Attracting female attention: the evolution of dimorphic courtship displays in the jumping spider *Maevia inclemens* (Araneae: Salticidae)

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Males of the dimorphic jumping spider (*Maevia inclemens*) differ in both their morphologies and courtship displays (i.e. phase I). The tufted morph stilts and waves from an average distance of 9 cm from a female, whereas the grey morph crouches and sidles from an average distance of 3 cm from a female. The objective of this study was to determine the significance of the different courtship displays using computer-animated versions of males performing phase I courtship in a Y-maze where first male movement and then the distance of the stimulus was controlled. Females selected the first male that they orientated to at the close distance of 4 cm and at the far distance of 16 cm. However, there was no preference for the first male at the intermediate distance of 8 cm or the furthest distance of 24 cm. In addition, males have morph-specific advantages regarding the time it takes to attract female attention. Grey males attracted female attention in less time than tufted males at 4 and 8 cm. However, tufted males attracted female attention in less time than grey males at 16 cm. These results suggest a mechanism for the evolution of two different courtship displays whereby each morph has an advantage at different distances from the female.

Keywords: male dimorphism; alternative strategies; female choice; spider

1. INTRODUCTION

Current views of behavioural evolution are based on the theory that animals behave in such a way as to maximize their genetic contribution to future generations (Williams 1966; Arak 1984; Pomiankowski *et al.* 1991). Darwin (1871) was the first to propose the theory of sexual selection, suggesting that certain individuals have advantages over others of the same species and sex with regard to success in mating and reproduction. Many studies have provided considerable evidence since Darwin (1871) that the courtship displays of males affect the mating decisions of females (see the review by Andersson 1994). Selection has therefore favoured males that invest in behaviours and morphologies that increase their chances of finding and attracting females (Searcy & Anderson 1986; Arak 1988; Ryan 1990). Determining how these male characteristics evolve can be difficult and experimentally manipulating males may produce inappropriate behaviour patterns or incorrect morphological cues. However, species exhibiting male dimorphism, where males are naturally distinct and divided into two discrete categories, can be useful in elucidating the evolution of alternative mating tactics. In this study, we examined how attracting female attention may have influenced the evolution of the two distinctly different courtship strategies found in the dimorphic jumping spider *Maevia inclemens*.

The dimorphic jumping spider *M. inclemens*, Walckenaer (that is also known under the name *Maevia vittatta*) is commonly found throughout eastern and midwestern regions of the USA. The two male morphs differ dramatically in both their morphologies and courtship behaviours (Clark 1994). The tufted morph has three

rows of setae on its anterior cephalothorax, a black-coloured body, white legs and black-coloured pedipalps. The grey morph lacks the tufts, but has a white stripe above its eyes, its body and legs are striped and its pedipalps are bright orange in colour. Females do not resemble either morph: they lack the tufts and orange palps and their bodies are brown in coloration with a prominent white stripe below the eyes (Barnes 1955; Kaston 1972).

In addition to distinct morphologies, the two male morphs behave differently when performing the initial phase of courtship (henceforth called phase I). The tufted morph begins its courtship display, at an average distance of 9 cm from a female, by standing up and waving its first pair of legs vigorously from forward to back while at the same time swinging its abdomen from side to side. In contrast, the grey morph initiates courtship, at an average distance of 3 cm from a female, by lowering to the substratum and sidling back and forth in a prone posture with its first two pairs of legs pointed forward in a triangle-like configuration (Clark & Uetz 1993; Clark 1994). These differences in male morphology and behaviour raise the question of how attracting female attention at two different distances might serve as a selective mechanism in the evolution of this species.

It was recently demonstrated that the two male morphs of *M. inclemens* achieve equal levels of mating success (Clark & Biesiadecki 2002). The two male morphs did not differ in their copulation success, frequency or duration and, importantly, there was no difference in the numbers of offspring produced by either morph. The only difference reported was latency of visual orientation by the female to the courting male as a function of distance. The courtship distance from the female was divided into two areas in open arena observations, namely close to the female (0–8 cm) and far from the female (≥ 9 cm). Grey

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males courted for significantly less time than tufted males before the female orientated in the close area. Conversely, tufted males courted females for significantly less time than grey males in the far area. The results of these observations suggest that the two male morphs may have selective advantages with regard to mate choice as a function of distance from a female, although this hypothesis has not, to our knowledge, been tested.

