

**How Spatial Constraints on Efficacy and Dynamic Signaling Alignment Shape Animal
Communication**

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University of Pittsburgh, 2020

Effective communication is important to the survival and reproduction of many organisms. Signal transmission and reception have spatial constraints that interact to determine effectiveness. Signals are often best perceived from specific angles, and sensory systems may be limited in their ability to detect or interpret incoming stimuli from certain directions. Alignment between these directional biases can be critical to effective communication. Misalignment of either signal or sensor may disrupt signal perception. Signals also degrade during the distance traveled from signaler to receiver. Thus, how animals position themselves during communication may be under selection. Despite this, we know little about the spatial arrangement of signalers and receivers, what behaviors influence positioning, or the causes and consequences of variation in positioning. To address this fundamental gap in knowledge, I developed a geometric framework for studying the spatial constraints of communication and how they shape positioning across visual, sound, and chemical signaling. To investigate respective roles of signaler and receiver in managing these spatial constraints, I then characterized the spatial dynamics of visual signaling in the jumping spider *Habronattus pyrrithrix*. Males perform an elaborate courtship dance which includes arm waves and colorful ornaments; the latter are not visible from the side. The female can only perceive colors of male displays when they are presented in her frontal field of view. I recorded relative positions and orientations of both actors throughout courtship and established the role of each sex in maintaining signaling alignment. Finally, I tested how males control female orientation, and

respond to signaling challenges. Using video playback, I asked how males' arm-waving display and the visual environment determine how effectively they attracted female attention, as well as how males respond to variation in their signaling environment. These studies reveal that signaling alignment is frequently disrupted by females turning away from males, but that male arm-waving effectively re-captures her attention. Males also modulate displays in response to changing spatial and environmental conditions. Overall, this dissertation reveals the widespread role of spatial constraints in driving signaling behavior, and demonstrates that the spatial arrangement of signaler and receiver must be managed dynamically through behavioral responses.

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Preface

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1.0 Signals in Space: Geometry as a Framework to Analyze the Inherent Spatial Constraints on Communication Efficacy

1.1 Introduction

Communication of information between two separate individuals is crucial to many key ecological functions (e.g., contests over resources, coordination of social behavior, mating), and the traits and behaviors involved in communication are incredibly diverse (Bradbury and Vehrencamp 2011). What selective pressures drive the evolution of signals and signaling interactions? The theory of sensory drive states that communication systems may evolve under selection for effective transmission and reception of signals, as shaped by the constraints and biases imposed by the species' physiology and sensory ecology (J. A. Endler 1992; 1993a; J. A. Endler et al. 1998; 2005). Selection will favor signal traits and signaling behaviors that improve how effectively a signal travels through the environment from signaler to receiver, and/or the likelihood that a receiver's sensory system will detect the signal and act on the information as intended (i.e., increases in signal efficacy). For example, signalers may be under selection to sing at a pitch that stands out in contrast with other concurrent or frequent noises (Nemeth and Brumm 2009). Or, signalers may be under selection to display with the same colors that receivers' visual systems have evolved to seek out in the environment (e.g., those associated with food (Kolm et al. 2012)). In the 28 years since sensory drive theory was proposed, a robust body of research has provided strong evidence for how constraints such as ambient light (Terai et al. 2006; J. A. Endler 1993b), background noise (Slabbekoorn and Smith 2002), and receiver sensory biases (Cole and Endler 2018; Makowicz et al. 2015; Ninnes et al. 2015) shape signal evolution via selection for efficacy

(reviewed in (Cummings and Endler 2018)). However, spatial constraints inherent to each step of communication may also have consequences for signal efficacy, and we know comparatively little about how these shape selection on signals and signaling behavior.

Signal transmission and reception can often be spatially heterogenous. Signals may transmit better in certain directions than others, and degrade as they travel the distance from signaler to receiver (Bradbury and Vehrencamp 2011; G. G. Rosenthal 2007). Likewise, receivers may only be able to detect signals, or be more or less sensitive to different types of stimuli, if they arrive from certain directions (Michael F Land and Nilsson 2012; M. F. Land 1999; Kühne and Lewis 1985; Rosowski 1994; Bradbury and Vehrencamp 2011). Environmental conditions, such as physical obstructions and movement of the transmission medium, may distort a signal, change its directional of travel, and/or block transmission entirely (Book et al. 2012; D. R. Webster and Weissburg 2009; Pijanowski et al. 2011; G. G. Rosenthal 2007).

For example, consider the spatial constraints faced by a male Anna's hummingbird (*Calypte anna*) when displaying at conspecifics who enter his territory. Males perform "aerial power dives" at target conspecifics while presenting their brilliant purple feathers (Hamilton 1965). However, these feathers only cover a forward-facing patch on his head (the gorget), and so are not visible from some angles. In addition, these colorful feathers are iridescent, meaning that their brightness and color depends on angle of incident sunlight relative to the surface of the feathers; from the wrong angle, the gorget appears completely black. Hamilton (1965) hypothesized that if males are under selection to maximize the visibility of their purple feathers to a target individual, they may experience selection on their spatial positioning during communication. A male must direct his gorget towards the target and manage his position with respect to both the target and the sun to maintain an appropriate angle of illumination (Hamilton

1965). In addition to these directional constraints on signal transmission, how a male's display is perceived is also a function of where the target is looking. Depending on where the displaying male appears within the target's field of view, his purple feathers may only be seen peripherally, or not at all. As a result, moment-to-moment changes in how signaler and receiver position themselves relative to each other and the environment can strongly affect signal efficacy, and thus such positioning may itself be a target of selection. Indeed, recent work on related iridescent hummingbirds shows that how males orient and position themselves has evolved to directly manage the spatial constraints of his display (Simpson and McGraw 2018a; 2018c; Hogan and Stoddard 2018).

Analogous geometric constraints exist for other visual signals, as well as sound and chemical communication (R. H. Wiley and Richards 1982; Muller-Schwarze 2006; D. R. Webster and Weissburg 2009; Bradbury and Vehrencamp 2011). Despite this, much previous work on animal communication has implicitly relied on assumptions about one or more of the geometric considerations discussed above. Signalers are assumed to direct their displays at the receiver throughout communication. Receivers are likewise assumed to have a relatively constant sensory perception of the display without looking away or turning away. While the role of coarse-scale environmental features in shaping communication traits have been the subject of rigorous study, how animals position themselves within these environments on fine spatial and temporal scales has received much less attention. Such assumptions may have begun as necessary steps to facilitate the study of complex signaling interactions. However, by continuing to ignore the consequences of directional constraints, we underestimate the challenges involved in effective visual communication and therefore the axes along which selection may act. Thus, we have a limited understanding of several fundamental questions on communication, including:

- What are the spatial constraints on effective communication?
- How do these constraints select for specific geometries of signaler and receiver within the physical environment?
- How do signaler and receiver position and orient themselves during communication, and what are the functional consequences for signaling outcomes?
- How does positioning behavior evolve, and potentially co-evolve, with spatial constraints?

As these questions are fundamentally spatial in nature, we propose the development of a framework based on the tools of geometry: a description of the spatial properties and arrangements of elements in a system. The groundwork laid in the past few decades by separate ecological, behavioral and physiological studies provides a powerful understanding of the physical and ecological constraints experienced by signalers and receivers. We can quantify how a signal travels in different directions, how it is modified *en route* via interactions with the environment, and how well it is detected by the receiver's sensory system depending on the angle of incidence. Combined with modern improvements in tracking the position and orientation of actors, we can now analyze the spatial aspects of signaling at each step of communication. In this chapter, we will outline the critical elements of signaling geometry, review the compelling empirical evidence for their roles in shaping communication, and propose directions for future study.

1.2 Geometry of Visual Communication

We begin with a survey of visual communication because this modality is subject to especially strong geometric constraints. Light waves, unlike sound waves or diffusing chemical

signals, travel only in straight lines and cannot pass through most natural materials (Johnsen 2012). As a result, signal and sensor directionality both have strict boundaries, and visual communication typically operates on the eponymous “line of sight.” Light from a signal must be able to follow an unobstructed path to the receiver’s eye, and the receiver must be looking towards that incoming light. A robust body of visual physiology research has described the spatial constraints on how eyes perceive for many systems (Michael F Land and Nilsson 2012; Johnsen 2012), and over years of iterative work, researchers have developed effective methodologies for measuring signal directionality (e.g., (White, Zeil, and Kemp 2015; Santos et al. 2007; Meadows et al. 2009)). By integrating these pieces, we are now able to rigorously investigate how the positioning of signaler and receiver during communication affect signal efficacy.

1.2.1 Viewing Distance

The appearance, perception, and even function of visual signals can change dramatically with the distance between signal and receiver (termed here and in the literature as “viewing distance”, “receiver distance”, or “communication distance”). As this viewing distance increases, the image of the signal formed in a receiver’s eye grows smaller, and takes up less of their field of view. Smaller images are detected by fewer photoreceptors, and as a result, the receiver loses some ability to distinguish details within the signal (Michael F Land and Nilsson 2012; E. M. Caves, Brandley, and Johnsen 2018; Bradbury and Vehrencamp 2011; Cronin et al. 2014). As distance increases and details blur together, contrast between the signal and its surroundings can also decrease. Eventually, with enough distance, the receiver will not be able to tell the signal apart from other nearby stimuli. Signal perception can also become compromised if the distance between signaler and receiver is outside of the range within which the receiver’s eye can focus on

objects. If the distance between the signaler and receiver is smaller than the minimum focusing distance, or greater than the maximum focusing distance, the result is a blurry image (Michael F Land and Nilsson 2012). All else being equal, smaller and/or blurrier signals compromise visual information transfer and tend to be less salient (Fig. 1, (Michael F Land and Nilsson 2012; E. M. Caves, Brandley, and Johnsen 2018)). In addition, signals seen at an extremely close range may not “fit” within the receiver’s field of view and therefore may not be visible in their entirety. Thus, we can generally expect signal efficacy to be influenced by distance from receiver, to decrease with increasing distance, but with species-specific variation depending on focusing range and the physical size of the signal. It follows that signalers are likely under selection to (a) assess receiver distance, (b) compensate for effects of viewing distance through changes in signal properties and/or usage, and (c) control viewing distance by moving either themselves and/or the receiver.

Several mechanisms exist that allow signalers to estimate object distance either visually, and/or via cues from other senses (e.g., sound or olfaction), and these are reviewed elsewhere (Naguib and Wiley 2001; Michael F Land and Nilsson 2012; Cronin et al. 2014). While the mechanisms may vary among species, evidence of distance-dependent signaling behavior indicates that signalers can and do use this type of spatial information during communication. Signalers can actively change their visual displays to improve signal saliency at different distances. This active distance-dependent signal modification has been most studied in species that use movement-based displays. In these systems, signalers generally increase the intensity of their movements for more distant receivers. For example, in the jumping spider *Habronattus pyrrithrix*, males increase the amplitude of the arm-waving display of their courtship dance when further from the female (Chapter 3). Likewise, signaling males of the lizard *Anolis gundlachi* respond to

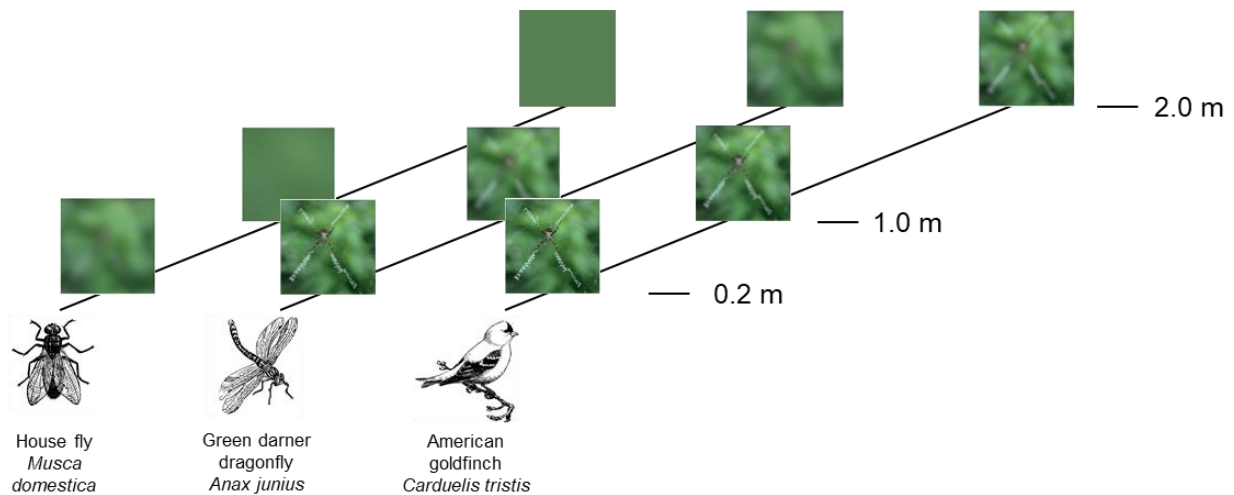


Figure 1. Visual signal appearance is affected by viewing distance and receiver acuity

Estimated views of orbweaver stabilimentum by three potential receivers, adapted from (Caves, Brandley, and Johnsen 2018). As viewing distance increases, signals appear blurrier, but the maximum range of detectability depends on the visual acuity of the signaler. Differences in color vision are not represented here.

increased viewing distance by also increasing the amplitude of their head-bob display (Steinberg and Leal 2013). In both cases, the signaler increases signal intensity approximately linearly with distance, and this modulation increases salience (relative to an unmodified signal), but does not fully compensate for the effect of viewing distance. This suggests possible limitations on signaling plasticity, and/or the functional benefits of these adjustments. In *A. gundlachi*, the extent of signal modulation seems to be matched to the amplitudes that best stimulate the species' visual system (Steinberg and Leal 2013). Signalers may also qualitatively change their signal in response to viewing distance. For example, *A. gundlachi* males append an additional signal component to their display when signaling at a farther distance (Steinberg and Leal 2013). Such facultative signal modifications provide another option for signalers to compensate for distance, especially if modulation of the primary signal may alter its information content.

We also note that signalers may employ distance-dependent signals for reasons other than compensating for decreased salience at larger distances. For example, male fiddler crabs (*Uca perplexa*) change their claw-waving display with distance, but, contrary to other examples, *increase* display intensity as females approach. Males may do this to communicate different messages at different viewing distances, or to avoid females misinterpreting their display as a predator cue (How et al. 2008).

The taxonomic breadth of confirmed descriptions of distance-dependent visual signal modification (jumping spiders, crabs, lizards) strongly suggests that this ability has evolved repeatedly, and may be more common than current evidence suggests. For example, anecdotal observations suggest that humans also engage in distance-dependent signal modification of a movement-based signal; when waving arms to get others' attention, signaling humans often increase the speed and amplitude of their waves with increasing distance from intended receivers. However, the extent of this behavior, and its impact on signal effectiveness, has yet to be tested. We know even less about distance-dependent signaling for visual signals that are not movement-based. Signalers capable of rapid color and pattern change (e.g., paradise whiptail fish, chameleons, cuttlefish and other cephalopods; reviewed in (Hutton et al. 2015)) may use this ability for signal modulation if certain colors are better able to reach a distant receiver, as in the case in marine environments (see below).

Which features within a visual signal are most salient will also change with viewing distance. At greater viewing distances, coarser-scale features will dominate the perceived image, while at closer distances, fine-scale features are likely more noticeable. When the coarse-scale and fine-scale features of display are sufficiently different, displays can have distance-dependent appearances. Indeed, distance-dependent functions without the need for distance-dependent

behaviors or movement on the part of the signaler have been identified for a number of animal signals (Kelley and Kelley 2014; Barnett and Cuthill 2014; Barnett et al. 2017). In humans, this property of visual perception is used to create “hybrid-image” illusions, where one image transitions into another as the viewer stands further away (or otherwise blurs their vision, such as by squinting) (Kelley and Kelley 2014). In nature, this phenomenon allows signals to evolve to simultaneously have two separate, often contradictory functions. Aposematic animals, for example, use conspicuous colors and patterns to alert predators to their (purported) inedibility. However, at greater distances, such displays may, through color mixing, end up being cryptic, thereby serving as camouflage and allowing these animals to avoid detection at all. For example, the striped aposematic patterns of many lepidopteran larvae (Barnett and Cuthill 2014; Barnett, Cuthill, and Scott-Samuel 2018; Tullberg, Merilaita, and Wiklund 2005; Bohlin, Tullberg, and Merilaita 2008), skunks (Caro 2013), and frogs (Barnett et al. 2018) have been shown to function as aposematic markings up close, and as camouflage at a greater distance (e.g. “distance-dependent defensive coloration” *sensu* (Barnett and Cuthill 2014)). Similarly, several species of reef fish have pointillist coloration patterns: many small dots and stripes that are resolved as discrete, distinctly colored elements from shorter distances but appear uniform and monochrome over long distances. Such coloration allows for species discrimination at close range, but camouflage from more distant predators (Marshall 2000; reviewed in Stevens 2007). It is likely that other species with bold markings, either for aposematism or social communication, will benefit from distance-dependent cryptic patterning, suggesting that these dual-function signals may be more common than the scope of current work suggests.

Distance-dependent perception may also shape the evolution of signaling polymorphisms. In the dimorphic jumping spider *Maevia inclemens*, males come in ‘grey’ and ‘tufted’ morphs,

which have specialized courtship displays that most effectively attract a female's attention at nearer versus farther viewing distances, respectively (David L Clark and Uetz 1993). As initial viewing distance can vary between male-female encounters, and the initial capture of a female's attention strongly influences mating success, both morphs are able to persist in the species (David L Clark and Biesiadecki 2002; D L Clark and Morjan 2001). However, whether this effect may play a role in other polymorphic systems is an interesting question for future study.

Importantly, the strength of distance dependent effects (e.g., the rate at which images become blurry with increasing distance) in any given signaling interaction depends largely on the receiver's visual system. Species with greater acuity ("sharper" vision as a result of larger eyes and/or more densely packed photoreceptor arrays) will likely be able to perceive signals at greater viewing distances (given that the eye is also capable of focusing the image at that distance; (Michael F Land and Nilsson 2012). Visual acuity may thus limit the distances at which communication can occur (i.e., the active space of a signal (H C Gerhardt 2017)). For example, individual paper wasps (*Polistes fuscatus*) have unique facial markings, but the size of pattern elements and the acuity of the species' eyes indicates that individuals cannot visually recognize each other beyond distances of 5.7cm at the most (Tibbetts 2002; E. M. Caves, Brandley, and Johnsen 2018). Visual acuity can vary by three orders of magnitude between species, such that a community of heterospecific receivers may have drastically different perception of a signal from the same distance (Fig. 1, (reviewed in Caves, Brandley, and Johnsen 2018)). Species disparities in visual acuity may also allow for semi-private communication channels—at certain viewing distances, one species may be able to clearly perceive a signal, while another may perceive the image differently, or not be able to detect it at all. For example, the bright white X-shaped webbed decorations ("stabilimenta") made by some orbweaver spiders are salient to an approaching bird,

but not a prey insect at the same distance, as a result of the disparity in acuity between the two species. In this manner, the stabilimenta may be a warning signal to birds (so they avoid flying into the web and damaging it), while not being visible to flying insects (E. M. Caves, Brandley, and Johnsen 2018; Matthew J. Bruce, Heiling, and Herberstein 2005); but see (M. J. Bruce 2006) for review of alternative hypotheses including prey attraction). Jellyfish may exploit a similar acuity disparity to avoid destruction of their stinging tentacles by adult fish while remaining cryptic to pelagic crustaceans and adult fish (E. M. Caves, Brandley, and Johnsen 2018).

Finally, the effects of viewing distance are also modified by environmental conditions. Signal perception degrades more quickly with viewing distance in dim light than in bright light. To compensate, male guppies (*Poecilia reticulata*) move closer to females when courting in dimmer lighting (Long and Rosenqvist 1998). In addition, the quality and density of particles in the transmission medium (e.g., in air or in water) will determine how light is scattered and/or absorbed per unit distance. This attenuation effect further reduces the range of effective viewing distance beyond that established by limits of the visual system. The transmission medium may also interact with certain wavelengths of light such that some colors attenuate more quickly than others. The rate of attenuation depends on particle density, and as a result visual signals degrade more quickly with distance when underwater than in air (Johnsen 2012; Cronin et al. 2014). However, weather conditions (e.g., fog, rain, and dust storms) may transiently produce similar effects on land. The sharp disparity in distance-dependent effects between air and land may create a unique situation for amphibious signalers that are viewed in both environments, although this remains to be investigated.

1.2.2 Directionality of Visual Signals

In addition to distance-dependent effects, the appearance of a visual signal often depends on the direction from which it is viewed. This effect can result in strong selection on signalers to manage the orientation of their signal relative to the receiver's location (Bradbury and Vehrencamp 2011; G. G. Rosenthal 2007; Hutton et al. 2015). Consider the tail-fan display of a male peafowl. For this forward-facing, approximately flat display, an appropriate measurement of the viewing angle would be the angle between the vector from the receiver to the signaler and the perpendicular vector from the center of the display (Fig. 2). When seen "head-on" (i.e., at a viewing angle of 0), the elements of the display are fully visible with their familiar eyespots arrayed in a fan-like shape (Fig. 2A). However, if the male were to turn towards the right, this display would be seen from an increasingly skewed perspective. Eventually, the peacock is seen in profile (i.e., at a viewing angle of 90 degrees), and the eye spots are no longer visible (Fig 2B). Other signal elements, however, such the male's orange wings, may now be visible from this perspective. So, to ensure that females can see display elements, courting peacocks must track a female's relative position, and orient their display appropriately. Indeed, males change their orientation towards females to expose different ornaments depending on the display being performed (Dakin and Montgomerie 2009). Signaler behaviors that work to manage the directionality of their displays are expected to be a common feature of visual communication, shaped by selection for effective communication (G. G. Rosenthal 2007; J. A. Endler 1992; Echeverri, Morehouse, and Zurek 2017).

The strength of this selection likely depends in part on the extent of signal directionality. Hypothetically, a perfectly smooth and matte sphere of uniform color and brightness would act as an omnidirectional signal (if a message was coded by reflectance information), as its appearance would remain constant irrespective of viewing angle. However, much like the proverbial

“spherical cow” used to simplify thought experiments in physics, no such omnidirectional signal exists in nature to our knowledge. We can then classify natural signals on an axis from weakly directional to strongly directional. The peacock’s tail is an example of a strongly directional signal, where appearance and effectiveness change dramatically with viewing angle (Fig. 2A, B). Visual signals tend to be strongly directional if (Fig. 3):

- (a) they are formed by approximately flat surfaces (e.g., flattened tail feathers arranged in a plane in peafowl and relatives (Dakin and Montgomerie 2009) and other birds (e.g., great bustards (Olea et al. 2010) and birds of paradise (Scholes 2008b)), clypeal coloration in jumping spiders (e.g., (Echeverri, Morehouse, and Zurek 2017; Elias et al. 2012)), dewlaps in *Anolis* (Leo J. Fleishman et al. 2015; Gartner et al. 2013; Losos et al. 2017) and other lizards (Klomp et al. 2017), butterfly wings (White, Zeil, and Kemp 2015; Rutowski et al. 2007a)),
- (b) they have a directionally asymmetric design (e.g., the dewlap of *Anolis lineatus*, which is colored differently on the left versus right side (Losos et al. 2017; Gartner et al. 2013) or have dorso-ventral countershading, as in many marine organisms (Cuthill et al. 2016)),
- (c) signaled information is coded by the area (or volume) of the signal, as less of this area will be seen if viewed from a skewed angle (e.g., displays that serve to exaggerate the signalers size, such as deimatic displays in mantises (Maldonado 1970), the neuropteran *Palmipenna aeoleoptera* (Picker, Leon, and Londt 1991), and other species (Umbers, Lehtonen, and Mappes 2015))

and/or

(d) the material that forms the signal reflects light in a specular (mirror-like) or iridescent (color-changing depending on viewing angle) manner (e.g., feathers of some hummingbirds (Simpson and McGraw 2018b; Hamilton 1965; Hogan and Stoddard 2018) and birds of paradise (Scholes 2008b), and the wing scales of some butterflies (White, Zeil, and Kemp 2015); reviewed in Meadows et al. 2009; Doucet and Meadows 2009).

