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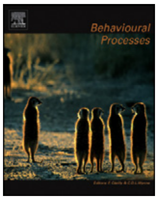

Weaponry, color, and contest success in the jumping spider *Lyssomanes viridis*

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ABSTRACT

Weaponry and color badges are commonly theorized to function as visual signals of aggressiveness or fighting ability. However, few studies have supported a signaling function of weaponry, and the role of color in invertebrate competitive interactions remains virtually unexplored. Jumping spiders (Salticidae) make excellent invertebrate models for studying weaponry and color because males of many species are colorful and possess exaggerated chelicerae, which are used as weapons in escalated contests. To determine whether color or weaponry might function as visual signals in male–male competitions, we investigated relationships between contest success, cheliceral length, and red coloration in *Lyssomanes viridis*. Males having longer chelicerae than their opponents were significantly more likely to win ($p = 0.0008$). Males who won, despite being smaller than their opponents, had significantly less red chelicerae than their opponents ($p = 0.01$). Male and female cheliceral length, as well as foreleg length, correlated tightly with body size. Cheliceral and foreleg length showed significantly stronger positive allometry in males than in females. We conclude that male chelicerae and forelegs are under strong positive selection for their use in physical fights and/or as visual signals of fighting ability.

1. Introduction

Male–male competition for access to females is a widespread phenomenon in the animal kingdom. Many such contests seem to be resolved by visual signals, which typically fall into two categories: displays of weaponry and badges of status (Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005). Weapons are specialized structures or elaborated body parts designed to inflict damage during physical fights, such as antlers, teeth, crustacean chelae, and spider chelicerae. Weapon size could, in theory, be evolutionarily co-opted to function as a visual signal of fighting ability or aggressiveness. Badges of status are theorized to be patches of color(s) whose hue, brightness, darkness, contrast, size, shape, or pattern indicate a willingness or ability to fight. Badges and weaponry may, in some species, evolve dual signaling functions in both intrasexual and intersexual contexts (Berglund et al., 1996).

Although weapon size has been found to correlate with body size in both vertebrate and invertebrate taxa (e.g. Huxley, 1932; Pomfret and Knell, 2006), little is known as to whether or not weapons tend to function as visual signals of fighting ability. In the Cervidae (deer and their allies), for example, there is no conclusive experimental evidence that antler size or branching patterns are used to assess fighting ability (reviewed by Clutton-Brock, 1982). Chela size appears to be a rough predictor of contest success in snapping shrimp (*Alpheus heterochaelis*) (Hughes, 1996) and slender crayfish (*Cherax dispar*) (Wilson et al., 2007). However, evidence suggests that these signals do not honestly convey actual fighting ability (Hughes, 2000; Wilson et al., 2007). Further work is needed to clarify the signaling function of weaponry in both vertebrate and invertebrate taxa.

Experimental manipulations of avian color badges have provided strong support for the theory that color patches can signal fighting ability or aggressiveness (e.g. Fugle et al., 1984; Rohwer, 1985; Pryke et al., 2002; Pryke and Andersson, 2003). However, little is known about the role of color in the agonistic interactions of other taxa, particularly invertebrates. The few studies that have explored the relationship between invertebrate color patterns in aggressive interactions suggest that invertebrates are capable of associating fighting ability with the size of a color patch (Grether, 1996) or the patterning of light and dark elements (Tibbetts and Dale, 2004; Tibbetts and Curtis, 2007). However, the roles of other spectral properties, like dominant wavelength and spectral purity, are unknown.

1.1. Salticids as a model system

Jumping spiders (Salticidae) make excellent invertebrate subjects for studies of both weaponry and badges of status because in many species, males possess exaggerated chelicerae, which function as weapons in escalated contests, as well as colorful patches of hair or cuticle on the face and/or abdomen, which may function as badges of status. Females do not have exaggerated chelicerae and

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Fig. 1. Female (left) and male (right) *Lyssomanes viridis*. Photos by CT (left) and Jay Barnes (right).

are typically more cryptically colored. Salticids are diurnal and have excellent vision; measurements of *Portia fimbriata's* photoreceptor spacing and optics suggest a resolvable angle of 0.04° (Williams and McIntyre, 1980). This is much finer than the 0.24° inter-ommatidial angle of the compound eye of the dragonfly *Anax junius*, which possesses the finest known spatial acuity of any insect (Land and Nilsson, 2004). The saliticid *Menemerus confusus* was found to possess four different photoreceptor classes whose peak sensitivities span the spectrum from UV (360 nm) to yellow-orange (580 nm) (Yamashita and Tateda, 1976). Behavioral observations of *Lyssomanes* suggest a strong role for vision in predation and intraspecific interactions, although *Lyssomanes'* visual acuity may be somewhat lower than that of *Portia* (see Blest and Sigmund, 1984). Male *Lyssomanes* and other salticid species wave their legs at each other in stereotypical patterns when competing over females, so it seems likely they are visually evaluating one another.

