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Mating and egg-laying behavior of *Hasarius adansoni* (Araneae: Salticidae) and the influence of sexual selection

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Abstract. Jumping spiders perform multi-modal displays during courtship and this has been used to study sexual selection and mate choice. However, studies have focused on only a few groups of spiders. Here we describe for the first time the breeding behavior of the tropical jumping spider *Hasarius adansoni* (Audouin, 1826). Animals were collected in the field and reared in the laboratory until adulthood. We took male body measurements, paired couples in mating trials, and then collected subsequent clutches. We confirmed the presence of a multi-modal display with visual and vibratory signals (tremulations) by the males. Females responded with their own tremulations and occasionally a receptive posture. Otherwise, they avoid mating by attacking or running away from the male. No measured male morphological attributes were important for male mating success and future studies should focus on other morphological measurements to understand how the mate choice process functions in this species. Multiple matings were common and females laid numerous clutches while enclosed in silk cocoons. Number of young per clutch decreased over the course of laying bouts.

Keywords: Jumping spiders, multi-modal display, mate choice

Salticid spiders have excellent vision (Levi & Levi 1990; Hill & Richman 2009) and most of their behaviors are visually guided (Richman & Jackson 1992). Courting behavior is no exception, and males from this family are known for performing extravagant visual and vibratory displays to attract females (e.g., Jackson & Macnab 1989a, b; Hill & Richman 2009; Girard et al. 2011). In many species, females respond with their own display behavior (Levi & Levi 1990; Cross et al. 2007). Recent work has shown that jumping spiders also produce vibratory signals, and these are often complex and coordinated with visual displays (Foelix 2011; Elias et al. 2012). For these reasons, salticids are important models for studies of the evolution of communication, including hypotheses about signal elaboration, multi-modal signals, and signal function across diverse habitats. Moreover, male sexual displays in Salticidae are important in speciation and can be key characters for taxonomic classification (Richman 1982; Masta & Maddison 2002). Richman (1982) presented a comprehensive description of the displays of species across genera, information that is critical for salticid systematics. However, as is the case for many spider families, behavioral data are available for relatively few species, and there are entire genera with little or no information available. In the case of salticids, behavioral studies are concentrated in groups of the genera *Habronattus* F.O. Pickard-Cambridge, 1901 and *Phidippus* C.L. Koch, 1846, focusing mostly on breeding behavior (e.g., Sivalinghem et al. 2010; Elias et al. 2012; but see Clark & Morjan 2001 and Lim et al. 2007 for examples in other genera). This hampers studies of the evolutionary history of this group and precludes comparative analyses of signal evolution.

Here, we examine the breeding behavior and sexual signals of *Hasarius adansoni* (Audouin, 1826), a salticid that is common in urban environments throughout the tropics (Levi & Levi 1990). Despite its widespread distribution, (Levi & Levi 1990; Zabka & Pollard 2002), this species has been the subject of only one behavioral study to date. Cloudsley-Thompson (1949) provided some descriptive notes about *H. adansoni* sexual behavior, including display, copulation and egg-laying behaviors. However, this was based on a very small sample size, largely anecdotal observations, and since no viable eggs were produced it is unclear whether matings were successful. However, Cloudsley-Thompson's description suggests *H. adansoni* males produce visual signals, and this is also suggested by their sexually dimorphic coloration; while females are cryptic brown, males are black with conspicuous white patches on their palps (Levi & Levi 1990; Fig. 1). Thus, the objective of this study is to describe this species' display, copulation and egg-laying behaviors. Specimens of both sexes of *H. adansoni* are deposited in the arachnid collection of the Universidade de Brasília (UnB), Laboratório de Aracnídeos, collection number 4304.

METHODS

Rearing.—A total of 94 animals were used in mating experiments. We captured *H. adansoni* juveniles before their last instar on urban walls and buildings around the city of Brasília, Brazil (15°45′47.4″ S, 47°52′14.3″ W) and brought them to the Laboratório de Comportamento Animal in Universidade de Brasília (UnB) where mating trials were conducted. Vibratory signals produced by one pair were recorded at the University of Toronto Scarborough (43°47′1.47″ N, 79°11′15.66″ W). We could not repeat vibratory analysis with other pairs, since most of those transferred to Canada were part of other experiments. No permits were needed to transport the live spiders to Canada. All animals were kept in cylindrical glass containers measuring 9 cm X 4.5 cm in natural photoperiod and room temperature. A piece of wet cotton was kept inside each container to

Figure 1.—Sexual dimorphism in *Hasarius adansoni*. A. Female; B. Male.

maintain moisture. Spiders brought to Canada were maintained in similar conditions. Animals were fed every four to seven days. In each feeding episode, individuals were given 10 to 15 *Drosophila* spp. and one young *Gryllus* cricket. We also fed the spiders on the day before conducting the mating experiment described below.

