



Original Article

Control of signaling alignment during the dynamic courtship display of a jumping spider

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During communication, alignment between signals and sensors can be critical. Signals are often best perceived from specific angles, and sensory systems can also exhibit strong directional biases. However, we know little about how animals establish and maintain such signaling alignment during communication. To investigate this, we characterized the spatial dynamics of visual courtship signaling in the jumping spider *Habronattus pyrithrix*. The male performs forward-facing displays involving complex color and movement patterns, with distinct long- and short-range phases. The female views displays with 2 distinct eye types and can only perceive colors and fine patterns of male displays when they are presented in her frontal field of view. Whether and how courtship interactions produce such alignment between male display and female field of view is unknown. We recorded relative positions and orientations of both actors throughout courtship and established the role of each sex in maintaining signaling alignment. Males always oriented their displays toward the female. However, when females were free to move, male displays were consistently aligned with female principal eyes only during short-range courtship. When female position was fixed, signaling alignment consistently occurred during both phases, suggesting that female movement reduces communication efficacy. When female models were experimentally rotated to face away during courtship, males rarely repositioned themselves to re-align their display. However, males were more likely to present certain display elements after females turned to face them. Thus, although signaling alignment is a function of both sexes, males appear to rely on female behavior for effective communication.

Key words: communication efficacy, signaling behavior, visual ecology, Salticidae, spider vision.

INTRODUCTION

In animal communication, directional biases in signal transmission and reception can have a strong influence on signaling effectiveness. While this is likely to be true for many signaling modalities, it is particularly pronounced in visual signaling. Both visual signals and visual systems often have strong directional biases, and this places a number of distinct constraints on signaling in this modality. First, because the appearance of visual signals is often angle-dependent, visual signals face spatial constraints on their visibility. For example, from certain vantage points, signaling surfaces may be partially or fully obscured by the signaler's body, or may transmit and/or reflect light differently. The latter situation is particularly pronounced for specular or iridescent signals (Osorio and Ham 2002; Doucet and Meadows 2009; Fleishman et al. 2015;

Hutton et al. 2015). Thus, signalers may need to carefully monitor their own position relative to receivers to make sure that their signals are detectable. Second, visual systems have inherent biases in sensitivity as a result of the directionality of lens optics combined with regionalization of retinal function (e.g. foveal areas; Temple 2011; Land and Nilsson 2012). Eyes can only evaluate stimuli that fall within their field of view, and photoreceptor mosaics are rarely, if ever, homogenous across the retina. Instead, most retinas exhibit strong regionalization of visual functions such as color perception, spatial acuity, and motion detection (Land and Nilsson 2012). Such regionalization means that receivers cannot see all types of visual information everywhere all at the same time. Thus, perception of visual signal characteristics (e.g. color, pattern) will often strongly depend on their position within the receiver's field of view.

As a result of these directional biases in signal propagation and signal reception, alignment of these 2 aspects of visual signaling (hereafter “signaling alignment”) is likely to often be important for communication efficacy. Spatial arrangements that align key signal

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features with the appropriate regions of the receiver's visual field will increase signaling efficacy, whereas misalignment may reduce or even eliminate signal perception. While selection for communication efficacy should thus favor behaviors that establish and maintain signaling alignment (Endler 1992), we know little about the extent to which signaling alignment actually occurs, let alone how signaler and receiver contribute to its establishment and maintenance. Previous work has shown that some signalers employ color and motion elements designed to be particularly salient in their visual environment (e.g. Fleishman 1992; Peters and Evans 2003; Fleishman et al. 2015), and may also deliberately position themselves relative to the sun to augment the salience of directional visual signals (Hamilton 1965; Dakin and Montgomerie 2009; Olea et al. 2010; White et al. 2015; Klomp et al. 2017). For example, males with iridescent color ornaments have been shown to aim their displays toward prospective mates (e.g. Anna's hummingbirds, *Calypte anna*, Hamilton 1965; and common eggfly butterflies, *Hypolimnas bolina*, White et al. 2015). However, we know much less about how receivers direct the focus of their visual systems during communication. For example, none of the studies cited above have explicitly measured how dynamic responses of receiver body position or eye orientation might promote or impede optimal signaling alignment. The result is an implicit assumption that receiver position always supports optimal evaluation of the male display. Pivotal work by Yorzinski et al. (2013) concerning where peahens (*Pavo cristatus*) look during peacock displays reveals that receiver behavior need not match such expectations of optimality. Instead, displays may be under selection explicitly to capture and retain the visual attention of distractible receivers (Dukas 2002; Számadó 2015). Work to investigate this more dynamic view of visual signaling is sorely needed.

To better understand signaling alignment over the course of a dynamic signaling interaction, we studied both male and female position during courtship in the jumping spider *Habronattus pyrrithrix* (Chamberlin 1924; Aranea: Salticidae). Both the visual signals and visual system of this species have clear directional biases. First, male displays are forward facing. During courtship, males produce a series of distinctive displays that include stereotypical movements and brightly colored ornaments (Taylor et al. 2010; Taylor and McGraw 2013). These display routines can be divided into long-range and short-range bouts distinguished by differences in not only distance from receiver, but also distinct posture and movement repertoires (Figure 1a and b; Elias et al. 2012). Males initiate courtship with the long-range phase, which involves sidling, forelimb waving, and palp movements that reveal the underlying red male clypeus (Figure 1a). After approaching the female, males then switch to the close-range phase, which is characterized by rapid movements of the black-and-white tarsi of the raised first leg pair, and ratchet-like movements of third leg pair that bring conspicuous orange patches on the femur ("knees") into view above the male's head (Figure 1b). Male appearance, particularly the red male clypeus, affects male success during courtship (Taylor and McGraw 2013). Many of the prominent visual elements of these displays are partially or entirely obscured when viewed from the side (Figure 1c). Thus, males should benefit from directing these displays toward the appropriate region of the female field of view.