Conversely, certain signals may be weakly directional, with appearance and effectiveness remaining relatively constant from many viewing angles. Visual signals are likely to be weakly directional if:

- (a) signal components are distributed uniformly or nearly uniformly over the signaler's body such that the signaled information is accessible from many angles (e.g., red body coloration of a male cardinal (Fig. 2C, D), or non-iridescent aposematic stripes that wrap all the way around a caterpillar)
- (b) signaled information is coded by a spatially simple design (e.g., stripes of 2 alternating colors) and/or by traits that do not depend on apparent area or volume (e.g., color hue instead of area of color patch). Spatially complex designs and size-dependent signals may not be fully visible from skewed angles.

and

- (c) the material that forms the signal reflects light in diffuse or matte manner, such that the angle of incident light only weakly affects the properties of the reflected light. Many pigment-based colors fulfill this condition.

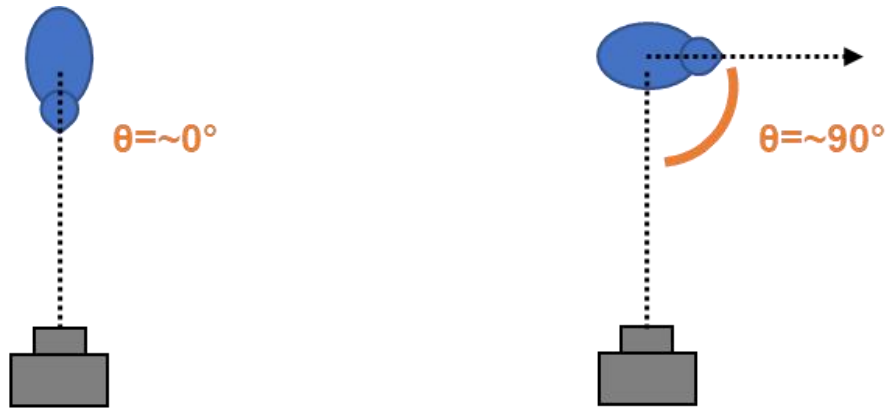


Figure 2. Visual signal appearance is affected by viewing direction

The appearance of a strongly directional visual signal (tail train of a peacock, *Pavo cristatus*) changes dramatically when “head-on” (A), and in profile (B). The appearance of a weakly directional visual signal (red coloration of a male cardinal, *Cardinalis cardinalis*) changes only slightly with viewing angle (C, D). Images from Wikimedia Commons users Jennie Kondo (A), “Arpingstone” (B), Jocelyn Anderson (C, D).

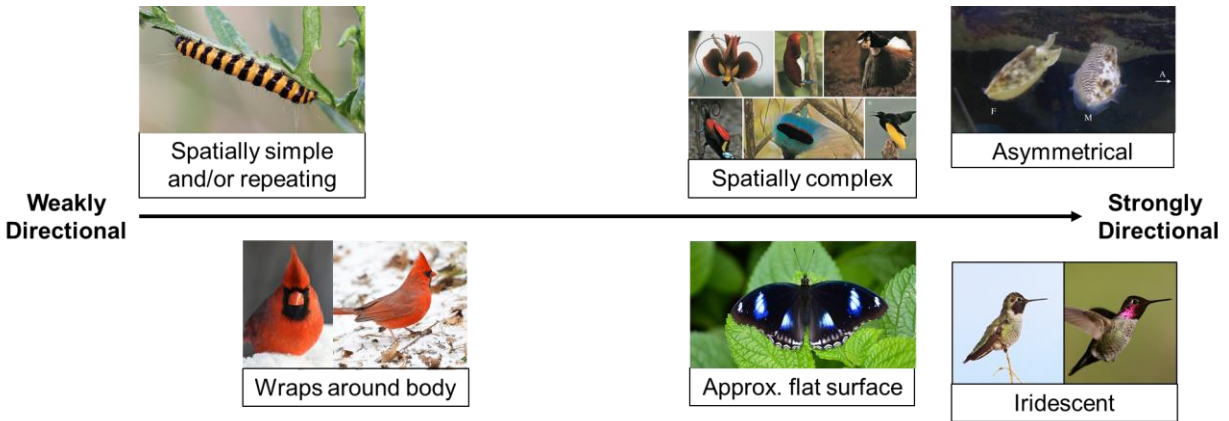


Figure 3. Visual signal directionality is affected by signal properties

Visual signals can be classified on an axis from weakly directional to strongly directional. The extent of this directionality is affected by the physical shape of the signal, how its component material interact with light, and/or its location on the signaler’s body. Images by (top row, left to right) Wikimedia user “Stu’s Images”, Scholes 2008, Brown et al 2012; (bottom row, left to right) Jocelyn Anderson, Vedant Kasambe, Steve Berardi, USFWS Pacific Southwest.

Iridescent signals, where color changes based on viewing angle, are perhaps the most famous and well-studied examples of highly directional visual signals (reviewed in (Meadows et al. 2009; Doucet and Meadows 2009). Iridescent signals are phylogenetically widespread, and can have especially narrow effective viewing angles. Consequently, signaler behaviors that effectively orient their iridescent signal towards receivers are quite common, having been observed in hummingbirds (e.g., (Simpson and McGraw 2018b; Hamilton 1965; Hogan and Stoddard 2018)), birds of paradise (Scholes 2008b), and butterflies (White, Zeil, and Kemp 2015; Rutowski et al. 2007b). However, the appearance of iridescent signals depends on not just the viewing angle relative to the receiver, but also the direction of the light source. For the moment, we will focus on the consequences of directionality agnostic of lighting, but will return to this additional complication when we discuss the geometric considerations of the visual environment within which signaling occurs.

Unfortunately, we know relatively little about signal directionality and its consequences for signaler behavior outside of iridescent systems, despite that non-iridescent signals can exhibit strong directionality. While it is generally assumed that the appearance of non-iridescent, pigment-based colors is not angle-dependent, in the rare case that this assumption has actually been tested, it has proven false. An exemplary study on the blue-fronted Amazon parrot (*Amazona aestiva*) shows that several measures of pigmentary color signals (intensity, hue, and within-ornament contrast) can vary solely based on viewing angle (Santos et al. 2007). Indeed, any surface that is rough on a fine scale, such as a bird's feather, will reflect light in an angle-dependent way, even if it reflects light diffusely (Oren and Nayar 1995). Only a perfectly smooth and matte surface will not do so. Thus, it is likely that color signals in more species also have directional changes in coloration. We note that studies on iridescent color signal directionality may also measure non-iridescent colors as a baseline for comparison (e.g., (Kemp and Rutowski 2007)). Although the angle-dependent changes of these non-iridescent colors may not be prominently discussed in publications, such datasets may provide a useful resource for expanding our understanding of visual signal directionality.

Signalers may be under selection to, when possible, aim their directional signal towards the receiver. In great bustards, males orient their bright tail displays towards females (Olea et al. 2010), though as with peafowl, the extent to which they do so varies with specific phases of courtship and the sun's location (Dakin and Montgomerie 2009). In the lizard *Anolis linneatus*, however, while males have an asymmetrically colored dewlap (one side being orange and the other yellow), they do not appear to preferentially show either side to a receiver during communication (Gartner et al. 2013; Losos et al. 2017). This suggests that *A. linneatus* males are under little

selection to do so, and thus that, despite the directionality of dewlap color, this does not affect signal function in this case.

Signalers that construct a physical structure as a visual signal, as opposed to displaying with their own body, (i.e., a type of extended phenotype signal *sensu* (Schaedelin and Taborsky 2009) may require alternative strategies to ensure these structures are viewed from an effective angle. While no longer obscured or limited by the signaler's own anatomy, these external signals can also be highly directional, and often cannot easily be reoriented during communication (Schaedelin and Taborsky 2009). Instead, signalers may use strategies that control receiver position. Male great bowerbirds (*Chlamydera nuchalis*) arrange rocks in their bowers to create a visual illusion that may amplify the perceived size of the male (J. A. Endler, Mielke, and Kelley 2012). This illusion relies on forced perspective, requiring that females view the structure from a very specific angle to perceive the signal (Kelley and Endler 2012). Males build an entranceway that restricts females to viewing the bower from within the limited viewing angle of the illusion (J. A. Endler, Mielke, and Kelley 2012). Signalers may also rely on predictable movement of receivers. In *Vargula annecohenae*, a marine ostracod, males eject luminescent materials while swimming in a complex three-dimensional pattern to create a visual display that persists briefly in the water column (Rivers and Morin 2008). Females are free to move when viewing this display, but swim towards males in a simple intercept course, thereby allowing males to reasonably predict females' viewing angles (Rivers and Morin 2006; 2008). Other species that construct physical structures as possible visual signals (e.g., sand pyramids built by male ghost crabs (Linsenmair 1967), and ornaments in bird nests; reviewed in (Schaedelin and Taborsky 2009)) are exciting opportunities to understand how signalers control receivers' perspective.

Signalers with more traditional displays may create physical structures to constrain the range of viewing angles receivers have access to. For instance, several birds of paradise clear courtship stages underneath low hanging tree branches. These branches serve as a perch for females to view the male's display from above, where the full design of the male's elaborate ornaments can be seen (Scholes 2008a; 2008b). By constraining possible viewing angles ahead of the communication interaction, signalers can ensure optimal viewing and reduce the cognitive load required to track receiver position during communication and reorient. However, in both cases, this strategy is dependent on communication occurring at a known location that the signaler can manipulate beforehand. The development of this strategy may thus be evolutionarily associated with territoriality and/or landmark-based social behavior (e.g., "hill-topping" in many insects (Alcock 1987)).

Signaling interactions where orienting a signal is challenging may also select for weakly directional signals. This may be the case when there are multiple receivers or when receiver location is rapidly changing or simply unknown. This suggests that broadcast displays, such as camouflage patterns or body coloration that indicate territorial or social ranking, may have undergone selection for weaker directionality than that of dyadic displays (e.g., a courtship signal directed at a single female). Broadcast signals that are strongly directional, such as dorsoventral countershading in marine organisms, seabirds, and some primates (Cuthill et al. 2016; Ruxton, Speed, and Kelly 2004; Kamilar and Bradley 2011), likely have coevolved with morphology and typical body orientation to increase the chance that receivers view the signal from an effective direction (Johnsen 2002; Donohue, Hemmi, and Kelley 2020).

While previous work provides clear evidence for the role of signal directionality in visual signaling efficacy, many questions remain to be investigated. There have been very few studies

quantifying the directionality of non-iridescent signals. Work by Santos et al. (2007) demonstrated the angle-dependent appearance of a pigmentary color ornament. However, how such methods can best be adapted to quantify angle-dependent changes in the visibility of spatially complex patterns (as opposed to coloration changes) remains a pressing need. Furthermore, few studies have tested the consequences of signal directionality on signaling outcomes. Work on iridescent warning colors on butterflies has, as a proxy for viewing the iridescence from suboptimal angles, removed these colors from a clay model used in predation experiments (e.g., (Pegram, Han, and Rutowski 2015)). But what are the consequences for iridescent colors viewed at intermediate angles, or for non-iridescent signals? It is clear that at extreme viewing angles, many highly directional signals are entirely obscured and likely ineffective. But how effective is a peacock that faces his display 30 degrees away from the female? 45 degrees? What is the rate of change (linear? exponential?) of signal effectiveness, and what factors (signal complexity? signaler anatomy?) influence this rate? The answers to these questions are important to understanding the strength of selection on signaler orientation and positioning during communication, and thus for making hypotheses about the evolution of such behavior as has been done for iridescent displays. We encourage researchers to more widely measure the effective viewing angles of non-iridescent signals, how these constraints drive communication outcomes, and how signalers manage this effect.

In addition, the majority of published work regarding directional signals has dealt with dyadic signaling situations (i.e., between two individuals). But in cases where there are multiple receivers (e.g., in a lek), signalers are constrained in their ability to orient their display towards more than one receiver. How do signalers manage this potential conflict of interest? Do lekking males select one female to aim their display at, or orient themselves such that the greatest number of receivers have an adequate, if sub-optimal, viewing angle? And what influences these decisions?

While lekking great bustards do orient their signals towards a female, the consistency of this behavior (only ~20% of the time (Olea et al. 2010)) is far less than what is seen in dyadic interactions between peafowl (~60% of the time (Dakin and Montgomerie 2009)) and jumping spiders (~99% of the time (Echeverri, Morehouse, and Zurek 2017)). This suggests that courting multiple females may indeed challenge signalers' abilities to orient their displays appropriately.

Finally, we note that signal directionality interacts strongly with the directionality of the receiver's visual system (see following section), such that the effects of one may compliment or exacerbate those of the other. Therefore, we strongly recommend that researchers assess both factors when possible.

1.2.3 Directionality of Sight

Just as signal appearance changes with viewing angle, how eyes detect and process visual information is also subject to directional biases. The distribution of photoreceptors is rarely, if ever, uniform across the retina. In many species certain areas of the retina (e.g., foveal areas or retinal streaks) have a much greater density of receptors than others (e.g. the retinal periphery) (Temple 2011; Michael F Land and Nilsson 2012; Cronin et al. 2014). Likewise, the required photoreceptor types and neural wiring for different visual functions, such as color perception, spatial acuity, and motion detection tend to be regionalized within the retina (Michael F Land and Nilsson 2012). Consequently, what visual information is available to receivers depends on the moment-to-moment position of the signal within their field of view.

The precise nature of these specialized retinal regions varies among species, between sexes of the same species, and between eyes of an individual (Michael F Land and Nilsson 2012; Cronin et al. 2014). While most vertebrates only have one set of physiologically similar eyes, many

invertebrates have multiple sets, each of which can be physiologically different. Vision in these animals can be modular in nature, with each set of eyes specialized for distinct visual functions, and with distinct directional limitations. Within arachnids, for example, the arrangement and function of eye pairs varies greatly amongst spiders (Foelix 2011). A particularly notable example is the vision of jumping spiders, where the anterior median eyes are specialized for high acuity and color vision, while two of the remaining three sets of lateral eyes excel at motion detection, but achromatically and with reduced resolution (Harland, Li, and Jackson 2011; M F Land 1985). Thus, while the overall field of view of the entire spider is quite wide (approaching 360 degrees), how a visual stimulus is processed depends on which eye can see the stimulus. Likewise, insects often have one set of compound eyes and several simple ocelli, and many marine invertebrates have numerous sets of eyes (Michael F Land and Nilsson 2012).

As a result of spatial heterogeneity in visual system function, even the perception of an otherwise static display can become dynamic if the receiver changes their field of view by looking around (e.g., bringing the display from the periphery to the foveal region or vice versa) (G. G. Rosenthal 2007; Hutton et al. 2015). Indeed, such gaze movements, (of the eye itself, the head, and/or body) are a common evolutionary solution to the directional limitations of vision (reviewed in M. F. Land 1999).

Despite extensive physiological and neurological research on functional regionalization of visual systems available for many species (Temple 2011), this information has rarely been incorporated into signaling research. Instead, receivers are often implicitly assumed to look at signals uniformly and consistently. It is commonplace, even in studies on directional biases in signal propagation (Olea et al. 2010; Dakin and Montgomerie 2009; White, Zeil, and Kemp 2015; Stavenga et al. 2011; Vukusic et al. 2002; Hamilton 1965) to neglect or not report the orientation

of receiver's gaze or field of view. However, when receiver gaze *has* been measured during a signaling interaction, it is clear that visual attention is temporally and spatially dynamic. Pivotal work in tracking gaze of peahens viewing courting peacocks shows that females view only certain display elements (the bottom edge of the males' train, and his body, but *not* individual eyespots) with their highest acuity (foveal) vision (Jessica L Yorzinski et al. 2013; J. L. Yorzinski et al. 2015). In addition, this work found that females often (63% of the time) looked *away* from the male during communication, such that males would be viewed entirely with the female's peripheral vision or not at all. Likewise, in *Habronattus pyrrithrix* jumping spiders, females looked away from males for over 73% of the interaction (Echeverri, Morehouse, and Zurek 2017). Because of their unique visual system, males were likely visible to the female throughout this period, but only achromatically, and at a reduced resolution.

Furthermore, eyes that are (or appear to be) anatomically identical, may be preferentially used for a certain visual task based on which lateral hemisphere of the brain they are associated with (i.e. left or right). Here, the geometric constraints on perception are a consequence of asymmetrical neurophysiology, and not limitations to the visual "hardware". This visual "handedness", or lateralization, means that which eye is used to see the signal, (especially for species with fields of view with small or no binocular overlap) may change how visual information is integrated and acted upon (reviewed in (Salva et al. 2012)). For instance, male zebra finches use female coloration to decide which individuals to court, with a strong preference for females of the same color morph. However, males are only able to make this distinction when viewing females with their right eye (Templeton et al. 2012). This implies that courting males must orient themselves to keep prospective females to their right-hand side, and/or that females should position themselves appropriately so as to have the best opportunity to be evaluated or even to avoid critical

evaluation. Lateralization in this system appears to be a consequence of avian brain structure, suggesting that such biases may be common in birds. Lateralized visual function may be a mechanism by which neurophysiology may drive the evolution of signaling behavior in other systems. However, such comparative work remains to be done.

Tracking how receivers orient their visual system, in combination with physiological and neurological research on the regionalization of the visual field, allows for inferences about what visual information is available to the receiver and when. Using this, we can better understand how receivers make decisions about signaling outcomes, and thus more precisely track selection on signal components. Luckily, the technology needed to track receiver orientation is increasingly accessible. Gaze-tracking technology has been developed for primates, canines, peafowl (Jessica L Yorzinski et al. 2013), and jumping spiders (Canavesi et al. 2011), and may be adapted for related species. In species where eyes do not move independently of the head (e.g., most arthropods, amphibians, and reptiles), measuring the head's facing direction can be sufficient to track a receiver's visual field (M. F. Land 1999).

1.2.4 Positioning within the Visual Environment

Until now, we have largely discussed the role of geometry inherent in interactions between visual signals and receivers in general, without fully placing these interactions in the real-world context of the visual environment, with the additional complexities that such environments bring. However, signal effectiveness also changes as a function of the spatial arrangement of signaler and receiver within the physical environment around them (G. G. Rosenthal 2007; Ryan and Cummings 2013). Illumination, obscuring physical objects, and the backdrop against which signalers display can all affect signal efficacy, and natural environments are often heterogenous in

these spatio-visual properties (J. A. Endler 1992; G. G. Rosenthal 2007). Space use during communication may thus be a result of selection for behaviors that result in effective geometries of signaler, receiver, and environment.

1.2.4.1 Directional Illumination

Signal appearance is dependent on the direction of illumination, and how a signal's constitutive material(s) reflect oncoming light from different angles. With the notable exception of phosphorescent/luminescent animals, signalers must rely on an external source for the light necessary for signal transmission. The light source's position relative to the signaler and receiver will determine the extent to which the receiver sees the signal as brightly lit or in silhouette. This will be influenced by the relative position of signal, receiver, and the illumination source. In addition, different materials reflect incoming light differently, modulating the effects of illumination (Bradbury and Vehrencamp 2011). Diffusely reflective surfaces, which "spread out" reflected light, can result in signals that are weakly directional with respect to illumination angle. In contrast, specularly (i.e., mirror-like) reflecting surfaces produce signals that are highly directional with respect to illumination angle. In the extreme case of iridescent reflection, the color of reflected light will change depending on the angles of illumination and viewing, resulting in some of the best studied examples of highly directional visual signals. The physical mechanisms underlying iridescence have been well described (Doucet and Meadows 2009; Meadows et al. 2009; Seago et al. 2009), but there are ongoing questions regarding the evolution, function, and use of these signals.

As with other highly directional signals, the angle-dependent appearance of iridescent signals may select for signalers to aim their display such that the bright iridescent color is visible by the receiver. However, signalers using iridescence are more constrained in their possible

positions and orientations, as they must also manage the angle of illumination as well as that of the receiver's position. Males of common eggfly butterflies (*Hypolimnas bolina* (White, Zeil, and Kemp 2015)) and broad-tailed hummingbirds (*Selaphorus platycercus* (Hogan and Stoddard 2018)) have been shown to position themselves in relation to the sun and the intended receiver so as to maximize the brightness of their signal in the eye of the receiver. Male Anna's hummingbirds (*Calypte anna*) also display their iridescent gorgets towards the sun when displaying at a focal female, though whether this behavior indeed improves brightness remains to be formally tested (Hamilton 1965).

In addition to producing particularly bright colors, iridescent signal elements can also be used to produce a "flashing" effect because of their rapid directional color changes (e.g., as in *Colias eurytheme* butterflies (Kemp and Rutowski 2007; Rutowski et al. 2007b)). Such flashy signals may be effective at capturing a receiver's attention due to their changing appearance (G. G. Rosenthal 2007; Számadó 2015; Doucet and Meadows 2009), but require potentially more complex signaler behavior. To increase flashiness, signalers can oscillate their positions between those corresponding to the viewing angles of most and least reflectance. In the butterfly *C. eurytheme*, the iridescent color patches are located on the wings, so that flashing effects are a byproduct of flight (Kemp and Rutowski 2007). Recent work shows that in bee hummingbirds, positioning during display and iridescent signal directionality appear to be tightly evolutionarily linked to produce flashy signals (Simpson and McGraw 2019). However, these two display strategies (maintaining a bright iridescent color vs producing a flashy signal) may also be exhibited within a species. In broad-tailed hummingbirds (*Selaphorus platycercus*), some males oriented more towards the sun and produced flashier displays, while other males maintained a more consistent coloration (Simpson and McGraw 2018c).

Iridescent color changes have been quantified for various Lepidoptera (Kemp 2008; Rutowski et al. 2007a; Vukusic et al. 2002; Lind et al. 2017; Rutowski, Nahm, and Macedonia 2010), birds of paradise (Stavenga et al. 2011), and beetles (Seago et al. 2009), amongst others (Meadows et al. 2009), and the methods to do so have been well described by (Meadows et al. 2011). However, whether these signalers' positioning during communication presents their iridescent colors effectively remains to be tested outside of a few systems.

Even for non-iridescent signals, the relative position of illumination can affect signal appearance. Pigment-based color patches of the blue-fronted Amazon parrot have been shown to change in brightness, hue, and within-patch contrast as a function of illumination angle, and such effects are suggested to be widespread (Santos et al. 2007). In addition, the non-iridescent plumage of the summer tanager (*Tersina viridis*) also shows dramatic color change depending on whether the illumination source is behind the receiver or behind the signaler (Skigin et al. 2019; Barreira et al. 2016). In addition to possible color-changing effects, most displays will appear brighter with direct illumination. Thus, non-iridescent signalers can also experience selection to orient their display towards the sun. Great bustards (*Otis tarda*) orient their bright white tail displays towards the sun, particularly when the sun is low in the sky and thus best positioned to shine upon the male's vertically-held tail feathers (Olea et al. 2010). Likewise, snowy owls (*Bubo scandiacus*) seem to orient their white breast feathers towards and the sun in order to increase brightness ((Bortolotti, Stoffel, and Galván 2011), but see (Wiebe and Chang 2018)). To determine how and why non-iridescent signalers orient themselves with respect to the sun, we encourage future research to build on work by applying the robust methodology used in iridescent systems to non-iridescent ones.

1.2.4.2 Physical Structures

Unlike some other modes of communication, light cannot flow around solid objects in its path (at least not on behaviorally-relevant spatial and gravitational scales) and so such obstructions shape which positions of signaler, receiver, and illumination are most effective. Most simply, objects located between signaler and receiver may partially or fully obscure signal visibility (G. G. Rosenthal 2007). To establish a clear line of sight for receivers, signalers may experience selection to maneuver around intervening objects during communication, and/or directly modify the local environment by clearing objects in advance of signaling. The latter strategy, however, depends on signalers having the opportunity to control when and where signaling will occur. In cases where signalers encounter receivers in variable locations (e.g., a male happens upon a moving female and begins courtship), signalers will likely have less control over the physical environment. In dense microhabitats, navigating physical obstructions while displaying may be cognitively demanding for signalers. There is little research on how signalers navigate fine-scale obstacles during communication, and the extent to which this imposes an additional challenge for signalers.

