

## Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*

(video/communication/mate recognition/sensory exploitation)

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**ABSTRACT** An extreme form of male dimorphism occurs in the jumping spider, *Maevia inclemens*, where two male morphs differ dramatically in both morphology and behavior. We examined the visual signals transmitted to females by the two different morphs during courtship display. Even though the display of each male is different, as a function of behavior and courtship distance, the males present females with images that are almost identical in height and visual target area. By substituting live males with computer-animated sequences of male courtship behavior, the male morphs were superimposed upon each other, and females were determined to have two distinct male-recognition templates. We hypothesize that the dimorphic males of this species evolved through sensory exploitation and selection for alternative male strategies that stimulate different fields of the female visual range.

Although a great deal is known about animal communication (1–3), the selective pressures shaping the evolution of signal design and efficacy are poorly understood. Much recent attention has focused on courtship communication and how male behaviors and morphological characteristics convey information that influences female mate choice (4–6). Although male characteristics may be highly variable, for most species there is usually only one male morph that females must recognize. However, in species with polymorphic males this issue is complicated, for females are required to distinguish between different male types. In these species, do males send distinctly different species-recognition signals, where females have more than one male-recognition template (7), or do the individual males transmit signals that overlap in signal design, or is it some combination of these characteristics?

Here we examine the courtship display of a species of jumping spider, *Maevia inclemens*, where males are so morphologically and behaviorally distinct that they appear to belong to different species (8–10; Fig. 1 A and B). The tufted morph (named because of three tufts of setae on the anterior cephalothorax) has a black body with white legs and stilts during the initial phase of courtship. In contrast, the gray morph has a striped colored body, has orange-colored pedipalps, and assumes a prone posture during the initial phase of courtship. Previous studies (10) have demonstrated that the male dimorphism is genetically based and that a single female will mate readily with either male morph (producing both male morphs in the offspring). Additionally, males have been found in equal abundance (i.e., 50:50) at all field sites sampled so far.

Although it is difficult to determine which morph evolved first, morphological and behavioral comparison with other members of the genus *Maevia* suggests that the gray morph is plesiomorphic to the unusual tufted morph. This plesio-

morphism is likely because within the genus *Maevia*, *Maevia inclemens* is the only member to exhibit this type of male dimorphism, and other males within the genus resemble and behave much like the gray morph of *M. inclemens*. Also, in *M. inclemens*, all juveniles resemble the adult gray morph and are not distinguishable as different male morphs until their final molt.

An earlier study proposed that dimorphic males evolved by sexual selection through female choice (8), where females were presumed to have a mating preference for the tufted morph. However, it was recently demonstrated that mate selection is independent of male morphology (11) and that female *M. inclemens* select mates based on initial male movement (i.e., the male that captured the female's attention first was allowed to mate). Given that jumping spiders orient visually toward moving objects which stimulate the motion-sensitive posterior lateral eyes (the stimulus is then aligned in the acute visual field of the anterior median eyes; refs. 12 and 13), a male that attracts female attention first would appear to have a distinct mating advantage. However, simply capturing female attention is not sufficient, as the male must also be recognized as a conspecific. Because any divergence in form and behavior most likely evolved from a polymorphism, it is unclear how two distinct male morphs might be recognized by females as conspecifics.

Recent advancements in animal behavior research using television to present stimuli to test subjects have allowed detailed questions about animal perception to be addressed (11, 14–16). To investigate the male phenotype-matching template of females (7), video and computer animation was used to switch and superimpose the behavior and morphology of the two male morphs. By evaluating female sexual-receptivity response to normal and superimposed versions of the two male morphs, the neurological templates of females could be examined. This species provides an excellent opportunity to investigate the criteria females use for mate identification and thereby to gain insight into the evolution of this unusual male dimorphism.

Preliminary observations of male courtship behavior showed that the courtship display of each morph differed dramatically. After sighting a female, the tufted morph stands up, whereas the gray morph crouches down in a prone position (Fig. 1 A and B). In addition to posture differences, the male morphs initiate courtship display at significantly different distances from the female (gray:  $\bar{x}$ , 34  $\pm$  3 mm SEM;  $n$  = 36; tufted;  $\bar{x}$ , 86  $\pm$  6.8 mm SEM;  $n$  = 27; Mann-Whitney  $U$  test;  $P$  < 0.001).

