of size difference in our current models. Thus, in models including this variable, we specified nonproportional odds for the size difference variable by including an interaction term between size difference and the dependent variable's threshold parameters. A few males courted their opponents (a courtship display is very distinct from a threat display in this species; Tedore and Johnsen 2013); we assumed these displays reflected recognition errors and hence excluded them from analysis. We used the software program SuperMix for all analyses (Scientific Software International, Skokie, IL). Out of the set of models in which all fixed effects were significant, we determined the best-fitting model using Akaike's information criterion (AIC), together with its associated relative likelihood (Akaike 1983).

For the Weapon Size Experiment, we tested for an effect of manipulated appendage lengths on escalation intensity, again using ordinal generalized linear mixed models, with animated opponent treatment as a fixed effect and male identity as a random effect. We also tested whether the size distributions of the males we ran in the Overall Size Experiment versus the Weapon Size Experiment differed using a Kolmogorov–Smirnov test.

RESULTS

The range of cheliceral lengths of all animated opponents was within the natural size range of our experimental subjects (Figure 2). The distributions of focal male sizes across the 2 experiments were not significantly different (Kolmogorov–Smirnov $D = 0.17$, $P = 0.68$).

Overall Size Experiment

The model with the lowest (i.e., best-fitting) AIC included the size difference between the focal male and his animated opponent as the only fixed effect (Table 1 and Figure 3). The next best-fitting model included opponent size as the only fixed effect ($P < 0.0001$), but its relative likelihood compared with the best-fitting model was only 0.11. Importantly, when size difference and opponent size were included in the same model, the effect of size difference remained significant ($P = 0.046$), whereas the significant effect of opponent disappeared ($P = 0.23$). We found no effect of focal male size on escalation intensity in any model. Intraindividual patterns of responses to the different-sized animations can be seen in Figure 4.

Weapon Size Experiment

The 3 experimental treatments had no effect on escalation intensity relative to the control. Males escalated to the same level when presented with animations having 1) elongated legs 2–4 ($P = 0.25$), 2) elongated chelicerae ($P = 0.98$), and 3) elongated forelegs ($P = 0.58$), as they did when they were presented with the
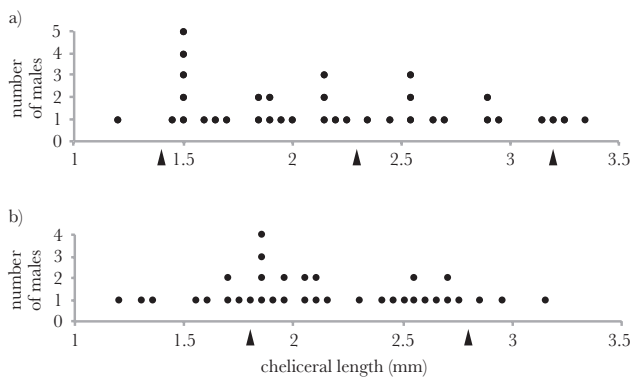
Figure 2

Cheliceral lengths of the subjects in (a) the Overall Size Experiment and (b) the Weapon Size Experiment. Each point corresponds to a unique individual. In (a), the leftmost pointer below the x axis indicates the cheliceral length of the small animation (1.4 mm), the middle pointer indicates the cheliceral length of the medium animation (2.3 mm), and the rightmost pointer indicates the cheliceral length of the large animation (3.2 mm). In (b), the right-hand pointer indicates the cheliceral length of the animation with elongated chelicerae (2.80 mm) and the left-hand pointer indicates the length of the chelicerae of the control animation and of the other 2 experimental animations (1.80 mm).

control animation (Table 2). The lack of intraindividual patterns of responses to the different experimental treatments can be seen in Figure 5.

