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Predation on reproducing wolf spiders: access to information has differential effects on male and female survival

Ann L. Rypstra [a, *], Chad D. Hoefler [b, 1], Matthew H. Persons [c, 2]

[a] Department of Biology, Miami University, Hamilton, OH, U.S.A.
[b] Department of Biology, Arcadia University, Glenside, PA, U.S.A.
[c] Department of Biology, Susquehanna University, Selinsgrove, PA, U.S.A.

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Predation has widespread influences on animal behaviour, and reproductive activities can be particularly dangerous. Males and females differ in their reactions to sensory stimuli from predators and potential mates, which affects the risk experienced by each sex. Thus, the information available can cause differential survival and have profound implications for mating opportunities and population structure. The wolf spider, *Pardosa milvina*, detects and responds in a risk-sensitive manner to chemotactile information from a larger predator, the wolf spider *Tigrosa helluo*. Male *P. milvina* use similar chemotactile cues to find females whereas female *P. milvina* focus on the visual, and perhaps vibratory, aspects of the male display. Our aim was to document the risk posed by *T. helluo* predators on *P. milvina* during reproduction and to determine whether augmenting chemotactile information would affect that outcome. In the laboratory, we explored the effects of adding predator and/or female cues on the predatory success of *T. helluo* on *P. milvina* males or observing females. Additional cues from prospective mates or from predators enhanced male survival. The addition of female cues increased predation on females whereas predator cues augmented female survival. In field enclosures, we documented the impact of *T. helluo*, with and without additional predator cues, on the sex ratio of survivors and the reproductive success of females. Additional predator cues shifted the sex ratio towards males, however, 90% of the remaining females in that treatment produced eggsacs whereas less than 60% reproduced in female-biased populations. Thus, augmenting the available predator information shifted the risk from males to females, presumably due to differences in their sensory priorities. By altering the availability of potential mates, this shift appears to have influenced the intensity of sexual selection for this spider.

Males and females experience different levels of predation risk due to the contrasting sex roles that are implicit in any breeding system (Emlen & Oring, 1977; Kokko & Jennions, 2008; Székely, Liker, Freckleton, Fichtel, & Kappeler, 2014; Székely, Weissing, & Komdeur, 2014). By necessity, the behavioural responses of each sex are distinct but, because males and females must ultimately come together for reproduction, the reactions of one can affect the success of the other. Thus, these interactions may influence differential predation and affect the adult sex ratio of the population (Székely, Liker et al., 2014; Székely, Weissing et al., 2014). Ultimately, any shifts in the sex ratio can feedback to influence the efficacy of the mating system and further distinguish the sex roles (Fitze & Le Galliard, 2008; Liker, Freckleton, & Székely, 2013).

The detectability of the signals exchanged by males and females is a major factor that drives differential predation. In species with 'classical' sex roles, males have more outlandish characters and/or engage in more conspicuous activities that are meant to persuade females and, as a result, they are putatively under more predation pressure (Clark, Zeeff, Karson, Roberts, & Uetz, 2016; Costantini, Bruner, Fanfani, Dell'Omo, 2007; Székely, Weissing et al., 2014; Zuk & Kolluru, 1998). On the other hand, while these prominent male features attract the unwanted attention of predators, they may distract approaching females who are then targeted by the predators (Hughes, Kelley, & Banks, 2009, 2012). For example, the calls of male crickets (*Gryllodes supplicans*) are intended as an advertisement to females but end up attracting gecko (*Hemidactylus tursicus*) predators that then preferentially prey on the females (Sakaluk & Belwood, 1984). Similarly, pike cichlids (*Crenicichla alta*) approach the male mating displays of guppies, *Poecilia*

* Correspondence: A. L. Rypstra, Department of Biology, 1601 University Blvd, Miami University, Hamilton, OH 45011, U.S.A.
E-mail address: rypstral@miamioh.edu (A. L. Rypstra).
[1] *E-mail address*: hoeflerc@arcadia.edu (C. D. Hoefler).
[2] *E-mail address*: persons@susqu.edu (M. H. Persons).

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reticulata, and then consume the drab females nearby (Pocklington & Dill, 1995). Thus, the relative risk experienced by males and females during courtship and mating are not necessarily easy to predict, even when there are obvious differences in the detectability of their signals.

Some proportion of the susceptibility of animals is related to the need to communicate, which typically involves the exchange of a diversity of messages that engage multiple sensory modalities (Hebets & Papaj, 2005; Higham & Hebets, 2013; Partan & Marler, 1999, 2005; Uetz & Roberts, 2002). Cognitive limitations place constraints on the amount of information that can be processed and interpreted, thus the attention focused on one set of signals reduces the ability of animals to receive and react to other inputs (Dukas, 2002, 2004; Schmidt, Dall, & van Gils, 2010). Existing evidence suggests that the complexity of the sensory involvement, including the spatial and temporal sequence in which cues are received, affects whether and when they elicit a reaction (Clark et al., 2016; Hebets & Papaj, 2005; Munoz & Blumstein, 2012; Stephenson, 2016). In some cases, an initial stimulus serves to alert the recipient and enhance the detectability and discriminability of subsequent signals that enlist additional sensory modalities (Driver & Spence, 2004; Munoz & Blumstein, 2012; Rowe, 1999). For example, when glowlight tetras (*Hemigrammus erythrozonus*) are exposed to chemical cues from predators, they respond in a stronger and more specific manner to visual cues (Brown, Poirier, & Adrian, 2004; Wisenden, Vollbrecht, & Brown, 2004). In other instances, one sensory modality may take precedence as the primary source of environmental information or even distract individuals from making biologically relevant assessments (Blumstein, 2014; Dukas, 2004; Hartman & Abrahams, 2000). For example, when male noctuid moths (*Spodoptera littolalis*) focus their attention on the quality and quantity of female sex pheromones, they are effectively deaf to the sonar signals from predatory bats (Skals, Anderson, Kanneworff, Löfstedt, & Surlykke, 2005). These examples underscore the importance of cognitive capacity of males and females and the manner in which they prioritize their limited attention. Sex-based differences in sensory modalities, timing of information transfer and ability to react to appropriately to predator cues may translate into differences in predation risk. In this way, the sensory landscape can influence the adult sex ratio and potentially place selective pressure on the breeding system (Bro-Jørgensen, 2010).