The significance of the morph-specific courtship behaviors was revealed after measuring the height of males in courtship stance (tufted:  $\bar{x}$ , 10.5  $\pm$  0.5 mm SEM; gray:  $\bar{x}$ , 3.1  $\pm$  0.25 mm

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Abbreviations: TT, tufted morphology with tufted behavior; GG, gray morphology with gray behavior; TG, tufted morphology with gray behavior; GT, gray morphology with tufted behavior.

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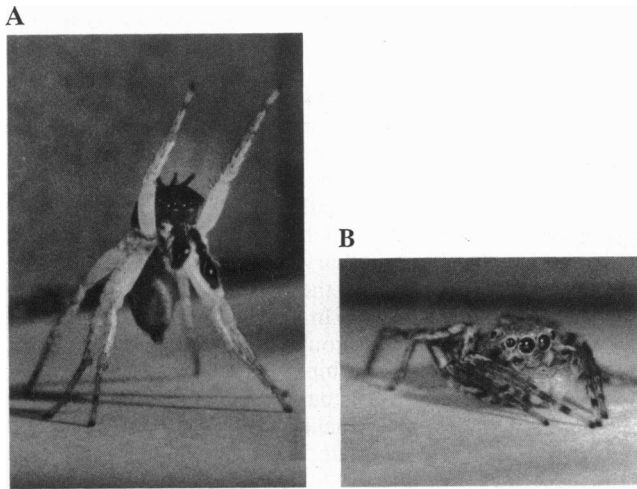


FIG. 1. Male morphs of the dimorphic jumping spider *M. inclemens*, illustrating differences in appearance and behavior in initial (phase I) courtship. (A) tufted morph, showing the three tufts of setae above the anterior median eyes, black body coloration, and white legs. In phase I courtship the tufted morph stands up with legs I waving above the head and swings the abdomen from side-to-side. (B) gray morph, showing black-and-white striped body coloration, white-color band above the anterior median eyes (no tufts), and orange-colored pedipalps. In phase I courtship the gray morph crouches down with legs I and II pointed forward in a triangle-like configuration and sidles from side-to-side. In phase II (approaching the female), both morphs converge in behavior, with zigzagging movements and waving of legs I together approximately five times per sec.

SEM;  $n = 5$ , respectively) and computing the angle subtended by each male relative to its position from the female

(17). From the female's perspective, there was no significant difference in the angles subtended by the two male morphs (gray:  $\bar{x}$ ,  $7.2 \pm 0.76^\circ$  SEM;  $n = 36$ ; and tufted:  $\bar{x}$ ,  $8.1 \pm 0.70^\circ$  SEM;  $n = 27$ ; Watson-Williams test:  $F = 1.36$ ;  $df = 2, 61$ ;  $P > 0.50$ ; Fig. 2A), demonstrating that as a function of male behavior and distance, both morphs present the female with images that are similar in height (mean angle for both morphs,  $7.6^\circ$ ).

On the basis of the angle subtended by each male morph relative to its distance from the female, the visual target area of the males in courtship display was estimated by using the following mathematical formula:

$$Ap = \left( \frac{Dv - Df}{Aa} \right)^2 Aa,$$

where  $Ap$  is the apparent area of a male in phase I courtship display perceived by the female,  $Dv$  is the vanishing-point distance of a phase I male,  $Df$  is the distance from female to male, and  $Aa$  is the absolute target area of male. Vanishing-point distances ( $Dv$ ) (i.e., the distance that females failed to respond visually to the stimulus) were determined by presenting females with life-size models of males (constructed from plastic beads and wire) positioned in phase I courtship stance. Females were placed in a 40-mm  $\times$  30-mm  $\times$  25-mm plastic box with a 0.2-mm-thick glass front ( $n = 30$ ). Models were attached to a plastic strip, positioned out of the female's visual range, and presented by moving them closer at a constant speed. Females were scored as seeing the model when they swiveled and oriented to the model. The farthest distance (+5 mm) from the female that the model elicited an orientation response was used as the vanishing point (tufted, 160 mm; gray, 90 mm). The absolute target area ( $Aa$ ) of