Vibratory signals.—Since substrate-borne vibratory signals are common in salticid spiders (Foelix 2011), we used one pair of spiders to determine whether such signals occur for this species. The pair was placed together in a circular mating arena (11 cm diameter) on a turntable covered in stretched nylon and with all sides composed of a clear plastic wall. This type of arena has been previously shown to transmit salticid courtship signals (Elias et al. 2003). Laser Doppler vibrometry (LDV, PDV100 portable laser vibrometer, Polytec, Tustin CA, USA) was used to detect the occurrence of substrate vibrations during the pair's interactions. Vibratory signals were recorded, along with detailed videos with sound available that made it possible to detect any movements causing vibrations by the animals. Three small pieces of lightweight reflective tape (~1 mm) were placed near the center of the nylon-covered turntable and used as measurement points for the laser. Laser output was fed through a speaker to allow real-time audio monitoring of vibratory signals. Simultaneously, the pair was filmed using a digital high-speed camera (500 frames s^{-1}; PCI 1000; RedLake Motionscope, San Diego, CA, USA) while the spiders were illuminated with a Minifill light, manufactured by Frezzi. For this exploratory analysis, we monitored the high-speed video while listening to the LDV output to determine candidate body movements that might generate vibratory signals (e.g., Elias et al. 2012).

Mating trials.—A total of 47 mating trials were recorded on digital video during the experiments (excluding the trial on vibratory signals), and males and females were used only once. For these trials, the mating arena consisted of a square acrylic container (13 cm x 13 cm X 4 cm) with two opaque dividers that allowed two spiders to be held simultaneously without visual contact. The container also had niches in the four corners where spiders could avoid each other. For every trial, one adult male and one adult female were held inside the arena but kept apart by the opaque dividers, which were simultaneously opened to start the experiment after a 1-h acclimatization period (Fig. 2). Age, measured as days since last molt, were 50.8 (±70.2) days for males and 51.2 (±73.81) days for females. Each pair was videotaped for 3h (Kodak Zx1 Pocket Video Camera), from the upper side of the arena, and all experiments were conducted under a natural light-simulating lamp (Arcadia Bird lamp. Model FB 36).

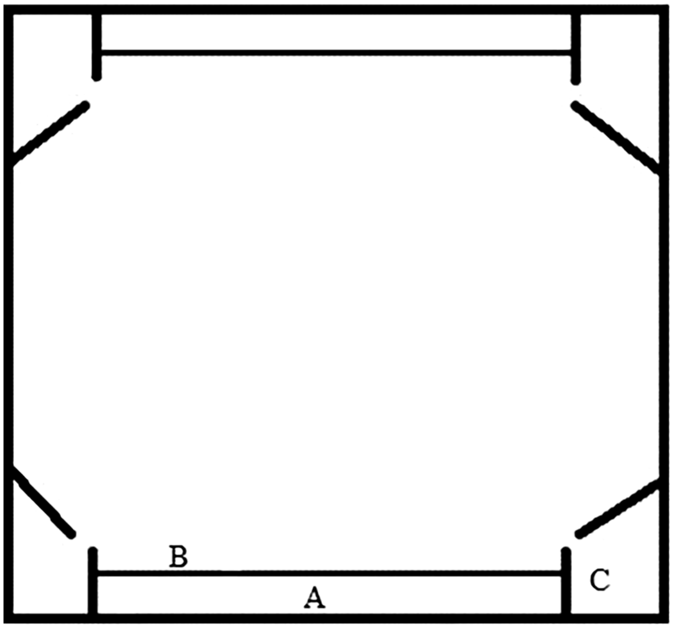

Figure 2.—Upper view of the mating arena. A. Compartment to hold spiders; B. Opaque doors that can be opened; C. Refuge. Arena dimensions: 13 × 13 × 4 cm.

The videos were then analyzed to develop an ethogram of the three stages of breeding for both males and females: (i) pre-copulation display and response; (ii) copulation behavior; and (iii) post-copulation behavior (i.e., egg-laying behavior). Below we describe the behavioral repertoires, time spent in each of these phases and number of eggs and young produced by *H. adansoni*.