Alternatively, physical objects in the signaling environment also provide an opportunity for signalers to strictly control what receivers see. Male great bowerbirds (*Chlamydera nuchalis*) build an “avenue” of reeds that function to block females from viewing the male’s bower from all but head-on, preserving the directional visual illusion of the bower display (J. A. Endler, Mielke, and Kelley 2012; Kelley and Endler 2012). Signalers may also use obstructions for “peek-a-boo” displays, repeatedly presenting and hiding the signal from behind cover, as seen in some jumping spiders (genera *Saitis* and *Jotus* (Hill 2009; Otto and Hill 2016)). Such interactions have been studied in the context of human development (e.g., (Greenfield 1972), but not in communication

of other animals. These peek-a-boo displays may allow signalers to avoid visual desensitization and/or exploit biases for novel stimuli. However, they require signalers to track the receiver's position without a clear line of sight, as the peek-a-boo only functions if the obscuring object remains between signaler and receiver.

How do signalers navigate this and other cognitive and sensory challenges regarding physical objects? If signalers are using an obstruction to control the receiver's field of view, this may require some ability to estimate what the receiver will see based on current conditions, especially if the signaler cannot establish a line-of-sight (e.g., if only showing a part of its body in a peekaboo type display). And how do signalers compensate if no suitable object is available? Testing signaling interactions in physical environments with similar structures to the species' natural conditions is important for beginning to answer these questions. Such observations may exist in species descriptions or in video form, but we strongly encourage future work to conduct observations in natural environments, and/or reproduce similar physical obstructions in lab environments.

1.2.4.3 Visual Background

Signals are not perceived as isolated stimuli; instead, they are perceptually weighted against their surrounding stimuli (i.e., the visual background) (G. G. Rosenthal 2007; Cronin et al. 2014; Ord et al. 2007; R. Peters, Hemmi, and Zeil 2008; Cole 2013). The properties of the background (color, complexity, illumination, movement, etc.) interact with those of the signal to affect signal efficacy. The position of signaler and receiver within their environment will change this background in all but exceptionally homogenous habitats.

How signaling efficacy is affected by any specific background, and thus how selection acts on positioning, depends on signal function. Species with cryptic body patterning experience

selection to position themselves such that they are viewed against a background with similar visual properties (Stevens and Ruxton 2019; Cuthill et al. 2016; Cronin et al. 2014). Species with countershading colorations must keep themselves oriented with respect to the direction of illumination, so that they more closely match the brightness and color of their background when viewed from above and/or below (Cuthill et al. 2016; Ruxton, Speed, and Kelly 2004). While frequently discussed in terms of marine organisms (Johnsen 2002), countershading may also benefit caterpillars in forests (Rowland et al. 2008).

Species with cryptic coloration may experience selection to match the directional properties of physical features in their visual environment. The geometrid moth (*Jankowskia fuscaria*) has a bark-like pattern on its wings, but when viewed against non-pattern-matching trees experiences greater predation. Even on pattern-matching trees, however, the moths must also orient their bodies such that the direction of their markings matches that of the tree because the pattern of bark is itself directional (R. J. Webster et al. 2009). Individuals do not orient themselves from a distance, but conduct short re-orientation movements after landing that allow them to hone-in on the proper orientation. As the moth may not be able to resolve the bark pattern while on the tree, it may detect the orientation of the bark through touch, and use this information to inform its visual signaling behavior (Changku Kang et al. 2015; Chang ku Kang et al. 2013).

The extent to which geometry affects the visual background also depends on habitat homogeneity. In heterogenous environments, especially at boundaries between different microhabitats, changes in relative positioning can have stronger effects (e.g., by changing which microhabitat is behind the signaler). In homogenous environments, such as in the open ocean or an open field, changes in positioning within certain planes (e.g., horizontally at the same depth in the water column) can be much more constrained (Johnsen 2002; 2012). In addition, much as

viewing distance affects signal perception, the distance between the signaler and the background behind them may determine whether the signal and background are perceived at similar levels of detail (E. M. Caves, Brandley, and Johnsen 2018).

As with other physical properties, in some systems signalers may be able to select or modify their visual environment prior to communication (e.g., clearing debris from a display court in manakins (Uy and Endler 2004)) . However, when signaling interactions are unpredictable in location, signalers may be under selection to assess their environment, and reposition themselves during communication. In the jumping spider *Habronattus pyrrithrix*, males move closer to females when courting against more spatially and temporally complex backgrounds (Chapter 3). Jumping spiders have a particularly wide field of view, and may be able to assess their background without turning away from the receiver. Other animals with laterally-oriented eyes (e.g., many birds and mammals) may also be able to simultaneously view the receiver and the visual background if they position themselves appropriately. However, many species lack such a wide field of view. How is the visual environment assessed during communication, if at all? Do signalers incur a cost by moving their visual attention away from the receiver in order to assess their own background, either by missing potential cues or by inadvertently showing disinterest? We encourage future work to pursue these questions to determine how signalers select and position themselves to control their visual background.

1.2.5 Critical Needs and Opportunities

Previous studies have developed a useful methodological toolbox for analyzing visual signal geometry, and many exciting hypotheses to test. Perhaps the most important is a suite of tools for tracking body position and movement of individuals (e.g., standalone programs such as

DeepLabCut (Nath et al. 2019) and TrajR (McLean and Skowron Volponi 2018), MATLAB-based package DLTdv5 (Hedrick 2008)), and/or general image analysis programs such as ImageJ (Schneider, Rasband, and Eliceiri 2012; Schindelin et al. 2012; Hedrick 2008; R. A. Peters 2010). Signalers can then be filmed courting with freely moving receiver(s) and/or with experimenter-controlled model receivers (e.g., (Echeverri, Morehouse, and Zurek 2017; Olea et al. 2010; Patricelli et al. 2002)), and the positioning of all actors can be measured throughout communication. We can also quantify directional changes in signal appearance, by photographing a signal from a range of viewing angles and illumination angles, a technique refined by many studies on iridescent colors (Gruson et al. 2019; Rutowski et al. 2007a; White, Zeil, and Kemp 2015; Stevens et al. 2007; Santos et al. 2007). For some species, presenting each of these incrementally rotated views to receivers in a video-playback experiment allows for measurement of signal effectiveness based on the extent or likelihood of the intended receiver response (Nelson and Fijn 2013). Software packages such as AcuityView (E. Caves and Johnsen 2017; E. M. Caves, Brandley, and Johnsen 2018) can also estimate the effects of acuity and viewing distance on signal appearances. Virtual reality (VR) systems for animals, especially those with closed-loop designs that allows individuals to “move” within a virtual space, have the potential to allow for full control over the visual environment experienced by an individual (Peckmezian and Taylor 2015; Stowers et al. 2017). Taken together, these techniques allow for an effective estimation of how signal appearance changes moment-to-moment with positioning of signaler and receiver in many systems, and how individuals respond. As a result, visual communication as a field is poised to tackle a broad range of questions regarding signaling geometry.

One particularly promising direction for future work is to investigate the psychological and neuro-physiological mechanisms used by signalers and receivers to manage their positions during

communication. Much work has studied how animals navigate to different geographic locations and around physical obstacles (reviewed in Collett and Graham 2004; Berdahl et al. 2018), but we know much less about how individuals handle navigation with respect to a communication partner. Unlike in geographic navigation, the sensory cues and “landmarks” (physical appearance, e.g., the extent to which eyes are visible) associated with signal and sensor orientation are not fixed in space, due to the movement of both signaler and receiver(s). This may preclude simple navigational strategies such as path integration and a static mental map. Instead, communicators may require new strategies or heuristics focused on signaling-relevant cue. What these strategies are, how they vary and evolve, and what their role is in communication efficacy remain exciting open questions.

1.3 Geometry of Sound Communication

Many of the same geometric constraints that are important to visual signaling also shape the efficacy of acoustic signals. Sound also travels as a wave, sound signals are often directional, and are detected by sensors with directional biases. However, unlike the electromagnetic waves of light, sounds are mechanical waves, and can travel through a much greater diversity of materials than light waves. In addition to traveling as a pressure wave in air or water, sound signals may also transmit as vibrational waves, either on a surface (e.g., ripples on the water) or through an object (e.g., a rock or leaf). As a result, sound waves interact in complex ways with the environment, and this complexity affects how signalers and receivers position themselves.

1.3.1 Distance of Sound Communication

Sound waves attenuate in several ways as they travel, reducing signal detectability. As a wave spreads from the point of origin, the amplitude (volume or loudness) of the wave decreases because the initial kinetic energy is spread out over more and more molecules. In addition, at each collision of molecules that propagates the wave, additional energy is lost in the form of heat to entropy. Environmental effects notwithstanding, sound signals continuously degrade through the combined action of these two forms of attenuation, called spreading loss and heat loss respectively, such that sound information becomes harder for receivers to extract as communication distance increases (Bradbury and Vehrencamp 2011; R. Haven Wiley and Richards 1978)). Past a certain distance, the signal is no longer detectable.

In addition to these distance-dependent issues due to attenuation, the distance between sender and receiver of sound signals impacts whether such signals can be perceived as near-field or far-field sounds. The mechanism of sound signal transmission changes across the boundary between these two types of sound (Fig. 4, (Bradbury and Vehrencamp 2011; R. Haven Wiley and Richards 1978)). Very close to the origin of the sound (within the “near field”; within approximately $1/6$ of the wavelength of the sound), receivers can detect the tidal movement of molecules pushed by the sound wave. However, past this boundary (e.g., in the “far field” of the sound), receivers only have access to the pressure changes caused by the sound, which are much harder to detect (Bradbury and Vehrencamp 2011). The sensory structures needed for near- vs. far- field signals are typically distinct, and so consequences of this boundary depends on the sensory capabilities of the receivers. If receivers are only able detect near-field sounds, effective communication distance would be strictly limited. If instead receivers are able to detect both types of sound, signalers could improve signal detection by adjusting their position (or signal wavelength) such that receivers

remain within the near field of the sound. However, to our knowledge, no study has specifically tested for such behaviors, or studied the consequences of the near vs. far field on positioning for sound communication.

As seen in visual communication, one possible consequence of distance-dependent signal quality is selection on signalers to assess receiver distance and compensate for attenuation as needed. If receivers are within line of sight, signalers may assess distance visually. However, in many cases, receivers may be out of sight. If the receiver has themselves made a noise (either their own sound signal or simply through sound cues from movement), signalers may use the various effects of sound attenuation to estimate distance. Signalers are known to use the reverberation (echoes), overall amplitude (volume), and frequency intensity (relative volume of different pitches) of sounds to estimate their relative and/or absolute distance, although their ability to do so may rely in part on prior experience (reviewed in (Naguib and Wiley 2001)).

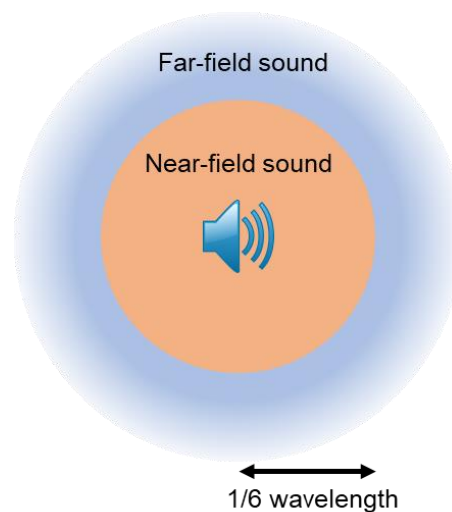


Figure 4. The mechanism of sound transmission changes with distance

Very close to the origin of the sound (within the “near field”; within approximately 1/6 of the wavelength of the sound), receivers can detect the tidal movement of molecules pushed by the sound wave. However, past this (in the “far field” of the sound), receivers only have access to the pressure changes caused by the sound, which are much harder to detect.

It follows that signalers may adjust their sound signal to compensate for the effects of attenuation, thus increasing the range at which the sound signal is effective (active space). However, evidence of distance-dependent modulation in acoustic signals comes primarily in the form of adjustment of overall amplitude. Both zebra finches (Brumm and Slater 2006) and humans (A. H. Marshall and Meyer 1985) produce quieter (lower amplitude) calls when closer to a focal receiver, and louder calls when further away. Other songbirds also have the ability to modulate song amplitude, but whether they, or other species, specifically do so in response to receiver distance is an open avenue for future research. Likewise, it is unknown if signalers compensate for other forms of sound attenuation in a distance-dependent manner. Because higher frequencies attenuate more quickly with distance, signalers might be able to selectively boost the higher frequency components within the signal when communicating with more distant receivers. As with the analogous distance-dependent signal modulation, the extent of this strategy as compensation for attenuation remains to be explored, although some species of frogs and birds are known to change frequency in response to environmental noise (Parris, Velik-lord, and North 2009; Nemeth and Brumm 2009).

Alternatively, attenuation with distance may be a part of an intended signal function. Signalers may use sound signals to provide receivers with relative location information (termed “ranging” in literature (Naguib and Wiley 2001)), especially when out of visual contact. If a signal has evolved to give accurate information, signalers then benefit from explicitly avoiding compensating for distance-dependent attenuation. In theory, signalers may even be under selection to enhance the perception of attenuation so as to facilitate ranging by receivers. Signals that include wide frequency sweeps (“trills”) could allow receivers to better estimate distance via the extent of frequency-specific attenuation. Pygmy marmosets, *Cebuella pygmaea*, for example, produce three

calls which vary in how effectively their trills give distance information. The most informative trill is used when receiver distance is larger, and vice versa (Snowdon and Hodun 1981). A similar function may explain the usage of trills by some forest bird species in their long-range songs, despite that trills tend to be more easily obscured by the structure of the forest environment (Naguib and Wiley 2001).

Signalers may also use distance-dependent signaling strategies to exclude unintended receivers (e.g., eavesdroppers such as predators) from accessing distance information. In Richardson's ground squirrels, individuals were more likely to make ultrasonic frequency alarm calls upon initially sighting a predator if that predator was further away. Such calls will degrade more quickly than the species' lower frequency alarm calls, possibly reducing the chances that a distant predator will hear it while still alerting nearby conspecifics (Wilson and Hare 2006). Switching between qualitatively different signal types, each specialized for short- or long-range communication, may be another way in which signalers respond to changes in receiver distance.

In theory, signalers could even exploit predictable patterns of sound attenuation to produce deceptive distance information by mimicking the effects of degradation themselves (Naguib and Wiley 2001). Howling monkeys (*Alouatta palliata*), for example, produce both a normal grunt call, and a grunt with additional reverberation that may be perceived as deceptively distant (Whitehead 1987). These deceptive signals may allow the signalers to avoid confrontation with other groups of conspecifics. Signalers might also create falsely distant-sounding signals by selectively decreasing the amplitude of high frequency elements within a call, although this has yet to be observed. How common are falsely distant signals, and other possible illusions in sound communication? Is their usage limited by constraints in producing them and/or from limited functional utility? How receivers perceive and possibly distinguish between honest and false

distance information in sound signals may also be an exciting avenue for future neurophysiological research.

1.3.2 Directionality of Sound Signals

Many sound signals are directional, radiating with greater intensity in certain directions than in others. As with visual signals, sound signal directionality can affect how and when signalers produce sounds, effectiveness of different types of signal functions, and how receivers act upon signals. The directionality of a sound signal is largely shaped by the morphology that a signaler uses to create the sound. Sound-producing organs are incredibly diverse, but many are located on one or a few places on a signalers body. Sound waves originating from these organs will more quickly propagate into the transmission medium from certain directions (e.g., out of the mouth of a singing bird), but are blocked and/or dampened by the receiver's body in other directions. In addition, external (e.g., nose cones in several species of bats , an open mouth or beak in mammals and birds) and internal (e.g., dish-like skulls of whales) structures can act as sound emission horns, further concentrating sound energy in certain directions (Bradbury and Vehrencamp 2011). Signalers may control directionality by adjusting the horn shape and body posture.

In general, sound produced by a single internal source, such as vocalizations in many birds and mammals, will produce a sound that is bilaterally symmetrical and loudest in front of the animals' mouth (or other sound emission structure) (Hunter et al. 1986). Sound signal directionality has been measured for a variety of vertebrates (Brumm, Robertson, and Nemeth 2011; Dantzker, Deane, and Bradbury 1999; Holt et al. 2010; Chaverri and Gillam 2013; Frommolt and Gebler 2004; Lammers and Au 2003; Blackwell et al. 2012; H Carl Gerhardt 1975), as well as in crickets (Forrest 1991). These studies indicate extreme variation in the extent of sound

directionality, ranging from weakly directional (e.g., human speech (A. H. Marshall and Meyer 1985)) to highly directional (e.g., a 30 decibel difference from loudest to quietest direction in elephant seal calls (Holt et al. 2010)).

Signalers that produce sound with different internal and/or external structures may produce different patterns of directionality. In ruffed grouse (*Bonasa umbellus*), for example, males signal by drumming on logs. As a consequence of the log's shape, this produces a sound that is bi-directional, with two opposite facing lobes aligned with the long axis of the log (Garcia, Charrier, and Iwaniuk 2012). These birds and other signalers that use separate physical structures to produce sound may be limited in their ability to orient their signals.

As with visual signals, the constraints of directional sounds suggest that signalers would be under selection to accurately aim strongly directional sounds towards intended receivers to improve signal efficacy. Indeed, nightingales and sedge warblers orient towards a single rival when producing a territorial defense call (Brumm and Todt 2003; Brumm, Robertson, and Nemeth 2011). In these experiments, rival birds were simulated by playing back conspecific song on a speaker, indicating that signalers can use sound information to assess receiver position, likely in addition to the visual mechanisms described above.

When the position of the intended receiver is unknown (or a signal must reach multiple receivers), however, signalers may compensate by producing their signal in multiple directions to increase the chances of facing a receiver. Both nightingales and sedge warblers rotate on their perch while calling, much like a rotating siren when receiver position is unclear. Similar patterns of spatial positioning have been observed in northern mockingbirds (Breitwisch and Whitesides 1987), red-winged blackbirds (Brenowitz 1982; Patricelli, Dantzker, and Bradbury 2007), and crickets (Forrest 1991). This suggests that aiming a strongly directional sound at a known receiver,

and rotating while signaling to unknown receiver(s) may be a frequently evolved solution to the constraints of directional sound. In addition, observing a signaler's orientation movements can help to identify intended receivers, and thus be a particularly useful tool for determining signal function(s) (Brumm, Robertson, and Nemeth 2011).

Likewise, the extent of sound directionality can itself be strongly tied to signal function. A sound's directionality determines in large part where the signal can be heard; signalers may exploit this to control what sound information is available to potential receivers. Red-winged blackbirds (*Agelaius phoeniceus*), for example, produce at least five different call types, which co-vary in their directionality and function. Strongly directional calls are used for dyadic interactions where receiver position is known (courtship and copulation solicitation, Fig. 5A), while weakly directional calls are used to communicate with receivers located in potentially many different directions (alarming conspecifics to danger) (Patricelli, Dantzker, and Bradbury 2007). Likewise, the antipredator calls of nine other songbird species are also less directional than their courtship calls (Fig. 5B (Jessica L. Yorzinski and Patricelli 2010)).

In addition, signalers may modulate the directionality of a specific sound in response to the spatial arrangement of receivers. Dark-eyed juncos, and yellow-rumped warblers all increase the directionality of their weakly directional alarm calls such that the sound is louder towards the location of a predator (Jessica L. Yorzinski and Patricelli 2010). This may improve the efficacy of a signaled message to the predator (e.g., that the predator has been detected and the hunt will not be successful), indicating that alarm calls in these species might serve dual functions. Signalers might also weaken the directionality of a strongly directional sound signal if the number of receivers increases. This, however, has yet to be observed. Nevertheless, modulation of

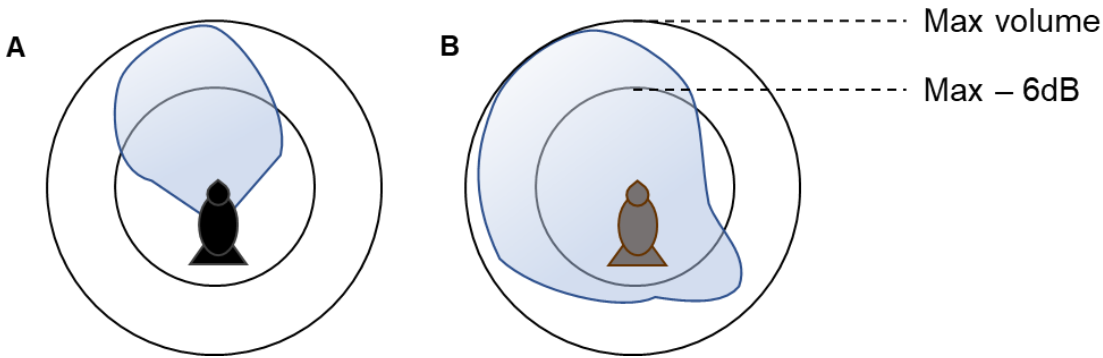


Figure 5. Variation in sound signal directionality can be associated with function

Strongly directional sounds, like the precopulatory song of a red-winged blackbird (A), are often used in dyadic interactions, and may be aimed at the receiver. Weakly directional sounds, like the alarm call of the yellow-rumped warbler (B), can be used to reach multiple receivers or receivers at a greater variety of locations. Distance from the center of the circle with the volume of the call in that direction. Redrawn from (Patricelli, Dantzker, and Bradbury 2007; Yorzinski and Patricelli 2010).

directionality may be an important mechanism—potentially unique to sound signaling—for compromise between signal functions with conflicting spatial constraints.

If receivers have experience with the directionality of a specific sound signal, and some information about the signaler’s location, they may use the properties of the sound they receive as an indication for signaler orientation and possibly intention. For strongly directional sounds, receiving a high amplitude can indicate that a signaler is directing their sound towards—and therefore paying more attention to—the receiver, and vice versa. Male elephant seals (*Mirounga angustirostris*), for example, produce a directional threat call that dominant males use to repel subordinate males from breeding females. However, subordinate males do *not* back away when they hear a call that sounds like the dominant male is facing away, indicating that subordinates use directionality to assess the likelihood of confrontation (Holt et al. 2010). In this manner, sound directionality and signaler orientation may be critical in mediating receiver responses; this hypothesis remains a particularly promising and unexplored direction for future research.

Relative spatial information between sender and receiver can also be encoded in sound signals in the form of Doppler shifts. A moving signaler will produce relatively crowded sound waves in the direction of travel, and relatively spaced out waves in the opposite direction. As a result, a receiver will experience an overall shift in the received frequency of the sound: higher frequency if the signaler is approaching, and lower frequency if the signaler is moving away. In situations where signal function is tied to approaching the receiver (e.g., during courtship, or agonistic interactions), these Doppler shifts may affect signal function and/or provide information on signaler speed. The extent of this Doppler shift is determined by the speed of relative motion and the speed of sound (Bradbury and Vehrencamp 2011). In air, signalers moving at 10m/s (e.g., a fast bat or bird) will only produce a Doppler shift of about ~3% (Bradbury and Vehrencamp 2011), suggesting that the effect of this phenomenon on communication may be negligible. However, flying signalers may produce a significant Doppler shift when producing sound while diving towards a receiver, as seen in the courtship displays of many hummingbirds. Male Costa's hummingbirds have special feathers that produce a tone while diving at females, the pitch of which can change by up to 28% (from 7 to 9 kHz) due to Doppler shift (C. J. Clark and Mistick 2018). Males, however, minimize the frequency shift experienced by females by diving not at the female directly, but at a point displaced to her side. C. J. Clark and Mistick (2018) hypothesize that this change in positioning suggests that males are attempting to control the information available to females, who could otherwise assess dive speed (via the extent of the Doppler shift) as a proxy for males' physical ability.