Despite their colorfulness, the relationship between natural variation in male salticid color patterns and success in agonistic encounters has not been examined. In *Habronattus pyrrithrix*, Taylor et al. (2011) found the inflection point and spectral purity of red facial coloration, as well as the darkness of green forelegs, to be condition-dependent. Whether conspecific observers actually use the information embedded in coloration, however, remains unknown. In several salticid species, including *Phidippus johnsoni*, *Euophrys parvula*, *Zygoballus rufipes*, *Trite planiceps*, *Plexippus paykulli*, *Evarcha culicivora*, and *Phidippus clarus*, larger-bodied males have been found to be more likely to win male–male competitive interactions and to gain access to females (Jackson, 1980; Wells, 1988; Faber and Bayliss, 1993; Taylor and Jackson, 1999; Taylor et al., 2001; Cross and Jackson, 2007; Elias et al., 2008), but the relationship between weapon size and contest success remains unexplored.

1.2. Specific aims

The goal of the present study was to evaluate the relationships between contest success, weapon size, and color in the sexually dimorphic jumping spider *Lyssomanes viridis*. Male *L. viridis* have reddish-brown chelicerae that are exaggerated in length, as well as boldly striped legs and a larger patch of red hairs on the forehead than females. Females are cryptically colored translucent green, except for a red ring of hairs against a background of white hairs on top of the head, and have comparatively short, green chelicerae (Fig. 1). In escalated contests, males press their chelicerae and forelegs against each other and push until one of them gives way and retreats. Thus, for the purposes of this paper, we considered both the chelicerae and forelegs to be weapons. Specifically, we staged contests between pairs of males, and asked the following: (1) Does male weapon length (i.e. cheliceral and foreleg length) correlate with contest success? (2) Does the spectral composition or overall brightness of male foreheads or chelicerae correlate with contest success? and (3) Does weapon length correlate with body size?

2. Methods

2.1. Subjects and housing

Thirteen juvenile male and eight juvenile female *Lyssomanes viridis* were collected by beating sweet gum (*Liquidambar styraciflua*) trees along the Black Creek Greenway (35°49.3′N, 78°47.1′W) in Wake County, North Carolina, USA, in February 2009. Eleven additional mature males and one immature female were collected from the same area and from the Jordan Lake State Recreation Area (35°50.0′N, 78°58.0′W) in Chatham County, North Carolina, USA, in May 2009. All spiders molted to sexual maturity prior to being run in experimental trials. Fifty-four additional females and fifty-five additional males were captured for morphological measurements between July 2009 and April 2010, from the Jordan Lake State Recreation Area, the Black Creek Greenway, and the Duke University campus.

Spiders were individually housed in 10 × 10 × 10 cm clear plastic boxes on a wire shelving unit. Each shelf was illuminated by two full-spectrum (including UV) fluorescent mercury vapor tubes (T8, 32 Watt, 48 inch, Duro-Test Lighting's Vita-Lite, Philadelphia, PA, USA) installed in high-frequency (electronic ballast) light fixtures. To simulate the leaves they normally perch under, a 10 × 10 cm piece of green tissue paper was placed on top of each box, and a 10 × 15 cm piece of green tissue paper was crumpled slightly and placed inside each box. Boxes were visually isolated from one another by white paperboard barriers. The light cycle was altered gradually to mimic the outdoor diurnal light cycle and the room temperature was held constant at 27 °C. During the weeks leading up to experiments, spiders were fed four *Drosophila* three times per week. Seven days before behavioral trials began, we increased feeding frequency, providing each spider with four *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. To ensure spiders were well-hydrated, we accompanied each feeding with a light misting of filtered water.

Before the experiment began, all male spiders were run in a variable number of preliminary trials in which one or two males and a female were allowed to interact. Males were allowed to

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mount females, but were separated before intromission. Additionally, 11 of the 24 males used in the experiment were mature when caught. Thus, males had varying levels of experience with mature conspecifics prior to the experiment described in this paper.

2.2. Experimental arena

Behavioral experiments were run in a 10 × 10 × 10 cm clear plastic box illuminated by two overhead full-spectrum fluorescent lights (described above). Boxes were surrounded on all six sides by white translucent vellum, a high-quality paper which diffuses direct illumination. Because salticids see UV radiation, we measured absolute irradiance from 300 to 750 nm through the plastic box/vellum combination, and found that UV radiation made up 1.8% of total irradiance in photons. Trials were recorded by a video camera (Logitech QuickCam Pro for notebooks, Fremont CA, USA) directed through a window in the vellum exterior. Between trials, boxes were soaked in a solution of bleach (sodium hypochlorite (NaClO) and sodium hydroxide (NaOH)) for at least thirty minutes, scrubbed with a sponge, and rinsed to eliminate residual olfactory cues.

2.3. Experimental procedure

A randomly selected sexually mature virgin female was placed in the experimental arena for 20 min to lay down silk, which in preliminary trials seemed to increase the probability of male–male aggressive interactions. The female was removed and two randomly selected males were then placed in the arena in quick succession (within at most 10 s of each other) and in random order. When disturbed, *L. viridis* often runs in random directions for several seconds before pausing to examine its surroundings, so initial placement within the arena was not a factor we could control. Before placing pairs of males in the arena, we visually inspected each spider and noted distinguishing features that would allow us to tell them apart at the end of the trial. Video recording commenced just before males were placed in the arena. We recorded the order in which the two males were placed in the arena so that the identity of each spider could later be tracked during video analyses. The behavior of the two spiders was recorded for ten minutes, after which males were returned to their home boxes. Most individuals were run in one trial per day on June 8–11, 14, and 20–22. A few individuals died before the experiment was over. On days when we had an odd number of experimental subjects, we randomly selected one spider not to run in a trial that day. The result of this was that individuals ran in anywhere from two to eight trials. A total of 75 pairs of 24 different males were run. Seven pairings were identical and were removed from our analyses to avoid pseudoreplication, resulting in a total of 68 trials analyzed.

