10-2014

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Herberstein, Marie E.; Wignall, Anne E.; Hebets, Eileen; and Schneider, Jutta M., "Dangerous mating systems: Signal complexity, signal content and neural capacity in spiders" (2014). *Eileen Hebets Publications*. 53.
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REVIEW

Dangerous mating systems: Signal complexity, signal content and neural capacity in spiders

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Abstract

Spiders are highly efficient predators in possession of exquisite sensory capacities for ambushing prey, combined with machinery for launching rapid and determined attacks. As a consequence, any sexually motivated approach carries a risk of ending up as prey rather than as a mate. Sexual selection has shaped courtship to effectively communicate the presence, identity, motivation and/or quality of potential mates, which help ameliorate these risks. Spiders communicate this information via several sensory channels, including mechanical (e.g. vibrational), visual and/or chemical, with examples of multimodal signaling beginning to emerge in the literature. The diverse environments that spiders inhabit have further shaped courtship content and form. While our understanding of spider neurobiology remains in its infancy, recent studies are highlighting the unique and considerable capacities of spiders to process and respond to complex sexual signals. As a result, the dangerous mating systems of spiders are providing important insights into how ecology shapes the evolution of communication systems, with future work offering the potential to link this complex communication with its neural processes.

Keywords: spider, communication, vibrations, multi-modal signals, sexual cannibalism

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1. Introduction

“The male is extremely cautious in making his advances, as the female carries her coyness to a dangerous pitch” (*a description of the behavior of a male spider*, Darwin, 1871, Chapter IX, pp. 339).

The true spiders (Araneomorphae) are **all predatory** with highly diverse behavior, morphology and physiology. They are exceedingly efficient hunters possessing exquisite sensory capacities and neural motor-control (Barth, 2002). Spiders rely on taking their victims by surprise with their unexpected, rapid attacks.

For example, orb-web spiders only require a few seconds to locate and overwhelm a prey item once it hits their web (Briceño and Eberhard, 2011 and references therein). Indeed, spiders manage perfectly the transition from an absolutely motionless posture into a burst of activity.

Spiders have evolved a variety of prey capture strategies, some of which involve the use of webs. Others are ambush hunters with effective camouflage, (e.g. the jumping spider *Portia* resembles detritus; Wilcox and Jackson, 1998), while others still mimic their prey (e.g. ant mimics; Nelson and Jackson, 2011). In addition to these gross differences, hunting strategies are highly flexible and can be adjusted to the prevailing environment, even within the individual (Nelson and Jackson, 2011). However, hunting strategies entail risks of costly failure and of perception errors, as many prey can cause a spider injury or even death. Hence, it might not be surprising that spiders are capable of estimating the quality and danger posed by a potential prey or enemy before deciding how to respond (Stankowich, 2009).

The prey spectrum of spiders ranges from very broad to highly specialized. Spiders have been reported to occasionally capture vertebrates: fish, bats, birds, lizards (Nyffeler and Knornschild, 2013), but they mostly prey on insects and other spiders (Wise, 2006). **Cannibalism** is common in spiders, and conspecifics can comprise a major component of their diet (Fox, 1975). Interspecific and intraspecific cannibalism affect population dynamics and are proposed to regulate density in many species (see Wise, 2006 for a review) with the exception of social or colonial spiders that show remarkable tolerance towards conspecifics (Bilde and Lubin, 2011). When cannibalism does occur, the relative size difference between two individuals often decides who eats whom (Dor and Hénaut, 2013). Hence, for spiders it is crucial to assess the risks of becoming or gaining a meal. It is therefore likely that spiders can detect even small cues that indicate danger, and during an approach of a potentially dangerous prey, these predators can benefit from disguise and deception. Airflow, for example, is a subtle cue used to detect prey and airflow detection appears to be very acute in spiders (Bathellier et al., 2012). At the same time, spiders adjust the airstream they generate during prey approach to minimize detection by their prey, which could be other spiders (Dangles et al., 2006).

In the public perception spiders are fast and ferocious hunters but in ecology they are generally considered to be food limited (e.g. Chen and Wise, 1999) with the ability to withstand long periods of hunger (Nakamura, 1986). Foraging success has direct fitness consequences, as fitness is size and condition dependent in both sexes (Foellmer and Moya-Larano, 2007). For example, in females, fecundity is directly correlated to adult body size and to how many nutrients are stored (e.g. Head, 1995). In males, large body size generally determines resource holding capacity and mating success although life-history trade-offs might alter this relationship (Kasumovic and Andrade, 2009).

We have drawn an ecological scenario in which selection favors excellent capabilities to assess the costs and benefits of responding to prey, predators and competitors as well as rapid motor-reactions when a positive decision has been made. It is largely unknown which cues a hunting spider uses to make decisions of whether to attack or not—an interesting field in its own. Here, we are interested in exploring *how such a predatory life-style shapes mating interactions* as the curious reproductive biology of spiders sets this taxon apart from most other animals (Herberstein et al., 2011). For example, during a typical mating approach, the male has to approach a female that is very likely in hunting mode—highly alert and often considerably larger. In web-building species, the male may even have to enter her trap. It is well known that this approach can end in the death of the male through sexual cannibalism.

