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Aspects of courtship risks and mating success in the dimorphic jumping spider, *Maevia inclemens* (Araneae: Salticidae)

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Abstract. The jumping spider *Maevia inclemens* (Walckenaer, 1837) is unusual because there are two male types, tufted (T) and gray (G). We investigated the risks of predation associated with the different courtship strategies by testing the response of the predatory jumping spider *Phidippus audax* (Hentz, 1845) to T and G courtship display, to ascertain if the two morphs were equally noticeable. We then tested the courting responses of T and G in the presence of a conspecific mate and a potential predator (*P. audax*). For the first experiment, we used computer-animation techniques to present two different views of courting males: *face-on* view as a female might see a courting male; and *45°-above* view as may be seen from the perspective of a predator hunting in the vegetation. Visual orientation distance to the courting male images was used as an estimate of predation risk. Results demonstrated that risk of visual detection was not equal for the males; *P. audax* oriented to G at significantly greater distances than to T. From the *45°-above* view, the apparent size of courting G males measured approximately three times greater than that of T males, suggesting that from this point of view, T may be less conspicuous to predators. In our second experiment, T and G responded differently when courting a conspecific female if a live predator had recently been or remained in view of the male. Fewer G males courted than T males and the courtship latency was significantly longer for G than for T. The visibility of T and G males to both females and potential predators may help to understand how these different, but equally successful, courtship strategies are maintained.

Keywords: Predation risk, predator attraction, male dimorphism, video playback, computer animated stimuli

Male courtship displays have evolved to attract female attention and this can ultimately lead to successful mating (Darwin 1871; Andersson 1994; Busso & Rabosky 2016). However, the obvious benefits of courtship are not without risk. Conspicuous male displays and coloration may be energetically costly, attract predators, or reduce opportunities for escape from hungry conspecific females (Moodie 1972; Haas 1976; Daly 1978; Burk 1982; Gwynne 1989; Lima & Dill 1990; Magnhagen 1991; Candolin & Voigt 1998; Fowler-Finn & Hebets 2011; Marshall et al. 2015; Clark et al. 2016). Courting males of some species may reduce how detectable they are to a potential predator by decreasing the intensity of their courtship display (Hastings 1991; Fuller & Berglund 1996), or switching to alternative reproductive strategies (Cade 1979; Lloyd 1984; Godin 1995). For very small species such as spiders, conspicuous male displays seem particularly risky. Clark et al. (2016) found that courting male wolf spiders *Schizocosa ocreata* (Hentz, 1844) have a higher risk of visual detection by predatory toads than do non-courting (walking) males. In jumping spiders (Salticidae), Bulbert et al. (2015) demonstrated that female *Cosmophasis umbratica* Simon, 1903 are more attracted to males that reflect UV; however, the predatory jumping spider *Portia labiata* (Thorell, 1887) uses UV reflectance to cue in on prey, putting UV attractive males at higher risk of predation.

Species exhibiting polymorphism, or the presence of at least two variants within a population, are relatively common in nature (Gray & McKinnon 2007). Polymorphic species can be useful for investigating the evolution of male traits because different selection pressures are likely to have favored the different male variants within the population (Clark & Morjan 2001). Here, we explore how predation risk may have influenced the evolution of different courtship displays in the dimorphic jumping spider, *Maevia inclemens* (Walckenaer, 1837).

Maevia inclemens is an unusual jumping spider (Salticidae) because there are two male morphs that are strikingly distinct not only in morphology but also in courtship behavior (Clark 1994). The tufted (T) male morph has a black body, three rows of setae on the anterior cephalothorax, black pedipalps and white legs. After orienting to the female, the T male generally begins courting by standing up in place, assuming a stilting posture approximately 9 cm from her. He then begins wagging his abdomen side-to-side and simultaneously waving the first pair of legs back and forth vigorously towards her. The gray (G) male morph lacks the tufts but has a white stripe above the eyes; the body and legs are striped and the pedipalps are bright orange in color. The G male initiates courtship much closer to the female (about 3 cm) by lowering his body to the substratum, pointing the first two pair of walking legs forward in a triangle-like configuration, and sidling back and forth (Clark & Uetz 1993; Clark 1994). Although males differ dramatically in behavior and morphology, a receptive female generally mates with the first male that attracts her attention without preferring one male type over the other (Clark & Uetz 1992).