1.3.3 Directionality of Sound Sensors

Sound reception can also have directional biases, with the extent of this likely determined by, as with sound signals, sensor structure and location on the receiver's body. We note that the term "directional hearing" has, perhaps confusingly, also been used to describe an animal's ability to identify the relative location of a sound (i.e., "hear" its direction) (Bradbury and Vehrencamp 2011). However, in the context of this review, we will use "hearing directionality" to describe how an animal's ability to detect different types of sound information varies with the direction from which that sound reaches the receiver. While the vast majority of previous work has focused on sound locating abilities, a receiver's orientation can also affect sound perception. For sensory organs located on only one or a few parts of the body, approaching sound may be blocked and/or distorted by refraction by the receiver's body (Bradbury and Vehrencamp 2011). In addition, many animals (but especially mammals and some birds) have sound detection horns in the form of external ears (pinna) that amplify incoming sounds for an internal ear where actual detection occurs (Kühne and Lewis 1985; Rosowski 1994). Much like emission horns, detection horns are directional; they capture more sound from certain directions. It follows that how incoming sound from different directions is detected will be affected by sensor shape and orientation. Thus, receivers are likely under selection to orient their sensors towards sound signals. Species with pinna may be under stronger selection to do so as a result of increased directional biases in reception. Pinna are known to move in response to sound, although these movements have been primarily studied in the context of determining the location of a sound ("localization"; e.g., in cats (Populin and Yin 1998)), as opposed to explicitly for improving signal reception. Other animals that lack moveable pinnae may use whole head or body movements for a similar effect (e.g., owls (Knudsen, Blasdel, and Konishi 1979)). Presumably, localization is followed by pinna

reorientation towards the sound to improve reception, but this may not always be the case. As seen with eye movements (see Chapter 1.2.3), the dynamics of sound sensor orientation may also be complex and not optimal for signal reception. How receivers control sound sensor directionality during communication, and how this impacts reception of different types of sound information, remain as crucial gaps in our understanding of sound communication.

1.3.4 Positioning within the Sound Environment

Spatial heterogeneity in sound environments can affect sound wave transmission, and therefore how signalers and receivers might position themselves within the environment. When sound waves encounter objects within their transmission medium, and/or if the medium itself changes in properties that affect the speed of sound (e.g., temperature, pressure, fluid flow), the wave can be reflected, refracted (bent) and/or scattered. The nature and extent of these effects depend on the relative properties of adjacent layers of the transmission medium (or the medium and an object within it), and can be complex (Pijanowski et al. 2011; Farina 2014). While a detailed analysis of each of these effects is outside of the scope of this review (but see Bradbury and Vehrencamp 2011), we highlight one phenomenon, which evidence demonstrates is particularly likely to affect how animals position themselves during communication.

To increase signal transmission, signalers may be under selection to adjust their vertical positioning during communication. Refraction of sound waves within different layers of a medium can affect the distance a signal can travel. Transitions between warm and cold layers of a transmission medium bend sound waves towards the colder layer, as a result of the difference in speed of sound between the two. For example, in an open habitat, sound signals produced near the

ground on a hot day will bend upwards, and thus away from a distant receiver located the same height from the signaler. This temperature gradient refraction creates a space where the sound waves have bent too far upward for a receiver at ground level to hear them clearly, termed a “shadow zone”. The distance at which the shadow zone begins is, however, a function of the height at which the sound was produced (R. H. Wiley and Richards 1982). Thus, terrestrial signalers may be under selection to call from a greater height above the ground such that the shadow zone occurs further than the receiver’s location, either by adjusting their posture and/or position during communication. Although we focus here on terrestrial examples, similar phenomena occur in aquatic systems.

Several bird species (e.g., Eurasian wrens (Mathevon, Aubin, and Dabelsteen 1996), rufous-and-white-wrens (Barker and Mennill 2009)) move into high perches when singing, increasing the range of their song (R. H. Wiley and Richards 1982). These behaviors may have the added effect of avoiding scattering from low vegetation, but may also expose signalers to predators and/or other eavesdroppers (Campos et al. 2009). Likewise, receivers may benefit from improved signal transmission at different heights. King penguins listening for a call from their mate, for example, receive a less degraded (as thus more easily identifiable) sound when standing upright (as opposed to lying down; Lengagne et al. 1999). We also note that signalers may also respond to temperature gradient refraction, not via positioning, but by waiting until environmental conditions change before signaling. For example, at night, air closer to the ground is cooler than air above, and the effects of refraction instead act to improve signal transmission by curving sound waves (that would otherwise pass over the receiver) back down towards the ground (Henwood and Fabrick 1979). By calling at night, male bladder grasshoppers improve the range of their signals from 150 meters (in the day) to over 1.5 kilometers (Van Staaden and Römer 1997). Dawn

choruses, common in a variety of birds, may also have evolved to exploit this phenomenon (Henwood and Fabrick 1979).

Much like temperature gradients, differences in fluid flow can also refract sound (Bradbury and Vehrencamp 2011). Sound signals will travel further when aligned with the direction of fluid flow (as observed in red-winged blackbird calls (Brenowitz 1982)), with this effect being more noticeable for wind than for water currents. Signalers may benefit from monitoring wind direction and orienting in the same direction. However, this strategy could limit transmission to receivers in other directions. Whether signalers choose to “sing with the wind”, and how they manage possible countervailing selection (e.g., noise produced by the wind, increased thermoregulatory costs from exposure (Ward and Slater 2005)) on this behavior remain to be investigated.

Finally, signalers may use physical structures in the environment to increase signal range. Signalers may use sound emission horns to amplify their calls and increase their directionality. These horns may be naturally occurring (e.g., tree-hole frogs and their eponymous use of tree cavities (Lardner and Bin Lakim 2002), or Spix’s disc-winged bat’s use of curled leaves (Chaverri and Gillam 2013)), or constructed (e.g., burrows made by mole crickets (Bennet-clark 1987)). For signalers that use vibratory sounds, signal efficacy may depend on whether signaler and receiver are touching the same object, and how well that object transmits vibrations (D. O. Elias, Mason, and Hebets 2010; M. F. Rosenthal et al. 2019; D. O. Elias, Mason, and Hoy 2004). A signaler’s ability to find or create appropriately shaped environmental features may be critical to effective communication in such systems.

1.3.5 Critical Needs and Opportunities

Previous work in sound communication has created a powerful foundation for investigating the geometric constraints on the modality and their evolutionary consequences. Many studies have explored the physical and environmental factors that determine how sounds degrade as they travel from signaler to receiver, and how signalers may compensate for these effects. Several studies have developed robust techniques for measuring sound signal directionality and observing how signalers orient these sounds (e.g., (Patricelli, Dantzker, and Bradbury 2008; Brumm, Robertson, and Nemeth 2011; Jessica L. Yorzinski and Patricelli 2010)). The general system of a circular array of microphones, speakers, and cameras described in these studies of is broadly adaptable.

Several key questions stand out as important future directions. We know much less about the directionality of sound and sound detection for waves traveling across ground or water surfaces, leaves, or other approximately flat surfaces. How can signalers control sound directionality for these types of signals, if at all? In addition, we know very little about the directionality of sound reception, unlike for visual systems. How does the relative orientation of a receiver's sound sensors and/or pinna affect how effectively they can detect and interpret incoming signals? During communication, how much do receivers track signalers and orient their sound sensors appropriately? How might signalers' behaviors have evolved to influence receiver sensor orientation? Do receivers use environmental structures (e.g., sound detection horns) to improve reception, as they do with sound signal production? We strongly encourage a new push for work on sound sensor directionality. This will facilitate testing of the importance of alignment between the directional biases of signal and sensor, as is beginning to occur for visual communication.

1.4 Geometry of Chemical Communication

The mechanisms and geometric constraints of chemical communication are markedly different from those of other modalities. Unlike visual and sound signals, which travel as waves, chemical communication relies upon the travel of individual molecules whose chemical properties carry the signaled information (i.e., semiochemicals). In practice, the transmission of these semiochemicals (except those delivered by touch) is often driven by interactions with the spatial properties of the signaling environment (Atema 1995; Alberts, Winkler, and Hall 1992; Muller-Schwarze 2006). As with other signaling modalities, the detectability of chemical signals tends to decrease with increasing distance from the origin of the signal. In the absence of fluid flow in the transmission medium, released semiochemicals will spread via simple diffusion. Apart from weak directionality introduced if the signaler's body blocks molecular movement in a direction, the signal will spread evenly as an expanding sphere. As this sphere grows, the concentration of semiochemicals will decrease, reducing the number of molecules that can be detected by a receiver. The rate of diffusion depends on the chemical properties of the signal molecule and of the medium it is diffusing into. At a certain distance from the location of emission—or after enough time has passed—the concentration will decrease below the receiver's threshold for detection.

Receivers can assess this concentration gradient to determine the location of the signal's emission; indeed, this appears to be one of the primary functions of many chemical signals, (e.g., mate attractant pheromones in many insects (Pokorny et al. 2017; Miller, Loudon, and Freed 2007; Andersson et al. 2011; Graham et al. 2012; Williams et al. 2013)). A large volume of research has studied how receivers find and use this directional information (reviewed in (Moore and Crimaldi 2004)). However, there is little evidence that signalers assess receiver distance and adjust the intensity of their chemical signals during communication, as seen in other modalities. This may be

because of this information may only be rarely available to signalers, due to the relatively slow speed of diffusion (compared to visual and sound signals) and the resulting asynchronous nature of long-range chemical communication. A receiver is likely to have moved before a newly emitted, more intense signal will have reached them. Instead, how semiochemicals travel from signaler to receiver is almost always driven by patterns of molecular movement in the environment (“fluid flow;” either natural, or signaler-generated) (Atema 1995; Alberts, Winkler, and Hall 1992). As such, efficacy of chemical communication tends to be influenced by how signaler and receiver position themselves with respect to fluid flow dynamics within the environment more so than in other modalities, and so we will focus on these factors here.

1.4.1 Fluid Flow and the Directionality of Semiochemical Movement

Signalers may be under selection to improve signal efficacy by orienting themselves with respect to natural fluid flows in the environment, and/or generating their own. In most natural conditions, fluid flow will dominate over the effects of simple diffusion (Atema 1995; Alberts, Winkler, and Hall 1992; Muller-Schwarze 2006). Chemical signal molecules will be pushed along by the movement of molecules of the transmission medium, and so the direction of fluid flow will largely define the signals’ directionality and active space.

Signalers can improve transmission by assessing receiver location and positioning themselves such that fluid flow will carry the chemical signal to a nearby receiver (Fig. 6). Tilapia (Li and Buchinger 2014) and swordtail fish (G. G. Rosenthal et al. 2011) both release urinary chemical signals when upstream of a target receiver. Given the preponderance of currents in many aquatic habitats, this may be a more widespread strategy than current work indicates. Terrestrial

organisms may also release semiochemicals from upwind to aim their signal at a known downwind receiver, but this also remains to be investigated.

When receiver position is unknown, signalers may position themselves within the environment to increase the dispersive effects of fluid flow. Many terrestrial insects, for example, produce mate-attractant pheromones to advertise their location (confusingly termed “calling”). Signalers engaging in chemical calling may select elevated locations in order to access faster and/or more consistent fluid flows (Bradbury and Vehrencamp 2011; Moore and Crimaldi 2004). A robust body of work, especially from the field of pest monitoring, has tested and modeled how wind speed and signaling height influence the dispersion rate and range of chemical signals (e.g., (Murlis, Willis, and Cardé 2000; Andersson et al. 2011; Witzgall et al. 2008; Williams et al. 2013; Graham et al. 2012)). However, work on orchid bees suggests that signalers may also be under selection to avoid chemical “noise” from other signalers by partitioning signaling heights (Pokorny et al. 2017). The same study shows that signalers may align themselves with the direction of fluid flow when calling to increase signal transmission. Calling males rest on the downwind side of trees while calling in windy conditions, so as to avoid fluid flows being blocked by the tree itself (Pokorny et al. 2017). Receivers may likewise improve signal detection by resting on the upwind side of objects. While this hypothesis has not been widely tested, evidence from the resting orientation of wood cockroaches on trees (genus *Parcoblatta*) suggests that air flows are not sufficiently blocked by trees to affect behavior (Miller, Loudon, and Freed 2007).

In addition to exploiting naturally occurring fluid flows, signalers may create their own (e. g., by spraying semiochemicals in liquid, or through body movement). In this way, signalers may exert more direct control over when receivers access chemical information. For example,

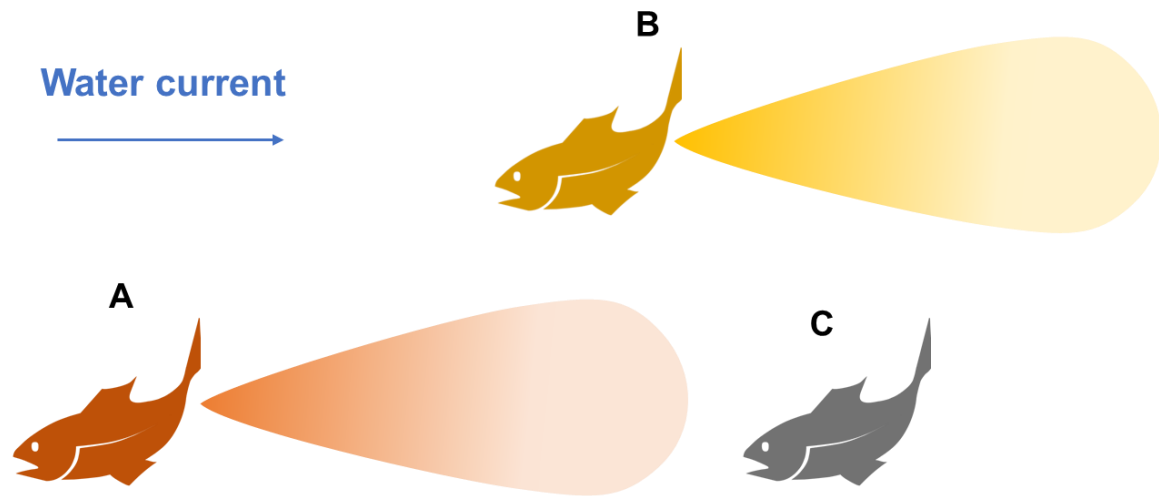


Figure 6. Fluid flows often control the directionality of chemical signals

The relative position of signaler and receiver within a fluid flow may determine the efficacy of a chemical signal. Many marine organisms release semiochemicals with their urine. Signalers that urinate from directly upstream (A) will increase the likelihood that the signal reaches the intended receiver (C). Signalers urinating from other positions (B) may not have their signals reach the receiver.

crayfish use gill movement to generate their own flow currents and use these to direct urine towards the receiver (Bergman, Martin, and Moore 2005). Similar behaviors are seen in lobsters, newts, and bats (Atema 1995). Likewise, terrestrial animals may directly spray urine at a receiver. For example, female mara (a large rodent), spray urine at other females, the scent of which serves to reduce harassment from males (Ottway, Pankhurst, and Waterhouse 2005)). The extent to which this behavior occurs in other terrestrial systems has not been well explored, but it is likely associated with communication interactions where the receiver's position is known (as opposed to the 'broadcast' communication described above).

1.4.2 Critical Needs and Opportunities

We have a growing understanding of how natural fluid flow shapes the positioning of signalers during chemical communication, and several studies provide examples for how to address the challenges of measuring the associated geometry. Fluid flow may be measured with specialized equipment (e.g., a three-dimensional anemometer (Girling, Higbee, and Cardé 2013)), or relatively low-tech approximation (e.g., the novel “feather boa” technique employed by (Miller, Loudon, and Freed 2007)). Researchers with access to air tunnels and flow chambers may use these to test hypotheses by manipulating fluid motion, although these (esp. air movement tests) can also sometimes be approximated with household solutions, such as a portable fan (Miller, Loudon, and Freed 2007). Measuring the actual movement of semiochemicals in real-time remains a more involved process, which may be why many studies prefer to use signaling outcomes as a proxy (e.g., the number of conspecifics attracted by a pheromone trap (Girling, Higbee, and Cardé 2013)) (Muller-Schwarze 2006; Riffell, Abrell, and Hildebrand 2008).

There are several open directions for future research. We know perhaps the least about the directionality of reception for chemical signals. Due to the specific location of chemical sensors on the body (generally the head or on antennae or other limbs), fluid flows carrying semiochemicals may be blocked or slowed from certain directions. Work on fluid dynamics has shown that the shape of the sensor and surrounding morphology will affect how fluid flows in and through the sensor, loosely defining a volume of surrounding space that feeds into the sensory cells (Jaffar-Bandjee, Krijnen, and Casas 2020; Craven, Paterson, and Settles 2010). Many species repeatedly reorient their body and/or antennae to track the direction of a chemical plume back to its source (Atema 1995; Breithaupt and Thiel 2011), indicating that these chemical sensors have some directional biases. Likewise, many species engage in “sniffing” behaviors to increase fluid

flow over and/or through their chemical sensors. However, slower timescales of chemical communication along with its often asynchronous nature likely precludes the complex interactions of signal and sensor orientation as seen in other modalities.

Also interesting are the possible consequences of variation in spatial positioning. How do signalers vary in their efforts to signal from upstream of a receiver, or to create a fluid flow in that direction? And how might this variation affect signaling outcomes? It is possible that diffusion across short distances may relax pressure on signal aiming, especially compared to other modalities. In addition, the asynchronous nature of many chemical signaling interactions would preclude the importance of moment-to-moment alignment of the directional chemical signals and chemical sensors. However, signaling alignment may still influence effectiveness in close-range communication with signaler-generated fluid flows (e.g., signaling via urine spraying), and we encourage future work to explore this possibility.

1.5 Conclusions

In summary, effective communication is often reliant on the interaction between the inherent directional constraints of signal transmission and reception, and the positioning of signaler and receiver on fine spatial and temporal scales. Signal efficacy tends to decrease with increasing distance between signaler and receiver, either as a consequence of shrinking image size, fading and echoing sound, or rarefaction of semiochemicals. Signals themselves propagate further in certain directions than in others, and the physiological design of sensory organs means that receivers ability to detect stimuli also varies with the direction of the incoming stimulus. Environmental conditions may modify the extent of these directional constraints, or impose their

own (e.g., fluid flow). The growing body of work reviewed here show that across three major signaling modalities and a diversity of species, signalers and receivers likely experience selection to manage their positioning during communication.

We find frequent evidence that signalers assess and manage their positioning so as to improve signal effectiveness. Generally, signalers may increase signal intensity to compensate for degradation at increased distance (e.g., (Brumm and Slater 2006; Echeverri, Zurek, and Morehouse 2020; Steinberg and Leal 2013)), aim directional signals towards receivers (e.g., (White, Zeil, and Kemp 2015; Olea et al. 2010; Jessica L. Yorzinski and Patricelli 2010), and/or position themselves with respect to environmental features that increase transmission (Mathevon, Aubin, and Dabelsteen 1996; Dakin and Montgomerie 2009; Olea et al. 2010; Pokorny et al. 2017). Signaler behavior has been shown to co-evolve with signal directionality to improve efficacy, although this work is currently limited to hummingbirds (Simpson and McGraw 2019). In contrast, we know comparatively little about the spatial behavior of receivers, and its consequences for communication. In particular, very few studies have measured how receivers orient their sensory systems. This lack of research is evidence of an unspoken and largely untested assumption that receivers will orient so as to maximize signal reception. So far, this assumption has only been tested for visual signals, but that research shows that, contrary to expectations, where receivers look during visual communication can be dynamic and often suboptimal for signal reception (Jessica L Yorzinski et al. 2013; J. L. Yorzinski et al. 2015; Echeverri, Morehouse, and Zurek 2017). This suggests that receivers' spatial behavior may be under different selective pressures than those of signalers.

Perhaps the most promising direction for future research is investigating the dynamics of signaling alignment, and its consequences for signal efficacy. To increase signal efficacy, signaler

and receiver should position themselves so as to align a signal's effective transmission angles with the regions of the receiver's sensory field appropriate for detecting that type of information (G. G. Rosenthal 2007). Generally, signals must face towards the receiver, *and* the receiver must face their sensory organ towards the signal. Misalignment of either signal *or* sensor may impair signal perception, or completely eliminate it. Selection for effective communication should thus favor behaviors that establish and maintain signaling alignment.

However, we know unfortunately little about the extent to which signaling alignment actually occurs, let alone how signaler and receiver have evolved to control it. Instead, it is a largely unspoken and untested assumption in that signaling alignment occurs throughout communication. Some visual communication studies have measured signal orientation or receiver gaze, but rarely both in conjunction. In one such example, (Echeverri, Morehouse, and Zurek 2017; Chapter 2) found that in the jumping spider *Habronattus pyrrithrix*, signaling alignment between female and a courting male can be infrequent and often disrupted. While males aimed their displays at the female, females looked away from males for, on average, 73% of the interaction. This is in spite of the fact that alignment is crucial for females to see male coloration, which is known to be used for mate choice (L. A. Taylor and McGraw 2013). This suggests that females in this system, and perhaps others, must balance the need to effectively evaluate males with other visual tasks (e.g., predator avoidance). How do signalers maintain alignment in spite of this challenge? What are the dynamics of signaling alignment for other sensory modalities? Much work is needed, especially comparative work in diverse taxa, to assess how frequently signaling alignment is achieved during communication and how signaler and receiver movement determine signal efficacy in tandem.

To facilitate future work on this and other questions about spatial behavior during communication, we provide a series of broadly applicable experimental questions, promising

hypotheses, and examples of best practices. We encourage researchers to consider the following questions to assess what is known about signaling geometry in their system, and use gaps in knowledge as inspiration for new research:

- What are the applicable spatial constraints on signal transmission and reception?
- How do different geometries of signalers, receiver, and/or environmental conditions change how detectable signals are to the receiver? What spatial arrangements are most likely to lead to effective communication of the signaled information?
- How often are these geometries achieved during communication?
- How do signaler and receiver behaviors contribute to or detract from effective positioning?
- What are the signaling and associated selective consequences of ineffective geometries?
- How does positioning behavior, signal directionality, and/or sensor directionality evolve or co-evolve? How does do these spatial constraints vary between close relatives?
- How do signalers and receivers handle sub-optimal signaling geometries? How do signalers and receiver position themselves when, for example, environmental conditions for effective transmission are at odds with directing the signal towards the receiver, or when communicating with multiple receivers?
- What neurological processing is required for signaler and receiver each to manage geometries? What information must they process and when?

- How do signalers vary in their ability to manage geometric constraints during communication? What traits (e.g., body condition, age, cognitive ability) affect signalers' abilities to do so?

To interpret resulting observations, we adapt and expand upon several hypotheses regarding how animals may position themselves during communication:

- **Signaler-driven optimization:** This predicts that signalers will position themselves and their signals in with respect to the receiver and the environment to optimize signal transmission and reception. Signaler behavior will thus increase alignment between directional biases in transmission and reception and/or compensate for distance-dependent effects. This hypothesis is an extension of selection for signal efficacy as predicated by sensory drive (J. A. Endler 1992; 1993a; G. G. Rosenthal 2007), and is well supported for all three signaling modalities.
- **Receiver-driven optimization (proposed by (Hutton et al. 2015):** This hypothesis predicts that receivers will position themselves to maximize stimulation received from signals. As such, receiver behaviors will increase signaling alignment (e.g., turning their pinna towards a calling signaler).
- **Receiver-imposed handicap (proposed by (Hutton et al. 2015):** This predicts that receivers will position themselves in a manner that is suboptimal for signal transmission. As such, receiver behaviors will decrease signaling alignment (e.g., looking away from a visual signal, moving behind a physical obstruction or onto a different sound transmission medium). Receivers may do so to evaluate signalers' ability to assess and adapt to spatial signaling challenges (i.e., their spatio-social skill (Sih, Chang, and Wey 2014; Echeverri,

Morehouse, and Zurek 2017; Sih, Sinn, and Patricelli 2019)), and/or if a cumulative assessment of a signal is informative (e.g., if signal directionality is tied to signaler quality).

- Limited attention (adapted from (Reuven Dukas 2004; R Dukas 2002)): This hypothesis predicts that how receivers position themselves reflects a dynamic trade-off between optimal geometries for signal evaluation, and those necessary for other ecological tasks (e.g., predator avoidance). The extent to which receiver behavior increases or decreases signaling alignment will be driven by the urgency of the task (e.g., receivers spend more time looking towards a signaler when predator cues are absent).