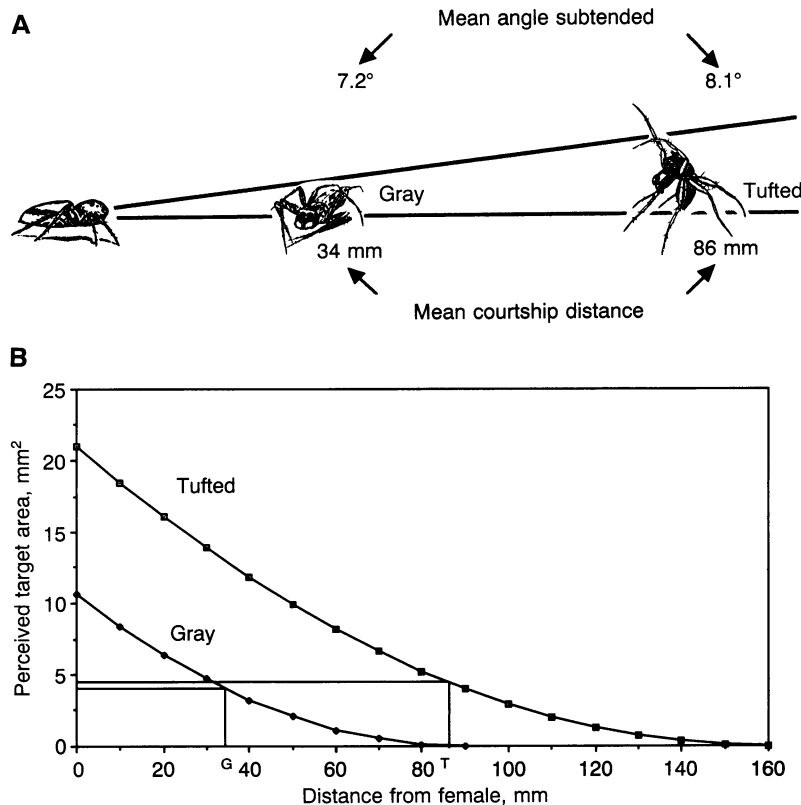


FIG. 2. (A) Phase I courtship distance of each morph relative to the female and the angle subtended by the males in courtship stance (mean height of gray male, 3.1 mm; mean height of tufted male, 10.5 mm). (B) Graphic model showing how the perceived area of a male in phase I courtship changes as a function of distance from the female. Curves show that male area decreases as a function of distance from the female. Uppercase letters on the x axis designate mean phase I courtship distance for each male (G, gray; T, tufted).

courting males was calculated from computer-digitized photos by using the PIXMATE software program (tufted, 21.04 mm<sup>2</sup>; gray, 10.67 mm<sup>2</sup>).

As expected, this model shows that the visual target area of each morph decreases as a function of male distance from the female. However, at their mean courtship distance, the visual target area of each male morph was almost identical (tufted:  $\bar{x}$ , 4.5 mm<sup>2</sup>; gray:  $\bar{x}$ , 4.1 mm<sup>2</sup>; Fig. 2B).

These data suggest that the two different male morphs of *M. inclemens* present females with courtship signals that contain overlapping bits of information for species identification (i.e., as a function of different courtship postures and distances from the female, each morph presents females with images of similar height and visual target area). However, it is not clear whether females have one recognition template satisfied by both male morphs (where the behavior and the morphology of the two males are interchangeable), or whether females have two independent recognition templates—one for each male morph.