Although we still do not understand the selection pressures that produced two completely different male strategies for female attraction (see Busso & Rabosky 2016 for a recent review), cannibalistic predation pressure from females may have been important in the evolution of the male dimorphism for *M. inclemens*. In a study testing female *M. inclemens* attraction to male courtship behavior, Clark & Morjan (2001) found a trade-off between the benefits of attracting her attention at a distance and initiating courtship in close proximity to the female. Whereas T males have the advantage of female attraction at greater distances than G males, T males courting within 4 cm of the female experienced a higher risk of attack than the G males courting within the same proximity. These results support the hypothesis that predation pressure from cannibalistic females may impose different risks for the dimorphic males.

These small male spiders live in a world of multiple predation risks, including conspecific females, heterospecific spiders and other predatory invertebrates and vertebrates. However, it is still unknown if the different courtship displays also attract the attention of nearby predators. Might a predatory spider respond differently to these displaying males, and conversely might the males alter their behaviors when they sense a nearby threat? If male courtship display reduces effort or increases the success of attracting a female, the cost of courtship display can be measured by the conspicuousness to predators and the alteration of behavior in response to a potential predator. To explore how the risk of predation may have selected for different courtship behaviors in *M. inclemens,* we used a two-fold approach. First, we examined the responses of a predatory heterospecific jumping spider, *Phidippus audax* (Hentz, 1845), to courting male *M. inclemens* (both T & G) to determine if the male morphs were equally attractive to the predator. Second, we explored the influences of the presence of a predatory spider on the courting activities of male *M. inclemens* (both T & G).

METHODS

Mature male and female *M. inclemens* and mature female *P. audax* were collected by hand and sweep net in May–June of 1995 in southwestern Ohio, at the Cincinnati Nature Center in Clermont Co., OH, U.S.A. The daring or bold jumping spider, *P. audax (*Araneae: Salticidae), is a known araneophagic species (Edwards & Jackson 1993) and was chosen as the potential predator for this study because they occur sympatrically with *M. inclemens* and have been seen to prey upon them in the field (Clark, unpublished data). All spiders were maintained in the laboratory at Alma College, housed in circular plastic deli containers measuring 12 cm (diam) x 4 cm (height). A diet of domestic crickets, *Acheta domesticus* (Linnaeus, 1758), obtained from Flukers Cricket Farm (Portland, LA) and fruit flies *(Drosophila* sp.) cultured at Alma College was provided weekly, and water was available *ad libitum*. Voucher specimens of *M. inclemens and P. audax* are on deposit at University of Cincinnati and Alma College. To ensure that the predators were hungry and therefore more likely to respond to prey, each *P. audax* was food deprived for two days prior to being used in an experiment. All *P. audax* used throughout these experiments were adult and similar in size. Since male jumping spiders rarely court heterospecifics and since salticids are known to respond appropriately to computer-animated stimuli (hereafter CAS) (Clark & Uetz 1990, 1992, 1993), female *P. audax* were shown CAS sequences of each male morph (T and G) performing its morph-specific phase I courtship display (see Clark 1994). Specifically, both face-on and 45°-above view CAS were created of courting T and G males, for a total of four stimuli to be shown to the predator test subjects (see video S1 Gray-3D, online at http://dx.doi.org/101636/JoA-S-16-029.s1 and video S2 Tuft-3D, online at http://dx.doi.org/101636/JoA-S-16-029.s2). Although similar in physical size, when T and G court they assume different postures and initiate courtship at different distances from the female. The T male stands up, making himself appear as large as possible, but courts further from the female. The G male crouches, minimizing his apparent size, and courts more closely to the female. At their morph-specific courting distance, they present essentially the same size visual image (=visual target area) to the female (see Clark & Uetz 1993).