Color and high acuity vision in *H. pyrrithrix* is also forward facing. Like all jumping spiders, *H. pyrrithrix* has 2 principal eyes and 6 lateral eyes. Only the 2 principal eyes are capable of detail and color discrimination (Land 1969; Blest et al. 1981; Zurek et al. 2015). While the movable retinas of the principal eyes can scan within

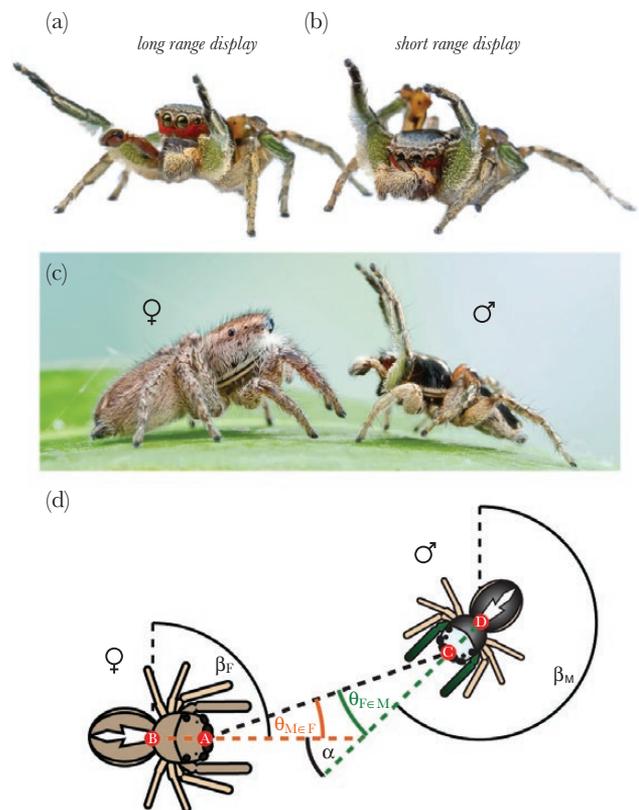


Figure 1

Male posture during (a) long-range and (b) short-range phases of courtship, (c) side view of short-range courtship interaction (photo by Colin Hutton), and (d) coordinates and angles determined: distance between male and female (point A to point C), absolute angle of each spider relative to the arena (β), male azimuth in female field of view (θ_{MeF}), female azimuth in male field of view (θ_{FeM}), alignment angle between male and female body axes (α).

their movement range, this is limited to a cone of approximately 60 degrees in front of the animal (Land 1969). Thus, the field of color vision is restricted to a 60-degree cone centered around the spider's facing direction. This is in contrast to the lateral eyes, which function as monochromatic motion trackers and have a combined field of view of up to 360 degrees (Duelli 1978; Land 1985; Zurek and Nelson 2012).

Because both male color displays and female color vision are forward facing, female perception of male coloration is strongly influenced by position and orientation of both actors. If males do not orient their display towards the female, and/or if a displaying male is not within the field of view of a female's principal eyes, male color and pattern information will not be visible for female evaluation. Both actors may therefore be under selection to establish and maintain signaling alignment.

Our focus here is on visual signaling, because this modality exhibits the strong directional biases described above. It is important to note that courtship in *H. pyrrithrix* and other salticids also involves other modalities. Males often perform complex vibrational songs alongside their visual display behaviors (Elias et al. 2012), and these vibrational elements are likewise important to mate choice (Elias et al. 2005). However, under our experimental conditions, these vibrational songs are unlikely to have strongly directional properties, and in the field, directional propagation of these

vibrations will be haphazardly determined by substrate properties (Elias et al. 2004). In addition, both sexes deposit silk draglines during normal locomotion, which may serve as chemo-tactile spatial cues of an individual's previous path, and males may use these silk lines to track down females in the field (Jackson 1987). However, any given silk deposit is an unreliable indicator of its creator's current position, as it does not account for subsequent movement and direction changes following silk deposition. While both substrate-borne vibrations and chemical signals contain spatial information, communication efficacy in these modalities is less strongly tied to the geometry of signaler and receiver. Here, we chose to focus on the more predictably directional challenges of visual signaling, but return to potential functions of vibrational signaling in particular in the Discussion.

In this study, we asked 2 main questions. First, we sought to determine to what extent signaling alignment is established and maintained throughout a signaling interaction. Second, we asked how signaler and receiver each contribute to signaling alignment. While both males and females stand to benefit from effective communication, control of alignment need not be evenly split. We addressed these questions by first measuring the position and orientation of live males and females during live courtship interactions. We then followed up on these live interactions by quantifying male position when males courted non-living female models. This second series of experiments allowed us to separate male signaling behavior from female behavioral responses, and to determine how males responded to experimentally induced changes in female orientation.