Our goal was to examine how the availability of various cues would affect the success of a predator housed with males and females during courtship. We then documented whether the differences in predation on the sexes were sufficient to affect the adult sex ratio and reproductive success of females in seminatural populations. Wolf spiders (Lycosidae) are a useful group with which to investigate complex signalling and its impact on ecology (Clark et al., 2016; Hebets, 2011; Hebets & Papaj, 2005; Roberts, Taylor, & Uetz, 2007; Uetz, 2000). Members of this group communicate using multiple sensory modalities during foraging (Persons, 1999; Persons & Uetz, 1996), courtship (Hebets & Papaj, 2005) and mating (Uetz & Roberts, 2002). In addition, wolf spiders are amenable to manipulative studies aimed to tease apart how each one of these factors affects mating success (Rypstra, Wieg, Walker, & Persons, 2003), foraging (Persons, Walker, & Rypstra, 2002) and their susceptibility to predation (Persons, Walker, Rypstra, & Marshall, 2001). We deployed a well-characterized wolf spider system where females attract males with substrate-borne chemical and tactile cues that cause those males to respond with a conspicuous visual courtship display, possibly accompanied by vibratory signals (Rypstra et al., 2003). Both males and females can extract specific information about a common coexisting predator, also a wolf spider, from its chemical and tactile cues (Bell, Rypstra, & Persons, 2006; Persons & Rypstra, 2001; Persons et al., 2001). Thus, the nature of the cues used to detect this predator are similar to those that are used by females to attract males, but the cues used by males to attract females stimulate different sensory modalities. We predicted that the presence of predator cues would alter the survival of males and females and result in a biased sex ratio that would also affect reproductive success. Specifically, the attention that males must focus on chemotactile cues as they search for females should allow them to detect and respond to risk sooner when the same type of predator information is available. On the other hand, females, with their attention directed towards assessing the male's conspicuous display, may be less likely or less able to respond to other environmental information.

STUDY SYSTEM

The wolf spider, *Pardosa milvina* (Araneae, Lycosidae), is a particularly apt species with which to address these questions. Females advertise to males using air- and substrate-borne chemical cues (Rypstra et al., 2003; Searcy, Persons, & Rypstra, 1999). Males garner information about the female's mating status and hunger level from chemotactile cues (silk, faeces and other excreta) deposited on a surface that has been occupied by a female (Rypstra, Schlosser, Sutton, & Persons, 2009; Rypstra et al., 2003; Schlosser, 2005). Once males detect female cues, they begin to court, which ultimately lures females out of hiding places to observe and possibly mate with the male (Rypstra, Walker, & Persons, 2016; Rypstra et al., 2003). Male and female *Pardosa* also detect air- and substrate-borne chemotactile cues from a common predator, the larger wolf spider, *Tigrosa helluo* (Araneae, Lycosidae) (Persons et al., 2001; Shonewolf, Bell, Rypstra, & Persons, 2006). Their response to the chemotactile cues of *T. helluo* is costly (Persons et al., 2002) but effectively increases survival (Persons et al., 2001). Indeed, the reactions of *P. milvina* are accurately gauged to the risk posed by the *T. helluo* individual that produces the cues; *P. milvina* detect and adjust their response in a threat-sensitive manner that reflects the potential predator's size (Persons & Rypstra, 2001), sex (Lehmann, Walker, & Persons, 2004), hunger level (Bell et al., 2006) and recent diet (Persons et al., 2001). Notably, the courtship display of male *P. milvina* render them more susceptible to attack by *T. helluo*, but courting males in good condition are better able to survive than those in poor condition (Hoefler, Persons, & Rypstra, 2008).

Here we report the results of two experiments that aimed to explore the effects of chemotactile cues on the relative success of *T. helluo* preying on male or female *P. milvina* during courtship and mating. In our designs, we added additional cues in order to ensure that the subjects could detect and react to the information immediately upon entering the experimental arena. In a laboratory experiment, we tested the hypothesis that abundant chemical information regarding females and/or predators would have differential effects on the mortality of male and female *P. milvina* during courtship. Because the impact of *T. helluo* cues on behaviour and sexual selection in *P. milvina* has been documented in a variety of other situations (Hoefler et al., 2008; Persons et al., 2002, 2001; Rypstra et al., 2016), we conducted a field experiment to determine whether the effect of abundant predator information that has been observed in the laboratory was sufficient to affect the adult sex ratio and mating success of *P. milvina* populations housed with *T. helluo* in a more natural situation.

METHODS

Basic Laboratory Maintenance

All spiders were collected from fields at Miami University's Ecology Research Center, Oxford, Ohio, U.S.A. (39°31′52.68″,