DISCUSSION

Our results indicate that male *L. viridis* compare their opponents' sizes to their own during the precontact phase of a contest and that they are capable of using visual cues to do so. Importantly, computer animation allowed us to manipulate one size-related variable at a time, which allowed us to exclude alternative possible explanations (e.g., coloration, behavior, chemical cues, and seismic cues) for males' differential responses to the different-sized animations. In the Overall Size Experiment, although the effects of size difference and opponent size were both highly significant, with opposite effects when run in separate models, the effect of opponent size disappeared when the 2 variables were included in the same model. This indicates that size difference explains more of the variation in escalation intensity than opponent size does. The lower AIC and higher relative likelihood of the model including size difference as the only fixed effect adds further evidence that size difference is a better predictor of escalation intensity than opponent size. Interestingly, there was no significant effect of focal individual size in any of our models, which argues against a strong role for self-assessment in this species. When we removed the random effect term from the model that included focal individual size as the only fixed effect, focal individual size was still not a significant predictor of escalation intensity. This indicates that any possible effect of focal individual size was not masked by a correction for random effects.

The evidence here for mutual assessment stands in contrast to previous work on jumping spider contests in the species *Phidippus clarus* and *Plexippus paykulli*, in which the weight of evidence pointed toward a self-assessment strategy (Taylor et al. 2001; Elias et al. 2008; Kasumovic et al. 2011). Whether this reflects a true difference in assessment strategies across species, or rather a difference in experimental approaches or analyses, is an interesting question. In the current study, we were able to control for the behavior of one of the individuals in the contest (the computer-animated spider) and focus on the behavior of a single individual during the precontact phase only. Not only did the use of computer-animated opponents reduce the amount of noise in our data by cutting down on the number of unknown and unquantified and potentially confounding variables but it also confined our analysis to the precontact phase, during which animals may employ a different assessment

Table 1

Models tested for Overall Size Experiment

Model	Fixed effect (FE)	Random effect (RE)	Mean β-coefficient	AIC	Relative likelihood	FE P-values	RE P-value	ICC
1	Focal–opponent	Male ID	5.14	222.6	1	<0.0001	0.094	0.60
2	Opponent	Male ID	−5.33	227.1	0.11	<0.0001	0.085	0.56
3	Focal	Male ID	1.58			0.19	0.25	0.21
4	Focal		1.35			0.12		
5	Focal–opponent	Male ID	2.76			0.046	0.096	0.57
	Opponent		−2.71			0.23		
6	Focal–opponent	Male ID	5.47			<0.0001	0.096	0.57
	Focal		−2.71			0.22		
7	Opponent	Male ID	−5.33			<0.0001	0.092	0.54
	Focal		2.54			0.19		
8	Order	Male ID	−0.04			0.86	0.21	0.24
9	Focal–opponent	Male ID	5.29			<0.0001	0.092	0.59
	Order		−0.25			0.39		

Figure 3
Male threat escalation intensity directed toward the small, medium, and large animations in the Overall Size Experiment as a function of the difference in size between the focal male and his animated opponent. Although overall size was the parameter being manipulated, cheliceral length was used as a proxy for size. Animated opponent size for each data point is indicated as follows: small (open circle), medium (gray circle), and large (filled circle).

strategy than they do during the contact phase of a contest. There is evidence that some taxa do employ different assessment strategies during different contest phases (Morrell et al. 2005; Hsu et al. 2008; Keil and Watson 2010). Grouping the precontact and contact phases together into one analysis, as is usually done, could cause the evidence for the contact phase assessment strategy to overshadow the evidence for the precontact phase assessment strategy, or vice versa (Hsu et al. 2008). The best approach, in contests between live males, is to analyze contests that were resolved during the precontact phase separately from contests that were resolved during the contact phase. If one is specifically interested in the precontact phase of a contest, the use of virtual opponents may, in many cases, be a more efficient and well-controlled methodology than staging contests between live males. With more studies using virtual opponents and/or analyzing different stages of contests separately, over time, we should begin to get a clearer picture as to the distribution of assessment strategies across different contest phases as well as across the animal kingdom.