METHODS

Study species and maintenance

Habronattus pyrrithrix is a small, sexually dimorphic jumping spider found in riparian habitats and grassy agricultural and urban areas ranging from southern California and Arizona to Sinaloa, Mexico. We collected adult and sub-adult individuals from 2 high-density populations in Queen Creek, Arizona (33°13'16" N, 111°35'50" W), and Yuma, Arizona (32°43'53" N, 114°36'49" W) in May 2014 and June 2015. Following field capture, we housed spiders individually in translucent cylindrical plastic containers (7 cm diameter, 6 cm tall) in a climate-controlled chamber that maintained a constant temperature (24 °C), constant humidity (55% RH), and a 16:8 h light:dark cycle. The material of the housing containers prevented adjacent individuals from seeing each other clearly, if at all. We fed each spider once per week with cricket nymphs (1st–3rd instar *Acheta domesticus* or *Grylodes sigillatus*) in quantities approximately equal to twice the spider's mass. We ran courtship trials between September and December 2014 for animals collected in May 2014, and between September and October 2015 for animals collected in June 2015.

Courtship interactions

Courtship interactions took place in a custom-built arena consisting of a 16cm diameter disc of 3mm thick matte white polystyrene (Plastics 2000, Modesto, CA) affixed atop a cylinder. Spiders were free to leave this platform at any point during trials. The polystyrene surface should allow for the transmission of at least some frequencies of male vibrational song (Elias D, personal communication). Thus, females in live trials experienced both visual and vibratory elements of male courtship displays. For trials involving female

models, a vertical rod protruding 1–2 mm from the center of the arena floor allowed us to mount models by their ventral surface, and to rotate them with a mechanism below the setup. All trials took place under full-spectrum natural light in a greenhouse. Trials were filmed from above the center of the arena, with a Nikon D7000 (1920 × 1080 pixels, 24 frames/second) in 2014, and with a Panasonic Lumix DMC-GH4 (3840 × 2160 pixels, 30 frames/second) in 2015. Supplemental lighting was provided by 2 Neewer DN-160 LED light panels. To remove silk and odor cues from previous interactions, we wiped down the arena surface with 95% ethanol following each trial.

Interactions between live males and females

To characterize the degree to which signaling alignment naturally occurs in courtship, we filmed courtship between unrestrained adult male and female pairs. Because male jumping spiders often use dragline silk as a cue of female proximity (Elias et al. 2011), we placed the female atop the arena before introducing the male and allowed her to lay silk draglines. If males did not begin courting within 5 min, we removed both animals and ended the trial. If either animal left the arena during this period, we returned them to the arena top and allowed them another chance to initiate courtship.

Once males began to court females, we allowed courtship to proceed for 10 min, until males attempted to copulate, or until aggression by the female occurred, whichever occurred first. In our experience, this 10-min period permits males to progress through both long-range and short-range courtship phases. We excluded from subsequent analyses any trial where courtship did not include both long-range and short-range display types, resulting in useable data from 18 pairs. All males and females were only used once. Individuals comprising 8 of the 18 pairs were captured in the field as adults, and were thus of uncertain mating status. The other 10 pairs were captured as sub-adults and lab-raised to maturity, and thus known to be virgin. We did not find significant differences in different measures of courtship and alignment behavior between these 2 groups (field-matured vs. lab-matured, see Results), and thus pooled all trials with live pairs in subsequent analyses.

Interactions between live males and female models

To investigate the contribution of male behaviors to signaling alignment in the absence of female movement, we filmed adult males displaying to female models. Models were created by ventrally mounting a dead female onto a rotating rod protruding from the floor of the arena. These females were adults from our lab colony who died of natural causes, and were frozen at –80 °C within 24 h of death. Before introducing the male, we allowed a live lab-matured female to walk about the arena in order to deposit silk and other chemical cues, which we found increased male propensity to remain on the arena until visually noticing the model. The same female was used for all model trials, and was not re-used for any other part of the study. Consistent with previous studies of *Habronattus* jumping spiders (e.g. Elias et al. 2012), males were observed to readily court these dead females. Female models were only used for a maximum of 2 days of filming. Models did not include any females from the live courtship trials. Males used for live female interactions were not used for interactions with model females, with the exception of 3 field-matured males.

We used a paired design to evaluate male courtship of stationary ($n = 14$) and ($n = 12$) turning models. To prevent sequence effects, individual males randomly experienced either the stationary or turning model first, utilizing a list randomizer from <http://random.org>. To encourage initiation of courtship following introduction of the male into the arena, we rotated the female model to imitate typical female scanning behavior. For the stationary-model treatment, we did not move the female model after courtship had commenced, and allowed the male to court for 10 min or until he attempted to mount the model.

We investigated how males respond when females turn away during courtship by quantifying male courtship behaviors following experimental reorientation of female models. We allowed male courtship to proceed until males began their short-range phase of courtship. After 5 s of short-range male display, we rotated the model so that it faced away (approximately 180 degrees) from the male. This turn magnitude is common in live interactions, and was chosen to present males with maximal misalignment. Following rotation, we then left the female model stationary for the remainder of the trial (10 min of courting or until a mounting attempt).

For stationary-model trials, we excluded any trials that did not contain both long-range and short-range displays. For the turning-model condition, we only excluded trials that did not contain short-range displays.