2.4. Video analyses

Interactions normally consisted of either one or both males posturing at each other, but for the purposes of scoring, we defined an interaction as two males pausing in their movements and looking at each other with their anteromedian eyes. The direction of visual attention in salticids is easy to judge because of the anteromedian eyes' narrow visual field and because salticids reflexively rotate their bodies to orient towards moving stimuli detected by the lateral eyes. We noted which male disengaged from each interaction first. Each disengagement was classified as either a retreat or a neutral disengagement. A retreat was defined as continuous movement away from the opposing spider for at least five cm without pausing or investigating female silk cues with the pedipalps. A neutral disengagement was defined as a walking or turning away from the opponent, moving less than five cm before pausing and/or investigating female silk cues. Five centimeters was easy to visually estimate because it was half the distance across the experimental arena. The first spider to retreat three times in a row was considered the loser, and his opponent the winner. The number three, as opposed to one, was designed to average out any ambiguities in the spiders' behavior and/or our interpretations of the spiders' behavior.

2.5. Photographic measurements of size and color

Each spider's visual characteristics were measured no later than 24 h after its death. Three individuals' colors were not measured within 24 h and were excluded from subsequent color analyses. Spiders either died naturally or were sacrificed via overanesthesia with carbon dioxide. Size attributes, including cheliceral length, foreleg breadth, and prosoma diameter (our measure of body size) were measured by photographing spiders through a microscope next to an ocular micrometer. Body size endpoints are shown in Fig. 2.

Repeatable color measurements were impossible to obtain using our spectrometry equipment due to the tiny size of these spiders. Small changes in the position or angle of the measurement probe and light source relative to the spider's color patch gave very different results, even when working under a microscope with the probes clamped into place. Some spiders had sparse hairs and were particularly difficult to measure because, depending on the positioning of the measurement probe, one might be measuring hair or cuticle or some varying combination of both. The chelicerae were also difficult to measure because of variation in pigmentation over small areas and because cuticle is susceptible to specular reflection when illuminated by a bright standardized light source. Because we wanted to measure entire color patches, as spiders likely perceive them, and because *L. viridis*' red foreheads and chelicerae did not reflect UV light in any of our spectroscopic measurements, we devised a highly repeatable method of calculating color from photographs taken through a microscope, similar to that described by Stevens et al. (2007). Spiders were photographed at an ISO of 200 (using uncompressed TIFF format) next to a series of nine gray squares, constructed from Color-aid's Gray Set (Hudson Falls NY, USA), which is a series of high-quality, spectrally flat papers, covering a wide range of grays from black to white. We verified the papers' spectral flatness by measuring their reflectances. To measure reflectance, we placed each paper under an integrating sphere (ISP-REF, Ocean Optics Inc., Dunedin, FL, USA), which was connected by a fiber optic cable to a spectrometer (USB2000, Ocean Optics Inc., Dunedin, FL, USA).

When taking photographs through the microscope, the spider and gray series were surrounded by a cylinder of translucent white vellum, which served to create an even light field throughout the photograph. Sufficient depth of field was achieved using the extended focal imaging function in Olympus' Microsuite FIVE software (Center Valley, PA, USA), which montages photos taken at different focal planes to create a single in-focus image with an enhanced depth of field.

Before taking each photograph, color cast was neutralized using Microsuite FIVE's white balance function, which allows one to select a specific region in the camera's field of view and to designate that region as gray, or spectrally neutral. In each photograph, we selected the pixels making up the lightest gray of the gray series, taking care not to overexpose this gray. For each of these selected pixels, the software calculates the average intensity registered by the R, G, and B sensors. A pixel-specific correction factor is then calculated for each of the R, G, and B channels by dividing the average value across channels by the actual intensity value in each channel. This is done for each pixel in the selected region. The software then calculates the average correction factor for each

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channel in the selected region. These correction factors are then applied to the entire image. Because all of the Color-Aid papers in the gray series were spectrally flat, this resulted in identical, or near-identical, intensity values in the R, G, and B channels in each of the gray squares.

After image capture, photographs were opened using Photoshop CS2 (Adobe, Inc., San Jose, CA, USA). Each of the R, G, and B channels were 8-bit with an intensity value that could range from 0 to 255. Each gray square was selected individually and treated with an averaging blur, which calculates the average intensity value in each of the R, G, and B channels, and fills in the selected region with the resulting color. This, in effect, blurred out the grain of the gray paper, which was visible under the microscope.

A unique calibration curve was calculated for each photograph by plotting the average intensity value for each gray in the gray series against its reflectance, as measured above by a spectrometer. An exponential equation was then fitted to this plot, which served to convert the camera's intensity values into reflectances. Because the gray series was spectrally flat, and because the white balance in the Microsuite FIVE software adjusted the color balance of each photograph to ensure that each gray square's R, G, and B intensity values were nearly identical, it was not necessary to construct a separate calibration curve for each channel. As described below, we applied the same calibration curve to each of the R, G, and B channels.