Construction of computer-animated courtship displays.—*Face-on computer-animated stimuli (CAS):* Face-on CAS were constructed by digitizing raw video footage of courting males of T and G morphs in phase I courtship display (see Clark & Uetz 1990, 1992, 1993 for details on constructing and appropriately sizing video stimuli). Each CAS sequence was standardized by placing the courting male against a plain background (Pantone 312 CVU), and then set to the mean movement rate of live courting males: T morph (n = 8): leg waves, $\bar{X} = 10.37$/sec, $SD = 1.7$; abdominal swings, $\bar{X} = 2.5$/sec, $SD = 0.75$; pedipalp waves, $\bar{X} = 4.3$/sec, $SD = 1.1$; G morph (n = 8): sidle back and forth, $\bar{X} = 14.25$ mm/sec, $SD = 3.1$. The individual video frames were sequenced into a QuickTime movie loop with pixel dimensions of 640 (w) x 480 (h) and a frame rate of 29.97 frames per second. Each CAS was then downloaded to a Panasonic AG-1970 videocassette recorder (VCR) and stored on separate S-VHS tapes. Finally, the courting male CAS were presented life-size on a Sony Watchman (FDL 310) mini-television.

45°-above view computer-animated stimuli: Since a predatory spider may be hunting in the vegetation somewhere above the courting male, we constructed 3-dimensional CAS that simulated the view a predator would see from a 45° angle above the T and G morphs performing phase I courtship displays. These life-size animations were created using Swivel 3D Professional (v 2.0.4) by first building a 3-D skeleton over raw video footage of courting males and then superimposing digital "skins" on the skeleton. The "skins" used color patterns derived from photos of live T and G males. Morph-specific postures and movements (set to the average display movements described above for the *Face-on* CAS) were animated and then rotated to create the 45°-above view CAS.

Visual target area.—Although the T and G males are similar in absolute size, both their courting postures (stilting or body-lowered) as well as the angle from which they are viewed (*Face-on* and *45°-above*) change their apparent sizes (i.e., the visual target area). The CAS were carefully scaled to reflect these morph-specific differences. The visual target area was estimated from digital still photographs of courting males using NIH Image (v 1.59) (Fig. 1). Eight different males of each morph were photographed in a slightly different position of their morph-specific phase I courtship display. Using NIH Image and a mm ruler size standard, the perimeter of each male was traced and the visual target area of the image was estimated. To be consistent, eight different positions of the 3D computer-animated male stimuli were digitally "captured" using the camera snapshot mode in Swivel and the area was estimated from jpeg pictures using NIH Image.

Experiment I: Predator attraction to male *M. inclemens* morph-specific courtship behaviors.—*Predator to prey orientation distance:* Ten female predators (*P. audax*) were randomly assigned to view each of the four stimuli (n = 40 trials). All

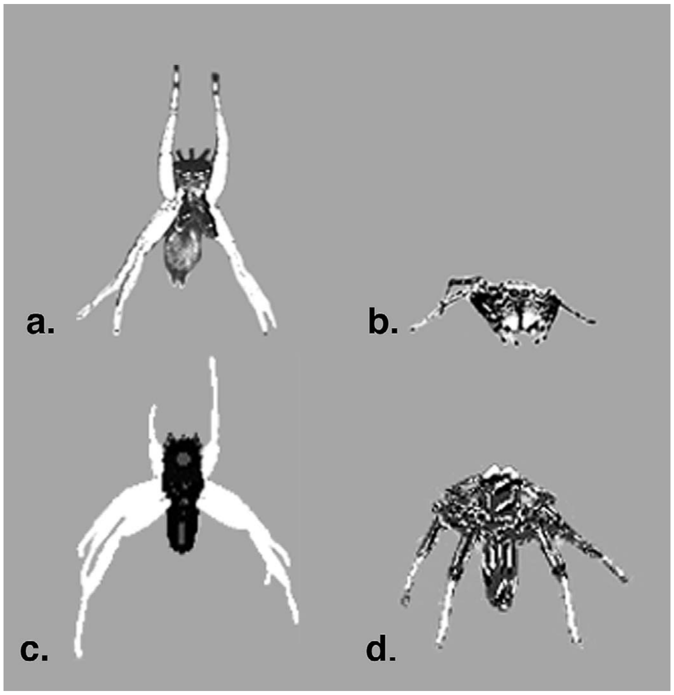

Figure 1.—Views of the video stimuli used to test predator orientation response: face-on view (a) tufted morph phase I courtship posture; (b) gray morph phase I courtship posture; 45°-view (c) tufted morph; (d) gray morph.

trials were videotaped from above using a Panasonic HD 5100HS video camera and recorded on a VCR. Each *P. audax* (predator) was scored for the furthest distance at which it oriented to the courting male *M. inclemens* stimulus.