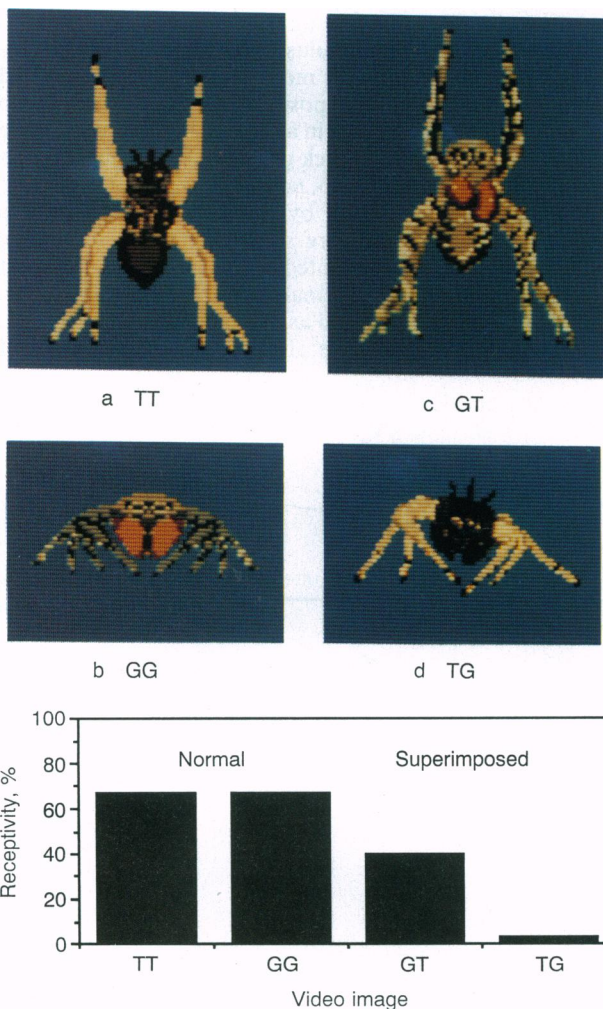


FIG. 3. Computer-animated versions of male courtship display shown to females using a small television monitor. The morphology of the male stimulus is given first, followed by the corresponding behavior of the animated sequence: (a) TT, normal tufted male courtship sequence with tufted morphology and tufted behavior; (b) GG, normal gray male courtship sequence with gray morphology and gray behavior; (c) GT, superimposed male courtship sequence with gray morphology and tufted behavior; (d) TG, superimposed male courtship sequence with tufted morphology and gray behavior. Histogram shows percentage of females showing sexual-receptivity behavior to the corresponding male stimulus (TT and GG,  $n = 24$ ; GT and TG,  $n = 30$ ; see text for statistical inference).

On the basis of studies demonstrating that jumping spiders respond appropriately to televised images of prey (e.g., stalking and attack), predators (e.g., retreat), and conspecifics (e.g., sexual behavior) (11, 14), questions regarding morph recognition by females were further investigated by using a recently developed computer-assisted video animation technique. By using computer-animated sequences of male courtship behavior, the morph-specific behavior and the morphology of the two males were switched and superimposed. Thus, all bits of information necessary for male and species recognition were conserved, but the signals were presented to females opposite of normal. In this manner, the number of male-recognition templates could be determined.

Sequences of male courtship behavior were digitized by using an Amiga model 2000 computer and an external frame grabber (real time video image digitizer, peripherals, and software). The individual frames of the animated sequences were modified by using the Deluxe Paint III software package (Electronic Arts) in the same manner as described by Clark and Uetz (11). Females were randomly assigned to view each stimulus: normal males—tufted morphology with tufted behavior (TT); gray morphology with gray behavior (GG) ( $n = 24$  females); and superimposed males—tufted morphology with gray behavior (TG); gray morphology with tufted behavior (GT) ( $n = 30$  females) (Fig. 3).

Presentation of video images to female spiders was done in a trapezoid-shaped video chamber that accommodated three liquid crystal display color Sony Watchman television units (model FDL-310; screen diameter, 7 cm; diagrammed in Fig. 4). Females were shown only one stimulus per trial and were scored as positive when they exhibited sexual-receptivity behavior toward the animated male (i.e., approach with leg frontal display and body posturing). Contingency table design and the  $\chi^2$  test were used for statistical analysis.

Females differed significantly in sexual receptivity shown toward the different male stimuli ( $\chi^2 = 30.51$ ;  $df = 3$ ;  $P < 0.001$ ; Fig. 2B). Pairwise comparisons showed that receptivity response was not significantly different for the two normal males (TT  $\times$  GG;  $\chi^2 = 0.09$ ;  $df = 1$ ;  $P > 0.75$ ;  $n = 24$ ). Although the level of sexual receptivity behavior toward the male with gray morphology and tufted behavior (GT) was lower, it was not significantly different from the response toward the normal males (GT compared with TT and GG, respectively;  $\chi^2 = 2.8$ ;  $df = 1$ ;  $P > 0.05$ ;  $n = 30$ ). However, when the male image with TG was compared with the normal males, female sexual-receptivity behavior was significantly lower (TG compared with TT and GG, respectively;  $\chi^2 =$