Sexual cannibalism, which is defined as the capture and consumption of potential or actual mating partners (Elgar, 1992), occurs in many spider species. While it is an inherent component of the mating system in at least four spider families (Miller, 2007; Schneider and Fromhage, 2010; Schwartz et al., 2013), it poses a significant threat to male and female reproductive success in most other spiders (Elgar and Schneider, 2004). Sexual cannibalism before copulation clearly entails a large cost for the male, but also for the female if she remains unmated (see Kralj-Fišer et al., 2013). Nevertheless, a male may constitute a substantial meal for a female, which may increase her survival and future reproductive prospects (Moya-Laraño et al., 2003). *The risk of cannibalism for a courting male varies with the state and the personality of a female* (Rabaneda-Bueno et al., 2008; Berning et al., 2012) as well as with the relative size differences between the sexes (Johnson, 2005; Wilder and Rypstra, 2008).

In approaching an aggressive and potentially cannibalistic female, males are expected to perceive and process information about the risks and benefits of approaching. Conversely, females should quickly recognize a mating partner and suppress the natural attack response towards movement in the web or the visual field (if she is indeed interested in mating with that particular male). The courtship display dynamics and interactions between males and females (Figure 1) likely reflect these scenarios and *here we summarize recent work on the nature of courtship signals and their perception*. Spiders, due to their fine sensorial-perceptive capacities, are able to process and respond to complex signals, although proximate neural mechanisms to date are poorly investigated.

2. Signal complexity & content

Signal complexity can be thought of as the combination of distinct, yet interconnected, components. With respect to signaling, such complexity is often categorized by the physical form, or **sensory modality**, of these distinct components. For example, *a complex signal could have multiple components that are transmitted within one or more sensory modalities* (e.g. acoustic, visual, chemical, etc.), making them *multicomponent or multimodal signals*, respectively (*sensu* Hebets and Papaj, 2005; see Fusani et al., this issue, about the complex displays of manachins).

In the most common mating systems, where males initiate courtship with prospective females, courtship signals must travel effectively through the environment, must be detected by a receptive female, and must elicit the appropriate female response (i.e. mating behavior) for a male to ultimately acquire a mating. Simultaneously, due to their cannibalistic nature, males must avoid being eaten by the female. In cannibalistic spiders, success in all stages of courtship communication (i.e. signal production, transmission, perception, and processing) is especially important, and signal form is likely influenced not only by selection for increased efficacy and information transfer, but also by selection to reduce or evade female aggression. In fact, it has been proposed that *male mate choice may be heavily selected for within these dangerous mating systems* (Bonduriansky, 2001; but see Edward and Chapman, 2011 & Beani et al., this issue [*Neuroscience & Biobehavioral Reviews* 46:4], about male mate choice in insects).

Many spider courtship displays are sequential in nature. For example, in *Cupiennius* spiders the display starts with a vibratory phase where the male and female duet, before moving onto a tactile phase (Barth, 2002). Similarly, orb-web spiders first generate vibrations as they move through the web before reaching the female where they tap her (Wignall and Herberstein, 2013a). Considering the aggressive nature of females, staggering the different elements of courtship is intuitive and may help ameliorate some of the risks involved in approaching another spider. For instance, the stages of courtship (i.e.

Figure 1. Simplified schematic of courtship signaling dynamics in spiders, with reference to neurological processing pathways (in blue). Points at which strong potential for selection has been identified are shown in red. For males of many species, errors at any stage in the process may result in him being cannibalized by the female. Note that in the initial and final stages of courtship important information (e.g. identity, intent) is exchanged between the male and female that reduces the risks of pre-copulatory cannibalism.

calling/broadcast signaling; directed courtship; tactile courtship and copulation) contain varying levels of risk, which may in turn lead to the evolution of more complex signals during riskier contexts.

The types of male courtship signals that have attracted most research include visual and vibratory signals. While chemical signals are also likely to play an important role in spider courtship, it is usually the female that emits chemical signals (e.g. Chinta et al., 2010; Gaskett, 2007). Nevertheless, it is possible that males also transmit some chemical information to females during courtship, but the identity and function of such chemicals are not well understood. Due to the paucity of information regarding male chemical signals, we limit our review to vibratory and visual courtship signals.

We focus on two main groups of spiders that utilize very different prey capture strategies and hence sensory worlds. The first group includes the web-building spiders, which encompasses orb-web, sheet-web, cob-web and gum-foot-web spiders. The second group contains the cursorial spiders, represented in this review by tropical wandering spiders, wolf spiders and jumping spiders. Below, we discuss signal complexity and signal content in these two groups. Then, we describe our current knowledge about the neural capacity of spiders in integrating courtship signals. Finally we suggest future avenues and the advances to scientific theory that may be made by studying spider communication.