Spiders were placed in a covered rectangular plastic viewing container measuring 5.3 cm (l) x 4.1 cm (w) x 2.7 cm (h) with a thin glass front (0.6 mm). To present the video stimuli to the test subjects, a Sony Watchman (FDL-310) television was fixed to one end of a 75 cm long runway that was marked off in 1 cm increments. The spider was placed on the runway outside of its visual response range of the stimulus (60 cm). The CAS was then started and the cover of the viewing container was removed. The test spider was given one minute to visually orient to the CAS. If no response occurred within the allotted time, the cover was replaced and the viewing container was moved closer to the CAS in 10 cm increments. When a visual orientation did occur, the viewing container was covered, moved back 10 cm, then uncovered again and moved ahead incrementally 1 cm at a time until visual orientation occurred. This technique allowed us to determine the maximum visual orientation distance (to the nearest cm).

Experiment II: Male *M. inclemens* courtship while in the presence of a potential predator.—Three experimental treatments were designed to determine how the presence of a potential predator might influence the initiation of courtship behavior for male T and G *M. inclemens*: (a) control—no predator present; (b) visual exposure to the predator for three minutes followed by removal of the predator from view; and (c) sustained visual exposure to the predator.

An arena measuring 20 cm (l) x 8 cm (w) x 4 cm (h) with removable partitions on either side of the middle compartment was constructed. The middle compartment (compartment B) was separated from the end compartments (A and C) by 0.6-mm glass and the inner walls were lightly coated with petroleum jelly to prevent the spiders from escaping. To elicit courtship behavior, a female *M. inclemens* was anesthetized with CO_2, affixed to a cardboard strip using non-toxic wax adhesive and placed in the center of compartment A of the arena. A total of five females were used as stimuli and were released unharmed after the experiments were conducted. For the predator, 10 different adult female *P. audax* were used throughout these experiments. Fifteen males of each morph were randomly assigned to one of the three experimental treatments (T, $n = 45$; G, $n = 45$); males were tested one time and not repeated throughout the experiment. For all treatments, the *M. inclemens* female was placed in compartment A, the *M. inclemens* male (either T or G morph) was placed in compartment B and the predator (*P. audax*) was placed in compartment C. In compartment B, the paper was changed between each new male tested. The number of males that courted and the courtship latency (= time to initiate courtship once the male visually oriented to the female) was recorded for each experimental treatment.

Treatment 1 (control): A female was placed in the center of compartment A behind a partition and a male was placed in compartment B. After a three-minute acclimation period, the partition was removed and the male courtship behavior was scored.

Treatment 2: A female was placed in compartment A behind the partition, the male was placed in compartment B and a predator was placed in compartment C. The experiment began by removing the partition between compartments of the male (B) and the predator (C), so that the predator was in full view of the male. After three minutes, the partition between B and C was lowered and the partition between the male and the female was raised.

Treatment 3: The procedure was the same as treatment 2, except the partition between the male and predator remained open so that the predator was in full view of the male at all times. After three minutes, the partition between A and B was removed and courtship was scored. For all treatments, males were given a maximum of five minutes to respond.

RESULTS

Experiment I: Predator attraction to male *M. inclemens* morph-specific courtship behaviors.—*Predator-prey orientation distance:* The predator, *P. audax*, visually oriented to the face-on view of the G male at a significantly greater distance than to the face-on view of the T male ($\bar{X} \pm$ SE: G = 21.7 cm ± 0.51; T = 12.5 cm ± 0.67; *t*-test: $t_{18} = 10.85$; $P < 0.0001$; Fig. 2). Likewise, the predator visually oriented to the 45°-view of the G male at a significantly greater distance than to the 45°-view of the T male ($\bar{X} \pm$ SE: G = 35.7 cm ± 1.63; T = 12.8 cm ± 0.61; *t*-test: $t_{18} = 13.13$; $P < 0.0001$; Fig. 2). The predator also responded to the 45°-above view of G at greater mean distances compared to the face-on view of the G male (*t*-test: $t_{18} = 8.17$; $P < 0.0001$; Fig. 2). However, when the mean response distance to the face-on view of T was compared to the 45°-view of T, mean predator orientation distances did not differ significantly (*t*-test: $t_{18} = 0.33$, NS; Fig. 2).