As best practices for measuring spatial constraints and positioning depend in part on signaling modality, we direct researchers to exemplary studies within each modality (Table 1). A combination of extensive monitoring equipment (e.g., multi-angle camera arrays) and computationally-intensive manipulations (e.g., virtual reality paradigms) will likely become commonplace for this research. However, such studies should continue to be based on and compared to observations of free-moving animals in natural settings, as this is the gold standard for this research. In addition, we emphasize that researchers can still measure signaling geometry and test hypotheses with widely accessible equipment, especially for visual and sound communication. Even a single basic sensor (camera or microphone) can be provide for a coarse but effective measurement of signal directionality. Filming signaling interactions, even if just with a single top-down or side view can be sufficient to the extent of signaling alignment, especially when combined with basic information about sensor directionality potentially available in physiology research (e.g., field of view). Body, head, and/or eye orientation of signaler and receiver can be analyzed from video footage using free programs such as ImageJ, and the relative orientation of both actors can be used to calculate the extent to which they face each other (for

example, see Echeverri, Morehouse, and Zurek 2017)). We strongly encourage researchers to use the tools available to incorporate a geometric framework into future studies on signal efficacy, even if only some parameters can be measured.

Finally, we call attention to the potential role of multimodal signaling in affecting positioning and signaling geometry. While we have thus far considered the geometric constraints of each modality in isolation, many animal signals involve two or more modalities (e.g., a visual display paired with a song, as in many birds and jumping spiders). As discussed in this review, each modality differs, often greatly, in its inherent spatial constraints on transmission and reception. As a result, the selection on positioning for multimodal signals may be complex, and we call for signaling geometry to be included in the ongoing research on the function and evolution of multimodal signals (Hebets and Papaj 2005; Partan 2013). In communication interactions where multimodal signal components are both informative, for example, signalers and receivers may experience particularly strong selection on behaviors that achieve effective signaling geometries for both modalities. Given that certain modalities may be more directional than others, it is also possible that one modality of the signal may function to manage signaling alignment for effective communication in another modality. A weakly directional sound signal, for example, may serve to indicate the location of the signaler, cueing the receiver to reorient their field of view towards a visual signal that is produced in synchrony or shortly after the sound. This “guiding” of signaling alignment may be a widespread function of multimodal signals that contain one or more strongly directional components, and we encourage a thorough investigation of this hypothesis.

Table 1. The elements of signal geometry, their causes, consequences, and key examples

Element of Signaling Geometry	Common Causes		Consequence(s) for Signal Efficacy		Measurement Methodology		Key Examples
Communication distance: The linear distance between signaler and receiver. Alternatively termed "receiver distance", "viewing distance"	Visual	Signaler and receiver are spatially separated	Visual	Image size decreases with distance, Image blurs outside of focusing range	Visual	AcuityView software package (requires acuity information)	(E. Caves and Johnsen 2017; E. M. Caves, Brandley, and Johnsen 2018; How et al. 2008; Steinberg and Leal 2013)
	Sound		Sound	Sounds attenuate with distance	Sound	Microphone(s) (or vibration sensor) at range of distances from signaler	(Brumm and Slater 2006)
	Chemical		Chemical	Semiochemicals diffuse over time	Chemical	Compare semiochemical concentration from samples at different distances over time. Can also estimate based on response rate of receivers located at different distances	Remains to be well studied
Signal directionality: The extent to which signal properties (e.g., color, visibility, volume, semiochemical concentration) vary when observed from different directions	Visual	Signaler's body blocks viewing, appearance changes with viewing angle (e.g., iridescence)	Visual	Signal only visible from certain angles, color changes with angle (iridescence)	Visual	Sequential imaging of signal from different angles	(Santos et al. 2007; White, Zeil, and Kemp 2015; Gruson et al. 2019; Meadows et al. 2011; Skigin et al. 2019)
	Sound	Physical objects direct and/or dampen sound, emission horns focus sounds in a direction	Sound	Volume varies with direction, directional loss of certain signal elements (e.g., high frequency sounds, harmonics)	Sound	Microphone(s) (or vibration sensor) at range of angles	(Brumm, Robertson, and Nemeth 2011; Patricelli, Dantzker, and Bradbury 2008; Garcia, Charrier, and Iwaniuk 2012; Patricelli, Dantzker, and Bradbury 2007)
	Chemical	Fluid flows directs spread of semiochemicals	Chemical	Travel and concentration of semiochemicals	Chemical	Can be estimated from releasing visible chemicals in same fluid flow	See fluid flow, below

				follows direction of fluid flow			
Sensor directionality: The extent to which sensor capabilities (e.g., sensitivity) and/or neurological processing changes with stimulus direction	Visual	Location and field of view of eyes, spatial heterogeneity of retina, neural lateralization	Visual	Sensitivity depends with direction that the sensor is facing	Visual	Retina mapping and/or behaviorally from responses to stimuli at different angles	(M. F. Land 1999; Temple 2011; Templeton et al. 2012)
	Sound	Location of sensors, reception horns (pinna) pick up sounds better from certain directions	Sound		Sound	Remains to be well studied in the context of communication, but see work on sound localization	(Populin and Yin 1998; Knudsen, Blasdel, and Konishi 1979)
	Chemical	Location of sensor on body, shape of sensor and surround morphology	Chemical		Chemical	Modeling and measurement of fluid flow dynamics in and around sensor	(Jaffar-Bandjee, Krijnen, and Casas 2020; Craven, Paterson, and Settles 2010)
Signaling alignment: The extent to which the direction of best signal transmission aligns with the direction of best signal reception	Visual	Extent to which signal faces receiver and receiver looks at signal	Visual	Limits what types of visual information available to receiver, and eye's sensitivity	Visual	Angle between maximal signal transmission and appropriate field of view (e.g., fovea)	(Echeverri, Morehouse, and Zurek 2017; Simpson and McGraw 2018a)
	Sound	Extent to which sound is aimed at receiver and receiver orients sensors toward sound	Sound	May affect signal detectability; remains to be well studied	Sound	Angle between maximal sound transmission and maximal reception for given frequency	Remains to be well studied
	Chemical	Extent to which semiochemical diffusion is aimed at receiver, and receiver orient sensor towards semiochemical flow, remains to be well studied	Chemical	May affect signal detectability; remains to be well studied	Chemical	Angle between movement vector of semiochemical diffusion and intake for chemical sensors	Remains to be well studied
Physical objects in the environment	Visual	n/a	Visual	Blocks visibility from certain directions	Visual	Image signal from perspective of receiver	(Kelley and Endler 2012)

	Sound		Sound	Reflects and/or refracts sound, net effect on transmission varies	Sound	Measure sound transmission in different physical environments	(Mathevon, Aubin, and Dabelsteen 1996; Barker and Mennill 2009; R. Haven Wiley and Richards 1978)
	Chemical		Chemical	May redirect fluid flow, or allow access to areas of different flow	Chemical	Measure fluid flow in different physical environments	(Pokorny et al. 2017; Girling, Higbee, and Cardé 2013; Moore and Crimaldi 2004)
Fluid flow: Directional movement of the transmission medium	Visual	n/a	Visual	n/a	Visual	n/a	n/a
	Sound		Sound	Increases wave transmission in direction of flow, decreases in opposite direction	Sound	Flow measurement tools	(Brenowitz 1982)
	Chemical		Chemical	Carries semiochemicals in direction of fluid flow	Chemical	Flow measurement tools	(Girling, Higbee, and Cardé 2013; Miller, Loudon, and Freed 2007)

2.0 Control of Signaling Alignment During the Dynamic Courtship Display of a Jumping Spider

The contents of this chapter are adapted from a published article of the same name. © 2017 Echeverri et al. Originally published in the journal *Behavioral Ecology*. <https://doi.org/10.1093/beheco/axx107>

2.1 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; Hutton et al. 2015; Leo J. Fleishman 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 two aspects of visual signaling (hereafter “signaling alignment”) is likely to often be important for communication efficacy. Spatial arrangements that align key signal 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, Zeil, and Kemp 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, *Hypolimnna 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 (R 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 (Fig. 7a,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 (Fig. 7a). 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 (Fig. 7b). 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 (Fig. 7c). 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* are also forward-facing. Like all jumping spiders, *H. pyrrithrix* has two principal eyes and six lateral eyes. Only the two 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 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; M F Land 1985; Zurek and Nelson 2012b).

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 (D. 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 (D. O.

Elias, Mason, and Hoy 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 (R. 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 two 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.

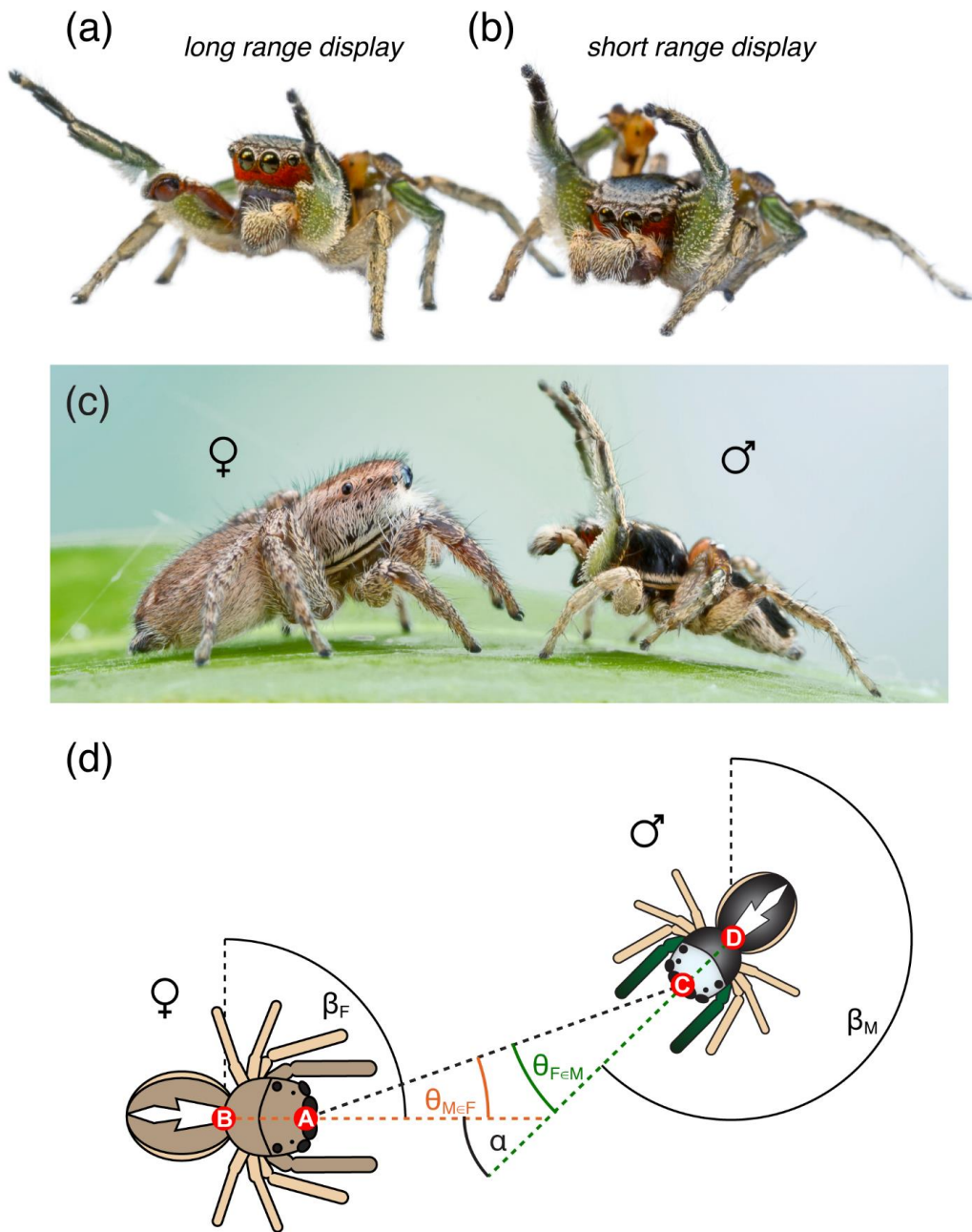


Figure 7. *Habronattus pyrrithrix* courtship

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 ($\theta_{M \in F}$), female azimuth in male field of view ($\theta_{F \in M}$), alignment angle between male and female body axes (α).

2.2 Methods

2.2.1 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 two 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 (7cm diameter, 6cm tall) in a climate-controlled chamber that maintained a constant temperature (24°C), constant humidity (55% RH), and a 16:8h 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 *Grylloides 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.

2.2.2 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 (D. Elias, 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 (1920x1080 pixels, 24 frames/second) in 2014, and with a Panasonic Lumix DMC-GH4 (3840x2160 pixels, 30 frames/second) in 2015. Supplemental lighting was provided by two 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.

2.2.3 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 (D. O. Elias, Andrade, and Kasumovic 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 minutes, 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 minutes, until males attempted to copulate, or until aggression by the female occurred, whichever occurred first. In our experience, this 10-minute 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 two groups (field-matured versus lab-matured, see Results), and thus pooled all trials with live pairs in subsequent analyses.

2.2.4 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 hours 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 two 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 three 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 ten minutes 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 five seconds 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 minutes 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.

2.2.5 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 60s 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 Fig. 7d) and the point between the principal eye lenses (A, C in Fig. 7d) 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 Fig. 7d), 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 re-orientation toward the male display.

2.2.6 Statistical Methods

All statistical tests were carried out using R version 3.2.2 (R Core Team 2015). 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 (Jammalamadaka and Sengupta 2001; Russell and Levitin 1995; Rao 1976). 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 two or more samples of circular data. This test performs better than circular ANOVA when sample sizes are small (Tasdan et al. 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.

2.3 Results

Analysis and experimental manipulation of the geometry of *H. pyrithrix* 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).

2.3.1 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

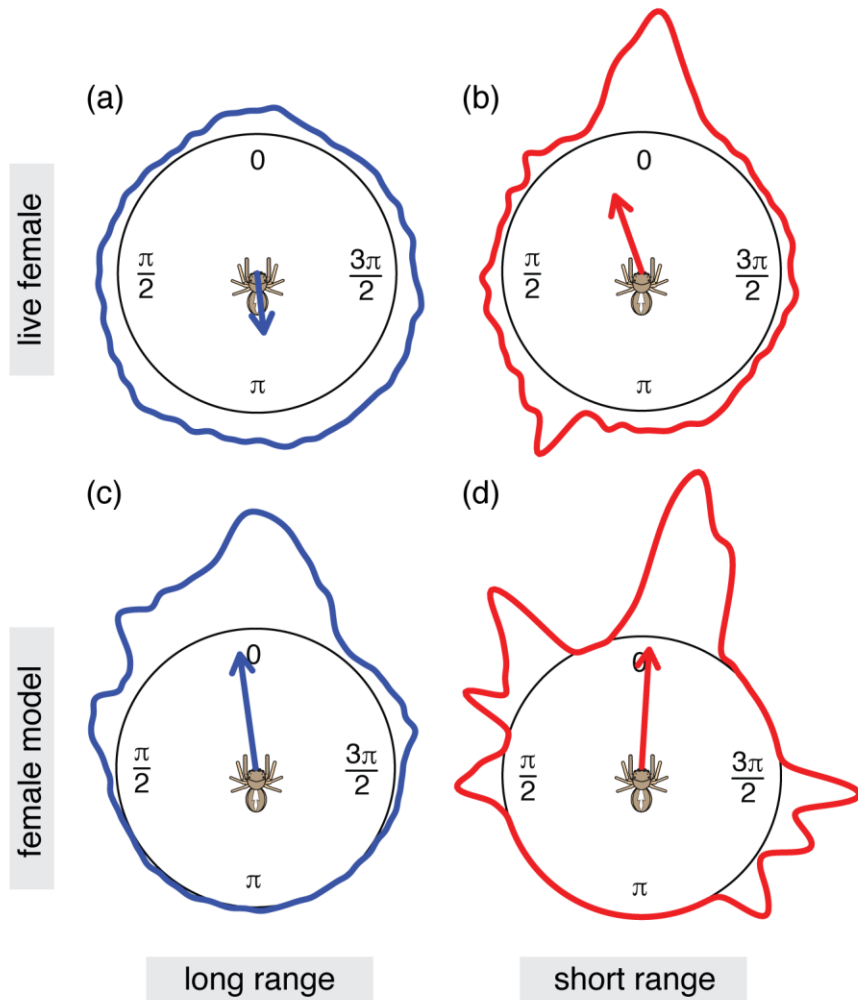


Figure 8. Signaling alignment during courtship

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_α), and thereby serves as a measure for the consistency of alignment. Colored lines outside of circular axes represent mean density distribution of observations.

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 (Fig. 8a).

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 8b; 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 (Fig. 9a). Subsequent cross-correlation analysis revealed that initiation of knee raise bouts was most likely to occur 200ms after the female

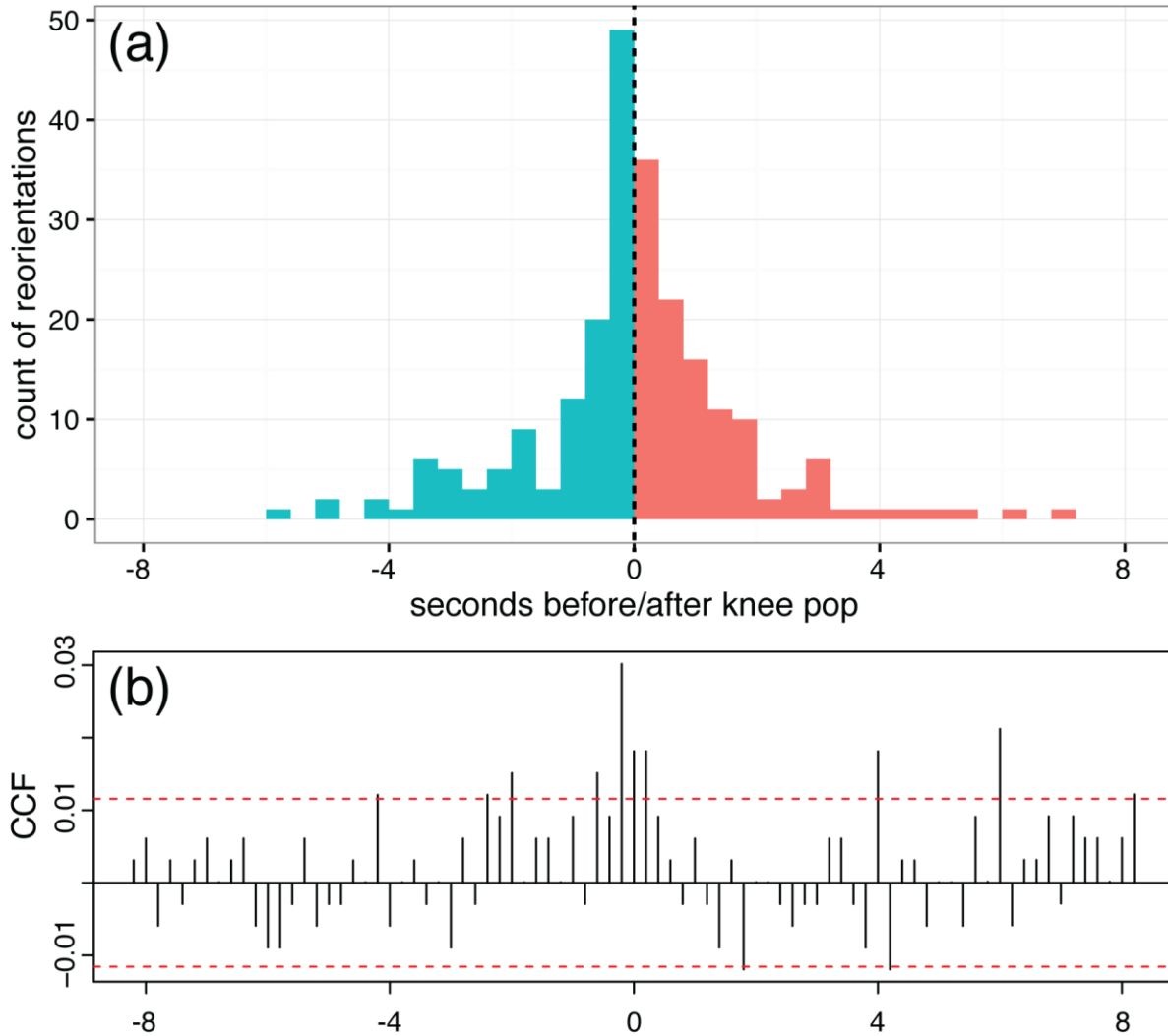


Figure 9. Timing of 'knee-pop' displays

(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 $-0.2s$, meaning that males are most likely to raise their knees $0.2s$ after a female reorients to face him.

turned towards the male (at a 200ms lag, Fig. 9b, dominant cross-correlation = 0.03, mean \pm 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 $\rho_{\beta F}$ (field 0.52 ± 0.23 , lab 0.41 ± 0.21 , Welch's t-test, $t_{14.2} = 1.06$, $p = 0.308$).

2.3.2 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 8c). 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 two conditions (Fig. 8b, 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

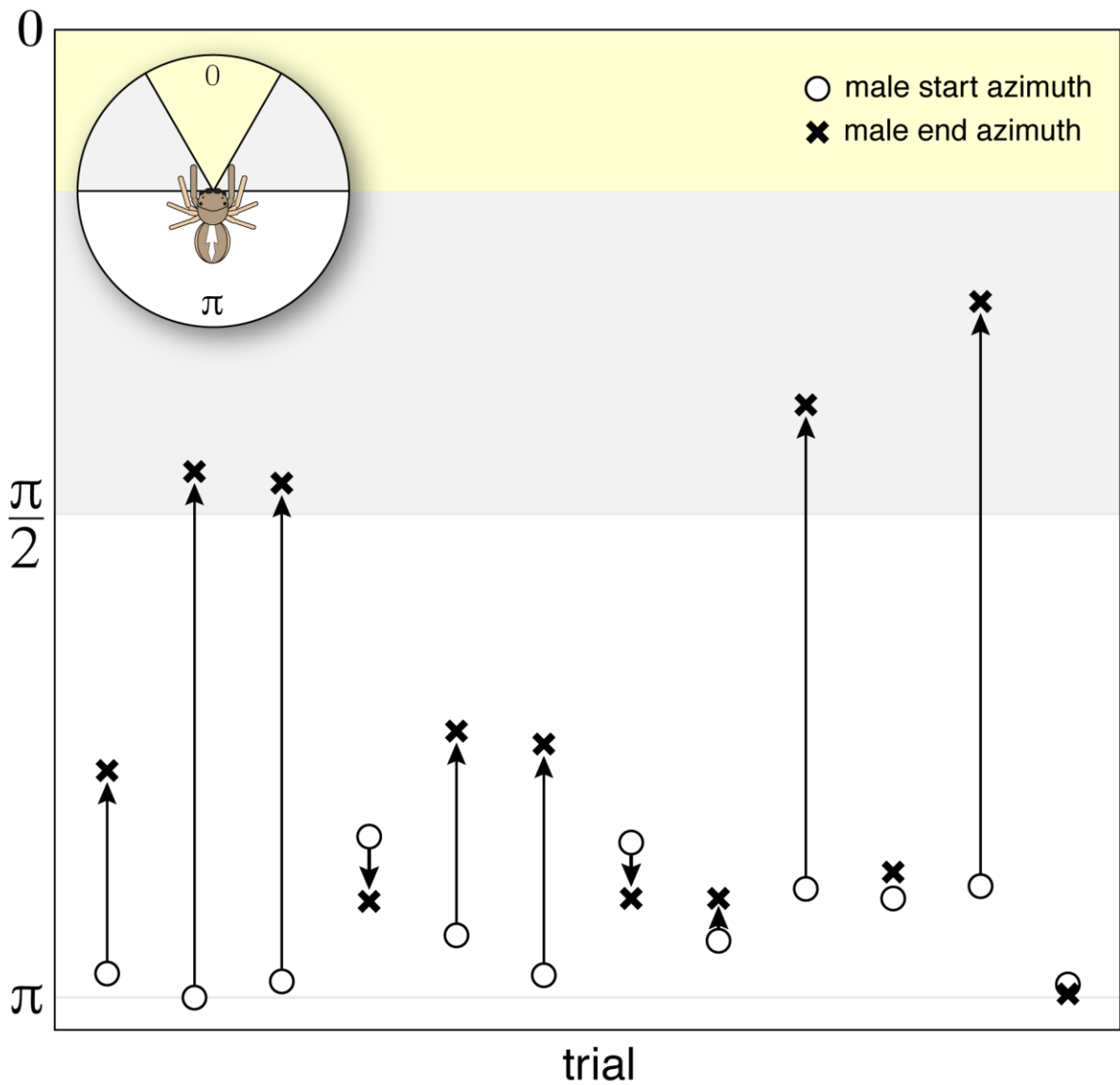


Figure 10. Male responses to female looking away

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.

towards the front of the model (Fig. 10, 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, Fig. 10), and no males reached the field of view of the model's principal eyes.

