Consequences of complex signaling: predator detection of multimodal cues

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Animals often evolve complex signals to enhance their detectability by intended receivers. But signals that are more detectable by intended receivers may also be more likely to be intercepted by others, including predators. Courtship signaling in male *Schizocosa ocreata* wolf spiders (Lycosidae) includes morphological traits (prominent foreleg tufts) and active behaviors that together produce a complex signal with simultaneous broadcast of visual and seismic components. Females respond more readily to males with large tufts and are more likely to respond when multiple modalities (visual and seismic) are present in a complex signal. These spiders cooccur with active predators that may intercept these conspicuous courtship signals and use them as hunting cues. We used video/seismic playback to experimentally isolate and manipulate aspects of the complex signal produced by male *S. ocreata*. We found that increasing the size of a visual signal (male tufts) and increasing the complexity of the courtship signal by adding a second modality (visual plus seismic versus visual alone) increased the speed with which a common predator, the jumping spider *Phidippus clarus* (Salticidae), responded to playbacks of courting male *S. ocreata*. These results indicate that the benefits of increased signaling efficacy of large visual signaling ornaments and complex, multimodal signaling may be countered by increased predation risks. *Key words:* complex signals, Lycosidae, playback, predation, Salticidae, spider. *[Behav Ecol 18:236–240 (2007)]*

Detectability is one of the primary sources of selection acting on animal signals, and signal detection theory predicts that animals will produce courtship signals that enhance the transfer of information by standing out against background noise (Guilford and Dawkins 1991; Wiley 1994; Johnstone 1998; Rowe 1999). A growing volume of research has revealed widespread use of complex signals (Candolin 2003; Hebets and Papaj 2005; Partan and Marler 2005), involving simultaneous implementation of multiple signal components in a given mode (multicomponent signaling) or in multiple modes (multimodal signaling) (Partan and Marler 1999, 2005). Complex signals are thought to enhance efficacy by enabling signals to reliably exceed detection thresholds, increasing the probability of detection, and lowering the reaction latency of intended receivers (Rowe 1999; Candolin 2003; Hebets and Papaj 2005; Partan and Marler 2005).

One trade off of greater detectability by intended receivers is the potential for increased detectability by enemies (reviews in Burk 1982; Magnhagen 1991; Zuk and Kolluru 1998; Haynes and Yeargan 1999; Kotiaho 2001). For example, male courtship signals that are conspicuous to female receivers are also likely to become "public information" that is open to interception by others within the signal active space. This includes cue-reading predators for which the information content could be less important but for whom the signal itself reveals the presence of potential prey (Brenowitz 1982; Bradbury and Vehrencamp 1998; Zuk and Kolluru 1998; McGregor and Peake 2000; Shier 2002). There are numerous examples of predator exploitation of sexual signaling encompassing a variety of animal taxa including geckos (*Hemidactylus tursicus*, Sakaluk and Belwood 1984), wolf spiders (*Hygrolycosa rubrofasciata*, Kotiaho et al. 1998), and swordtail fish (*Xiphophorus helleri*, Basolo and

Wagner 2004; *Xiphophorus multilineatus*, Rosenthal et al. 2001). Previous studies have focused on individual signal components or signaling modes, despite the fact that communication in many animal signaler/receiver models is considerably more complex (Zuk and Kolluru 1998), and although complex communication has attracted increasing attention in recent years, there has been surprisingly little research investigating the associated costs (Hebets and Papaj 2005).