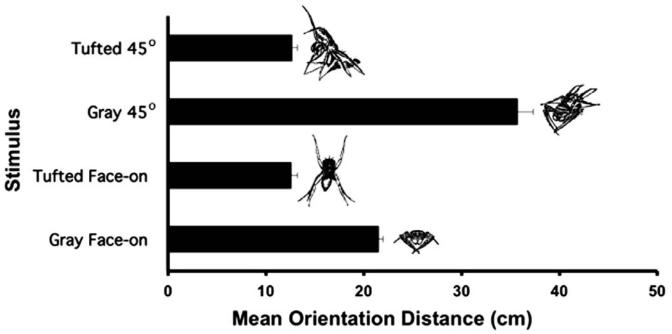

Figure 2.—Mean orientation distance of the predator *P. audax* in response to face-on and 45° views of *M. inclemens* male courtship behavior.

Experiment II: Male *M. inclemens* courtship while in the presence of a potential predator.—*Treatment 1 (control – no predator present):* The number of T and G males that courted (T = 13 (87%); G = 14 (93%)) did not differ in control treatment 1 (chi square test: $\chi^2_1 = 0.037$, NS; Fig. 3a). The numbers of males that courted in treatments 2 and 3 were compared to the number of similar males that courted in the control treatment 1.

Treatment 2 (3-minute visual exposure to predator, then removal of predator from view): The number of courting T males in treatment 2 did not differ significantly from controls (T = 6 (46%): chi square test: $\chi^2_1 = 2.5$, NS; Fig. 3a). However, the number of G males that courted was significantly lower than the controls (G = 3 (21%); chi square test: $\chi^2_1 = 7.1$, $P < 0.008$; Fig. 3a).

Treatment 3 (3-minute visual exposure to the predator, predator remains in view): The number of T males that courted in treatment 3 was significantly lower than the number of T males that courted in the controls (T = 4 (30%): chi square test: $\chi^2_1 = 4.7$, $P < 0.03$; Fig. 3a). Likewise, the number of G males that courted in treatment 3 was significantly lower than the number of G males that courted in the controls (G = 2 (14%); chi square test: $\chi^2_1 = 9.0$, $P < 0.003$; Fig. 3a).

Courtship latency time: For treatment 1 (no exposure to a potential predator), there was no significant difference in the latency time to courting of T and G after visually orienting to the female ($\bar{X} \pm$ SE: T = 5.3 sec ± 0.97; G = 5.5 sec ± 0.88; t-test: $t_{25} = 0.08$, NS; Fig. 3b). For treatment 2 (3-minute exposure to the predator, predator not in view), there was a significant difference in courtship latency between T and G males ($\bar{X} \pm$ SE: T = 33.0 sec ± 1.9; G = 51 sec ± 2.8; *t*-test: $t_7 = 5.08$, $P < 0.01$; Fig. 3b). Likewise, for treatment 3 (3-minute exposure to the predator, predator remains in view) the courtship latency was significantly longer for G males than it was for T males ($\bar{X} \pm$ SE: T = 27.25 sec ± 2.8; G = 41.5 ± 4.5; *t*-test: $t_4 = 2.78$, $P < 0.05$; Fig. 3b).

Prey visual target sizes.—By altering posture, the males can make themselves appear larger or smaller. To explore how this may influence the predator's responses, the visual target areas of the males in the different stimuli were compared. There was no significant difference between the mean areas of the face-on view of the T morph and the 3-dimensional 45°-view of the T morph ($\bar{X} \pm$ SE: T face-on = 21.04 ± 0.53; 45° = 21.48 ± 0.2; *t*-test: $t_8 = 0.76$; NS; Fig. 1a, c). However, the area of the face-on view of the G morph was significantly smaller than the area of 3-dimensional 45°-view of the G morph ($\bar{X} \pm$ SE: G face-on = 10.6 ± 0.17; G 45° = 32.6 ± 0.29; *t*-test: $t_8 = 63.7$, $P < 0.0001$; Fig. 1b, d).