2.4 Discussion

2.4.1 Control of Signaling Alignment

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. pyrrithrix* 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).

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.

2.4.2 Implications for Communication

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. pyrrithrix*, 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 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 (R Dukas 2002; Reuven 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. pyrrithrix* 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 (J. 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.

2.4.3 Selection for Control of Receiver Attention

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 (J. A. Endler 1992; R Dukas 2002; G. G. 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 1981b; Guilford and Dawkins 1991; Leo J. Fleishman 1988). The forelimb waving characteristic of long-range display in *Habronattus* and other jumping spiders (Herberstein 2012; D. O. Elias et al. 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. pyrrithrix*, 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 (L. A. Taylor, Powell, and McGraw 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 (M F Land 1969b). *H. pyrrithrix* 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-born 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 (D. 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.

2.4.4 Signaling Behavior in Response to Spatio-social Cues

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. pyrrithrix* 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 (R. R. 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. pyrrithrix* (12 of 36 trials involving 48hrs 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. pyrrithrix*. 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 signaling 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, Coleman, and Borgia 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.

2.4.5 Conclusions

In summary, directional biases in both vision and visual signaling predict that effective communication requires behavioral alignment of these two 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. pyrrithrix*, 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, Dantzker, and Bradbury 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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3.0 Jumping Spider Adjusts Attention-Grabbing Display to Spatial and Environmental Context

3.1 Introduction

A major challenge for visual signalers, especially those in complex environments, is to attract and retain the attention of intended receivers (Reuven Dukas 2004; R Dukas 2002; Számadó and Penn 2015; J. A. Endler 1992; G. G. Rosenthal 2007; Számadó 2015). This is because animals face physiological and cognitive limitations on their ability to attend to multiple visual stimuli (Reuven Dukas 2004), and natural environments are cluttered with an excess of potentially important visual stimuli (e.g., cues associated with predators, prey, and ecological needs). Because processing visual information is computationally demanding, handling multiple visual tasks concurrently decreases performance in each (Broadbent and Gregory 1965; Milinski 1990; Reuven Dukas 1998; Kastner and Ungerleider 2000; R Dukas 2002). As a result, animals often reduce this cognitive load by preferentially attending to only select few stimuli (R Dukas 2002; Reuven Dukas 2004), while filtering out the vast majority of detectable visual information (e.g., 99.98% in primates (Van Essen et al. 1991; Van Essen, Anderson, and Felleman 1992)). Thus, even if a signal is detectable, a receiver may not devote the cognitive resources required to process the signal (R Dukas 2002; J. A. Endler et al. 1998; Guilford and Dawkins 1991). Consequently, we expect that signalers may be under strong selection to “outcompete” distracting stimuli.

One potential solution to this challenge that has evolved repeatedly is for signalers to precede their complex visual displays with a particularly salient signal that captures the receiver’s attention (Richards 1981b; R Dukas 2002; Számadó 2015; Bradbury and Vehrencamp 2011; G. G.

Rosenthal 2007; Swan and Hare 2008). Such “alerting” displays are predicted to be structurally simple (e.g., a brief, rapid movement), and taxonomically widespread (R Dukas 2002; Bradbury and Vehrencamp 2011; Számadó 2015). Introductory elements of otherwise longer and more complex visual displays have been suggested to function as alerts in many species (Számadó 2015; Hebets and Papaj 2005; G. G. Rosenthal 2007; Rivers and Morin 2008). We note that signals that function to warn of a nearby predator are sometimes also termed ‘alert signals,’ but here we focus solely on signals that function primarily to capture receiver attention (i.e., attention-seeking displays, *sensu* (Számadó 2015)). Even if alerts only inform a receiver about an upcoming complex signal (e.g., do not inform about the signalers’ condition), theoretical modeling indicates that these signals are still evolutionarily stable (Számadó 2015).

The effectiveness of an alerting display may depend not only on the properties of the display itself, but also the nature of other stimuli in the environment that compete for the receiver’s attention. Background stimuli can reduce the likelihood of signal detection. For visual signals in terrestrial environments, wind-blown vegetation is the primary source of distracting motion “noise” (Bradbury and Vehrencamp 2011; Cronin et al. 2014; R. Peters, Hemmi, and Zeil 2008; Richard A Peters 2013). Thus, alerting displays must contrast with such background motion in order to be readily detectable (Leo J. Fleishman 1992; R. Peters, Hemmi, and Zeil 2008; Ord and Stamps 2008). To increase salience, alert signals may evolve to exploit particular pre-existing sensory biases in the receiver’s visual system (Michael F Land and Nilsson 2012; Bradbury and Vehrencamp 2011; J. A. Endler 1992; Guilford and Dawkins 1991; R Dukas 2002), and/or to be qualitatively different from environmental motion (G. G. Rosenthal 2007; R. Peters, Hemmi, and Zeil 2008; Richard A Peters 2013).

Signalers must compete not only with static properties of their environments, but also dynamic changes to environmental conditions, such as rapid increases or decreases in wind-blown vegetation. Thus signalers may often experience selection for behavioral plasticity such that they are able to adjust their alert display in response to the current visual environment (Richard A. Peters, Hemmi, and Zeil 2007; McNett, Luan, and Cocroft 2010; R. Peters, Hemmi, and Zeil 2008; McGregor et al. 2013; Ord and Stamps 2008; R Dukas 2002; Ord et al. 2016). However, assessing environmental conditions may itself be a demanding cognitive task for signalers, especially while simultaneously performing a complex display. In addition, changing the properties (e.g., speed, and direction of motion) of a signal may reduce how effectively they address receiver preferences. Thus, background motion may result in selection that conflicts with receiver-based selective pressures.

Despite the predicted importance and ubiquity of alerting displays, previous research on alerting signals is limited in number and phylogenetic scope. To date, visual alerting displays have only been explicitly studied in vertebrate systems (*Anolis* lizards (Ord and Stamps 2008), *Amphibolurus* lizards (Richard A. Peters, Hemmi, and Zeil 2007), but see also (Swan and Hare 2008; Richards 1981a) for acoustic communication examples in mammalian and avian systems). Even within this limited body of work, however, we see a diversity of responses to adverse environmental conditions. *Amphibolurus* lizards change signal duration and structure (Richard A. Peters, Hemmi, and Zeil 2007) in response to changing environmental conditions, while some *Anolis* lizards increase display speed (Ord, Stamps, and Losos 2010; Ord et al. 2016; 2007) and/or timing (Ord, Charles, and Hofer 2010). These differences suggest that selection on alert displays may result in the evolution of a diversity of solutions, even within one phylogenetic group. Outside of lizards, we know little about the role of attention and attention-seeking signals. This is

particularly true in arthropod communication, despite many species being known for their complex visual displays (e.g., jumping spiders and wolf spiders (D. O. Elias et al. 2012; Girard, Kasumovic, and Elias 2011; Uetz et al. 2011), butterflies (White, Zeil, and Kemp 2015), marine ostracods (Rivers and Morin 2008)). Due to their small eyes and brains (compared to those of many vertebrates), many arthropods likely face stricter limits on how much visual information they can attend to at any given time.

Here, we investigate variation in alert signals in the courtship display of the jumping spider *Habronattus pyrrithrix* (Chamberlin 1924; Aranea: Salticidae), the challenges posed by variation in environmental conditions during these displays, and how males address these challenges while displaying. *H. pyrrithrix* is a small, sexually dimorphic jumping spider found in riparian habitats, agricultural settings, and grassy urban areas ranging from southern California and Arizona to Sinaloa, Mexico (Griswold 1987). Because of their complex courtship displays (D. O. Elias et al. 2012) and unique visual system (Zurek et al. 2015), this species provides an excellent opportunity to study how signalers use alerts to capture receiver attention.

Female visual attention is important to male courtship communication in *H. pyrrithrix*. Males are colorful and ornamented, and perform an elaborate courtship dance consisting of stereotyped sequences of movements (D. O. Elias et al. 2012; Maddison and Hedin 2003). Females are choosy, selecting males at least in part based on their coloration (Blackburn and Maddison 2014; Masta and Maddison 2011; L. A. Taylor and McGraw 2013). However, whether or not females are able to see male colors is limited by where females direct their attention. Only two of a jumping spider's eight eyes, the forward-facing principal eyes, provide the animal with color vision and high spatial resolution (Harland, Li, and Jackson 2011; Zurek et al. 2015; M F Land 1969a; Blest et al. 1981; Blest 1985). The gaze of principal eyes can be moved to look around the

world via muscular movements of the underlying retina, but only within an approximately 60-degree cone in front of the spider (M F Land 1985). In contrast, the four lateral eyes function as lower-resolution monochromatic motion detectors with a combined field of view of nearly 360 degrees (M F Land 1985; Duelli 1978; Zurek et al. 2010). Thus, while a female may be able to detect a courting male from almost any direction, she can only see his colors if she turns to face him. Females, however, frequently turn away from actively courting males (Echeverri, Morehouse, and Zurek 2017). Thus, males are likely under selection not only to attract female visual attention, but also to retain it.

Habronattus pyrrithrix courtship consists of two distinct stages, the first of which may serve to capture attention in advance of the second. Courtship begins with a relatively simple, long-range display, followed by a more complex, close-range display (D. O. Elias et al. 2012). As males approach a female, they perform the long-range display, raising and lowering (“waving”) their first leg pair while walking from side to side and exposing their red clypeus (Fig. 11A, B). If males successfully transition from the long-range to the close-range display, males then rapidly twitch the tarsi (final segments) of their raised first legs while repeatedly raising their third legs to expose and hide conspicuous orange ornaments on the distal femur of these legs (D. O. Elias et al. 2012). We hypothesize that the conspicuous arm waves that males perform during long-range courtship function as alerting signals, thereby capturing female visual attention prior to initiation of the short-range courtship display. Jumping spiders are known to turn towards movement seen by their lateral eyes (Echeverri, Morehouse, and Zurek 2017), so male waving displays may have evolved to target this sensitivity in prospective female mates.

Several factors may influence the effectiveness of male alerts. First, the ecology of *H. pyrrithrix* suggests that males may experience a visual environment that reduces signal salience.

Males actively search for females, and initiate courtship whenever they encounter a female (L. A. Taylor, Powell, and McGraw 2017; Blackburn, Maddison, and Blackburn 2015). As a result, males have relatively little control of over the visual environment during courtship (unlike in species that prepare a specific location for displaying, e.g. manakins (Uy and Endler 2004)). Second, because the species is often found in or near vegetation, the visual noise of wind-blown motion may be a frequent signaling challenge. Finally, preliminary data showed intraspecific variation in waving displays (SAE, unpublished data), but the causes and consequences of this variation are unknown.

In this study, we investigated the role of the male *H. pyrrithrix* arm waving display as an alert signal, and how this function might be affected by signaling conditions. First, we used to video playback to ask whether or not arm waves captured female attention. We then tested how signal variation and visual environment complexity affected this alerting function. Finally, we observed male courtship under different environmental conditions to ask if and how males adjusted their alerting display in response to the visual environment.

3.2 Methods

3.2.1 Collection and Maintenance

We collected sub-adult individuals from a high-density population in Queen Creek, Arizona (33°13'16" N, 111°35'50" W) in May 2016. Following field capture, spiders individually were reared to maturity in opaque cylindrical plastic containers (7cm diameter, 6cm tall) in a chamber at constant temperature (21°C) and a 12:12h light:dark cycle. We fed each spider twice per week with cricket nymphs (1st-3rd instar *Grylloides sigillatus*) in quantities approximately

equal to twice the spider's mass. Video playback experiments were conducted between August and November 2016, and courtship trials between September and December 2016.

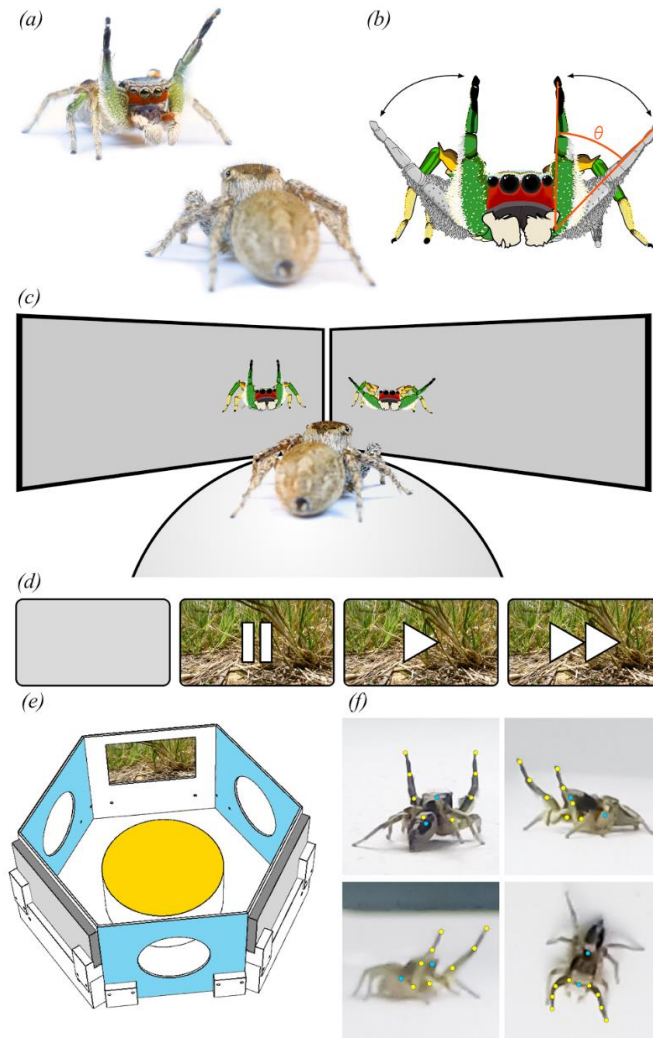


Figure 11. *Habronattus pyrrithrix* courtship and experimental design

(a) *Habronattus pyrrithrix* males initiate courtship with a waving display of the first leg pair. (b) Animated stimuli were designed with range of amplitudes (Θ) and angular velocities ($^{\circ}/s$) designed to span the range of natural variation. (c) Females viewed competing waving and non-waving stimuli, and their attempts to orient towards either were recorded as movement of the “treadball” held by their feet. (d) Stimuli were presented against four backgrounds: 50% grey, a habitat photo, a habitat video, and a habitat video played at 1.5x speed. (e) In a separate experiment, males courted females on a circular stage while experiencing one of the same four background conditions (Grey, Habitat Still, Habitat Video, Fast Habitat Video at 1.5x speed) displayed on three surrounding video screens. Four cameras positioned overhead (1) or in front of openings in the arena walls (3) recorded the scene at 30 frames per second. (f) Tracking of 14 morphological landmarks allowed for 3D reconstruction and quantification of male waving displays.

3.2.2 Video Playback Experiments

To assess how waving displays capture female attention, we filmed the reaction of females to competing animations of waving and non-waving males. Females viewed video stimuli in a custom-built “theater” consisting of two computer monitors arranged in an L-shape (2560x1440 pixel resolution, 120hz; Acer XB270HU; Fig 11c). During the experiment, females viewed the monitors from a location of 43cm along the angular bisector (i.e., 45° from each monitor) and centered vertically with respect to the monitors’ height. To maintain a consistent viewing position and orientation, females were suspended from a metal rod that connected to a neodymium disc magnet (1mm diameter, 0.5mm thickness, .07lb pull force; SuperMagnetMan N50 D1005) glued to the top of their cephalothorax with UV-activated glue (Bondic, Laser Bonding Tech, Inc.). Magnets allowed us to easily remove and replace females between experiments. The metal rod was held by a micromanipulator, which was used to fine tune the position and orientation of the spider such that the female’s body axis aligned with the angular bisector of the two monitors. We rested the micromanipulator base atop a foam cushion to dampen stray vibrations. While suspended, females held a lightweight grey foam ball (diameter approximately 1cm) that was marked with spots of white paint to facilitate tracking of movement. We positioned a piece of cardstock 3cm behind the female to prevent her from seeing the rest of the room or the experimenter with her posterior eyes. This cardstock was covered in matte black paper on the side facing the spider. We filmed all experiments with a GoPro Hero 4 Black (1280x720p, 60fps) through a small notch cut into the bottom of the cardstock behind the female. All trials took place in an isolated, windowless room lit by four incandescent 60W bulbs to ensure a consistent visual environment.

3.2.3 Stimulus Design

Video stimuli were created by superimposing animations of male courtship displays on manipulated backgrounds. Animations, created using Adobe Animate CC v9.1 (Adobe Systems Inc., San Jose, CA, USA), were based on high-magnification recordings of male *H. pyrrithrix* (Fig. 11a, b) and allowed for manipulation of the motion characteristics of the male first leg waves. We produced 100 versions of the animation with different wave characteristics, corresponding to factorial combination of ten levels of wave velocity (10, 50, 100, 150, 200, 250, 300, 500, 750, 1000 degrees/second) and amplitude (10, 20, 30, 40, 50, 60, 70, 80, 90, 100 degrees). We selected these values to bracket the range of variation previously recorded from male wave displays ($n = 30$ displays measured from $n = 5$ males, velocity range = 64-398 degrees/second, amplitude range = 11-98 degrees, SAE unpublished data). Animations were then superimposed onto four different backgrounds using Adobe Premiere Pro CC v9.1. We used a still frame from a habitat video (“Habitat Still”), the unaltered habitat video (“Habitat Video”), a 1.5x sped-up version of the same video (“Fast Habitat Video”), and a control of uniform 50% grey (“Grey”) as stimulus backgrounds (Fig. 11d). Habitat backgrounds were based on a video taken at the capture location of an adult female *H. pyrrithrix* at the Queen Creek, AZ site in May 2016. Settings for this habitat video were chosen to closely approximate salticid optics (84 degrees field of view, close focus with maximal depth of field), using a Panasonic Lumix DMC-GH4 camera (1920*1080px, 60fps) with an Olympus M.Zuiko Digital ED 60mm f/2.8 macro lens. Stimuli were presented as pairs consisting of a waving male opposite a non-waving male. Females viewed five seconds of the background alone, followed by 20 seconds of simultaneous presentation of the animated males. Competing males within a stimulus pair always appeared against the same background, and on separate monitors. We produced two types of experimental stimuli: a full set wherein both males remained

in the same location on screen (i.e., “standing and waving”; hereafter “SW”), and a subset wherein both males walked across the screen (i.e., “walking and waving”; hereafter “WW”, see below).

3.2.4 Female Response to Waving Displays from Walking Males (WW Experiment)

To determine how female responses were affected by males walking while displaying, we also filmed the reaction of females ($n = 10$) to the WW stimuli. WW stimulus pairs were created as described above but were designed such that both displaying and non-displaying males appeared at the outer edges of the monitors (i.e., in the female’s periphery), and walked towards the center of the female’s field of view. This experiment also served to determine whether female responses in the SW experiment were driven purely by the presence vs absence of movement in each stimulus pair.

Waving displays in the WW stimuli consisted of a limited set of wave parameters chosen to approximate typical displays of live males: three levels of amplitude (30, 50, 70 degrees) and four levels of velocity (100, 150, 200, 250 degree/s). WW stimuli were only presented on the grey background. No females were re-used between this and the SW experiment. Each female experienced a singular experimental session consisting of five repeats of all 12 combinations of WW stimuli. Stimulus order was randomized within a repeat. Following each repeat, playback was paused for 5 minutes to reduce desensitization.

3.2.5 Female Response to Waving Displays in Different Visual Environments (SW Experiment)

To assess how responses were affected by display parameters and the visual environment, we filmed the reaction of females ($n = 40$) to the SW stimuli. Stimuli pairs were shown in sessions consisting of 50 pairs on the same background. Thus, for each background condition, two sessions were required for the female to view all combinations of male waving display parameters. These two sessions of the same background type occurred on consecutive days. The order of stimuli and the monitor on which the waving male appeared on were randomized. Within each session, playback was paused for a 5-minute break following the 25th stimulus to reduce desensitization. For logistical purposes, the 40 females were tested in cohorts of 10.

3.2.6 Measurement of Female Responses

Because females were mounted in place and could not turn, female attempts to orient toward a stimulus translated instead to turns of the foam ball. We therefore scored female responses to video stimuli by tracking the movement of the foam ball held by the female. For each stimulus, we determined four primary response variables: (1) Total number of turns to either direction, (2) Total number of turns towards the waving male, (3) Direction of first choice (which stimulus the female attempted to turn toward first), (4) Proportion of turns to wave ($\# \text{ turns toward waving male} / \text{total turns}$, excluding trials where the female did respond to either stimulus).

Due to the large volume of footage, the SW experiment was scored by four scorers, who were trained on partial videos until the entire group's pair-wise measurement repeatability was greater than 70%. The WW experiment was scored by one individual.

3.2.7 Male Courtship in Different Visual Environments

To assess male signaling behavior in different visual environments, we recorded long-distance courtship of male *H. pyrithrix* ($n = 20$) displaying under four different background conditions (uniform 50% grey, habitat still image, habitat video, habitat video played at 1.5x speed; see above). Male courtship displays were elicited in a custom-built arena (Fig. 11e). The arena consisted of the circular top surface of a 13.6kg steel drum (10cm diameter), surrounded by a hexagonal wall. Heavy steel was chosen in order to eliminate transmission of vibrations produced by the male, thereby eliminating the potential confound of independent variation in male vibratory signaling from our analyses. The six sides of the hexagonal arena wall contained three video screens and three camera mounts. An additional 4th camera mount was located on an arm above the arena. A freshly killed conspecific female was mounted on the tip of a rotatable brass rod that extended from the arena center to below the setup. Before each trial, a virgin female was allowed to walk about the arena to deposit dragline silk and any other chemical cues. Male waving displays were then elicited by rotating the female model mounted on the rod in the arena center, imitating characteristic female reorienting turns. Throughout each trial, all three video monitors displayed the same background stimulus. Males courted females once per background condition, and background conditions were presented in random order.

The four cameras (GoPro Hero 4 Black with Polar Pro macro lenses) allowed us to capture male movements in the arena without blind spots, at 1920x1080 pixels resolution and 120 frames per second. Male displays were recorded for 30s, starting as soon as males began lifting their front legs to initiate courtship. Filming by the four cameras was simultaneously triggered using a

wireless remote control. The arena was cleaned with 95% ethanol between consecutive trials to remove previous scent and silk cues. Experiments were carried out under direct sunlight in August and September 2016 between 10am and 4pm. Only 66 of an intended 80 trials were included in the full analysis, because some males died of natural causes before experiencing all trial conditions ($n = 3$ trials), males failed to display ($n = 8$ trials), or we determined that recorded movements were locomotory upon inspection ($n = 3$ trials).

To calculate properties of male waving displays, we first determined the frames in which a wave of either left or right leg began or ended in trial. When multiple movements in the same direction (up or down) occurred in sequence, they were treated as separate waves in the rare instances when there was a pause of 500 ms or more between them. In each of these start/end frames, we marked the xy pixel coordinates of 14 morphological landmarks from each of the four perspectives (Fig. 11f). We then used direct linear transformation to calculate 3D coordinates with confidence intervals for each landmark. Some landmarks were hidden behind the male body from some perspectives, but all landmarks remained visible in at least two of the four perspectives so that a 3D coordinate could be calculated. The cameras were calibrated in the MATLAB-based digitizing environment DLTdv5 (version 5 from 2014-10-16 (Hedrick 2008)) using an 80-point calibration object. All recordings were synchronized based on an audio cue in Adobe Premiere.

