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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 signalling 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.

Contents

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 behaviour of a male spider, Darwin, 1871, Chapter IX, pp. 339).

The true spiders (Araneomorphae) are **all predatory** with highly diverse behaviour, morphology and physiology. They are exceedingly efficient hunters possessing exquisite sensory capacities and

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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 favours 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 (Fig. 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 signalling, 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 behaviour) 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 and Beani et al., this issue, 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. calling/broadcast signalling; directed courtship;