In the studies that have analyzed contests that were resolved in the precontact phase separately from those that were resolved during the contact phase, it has generally been found that contestants switch from a mutual assessment strategy in the early, noncontact phases of a contest to a self-assessment strategy in the contact portions of a contest (Morrell et al. 2005; Hsu et al. 2008; Keil and Watson 2010). This pattern makes sense and seems to validate the visual displays that precede physical combat in so many systems. It has indeed been alarming that the implementation of Elwood and colleagues' statistical model across diverse taxa has so far seemed to suggest that mutual assessment is a rare phenomenon, even among animals with obvious visual agonistic displays (Taylor et al. 2001; Stuart-Fox 2006; Elias et al. 2008; Brandt and Swallow 2009; Kasumovic et al. 2011; Tsai et al. 2014). The common practice of not analyzing precontact and contact phases separately could be a possible explanation for this.

There was a marginally significant random effect of individual in the present study, as well as a high intracluster correlation coefficient (ICC), in all of our most parsimonious models (Table 1). The ICC corresponds to the proportion of variance in the data explained by differences among individuals. The high ICCs that we observed indicate that a male's propensity to threaten an opponent was also

influenced by behavioral syndrome and/or by interindividual variation in levels of assessment or motivation during different stages of a contest. Some males may not assess their opponents at all prior to their first display but rather threaten all opponents regardless of relative size, and only make a decision to retreat or advance after a few displays have been exchanged, and/or after they have stepped closer to their opponent for a better look. Others may never assess but instead respond in the same way to all of their opponents or in a probabilistic fashion according to genetically inherited knowledge of the RHP distribution in the population, both of which are strategies that could confer energetic advantages to individuals for whom the costs of assessment are high. Similarly, some males may assess, but do so with varying degrees of investment and, hence, error, according to resource value and individual-specific costs of assessment and/or escalation (Mesterton-Gibbons and Heap 2014). In the present experiment, each male was exposed to silk from a different female as a priming stimulus for combat. Different females likely had different genetic qualities and were therefore perceived as resources of different values, which may have differentially affected individual males' investments in assessment. Males may also vary in their sensory or cognitive capacity to make accurate assessments (Elwood and Arnott 2012; Mesterton-Gibbons and Heap 2014). Behavioral syndrome, as mentioned above, may also be responsible, at least in part, for the high ICCs that we observed, as aggressiveness is generally found to vary across individuals and to covary with other boldness-related traits, such as exploratory behavior in novel environments and activity under predation risk. Such behavioral syndromes are found in taxa as diverse as birds, fish, crickets, and spiders (including the jumping spider *Eris militaris*) (Bell and Stamps 2004; Kortet and Hedrick 2007; Bourne and Sammons 2008; Webster et al. 2009; Eriksson et al. 2010; Colléter and Brown 2011; Barnett et al. 2012; Mowles et al. 2012; Pruitt et al. 2012; Scales et al. 2013; Royauté et al. 2014). Whatever the cause of interindividual variation, when it is as high as it was in the present study, there is a risk that it could obscure correlations diagnostic of different assessment strategies in an experiment in which intraindividual correlation coefficients are not calculated or controlled for. Thus, there is a distinct benefit to using a repeated-measures experimental design in studies of assessment strategies because the effect of individual can be controlled for.

Although males clearly distinguished between the different-sized animations in the Overall Size Experiment, they did not seem to make any distinction between males with versus without select elongated appendages in the Weapon Size Experiment. This suggests that males do not attend to the lengths of specific appendages relative to other body part(s). To determine whether or not our
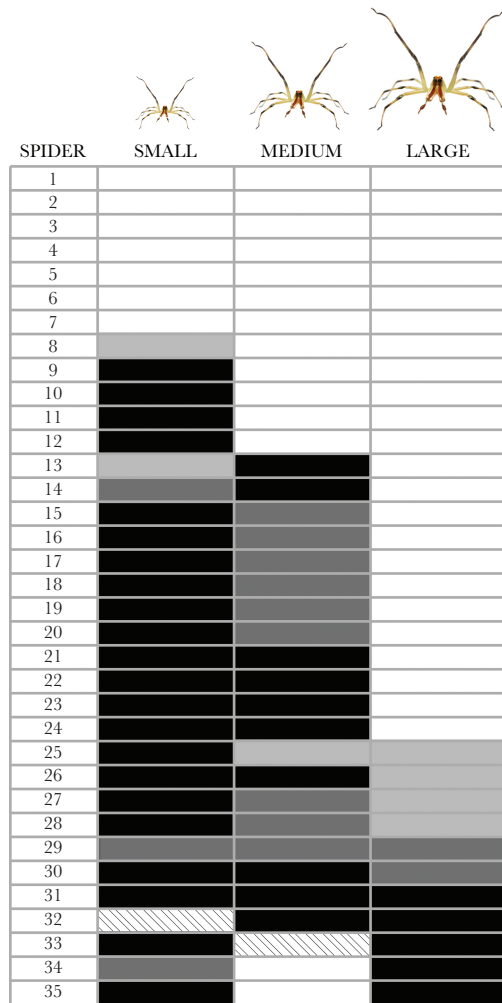
Figure 4