To measure the color of the red forehead spot, we selected the polygon bound by the antero-median and antero-lateral eyes (Fig. 3a). To measure the color of the chelicerae, we selected the proximal portion of the right chelicera, from the base of the chelicera to the first prominent hair with a small spot of pigmentation at its base (Fig. 3b). We obtained the average intensity value in each of the R, G, and B channels within the selected region. The average intensity of the B channel in these red patches was very low (below five) in nearly every photograph. This simply means that the red patches reflected very little blue light, which is to be expected of a red color patch. These average intensity values were calculated from a range of intensity values; averages less than five were calculated from a range of values which often included zero. Thus, the B channel may have been underexposed in many of these red patches. We therefore excluded the B channel from subsequent analyses of red color patches. Using an image's unique calibration curve (described above), we calculated reflectance in the R channel and in the G channel. We then created an index of total reflectance, or brightness, by summing the reflectances in the R and G channels (R + G). Finally, we calculated the difference between R and G reflectances, normalized by total reflectance (R − G)/(R + G). This latter color attribute describes the relative amount of light captured by the red channel versus the green channel of the camera's sensors. We used these camera-specific reflectance values to approximate color and brightness. Converting these values to human CIE color space or to photoreceptor quantum catches, as in Stevens et al. (2007), would not useful or feasible here because (1) human color space is irrelevant to spiders and would unnecessarily obfuscate the parameters we actually measured, and (2) salticid spectral sensitivities have not been thoroughly investigated, and the number of photoreceptor classes may vary across species. Yamashita and Tateda (1976) found four distinct photoreceptor classes (at 360, 480–500, 520–540 and 580 nm) in *Menemerus confusus*, whereas DeVoe (1975) found three (at 370, 532, and one with dual peaks at

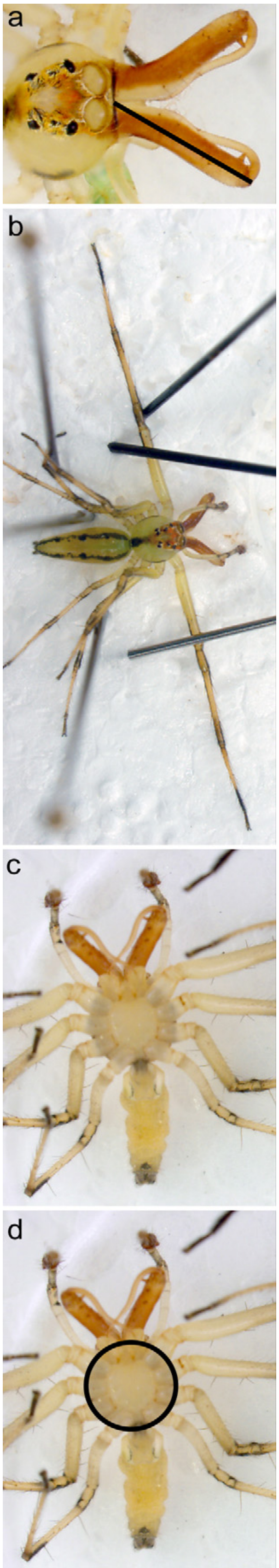

Fig. 2. Size endpoints of body parts. (a) Cheliceral length (indicated by a black line) was measured from the medial proximal corner of the chelicera to the connection between the basal segment and the fang. (b) Foreleg breadth was measured as the distance spanned by the laterally extended forelegs, from the distal ends of the left tarsal claws to the distal ends of the right tarsal claws. (c) The spider was flipped onto its dorsal side for measurements of prosoma diameter. The sternum was aligned horizontally for a consistent orientation across all subjects. In this configuration, the outline of the prosoma was visible between the legs' coxae. This allowed us to draw a circle of best fit around the prosoma (d), from which we obtained a diameter, i.e. 'prosoma diameter.'.

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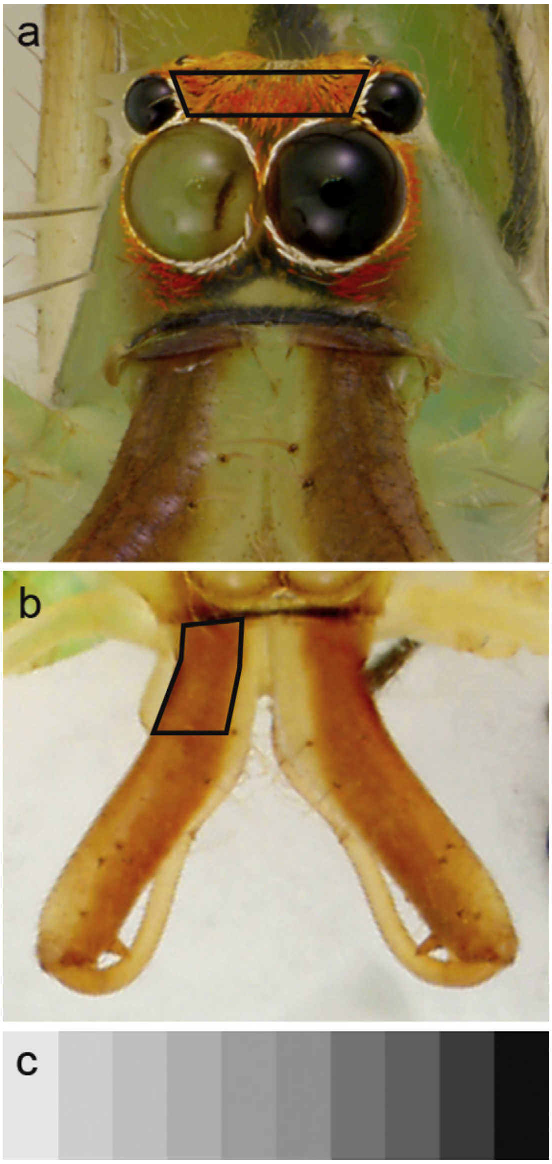