Previous studies on mate choice have demonstrated that female *M. inclemens* select mates according to which male attracts their attention first, independent of male morphology (Clark & Uetz 1992). Experiments were designed for testing female mating preferences based solely on male morphological differences. Clark & Uetz (1992) used computer-animated sequences of the two morphs performing the second phase of courtship, where males behave identically (Clark 1994), in order to control for the behavioural differences between males. It was determined that females do not show a preference for males based on their morphological differences, but show a strong preference for the male that attracts their attention first. These results raise important questions about the significance of phase I courtship, where males do show behavioural differences that are probably linked to attracting female attention. The objective of the current study was to determine whether males use phase I courtship differentially in order to attract female attention and how distance from a female might influence the efficacy of the morph-specific courtship signal.

2. METHODS

Male and female *M. inclemens* were captured by hand and sweep nets at several field locations in the greater Cincinnati, Ohio and Northern Kentucky area in May 1994 and 1995. The spiders were maintained in the laboratory and housed in cylindrical plastic containers measuring 12 cm × 4 cm (depth × height). A diet of domestic crickets (*Acheta domesticus*) and fruit flies (*Drosophila* sp.) was provided on a weekly basis and water was available *ad libitum*. All experiments occurred in midsummer 1994 and 1995 and, in order to control for the possible effects of previous mating experience on mate choice (Jackson 1981), only virgin females were used.

The experiments were designed for testing female responses to the movement of the first male mover as functions of morph-specific courtship behaviour and the distance of the display from the females. Since it is often difficult to control the courtship behaviour of live males and since *M. inclemens* responds to video-simulated stimuli appropriately (Clark & Uetz 1992, 1993), females were shown computer-animated video sequences of each male performing its morph-specific phase I courtship display. The stimuli were derived from raw video footage of courting males (see Clark & Uetz (1992, 1993) for details on constructing the video stimuli). A Macintosh 8100/80 AV desktop computer was used for digitizing and editing the video sequences into the QUICKTIME file format. Each stimulus sequence was set against a blue-coloured background (Pantone 312 CVU) using ADOBE PHOTOSHOP (v. 3.0) and MACROMEDIA DIRECTOR (v. 5.0). ADOBE PREMIERE (v. 4.2) was used for compiling the video frames into a QUICKTIME movie loop with dimensions of 640 pixels × 480 pixels (width × height) and a frame rate of 29.97 frames s⁻¹. The stimuli were then downloaded to a Panasonic AG-1970 videocassette recorder (VCR)

and stored on separate S-VHS tapes. Finally, the courting male stimuli were presented at life size on one of two Sony Watchman (FDL 310) mini-televisions using a Panasonic AG-1970 VCR attached to each television. The use of separate VCRs allowed for random assignment of the side of the Y-maze on which each morph was displayed (figure 1) and the freeze-frame capability of these VCRs allowed for precise control of the courting-male stimuli. In order to elicit an orientation response by the female to one male before the other, the start of a display was linked to the pause/play button on the VCR. By pressing 'play' for one side, the stimulus started courting and, at the same time, the other side was held motionless until an orientation response was observed to the courting male stimulus, at which time 'play' was pushed and the paused male started to display.

The Y-maze that was used for these experiments was designed with tracks that allowed the courting male stimuli to be presented to females at the following distances: 4 cm (close), 8 cm (intermediate), 16 cm (far) and 24 cm (furthest) (figure 1). These distances correspond to the courtship distances of live males, that range from 3 to 18 cm. The furthest distance of 24 cm was chosen because it was beyond the courtship range of both males but still within the visual range of females. Twenty females were randomly assigned to a distance and first male movement category (i.e. 4 cm with tufted male moving first, 4 cm with grey male moving first, etc.). If a female did not orientate to the stimulus within 5 min, she was removed from the Y-maze and the trial was scored as 'no response'. Only those females that visually orientated and made a choice were used in subsequent statistical analysis ($n = 136$ females).