Video analysis

We used Adobe Premiere Pro CC v9.1 (Adobe Systems Inc., San Jose, CA, USA) to trim each trial video to only include the longest continuous courtship sequence. We defined a continuous sequence as beginning when the male initiated his courtship display, and ending when the male ceased displaying for more than 60 s despite remaining oriented toward the female, left the arena top, or when the end of the trial was reached. Videos were down-sampled to 5 frames per second (fps) for analysis because our preliminary analyses indicated that this frame rate allowed us to resolve even the briefest time period between male reorientation movements observable in unedited 30 fps footage. We used ImageJ (v.2.0.0-rc-34/1.50a, [Schneider et al. 2012](#); [Schindelin et al. 2012](#)) to mark the locations of the pedicel (B, D in [Figure 1d](#)) and the point between the principal eye lenses (A, C in [Figure 1d](#)) in both spiders. We calculated the following measurements for each video frame using MATLAB (r2014a, The MathWorks, Inc., Torrance, CA, USA): distance between male and female (distance from A to C in [Figure 1d](#)), male azimuth in female field of view ($\theta_{M \in F}$), female azimuth in male field of view ($\theta_{F \in M}$), alignment angle between male and female body axes (α), and absolute angles of male (β_M) and female (β_F) body axes relative to the top left corner of the video frame. All angles are reported in radians. For each trial, we scored male display phase as long-range (sidling movement with large amplitude lateral waves of the 1st leg pair) or short-range (stationary with both 1st legs raised high). Lastly, for short-range courtship involving live males and females, we also quantified a conspicuous male behavior that may be related to capturing and/or retaining female visual attention: ratcheting movements that raise the orange patch on the 3rd leg femur above the cephalothorax, bringing these “knees” into the female’s field of view. The timing of these “knee raises” was considered explicitly in relation to female position and reorientation behavior to determine whether males employ these either 1) to elicit female reorientation toward the male display, or 2) as a response to female reorientation toward the male display.

Statistical methods

All statistical tests were carried out using R version 3.2.2 (R Core Team 2013). We determined the distances at which males initiated long- and short-range courtship stages, and tested whether these differed between trials with live and model females using Welch’s unequal variances t -tests.

Tests on circular data used the R package ‘circular’ v0.4–7 ([Agostinelli and Lund 2013](#)). For short- and long-range courtship phases in each trial, we calculated the mean vector of the observations of alignment angle α in each video frame. The direction α of this vector represents mean signaling alignment during the phase and trial, with a value of 0, or 2π , representing perfect alignment of viewing direction (i.e. male and female directly facing each other), and a value of π representing the female facing directly away from the male. The resultant length of this vector, ρ_α , represents the density of observations at mean α , and thereby serves as a measure for the consistency of alignment during each phase and trial. Equivalent vectors were also calculated for the absolute facing angles of male and female (β_M and β_F), and the azimuth of the other spider from the perspective of male and female ($\theta_{M \in F}$ and $\theta_{F \in M}$). We determined the mean alignment angle of each category by taking the circular mean of α values in each trial. We also calculated the proportion of time the female spent within a 60° cone in front of the male (F \in M) and vice versa (M \in F).

To determine whether males initiated courtship phases in specific positions relative to the female, we tested whether α at phase initiation was nonrandom using Rao’s spacing test of uniformity ([Rao 1976](#); [Russell and Levitin 1995](#); [Jammalamadaka and Sengupta 2001](#)). Differences in mean α between trial types (live vs. model), display types (long-range vs. short-range), and rearing history (lab-matured vs. field-matured), as well as sex differences in mean θ were tested using Mardia-Watson-Wheeler tests ([Wheeler and Watson 1964](#); [Mardia 1972](#); [Jammalamadaka and Sengupta 2001](#)). Also called uniform scores test, this non-parametric test compares the homogeneity of 2 or more samples of circular data. This test performs better than circular Anova when sample sizes are small ([Taşdan and Yeniay 2014](#)).

We observed that male “knee raises” are carried out during periods when males and females are close to or in alignment. Thus, this display motif may function to elicit female reorientation or as a reaction of the male to increased alignment resulting from female reorientation towards him. To distinguish between these potential functions, we computed the cross-correlation function (ccf) of the time lag between the initial frame of female reorientation towards the male and the initial frame of a bout of male knee raises across all occurrences of knee raises in live trials.

RESULTS

Analysis and experimental manipulation of the geometry of *H. pyrrithrix* courtship reveal a dynamic interaction in which both partners react to visual cues from the other. Males readily accepted model females as courtship partners, initiating courtship elements at similar distances as with live females (mean \pm SD distance at long-range courtship initiation: live 34.4 ± 16.3 mm, model 23.7 ± 21.3 mm, Welch’s t -test, $t_{38.99} = 1.829$, $P = 0.075$; short-range courtship initiation: live 9.0 ± 4.0 mm, model 7.1 ± 6.2 mm, Welch’s t -test, $t_{37.85} = 1.198$, $P = 0.238$), but we observed key differences in relative angular positioning during courtship sequences (see below).

Interactions between live males and females

Interactions between live males and females allowed us to evaluate how male forward-facing displays were aligned with the frontal female field of view, and to some extent which sex was responsible for this alignment. Males nearly always remained fixated on the female, whereas females faced away from the male for much of the time (male: $\theta_{FEM} = -0.056 \pm 0.054$ rad, $\rho = 0.999$, female: $\theta_{MEF} = 1.678 \pm 2.075$ rad, $\rho = 0.116$, Mardia-Watson-Wheeler test, $W(2) = 25.267$, $P < 0.0001$). In addition, males most commonly initiated long-range courtship displays when their facing direction was aligned with that of the female (mean α at display initiation \pm SD: -0.12 ± 1.34 rad; circular distribution of display initiations was non-uniform, Rao statistic 159.374, $P < 0.05$). Following initiation of this long-range phase, the male waved his front legs while walking sideways, approaching the female on a zig-zag course. Females rarely tracked males with their frontal visual field during this approach, leading to long-range displays being carried out evenly around the female (Figure 2a).

