ANIMAL BEHAVIOUR, 2006, **71**, 135–140
doi:10.1016/j.anbehav.2005.04.007

Location, location, location: stripe position effects on female sword preference

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*(Received 10 May 2004; initial acceptance 29 October 2004;
final acceptance 4 April 2005; published online 28 November 2005; MS. number: A9876R)*

The evolution of complex signals via sexual selection is becoming a primary focus in mate choice studies. Male swordtail fish, *Xiphophorus helleri*, have a secondary sexual trait, the sword, which is a composite trait consisting of four components favoured by sexual selection via female mate choice. The components include three coloured stripes and size. Although a complete sword is most attractive to female green swordtails, females prefer partial swords containing complete black stripes to incomplete swords lacking black coloration. Female swordtails also prefer longer swords. We addressed how subcomponents of the sword affect female mate choice. Digitally altered videos were used to investigate whether females respond differently to swords with proximal black stripes than to swords with distal black stripes. Although females preferred complete swords to both of the stimuli with partial stripes, they preferred males with distally striped swords to males with proximally striped swords. These results are discussed in light of hypotheses concerning the evolution of mating preferences for multicomponent traits. This study contributes to the growing body of information regarding the response of females to multicomponent visual traits.

The evolution of complex signals is becoming a focus of both theoretical and experimental studies in the field of sexual selection (Møller & Pomiankowski 1993; Iwasa & Pomiankowski 1994; Johnstone 1996; Partan & Marler 1999; Basolo & Trainor 2002). In the study of intersexual selection, investigation of the effects of mating preferences on sexual ornaments has led to an appreciation that males often have not just one but multiple traits that are favoured by females (Zuk et al. 1990; Omland 1996; Wagner 1996; Marchetti 1998; Basolo & Trainor 2002). Increased complexity in mating signals can evolve in several ways. First, males may express multiple components that form a composite trait that is attractive to females (Basolo & Trainor 2002). For example, the trains of male peacocks, *Pavo cristatus*, incorporate several colour components as well as a size component (Petrie et al. 1996), and females prefer both longer tail feathers (Petrie et al. 1991) and more multicoloured feather eyespots (Petrie & Halliday 1994). Female preferences for different components of the male train could allow females to assess different aspects of a male's condition, because train length is positively correlated with fat reserves, but eyespot number is positively correlated with muscle mass (Petrie et al. 1996). In guppies, it has been suggested that two elements of coloration, colour contrast and brightness contrast, combine additively to make males more attractive to females than either single element alone (Endler & Houde 1995). Second, multiple signals in the same modality may be combined. In junglefowl, *Gallus gallus*, several distinct visual cues appear to affect female mate choice, including combs, eyes and tails (Zuk et al. 1990), and mice, *Mus domesticus*, assess complex chemical cues to choose mates (Roberts & Gosling 2003). Third, males may signal in multiple sensory modalities, such as combining visual with acoustic signals in male birds (Partan & Marler 1999) and spiders (*Schizocosa ocreata*: Uetz & Roberts 2002) and combining visual with chemical signals in swordtails (*Xiphophorus* sp.: McLennan & Ryan 1997; Hankison & Morris 2003) and guppies (*X. pygmaeus*: Shohet & Watt 2004). Understanding how receivers process and respond to complex multicomponent signals, multiple signals in the same modality and multimodal signals is important to our understanding of the contribution of receivers to the evolution of complex phenotypes.