Courtship signaling in male wolf spiders of the genus *Schizocosa* often involves multiple modes (Uetz 2000; Uetz and Roberts 2002; Hebets and Papaj 2005), usually concurrent visual and seismic components (Hebets and Uetz 1999). In male *Schizocosa ocreata*, courtship includes active behaviors (waving and tapping of the forelegs, seismic communication by stridulation and percussion) and static morphological traits (tufts of bristles on the forelegs) that are presented simultaneously to females as components of a complex signal (reviewed in Uetz 2000; Uetz and Roberts 2002). Males broadcast sexual signals as they search for females in their complex leaf-litter habitat (Scheffer et al. 1996). In laboratory studies, females prefer males with larger and/or more vigorous signal attributes, and this is thought to have resulted from selection for increased conspicuousness of male signals in each modality (Uetz 2000), but has selection for increased detectability of signals been countered by increased risk of predation? In this study, we use video and seismic playback experiments to investigate whether complex signaling traits that result in increased efficacy of intersexual communication (i.e., multimodal, visual and seismic signals, and enlarged leg tufts of *S. ocreata* males) are associated with heightened predation risk from a common predator.

METHODS

General methods

In this study, jumping spiders were chosen as representative predators for several reasons. Jumping spiders rely on visual

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cues when hunting (Forster 1982; Foelix 1996) but can also use seismic cues (Elias et al. 2003, 2005). Jumping spiders respond consistently with predatory behavior to video playback of "virtual prey" (Clark and Uetz 1990; Roberts JA, personal observation). Jumping spiders of the genus *Phidippus*, in particular, were chosen because 1) they are the largest jumping spiders occurring in North America and are similar in body size to *S. ocreata* (Kaston 1978; Maddison and Schulz 2004); 2) they are common generalist predators in a variety of habitats and actively hunt using both visual and seismic cues from prey (Jackson 1986; Foelix 1996); 3) several species are sympatric with *Schizocosa* and take *S. ocreata* as prey (Kaston 1978; Maddison and Schulz 2004; Roberts JA, personal observation; Wise and Chen 1999); 4) they are diurnally active, and their period of foraging activity overlaps with that of male *S. ocreata* courtship activity (Givens 1978; Cady 1984). *Phidippus clarus* were collected in summer 2001 by sweep netting in oldfield habitats in York County, Maine, USA. Only adult females were collected for use in these experiments as female spiders are generally more rapacious and likely to respond with predatory behavior (Givens 1978; Walker and Rypstra 2002).

Phidippus clarus were transported from the field to the laboratory in Cincinnati, Ohio, USA, where they were maintained individually in opaque plastic containers (480 ml, 100 mm diameter), visually isolated from other spiders. Each container was furnished with a 50-mm length of garden hose providing environmental complexity and space for the construction of a retreat (Carducci and Jakob 2000). All spiders were provided water ad libitum in a moistened cotton wick, and were fed one subadult cricket weekly (at the end of each day of trials during the testing period, maintaining a 7-day feeding cycle), to standardize hunger levels. Spiders were kept at a temperature of 22–24 °C and a light:dark photoperiod of 13:11 h.

Playback stimuli

To avoid pseudoreplication inherent to many playback studies (see McGregor 2000), 3 different "exemplars" were created for use in this study from recordings of individual male *S. ocreata*. In spring and summer of 2000, recordings of 26 courting male *S. ocreata* were made with a Canon XL1 DV camcorder with a HOYA +2 diopter close-up lens to create a video library of males from which to select exemplars. An accelerometer (PCB Piezotronics, New York, NY; model 352C65) was attached to the floor of the arena out of the camera's field of view and used to record seismic signals. Vibrations produced by the courting spider were recorded on the video sound track (16 bit, 48 kHz) by the accelerometer via an amplifying signal conditioner (PCB Piezotronics, New York, NY; model 480E09; X100 gain). To minimize background noise, recordings were made in a sound-attenuating room.

As exemplars for this study, we chose 3 males representing a range of different sizes from the suite of recordings where males performed a full repertoire of displays within camera view. Video/audio clips of male signaling behavior were transferred to computer using video capture and editing software (Adobe Premiere, v5.1). Clips of signaling behavior of each selected male were cut and pasted into a 30-s sequence of activity that was continuously looped during playback.