Males approached females until close enough to initiate their short-range display motif, at a mean (\pm SD) distance of 9 ± 4 mm. Short-range displays were initiated regardless of alignment (mean α at display initiation \pm SD = -0.12 ± 1.78 rad; circular distribution of display initiation was uniform, Rao statistic 145.474, $P > 0.05$). However, females often turned around so that short-range displays more often took place with both spiders facing each other than did long-range displays (Figure 2b; mean α during short-range display

\pm SD: 0.25 ± 1.67 rad versus mean α during long-range display \pm SD: 3.05 ± 1.21 rad, Mardia-Watson-Wheeler test, $W(2) = 6.743$, $P = 0.034$).

Knee raises were carried out by the male once he and the female became closely aligned during the short-range display phase. Analysis of the relative timing of female turn initiation towards the male and the beginning of a knee raising bout revealed that this display motif occurs more frequently following a female turn to face the male (Figure 3a). Subsequent cross-correlation analysis revealed that initiation of knee raise bouts was most likely to occur 200 ms after the female turned towards the male (at a 200-ms lag, Figure 3b, dominant cross-correlation = 0.03, c.i. = 0 ± 0.012).

We tested for possible behavioral differences between pairs with field-matured versus lab-matured females. We found no significant group differences in alignment α (Mardia-Watson-Wheeler test, $W(2) = 0.998$, $P = 0.607$), courtship duration (field 380 ± 327 s, lab 175 ± 166 s, Welch's t -test, $t_{9,85} = 1.62$, $P = 0.137$), fixation on the other spider (Male (θ_{FEM}) Mardia-Watson-Wheeler test, $W(2) = 0.05$, $P = 0.975$, female (θ_{MEF}) $W(2) = 0.08$, $P = 0.959$), duration of knee raise bouts (field 46 ± 42 s, lab 28 ± 36 s, Welch's t -test, $t_{13,9} = 0.938$, $P = 0.364$), and female locomotor activity as measured by the spread of facing direction ρ_{BF} (field 0.52 ± 0.23 , lab 0.41 ± 0.21 , Welch's t -test, $t_{14,2} = 1.06$, $P = 0.308$).

Interactions between live males and female models

During trials with female models, males approached females from the front and did not deviate much from the model's frontal cone during the approach (Figure 2c). This led to greater long-range display alignment during model trials when compared to live trials (mean $\alpha \pm$ SD, model: 0.14 ± 0.61 rad, live: 3.05 ± 1.21 rad, Mardia-Watson-Wheeler test, $W(2) = 20.575$, $P < 0.001$). As with live trials, short-range displays in model trials occurred predominantly face-to-face (mean $\alpha \pm$ SD, model: -0.06 ± 1.08 rad, live: 0.25 ± 1.67 rad), and a comparison of live versus model trials indicated no statistical difference in short-range display alignment between these 2 conditions (Figure 2b and d, Mardia-Watson-Wheeler test, $W(2) = 1.436$, $P = 0.488$).

In the model-turn condition, the model was initially positioned so that courting males carried out their short-range display directly in front of the female ($\alpha \approx 0$). When the model was then turned so that it faced directly away from the male, males most often responded by moving towards the front of the model (Figure 4, paired $t_{11} = -3.17$, $P = 0.009$). However, of the males that repositioned, only some moved into the model's frontal hemisphere (4 out of 7 individuals, Figure 4), and no males reached field of view of the model's principal eyes.

DISCUSSION

In many sensory modalities, both signals and sensors can have pronounced directional biases. When this is the case, signalers and receivers can maximize the efficiency of information transmission by spatially aligning themselves. We investigated to what extent the directional courtship displays of male *H. pyrithrix* are aligned with the forward-facing field of view of female receivers. Tight alignment would improve detection and evaluation of male courtship elements by the female, including aspects that would not be visible to the female without the specific input of her forward-facing principal eyes (i.e. color, fine detail).

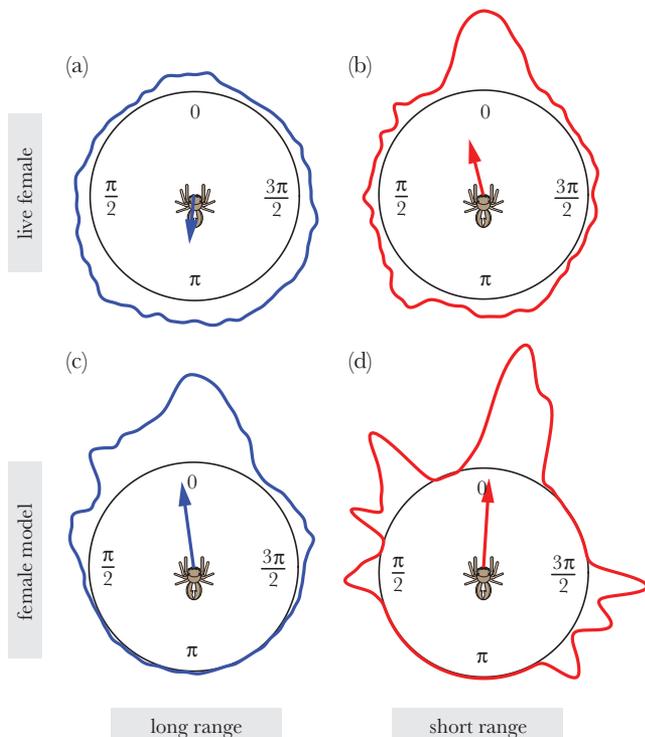


Figure 2

Alignment of facing directions of male and female spiders during (a, c) long-range and (b, d) short-range courtship phases. Arrow direction indicates the mean of α , the relative angle between male and female viewing direction (e.g. at 0 the spiders face each other). Arrow length indicates the density of observations at mean α (ρ_a), and thereby serves as a measure for the consistency of alignment. Colored lines outside of circular axes represent mean density distribution of observations.