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0003–3472/05/$30.00/0

Female mate choice may favour increased complexity in male traits for a number of nonmutually exclusive reasons. (1) Preexisting receiver biases (i.e. biases in the sensory and/or cognitive processing systems) can favour the evolution of new male traits (Basolo 1990; Ryan et al. 1990; Endler & Basolo 1998), and multiple biases may contribute to the evolution of single or multiple traits (Basolo & Trainor 2002). Preexisting biases can also favour greater elaboration of existing traits, if they have greater stimulatory value. Although preexisting biases appear to operate in a number of organisms (Basolo 1990; Ryan & Rand 1990; Clark & Uetz 1992; Proctor 1992), few experimental studies have directly tested how preexisting biases might affect the evolution of complex male traits and female responses to such traits (Johnstone 1996). (2) A trait favoured by females can be driven to fixation, resulting in all males expressing the trait. In this case, the trait may be retained as a ritualized trait even when variation for a different male trait arises and is favoured. (3) A trait can arise and be favoured by females because of a direct or indirect benefit, but cheating may result in females switching to another trait that is informative while the previous trait remains as a ritualized trait. This idea is akin to Andersson's (1980) reasoning for why there are multiple threat displays. (4) Increased complexity could reinforce female assessment of a direct or indirect benefit that could be gained by mating with a particular male because the combination provides information that is more reliable (Møller & Pomiankowski 1993). (5) One trait might reinforce female assessment of a direct or indirect benefit because it acts as an amplifier of another trait (Wilson 1975; Hasson 1989). (6) Different traits could provide females with information about different benefits that may be gained by mating with a particular male (Møller & Pomiankowski 1993). The last four explanations may involve indirect benefits (genetic benefits accrued to offspring of a female as a result of the female mating with a male with the preferred trait). However, indirect benefits models have difficulty in explaining the presence of multiple male traits, because these models generally predict the evolution of a single reliable trait rather than of multiple ornaments or traits (Møller & Pomiankowski 1993; Johnstone 1996); this is not a problem for direct benefits or a combination of direct and indirect benefits. Evidence suggests, however, that multiple indicator traits can be maintained by multiple sources of selection when different ornaments are important during male–male competition and female choice (Andersson et al. 2002) or when preferences are context dependent (Marchetti 1998). (7) Fisherian selection can maintain multiple preferences for multiple traits (Pomiankowski & Iwasa 1993).

An ideal group in which to study the evolution of complex sexual ornaments are swordtails in the genus *Xiphophorus*. Male swordtails have a multicomponent trait, the sword (Basolo 1996), which is preferred by females (Basolo 1990), and phylogenetic inference indicates that the preference stems from a preexisting bias favouring a sword (Basolo 1990, 1995, 2002). In the green swordtail, *Xiphophorus helleri*, the sword consists of at least three colour components, two black stripes and a green or orange/yellow stripe, as well as a size component involving lengthening of ventral rays at the base of the caudal fin forming an extension (Rauchenberger et al. 1990; Basolo 1996). Using live male presentations, Basolo (1990) found that female *X. helleri* prefer males with long swords to males with short swords, and the preference is an increasing function of sword length. Female preferences in green swordtails have also been tested with video males. Video stimuli presentation allows for precise manipulation of specific visual signals while controlling variation in other traits. This methodology has proven useful to investigate behaviour in a number of organisms, including spiders (Clark & Uetz 1992), fish (Kodric-Brown & Nicoletto 1997), lizards (Macedonia & Stamps 1994; Ord et al. 2002), frogs (Roster et al. 1995) and birds (Evans & Marler 1991). Female *X. helleri* respond to male video stimuli (Rosenthal & Evans 1998; Trainor & Basolo 2000). In another video study, Basolo & Trainor (2002) found that sword components can act in an additive manner; with an increase in the number of components, female response increased. Females also responded less to a sword lacking black coloration than to a sword with at least one black stripe. These results suggest that black coloration contributes to the sum effect of the sword in female response.

Thus, previous results suggest that, although the complete sword elicits the strongest female response, black coloration components themselves elicit a female response. We investigated the response of female green swordtails to black sword coloration further by considering the importance of the location of black stripes, either located on the distal half or on the proximal half of the sword. We interpret the results in light of several hypotheses for the evolution of female preferences and preferred male traits, including the hypothesis that black stripes bordering the portion of the sword extending beyond the caudal fin function in part as an amplifier of sword extension length.

METHODS

Test Subjects

Subjects were virgin female descendants of wild-caught *X. helleri* collected from Savannah Stream along the Great Western Highway, Belize, under a permit issued by the Belize Ministry of Fisheries. Fish were maintained in the laboratory on a 16:8 h light:dark cycle with broad-spectrum fluorescent lighting, and an average water temperature of 25 °C. Fish were fed three times per day: live brine shrimp nauplii in the morning, liver paste in the afternoon and Tetramin fish flakes in the evening. Before testing, females were housed as pairs in 6-litre tanks.