2.1. Signal complexity in web-building spiders

Web building spiders rely largely on vibrations transmitted through the web for information transfer in various contexts including foraging, predator avoidance and reproduction (Clemente et al., 2005; Herberstein and Wignall, 2011). Communication via vibrations holds a special fascination for researchers, perhaps because humans lack acute vibratory sensitivity and/or because of the complex technology required to quantify vibrations. With the

advent of non-contact methods of recording vibrations, such as **laser vibrometry**, the field has made substantial advances in recent years (e.g. Landolf and Barth, 1996; Elias et al., 2006; Hebets et al., 2008; Wignall and Herberstein, 2013a).

Laser vibrometry is now widely used to record vibrations from spider webs and other substrates. It uses the Doppler shift between the emitted laser beam and its returning reflection from the web to generate a digital representation of the vibrations (for methods see Masters, 1984; Elias et al., 2003). While this technology has become increasingly available and affordable to researchers, it does have some limitations, particularly when measuring vibrations in spider webs. Laser vibrometry has a limited capacity to record vibrations with large displacements, as the amplitudes generated by courting male spiders on a silk thread can be too large for the focal depth of the laser and can move the silk thread outside the plane of the laser beam. Another major limitation for recording vibrations in spider webs is that lasers are most effective in measuring transverse vibrations (McNett et al., 2006).

Transverse vibrations in webs describe silk movement that is perpendicular to the plane of the web (Masters et al., 1986; Landolf and Barth, 1996). Other types of web vibrations that may be important in information transfer are longitudinal, lateral and/or torsional vibrations. Longitudinal vibrations describe silk movement that is parallel to the silk thread and are the least attenuated in the web (Masters et al., 1986; Masters and Markl, 1981). Landolf and Barth (1996) have shown that longitudinal vibrations are particularly important for eliciting predatory responses in *Nephila clavata* orb-web spiders. However, our current technology is limited in recording longitudinal vibrations with large displacements that are characteristic of the vibrations generated by courting males (e.g. Wignall and Herberstein, 2013a). Lateral vibrations describe silk movement that is perpendicular to the silk thread and within the plane of the web; torsional vibrations describe silk movement that rotates (twists)

along the plane of the silk thread (Masters et al., 1986). Torsional vibrations in particular have been studied very little with respect to spider behavior due to our extremely limited ability to record these types of vibrations. Most of what is known about the importance of vibrations for spiders refers to transverse vibrations.

The vibrational stimuli that web-building spiders frequently come in contact with are those generated by prey. Prey vibrations are often characterized by an initial impact vibration of particularly high amplitude and subsequent vibrations containing fast transients (rapid changes in amplitude; Barth, 1982 & Wignall and Taylor, 2011). Due to the lack of visual acuity in most web-building females (e.g. Clemente et al., 2005), it is reasonable to assume that there is *acute selection pressure on males to generate courtship vibrations that are distinct from those generated by prey* (Barth, 1997) or alternatively, to take advantage of a female's response to such a stimulus for attracting her attention. Despite a limited number of studies to date, the former idea that courtship are signals distinct from prey, is supported by papers that have quantified male courtship in spider webs. For example, in the gumfooted-web spider *Parasteatoda* sp., males produce low amplitude but highly repetitive courtship vibrations (Wignall and Taylor, 2011), quite distinct from prey vibrations. Curiously, these *Parasteatoda* signals are remarkably similar to the courtship vibrations generated by the unrelated orb-web spider *Argiope keyserlingi* (Wignall and Herberstein, 2013a), the sheet-web spider *Frontinella pyramitela* (Suter and Renkes, 1984), and the black widow spider *Latrodectus hesperus* (Vibert et al., 2014). In *A. keyserlingi*, these '**shudder**' **courtship vibrations** are generated by the male rocking forwards and backwards as he walks through the web (Wignall and Herberstein, 2013a). Individual male characteristics that can potentially be coded in these vibrations, such as male size and weight, are likely to influence these courtship vibration parameters (Wignall et al., 2014).

Describing the diversity of courtship vibrations and their significance in web-building spiders is only in its infancy and is restricted to studies where males pluck and bounce on the web, thereby generating vibrations. Whether and how stridulatory organs (e.g. Agnarsson, 2004) contribute to web-borne vibrations is currently unknown. Preliminary studies suggest that males utilize many different types of vibrations that may contain salient information for their potential mates. For instance, in the kleptoparasitic spider *Argyrodes*, males perform up to 32 different displays in the web of their much larger host spider (*Eriophora*), and presumably each display generates distinct vibrations (Whitehouse and Jackson, 1994). In *A. keyserlingi*, four different types of courtship vibrations have been described: shudders, abdominal wags, plucks and bounces (Wignall and Herberstein, 2013a). In Asian and Australian *Argiope*, male courtship contains an additional phase in which the male spins a horizontal mating thread in the female's web on which he plucks and bounces, generating a vibratory dance that progressively increases in rate and amplitude (Robinson and Robinson, 1980; Wignall and Herberstein, 2013a). The vibrations on the mating threads appear very energetically expensive and so far we have only limited resolution of the features of these vibrations. However, the information contained within male courtship vibrations has recently been the focus of experimental studies.