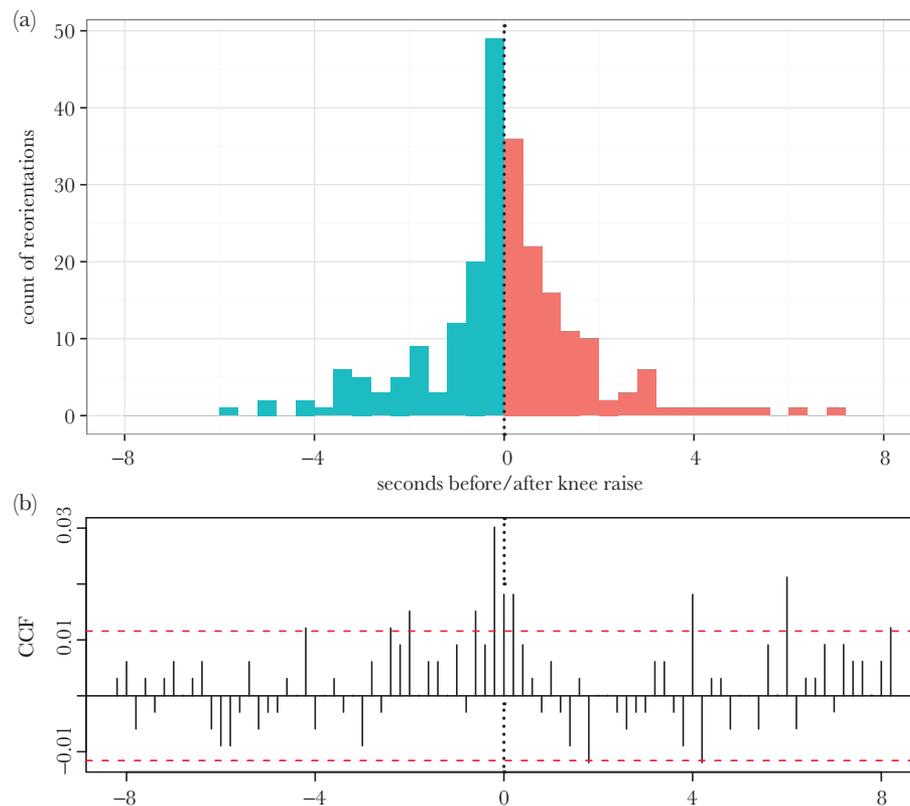


Figure 3

(a) Occurrences of female reorientation to face the male, relative to a male's initiation of knee raise display bouts. Histogram depicts summed counts of the first reorientations immediately before and after knee raise initiation ($t = 0$, dotted vertical line on x-axis) during 12 live interactions that included knee raises. (b) Cross-correlation plot of female facing direction (predictor) and male knee raise occurrence (recruit). Red horizontal lines indicate 95% confidence interval, and dotted vertical line illustrates the moment the female turns to face the displaying male. The dominant correlation occurs at -0.2 s, meaning that males are most likely to raise their knees 0.2 s after a female reorients to face him.

We found that males initiate courtship following establishment of frontal “eye contact” with females, but then continue long-range displays irrespective of their position in the female field of view. However, male short-range courtship displays are aligned with the female frontal field of view for much of the time, although this alignment is often transient.

How does each actor contribute to achievement or disruption of signaling alignment? Our results indicate that males actively manage their body orientation in relation to females such that their displays are almost always directed towards a focal female (>97% of the time). When we rotated female models to face away from males, most males repositioned themselves towards the front of the model. However, few males moved beyond the model's rear hemisphere, and no males moved into the model's frontal field of view. This suggests that while males adjust their position in response to changes in female orientation, they vary in the extent of their movement, and these responses alone are insufficient to maintain signaling alignment. Thus, successful alignment is not the result of male position alone, but rather the product of male position and female orientation in response to the male display.

We observed that female movement often disrupts alignment, especially during long-range displays. This is supported by our observation that male–female alignment during long-range courtship was substantially better when males courted a stationary model instead of a freely moving female. Because males nearly always oriented their displays toward females, the discrepancy in alignment between live and model trials can be largely attributed

to changes in orientation of live females. However, during short-range courtship, alignment was consistently high for both live and model trials. This is likely because live females remained more consistently oriented towards the male displays during this phase of courtship.

These results have several implications for courtship dynamics in this and other species. Signaling alignment should improve a female's ability to evaluate male color and pattern. Why then do females carry out movements that reduce this ability? The female-induced misalignment we observed at long range may suggest that females are rarely interested in the male display at this stage of courtship. Females may primarily assess male vibrational song (as in certain other species; Elias et al. 2005) and/or chemical signals, which are both unconstrained by viewing angle. It is also possible that females prioritize the motion elements of male courtship, as jumping spider motion detection has a very wide field of view (near 360° , Land 1985) and is thus not constrained by alignment with the female frontal visual field. However, previous work by Taylor and McGraw (2013) indicates that male coloration is indeed an axis of female mate choice in *H. pyrithrix*, and that this evaluation occurs, at least in part, during a male's long-range display, when misalignment is most frequent. It is possible that females only require a short period to conduct this evaluation. Importantly, males usually initiate their long-range displays within the field of female color vision. A brief glimpse of color information from long range might be sufficient for recognition of a potential mate, but preclude the longer evaluation necessary to assess more subtle differences in