Measurements.—Before every trial, males were weighed to the nearest 0.001g. After each trial males were measured and then sacrificed, and their palps and front legs (used in the courtship, see below) removed for measurement. Every measurement was done by photographing the animals with a stereomicroscope, keeping a ruler in the image for scale. Images were then entered in ImageJ for measurement. Carapace width was used as a measure of animal size. We also measured front leg length, white patch area and percentage of pedipalp covered with the white patch area. Areas were calculated drawing a polygon around palps and white patches and then extracting the area of the polygon. To summarize male morphology, cephalothorax width, leg length, male mass, white patch area and percentage of white patch cover were entered in a Principal Component Analysis (PCA). All morphological measurements were taken using pictures similar to those in Fig. 3. We assessed whether any morphological traits predicted mating success, using a regression analysis including the number of copulations as the response variable, along with male morphology (as predicted by the PCA) and male condition as predictive variables. Total duration of copulations was used as response variable in non-parametric regression analysis, since these data were highly overdispersed. Male condition was calculated as the residuals of the regression between male weight and male

Figure 3.—Morphological measurements taken from *Hasarius adansoni* individuals. A. Body size (carapace width; for males and females); B. Area of palp and area of white patch (males only); C. Length of leg I (males only).

cephalothorax width, as proposed by Jakob et al. (1996). Results are presented as mean ± standard deviation.

RESULTS

Mating trials.—We had nine trials in which animals did not see each other, and were considered unsuccessful and thus excluded from further analysis. Among our 38 successful trials (where animals saw each other), 23 (60.5%) resulted in copulations. Among those that did not result in copulations, only four were because males did not attempt copulation and one was because the female cannibalized the male. The other 10 were because females did not accept males (see description below).

When the male orients and moves towards the female, he typically spreads the first pair of legs and his palps (33/38 successful trials). Given the location of the white patches, this would reveal them to a female oriented towards him. From seeing a female and starting a display, males took a mean of 10.6 ±14 s, showing high variation in latency to court. The male then walks towards the female in a zig-zag fashion. Here, the female may respond in three ways: (i) facilitate palp insertion by curling her legs close to her abdomen and staying motionless; (ii) avoid palp insertion, by running away or (iii) avoid palp insertion, by attacking the male. If the first option happens (23/38 successful trials), the male can approach and mount the female, and she then exposes the side of her abdomen and this facilitates palp insertion. Latency to adopt receptive posture once the male is courting was 11.8 ±10.8 s, again showing high variation. Males courted females an average of 53.3 ± 30.86% of times they saw females. On the other hand, females rejected a mean of 45.5 ± 36.6% of males' attempts.

Palps are not inserted simultaneously, thus each insertion was counted as a separate copulation. Mean palp insertion duration was 22.96 ± 14.86 s. Pairs that copulated did so an average of 5.82 times (min = 1; max = 18). Although two separate insertions could happen in a row, multiple copulations were usually separated by a period of other behaviors, such as wandering around the arena, self-grooming, and many times, spiders lost visual contact with each other. Usually, males continued courting and mounting the female multiple times until she moved out of the receptive posture. Once this happened, females frequently adopted the second possible response to courtship (i.e., attacking or running away from the male). Cannibalism of the male by the female was extremely rare, and was observed only once in our 47 trials.

All the behaviors related to reproduction are represented in the ethogram in Table 1.

Vibratory signals.—We confirmed the presence of substrate-borne vibrations during courtship from both male and female. These appeared to be primarily tremulations, a type of substrate-borne vibration signal in which a part of the spider's body vibrates but does not touch the substrate. The energy of such vibrations, however, is transferred to the substrate by the spiders' legs and allows communication (Uhl & Elias 2011).

In this exploratory trial, when the male started moving towards the female, he used tremulation of the abdomen to create vibrations that were detected by the LDV and likely were also available to the female (Elias et al. 2004, 2005, 2006, 2012; Sivalinghem et al. 2010). Once in the receptive posture (i.e., legs curled but still touching the substrate), the female started her own abdominal tremulations as the male approached.

Reproduction.—An average of 36.25 ± 29.92 days after mating, females build a silk cocoon and stay enclosed for an average of 21.21 ± 12.1 days while laying eggs. Usually, after the female leaves the cocoon, the young molt for the first time and only then do they disperse. Among the females that mated, 69.5% ($n = 23$) laid viable eggs. Considering just the females that copulated, the number of copulations did not predict the likelihood of laying viable eggs (Binomial Model: $\beta = 0.054$; $P = 0.567$).