Fig. 3. Photographic color analysis. The analyzed portions of the forehead (a) and chelicerae (b) are outlined in black. An idealized series of grays (c) depicts the increments and range of brightnesses used to calibrate each photograph.

370 and 525 nm) in *Phidippus reqius*, and Blest et al. (1981) found two (at 360 and 520 nm) in *Plexippus validus*.

In Olympus digital cameras, the peak transmittances of the R and G filters, combined with the efficiency of the underlying photodiodes (i.e. quantum efficiency), are 645 nm and 540 nm, respectively (Turchetta et al., 2010). The quantum efficiency spectra of the R, G, and B filters are partially overlapping and roughly bell-shaped, similar to animal photopigment absorption curves. The G filter's peak quantum efficiency at 540 nm roughly coincides with a salticid photopigment absorption curve in each of the three studies described above. The R filter's peak quantum efficiency at 645 nm is more long-wavelength-shifted than the most red-shifted photopigment (at 580 nm) discovered by Yamashita and Tateda (1976), but is in an overlapping range. Between the three of them, the R, G, and B filters are highly transmissive to all visible wavelengths of light (Turchetta et al., 2010). Since the spiders' red spots had B-channel reflectances indistinguishable from zero, and since the G and B channels are overlapping, the sum of the R and G channels should have provided us with a reliable index of overall brightness in this system.

We tested the repeatability of forehead and cheliceral color measurements by taking five photos of the same spider in succession. Between each photograph, the spider was unpinned from its position, the light source moved out of the way, and the series of grays was moved. Different exposures were used for each photograph. Color measurements of both the chelicerae and forehead spot were highly repeatable (Supplementary Table 1). We also tested whether or not spider colors fade over time by measuring a live female's red forehead patch 45 days apart. The female's forehead patch did not fade over the course of 45 days (Day 1 R = 65.3%, Day 45 R = 66.8%, SE = 0.74%); Day 1 G = 24.2%, Day 45 G = 23.6%, SE = 0.33%).

2.6. Statistical analyses

Following Briffa & Elwood's (2010) recommendations for analyzing contest data, we ran a binomial multiple logistic regression in R (R Development Core Team, 2010) to evaluate the effect of size and color on contest success. Contest success (won/lost) was the binomial response variable. We randomly selected a focal individual from each contest and calculated the differences between that individual's size and color attributes and the attributes of his opponent. Color and size attributes included: (1) cheliceral length, (2) cheliceral reflectance in the R channel (R), (3) cheliceral reflectance in the G channel (G), (4) cheliceral R + G (index of brightness), (5) cheliceral (R – G)/(R + G) (redness normalized by brightness), (6) forehead reflectance in the R channel (R), (7) forehead reflectance in the G channel (G), (8) forehead R + G, and (9) forehead (R – G)/(R + G). We excluded foreleg breadth and prosoma diameter from the model because they were both tightly correlated with cheliceral length. Our maximal model included all possible second order interactions. We simplified our model by iteratively removing the least significant effect, beginning with second-order interactions and working our way down to first-order interactions until all that remained were significant effects.

In both male and female spiders, Pearson's product–moment correlation statistics between cheliceral length versus prosoma diameter and between foreleg breadth versus prosoma diameter were calculated and tested for significance. We also tested for pairwise correlations between male cheliceral length and cheliceral R, G, R + G, and (R – G)/(R + G), and forehead R, G, R + G, and (R – G)/(R + G), using Pearson Product Moment correlation statistics. We calculated and compared the ratios of foreleg breadth: prosoma diameter and cheliceral length: prosoma diameter in males and females using a two-sample *t*-test. To determine whether male weaponry scaled allometrically, or disproportionately, with body size, we performed reduced major axis regressions between weapon size and body size in males and females for comparison. Using the resulting regression lines, we calculated the percent increase in weapon size that should be associated with a five percent increase in body size for a theoretical male and theoretical female of average size. We performed analyses of covariance to compare the slopes of male regressions with female regressions.

The Benjamini–Hochberg correction for multiple comparisons was used to limit the number of Type I errors in all pairwise tests (Benjamini and Hochberg, 1995). We did a separate set of corrections for each set of related comparisons, which are separated into different figures and tables. Thus, each figure and table was treated as a group of multiple comparisons and the *p*-values were adjusted accordingly.