To collect reference data on which to base manipulations of male tuft size in the selected exemplars, a set of 60 male *S. ocreata* were collected as adults from the Cincinnati Nature Center, Clermont County, Ohio, USA, throughout the spring of 2000. Immediately on return to the laboratory, males were humanely sacrificed using CO_2 and placed in 70% ethanol to preserve them in "field condition." The cephalothorax and forelegs (bearing tufts) were digitally photographed using a Pixera-Pro, 1.3 megapixel camera attached to a Wild M3 stereomicroscope. Digital photographs were used to measure cephalothorax width (a common measure of spider body size) and tuft area of both foreleg tufts of each preserved specimen. Measurements were made using ImageTools (v1.2), a freeware program available from the University of Texas. Using the measurements of this set of males, we calculated the regression of average tuft area (average of both foreleg measurements) on cephalothorax width. The residuals of this regression, used to represent size-corrected variation in tuft area, were used in manipulations of tuft area of exemplar males.

The video channel (visual stimulus only) of each exemplar was manipulated frame-by-frame using Adobe Photoshop (v5.0) to adjust strictly male tuft size and create multiple representative visual stimuli. We adjusted tuft size to the appropriate fifth percentile (reduced tufts video), population mean (natural tufts video), and 95th percentile (enlarged tufts video) values for a given male size. The seismic component was not manipulated. Thus for each exemplar ($n = 3$), there were 6 possible playback combinations; 3 levels of tuft size (reduced, natural, enlarged), and for each tuft size, the presence or absence of the seismic component of male courtship. The end result was 2 levels of signal complexity (unimodal-visual vs. multimodal-visual and seismic) for each exemplar male.

Playback methods

The visual component of courtship, scaled to life size, was displayed on a 68.6 mm LCD video screen (RCA Thomson Consumer Electronics Inc., Indianapolis, IN; model 16-3051) in a circular video playback arena (150 mm diameter) used previously (McClintock and Uetz 1996; Uetz and Smith 1999), which kept predators between 10 and 160 mm from the video screen. The arena was modified to include a miniature speaker (Koss, Milwaukee, WI; model 115071) mounted below the substrate for playback of seismic courtship in the multimodal (complex) signal treatments (Uetz and Roberts 2002). The substrate in these experiments, sheet metal (brushed aluminum, $280 \times 200 \times 1$ mm) elevated above vibration-dampening insulation (Owens Corning, $300 \times 300 \times 100$ mm) with stainless steel bolts, was selected to provide a substrate with low seismic signal attenuation properties. Seismic playback accompanying each exemplar was calibrated with a Bruel and Kjaer accelerometer (type 4366) and sound level meter (type 2203) to levels produced by live male *S. ocreata* courting in the same apparatus.

Experimental design and analysis

Laboratory playback methodology was chosen for this study because predation events are unpredictable and difficult to observe in the field. Also, live predation experiments are difficult to stage in the laboratory where individual variation in prey activity and small differences in the relative orientation of predator to prey at the start of a trial may override variation in the characteristics of interest. We used a repeated measures design where each individual predator was presented with all of the 6 video/seismic combinations (see Playback stimuli above) of a given exemplar ($n = 21$ total spiders: 7 spiders randomly assigned to each exemplar at the start of the experiment, 3 exemplars). On each day of trials, individuals were selected in random order and presented with one of the 6 treatment categories (presentation order was determined prior to the start of experiments using a random numbers table) that varied in combination of tuft size or presence/absence of seismic courtship. In total, there were 6 days of trials for each predator, with 1 week separating each day of trials to control

Table 1

Summary of analysis of variance *F* values for model effects—reaction latency (ln transformed) of jumping spider predators (*P. clarus*) exposed to video and seismic playback exemplars of male *S. ocreata* courtship elements

Source	df	Mean square	*F*,df	*F*
Tuft size	2	2.471	2,4	8.4*
Modality	1	2.423	1,2	151.4***
Exemplar	2	0.086	2,18	0.1
Individual (exemplar)	18	1.095	—	—
Tuft size × modality	2	0.280	2,4	1.0
Tuft size × exemplar	4	0.296	4,36	0.7
Modality × exemplar	2	0.016	2,18	0.0
Modality × individual (exemplar)	18	0.692	—	—
Tuft size × individual (exemplar)	36	0.444	—	—
Tuft × modality × exemplar	4	0.280	4,35	0.4
Tuft × modality × individual (exemplar)	35	0.806	—	—

* $P < 0.05$; *** $P < 0.001$.