2.2. Signal content in web-building spiders

Courtship vibrations in the web are often discussed in terms of their function (e.g. Maklakov et al., 2003), thereby implying information content, although this is rarely tested explicitly. Potential functions include: *species identification*, *display of mate quality*, *suppression of aggression and/or stimulation of females* (e.g. Maklakov et al., 2003; Suter and Renkes, 1984; Robinson and Robinson, 1980). It is helpful to visualize the context of the courtship sequence as a guide for generating functional hypotheses related

Figure 2. Male and female St Andrew's Cross spiders, *Argiope keyserlingi*. The smaller male is at the hub of the web, performing courtship vibrations for the larger female.

to the information contained in vibrations. For example, in orb-web spiders, males enter the female orb-web via one of the anchor threads. He then traverses the dangerous prey capture region covered by sticky silks to arrive at the central hub, where the female resides (Robinson and Robinson, 1980; Figure 2).

The early stages of approach are the riskiest for any male spider but are particularly so for web-building spiders as the female may mistake him for prey entering her trap. The occurrence of such pre-copulatory cannibalism varies greatly amongst species (e.g. *Araneus*, Roggenbuck et al., 2011; *Argiope*, Herberstein et al., 2002 & Zimmer et al., 2012) and it is often difficult to discern the effects of mate rejection from mistaken identity (Wilder and Rypstra, 2008). It is logical to hypothesize however that males communicate information that inhibits attack to females (e.g. identity or intent) at these early stages. Correlative evidence supports this idea in *Argiope*: as the rate of consistent male shudders increases, female aggression (as measured by post-copulatory cannibalism rates) decreases (Wignall and Herberstein, 2013a). Manipulative playback experiments have further demonstrated that male shudder vibrations effectively delay female attack behavior, even in the presence of actual prey in the web (Wignall and Herberstein, 2013b). These results collectively suggest that shudder vibrations modulate the neural pathway that controls predatory behavior, an idea that is further supported by the apparently highly conserved nature of

shudder vibrations and their effect on females (Wignall and Herberstein, 2013b). Therefore, shudder vibrations may be tapping into very basal aspects of neural control in spiders—a promising and very exciting avenue for future exploration.

The next phase of courtship in *Argiope* is located at the central hub where the female resides (Robinson and Robinson, 1980; Wignall and Herberstein, 2013a). Despite the proximity of the male to the female at the hub, males are seemingly safe from female aggression during this stage as cannibalism is rarely observed (Herberstein and Wignall, pers obs). Whether this is the result of shudder vibrations or additional information that males provide (e.g. vibrational, pheromones, tactile stimuli, Gaskett et al., 2004; Herberstein et al., 2012) is at present unclear.

It is generally assumed that courtship displays contain quality information and vibrations may be suitable to convey such information. For example, **male size** is likely to influence the parameters of the vibrations that he can generate in the web (Reichert, 1978; Masters, 1984). Additionally, if females select for male endurance as a measure of male quality, this could be assessed via the rate and consistency of vibrations that he generates during courtship. Despite the intuitive nature of these predictions, *there is surprisingly only little and conflicting evidence to date that directly links male traits with the vibrations that he generates*. It is clear that generating vibrations is an important aspect for successful mating and fertilization (Schneider and Lesmono, 2009; Maklakov et al., 2003; Suter and Renkes, 1984); however, more recent studies that relate male traits with vibratory parameters have found surprisingly few correlations. For example, male condition did not correlate with vibratory performance (duration, rate or consistency) in *A. keyserlingi* (Wignall and Herberstein, 2013a). Similarly, *Stegodyphus lineatus* male courtship effort or condition did not correlate with his reproductive success (Maklakov et al., 2003). However, male condition positively correlated with courtship performance (rate and duration) in *Argiope radon* (Wignall et al., 2014). These conflicting results are particularly puzzling given that we have clear evidence that females prefer males that vibrate at high rates (with consistent duration) in some species (Wignall and Herberstein, 2013a). This apparent anomaly could be because we are measuring male traits that are not associated with condition, in which case more fine scale analyses of male traits may elucidate this, or due to differences in methodologies. Alternatively, vibration performance may be an honest signal of underlying genetic quality or overall performance capacity (Byers et al., 2010). Equally, these vibratory signals may be under runaway selection leading to good genes (sensu Chandler et al., 2013). While we cannot distinguish between these ultimate mechanisms, we have promising preliminary results that indicate that male *A. radon* performance is highly repeatable independent of female identity and male condition, suggesting a strong genetic component to vibratory courtship (Wignall et al., 2014).

In contrast, or in addition, to providing information, male courtship performance near the female may function to stimulate females to mate (Suter and Renkes, 1984; Maklakov et al., 2003). This may be particularly relevant in species in which mating occurs on a male-generated mating thread, requiring males to signal to the female the location of the thread for copulation (e.g. *Argiope*, Robinson and Robinson, 1980; *Araneus*, Elgar and Nash, 1988 & Roggenbuck et al., 2011; *Gasteracantha*; Elgar and Bathgate, 1996). It is unlikely that these diverse functions of courtship vibrations act in isolation. Rather, *information about male quality, identity and intent may equally contribute to stimulate the female*.