3. Results

3.1. Behavioral observations

During a typical trial, each male walked about the experimental arena and explored female silk cues with his pedipalps. Males

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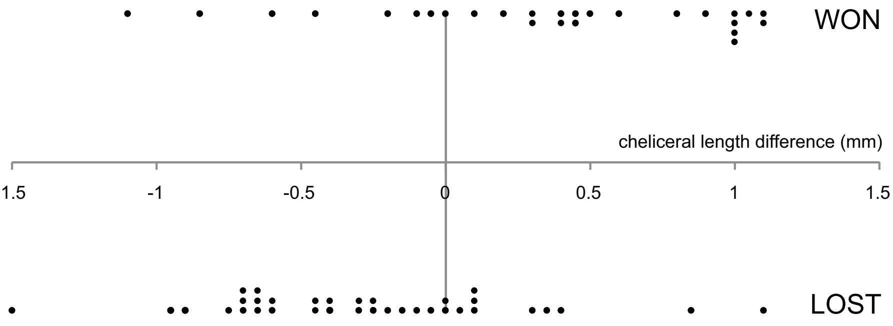

Fig. 4. Relationship between contest success and cheliceral length relative to one's opponent. A focal individual was randomly selected from each dyadic contest. Focal individuals who won are plotted above the *x*-axis; those who lost are plotted below the *x*-axis. Each data point's placement along the *x*-axis indicates the cheliceral length difference between the focal individual and his opponent. Logistic regression indicated a significant effect of relative cheliceral length on contest success ($p = 0.0008$).

periodically spotted one another and displayed until one of them retreated or neutrally disengaged. The same male invariably won all three interactions; there were only two experimental trials in which the winner and loser were reversed over the course of the trial. There was no clear winner in 7 of 68 (10%) of experimental trials; these trials merely consisted of a series of posturing interactions followed by neutral disengagements. The threat display consisted of an extension and periodic waving of the forelegs from near horizontal to near vertical, with the most common configuration being intermediate. During this display, the forelegs were either completely extended upwards or bent at the joint connecting the femur to the patella. Threat displays escalated to ritualized physical fights in 17 of 68 (25%) of experimental trials. When preparing for a physical fight (i.e. 'cheliceral fight'), males would slowly approach one another with their fangs extended. Cheliceral fights were initiated by one male quickly butting its chelicerae against his opponent's chelicerae. This would happen several times and occasionally one of the spiders would retreat after several bouts of cheliceral butting. More commonly, the two males would enter into an extended pushing contest in which they pressed their chelicerae and forelegs against each other for several seconds until one of them retreated. During some of these pushing contests, one of the males would disentangle his forelegs from his opponent's forelegs and reach underneath his opponent's abdomen, flipping his opponent into the air. Both males would sometimes lose their footing during pushing contests and grapple on the ground or while hanging by a dragline in mid-air. After a single cheliceral fight, the male that lost invariably became very submissive, retreating immediately when threatened. The male that won became highly aggressive if the loser persisted in the arena; he would abandon ritualized cheliceral fighting, and instead, chase and pounce on the loser. In a natural setting, the loser would be able to escape this aggression because he would not be limited to the confines of an experimental arena. To prevent the loser from being needlessly harmed, we separated the winner and loser after cheliceral fights, even if the trial had not run a full 10 min.

3.2. Weaponry and color

There were two significant fixed effects on contest success: (1) cheliceral length ($P = 0.0008$) and (2) the interaction between cheliceral length and cheliceral redness ($(R - G)/(R + G)$) ($P = 0.01$). In each dyad, the male with longer chelicerae was significantly more likely to win (Fig. 4). In 11 of 13 (85%) competitions in which the winner was smaller than his opponent, the winner was also less red (two-tailed exact binomial $P = 0.02$). In 19 of 42 (45%) competitions in which the winner was larger than his opponent, the winner was also less red (two-tailed exact binomial $P = 0.37$). Thus, males who were smaller than their opponents, but still won, had significantly less red chelicerae; however, color was not a predictive factor in competitions in which the winner was larger (Fig. 5).

Male and female foreleg breadth and cheliceral length were tightly correlated with prosoma diameter (Fig. 6). Reduced major axis regressions of cheliceral length versus prosoma diameter demonstrated that, for a theoretical average-sized male (prosoma diameter = 1.81 mm), a 5.0% percent increase in prosoma diameter would be accompanied by a 13.4% increase in cheliceral length. For a theoretical average-sized female (prosoma diameter = 2.18 mm), a 5.0% increase in prosoma diameter would be accompanied by a 7.4% increase in cheliceral length. The slope of the regression of male cheliceral length versus prosoma diameter was significantly different from the slope of the same regression in females (ANCOVA: $F_{1,133} = 564$, $P < 0.0001$).

Reduced major axis regressions of foreleg breadth versus prosoma diameter demonstrated that, for a theoretical average-sized male, a 5.0% increase in prosoma diameter would be accompanied by a 6.3% increase in foreleg breadth. For a theoretical average-sized female, a 5.0% increase in prosoma diameter would be accompanied by a 5.8% increase in foreleg breadth. The slope of the regression of male foreleg breadth versus prosoma diameter was