Figure 1
Mean reaction latency (s) (+standard error), pooled across exemplars, of jumping spider (*P. clarus*) predators ($N = 21$) exposed to playback stimuli of prey (male *S. ocreata*) courtship elements: visual stimulus only or visual stimulus plus seismic stimulus. For the tuft size treatment factor, shared letters above bars indicate no significant difference by Tukey–Kramer HSD post hoc analysis.

for hunger and maintain response rate while minimizing the potential for habituation (Pruden and Uetz 2004).

In each trial, the predator was placed under an opaque vial and allowed to acclimate for 2 min. Trials commenced when the vial was lifted. In trials involving seismic courtship, the sound channel was activated simultaneously with release of the predator from the vial. Latency to orient to the video stimulus (turning to direct the image-forming median eyes to a stimulus source, Clark and Uetz 1990) was scored for each individual. Trials were stopped prior to any capture attempt to minimize habituation. Trials were videotaped from above using a miniature video camera (Puget Sound Instrument Company Inc., Tacoma, WA; model WAT-902C) connected to a VCR, allowing an independent observer to verify latency to orient scores determined by the experimenter. Throughout the experiment, only 2 predators failed to respond to a stimulus within 5 min (in only a single trial each). These were scored as "no response" for that stimulus and as there were so few cases were left blank (missing cells) in the subsequent analysis.

Latency to event data is typically analyzed using survival regression analysis (Moya-Larano and Wise 2000). Unfortunately, this method is not sufficient to handle the nested, repeated measures data generated by multiple exemplar playback studies. As such, latency to orient (reaction latency) was analyzed using mixed model, nested analysis of variance, with appropriate *F* tests constructed following the method of Scheffé (1959) (Table 1). Latency data were not normally distributed and were natural log (ln) transformed for analysis. Two random factors, "exemplar" and "individual within exemplar," and 2 fixed factors, "tuft size" (small, average, large) and "modality," (visual vs. visual and seismic) were included in the model (Table 1). Mean square values for the calculation of *F* tests were obtained using SPSS (v11.0).

RESULTS

Phidippus clarus jumping spiders responded with orientation behavior to playback of male *S. ocreata* courtship elements in all combinations with an overall response rate of 98.4% (124 of 126 total trials) within the 5-min trial period. Latency from the onset of video stimulus presentation until orientation by *P. clarus* was significantly affected both by variation in foreleg tuft size of exemplar males and by signal complexity (Table 1, Figure 1). Predators oriented sooner when both visual and
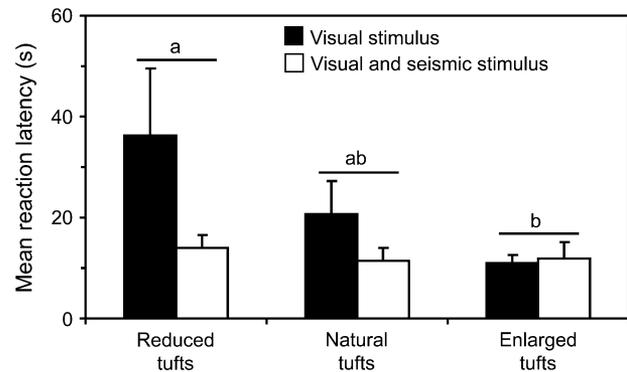
seismic modalities were present. Tukey post hoc analysis revealed that *P. clarus* responded sooner when presented with videos of "enlarged tuft" *S. ocreata* males than when presented with "reduced tuft" males (Zar 1999) (Figure 1).

