Courtship behavior and coloration influence conspicuousness of wolf spiders (*Schizocosa ocreata* (Hentz)) to avian predators

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A B S T R A C T

Signalers must balance the benefits of detection by intended receivers with the costs of detection by eavesdroppers. This trade-off is exemplified by sexual signaling systems, in which signalers experience sexual selection for conspicuousness to mates as well as natural selection for crypsis to predators. In this study, we examined how courtship behavior and body coloration influenced the conspicuousness of males to avian predators in the well-studied brush-legged wolf spider system (*Schizocosa ocreata* (Hentz)). We focused on three behaviors (courtship, walking, and freezing) and two coloration schemes (natural coloration and idealized background-matching coloration). We presented captive blue jays (*Cyanocitta cristata*) with video playbacks of male spiders in a presence-absence detection task and characterized conspicuousness by measuring response latency and detectability. We found that any type of motion significantly increased detectability, and that body coloration and behavior interacted to determine detectability while the spiders were in motion. Among spiders in motion, courting spiders were detected faster than walking spiders. Stationary (frozen) spiders, in contrast, were rarely detected. These results illustrate that male *S. ocreata* can be both highly conspicuous and highly cryptic to avian predators. Thus, while we find that courtship is conspicuous to avian predators in this system, we suggest that behavioral plasticity may mitigate some of the predation costs of the sexual signal.

1. Introduction

Signaling displays can only benefit signalers if they are detected by receivers. As a consequence, conspicuousness is a major force shaping signal design (Guilford and Dawkins, 1991, 1993; Wiley, 2006). Highly conspicuous signals provide the benefit of enhanced detection and discrimination by receivers; however, signals are broadcast within a "communication network" in which they are perceived by both intended and unintended receivers alike (Brenowitz, 1982; McGregor and Dabelsteen, 1996; McGregor and Peake, 2000; McGregor, 2005; Searcy and Nowicki, 2005). When unintended receivers (known as eavesdroppers) impose significant costs, signalers face a trade-off between the benefits of detectability to receivers and the costs of detectability to eavesdroppers. Courtship displays are a prime example of this trade-off. Conspicuous courtship signals function to attract the attention of conspecific mates, but they may also attract the attention of eavesdropping predators (Magnhagen, 1991; Zuk and Kolluru, 1998). Selection on courtship displays therefore involves a balance between reproductive success and predator avoidance, and courtship signals reflect a compromise between sexual selection for conspicuousness and natural selection for crypsis.

The brush-legged wolf spider, *Schizocosa ocreata* (Hentz), is an ideal study system in which to investigate this trade-off. Courting males use complex multimodal displays and conspicuous high-contrast coloration to attract potential mates (see review in Uetz et al., 2016). These signals are broadcast within a communication network (Uetz et al., 2013), and are perceived by both intended receivers (females) and eavesdroppers (predators and competitor males). Males signal visually by tapping, waving, and arching forelegs ornamented with dark tufts, as well as seismically by drumming their legs and abdomens on the substrate and stridulating using an organ located in the pedipalps (Stratton and Uetz, 1983, 1986; Uetz and Denterlein, 1979). These traits are honest indicators of male quality (Gibson and Uetz, 2012; Uetz et al., 2002) and influence female detection and preference (Gibson and Uetz, 2008; McClintock and Uetz, 1996; Uetz and Norton, 2007; Uetz et al., 2009). The spiders themselves contrast sharply with leaf litter backgrounds due to dark lateral body coloration (Clark et al., 2011), and body coloration enhances detection by prospective mates (Uetz et al., 2010).

These same qualities also increase detection by predators, which exploit both signaling traits (Roberts and Uetz, 2008; Pruden and Uetz, 2004; Roberts et al., 2006; Clark et al., 2016) and body coloration (Clark et al., 2016). *S. ocreata* are predated by a diverse predator community, and previous research has demonstrated that different predators exploit different components of the male courtship signal (see Uetz et al. (2016) for a comprehensive review).