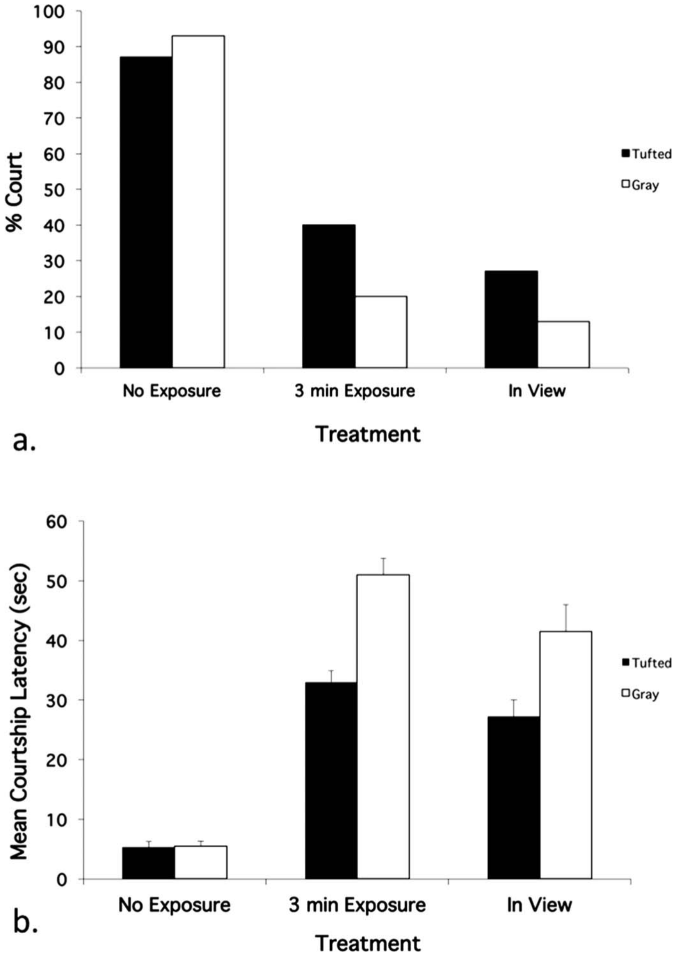

Figure 3.—Courtship response of *M. inclemens* males in the presence of a *P. audax* potential predator; (a) percent of the males that courted after exposure to the predator; (b) mean courtship latency after exposure to the predator.

DISCUSSION

Several studies have demonstrated that male courtship displays not only attract female attention (Houde 1987; Houde & Endler 1990; Andersson 1994; Godin & Briggs 1996) but also may garner unwelcome attention from predators (Burk 1982; Lima & Dill 1990; Magnhagen 1991; Sih 1994; Candolin 1997; Clark et al. 2016). In this study, we demonstrated that the uniquely dimorphic *M. inclemens* males that differ in coloration, presence/absence of tufts, courtship postures, movements and courting distances from the female (Clark & Uetz 1993; Clark 1994; Clark & Morjan 2001), also differ in visual detectability to a potential predator, a large jumping spider, *P. audax*. Although the *P. audax* in our experimental trials did not directly feed on *Maevia* test subjects, we believe that visual detection is the likely first phase of a predatory sequence; thus detectability is a legitimate measurement of predation risk. The G morph with its side-to-side movement attracted the predator's attention at significantly greater distances than did the stationary, stilting and leg-waving, courting posture of the T morph. The differences in visual detectability were also dependent on the perspective from which the predator viewed the displaying males. The predator visually oriented to the face-on view of the G morph display at approximately twice the distance at which it orients to the T morph display. This suggests that the G male display is more conspicuous than the display of the T male. However, neither would typically present a face-on view to a potential predator, consequently the 45° above-view of the courting male provides a more realistic view that a potential predator might see. From this perspective, the predator oriented to the displaying G male at approximately three times the distance that it oriented to the T morph. This difference may likely be due to two factors: the three-fold larger apparent size due to posture affecting visual target; and, to the sweeping, side-to-side movements of the G male. The result is that G male is more conspicuous to the predator than the T male; similarly, at close distances, the G male is also more conspicuous to the conspecific female (Clark & Morjan 2001).