Mated females laid between zero and nine clutches (mean = 3.13) after mating. The number of young per clutch varied from zero (eggs failed to hatch) to 41. The number of young per clutch decreased over the laying bout for each female (Fig. 4), as shown by a mixed-model with Gaussian error distribution, entering the number of young as response variable, clutch as predictor and female identity as a random factor. Number of young correlated negatively with clutch number ($\beta = -1.87$; $P < 0.01$), but did not correlate with female size (Spearman's $\rho = 0.07$; $P = 0.6$, $n = 19$). Female condition predicted the number of young (Spearman's $\rho = 0.64$; $P = 0.002$, $n = 19$). However, such a relationship disappeared after the removal of one single outlier (Spearman's $\rho = 0.19$; $P = 0.44$, $n = 18$).

Morphology and mating success.—The first principal component of the PCA explained 63.9% of the total variance in the traits measured and was highly correlated with leg length, cephalothorax width, and mass; and moderately correlated to white patch area. The second principal component explained another 23.28% of the variance and was highly correlated to

Table 1.—Ethogram of mating behaviors of the jumping spider *Hasarius adansoni*.

Behaviors	Description
Male behaviors	
Leg spreading	Spreading the first and, sometimes, second pair of legs in the horizontal plane
Tremulation	Vibrating the abdomen, but not touching it on the substrate. Vibrations are of long duration (~0.5s) and high amplitude
Zig-zag approaching	Walking towards the female in a zig-zag fashion while performing leg spreading and tremulation
Palp insertion	Inserting the palp in the female epigynum. It happens right after zig-zag walking. Male is mounted on the female's dorsal side, facing her abdomen. Right palp is inserted in left epigynum or left palp is inserted in right epigynum
Female behaviors	
Receptive posture	Female curves all 8 legs towards the center of the body and stands motionless
Tremulation	Vibrating the abdomen, but not touching it on the substrate. It happens while performing receptive posture and vibrations are of short duration (~0.25s) and low amplitude
Abdomen turning	Performed when the male is executing palp insertion. It consists of a small torsion of the abdomen in the vertical plane that facilitates palp insertion by the male

percentage of white patch cover and also moderately correlated to white patch area (Table 2). This shows that the variance in white patch area is partly associated with both body size and percentage of cover. Thus, we used the first principal component as a measure of body size and white patch size and the raw values of percentage of white patch cover in subsequent regression models.

Among the females that copulated, number of copulations was not predicted by male size or percentage of white patch cover (Negative Binomial Model; PC1: β = -0.29, P = 0.18; white cover: $\beta = 1.44$; $P = 0.58$). Among these females, number of copulations also did not correlate with male condition (Negative Binomial Model; Condition: β = 56.52; P = 0.43).

The probability of copulation was not predicted by male size or percentage of patch cover (Binomial Model; PC1: β = 0.47, $P = 0.26$; Percentage of white cover: β = -5.4, $P = 0.43$). Furthermore, male condition and probability of copulation were not correlated (Binomial Model; Condition: β = -82.55, P = 0.44).

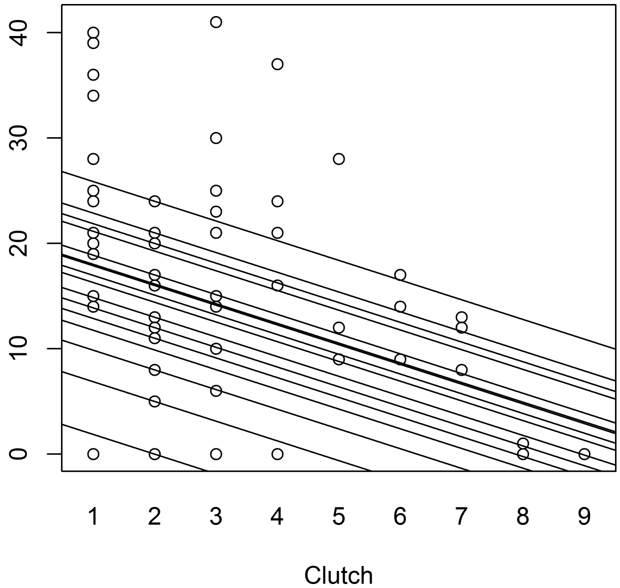

Figure 4.—Number of young and clutch number (i.e., 1st, 2nd, …ninth egg sac) laid by female *Hasarius adansoni*. Each line represents a different female. Individual intercepts and slopes were extracted from a mixed-model with Gaussian errors, including number of young as the response variable, clutch number as predictor and female identity as a random factor.

Total copulation time did not correlate with any of the predictor variables (PC1: Spearman's ρ = 0.15, P = 0.47; Percentage of patch cover: Spearman's ρ = -0.15, P = 0.45; Condition: Spearman's $\rho = 0.11$, $P = 0.52$).