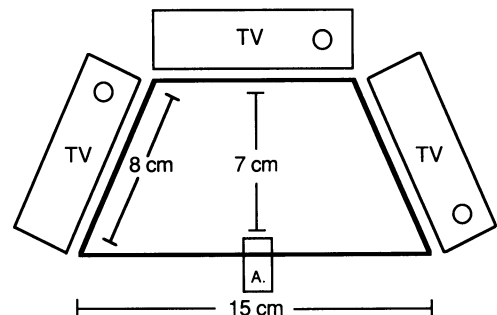


FIG. 4. Diagram of the video chamber used to present computer-animated male courtship stimuli to female jumping spiders. Females were released from vial (A.) and presented with the test image on the center screen only. The other two screens were provided to insure that females were not simply approaching a light source. Each television (TV) was calibrated to the same luminance using a Gossen Luna-Pro F light meter. Female behaviors were recorded on videotape from a video camera mounted directly above the chamber. Each female was given 5 min to respond to the male stimulus, after which the spider was removed and the paper substratum was replaced.

21.94;  $df = 1$ ;  $P < 0.001$ ). Furthermore, the level of sexual receptivity shown toward the two superimposed male images was significantly different ( $GT \times TG$ :  $\chi^2 = 9.8$ ;  $df = 1$ ;  $P < 0.001$ ).

Data presented here support a possible mechanism for the divergence of the two male morphs found in this species. As the courtship distance from the female increases, there is a proportional decrease in the visual size of the male image and at distances  $>8$  cm, females fail to visually orient to the gray male. It is plausible that any male mutation for attracting female attention at distances of 8 cm or greater would be favored by selection, particularly if the display contained information preestablished by the courtship display of the more primitive gray morph (the gray male is considered the primitive morph because of juvenile characteristics and behavioral and morphological similarities to other members of the genus *Maevia*). Importantly, the tufted morphology and display evolved as an alternative strategy for capturing female attention at distances where the gray male would fail to do so. It is no coincidence that the mean courtship distance of tufted males corresponds to the vanishing-point distance of gray males, for this greatly extends the visual range of females for finding a mate (up to 16 cm; Fig. 2B). Therefore, it seems that the visual range of the female is divided into two discrete courtship ranges, one for each morph, where the gray morph courts at close range, and the tufted morph courts at far range. It is plausible that male dimorphism in this species evolved as alternative mating strategies that exploit a sensory bias within females (18–21) for movement detection and males of a specific size class.

Although some elements of the male courtship display are similar for the two male morphs, females appear to have two noninterchangeable male-recognition templates. This fact was demonstrated by superimposing the behavior and morphology of the two male morphs with each other. If females had only one male-recognition template that was satisfied equally by either male morph, sexual receptivity should not have differed significantly between normal and superimposed males. However, when the morphology and the behavior of the two male morphs were switched, female receptivity decreased, and the male image that looked like a tufted male but behaved like a gray male (TG) released significantly lower sexual receptivity than all the other male images. Thus, females have evolved male-recognition templates that meet rather specific size requirements (as demonstrated by the angle subtended and target area of the males) and have selected for two different male displays that create images of this size from two different distances.

The evolution of animal signaling mechanisms has been an area of intensive investigation. It has been suggested that signal design has two components: "strategic design" and "efficacy" (3). The strategic design of a signal pertains to how natural selection shapes the information so that it can be acted upon by the receiver (i.e., signals allow assessment of sender's species, health, vigor, strength, etc., which may affect the fitness of the receiver). Efficacy concerns how the signal is designed to convey the information to the receiver (i.e., what is attention-getting, easily discriminable or memorable to the brain of the receiver). Recently, Hasson (25) argued that signals evolve which tend to decrease the cost of information transfer. Particularly relevant to these studies

are that certain signals can be attention getting or amplify a particular character (26) which improves the perception of informative cues. If male identification in this species required an image of a certain size and area, as assumed for the primitive gray morph, a distinctive male morph may have evolved by stimulating the nervous system of females in a manner that overlapped with these preestablished criteria. Furthermore, instead of a unidirectional male preference, females of this species appear to have two different male preferences, each favoring a different male morph and courtship strategy. On the basis of an earlier model proposed by Gadgil (22, 23), who suggested that a bimodal distribution in male characters can evolve by directional selection pressures, it is likely that strong intramorph selection has favored the evolution of these alternative male forms. Further studies are needed to test these hypotheses and investigate the relative importance of male behavior versus morphology in male recognition.

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