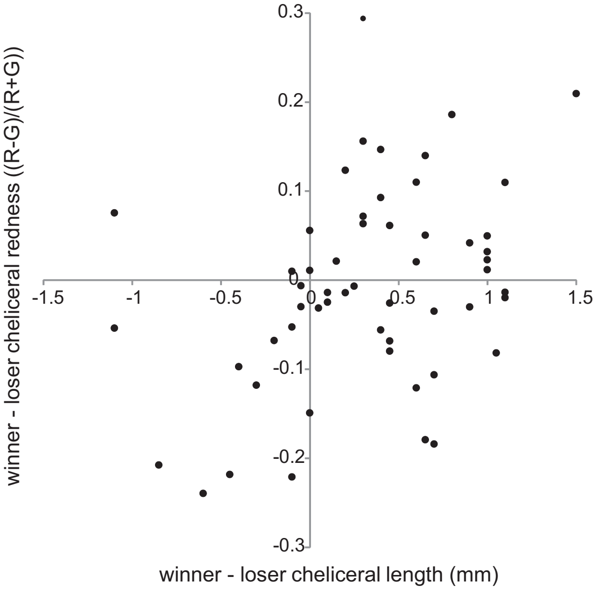

Fig. 5. Interaction between cheliceral length and cheliceral redness. The difference between the winner's and loser's cheliceral redness ($(R - G)/(R + G)$) is plotted against the difference between the winner's and loser's cheliceral lengths. Each data point represents a single trial. Males who were smaller than their opponents, but still won, had less red chelicerae ($p = 0.01$).

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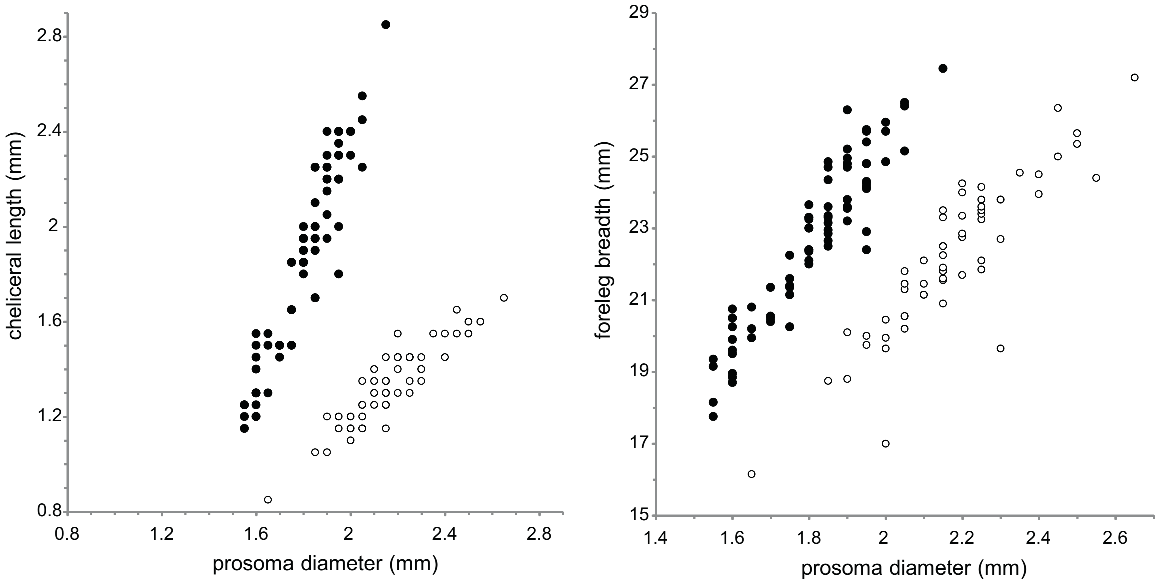

Fig. 6. Relationship between cheliceral length and prosoma diameter (left) and between foreleg breadth and prosoma diameter (right) in males (●) and females (○). Pearson's product–moment correlation statistics: Cheliceral length vs. prosoma diameter in males: $r = 0.94$, $N = 77$, two-tailed $p < 0.0001$; in females: $r = 0.91$, $N = 58$, two-tailed $p < 0.0001$. Foreleg breadth vs. prosoma diameter in males: $r = 0.82$, $N = 77$, two-tailed $p < 0.0001$; in females: $r = 0.89$, $N = 58$, two-tailed $p < 0.0001$.

Table 1
Ratios between weapons and body size in males ($N = 77$) and females ($N = 58$).

	Cheliceral length: prosoma diameter		Foreleg breadth: prosoma diameter	
	Mean	s.e.m.	Mean	s.e.m.
Males	1.03	0.02	12.45	0.09
Females	0.61	0.004	10.16	0.47
t (two-tailed)	21		19	
df	133		133	
P	<0.0001		<0.0001	

significantly different from the slope of the same regression in females (ANCOVA: $F_{1,133} = 408$, $P < 0.0001$).

The ratios of both foreleg breadth and cheliceral length to prosoma diameter were significantly higher in males than in females (Table 1). None of the color attributes of the forehead or chelicerae correlated with male cheliceral length (Table 2).

The order in which males were placed in the arena did not affect contest outcome. Of the 61 contests in which there was a distinct winner, 33 were won by a male who was placed in the arena first. Although pseudoreplicated trials were not used in any other analyses, we did find that five of seven replicated trials had the same outcome both times they were run.

Table 2
Correlations between male color and cheliceral length ($N = 21$).