In summary, the courtship vibrations generated by male orb-web spiders are characterized by highly repetitive motifs that are distinct from prey impact vibrations. It is likely that these courtship vibrations convey more information than simple identity. However, evidence that male quality information is encoded in courtship vibrations is still patchy. Evidence that courtship vibrations reduce

female aggression raises questions as to the neural mechanisms involved.

2.3. Signal complexity in cursorial spiders

Cursorial spiders, unlike web-builders, do not utilize silk to trap prey, but pounce on prey within their reach. While in some groups (e.g. jumping spiders), sight is the predominant sense for prey location, substrate vibrations still play an important role in predatory behavior and the sense organs involved in the detection of vibrations are essentially the same as in web-building spiders (e.g. lyri-form organs; Foelix, 2011 & Herberstein and Wignall, 2011). The courtship behavior of several cursorial spider species has been extensively studied, including tropical wandering spiders, jumping spiders and wolf spiders. In these cursorial spiders, vibratory and visual courtship signals are often described. Visual displays may include pigmentation and/or dynamic movements while vibrational signals may be coupled to a substratum and generated by percussion, and/or tremulation (Uhl and Elias, 2011; Jocqué, 2005). Not unlike bird songs, vibratory signals may consist of unique syllables or elements that may be repeated throughout the display.

2.3.1. Tropical wandering spiders

Tropical wandering spiders in the genus *Cupiennius* have received a significant amount of attention in all aspects of courtship signal form, function, reception, and processing (reviewed in Barth, 2002). Male courtship displays in this genus are species-specific and are predominantly vibratory, presumably due, at least in part, to their nocturnal lifestyle. There are two principal production sites for courtship vibrations in this group: (1) the **pedipalps** (male sperm transfer organs) and (2) the **opisthosoma** (abdomen). Vibrations produced by these body parts are coupled to the plant upon which the animal resides (by transmission through the legs) and are thus transmitted to females. Each production site generates distinct signal components—in *Cupiennius salei*, for example, courtship vibrations consist of up to 50 different syllables with frequency peaks at ~75 and ~100 Hz, produced by the opisthosoma (Barth, 2002), and high frequency components (>1 kHz) produced with the pedipalps (Baurecht and Barth, 1992). Frequencies consistent with male vibratory signals (~90 Hz) propagate well, with little attenuation, on the plants frequented by *Cupiennius* (Barth, 2002), demonstrating a correspondence between signal propagation and signal form, and *suggesting selection for effective signal transmission* (i.e. efficacy-based selection, Guilford and Dawkins, 1991).

The vibratory signals produced by males during courtship are detected by the **metatarsal lyri-form slit sense organ**, with different slits (of different length) specialized to represent different courtship signal components (Baurecht and Barth, 1992, 1993). For example, the pedipalpal signals elicit responses from all slits, while the opisthosomal signals elicit responses predominantly from the longer distal slits (Baurecht and Barth, 1992). Interestingly, the opisthosomal vibrations are processed in parallel by two different types of interneurons (i.e. type I and II; Friedel and Barth, 1995). Such *parallel processing of signal components raises interesting possibilities regarding the function of multicomponent signaling* (Hebets and Papaj, 2005).

2.3.2. Jumping spiders

In jumping spiders, males and females can be so morphologically distinct as to be initially considered separate species. Males often possess tremendously colorful and elaborate secondary sexual traits that suggest *a strong role of vision in courtship displays*. This is exemplified by the *extraordinarily colorful male peacock spiders* (Figure 3). However, the discovery of vibratory songs in *Habronattus* jumping spiders (e.g. *Habronattus dosseus*; Elias et al., 2003) has

Figure 3. A male peacock spider (*Maratus volans*) displaying to a female. Photo credit: Madeline Girard.

initiated a broader research approach to incorporate additional sensory modalities in understanding courtship behavior in these groups. Among isolated mountaintop populations of *Habronattus pugillis*, for example, songs were determined to be distinct with respect to both spectral and temporal properties (Elias et al., 2006). Among 11 *Habronattus coecatus* group species, the vibratory songs alone consist of up to 20 elements, organized into functional groupings. Interestingly, these vibratory components are frequently associated with dynamic motion displays that incorporate ornamented and/or colored or patterned male body parts (Elias et al., 2012), highlighting the multimodal nature of many spider courtship displays. Within and between species, there is in fact a tight correlation between visual and vibratory signal components, suggesting that synchronizing the two modalities is important (Elias et al., 2003, 2012). In addition to this complexity, the multimodal courtship displays of some species of *Habronattus* vary temporally as well (Elias et al., 2012). Research on *Habronattus* and other jumping spiders (e.g. Maddison and Stratton, 1988; Girard et al., 2011; Gwynne and Dadour, 1985) is focused upon quantifying and characterizing the complexity of the elaborate courtship, with a few studies examining the efficacy with which display components (vibratory signals) transmit through the environment (but see Elias et al., 2004). Results suggest selection for signal efficacy, and additional studies are required to determine the potential role of female choice and/or selection for reduced female aggression in *Habronattus*.