Male responses to the small, medium, and large animations in the Overall Size Experiment. Response type is color coded, such that a white box denotes a retreat, a light gray box denotes a threat display, a dark gray box indicates a threat display with advancement toward the computer screen, and a black box denotes a threat display with advancement culminating in contact with the computer screen. Hatched lines denote a courtship display. For clarity in the figure, subjects are grouped by their patterns of responses.
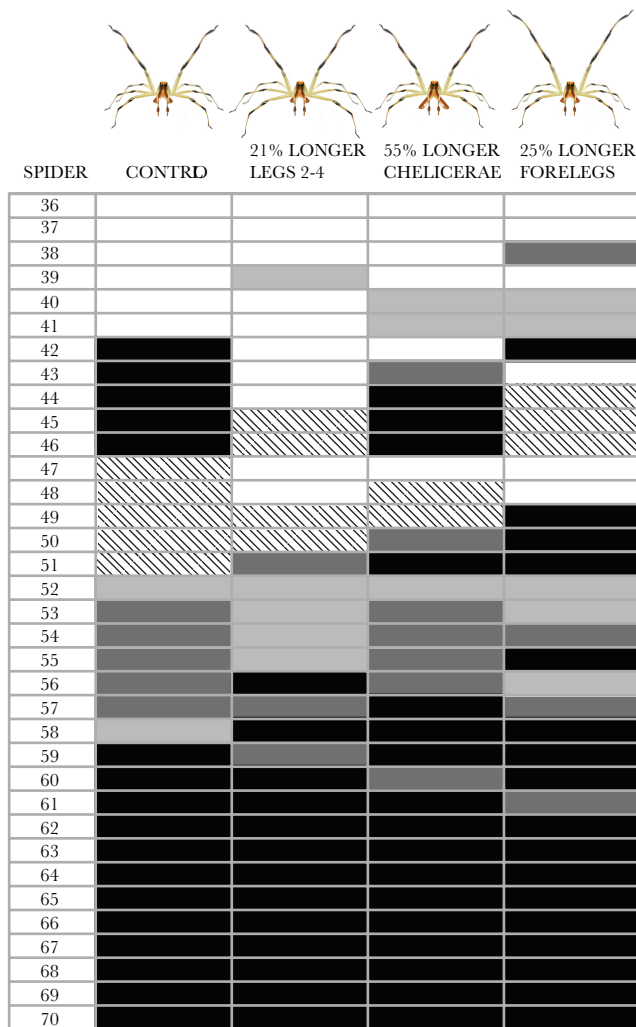
experiments also ruled out the possibility that males attend to the absolute lengths of specific appendages, without regard to their size relative to the rest of the body, we compared whether the length manipulations in the Weapon Size Experiment resulted in as big of a raw change in absolute length as the scaling of overall size did in the Overall Size Experiment. In doing this, we found that the chelicheral length manipulation in the Weapon Size Experiment resulted in a greater change in the absolute length of the chelicerae than the scaling of overall size did in the Overall Size Experiment. In contrast, we found that the foreleg and legs 2–4 length manipulations in the Weapon Size Experiment resulted in smaller changes in absolute length than the scaling of overall size did in the Overall Size Experiment. In conclusion, we can say that males do not attend to the absolute lengths of the chelicerae but that our experiments did not rule out the possibility that they attend to the absolute lengths of the forelegs and/or legs 2–4. Although no other study has been able to show that weapon size is visually evaluated in contests, the fact that *L. viridis*' red-pigmented, strongly allometric chelicerae did not appear to be evaluated is a good reminder that conspicuously colored, positively allometric weaponry is not necessarily evaluated in contests despite the intuitive appeal of the notion that it does.