Previous work in this system focused primarily on terrestrial predator species, including anurans (Roberts and Uetz, 2008; Clark et al., 2016) and arthropods (Roberts et al., 2006; Pruden and Uetz, 2004). In this paper we extend our focus to an avian predator. Birds are important predators of spiders in forest communities (see Gunnarsson, 2007 for review) and likely impose distinct selection pressures on *S. ocreata* relative to the predators tested thus far. Birds are highly visual predators with excellent visual acuity and sophisticated color vision (e.g., Bowmaker et al., 1997; Hart and Hunt, 2007; Jones et al., 2007). In addition, hunting birds approach spiders from an overhead perspective rather than a lateral perspective as both terrestrial predators and female conspecifics do. The difference in perspective between avian predators and potential mates suggests that dorsal coloration, unlike lateral coloration, may be at least partially unconstrained by the conspicuousness/crypsis tradeoff. Consistent with this idea, Clark et al. (2011) found that dorsal coloration (unlike lateral coloration) falls within the spectral reflectance values of natural backgrounds. This result suggests that body coloration might be simultaneously conspicuous from a lateral perspective and cryptic from an overhead perspective.

The aim of this study was to characterize the conspicuousness of visual courtship behavior and dorsal coloration in male *S. ocreata* to an avian predator. We presented captive blue jays with video playbacks of digitized male spiders in a standard "presence/absence" detection task, focusing on three behaviors (courting, walking, and freezing) and two dorsal color patterns (natural spider coloration and an idealized background-matching coloration). We assessed conspicuousness using two parameters: detectability and response latency. To quantify detectability, we used the parameter d' from signal detection theory (Tanner and Swets, 1954). This parameter is used in communication research to measure an animal's ability to detect a signal and reflects both characteristics of the signal itself and the perceptual abilities of the receiver (for an overview see Wiley (2006)). We used these measures to rank the conspicuousness of the tested behaviors and color patterns as perceived by an avian predator.

2. Methods

2.1. Overview

We presented captive blue jays with video playbacks of digitized male spiders in an operant-style "presence/absence" detection task. Our subjects were hand-reared in the lab and had limited or no experience with arthropods or live prey; therefore, we first trained subjects to identify *Schizocosa* on a neutral background and to peck buttons to register "present" and "absent" responses. Once the subjects could recognize *Schizocosa* we began the experiment. In the experiment itself the spiders were superimposed onto a leaf litter background. We presented subjects with video playbacks at regular intervals and they pecked buttons to indicate whether a spider was present or absent on the screen. They were rewarded with food pellets for correct responses. We tested three spider behaviors: courting, walking, and freezing (stationary). To explore the effect of body coloration, we tested two dorsal patterns: natural dorsal coloration and an idealized background-matching coloration. In the latter case, we digitally altered the spiders to match the average RGB values of the leaf litter background. We tested all subjects on all six combinations of these factors and analyzed the results following a within-subjects design. To assess the relative conspicuousness of the behaviors and coloration schemes, we tracked the detectability (quantified using the parameter d') and response

latency for each stimulus over the course of the experiment. All housing and experimental procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (protocol #1408-31752A).
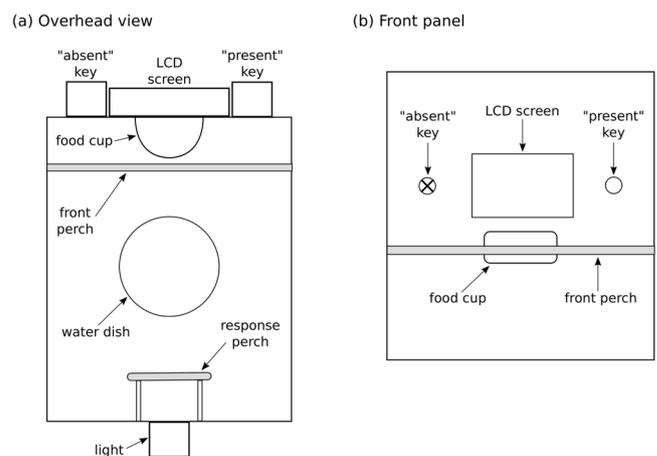
2.2. Subjects

Nine adult blue jays of unknown sex, randomly selected from a captive colony, served as our experimental predators. The birds were collected from the wild as hatchlings and hand-reared in the lab. During the experiment subjects were housed in the testing apparatus for 23 h/day (they were removed for an hour for cleaning and maintenance). Subjects ran trials from 7 am to 3 pm daily for the duration of the experiment. They received water *ad libitum* and were maintained on a 12 h light:dark cycle. The experiment operated in a closed economy; that is, subjects received all of their food from the experiment unless their body weight dropped dangerously low.