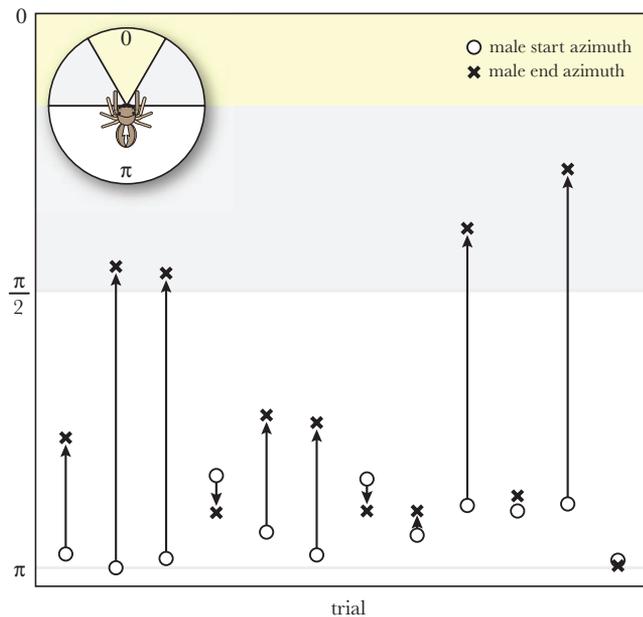


Figure 4

Change in absolute alignment angle in each “model-turn” trial. In all 12 trials, males (original angular position indicated with a circle) initiated courtship face-to-face with a female model (originally facing towards π). Five seconds after display initiation, the model was turned to face away from the male (to 0) by the experimenter. Male position was recorded until display stopped, with an x indicating the final male angular position. Colors indicate angular position in female’s visual field, as shown in inset.

male coloration that might be associated with male quality (Taylor et al. 2011).

Female movements that disrupt signaling alignment may also be a consequence of limited visual attention. These animals may face physiological and/or cognitive limitations that impede their ability to perform multiple visual tasks simultaneously, such as predation avoidance and mate evaluation (Dukas 2002; Dukas 2004). Orientation towards and away from the courting male may reflect how these different tasks compete for a female’s visual and cognitive resources. Here, *H. pyrithrix* females look away from courting males for the majority (over 73% of the time) of the interaction, similar to results in courted peahens (63% of the time, Yorzinski et al. 2013). Given that conspicuous male displays are susceptible to eavesdropping and attack from predators (Endler 1980; Zuk and Kolluru 1998; Woods et al. 2007), our results suggest that females may allocate more time to increased vigilance over male evaluation.

Because reduced receiver attention impairs signaling alignment, signalers may be under selection to capture receiver attention, retain attention once captured, and/or capitalize on transiently attentive receivers via strategic signaling behaviors (Endler 1992; Dukas 2002; Rosenthal 2007). One strategy is to use displays tailored to elicit females to turn, and then discourage them from turning away. In other words, aspects of male displays may function to capture and/or retain a female’s visual attention. To this end, signaling males may employ a simple but salient “alert” signal that primes female attention for a subsequent information-rich signal (Richards 1981; Fleishman 1988; Guilford and Dawkins 1991). The forelimb waving characteristic of long-range display in *Habronattus* and other jumping spiders (Elias et al. 2012; Herberstein 2012) is likely to serve as an introductory alert to establish signaling alignment in advance of the more complex short-range display.

In other taxa, similar exaggerated introductory movements improve signal detection (e.g. in Jacky dragons, *Amphibolus muricatus*, Peters et al. 2007; and *Anolis lizards* Ord and Stamps 2008; Fleishman and Pallus 2010) and gaze re-acquisition (in peafowl, Yorzinski et al. 2013). If long-range motion displays do indeed perform an attention-grabbing function in *H. pyrithrix*, it is possible that the effectiveness of such displays may depend on the properties of the visual environment (e.g. background motion, spatial complexity) within which they are performed (e.g. Peters 2008; Cole 2013; Wiley 2016). Given that even sympatric *Habronattus* species differ in their microhabitat use (Taylor et al. 2017), the need for a salient alert may have shaped intra- and interspecific display variation in this genus.

Once attention is captured, signaling males may then use subsequent display features to retain female attention. Here, we find that males may do so by targeting additional visual channels. For example, the timing and design of male “knee raises” suggests a function in maintenance of female visual attention. While males often initiate knee raises when the female is looking away, a male is most likely to initiate a bout immediately after a female turns to face him. By presenting, obscuring, and reintroducing their orange leg ornaments, males may seek to repeatedly attract the gaze of the female’s color sensitive principal eyes, as these eyes track and scan novel stimuli moving into their field of view (Land 1969). *H. pyrithrix* males also perform rapid bends of the first leg tarsi during short-range display; these “flicks” appear to be carried out at regular intervals regardless of alignment and are thus less likely to be involved in attention management. However, they were not reliably quantifiable in footage due to their small amplitude and short duration, and thus not specifically considered in this study. Experimental manipulation of male knee raises and flicks (e.g. color, pattern, rate) may prove to be fruitful in identifying precisely how female visual attention is retained, and how this retention impacts on signaling outcomes.