Jumping spiders are known to have excellent visual acuity (Blest 1985; Forster 1985) and the males of *M. inclemens* should easily notice a nearby predator orienting to them. To determine if male morphs respond differently in the presence of a potential predator, we conducted an experiment with live test subjects and varied the duration of visual exposure to a live potential predator. When the predator was absent, approximately 90% of males tested (both morphs) courted the female within 5 seconds of visually orienting to her. This is consistent with previous observations of courtship tendencies by the two male morphs, and supports the hypothesis that the "first male" the female notices has the mating advantage (Clark & Uetz 1992). However, when the predator was visually present, the courting activities of both T and G males changed. If first exposed to a potential predator before presentation of the female, fewer males courted and of those that did court, the latency to courtship display was longer than that of the controls. Dynamic changes in male behavior have been demonstrated in other species where males are known to adjust their behavior when a potential predator has been detected nearby. For example, some males adjust their courtship behavior by courting less actively (Candolin 1997; Godin & MacAulay 1997; Candolin & Voigt 1998). Such a change in behavior is not without cost and the dilemma is that males that court less actively in the presence of predators are also less attractive to females (Candolin 1997; Godin & MacAulay 1997), and males that court for a longer time to compensate for less activity, run the risk of being more conspicuous to predators (Burk 1982; Lima & Dill 1990; Magnhagen 1991).

In this study, we showed that the two male morphs responded differently to the presence of a potential predator. Fewer G males courted after predator exposure than T males. Of those G males that did finally court, they took significantly longer to initiate courtship than the T males. Being more conspicuous to females at relatively close distances has obvious advantages for the G morph; conversely being more conspicuous to potential predators has serious disadvantages for the G morph, and this may help us understand why G males tend to initiate courtship in close proximity to the female. Courting close to the female and attracting her attention quickly reduces the risk of visual detection by a potential predator. Furthermore, being in close proximity to the female significantly reduces the distance, or "travel time" to approach the female to mate. While we do not fully understand the mechanisms that might favor the "close to female" courtship behavior of the G males, T males are at higher risk of being preyed upon by females at closer range than are G males (Clark & Morjan 2001). Furthermore, Clark & Morjan (2001) suggested that courting G males might be more adroit than T males at escaping predation from the females, perhaps due to the G males' orange pedipalps, which may suppress the females' predation tendencies (see also Clark & Uetz 1993). By courting further from the female, the less-conspicuous-to-potential-predators T males can reduce their risk from hungry conspecific females and still optimize their mating opportunities. By assuming a stationary pose at a safe distance from the female, the risk of detection by a potential predator is relatively low, while at the same time being relatively conspicuous to, and safe from, the predatory advances of a conspecific female.

The interrelationships among posture, behavior, courting distance, lack of female preference, and predation risk management ultimately lead to equal courtship success for the two male *M. inclemens* morphs. This is helpful for understanding how the balance between the two morphs might be maintained. However, the evolution of these traits still remains elusive.

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LITERATURE CITED

Andersson. M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

Blest, A.D. 1985. The fine structure of spider photoreceptors in relation to function. Pp. 80–102. *In* Neurobiology of Arachnids (F.G. Barth, ed.). Springer-Verlag, New York.

Bulbert, M.W., J.C. O'Hanlon, S. Zappettini, S. Zhang & D. Li. 2015. Sexually selected UV signals in the tropical ornate jumping spider, *Cosmophasis umbratica* may incur costs from predation. Ecology and Evolution 5:914–920.

Burk, T. 1982. Evolutionary significance of predation on sexually signaling males. Florida Entomologist 65:90–104.

Busso, J.P. & A.R.D. Rabosky. 2016. Disruptive selection on male reproductive polymorphism in a jumping spider, *Maevia inclemens*. Animal Behaviour 120:1–10.

Cade, W. 1979. The evolution of alternative male reproductive strategies in field crickets. Pp. 343–380. *In* Sexual Selection and Reproductive Competition in Insects (M.S. Blum, N.A. Blum, eds.). Academic Press, New York.