DISCUSSION

Jumping spiders produce relatively intricate displays (Richman & Jackson 1992) and our observations show complex, multimodal displays are also a feature of mating in *H. adansoni*, with males producing tremulations during approach, and females responding with their own tremulations in turn. Even though our sample size for vibratory signals is just one, we confirmed tremulation by both sexes and previous studies have found abdomen vibrations to be ubiquitous in the Salticidae (Uhl & Elias 2011), so we believe it is also common in *H. adansoni*. We found high levels of prolonged courtship by male *H. adansoni*, and clear receptivity postures among females. Multiple copulations were common within pairs that mated. Among mating females, the first clutch typically had the most offspring, and this number declined with subsequent clutches. Surprisingly, despite a high frequency of mate rejection (11/38 pairings), we could detect no relationships between male body size and condition, or the white patch on male palps and any of our measures of mating success or copulation frequency. Notwithstanding these results, it remains clear that this species may be useful to test hypotheses about breeding behavior and sexual selection, given the combination of visual and vibrational signals in the male displays, and the different behavioral and vibrational responses from females.

The features that compose the visual display in *H. adansoni* (i.e., leg spreading, zig-zag walking and palp spreading) have been observed in other salticid species (Richman 1982). Similarly, substrate-borne vibrations have also been observed during courtship in many Salticidae, although the type of vibrations and repertoire size vary substantially (Elias et al. 2003, 2005, 2010, 2012; Sivalinghem et al. 2010; Girard et al. 2011). Such conspicuous traits and displays usually play a role

Table 2.—Correlations (*r*) between raw variables and the six components from the PCA.

	Principal Components					
Variables	PC1	PC2	PC3	PC4	PC5	PC6
Weight	0.93	-0.14	0.04	0.13	0.3	0.04
Cephalothorax width	0.89	-0.12	0.22	0.31	-0.18	-0.03
Front leg 1	0.93	-0.20	-0.20	-0.16	0.003	-0.15
Front leg 2	0.93	-0.15	-0.21	-0.13	-0.12	0.14
White patch	0.62	0.66	0.31	-0.27	-0.00	0.004
% of white patch cover	0.17	0.93	-0.26	0.20	0.002	-0.01

in sexual selection and mate choice (Andersson 1994). Both visual (Huber 2005; Uhl & Elias 2011), and vibratory displays (Elias et al. 2004, 2005, 2006, 2010; Sivalinghem et al. 2010) are used by female jumping spiders to assess potential males for mating during courtship. These display characteristics typically convey male condition, which may influence brood survival and success (Uhl & Elias 2011). For another salticid species, *Habronattus pyrrithrix* (Chamberlin, 1924), male coloration is related to diet (Taylor et al. 2011), and males without sexual displays are not chosen by females (Taylor & McGraw 2013, but see Taylor et al. 2014). Vibratory signals are also important in female choice in the same genus (Elias et al. 2004, 2005). In *Phidippus*, another well studied genus, vibration is also important for female mate choice (Sivalinghem et al. 2010). In contrast to these results, in *H. adansoni*, no morphological character we measured, nor the white patch area or percent of white coverage were related to female response. However, we found that *H. adansoni* also exhibits vibratory signals that might be important in sexual selection, but these have not yet been explored. Moreover, although white patch area does not predict female choice, it is possible that colorimetric variables, such as reflectance in different wave lengths, play a role in sexual selection. Finally, for such multi-modal signals, it may be a combination of traits that is critical for female preference (see Girard et al. 2011). We had a big variation in age of animals in our experiments. Although we did not have a large enough sample size to add it as another factor in our models, we believe this should be focus of future studies, since age might play a role in sexual selection and mate choice.

Most of the pairs that failed to copulate did so because of female rejection. Remating of the same pair, as observed here, has been reported in other jumping spiders (Jackson & Macnab 1989a,b). Females usually determine the end of remating by not accepting further attempts by a particular male. Long copulation durations have been suggested as a strategy of mate guarding in other spiders. Since monogamy is rare in spiders (Schneider & Andrade 2011), and first sperm priority is common (Huber 2005), males may try to prolong copulations (Huber 2005; see also Drengsgaard & Toft 1999), which may partly explain the high copulation rates observed in this study. In the field, males and females have territories with very little overlap (personal observation), which may select for both sexes to engage in copulation multiple times and for long durations if the encounter rates are low in natural populations.

This is the first study to describe the breeding behavior of *H. adansoni* in detail and, as expected for a jumping spider, male courtship was complex and involved multimodal features. Morphological traits did not predict male mating success, and future work should focus on the vibratory display and reflectance of the white patch to fully understand female mate choice in this species.

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