DISCUSSION

Together, results indicate that increases in size of a visual signaling ornament and the addition of multiple sensory cues can both result in added risk of detection by predators for species using complex signals in communication. The predatory jumping spider *P. clarus* oriented sooner when size of leg tufts in male *S. ocreata* wolf spiders was increased (Table 1, Figure 1). This suggests that for *S. ocreata* males, investment in a morphological visual signaling trait that increases sexual success (Uetz 2000; Uetz and Roberts 2002) also carries a burden of increased risk of detection by predators. Additionally, increased signal complexity (by incorporation of seismic and visual cues into multimodal male courtship using simultaneous video and seismic playback) lowered overall reaction latency of *P. clarus* (Table 1, Figure 1), suggesting increased risk of predation when both modalities are present and detectable.

We used high contrast video and seismic playback to present multiple components of male *S. ocreata* wolf spider courtship to jumping spider predators (*P. clarus*) because playback experiments allow specific manipulation of aspects of the signal itself while holding all other aspects of signaler behavior, such as vigor or intensity, constant (reviewed in Oliviera et al. 2000). This approach ensured that signals were above detection thresholds and would be readily detectable against background noise (Rowe 1999). The high response rate (98.4%) for this predator species indicates that both the detection threshold and detection probability factors were met.

The seemingly uniform response of jumping spider predators to multimodal cues regardless of tuft size (Figure 1) may argue for consideration of "intersensory facilitation," where simultaneous processing of signals in 2 sensory modes results in greatly reduced latency of response (see Rowe 1999). If that is the case, the presence of signals in multiple modes may serve to prime the dominant sensory mode (in this case visual), reducing latency to orient to levels where variation due to differences in visual signals is no longer detectable. Alternatively, the overall decreased latency to orient may suggest that seismic signals are more important to these predators

than information in visual cues. However, this seems unlikely, given that jumping spiders are thought to rely on visual cues (Forster 1982, 1985; Jackson 1982, 1986). To address this issue, at the conclusion of the experiment we tested each jumping spider predator for latency to orient to seismic cues alone. The overall response rate to seismic cues alone was 90% (19/21), and the mean latency to orient to seismic cues, across exemplars, was 25 ± 8.3 s. Although not directly comparable statistically, this value is approximately equivalent to the mean latency to orient to visual cues (20.7 ± 6.5 s) and somewhat longer than the mean latency to orient to multimodal cues (11.3 ± 2.6 s), across exemplars. These results suggest visual cues may be more important than seismic cues, as predicted, and that orientation to courting male *S. ocreata* by predatory *P. clarus* is facilitated by complex signals containing seismic and visual cues.

Elaborate, complex courtship signals may arise through sexual selection and/or constraints on signal efficacy imposed by the environment selecting for high contrast, detectable signals (Ryan 1994; Wiley 1994). Irrespective of how they evolved and are maintained in a given communication system, complex courtship signals are likely to increase predator detection (Zuk and Kolluru 1998; except see Stoddard 1999; Cummings et al. 2003). Male *S. ocreata* exhibit multiple morphological traits and behaviors that are important in mate attraction (review in Uetz 2000; Uetz and Roberts 2002), and these same traits are also likely to play a role in overcoming constraints on signal efficacy imposed by the complex leaf-litter habitat where the spiders interact. The complexity or "patchiness" of the leaf-litter environment increases the variability and unpredictability of single-mode transmission of visual or seismic signals (Scheffer et al. 1996). As male *S. ocreata* signal and move about frequently (Cady 1984), communication in different sensory modes is intermittently enabled and/or disabled as they move from surface to surface (Roberts JA and Uetz GW, personal observation). Complex multimodal courtship signals are assumed to be highly effective in this habitat (Scheffer et al. 1996), but the results of this study clearly indicate that aspects of signals that enable detection by females also have the potential to significantly increase predation risk.

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