Of course, rather than length, it is possible that males attend to a different size-related feature of the appendages. Males may attend more to the girth or shape of an appendage than to its length. Alternatively, males may not attend to the appendages at all but instead assess the size of the prosoma or specific features on the prosoma, which were unmanipulated in the Weapon Size Experiment. It is also possible that different individuals assess different body parts. In this case, it would be difficult to uncover general patterns without much larger sample sizes than those used in the present study. It may also be easier to obtain a larger number of differential responses to different animations if we were to begin with a larger (and hence "scarier") control animation. One could argue that assessing overall size or prosoma size could be a superior strategy to assessing weapon size if some individuals in a population cheat by growing larger weapons relative to their prosoma size than other individuals. However, it seems unlikely that cheating plays an important role in the evolution of assessment in this species because weapon length correlates tightly with body size, especially among males ($R^2 = 0.89$ for both chelicheral length and foreleg length) (Tedore and Johnsen 2012). By contrast, the nonweapon second pair of legs correlates only loosely with body size ($R^2 = 0.31$), so evaluating nonweapon appendages would seem to provide less accurate information about fighting ability than evaluating the weapons would, unless, of course, we are underestimating the importance of nonweapon appendages in winning fights. Perhaps by spreading their weight out over a larger area, males with longer nonweapon legs are better able to hold their ground in pushing contests. Another possibility is that weapon length may

Table 2

Models tested for Weapon Size Experiment

Model	Fixed effect (FE)	Random effect (RE)	Mean β-coefficient	FE P-value	RE P-value	ICC
21% elongated legs 2–4 versus control						
1	Opponent	Male ID	−0.31	0.25	0.17	0.75
55% elongated chelicerae versus control						
2	Opponent	Male ID	0.02	0.98	0.15	0.85
25% elongated forelegs versus control						
3	Opponent	Male ID	0.11	0.58	0.19	0.85

SPIDER	CONTROL	21% LONGER LEGS 2-4	55% LONGER CHELICERAE	25% LONGER FORELEGS
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Figure 5

Male responses to the control and the 21% elongated legs 2–4, 55% elongated chelicerae, and 25% elongated forelegs treatments. As in Figure 4, response type is color coded, such that a white box denotes a retreat, a light gray box denotes a threat display, a dark gray box indicates a threat display with advancement toward the computer screen, and a black box denotes a threat display with advancement culminating in contact with the computer screen. Hatched lines denote a courtship display. For clarity in the figure, subjects are grouped by their patterns of responses.

not correlate strongly with weapon strength, as in the fiddler crab *Uca annulipes* (Backwell 2000) and the slender crayfish *Cherax dispar* (Wilson et al. 2007), both of which are able to bluff their opponents by displaying enlarged chelae that are weaker on average for their size. If the same were true in *L. viridis*, then an assessment of multiple body parts, including the second pair of legs, might provide a more accurate estimate of opponent RHP than an assessment of just the weapons would.

In summary, we have here presented evidence for visual mutual assessment of opponent size in a jumping spider, using a methodology that allows for the disentanglement of potentially correlated phenotypic traits both within and between different sensory modalities. Given the paucity of evidence for mutual assessment so far, despite its apparent adaptive advantages, we propose that by more frequently incorporating computer animation, robotics, and other types of virtual stimuli into studies of competitive interactions, we may be able to more easily find evidence of mutual assessment throughout the animal kingdom.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco. oxfordjournals.org/

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