Candolin, U. 1997. Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behavioral Ecology and Sociobiology 41:81–87.

Candolin, U. & H.-R. Voigt. 1998. Predator induced nest site preference: safe nests allow courtship in sticklebacks. Animal Behaviour 56:1205–1211.

Clark, D.L. 1994. Sequence analysis of courtship behavior in the dimorphic jumping spider, *Maevia inclemens*. Journal of Arachnology 22:94–107.

Clark, D.L. & C.L. Morjan. 2001. Attracting female attention: the evolution of dimorphic courtship displays in the jumping spider *Maevia inclemens* (Araneae: Salticidae). Proceedings of the Royal Society B 268:2461–2465.

Clark, D.L. & G.W. Uetz. 1990. Video image recognition by the jumping spider *Maevia inclemens*. Animal Behaviour 40:884–890.

Clark, D.L. & G.W. Uetz. 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behavior. Animal Behaviour 43:247–254.

Clark, D.L. & G.W. Uetz. 1993. Signal efficacy and the evolution of male dimorphism, Proceedings of the National Academy of Sciences 90:11954–11957.

Clark, D.L., C. Kizer Zeeff, A. Karson, J.A. Roberts & G.W. Uetz. 2016. Risky courtship: background contrast, ornamentation, and display behavior of wolf spiders affect visual detection by toad predators. Ethology 122:364–375.

Daly, M. 1978. The cost of mating. American Naturalist 112:771–774.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London.

Edwards, G.B. & R.R. Jackson. 1993. Use of prey-specific predatory behavior by North American jumping spiders (Araneae, Salticidae) of the genus *Phidippus*. Journal of Zoology, London 229:709–716.

Forster, L.M. 1985. Target discrimination in jumping spiders. Pp. 250–274. *In* Neurobiology of Arachnids (F.G. Barth, ed.). Springer-Verlag, New York.

Fowler-Finn, K. & E. Hebets. 2011. The degree of response to increased predation risk corresponds to male secondary sexual traits. Behavioral Ecology 22:268–275.

Fuller, R. & A. Berglund. 1996. Behavioural responses of a sex-role reversed pipefish to a gradient of perceived predation risk. Behavioral Ecology 7:69–75.

Godin, J.-G.J. 1995. Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). Oecologia 103:224–229.

Godin, J.-G.J. & S.E. Briggs. 1996. Female mate choice under predation risk in the guppy. Animal Behaviour 51:117–130.

Godin, J.-G.J. & A. MacAulay. 1997. Predator-mediated changes in male courtship affect female mate choice in sticklebacks. Advances in Ethology 32:205.

Gray, S.M., & J.S. McKinnon. 2007. Linking color polymorphism maintenance and speciation. Trends in Ecology & Evolution 22:71–79.

Gwynne, D.T. 1989. Does copulation increase the risk of predation? Trends in Ecology and Evolution 4:54–56.

Haas, R. 1976. Sexual selection in *Nothobranchius guentheri* (Pisces: Cyprinodontidae). Evolution 30:614–622.

Hastings, P.A. 1991. Flexible responses to predators in a marine fish. Ethology, Ecology and Evolution 3:177–184.

Houde, A.E. 1987. Mate choice based upon naturally occurring color pattern variation in a guppy population. Evolution 41:1–10.

Houde, A.E. & J.A. Endler. 1990. Correlated evolution of female mating preferences and male color patterns in the guppy *Poecilia reticulata*. Science 248:1405–1408.

Lima, S.L. & L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lloyd, J.E. 1984. On deception, a way of all flesh, and firefly signaling and systematics. Oxford Surveys in Evolutionary Biology 1:48–84.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends in Ecology and Evolution 6:183–186.

Marshall, K.L.A., K.E. Philpot & M. Stevens. 2015. Conspicuous male coloration impairs survival against avian predators in Aegean wall lizards, *Podarcis erhardii*. Ecology and Evolution 5:4115–4131.

Moodie, G.E.E. 1972. Predation, natural selection and adaptation in an unusual threespine stickleback. Heredity 28:155–167.

Sih, A. 1994. Predation risk and the evolutionary ecology of reproductive behaviour. Journal of Fish Biology 45:111–130.

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