2.3. Testing apparatus

Subjects were housed individually in the testing chambers for the duration of the experiment (Fig. 1). A perch lever was located at the rear of the box directly below an indicator light. At the front of the box (Fig. 1b), stimuli were presented on an LCD screen (Accelevision LCDP7W). The "present" and "absent" keys (standard pigeon keys – MED Associates ENV-123AM) were located on either side of the screen. The absent keys were marked with an X and present keys were unmarked, and the left-right position of the two keys was randomized across subjects. The food cup and magazine light were located directly under the screen. A single stationary perch spanning the width of the box allowed subjects to access the two keys and the food cup. A Med-PC computer program (Med Associates, Burlington, VT, USA) controlled inputs and outputs and recorded data.

2.4. Video stimuli

We presented subjects with high contrast video playbacks of male brush-legged wolf spiders superimposed on an image of a leaf litter background. To create the video sequences, we videotaped walking and courting males on a green screen surface from an overhead position. Males were stimulated to court by allowing female *S. ocreata* to deposit silk pheromones on the green screen surface prior to filming. Digital still photos of natural leaf litter backgrounds in sunlight were captured with a Canon EOS 60D digital camera. The video sequences of walking and courting spiders were superimposed over the digital leaf litter

Fig. 1. An example schematic of the testing apparatus. The positions of the "present" and "absent" keys were randomized across subjects. (a) Overhead view. (b) Front panel.

Fig. 2. Two example stationary spider stimuli. Courting and walking spiders looked very similar, but the spider was performing the appropriate motion. Spider-absent stimuli looked identical but with no spider present. The spider is located inside the gray box (this box was absent in experimental stimuli). Top panel: A spider with natural coloration. Bottom panel: A spider with background-matching coloration.

background using the chroma-key function with Final Cut Pro® (v 7) software. All backgrounds and spider stimuli were appropriately scaled to life-size for presentation on the LCD screens used in our experiment.

We tested three levels of behavior: courting, walking, and stationary. In both courting and walking videos, playbacks began with spiders in different starting locations and orientations and the spiders moved across the screen. If the spider reached the edge of the screen before the subject responded, it moved offscreen and then immediately reappeared from a different location along the edge of the screen. In all stimuli, the spider was fully onscreen for at least 4 seconds at the beginning of the stimulus presentation. In stationary videos, location and orientation varied but the spiders were motionless. Stationary spiders were always completely onscreen.

We also tested two levels of dorsal patterning: natural coloration and idealized background-matching coloration (Fig. 2). To produce a spider with idealized background-matching coloration, we used average RGB values of natural leaf litter backgrounds obtained with the Apple Utilities Digital Color Meter® app (v5.10, Copyright 2001–2014 Apple Inc.). With the aperture of the app set to a size of one pixel, we haphazardly collected ten RGB samples from ten different digital photographs of natural leaf litter captured in full natural sunlight. We averaged the samples to obtain an overall RGB average of leaf litter background coloration. The background-matching spiders were altered using Final Cut Pro® to match the average RGB values of the natural leaf litter background. Natural colored spiders were not modified.

Ideally every stimulus would be unique. However, it was necessary to repeat stimuli due to constraints on generating and presenting the videos. To maximize the variability of the stimuli, we generated four

unique videos per stimulus category (e.g., courting/background-matching), randomizing the starting position of the spider on the screen. In addition, we presented versions of each video that had been rotated 180 degrees. As a result, the spider could be in any of 48 unique positions at the start of the playback (eight different positions for each of the six stimulus categories). The blank leaf litter backgrounds (spider-absent) were generated to match the spider-present stimuli and presented at equal frequency; in other words, for each presentation of a given spider-present stimulus there was (on average) a presentation of an identical leaf litter background with no spider present.