From the 3D coordinate sets, we calculated absolute amplitude and velocity of waves. We measured the angle between the line from the spider's coxa to the tarsus (approximately "shoulder" to "wrist"), and the horizontal arena floor. We defined the amplitude as the difference between the initial and final angle. Furthermore, we calculated the angular velocity and distance moved by the male tarsus from the perspective of the female at the center of the arena.

3.2.8 Statistical Methods

To determine whether females paid more attention to male waving displays in general, we calculated the net turns to wave (# turns toward waving male - # turns toward non-waving male), and compared this metric against a hypothetical mean of 0 (equal attention to both stimuli) using a one-sample Student's t-test. We performed this test for both the SW experiment and WW experiments. All statistical tests were carried out using R version 3.3.2 (Team 2013).

To assess the influence of each of our three test variables (amplitude, velocity, and background) on how females in the SW experiment attended to waving males, we used Generalized Linear Mixed Models (GLMMs; as implemented in R package lme4 (Bates et al. 2014)). We modeled our four response variables (total number of turns, direction of first choice, number of turns to waving male, and proportion of turns to waving male) each as separate GLMMs. When modeling first choice and proportion of turns, we excluded trials where the female did not react to either stimulus. We modeled females' first choice and proportion of total turns towards the waving male using Binomial GLMMs with logit link, because these variables represented binary and proportion data, respectively. Total number of turns and turns toward the waving male were modeled using Poisson GLMMs with log link because these variables represented count data (Crawley 2003; 2005). All four of these global models shared the same effect structure, as follows:

$$\begin{aligned} \text{(Response Variable)} \sim & \text{amplitude} + \text{velocity} + \text{background} + \text{velocity} * \text{amplitude} + \text{amplitude} * \\ & \text{background} + \text{background} * \text{velocity} + \text{amplitude} * \text{velocity} * \text{background} + \text{wavingSide} \\ & + \text{scorer} + \text{cohort} + (1|\text{cohort:spiderID}) + (1|\text{session}) + (1|\text{stimulusOrder}) \end{aligned}$$

We treated the amplitude, velocity, and background of the stimulus, and all their interactions, as fixed factors. We centered and standardized amplitude and velocity to two standard deviations (SD) using the R package arm (Gelman and Hill 2007), so that effect sizes could be

compared between variables (Gelman 2008). We included the order of stimuli within an experimental session, the order of sessions, and individual identity as random factors. To account for possible variation in testing conditions and aging of the spiders, we included the experimental cohort in the model. However, due to the small number of levels for this factor (fewer than 5), we treated it as a fixed factor (following advice in (Crawley 2003; 2005)). For the same reason, we also modeled the scorer (4 levels) and which side the waving male appeared on (2 levels) as fixed factors. Spider identity was nested within experimental cohort. We excluded trials ($n = 200$) from the analysis when females did not grip the foam ball, experimental conditions were disrupted (e.g., by excessive noise in adjacent rooms), and when technical errors occurred during video playback.

For all response variables modeled, we computed all 38 possible sub-models of the global model and compared the quality of these models to each other using the Akaike information criterion (AIC). As the weight of the best model was less than 0.9 in all cases, we elected to use model averaging (following advice in (Grueber et al. 2011)). We selected models within 2 Δ AIC of the top model for averaging (R package MuMIn (K 2013)). As the goal of modeling in this study was to determine which factors had the strongest effects on the response variables, we used the full (i.e., “zero-method”) average when averaging over component models in all cases (Grueber et al. 2011; Nakagawa and Freckleton 2011).

We also used GLMMs to assess female responses in the WW experiment, but with a different effect structure, as follows:

$$\begin{aligned} \text{(Response Variable)} \sim & \text{amplitude} + \text{velocity} + \text{velocity} * \text{amplitude} + \text{wavingSide} + (1|\text{spiderID}) \\ & + (1|\text{repeatOrder}) + (1|\text{stimulusOrder}) \end{aligned}$$

Background, experimental cohort, experimental session, and scorer did not vary in the WW experiments, and so these were not included as factors. We included the order that repeated stimuli

were viewed as a random factor. Modeling and model averaging were otherwise carried out as described above.

To determine the effects of background treatment on male waving displays in the arena study, we created three linear mixed-effects models with wave amplitude, visual angle, and male-female distance as response variables, background condition as a fixed effect, and male ID as random effect (R package lme4 (Bates et al. 2014)). The effect of background treatment on response variables was then evaluated using a repeated-measures analysis-of-variance (rmANOVA) with Type III sums of squares.

3.3 Results

3.3.1 Female Response to Waving Displays in Different Visual Environments (SW Experiment)

3.3.1.1 Female Responses to Waving vs Non-Waving Males

Females in the SW experiment ($n = 40$) showed interest in the male stimuli by attempting to turn towards one of them in 61.82% of the trials (9767 of 15800 trials). When females responded, they typically made one or two turns in total (mean \pm SD total turns = 1.82 ± 0.93 , $n = 9767$). The averaged GLMM (average of 16 component models, Appendix Table 1) showed that there was no significant effect of wave amplitude ($Z = 0.797$, $p = 0.43$), velocity ($Z = 0.52$, $p = 0.60$), or their interaction ($Z = 0.368$, $p = 0.71$) on the total number of turns.

For the number of turns to wave, females turned towards the waving male approximately once (mean \pm SD turns to wave = 0.95 ± 0.52 , $n = 15800$). The averaged GLMM (average of 8

component models, Appendix Table 2) showed that there was no significant effect of wave amplitude ($Z = 0.551$, $p = 0.58$), velocity ($Z = 0.695$, $p = 0.49$), or their interactions (not included as factor in any component model) on turns to wave. Females oriented more times towards the waving male than towards the non-waving male (Fig. 12a, mean \pm SD net turns to wave = 0.74 ± 0.96 , $n = 15800$; Student's t-test, $t_{15799} = 91.467$, $p < 0.0001$).

For the direction of first choice, females were more likely to first turn towards the waving male before the non-waving male, but this preference, while highly significant, was only slightly above chance (i.e., effect size was small; mean \pm SD likelihood to turn toward waving male first = 0.54 ± 0.50 , $n = 9767$; Student's t-test, $t_{9766} = 7.0295$, $p < 0.0001$). Larger amplitude waves were more likely to draw a females' attention on her first choice, but the increase was small (mean \pm SD likelihood to turn toward waving male first: 10° amplitude 0.53 ± 0.50 , 100° amplitude 0.56 ± 0.50). The averaged GLMM (average of 3 component models, Appendix Table 2) indicated a significant positive effect of waving display amplitude on the direction of first choice ($Z = 1.124$, $p = 0.0263$). There was no significant effect of display velocity ($Z = 0.354$, $p = 0.72$), or the interaction of amplitude and velocity (not included as a factor in any component model) on the direction of first choice (Appendix Table 3).

For the proportion of turns to wave, females directed the large majority (89%) of their responses at the waving male (mean \pm SD proportion of turns to wave = 0.89 ± 0.21 , $n = 9767$; Student's t-test, $t_{9766} = 172.21$, $p < 0.0001$). The averaged GLMM (5 component models, Table 1) showed no significant effect of wave amplitude ($Z = 0.097$, $p = 0.92$), velocity ($Z = 0.156$, $p = 0.88$), or their interaction ($Z = 0.435$, $p = 0.66$), on the proportion of turns to wave.

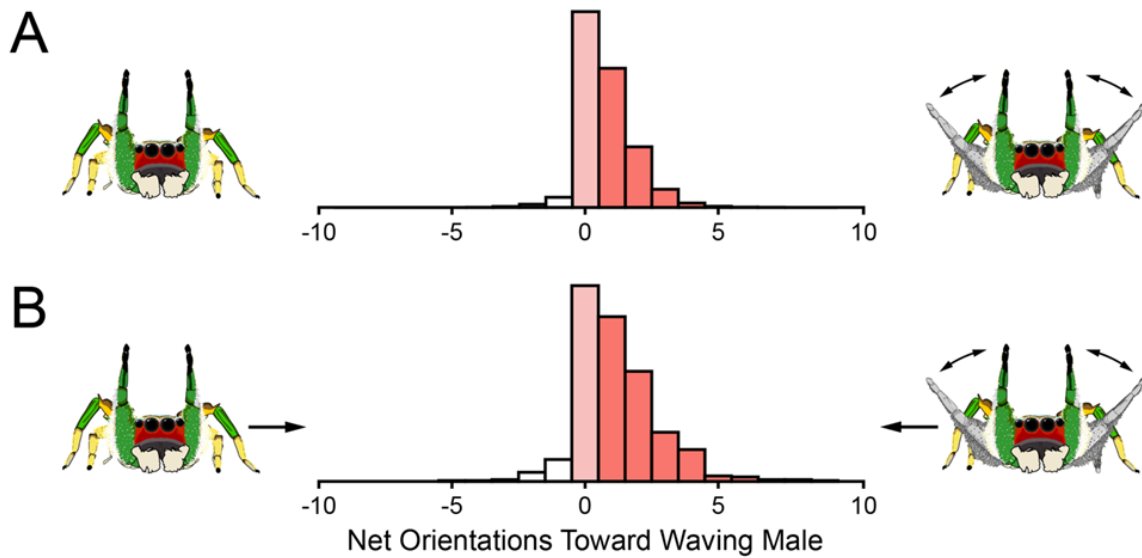


Figure 12. Female responses to competing male stimuli

Females turned toward waving males (dark pink bars) more often than toward non-waving males (white bars) when (a) animated males were presented in a stationary courtship posture ($n = 15800$ trials), and when (b) both animated males walked across the female's field of view ($n = 660$ trials). Central light pink bars correspond to cases where females engaged in an equal number of turns toward both stimuli, including cases where the female did not turn towards either stimulus.

3.3.1.2 Effect of Background on Female Responses

For the total number of turns, females were more responsive when viewing stimuli against stationary (Grey and Habitat Still) backgrounds than against moving backgrounds (mean \pm SD total turns: Grey 1.52 ± 1.17 , Habitat Still 1.14 ± 1.03 , Habitat Video 1.00 ± 0.95 , Fast Habitat Video 1.02 ± 0.98 , $n = 15800$). This difference in total turns between moving and stationary backgrounds is also represented in the averaged GLMM (average of 16 component models, Appendix Table 1), where the moving backgrounds both have significant negative effects on female turns (Habitat Video $Z = 12.052$, $p < 0.0001$, Fast Habitat Video $Z = 4.849$, $p < 0.0001$). For the turns to wave, females oriented to the waving male fewer times when viewing them against

moving backgrounds (mean \pm SD turns to waving male: Grey 1.15 ± 0.62 , Habitat Photo 1.00 ± 0.47 , Habitat Video 0.83 ± 0.41 , Fast Habitat Video 0.87 ± 0.42 , $n = 15800$). The averaged model (8 component models, Appendix Table 2) confirms a significant negative effect of the Habitat Video ($Z = 8.093$, $p < 0.0001$) and Fast Habitat Video ($Z = 2.3$, $p = 0.021$) backgrounds on the number of turns to wave.

For the direction of first choice, the averaged GLMM (average of 3 component models, Appendix Table 3) showed there was no significant effect of background (not included as a factor in any component model) on how likely females were to first turn towards the waving male.

For the proportion of turns to wave, females directed a greater proportion of responses towards the waving male when viewing stimuli against more complex backgrounds (Fig. 13, mean \pm SD proportion of turns to waving male: Grey 0.85 ± 0.22 , Habitat Photo 0.90 ± 0.19 , Habitat Video 0.91 ± 0.18 , Fast Habitat Video 0.92 ± 0.19 ; $n = 9767$). The averaged model (5 component models; Table 1) indicates a significant positive effect of the Habitat Photo ($Z = 5.012$, $p < 0.0001$), Habitat Video ($Z = 6.853$, $p < 0.0001$), and Fast Habitat Video ($Z = 6.411$, $p < 0.0001$) backgrounds.

3.3.2 Female Response to Waving Displays from Walking Males (WW Experiment)

Females in the WW experiment ($n = 10$) frequently responded to the animated stimuli (75.60%, 499 of 660 trials), and typically turned towards the stimuli 1-3 times (mean \pm SD total turns = 2.44 ± 1.41 , $n = 499$). Females again showed a preference to turn towards waving males first (mean \pm SD likelihood to turn toward waving male first = 0.63 ± 0.49 , $n = 499$; Student's t-test, $t_{498} = 4.5172$, $p < 0.0001$), and to orient to the waving male more often (Fig. 12b, mean \pm SD net turns to waving male = 1.51 ± 0.74 , Student's t-test, $t_{659} = 19.205$, $p < 0.0001$). The averaged

Table 2. Modeling of proportion of turns towards waving male

Effect of each parameter on the proportion of turns towards waving males in the SW experiment, as determined by binomial GLMM. Results represent model averaging of the top (2 ΔAIC) models (n = 5).

Asterisks following p-values indicate significance (* p < 0.05, ** p < 0.01, *** p < 0.0001). Relative

Importance scores indicate the proportion of models that include the variable.

* Effect sizes have been standardized on two SD following Gelman (Gelman 2008)

† BackgroundGrey was the reference category

†† ScorerSAE was the reference category

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value	Relative Importance
			2.5 %	97.5%			
(Intercept)	1.32871	0.079223	1.17	1.48	16.77	< 2 x 10⁻¹⁶	***
amplitude	-0.002152	0.022275	-0.08	0.07	0.097	0.92305	
velocity	-0.003576	0.022937	-0.09	0.07	0.156	0.876126	
amplitude:velocity	0.032687	0.075065	0.02	0.32	0.435	0.663242	
backgroundPhoto†	0.361307	0.07208	0.22	0.50	5.012	5.0 x 10⁻⁷	***
backgroundVid	0.473625	0.069102	0.34	0.61	6.853	< 2 x 10⁻¹⁶	***
backgroundVidFast	0.438317	0.068363	0.30	0.57	6.411	< 2 x 10⁻¹⁶	***
cohort	0.355644	0.127285	0.11	0.61	2.794	0.00521	**
scorerEL††	0.621976	0.09025	0.45	0.80	6.891	< 2 x 10⁻¹⁶	***
scorerJEK	-0.028933	0.065464	-0.16	0.10	0.442	0.658545	
scorerNAR	0.286032	0.078966	0.13	0.44	3.622	0.000293	***
wavingSide	-0.007236	0.022618	-0.11	0.04	0.32	0.749049	

GLMM of each response variable showed no significant effect of amplitude, velocity, or their interaction. Model details are presented in Appendix Tables 4-7.

3.3.3 Male Courtship in Different Visual Environments

We quantified male long-distance waving displays with respect to distance from the female, as well as visual background. Males carried out waves with an average amplitude of $28.9 \pm 7.0^\circ$ (upstroke) and $-28.8 \pm 7.0^\circ$ (downstroke), an average angular velocity of $88.4 \pm 22.9^\circ/\text{s}$ (upstroke), and $79.4 \pm 22.1^\circ/\text{s}$ (downstroke). Males performed a mean of 3.06 ± 0.94 (upstroke) and 3.09 ± 0.94 (downstroke) waves per second. Subsequent analyses were carried out using absolute values for wave amplitude regardless of wave direction.

Wave amplitude was strongly positively correlated with distance to the female (Fig. 14a, amplitude = $17.3 + 0.37 * \text{distance}$, $r^2 = 0.13$, $F_{60,41} = 7.6$, $p = 0.008$). However, these increases in male wave amplitude did not fully compensate for distance-based declines in the visual angle of male waves. From the perspective of the female, male waves performed from greater distances were smaller in visual angle compared to those performed closer (Fig. 14b). However, by waving with greater absolute amplitude at longer distances (i.e., by adopting a “dynamic wave” strategy), males’ increased the perceived visual angles in the female’s field of view more so than if they had waved at the same amplitude (i.e., a “static wave” strategy, see curves in Fig. 14b).

Males did not change the velocity of their waves when courting in different backgrounds ($F_3 = 0.86$, $p = 0.46$). However, we did find a significant decrease in wave amplitude, but only when courting against the Habitat Video background (Fig. 15a, $F_3=14.6$, $p < 0.0001$). Male courtship against the Fast Habitat Video background was not significantly different from courtship against Grey or Habitat Still backgrounds. We found that males consistently responded to different

backgrounds by altering their position in relation to females. Males displayed closer to the female when background complexity increased (Fig. 15b, $F_3 = 44.23$, $p < 0.0001$), leading to increased perceived movement (Fig. 15c, $F_3 = 12.26$, $p < 0.0001$).

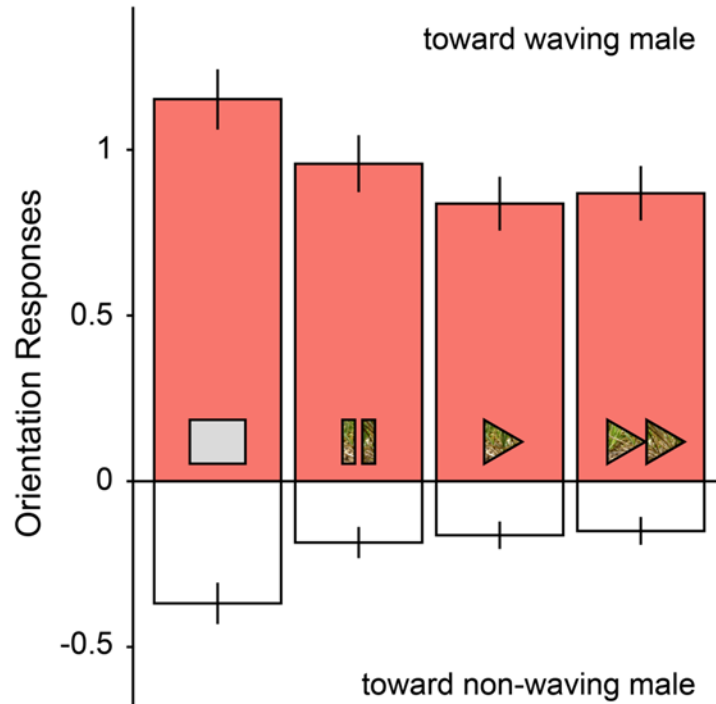


Figure 13. Female responses in different visual environments

Proportion of female orientation responses toward (dark pink bars) or away from (white bars) waving male stimuli, split by background type (L to R: grey, habitat still, habitat video, habitat fast video). Females were less responsive when viewing stimuli against moving backgrounds, but in these cases directed a greater proportion of their attention to waving males. Error bars represent ± 1 SE.

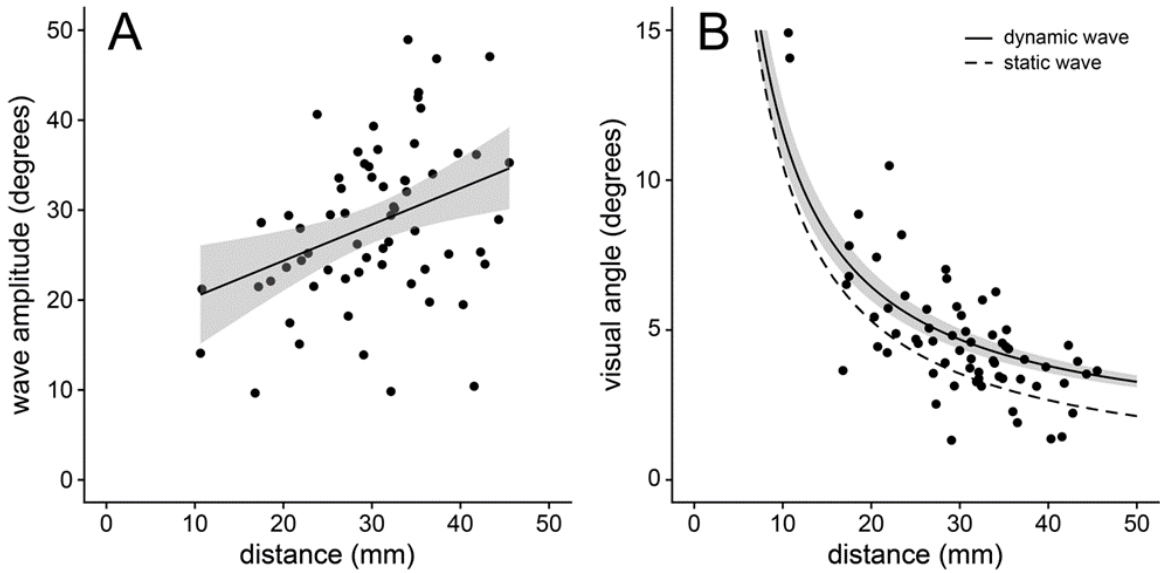


Figure 14. Males adjust waving displays with distance to receiver

(a) Males wave with greater amplitude at greater distances (linear regression, 95% CI in grey). (b) Visual angle of male wave as viewed by the focal females. Male wave visual angles decrease with increasing distance, but at a slower rate due to dynamic adjustment of wave amplitude (solid curve with grey confidence interval, dynamic wave: visual angle = $\tan^{-1}((a + b * \text{distance}) / \text{distance})$, with tarsus displacement of $a=2\text{mm}$ and wave increase factor of $b=0.1\text{mm}$), as compared to an unchanging wave amplitude (dashed curve, hypothetical static wave: visual angle = $\tan^{-1}(a / \text{distance})$). Data points represent the means of individual trials.

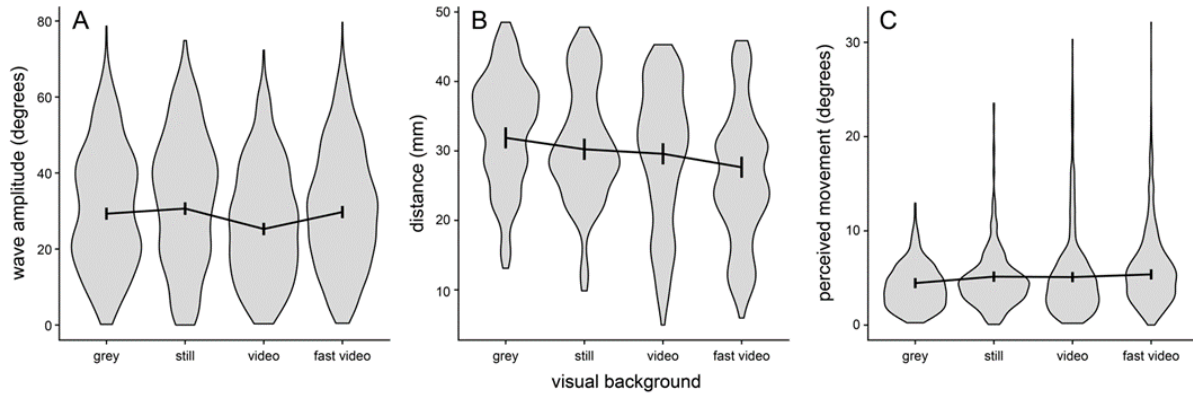


Figure 15. Male displays in different visual environments

(a) Males do not change leg wave amplitude when courting against more complex backgrounds, (b) but instead court at shorter distances from the female. (c) As a result, male leg movement as perceived by females is greater when backgrounds are more complex.

3.4 Discussion

3.4.1 Waving Displays as Alerting Signals

We demonstrate here that the waving displays of *H. pyrrithrix* have a robust attention-grabbing function. In the introductory, long-range phase of courtship, males display towards a focal female by raising and waving their outstretched forelegs. Females often face away from the courting male, but may notice these waves and subsequently attend to the male. Jumping spiders turn to fixate on stimuli of interest with their primary eyes (Harland, Li, and Jackson 2011; M. F. Land 1999; M F Land 1969b; Zurek and Nelson 2012b), allowing us to infer visual attention from these turning responses. Based on multiple measures of female response to competing videos of waving and non-waving males, we found that waving males are effective at capturing female visual attention. Females were more likely to respond to waving males first, and devoted a much greater

fraction of their attention (89% of all turns) to waving males than to non-waving males. Waving males were also attention-grabbing when both stimuli (waving and non-waving) walked across the female's field of view (Fig. 12), indicating that waving displays increase salience even in the presence of a competing source of male movement. In addition, waving-while-walking appeared to augment the alerting function of male displays, increasing the likelihood (by approximately 10%) that females would look at the waving male first. This advantage is consistent with the observation that males often sidle side-to-side while presenting these waving displays to females.