All trials were videotaped from above using a Panasonic HD 5100HS video camera and a Panasonic AG-1970 SVHS VCR. Females were scored for the following behaviours: (i) male first orientated to, (ii) elapsed time to first orientation of the courting male stimulus, and (iii) choice of male by approaching the displaying image beyond the end of the centre barrier. In order to control for scoring bias, an assistant who was unaware of which stimulus was started first conducted the analysis of the videotapes. Statistical comparisons were performed using the *G*-test for testing for preferences of the first male orientated to by the female and the Mann-Whitney *U*-test for analysis of the differences in elapsed time of the first orientation to the courting stimulus.

3. RESULTS

The females' preferences for the first male they orientated to were strongly influenced by distance (figure 2). The females selected the first male they orientated to at the closest distance of 4 cm, independent of male morphology (78% choice for the first male) ($G_1 = 11.76$, $p < 0.01$ and $n = 36$). Likewise, the females selected the first male they orientated to at 16 cm, independent of male morphology (70% choice for the first male) ($G_1 = 6.25$, $p < 0.02$ and $n = 37$). However, the females did not show a preference for the first male orientated to at 8 cm (47% choice for the first male) ($G_1 = 0.11$, $p > 0.74$ and $n = 38$) or 24 cm (52% choice for the first male) ($G_1 = 0.04$, $p > 0.84$ and $n = 25$).

Closer examination of female preference as a function of distance suggests that the two male morphs may have advantages at two different distances from the female (table 1). The females did not show a significant preference for the tufted morph when it attracted their

Figure 1. The Y-maze used for the female preference experiment showing the placement of the television monitors and the distance of the stimulus from the female when released into the test area.

attention first at the closest courtship distance of 4 cm (68% choice) ($G_1=2.64$, $p > 0.10$ and $n=19$). However, when the grey morph was the first to attract female attention at the same distance, the females showed a significant preference (88% choice) ($G_1=11.25$, $p < 0.01$ and $n=17$). The females did not show a preference for either morph when it was first to attract their attention at the intermediate distance of 8 cm (42% choice for tufted morph and 53% choice for the grey morph) ($G_1=0.47$, $p > 0.49$ and $n=19$ and $G_1=0.05$, $p > 0.81$ and $n=19$, respectively). The females showed a significant preference for the tufted morph when it was the first to attract their attention at the far courtship distance of 16 cm (77% choice) ($G_1=5.88$, $p < 0.02$ and $n=18$). Conversely, the females did not show a preference for the grey morph when it was first to attract their attention at 16 cm (63% choice) ($G_1=1.33$, $p > 0.24$ and $n=19$). The females did not show a preference for either male that attracted their attention first at the furthest courtship distance of 24 cm (64% choice for the tufted morph and 43% choice for the grey morph) ($G_1=0.82$, $p > 0.36$ and $n=11$ and $G_1=0.28$, $p > 0.59$ and $n=14$, respectively).

As a final assessment of courtship display as a function of distance, the elapsed time that a male displayed before the female visually orientated was measured (figure 3). Females were attracted to the courtship display of grey males in significantly less time than to tufted males at 4 and 8 cm (at 4 cm for tufted male, $\bar{X}=10.4$ s and s.e.=1.4 s, at 4 cm for grey male $\bar{X}=5.1$ s and s.e.=0.6 s, at 8 cm for tufted male $\bar{X}=12.1$ s and s.e.=1.6 s and at 8 cm for grey male $\bar{X}=6.1$ s and s.e.=0.8 s) (Mann–Whitney U -test, $U=48.5$, $p < 0.003$ and $n=32$ and $U=72.5$, $p < 0.01$ and $n=37$, respectively). Females were attracted to the courtship display of tufted males in significantly less time than to grey males at 16 cm (tufted male, $\bar{X}=12.2$ s and s.e.=1.6 s and grey male, $\bar{X}=19.5$ s and s.e.=2.7 s) (Mann–Whitney U -test, $U=93.5$, $p < 0.05$ and $n=35$). There was no significant difference between the males in elapsed time before the female orientated at the furthest distance of 24 cm (tufted male, $\bar{X}=39.1$ s and