2.5. Experiment progression

Prior to the start of the experiment, we trained subjects to identify *S. ocreata* and to peck keys to register "present" and "absent" responses. In this pre-experiment training, subjects were trained to identify all six categories of spider stimuli on a neutral gray background. Subjects moved on to the experiment once they had reached a detection threshold for all stimuli. This threshold was achieved when the proportion of correct present responses exceeded the proportion of incorrect present responses by at least 50% (following the terminology outlined in the Data Analysis section: P(Hit) − P(False alarm) ≥ 0.5). All birds readily achieved this criterion, indicating that they were able to detect all the categories of spider stimuli on a neutral gray background.

Once the pre-experiment training ended, subjects started the experiment the following morning. In the experiment itself, subjects were tested on the same six spider categories, but the spiders were superimposed onto a leaf litter background. All six stimulus categories were shuffled together and presented in a pseudo-random order; the randomization was restricted in order to balance the number of presentations of spider-present/spider-absent stimuli, the different stimulus categories, and the different stimulus versions in each category. The experiment continued until 2500 total trials had been completed, typically over the course of 12–13 days. For the analysis, these trials were arranged into blocks of 250, for a total of 10 blocks.

2.6. Trial walkthrough

Trials were separated by an intertrial interval (ITI) of 110 s. When the ITI had elapsed, the computer assigned the trial type (spider-present or spider-absent) and the stimulus. A flashing light at the rear of the box then indicated that the trial was ready to begin. Subjects began the trial by hopping to a perch lever at the rear of the box, causing the flashing light to extinguish, the two response keys to illuminate, and the video playback to begin. Once the video playback started, the timer to measure the reaction time began. Subjects responded by pecking either the present key or the absent key. Once the subject responded, the computer extinguished both response keys, ended the video playback, and delivered a food reward if applicable, accompanied by a flashing magazine light. Correct responses earned three food pellets (approximately 0.062 g) and incorrect responses earned no food. If a subject did not respond in 9 min, the trial aborted, the ITI restarted, and the trial was repeated.

2.7. Data analysis

We measured two parameters of conspicuousness: detectability and reaction time (response latency). All analyses were performed in R version 3.2.3 (RCoreTeam, 2015).

We quantified detectability with a frequently-used index from signal detection theory, d' (pronounced "d prime" – Tanner and Swets, 1954). In animal communication, signal detection theory is used to characterize the detectability or discriminability of signals and reflects both signal characteristics and the perceptual abilities of the receiver (e.g., Wiley, 2006; Leonard et al., 2011). Formally, our d' value represents the

distance between the peaks of two probability distributions: one corresponding to the perceived stimulus of a spider on the leaf litter background (spider-present) and the other corresponding to a leaf litter background with no spider (spider-absent). The area of overlap of these two distributions represents the bird's uncertainty about whether a spider is present: the closer together the two peaks (and lower the d' value), the more difficult the detection task (see Tanner and Swets (1954) or Macmillan (2002) for a more complete development). The absolute value of d' is context-dependent and may vary based on factors such as environmental noise and receiver motivation. In this study, we use d' to rank the relative detectability of our stimuli while controlling as much as possible for extrinsic factors.

In a presence/absence task such as this one, d' can be estimated based on the proportion of "hits" and "false alarms." A hit is a correct present response; that is, a spider is present and the subject correctly responds that a spider is present. A false alarm is an incorrect present response; that is, no spider is present on the screen but the subject incorrectly responds that a spider is present. We calculated d' using these measures following Stanislaw and Todorov (1999). Briefly, for each subject we calculated the hit and false alarm rates for each stimulus in each block. We applied a loglinear adjustment to these rates to correct for extreme values (this is necessary when hit and false alarm rates of 0 and 1 arise). We then used the inverse phi function to convert these rates into z scores and calculated d' by taking the difference between these scores ($d' = \phi^{-1}$(hit rate) $- \phi^{-1}$(false alarm rate) – see Stanislaw and Todorov, 1999, p. 142 for details).