Video Stimuli Preparation

The methods used to make the video stimuli have been described in detail elsewhere (Basolo & Trainor 2002). Briefly, a male with a standard length of 43.3 mm (measured from the anteriormost point to the point just posterior to the caudal fin vein) and a sword length of 40.4 mm (measured from the insertion of the fin rays at the base of the caudal fin to the distal tip of the sword) displaying courtship behaviour was videotaped as an exemplar for all video presentations. To record courtship behaviour, we placed the male and a female into a recording tank (30.5 × 20.3 × 30.5 cm), and after a 10-min acclimation period, we recorded courtship behaviour in 30-min intervals. The stimulus video included footage of three typical courtship behaviours: lateral presentation, backward swim and sigmoid flex. We also included two sequences of the male swimming to one of the two sides and then turning to reverse direction, resulting in a stimulus of a continuously swimming, courting male.

The video clips were imported into a Macintosh 7600/120 computer equipped with a Targa 2000 PCI video board using Adobe Premiere. Frames were exported as PICT files and manipulated using Adobe Photoshop. The PICT files were then imported into Director where the frames were linked to form a 12-s looping sequence producing a master tape. Three additional stimuli were created by modifying copies of the master tape of a complete sword. All stimuli were prepared by replacing portions of the black stripes of the sword with caudal fin coloration using the rubber stamp function in Photoshop. We prepared a stimulus without the two black stripes by replacing both stripes with caudal fin coloration (no-stripes stimulus). The second stimulus was prepared by replacing 20.2 mm of each black stripe at the proximal half of the sword with caudal fin coloration. This resulted in a stimulus with black stripes only at the distal half of the sword (distal stripes stimulus). The third stimulus was prepared by replacing 20.2 mm of each black stripe at the distal portion of the sword with caudal fin coloration. This resulted in a stimulus with black stripes only on the proximal half of the sword (proximal stripes stimulus). The original, unmanipulated master stimulus was used as a fourth stimulus (complete sword). We compared the area of black coloration in the distal and proximal sword stimuli in six frames using NIH-Image. The distal stripe stimulus had a mean ± SE of $38.5 \pm 1.28\ \text{mm}^2$ of black coloration and the proximal stimulus had $40.1 \pm 1.77\ \text{mm}^2$ of black coloration. This difference was not significant (Student's t test: $t_5 = 1.58$, $P = 0.17$). All video stimuli were transferred to high-quality S-video cassettes for playback.

To control for the effect of schooling behaviour on the measurement of female response to the male stimuli, we constructed a female video sequence and presented it on a screen at the opposite side of the test tank at which a male stimulus was presented. We made the female stimulus in the same manner as the male stimulus. We used two clips of a female (standard length = 43.3 mm) swimming across the recording tank and two clips of the female turning to reverse direction. In the completed video, the female appeared to swim back and forth across the screen at the same speed as the male stimulus and did not display courtship behaviour.

Video Playbacks

We measured female response using a single stimulus design, which has been suggested to be a more effective method for evaluating differences between female responses to male traits than traditional two-stimulus designs (Wagner 1998). The sword stimuli were presented in random order to each female. Females viewed one stimulus per day on consecutive days between 0800 and 1800 hours. The time of day at which an individual female was tested was held constant across sessions.