Figure 2. Percentage of overall selection for the first male orientated to as a function of distance. The shaded area indicates the zone of ambivalence where females did not show a preference for the first male orientated to in the choice experiments.

s.e.=4.1 s and grey male $\bar{X}=40.69$ s and s.e.=5.4 s) (Mann–Whitney U -test, $U=65$, $p > 0.9$ and $n=23$).

4. DISCUSSION

In this study, we purposely used one exemplar representing each morph as stimuli for attracting females and avoiding the influence of variations in male courtship display. This may raise some concern regarding methodological issues in such playback experiments (Kroodsmas *et al.* 2001) since it is possible that variation in male courtship display within and between morphs may produce different results. Despite using only one exemplar, we can still infer from our results that, in response to males performing phase I courtship displays, females showed a significant preference for the first male that received visual orientation (McGregor *et al.* 1992). While Clark & Uetz (1992) showed that female *M. inclemens* do not show a preference for males based on morphological differences, the current study using synthetic stimuli demonstrated that differences in morph-specific courtship behaviour could significantly influence female attraction and preference for a potential mate. Such a preference for a first male is consistent with previous studies on *M. inclemens* (Clark & Uetz 1992) and those on acoustic signalling in insects and anuran amphibians (Howard & Palmer 1995; Minckley *et al.* 1995). However, *M. inclemens* females appear to be unique with regard to their selection of males as a function of distance. In this study, females showed a significant preference for the first male they orientated to when both males were at the close distance of 4 cm and at the far courtship distance of 16 cm. In contrast, females did not show a preference for the first male they orientated to at the intermediate distance of 8 cm or the furthest courtship distance of 24 cm.

Finding no preference at 24 cm might be expected since this is well beyond the normal courtship range of both male morphs and far enough that species-specific cues might be obscured. However, it is intriguing that female *M. inclemens* do not show a preference for the first male orientated to at the intermediate courtship distance of 8 cm. This distance is within the range of courtship for both male morphs, although it is at the distant edge of the range for the grey male and at the near edge of the

Table 1. Summary of the results of the female preference experiment.

(The rows indicate the numbers and percentages of females that orientated and the selection for the first male that attracted their attention.)

distance	first move	selection	%	<i>G</i>	<i>p</i>
4 cm					
tufted	19	13	68	2.64	> 0.10
grey	17	15	88	11.25	< 0.01
8 cm					
tufted	19	8	42	0.47	> 0.49
grey	19	10	53	0.05	> 0.81
16 cm					
tufted	18	14	77	5.88	< 0.02
grey	19	12	63	1.33	> 0.24
24 cm					
tufted	11	7	64	0.82	> 0.36
grey	14	6	43	0.28	> 0.59

range for the tufted male. Since the females did not show a preference for the first male they orientated to here, nor was there a morph-specific bias, we refer to this intermediate distance as the 'zone of ambivalence'. This term refers to an area or zone where neither male appears to have an advantage over the other and where females may opt for the second male that attracts their attention. Essentially, this is an area of increased male competition (Halliday 1983) and in nature males should avoid initiating courtship in the zone of ambivalence due to the risk of losing the female to another male that starts courting. In support of this hypothesis, observations over 10 field seasons since 1988 have documented 14 instances of courtship (D. L. Clark, personal observations) and in three of these both male morphs were noted courting the female simultaneously. The distance of the males from the female in two of these three courtship episodes corresponded to the morph-specific courtship distances cited above, thereby suggesting that males in nature do avoid overlapping with each other during courtship.