For hits (correct present responses), we also measured the reaction time (i.e., response latency). We analyzed this measure for walking and courting spiders only; the hit rate for stationary spiders was very low, resulting in too few data points to characterize the reaction time. The timer started when the video playback appeared on the screen and stopped when the subject pecked a key to register a response.

We focused our analysis on stable responding behavior at the end of the experiment. Subjects completed 2,500 total trials (10 blocks of 250), and for the analysis we pooled responses from the final 750 trials (3 blocks). Detectability was calculated based on hit and false alarm rates as described above. The reaction time analysis was run on raw reaction time data. We analyzed these measures using a mixed effects model with fixed effects of behavior and coloration and a random effect of subject. For the detectability analysis, we used Tukey post-hoc comparisons to determine significant differences. We also characterized detectability over the course of the entire experiment using a mixed effect model with fixed factors of behavior, coloration, and block and a random effect of subject. When sphericity assumptions were violated, we reported Greenhouse-Geiser corrected values. Error bars in plots represent standard error values that have been normalized for within-subjects analyses following the Cousineau–Morey method (Cousineau, 2005; Morey, 2008).

3. Results

Hit rates for all spider stimuli stabilized by the end of the experiment, and ranged from near 100% to near 0% (Fig. 3). We characterized the conspicuousness of the stimuli by measuring detectability and reaction time in the final three blocks (shaded area in Fig. 3). Neither response variable showed significant effects of block or block interactions in the final three blocks, indicating that responses had stabilized. Therefore, we pooled responses from these three blocks for the following analyses. The data file and the R code for the analysis are available in the supplementary material.

3.1. Detectability

The analysis of detectability (d') over the last three blocks revealed a significant interaction between coloration and behavior (Fig. 4; mixed-effects model: $F_{2,16} = 8.04$, $p = 0.02$, Greenhouse-Geisser corrected).

Unsurprisingly, stationary spiders were much less detectable than moving spiders (both walking and courting). In stationary and courting spiders, detection rates did not differ based on coloration. Walking spiders, in contrast, varied in detectability based on coloration. For natural-colored spiders, there was no difference between walking and courting spiders. But background matching spiders were significantly less detectable when walking than when courting. These trends were reflected over the course of the entire experiment as well (behavior*coloration: $F_{2,16} = 15.71$, $p < 0.001$; behavior*block: $F_{2,16} = 9.82$, $p = 0.002$).

3.2. Reaction time

Courting spiders were detected significantly faster than walking spiders (Fig. 5; $F_{1,8} = 8.09$, $p = 0.022$). The coloration*behavior interaction and the main effect of coloration were not significant.

4. Discussion

This study supports the hypothesis that courting male *S. ocreata* are at an increased risk of predation by avian predators. Motion of any kind was highly detectable, and courting spiders were detected faster than walking spiders. However, our results illustrate that males can also be highly cryptic; stationary spiders were rarely detected. In other words, males can shift between conspicuous and cryptic states with simple behavioral changes. This suggests that behavioral plasticity could mitigate much of the predation cost of courtship displays. While our virtual spiders were unable to respond to predation risk, live spiders can (and do) alter their behavior in response to both acute and environmental predator cues. Focusing on the behaviors we measured in this study, we would expect males to shift their behavior down the axis of more conspicuous to more cryptic behaviors (courtship → walking → stationary). Several studies show precisely this trend when testing the responses of wolf spiders to predation risk.

The most striking effect we found was that our subjects were highly attuned to motion; stationary spiders were much less detectable than either walking or courting spiders. It is perhaps unsurprising then that freezing is an important anti-predation strategy in *S. ocreata*. Spiders freeze in response to predator cues and decrease locomotion overall in perceived high-predation environments (Fowler-Finn and Hebets, 2011; Lohrey et al., 2009). Lohrey et al. (2009) focused on avian predator cues specifically and found that both simulated beak-pecking and acoustic playbacks of bird calls stimulated freezing behavior. These authors also compared responses of *S. ocreata* to acoustic playbacks of blue jays and non-predatory mourning doves (*Zenaida macroura*) and found that blue jay calls elicited a greater freezing response. Our results suggest that freezing is likely to be a highly effective anti-predation strategy for *S. ocreata* when faced with avian predators.