What aspects of waving displays are responsible for capturing female visual attention? Waves may target a specific pre-existing sensory bias for a specific movement (e.g., as seen in the head-bob display of *Anolis* lizards (Steinberg and Leal 2013)). In such a case, we would expect that the effective combinations of signal properties (amplitude, velocity) would be constrained. However, while observed variation in male displays is clustered (low amplitude ($28.8 \pm 7.0^\circ$) and high velocity ($83.9 \pm 22.5^\circ/\text{s}$)) within the range tested in the SW experiment ($10\text{-}100^\circ$), we also observed that waves were similarly effective across the entire range. There was no decline in alerting function that would indicate the boundary of a strict sensory bias. Instead, our findings suggest that waving displays function to stimulate the general motion sensitivity of salticid lateral eyes (Zurek et al. 2010; Zurek and Nelson 2012a). Observed male variation may therefore be constrained for reasons distinct from their alerting function, such as body condition, and/or active female choice on waving displays (but see (d) below).

3.4.2 Effect of Background Motion

We also found that background motion impacts female responses to male waving displays. Females were less likely to respond to male stimuli when these were presented against moving

backgrounds. However, despite lower responsiveness in the presence of background motion, females directed proportionally more responses toward waving males in these circumstances (Fig. 13). This shows that waving displays are especially effective in capturing female attention in otherwise challenging visual environments.

The ecology of *H. pyrrithrix* suggests that background motion may be a frequent complication for this species, underscoring the attention-grabbing benefits of the waving display. In our experimental stimuli, background motion was the result of wind blowing over short grasses, filmed from the location and perspective of *H. pyrrithrix* individuals at our field site (see Methods). We expect that wind can produce similar effects across the species' range, given that this species inhabits grassy riparian terraces. Even if a courting male is not standing directly in front of vegetation, wind can still cause background movement by causing shadows cast by surrounding plants to shift (Richard A Peters 2013). Males begin courtship immediately upon encountering females (L. A. Taylor, Powell, and McGraw 2017), and thus do not have the opportunity to choose or change the visual environment when signaling. Therefore, having an alerting display that is robust to background motion allows males to initiate courtship while minimizing limitations from adverse signaling conditions.

Similar challenges are likely faced by a wide variety of organisms that use movement signals, but have been studied primarily in lizards [1,23,27, reviewed in 76]. In these systems, visual motion from wind-blown vegetation decreases detection and/or receiver response by masking the signal with visual “noise” with similar properties to the signal itself (R. Peters, Hemmi, and Zeil 2008; Ord et al. 2007; L J Fleishman and Pallus 2010). In turn, effective alerting signals may be able to stand out against a moving background by moving in a different way (Richard A Peters 2013; Ord, Charles, and Hofer 2010). Our results suggest that *H. pyrrithrix*

waving displays are qualitatively different enough from the movement of wind-blown grass to remain salient. To our knowledge, this study is the first evidence that movement from wind-blown vegetation is a source of visual noise for arthropod signalers. The role of such noise in the evolution of movement signals in this and other species is an exciting field for future study.

3.4.3 Contextual Plasticity in Waving Displays

We also report that *H. pyrrithrix* males actively respond to the visual and spatial conditions of a courtship interaction and adjust their waving displays to improve signal salience. While these responses did not take the form of changes to the average properties of their waves (i.e., males exhibited no changes to average wave velocity, and only idiosyncratic responses to average wave amplitude), males did exhibit changes to other behaviors that impact the salience of their displays from the female perspective. First, males increased the amplitude of their waving displays when courting from further away from the female (Fig. 14). Second, when courting against more spatio-temporally complex backgrounds, males moved closer to the female (Fig. 15). Both of these behaviors increase the visual angle of the male wave from the perspective of the female. In other words, these dynamic adjustments increase the perceived size of male waving displays, especially when compared to such waves had males not adjusted their signaling. Our results from the SW experiment (see above) show that larger waving displays are more likely to attract a female's attention first. Therefore, these forms of behavioral plasticity may improve the effectiveness of male alerting displays in changing conditions.

Many species produce distinct long- and short- range signals, but active modification of a signal in response to communication distance appears to be rarely studied. Previous work has described distance-dependent signal modification primarily in acoustic communication. By

adjusting amplitude, acoustic signalers are able to compensate for how sound waves degrade during travel (Cole 2013; Bradbury and Vehrencamp 2011). Humans (Michael, Siegel, and Pick Jr 1995) and zebra finches (Brumm and Slater 2006) both increase the loudness (amplitude) of their vocal communications when further from the focal receiver. Evidence for a similar strategy in visual signaling is limited, despite the fact that visual signals also “drop off” with increasing distance, appearing smaller from further away. Fiddler crabs (*Uca perplexa*) adjust the timing of their claw-waving displays with distance to the female, but also perform qualitative changes to the display structure that may correspond to different messages at different ranges (How et al. 2008). In the lizard *Anolis gundlachi*, signalers increase the amplitude of their head-bob display with increasing receiver distance (Steinberg and Leal 2013) (although the species also uses distance as a cue to facultatively add a separate alert signal before their display (Ord and Stamps 2008)). Similarly, *H. pyrrithrix* males appear to modify their visual display by increasing the perceived intensity of the signal without changing its overall structure.

We note that for the acoustic signals of humans and finches, as in *H. pyrrithrix* visual displays, signal modification did not fully compensate for the effect of distance. This suggests that there may be constraints on these animals’ ability to compensate, and/or the benefit in doing so (as seen for *Anolis gundlachi* (Steinberg and Leal 2013; Ord and Stamps 2008)). In addition, *Habronattus* jumping spiders are known to produce complex seismic songs in synchrony with their visual displays (D. O. Elias et al. 2012); do males also “sing” louder when courting from further away, or is their ability to compensate with distance limited to visual signaling? These questions are exciting avenues for future research.

To our knowledge, this is the first time that distance-dependent signal modification has been described in an arachnid. The phylogenetic range of distance-dependent signal modification

suggests that it may be a more widespread strategy for effective communication than current research indicates (How et al. 2008). Humans, for example, also wave their arms to attract attention, and common experience suggests they may also increase the intensity of their displays with communication distance. However, this observation surprisingly remains to be tested, along with how other animals might use this strategy in their communication.

Work on how signalers respond to increased motion noise in their environment is also limited. In general, signalers may attempt to change the properties of their signal to better stand out against background noise (e.g., the Lombard Effect, where acoustic signalers increase vocalization volume in noisy situations, reviewed in (Brumm and Zollinger 2011)), and/or adjust how and when signals are used (e.g., timing signal delivery when noise is minimized (McNett, Luan, and Cocroft 2010)). Previous work regarding movement-based signals is restricted to research on Jacky Dragon lizards (*Amphibolurus muricatus*) and *Anolis* lizards. These animals appear to follow a strategy analogous to the Lombard Effect. When faced with visual noise from wind-blown plants, *A. muricatus* increase the duration and changes the structure of their tail-flicking alerting signal (Richard A. Peters, Hemmi, and Zeil 2007), and two *Anolis* species (*A. gundlachi* and *A. cristatellus*) increases the speed of their head bob displays (Ord, Stamps, and Losos 2010; Ord et al. 2016; 2007). Several *Anolis* species also time their signaling for moments of decreased visual noise (Ord, Charles, and Hofer 2010). In contrast, *H. pyrrithrix* males respond primarily by changing their spatial positioning, moving closer to the female when in increasingly noisy visual environments. Some species with multimodal displays change between modalities when one is affected by environmental conditions (e.g., wolf spiders (Gordon and Uetz 2011)). Whether *H. pyrrithrix* similarly increases vibrational courtship in response to a noisy visual environment is another question open for future work.

3.4.4 Implications for Mate Choice

Observed natural variation in *H. pyrrithrix* waving displays and the effectiveness of different waves suggests that these signals may be subject to selection. Larger amplitude waves were more likely to attract a female's attention first, so it is possible that males experience selection to perform larger waves. Capturing attention early may improve mating success, as in the jumping spider *Maevia inclemens* (D L Clark and Morjan 2001). This hypothesis may explain why males responded to noisy signaling conditions by increasing the visual angle (apparent size) of their displays from the female's perspective; larger amplitude displays will also take up a larger visual angle. It is also possible that, in addition to the alerting effects of waving displays, females may assess wave amplitude in mate choice. Previous work shows that mating success improves with male body size in this species (L. A. Taylor and McGraw 2013), and larger males will, all else being equal, take up a larger visual angle in the female's field of view. Thus, the visual angle subtended by a display may be used by females as a proxy for overall body size, and male display adjustments may serve to communicate or exaggerate this metric of his size.

Females may also have the opportunity to directly judge males based on their ability to respond to changing conditions (Sih, Chang, and Wey 2014). Our findings suggest that males are continuously assessing receiver distance and background complexity during courtship, and this may be cognitively demanding. In addition, increasing wave amplitude requires males to invest more energy into their display; male effort is a common axis of female mate choice in other systems (Bradbury and Vehrencamp 2011), including in peacock jumping spiders (Girard, Elias, and Kasumovic 2015). Males vary in the extent of their response to these spatio-social cues (Fig 14, Fig 15), allowing females to potentially assess a combination of male cognitive skill and signaling effort. Disentangling how attention capture, display variation, and contextual plasticity

affect mating success in *H. pyrrithrix* will improve our understanding of the evolution of these complex visual displays.

3.4.5 Conclusions

In summary, we show that the introductory arm-waving display of *Habronattus pyrrithrix* reliably captures female visual attention, thus functioning as an alerting signal. We thus expand the phylogenetic extent of alerting signals to include jumping spiders, and follow others in suggesting that attention-grabbing components within complex displays are likely more common than current research shows (Ord and Stamps 2008; G. G. Rosenthal 2007; Számadó 2015). We also find that background motion from wind-blown vegetation is a source of sensory noise, decreasing female responsiveness. Previous work has shown that the visual displays of Jacky dragon lizards are affected by wind-blown vegetation ((Ord and Stamps 2008; Richard A. Peters, Hemmi, and Zeil 2007)), but we provide the first evidence that arthropod signalers face similar challenges. However, *H. pyrrithrix* waving displays are, in part, robust to these adverse conditions, capturing a greater proportion of female attention when background motion was present. In addition, displaying males appear to assess signaling conditions, including background complexity and distance from intended receiver, and adjust their signaling adaptively to increase the apparent size of their display. Males vary in the extent of this plastic response, possibly providing females information on cognitive ability, effort, and/or condition.

Our work has several implications for the evolution of communication systems in the *Habronattus* genus and other taxa. *Habronattus* species inhabit a wide range of habitats, and also exhibit diverse introductory motifs to their courtship sequences, many of which may be alerting displays (Leduc-Robert and Maddison 2018). Such putative alerts vary amongst even closely

related species in their amplitude, velocity, direction of motion, and even which limb (foreleg or pedipalp) is moved (D. O. Elias et al. 2012, SAE unpublished data). Do these represent distinct solutions to capturing female attention early in the male display? And if so, have they been shaped by ecological differences related to salience? *Habronattus* species also vary in their degree of microhabitat specialization, and thus vary in breadth of visual environments in which courtship occurs. How does alert salience vary between qualitatively different environments, and are such challenges met via signal evolution or adaptive plasticity (e.g., in *Anolis* lizards (Ord et al. 2016; Ord, Stamps, and Losos 2010))? Such questions are exciting prospects for future investigations on the evolution of alerting signals, in this and other arthropod groups.

3.5 Acknowledgements

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4.0 Conclusions

Through the above research, I have developed our understanding of the pervasive directional constraints in signal transmission and reception, how communicators position themselves with respect to these biases, and how signalers respond to dynamic alignment of signal and sensor. Previous work in animal communication has often operated under the untested assumptions that signaler and receiver behavior during communication facilitates signal perception. In my survey of communication literature, I found robust evidence for directional constraints on signal transmission and reception across species and signaling modalities. Taken together, these constraints indicate that even small changes in positioning may have strong effects on signal efficacy. However, while several studies have investigated how signalers orient themselves to manage signal directionality, there has been very little work that assesses how receivers direct their sensors (and thus their attention) during communication. For effective visual communication, it is not sufficient for signalers to orient their signals towards intended receivers. Receivers must also orient their sensor(s) towards these signals, and with the portion of their sensory field that is most sensitive to the type of information used by the signal (G. G. Rosenthal 2007).

I then empirically investigated the dynamics of such signaling alignment in the courtship of the fiery-haired jumping spider, *Habronattus pyrrithrix*. *Habronattus* jumping spiders have strong directional biases in visual signal transmission and reception. Males use colorful ornaments in their courtship dances, but these are only on the forward-facing surfaces of their bodies. Likewise, females can only see in color through their anterior median eyes, which sweep only a 60-degree cone in front of their body. Thus, the degree of alignment between male and female

facing directions serves as a reliable estimation of the effectiveness of color communication in this system. By characterizing signaling alignment throughout courtship, I discovered that the visibility of male coloration is dynamic, and ultimately determined by changes in receiver behavior. Females frequently looked away from courting males, and while males did sometimes reposition themselves in response, they did not move enough to regain a position in her frontal field of view. However, I also found evidence that males assessed the direction a female is facing, and used this information to make tactical decisions on when to display certain color ornaments. Males were most likely to show their orange “knees” to females immediately after she turned back to face him. Furthermore, female orientation towards males, and thus signaling alignment, increased significantly as courtship progressed from long to short-range display.

I tested one possible mechanism for how males might improve signal alignment by assessing the effectiveness of male arm-waving as “alert displays” that function to capture a female’s visual attention. Through a video playback experiment, I found that females frequently turned to look towards waving males, and the relative effectiveness of these displays increased in adverse signaling conditions. This suggests that such waving displays, which are widespread in *Habronattus* and other jumping spiders, may be a repeated or conserved adaptation for controlling receiver orientation. In addition, by quantifying male displays in increasingly complex signaling environments, I found that males assess and respond adaptively to their spatial and visual environment during communication.

In summary, this research demonstrates the importance of considering the inherent spatial constraints of signaling in shaping selection on communication behavior. The *Habronattus* group of jumping spiders provides an excellent springboard for future research on a variety of pressing questions. I found evidence of variation in males’ abilities to respond to spatial information,

suggesting that females have the potential to assess this spatio-social skill (Sih, Sinn, and Patricelli 2019) in mate choice. *Habronattus* species vary in the presence and elaboration of color ornaments, this raises the question of whether selection for behaviors that increase signaling alignment vary with the use of color in displays, and if this selection is relaxed in less colorful species. More broadly, assessing the frequency, control, and consequences of signaling alignment in other systems will help reveal previously unexplored axes on which selection may act to shape animal communication. Overall, this dissertation reveals the widespread role of spatial constraints in driving signaling behavior, and demonstrates that the spatial arrangement of signaler and receiver, and thus communication efficacy, must be managed dynamically through behavioral responses.

Appendix A Supplement to Chapter 3

Appendix Table 1. Modeling of total turns (SW experiment)

Effect of each parameter on the total number of turns towards both stimuli in the SW experiment, as determined by Poisson GLMM. Results represent model averaging of the top (2 Δ AIC) models (n = 16).

Asterisks following p-values indicate level of significance (* p < 0.05, ** p < 0.01, *** p < 0.0001). Relative

Importance scores indicate the proportion of models that include the variable.

* Effect sizes have been standardized on two SD following Gelman (Gelman 2008)

† BackgroundGrey was the reference category

†† ScorerSAE was the reference category

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value		Relative Importance
			2.5 %	97.5%				
(Intercept)	0.1527	0.1279	-0.10	0.40	1.194	0.23266		
amplitude	0.01208	0.01516	-0.01	0.05	0.797	0.42552		0.59
backgroundPhoto†	-0.06725	0.04023	-0.15	0.01	1.671	0.09466		1.00
backgroundVid	-0.3503	0.02906	-0.41	-0.29	12.052	< 2 x 10⁻¹⁶	***	1.00
backgroundVidFast	-0.1573	0.03244	-0.22	-0.09	4.849	0.0000012	***	1.00
velocity	-0.009877	0.019	-0.06	0.03	0.52	0.60326		0.69
amplitude:velocity	-0.007256	0.01973	-0.10	0.02	0.368	0.713		0.19
backgroundPhoto:velocity	0.000003898	0.02119	-0.08	0.08	0	0.99985		0.28
backgroundVid:velocity	-0.0223	0.04186	-0.16	0.00	0.533	0.59426		0.28
backgroundVidFast:velocity	0.003982	0.0227	-0.07	0.09	0.175	0.86078		0.28
cohort	-0.403	0.1228	-0.64	-0.16	3.281	0.00103	**	1.00
scorerEL††	-0.5888	0.02991	-0.65	-0.53	19.686	< 2 x 10⁻¹⁶	***	1.00
scorerJEK	0.06162	0.02572	0.01	0.11	2.396	0.01657	*	1.00
scorerNAR	-0.485	0.03054	-0.54	-0.43	15.877	< 2 x 10⁻¹⁶	***	1.00
wavingSide	-0.01031	0.01471	-0.05	0.01	0.701	0.48353		0.50

Appendix Table 2. Modeling of number of turns to waving male (SW experiment)

Effect of each parameter on the number of turns to the waving male in the SW experiment, as determined by binomial GLMM. Results represent model averaging of the top (2 ΔAIC) models (n = 8). Asterisks following p-values indicate level of significance (* p < 0.05, ** p < 0.01, *** p < 0.0001). Relative Importance scores indicate the proportion of models that include the variable.

* Effect sizes have been standardized on two SD following Gelman (Gelman 2008)

† BackgroundGrey was the reference category

†† ScorerSAE was the reference category

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value		Relative Importance
			2.5 %	97.5%				
(Intercept)	-0.067515	0.111272	-0.29	0.15	0.607	0.54404		
amplitude	0.00768	0.013927	-0.01	0.05	0.551	0.58133		0.41
backgroundPhoto†	-0.009425	0.043584	-0.09	0.08	0.216	0.82881		1.00
backgroundVid	-0.254278	0.031416	-0.32	-0.19	8.093	< 2 x 10⁻¹⁶	***	1.00
backgroundVidFast	-0.081237	0.035325	-0.15	-0.01	2.3	0.02147	*	1.00
velocity	-0.011326	0.016291	-0.06	0.01	0.695	0.48696		0.49
cohort	-0.346034	0.110347	-0.56	-0.13	3.136	0.00171	**	1.00
scorerEL††	-0.510907	0.03216	-0.57	-0.45	15.885	< 2 x 10⁻¹⁶	***	1.00
scorerJEK	0.0505	0.028651	-0.01	0.11	1.762	0.07799	.	1.00
scorerNAR	-0.440244	0.033601	-0.51	-0.37	13.101	< 2 x 10⁻¹⁶	***	1.00
wavingSide	-0.017651	0.018862	-0.06	0.00	0.936	0.34939		0.62

Appendix Table 3. Modeling of direction of first choice (SW experiment)

Effect of each parameter on direction of first choice (which stimuli the female turned towards first) in the SW experiment, as determined by binomial GLMM. Results represent model averaging of the top (2 ΔAIC) models (n = 3). Asterisks following p-values indicate level of significance (* p < 0.05, ** p < 0.01, * p < 0.0001). Relative Importance scores indicate the proportion of models that include the variable.**

*** Effect sizes have been standardized on two SD following Gelman (Gelman 2008)**

†† ScorerSAE was the reference category

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value	Relative Importance
			2.5 %	97.5%			
(Intercept)	0.247725	0.040152	0.17	0.33	6.169	< 2 x 10⁻¹⁶ ***	
amplitude	0.090896	0.040918	0.01	0.17	2.221	0.0263 *	1.00
velocity	0.009193	0.025988	-0.04	0.12	0.354	0.7235	0.26
cohort	-0.003964	0.056111	-0.11	0.11	0.071	0.9437	1.00
scorerEL††	-0.397417	0.072414	-0.54	-0.26	5.487	< 2 x 10⁻¹⁶ ***	1.00
scorerJEK	-0.443061	0.065228	-0.57	-0.32	6.792	< 2 x 10⁻¹⁶ ***	1.00
scorerNAR	0.009834	0.074959	-0.14	0.16	0.131	0.8956	1.00
wavingSide	0.053561	0.047635	-0.01	0.15	1.124	0.2609	0.73

Appendix Table 4. Modeling of total tuns (WW experiment)

Effect of each parameter on the total number of turns towards both stimuli in the WW experiment, as determined by Poisson GLMM. Results represent model averaging of the top (2 Δ AIC) models (n = 6).

Asterisks following p-values indicate level of significance (* p < 0.05, ** p < 0.01, * p < 0.0001). Relative**

Importance scores indicate the proportion of models that include the variable.

*** Effect sizes have been standardized on two SD following Gelman (Gelman 2008)**

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value	Relative Importance
			2.5 %	97.5%			
(Intercept)	0.5019141	0.1570053	0.19	0.81	3.191	0.00142 **	
amplitude	-0.0008328	0.028597	-0.12	0.11	0.029	0.97681	0.23
velocity	0.0514657	0.0612959	-0.03	0.20	0.839	0.40161	0.62
amplitude:velocity	-0.0241456	0.0754625	-0.42	0.04	0.32	0.74913	0.13
wavingSide	-0.0040041	0.0281332	-0.13	0.10	0.142	0.88702	0.21

Appendix Table 5. Modeling of number of turns to waving male (WW experiment)

Effect of each parameter on the number of turns to the waving male in the WW experiment, as determined by binomial GLMM. Results represent model averaging of the top (2 Δ AIC) models (n = 3). Asterisks following p-values indicate level of significance (* p < 0.05, ** p < 0.01, *** p < 0.0001). Relative Importance scores indicate the proportion of models that include the variable.

* Effect sizes have been standardized on two SD following Gelman (Gelman 2008)

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value	Relative Importance
			2.5 %	97.5%			
(Intercept)	0.32875	0.146199	0.04	0.62	2.244	0.0248	*
amplitude	-0.026186	0.056871	-0.16	0.09	0.46	0.6458	0.72
velocity	0.037488	0.059146	-0.07	0.18	0.633	0.5269	0.72
amplitude:velocity	-0.228533	0.179744	-0.57	-0.07	1.271	0.2039	0.72
wavingSide	0.001218	0.028472	-0.12	0.13	0.043	0.9659	0.19

Appendix Table 6. Modeling of direction of first choice (WW experiment)

Effect of each parameter on the direction of first choice (which stimuli the female turned towards first) in the WW experiment, as determined by binomial GLMM. Results represent model averaging of the top (2 Δ AIC) models (n = 4). Asterisks following p-values indicate level of significance (* p < 0.05, ** p < 0.01, * p < 0.0001). Relative Importance scores indicate the proportion of models that include the variable.**

*** Effect sizes have been standardized on two SD following Gelman (Gelman 2008)**

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value	Relative Importance
			2.5 %	97.5%			
(Intercept)	0.398493	0.106913	0.19	0.61	3.718	0.000201 ***	
amplitude	0.006513	0.078043	-0.32	0.40	0.083	0.933648	0.18
velocity	-0.013077	0.083505	-0.43	0.29	0.156	0.875824	0.19
wavingSide	-0.002518	0.076498	-0.38	0.35	0.033	0.973802	0.17

Appendix Table 7. Modeling of proportion of turns to waving male (WW experiment)

Effect of each parameter on the proportion of turns towards waving males in the WW experiment, as determined by binomial GLMM. Results represent model averaging of the top (2 Δ AIC) models (n = 6). Asterisks following p-values indicate level of significance (* p < 0.05, ** p < 0.01, *** p < 0.0001). Relative Importance scores indicate the proportion of models that include the variable.

* Effect sizes have been standardized on two SD following Gelman (Gelman 2008)

Parameter	Estimate*	Unconditional SE	95% C.I.		Z	p-value	Relative Importance
			2.5 %	97.5%			
(Intercept)	1.826388	0.203062	1.43	2.23	8.972	< 2 x 10 ⁻¹⁶	***
amplitude	-0.047963	0.119331	-0.43	0.21	0.401	0.688	0.43
velocity	-0.099738	0.151652	-0.52	0.12	0.657	0.511	0.50
amplitude:velocity	-0.11153	0.268185	-1.21	0.04	0.416	0.678	0.19
wavingSide	0.009243	0.058789	-0.23	0.39	0.157	0.875	0.11

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