We placed a monitor adjacent to each side of the test tank and positioned blinds between the tank and monitors. Before testing, females were fed brine shrimp, then placed into a glass tank (30.5 × 20.3 × 30.5 cm) with a live male to stimulate female sexual behaviour (a clear divider prevented direct male–female contact). Each female viewed the male for 10 min, and was then transferred to the test tank (30.5 × 30.5 × 30.5 cm) to acclimate for 30 min. The trial began when the blinds were removed, revealing the stimuli on the monitors. Data recording began when the female had entered all three sections of the test tank. We recorded female response, defined as the time spent by the female oriented towards the male and within three body lengths of him (Trainor & Basolo 2000), for 10 min. Immediately following this first trial, the blinds were replaced and the positions of the male and female video stimuli were switched. After an intertrial interval of 10 min, we conducted a second trial. These two trials together constituted a single session. When a session was completed, the female was returned to her home tank. Each female was used only once with each male stimulus. A female was considered to have a side bias if she spent more than 960 s (80%) on one side of the tank during a session. Females showing side biases were omitted from the analysis. Of 23 females introduced into the test tank and presented with the stimuli, two females showed a side bias, and two females did not swim actively in the test tank (i.e. never entered all three tank sections). These four females were omitted from analysis.

After checking that female response data met the assumptions of parametric tests, we first used a repeated measures ANOVA to test for effects of order of presentation. There was no significant effect of order of presentation ($F_{3,54} = 0.64$, $P = 0.59$), so we used a second repeated measures ANOVA to test for effects of sword video stimulus. We used Student–Newman–Keuls post hoc tests to compare female response to the different sword stimuli.

RESULTS

There were significant differences in female responses to the different sword stimuli ($F_{3,54} = 25.02$, $P < 0.001$; Fig. 1). Females responded significantly longer to the male video stimulus with a complete sword than to the other male video stimuli (proximal stripes: $P < 0.01$; distal stripes: $P < 0.05$; no stripes: $P < 0.01$). Females responded significantly longer to the male video with distal stripes stimulus than to both the proximal stripes stimulus ($P < 0.05$) and no-stripes stimulus ($P < 0.01$). There was no difference between responses to the proximal stripes

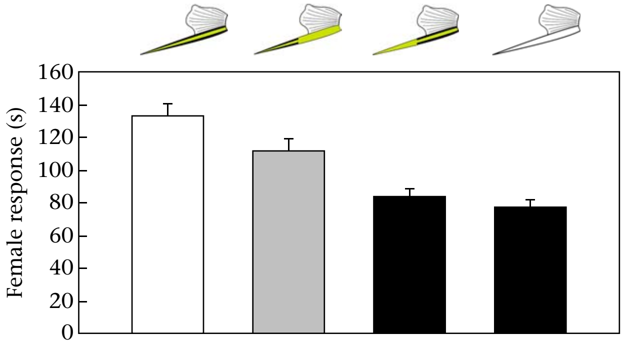

Figure 1. Female response to the four male video stimuli (pictured above each bar from left to right: complete sword, distal stripes, proximal stripes, no stripes). Bars with the same colour pattern did not differ significantly.

stimulus and the no-stripes stimulus ($P = 0.90$). The power to detect a difference of 30 s with an α of 0.05 was 0.90.

Females responded significantly longer to the male video stimuli than to the female video stimulus (paired *t* test: $t_{75} = 17.40$, $P < 0.0001$). There was no significant difference between female responses in the first and second trials of the test sessions (paired *t* test, $t_{75} = 0.73$, $P = 0.47$).

DISCUSSION

Female green swordtails showed differences in their responses to males based on differences in stripe location. Females preferred the male video stimulus with black stripes on the distal portion of the sword to the stimulus with black stripes on the proximal portion of the sword, even though the area of black coloration was equivalent in both videos. Thus, not only was the presence of black coloration important, but the position of the stripes also appeared to be important. However, despite their preference for distal stripes, females showed the strongest preference for the sword consisting of both proximal and distal stripes (the complete sword), suggesting that proximal stripes do contribute to the overall female response to the complete multicomponent sword.