We found some support for the hypothesis that courting spiders are more vulnerable to predation than walking spiders. The relative detectability of courting and walking spiders was influenced by coloration (see the discussion below), but courting spiders in general were detected significantly more quickly than walking spiders. Clark et al. (2016) found the same result in a similar study focusing on *S. ocreata* and another visually acute predator, the American toad (*Anaxyrus americanus*). There are various reasons that courting spiders might be more visually conspicuous. For example, courting spiders adopt a more winding path and move their abdomens as well as their legs. However, given the importance of motion discussed above, a compelling explanation is that courting spiders spend more time in motion than walking spiders. Walking spiders pause periodically as they go. Courting spiders follow a similar pattern of locomotion, but the forelegs of a courting spider are almost constantly in motion. When a walking spider is stopped, it looks very similar to a frozen spider; in contrast, a courting spider is almost never completely motionless. It is interesting to note that while courting spiders were detected significantly faster,
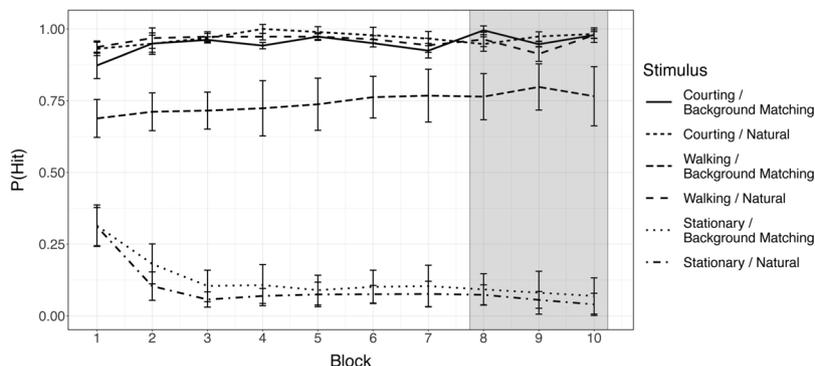
Fig. 3. Average proportion of hits (correct present responses) across subjects in each block. Error bars indicate normalized standard error. The shaded area indicates the blocks used to assess stable responding behavior in the detectability and reaction time analyses.
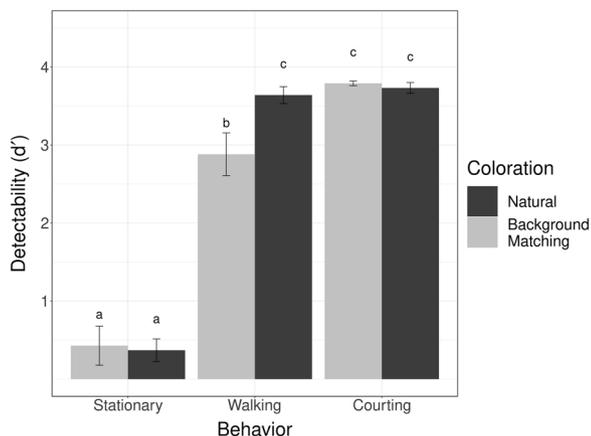

Fig. 4. Mean detectability (measured by *d′*) across subjects in the last three blocks. The variances were non-homogenous, so the reported statistics are Greenhouse-Geiser corrected values. Error bars indicate normalized standard error.
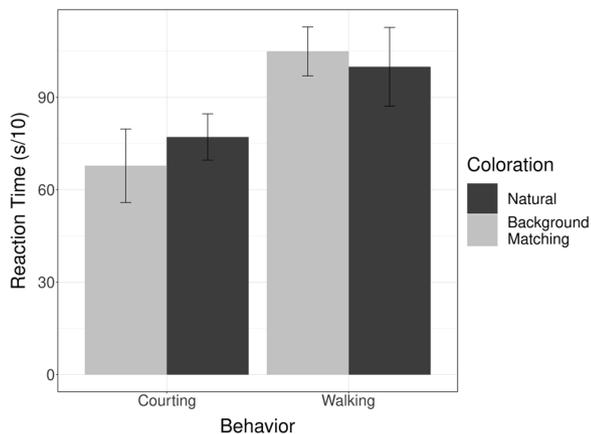