Size attribute	Color attribute	Pearson's *r*	*P* (two-tailed)
Cheliceral length	Forehead R	0.36	>0.3
	Forehead G	−0.30	>0.3
	Forehead R + G	0.07	>0.3
	Forehead (R − G)/(R + G)	0.45	>0.3
	Cheliceral R	−0.05	>0.3
	Cheliceral G	−0.32	>0.3
	Cheliceral R + G	−0.13	>0.3
	Cheliceral (R − G)/(R + G)	0.33	>0.3

R = reflectance in the red channel.
G = reflectance in the green channel.
R + G = sum of the reflectances in the red and green channels (i.e. an index of total brightness).
(R − G)/(R + G) = difference between R- and G-channel reflectances, normalized by R + G.

4. Discussion

4.1. Weaponry

Cheliceral length was an excellent predictor of success in male–male agonistic encounters, and was tightly correlated with foreleg breadth and prosoma diameter. Salticid displays usually include an extension and/or waving of the legs (Richman, 1982). Our results suggest that such displays could function as honest indicators of male body size. The highly disproportionate increase in male cheliceral length with body size, compared to the same relationship in females, was particularly striking, and likely reflects the importance of long chelicerae in winning physical fights. Male foreleg breadth also increased disproportionately with body size, compared to females, although to a lesser degree. One of seventeen cheliceral fights resulted in permanent damage to the loser's legs. If *L. viridis*' chelicerae and/or forelegs function as honest signals of fighting ability, then individuals having larger-than-normal chelicerae or forelegs relative to their body size, who escalate to physical combat, may be punished by a higher probability of injury. During some pushing contests, one of the males would disentangle his forelegs from his opponent's forelegs and reach under his opponent's abdomen to flip him into the air. The longer the forelegs, the easier it should be to reach this distance, which could be another selective force acting on male foreleg length.

L. viridis may have evolved its highly positively allometric chelicerae due to its high population densities. Among the Cervidae, Clutton-Brock et al. (1980) found that antler length increased not only with body size, but with social group size as well. Males living

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in large polygynous social groups should experience more intense competition for access to females than those living in small polygynous groups and, as a result, more intense intrasexual selection (Emlen and Oring, 1977). Although salticids do not live in social groups, we have found *L. viridis* and *Hentzia palmarum* (another salticid with exaggerated chelicerae) to occur at higher population densities than other sympatric salticids with shorter chelicerae. A high conspecific encounter rate may have similarly intensified competition over females, and selected more strongly for exaggerated chelicerae in *L. viridis* and *H. palmarum* than in other salticid species living at lower population densities. A detailed survey of salticid population densities and cheliceral lengths may reveal a parallel evolutionary pattern between vertebrate and invertebrate taxa.

4.2. Color

The only significant effect of color was the interaction between cheliceral length and cheliceral redness, measured as (R − G)/(R + G). Fig. 5 shows that males who were smaller than their opponents, but still won, had less red chelicerae. This result is puzzling and is the opposite of what one might expect if redness were functioning as a signal of fighting ability. One possible explanation is that males who win, despite being smaller, have allocated nutrients over the course of development in such a way as to increase their endurance or agility at the expense of being colorful. Another possibility is that jumping spiders are less sensitive to the red end of the spectrum and thus perceive red chelicerae as greyer, or more achromatic, than chelicerae with relatively more reflectance in the green portion of the spectrum. However, none of the color attributes we measured exhibited pairwise correlations with cheliceral length or with contest success, which argues against its evolution as a signal of fighting ability or aggression.

Interestingly, in the jumping spider *Habronattus pyrrithrix*, Taylor et al. (2011) found that juveniles fed a diet high in protein, calcium, and vitamins developed red scale coloration as adults that was richer in long wavelengths than the coloration of spiders fed a lower quality diet. This suggests that red scale coloration (as in *L. viridis*' forehead) has the potential to function as a signal of quality in jumping spiders, but more experimental data is needed to determine whether or not *H. pyrrithrix* actually evaluate the information embedded in coloration.

The biochemical basis of scale pigmentation in spiders has not been determined, although in some species, scale coloration is known to be structural (Foelix et al., 2009; Ingram et al., 2009, 2011). In the 14 families of spiders that have been tested, yellow, orange, red, brown, and black cuticular coloration has been found to be a result of ommochromes (Seligy, 1972; Holl, 1987), which are derived from the amino acid tryptophan. The degree to which tryptophan is a limiting nutrient in spiders is unknown. It is conceivable that in *L. viridis*, cheliceral color does not signal fighting ability or aggressiveness, but instead is correlated with some other trait that influences contest success, such as cuticular rigidity. High protein content and sclerotization of the cuticle increase its rigidity (Nation, 2002). If the rigidity of cheliceral cuticle influences contest success, and if protein consumption affects both cuticular rigidity and pigment deposition, this may explain the observed interaction between cheliceral color, size, and contest success in *L. viridis*.

Interestingly, *L. viridis* cheliceral coloration develops gradually in the days following the terminal molt, as the new cuticle hardens, suggesting a possible biochemical linkage between sclerotization and pigment deposition. Alternatively, pigment deposition may have evolved to coincide with the hardening of the cuticle to render a male visually inconspicuous to competitors while in a weakened state. Rather than functioning as a fine-grained signal of fighting ability or aggressiveness, reddish-brown cheliceral coloration may have evolved to provide visual contrast between the chelicerae and the spider's green body and its natural green leafy background. This visual contrast would be adaptive if males visually evaluate the size of each other's chelicerae or if exaggerated cheliceral length has evolved an additional function as a visual indicator of sex.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.beproc.2011.10.017.

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