Why might the distal location of the stripes contribute to eliciting a stronger female response? One possibility is that the distal black stripes bordering the extension portion of the sword act as a type of amplifier of one or more male traits, such as the extension component of the sword. The term amplifier has been used to describe a trait that reinforces female assessment of an informative trait (Hasson 1989). Males with greater sword extension have greater aerobic metabolism during routine and courtship swimming (Basolo & Alcaraz 2003) and recover from oxygen debt more quickly than males with a lesser degree of extension area (G. Alcaraz & A. L. Basolo, unpublished data). Although these results do not demonstrate that the sword extension component is an informative indicator of a female mating benefit, they are consistent with this hypothesis. A second possibility is that the distal stripes evolved as amplifiers of an uninformative male trait. In wolf spiders (*Schizocosa* sp.) auditory signals appear to have an amplifying effect on visual displays (Hebets & Uetz 2000), which are thought to exploit preexisting orientation biases that are elicited by prey movements (Clark & Uetz 1992). To support the hypothesis that distal stripes amplify some bias in females, outgroup species would need to be tested for their response to distal stripes. While a variety of studies have suggested that some male traits function as amplifiers of informative traits (Berglund 2000; Moya-Larano et al. 2003), to our knowledge, no studies have considered male traits that function as amplifiers of uninformative traits.

A second possible explanation for the difference in female response to distal versus proximal stripes is female avoidance of hybridization. Male southern platyfish, *Xiphophorus maculatus*, can express a black stripe at the base of the caudal fin, which resembles the proximal lower sword stripe of green swordtail males. Southern platyfish and green swordtails have a wide distribution and occur sympatrically in many coastal plain populations, including the site where the breeding population of swordtails for this study was collected. If these two species historically occurred together, female swordtails that mated with platyfish males with a stripe resembling the lower proximal stripe would have had lower reproductive success because of hybrid inferiority than females avoiding these males. Thus, even if proximal stripes increased the attractiveness of males, females that responded positively to this stimulus would risk mating with the wrong species, thereby lowering fitness. Females of several species have preferences that reduce the probability of hybridization (spadefoot toads: Pfennig 2000; pied flycatchers, *Ficedula hypoleuca*: Alatalo et al. 1994; cichlid fish: Couldridge & Alexander 2002), including multicomponent male traits (in treefrogs, *Hyla versicolor*: Gerhardt 1991; in crickets, *Allonemobius* sp.: Mousseau & Howard 1998). A third possible reason why females prefer distal stripes to proximal stripes is that they are an indicator of male age. Proximal stripes start to develop as a male nears sexual maturation and become completely formed soon thereafter; distal stripes, in contrast, are not completely formed until well after sexual maturation. Thus, females could use distal striping to distinguish older males from younger males. If mating with older males affords a benefit to females (Andersson 1994), the distal black stripes may be an indicator of the benefit.

Our results allow the rejection of several hypotheses for the evolution of preferences and preferred traits. We can reject the hypothesis that stripes serve only to increase the overall length (standard length plus fin length) of males because, although the distal stripes increased the overall length to the same degree as the complete sword, the complete sword elicited a stronger female response. This study contributes to the growing body of evidence on how male traits combine to elicit mating responses from females. We found that the location of identical components of a multicomponent male trait can affect female responses. We also propose a new class of amplifier traits, those that reinforce the effectiveness of an uninformative trait to stimulate a preexisting receiver bias or a female preference that evolved via a Fisherian sexual selection process (Fisher 1958). The results also indicate that, although the complete expression of a multicomponent trait may have the greatest effect on female response, some components can have a greater effect than others. Endler & Basolo (1998) noted that models such as the preexisting bias model emphasize signal design rather than signal content. Here, we found that combining the same components of a signal in different ways produces different responses in female receivers; thus, the design of the sword does contribute to mate attraction. Although this study answers some questions about the evolution of multicomponent traits, much remains to be investigated to more thoroughly understand the evolution of the multicomponent sword as well as other forms of complex male traits.

Acknowledgments

The authors thank J. Boughman & W. Wagner, Jr for critical input on this manuscript, J. Wise for sharing his knowledge of the animation programs and W. Feeney for developing illustrations for the figure. We also thank the Fisheries Ministry of Belize for issuing permits to A.L.B. for the study and collection of fish. B.C.T. was supported by National Institute of Mental Health-National Research Service Award F31 MH64328-01 during the preparation of this manuscript. This research was supported by a Grant-in-aid from Sigma Xi to B.C.T., and a University of Nebraska-Lincoln Layman grant and National Science Foundation grants IBN9629318 and IBN0112656 to A.L.B.

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