2.3.3. Wolf spiders

The wolf spider genus *Schizocosa* has become a classic system for studying complex, multimodal signaling (reviewed in Uetz and Roberts, 2002 & Hebets et al., 2013). The monophyletic North American genus includes 23 described (and numerous undescribed) species, showing species-specific variation in the use of visual and vibratory courtship signals (Stratton, 2005). For example, some species employ relatively simple, vibration-only courtship, while others incorporate complex vibratory signals (multicomponent) plus visual signals (multimodal) involving the waving/tapping of sexually dimorphic forelegs (reviewed in Hebets et al., 2013). To date, ~13 species have been the focus of behavioral studies (reviewed in Miller et al., 1998, Bern, 2011 & Hebets et al., 2013). Complexity scores have been calculated for both visual and vibratory signal form for 10 species and they range from 1 to 4 (vibratory) and 0 to 6 (visual) (Hebets et al., 2013; Figure 4). Artificial manipulations of display components, the use of video playbacks, and/or signal ablation techniques have verified the presence

of selection for male courtship components and have highlighted the importance of interactions between signaling modalities and the complexities of mating decisions (reviewed in Hebets et al., 2013 & Uetz and Roberts, 2002). For example, a female's attention to visual signal components is modified by the presence/absence of vibratory signaling (Hebets, 2005; Stafstrom and Hebets, 2013) and her choice of mates can be dependent upon an interaction between the signaling environment and a male's foraging history (Rundus et al., 2011). Additionally, males of some wolf spider species (*Rabidosa rabida* and *Schizocosa ocreata*) are known to be flexible in the composition of their courtship displays, adjusting the make-up of display components dependent upon current signaling environments (Taylor et al., 2005; Wilgers and Hebets, 2011). Surprisingly, despite the wealth of behavioral mate choice data in this system little is known about the peripheral or central processing of courtship signals or their modality-specific reliance during foraging. Future comparative studies examining the role of distinct sensory modalities in foraging across species that have been the focus of mating trials would be illuminating in terms of increasing our understanding of how selection for courtship signal content and efficacy interact with selection for decreasing receiver aggression or foraging instinct.

2.4. Selection for signal complexity in cursorial spiders

It has been proposed that complex, multicomponent and/or multimodal signals may function to overwhelm a receiver's sensory system and ability to process information, ultimately inhibiting an adverse behavioral response (sensory overload sensu Hebets and Papaj, 2005). The taxonomic group that provided the inspiration for this hypothesis was spiders. In laboratory mating trials of both jumping spiders and wolf spiders, one gets the sense that the successful males (i.e. those acquiring a mating) are those that are able to initiate no response from a female. The sensory overload hypothesis might predict that across closely related species, those with more complex displays would experience lower rates of cannibalism, as they were more likely to overwhelm a female's sensory system. Indeed, that general pattern holds across a small number of *Schizocosa* wolf spiders, where species exhibiting more extreme sexual dimorphism in the form of elaborated forelegs, which are waved and tapped during courtship, tend to experience less cannibalism (Hebets et al., 2013). It is intriguing to entertain the possibility that complexity in this system has been driven by selection to inhibit female behavioral responses. Regardless of the function, there is evidence of selection for signal complexity as a study across 10 *Schizocosa* species demonstrated a significant correlation between visual and vibratory signal complexity (Hebets et al., 2013; Figure 4).

Individual components, or combinations of components, in complex courtship displays may also experience different selective pressures. For example, the above-mentioned comparative study across 10 *Schizocosa* species found a correlation between the importance of visual signaling in mating success (a proxy of female choice for visual signals) and visual signal complexity—suggesting the role of sexual selection in visual signal elaboration. In contrast, no relationship was found between vibratory signal complexity and vibratory signal importance and the vibratory signals were hypothesized to be selected for signal efficacy. Indeed, studies on both jumping spiders (Elias et al., 2004) and wolf spiders (Hebets et al., 2008) have demonstrated that the spectral characteristics of the vibratory signal components correspond to low signal attenuation on substrate-types characteristic of their natural signaling environment (e.g. leaf litter), suggesting selection for signal efficacy. In short, signal complexity in cursorial spiders may be an intricate combination of selection from female mate choice, effective signal transmission, and potentially reduced female aggression by inhibiting female response.

Figure 4. (A) Bayesian consensus tree based on COI sequence data for 10 species of *Schizocosa* wolf spiders. Thickened bars represent species with tibial bristles present (from Stratton, 2005). Waveforms are placed next to the species of focus and lines beneath each waveform depict 1s of courtship (modified from Figure 1 in Hebets et al., 2013); (B) *S. retrorsa*; (C) *S. royneri*.