Signalers might also use multiple sensory “channels” to manage receiver attention, such that a signal in one modality may function as a conspicuous alert for a coordinated message in another (McLennan 2003; Hebets and Papaj 2005; Grafe and Wanger 2007). *Habronattus* males produce substrate-borne vibrations during courtship, which can be perceived by a nearby female regardless of facing direction and are often temporally synchronized with specific visual display motifs (Elias et al. 2012). Thus, vibrations could attract female attention despite visual misalignment and/or maintain attention while a visual display is performed. Muting male vibrations decreases mating success in another *Habronattus* species (Elias et al. 2005), but the extent to which male vibration may function as an alerting precursor to certain information-rich visual displays, a redundancy for a visual alert signal, or an independent information-rich sensory channel is open for further research.

If signalers are limited in their control of receiver attention, they can still benefit by attending to a receiver’s spatial information in order to capitalize on opportunities for effective signaling. Signalers may compensate for transient attention by orienting their displays towards the receiver’s position, even when the receiver is facing away. This behavior ensures that if the female does eventually face the male, his signal is immediately visible to her principal field of view. *H. pyrithrix* males show high fidelity in tracking a female’s location and orienting their displays towards her. However, the extent to which signalers in other systems similarly orient towards receivers, and the effects of this tactic on signaling efficacy, are relatively unknown. In the few systems in which this has been studied,

signalers do appear to actively face their displays towards the receiver's location (e.g. in Anna's hummingbirds, Hamilton 1965; peafowl, Dakin and Montgomerie 2009; great bustards, *Otis tarda*, Olea et al. 2010; common eggfly butterflies, White et al. 2015), but with considerable interspecific variation in the degree and pattern of male orientation. Imperfect orientation might stem from challenges in tracking receivers (e.g. due to fast moving and/or multiple receivers), environmental constraints on direction, and/or countervailing individual interests. In jumping spiders, for example, females are known to cannibalize males both pre- and post-copulation (Jackson et al. 1997). As a female's striking zone is directly in front of her (Foelix 2011), male efforts to maintain direct "face-to-face" alignment may carry an increased risk of attack and may thus be limited in the interest of survival. While laboratory experiments have shown relatively high rates of sexual cannibalism in *H. pyrithrix* (12 of 36 trials involving 48 h of cohabitation; Taylor and McGraw 2013), the extent of this behavior in natural populations, and its consequences for communication, is not well understood.

Signalers may also improve communication efficacy by using receiver spatial information to decide when to employ particular signals or signal elements. Opportunistic signaling may be particularly important for energetically costly displays, as it allows signalers to avoid their display falling on averted eyes. This is another possible explanation for the timing of knee raises in *H. pyrithrix*. Males may prefer to deploy their colorful knees when females are looking because this is when color information is most likely to be received.

It is also possible that female-induced misalignment is a deliberate strategy to assess male quality. Male efforts to improve and/or capitalize on signal alignment rely in large part on his ability to accurately attend to female orientation, determine her gaze direction (i.e. gaze sensitivity; Davidson et al. 2013) and react appropriately. This implies that more attentive males may be more successful communicators and, in turn, more valuable mates. Our results, and those of previous studies, suggest widespread intraspecific variation in signalers' ability (or propensity) to assess and respond to a receiver's spatial cues. Due to the energetic and cognitive costs of attending to the receiver's spatial cues (Davidson et al. 2013), an individual signaler's ability to do so may be a broad indicator of signaler quality that influences signaling alignment, and, in turn, signaling outcomes. By turning away from courting males, females may be attempting to assess his ability to maintain signaling alignment, and/or any of suite of correlated traits such as persistence, body condition, and motor performance that influence mate choice in many systems (Byers et al. 2010). Thus, we propose expanding the concept of "social skill" introduced by Sih and Bell (2008) to include a signaler's ability to assess and adaptively respond to a receiver's spatial cues. Previous work has noted that signaling males are able to adjust display intensity or tactics in response to female cues (Patricelli et al. 2006; Patricelli and Krakauer 2010; Sullivan-Beckers and Hebets 2014), and changes in receiver distance (e.g. How et al. 2008; Fleishman and Pallus 2010), potentially improving courtship success (but see Patricelli et al. 2006). Whether females use signaling alignment as a proxy for aspects of male quality, or whether improved courtship outcomes are strictly a result of increased signal efficacy remains an interesting direction for future work.

In summary, directional biases in both vision and visual signaling predict that effective communication requires behavioral alignment of these 2 directional elements during signaling. While previous work (e.g. Dakin and Montgomerie 2009; Olea et al. 2010; White et al. 2015) has shown that signalers often aim their signals towards the receiver's position, whether receivers also orient their visual field towards a signaling male has not been well investigated. We found that in the courtship of the jumping spider *H. pyrithrix*, females

often looked away from courting males, such that male display and the female frontal field of view were misaligned. Thus, although alignment is essential for females to be able to see and evaluate male display color and pattern, females appear to often undermine such alignment by reorienting to investigate other stimuli. These dynamic shifts in signaling alignment throughout courtship illustrate the challenge males face in contending with limited female visual attention, and highlight the potential importance of variation in male social skill when responding to female attentiveness and spatial positioning. Finally, we note that the directional biases in signal transmission and/or reception are not unique to visual communication. Acoustic signalers also employ directional calls (e.g. in grouse, Dantzker et al. 1999; whales, Holt et al. 2010), and some even actively modulate this directionality based on signal function (Patricelli et al. 2008). However, the importance of directionality on effective communication in visual, acoustic, and other modalities remains an interesting but largely uninvestigated avenue for further research. We encourage those interested to consider the active roles of both signalers and receivers in determining signaling alignment and efficacy.

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