If there are costs associated with losing the female to another male in the zone of ambivalence, selection may have favoured the evolution of morph-specific courtship distances. Indeed, the results of this study suggest that this is a plausible scenario. The females did not show a preference for the tufted morph when it was first to attract their attention at the closest courtship distance of 4 cm. However, if the grey morph was first to attract the attention of the female at 4 cm, they were likely to select it. This preference was reversed at the far courtship distance of 16 cm where females selected the tufted male when they orientated to it first, but not the grey morph. These data suggest that differential female preferences may have selected for males that initiate courtship at two different distances, where each has an advantage over the other morph.

Another reason why males may avoid the zone of ambivalence is that morph-specific cues are probably more acute on either side of the zone. An earlier study by Clark & Uetz (1993) suggested that males court at different distances in order to subtend angles of similar degree from the perspective of the female. Importantly, a grey male courting at 3 cm and a tufted male courting at

Figure 3. Elapsed time (s) before the female visually orientated to the stimulus of the courting male.

9 cm should appear similar in size on the retina of the anterior median eyes. If size is an important mate-recognition cue, selection should tend to favour those males that present the female with the appropriate size image during courtship. By assuming the different courtship postures at the different distances, the two male morphs avoid competition with each other and, at the same time, they each present the female with images that stimulate her visual system in a similar manner.

The results presented here also demonstrate that courtship distance could have a significant effect on the amount of time it takes a male to attract female attention. Grey males captured female attention in less time than tufted males at the close and intermediate courtship distances. This is probably due to the conspicuous side-to-side movement of the grey male during phase I courtship. Why the larger-appearing tufted male takes longer to attract female attention in the close areas is not understood. It may be related to inappropriate size cues and females may be hesitant to orientate and reveal their position until other species-specific cues have been processed. Interestingly, the advantage shifted to the tufted morph at the far distance of 16 cm where it was able to capture female attention in less courtship time than the grey male. Here, the size cues may be incorrect for the grey male where it appears too small and morph-specific cues, such as the white stripe above the eyes and orange pedipalps, may be obscured.

There were no morph-specific advantages for female attraction at the furthest courtship distance of 24 cm. Males courting at the furthest distance often displayed for 40 s before the female visually orientated, thereby suggesting that displaying at extreme distances may be risky because displaying males and watching females can attract attention from predators (Magnhagen 1991). Although this is true at any distance, courtship displays of relatively long duration would be selected against, thereby also selecting against courting females from excessively far distances.

Although not specifically tested in this study, it is interesting to note that the risk of predation on males by females may also have been important in the selection of the two different courtship distances. Like most spiders, courting males of *M. inclemens* must contend with the risk

that female attraction may lead to an attempt at predation. It is often difficult to determine whether the female is assessing the male as a mate or a meal in studies of spider courtship behaviour and it is probably both, since these may not be mutually exclusive to a female spider. While previous studies have reported a low incidence of sexual cannibalism in this species (Clark 1992; Clark & Uetz 1992; Clark & Biesiadecki 2002), attacks towards the courting-male stimuli were observed in this study. A total of seven predatory attacks towards the courting-male stimuli were documented and all of these occurred when males were at the closest courtship distance of 4 cm. Furthermore, five (or 72%) of the attacks were towards the tufted morph, while only two (or 28%) were towards the grey morph. These results are consistent with observations by Clark & Biesiadecki (2001) where sexual cannibalism occurred on a tufted male that initiated courtship at 4.5 cm from the female. If tufted males were at a higher risk of predation from females at close courtship distances than grey males, selection would have favoured tufted male courtship from a safe distance.

In conclusion, female preference for first male movement at two different courtship distances has been a strong selective mechanism in the evolution of male dimorphism in *M. inclemens*. The two male morphs have been selected for initiating courtship where each has a selective advantage over the other with regard to attracting females. This study raises many questions regarding other aspects associated with *M. inclemens* courtship behaviour, including how vibratory components to the male courtship display, if any, may interact with the visual display. In addition, males may experience different risks of predation by females or other predators hunting in the vegetation as a function of courtship distance. Further studies on courtship behaviour and on the risks associated with predation are required in order to gain a more comprehensive understanding of the evolution of male dimorphism in this species.

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