Complexity in courtship displays may also function through interacting signals, where receiver responses to one component are different in the presence/absence of another (Hebets and Papaj, 2005). For example, as mentioned previously, female *S. uetzi* wolf spiders increase receptivity in response to an increase in the degree of ornamentation in conspecific males, but only in the presence of a vibratory signal (Hebets, 2005). Similarly, females of the wolf spider *R. rabida* prefer males with foreleg ornamentation only in the presence of vibratory signals (Wilgers and Hebets, 2012). Finally, in the conspicuously brush-legged wolf spider *Schizocosa crassipes*, females are more likely to mate with males with brushes only in the presence of vibratory signaling (Stafstrom and Hebets, 2013). These studies highlight the importance of inter-signal interactions and ultimately, the complexity with which females make mate choice decisions. Whether the unique combination of signals inhibits aggressive female response or allows appropriate identification of males (vs potential prey) is at this stage not resolved.

2.5. Selection of signal content in cursorial spiders

Given the complexity inherent in many spider courtship displays, some researchers have focused upon the potential information content of individual components. Much of this research has involved either correlations between signal form and signaler attributes, or attempted manipulations of signaler quality (typically using diet manipulations) and subsequent quantification of signal form (reviewed in Wilgers and Hebets, in press). As mentioned previously for web-building spiders, studies often test for condition-dependence—or a positive correlation between signal expression and a proxy of individual condition. Given that most content-based hypotheses of complex signal function relate to signaler attributes, it seems unlikely that such selection would be influenced by the cannibalistic nature of spiders. Nonetheless, we will briefly review a few recent studies of courtship signal content in spiders.

In a brightly colored jumping spider, *Habronattus pyrrithrix*, field collected males have bright red facial patches whose size, hue, and

chroma were found to be positively correlated with a body condition index, providing females the ability to gain information about these male attributes (Taylor et al., 2011). Subsequent diet manipulation treatments confirmed that this red coloration is dependent upon feeding history during development (i.e. juvenile diet). Similarly, elements of the vibratory signals of the wolf spiders *S. ocreata* and *Hygrolycosa rubrofasciata* were found to be condition-dependent (Mappes et al., 1996; Gibson and Uetz, 2012). In *S. ocreata*, both frequency and temporal components were good predictors of female receptivity displays (Gibson and Uetz, 2008, 2012), while female *H. rubrofasciata* preferred male drums of longer duration, with no influence of pulse rate on female choice (Parri et al., 2002). In other wolf spiders (*Schizocosa floridana* and *R. rabida*), components of both visual and vibratory signals were also condition-dependent (Rundus et al., 2011; Wilgers and Hebets, 2011). Curiously, however, in *S. floridana*, female mate choice was only dependent upon these condition-dependent signals under certain environmental conditions. Specifically, high diet males only received higher mating success in environments where visual signals could not be perceived, yet all males mated more frequently and more quickly in the presence of visual signaling (Rundus et al., 2011). These last results highlight a potential trade-off between speed and accuracy in female mate choice and such a trade-off may be exacerbated in dangerous mating systems such as cannibalistic spiders. Additionally, they highlight the potential complexity with which selection works, as it may be environment or context dependent—in fact, this is one potential explanation for why so few studies find correlations between condition-dependent signals and courtship outcome in laboratory studies of spiders. Indeed, recent work examining how resource heterogeneity throughout a spiders life can influence both phenotypic trait expression and male mating success uncovered a complex interaction between juvenile diet, adult diet, and courtship rate on mating success (Rosenthal and Hebets, 2012), highlighting the complex nature of condition-dependent trait expression and its relationship with reproductive success. We argue that this complexity is not specific to spiders, however.

3. Neural capacity in spiders

Considering the wealth of information that males may provide females and the complexity of observed courtship displays across diverse spider groups, what evidence do we have that females are able to perceive and process this complexity? Similarly, how might males process female responses and formulate appropriate adjustments to their behavior? How does information travel from the sensory organs to the **central nervous system** (CNS) and how does this influence behavior? How has the cannibalistic nature of females and their associated sensory and processing system(s) influenced courtship signal evolution—or has it? These questions remain unanswered.

Our knowledge of the spider nervous systems to date is limited to a few target species (e.g. *Cupiennius*, *Phidippus*, *Araneus*; Babu and Barth, 1984, Weltzien and Barth, 1991, & Park and Moon, 2013). In contrast to their arthropod relatives, spiders have highly condensed CNS. While many of the other arthropod groups have a chain of interconnected ganglia that extend down the length of their body (e.g. crickets), spiders instead have two compact ganglia, termed the supraesophageal and subesophageal ganglion, located anteriorly in their prosoma and separated dorso-ventrally by the esophagus (thus the name). The latter (subesophageal ganglion) is a fusion of ganglia from the pedipalps, the eight legs, and the abdominal ganglia (Barth, 2002), while the former is called the “brain” and receives inputs from the optic nerves as well as the chelicerae. In *Cupiennius*, each ganglion (supra and subesophageal) consists of ~50,000 neurons equating to ~100,000 neurons in the entire CNS (Barth, 2002). The relative contribution of various neuropil areas to total brain volume across spider species varies widely. For example, 31% of a jumping spider’s brain volume consists of the optical center while in *Cupiennius* it is 20% and only ~2% in the web-building genera *Nephila* and *Epebopus* (Weltzien and Barth, 1991). How these differences may, or may not, translate into functional differences in any aspect of behavior (e.g. prey capture) remains an open question.