Fig. 5. Mean reaction time for courting and walking spiders in the last three blocks when the response was a hit. Error bars indicate normalized standard error.

they were not necessarily detected more often; walking natural-colored spiders had *d′* values similar to those of courting spiders. Detection speed and detectability are likely to be less independent in nature. For example, a walking spider may have more time than a courting spider to detect the presence of a predator and engage in antipredator response behaviors (such as freezing), which may result in reduced detection rates. Additionally, *S. ocreata* may alter their behavior before encountering a predator in the first place. Fowler-Finn and Hebets

(2011) tested male *S. ocreata* in the presence of chemical cues from a predatory spider (*Hogna georgicola*) and found that males decreased their courtship rate and increased their latency to begin courting. This effect was more pronounced in more highly ornamented males (Fowler-Finn and Hebets, 2011). Similar studies in other wolf spider species also found that chemical predator cues reduce or delay courtship behavior in males (Persons et al., 2001; Taylor et al., 2005; Wilgers et al., 2014). Though chemoreception of avian predator cues has not been tested, Lohrey et al. (2009) found that avian vocalizations cause male *S. ocreata* to cease courtship and to increase their latency to resume courtship relative to control sounds. This indicates that avian vocalizations could serve an analogous function to arthropod chemical cues in alerting *S. ocreata* to predation risk.

The effect of body coloration varied based on behavior. When spiders were stationary or courting, detection rates were similar for both color patterns. In contrast, when spiders were walking, spiders with natural coloration were significantly more detectable than background-matching spiders. The enhanced detectability of natural-colored spiders relative to background-matching spiders is not particularly surprising. As discussed in the introduction, lateral coloration shows high contrast with leaf litter backgrounds and enhances detection by conspecific mates (Uetz et al., 2010). Though *S. ocreata* have a broad dorsal stripe that overlaps significantly with the spectral reflectance of leaf litter background, the dark lateral coloration is also visible from an overhead perspective (Clark et al., 2011). Thus, dorsal coloration in *S. ocreata* may be the "best-case scenario" for crypticity, as it affords them some protection from overhead predators while still being conspicuous to females from a lateral perspective.

A more surprising result is that this effect was contingent upon behavior. Though natural-colored spiders were undetectable when stationary, any type of motion completely removed this effect. Background-matching spiders, in contrast, were still afforded some protection while walking. We can only speculate on the mechanism of this effect based on these data. One possibility is that stationary natural-colored spiders are actually more detectable than stationary cryptic spiders, but only when motion cues draw a predator's focus to a specific area. If a predator catches a glimpse of motion before a walking spider stops, it may be better able to locate the stationary spider once it knows where to look. For example, in our experiment a blue jay might be able to find stopped "walking" spiders if motion has directed its attention to a specific area on the screen, but might not be likely to find purely stationary spiders since it must scan the entire screen. Such effects are well-documented in the visual search literature, but our operant design did not allow us to characterize search behavior in detail.

Courting *S. ocreata* males exist within a complex communication network in which they must balance sexual selection for mate attraction and natural selection for avoidance of a diverse range of predators. This study adds a new node to this network by characterizing the role of avian predators. We find that avian predators are attuned to motion;

though courting males were highly conspicuous, stationary males were highly cryptic. These results indicate that behavioral responses could mitigate much of the cost of conspicuous courtship. Previous studies show that male wolf spiders shift away from conspicuous to cryptic behaviors in response to acute and environmental predator cues. Taken together with the results of this study, this suggests that behavioral plasticity may be an important mechanism for reducing predation by visually acute predators.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2018.12.023.

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