The organization of the arachnid brain can be discussed from three vantage points: *visual neuropils*, *olfactory centers*, and *mechanosensation* (Strausfeld, 2012). Given that our review focuses on vision and vibration, we retain that focus here. With respect to visual processing in spiders, the primary (anterior median) and secondary (all remaining) eyes send information to distinct visual neuropils (with some cross-talk in salticids). Secondary eyes supply the brain center termed the **mushroom body**. The arthropod mushroom body is hypothesized to be an ancestral brain structure that is generally characterized by parallel fibers that arise from a dense rostral cluster of globuli cells in the protocerebrum (Strausfeld and Andrew, 2011). In insects, the mushroom body is suggested to be involved in numerous complex behaviors such as sensory integration, visual navigation, place memory, motor control, and learning and memory—particularly olfactory learning and memory (reviewed in Farris, 2005). Unfortunately, in contrast to the abundance of research conducted on insect mushroom body structure and function, relatively little is known about arachnid mushroom bodies (but see Strausfeld et al., 1998, Strausfeld et al., 2006; Strausfeld, 2012). In spiders, unlike other arachnids, the mushroom bodies appear to have assumed a role in visual processing; specifically receiving information from secondary eyes which function primarily in movement detection (Strausfeld, 2012). In contrast, the primary eyes function predominantly in discriminating shape, color (in salticids), and other characteristics of a visual scene. The principle eyes supply a succession of neuropils distinct from the secondary eyes, ultimately extending to the **arcuate body** (the third

neuropil), which is hypothesized to be a multimodal integrator convergent with that seen in insects and crustaceans (Strausfeld, 2012). Thus, in wandering spiders, jumping spiders, and wolf spiders, the visual system provides two parallel streams of information: a motion-sensitive channel (secondary eyes) and a channel that discriminates visual details such as shapes, contours, colors, surfaces, etc. It is interesting to think about the morphologies and parallel processing of spider primary and secondary eyes in terms of the evolution of mating strategies and courtship displays. For example, Strausfeld (2012) suggests that the arrangement of centrally located color displays flanked by achromatic dynamic visual displays in some salticid courtships may function to exploit a female spider’s two visual processing systems.

Spiders are heavily equipped with sensory structures capable of detecting substrate-borne vibrations and air particle movements and these sensory investments (i.e. numerous sensilla of different types) are reflected in the size of the fused *subesophageal ganglion*, which accounts for the majority of the volume of the CNS. In general, mechanosensory inputs connect with networks of local interneurons, which lead to interganglionic relays and motor neurons. What little we know about the details of these connections comes from work done on *Cupiennius*, in which the subesophageal ganglionic mass accounts for ≥85% of the total CNS volume (Barth, 2002). The number of the cells in the periphery, however, far outnumbered the number of cells in the CNS (Barth, 2002), and the numerous nerves in the periphery have synaptic connections that are not present in insects. In arachnids (as well as crustaceans), the nervous system is characterized by a complex network of synapses on all parts of afferent neurons. Such architecture provides mechanisms for inhibition or enhancement of responses to detected stimuli (Torkkeli and Panek, 2002), and the functional implications of these numerous peripheral synaptic connections are manifold, yet remain unknown (Foelix, 2011).

The role of the central and peripheral nervous system in integrating signal information has only been studied in the tropical wandering spider, *Cupiennius*. In *C. salei*, electrophysiological recordings of vibration-sensitive interneurons identified 30 neurons that were responsive to the natural courtship vibrations of conspecifics; 19 of which had projections within the subesophageal ganglion (i.e. were plurisegmental neurons; Friedel and Barth, 1995 reviewed in Barth, 2002). The significance of this region of the CNS for processing vibrational stimuli is highlighted by the finding that none of the plurisegmental neurons appeared to project into the brain. However, in a study that explored 32 mechanosensory plurisegmental interneurons, nine were found to have branches in the subesophageal mass as well as the brain (Gronenberg, 1990). Clearly, it is still too early to draw any firm conclusions about how signals are integrated, and studies are urgently needed to elaborate our base knowledge.

4. Future avenues

The extraordinary biology of spiders coupled with considerable species and signal diversity offers us an excellent system in which to investigate the function and evolution of courtship signals. The most exciting and promising areas for future research are signal complexity and multimodal signaling where spiders are at the forefront of communication and sexual selection research. While such studies often examine the maintenance of traits and behavior, the well-established phylogenetic history of spiders coupled with desirable species diversity also offers excellent opportunity to investigate the evolutionary trajectory of courtship signals and their function. Finally, the highly centralized and relatively simple nervous system in spiders suggests itself to studies seeking to connect signal form and content to neural processing.

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