



# The conformation of a female preference for a composite male trait in green swordtails

ALEXANDRA L. BASOLO & BRIAN C. TRAINOR

School of Biological Sciences, University of Nebraska-Lincoln

(Received 12 December 2000; initial acceptance 24 January 2001;  
final acceptance 24 August 2001; MS. number: A8943)

Female green swordtails, *Xiphophorus helleri*, possess a preference for the multicomponent male sword. Previous work suggests that this female preference is a result of a pre-existing receiver bias favouring a sword and has contributed to sword evolution via intersexual selection. We use video presentations to investigate how females respond to components of this composite trait. Complete swords in this species have at least four individual components. Based on female response to video stimuli depicting males with intact swords and males in which sword components were digitally manipulated, it appears that males possessing complete swords elicit the strongest female response. Additionally, we found that females prefer stimuli with black sword coloration to those lacking black coloration. The results suggest that multiple components of the sword stimulate females, and that these components operate in conjunction to make the sword structure more attractive to females.

© 2002 The Association for the Study of Animal Behaviour

Intersexual selection explains the presence of mating preferences and preferred traits (Darwin 1871). Factors influencing the evolution of female preferences for elaborate male traits have been the focus of numerous theoretical and empirical studies (Andersson 1994 for review). Preferred male traits can be quite complex, requiring synthesis by female sensory and cognitive processes. Such synthesis may involve input from multiple male traits that are recognized by more than one female sensory modality (multimodal male traits), or synthesis of input for multiple male traits recognized by a single sensory modality (unimodal male traits). Unimodal processing involves either synthesis of input from multiple components of a composite male trait (e.g. cricket calls, peacock trains and swordtail swords), or synthesis of input from multiple male traits in a particular sensory modality (e.g. combs, eyes and tails in junglefowl: Zuk 1990a, b; orange coloration in guppies: Houde 1987; black spots in guppies: Endler 1983; caudal fin size in guppies: Bischoff et al. 1985). To evaluate whether different components of a composite trait contribute to male signals important to mate choice, the preference function for the multicomponent trait can be compared to the strength of the female preference to different subsets of the trait.

Correspondence and present address: A. L. Basolo, School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, Nebraska, 68588, U.S.A. (email: [basolo@cricket.unl.edu](mailto:basolo@cricket.unl.edu)). B. C. Trainor is now at the Department of Psychology, University of Wisconsin at Madison, 1202 W. Johnson Street, Madison, WI 53706, U.S.A.

Although the investigation of components of composite male acoustic signals is common (Andersson 1994), female responses to composite visual signals have not been as well studied (but see Zuk et al. 1992; Petrie & Halliday 1994; Endler & Houde 1995). Instead, the study of female preferences based on traits in the visual modality has tended to centre on either visual traits combined with traits recognized by other sensory modalities (Marler 1965; Wickler 1978; Burley 1981; Rowe & Guilford 1996; Marchetti 1998; Kilner et al. 1999), or multiple visual traits (Zuk et al. 1990a, b; Brooks & Caithness 1995; Omland 1996; Brooks & Couldridge 1999). This paucity of studies on how individual components of composite male traits affect female mating responses may be partially explained by the difficulty of manipulating the components of composite visual traits relative to acoustic composite traits.

An alternative to using live subjects to investigate visual signals is the use of video stimuli. Recent innovations in video technology allow precise control of stimuli; by digitally manipulating video clips, individual components of complex traits can be altered, while holding all other biologically significant attributes constant. Videos have been used with a number of animals to investigate receiver responses, including spiders (Clark & Uetz 1992), fish (McKinnon 1995; Balshine-Earn & Lotem 1998; Rosenthal & Evans 1998; Gonçalves et al. 2000), birds (Evans & Marler 1990; Adret 1997), frogs (Roster et al. 1995), lizards (Macedonia & Stamps 1994) and primates (Plimpton et al. 1981). Before using video

stimuli, however, it should be substantiated that the study animal responds to video and live stimuli similarly (see Fleishman et al. 1998 for review). One organism in which the effectiveness of using video stimuli has been demonstrated is the green swordtail, *Xiphophorus helleri*. Using digitally altered video, the strength of female response to variation in male sword length was measured; the results for both video (Trainor & Basolo 2000) and live presentations indicate that the strength of the sword preference increases with sword length.

Male green swordtails have composite swords that consist of at least four components involving ventral caudal fin rays 1 through 13: (1) a lower black stripe extending along the ventral margin of the caudal fin from the proximal insertion to the distal tip of rays 1–10, (2) an upper black stripe extending from the proximal insertion to the distal tip of rays 12–13, (3) a single or bilayer of orange/yellow or green between the two black stripes (rays 10–12), and (4) elongation of ventral caudal fin rays 10–12. Thus, the sword is a tri- or quadchromatic array extending from the insertion of 12 ventral caudal rays to their distal tip. Evidence for the swordtail *X. alvarezii* indicates a genetic basis for one sword component; internal coloration is an autosomal trait (Kallman & Bao 1987).

A preference for a composite male trait such as the sword may be specific for the complete trait per se, or, females may have preferences based on variation in individual components. A preference favouring sworded males has been found in female green swordtails and phylogenetic evidence suggests that this preference arose prior to the appearance of swords in *Xiphophorus* (Basolo 1995b). This pre-existing response bias could result from a single sensory or cognitive bias for that trait per se, or it may result from the synthesis of multiple biases, each contributing to the sword bias. Here, we investigate the relative importance of sword components to females using digital video technology to determine how the different components interact to affect female response.

## MATERIALS AND METHODS

Green swordtails are freshwater, live-bearing fish in the subfamily Poeciliinae (Parenti & Rauchenberger 1989). Test subjects were first- or second-generation offspring of female swordtails collected by permission from the Ministry of Fishes from Savannah Stream, Western Highway Mileage Marker 28, Belize. We tested virgin females when they reached sexual maturation. Three ad libitum daily feedings included live brine shrimp, liver paste and fish flakes. Broad-spectrum lighting was provided on a 16:8 h light:dark cycle.

### Preparation of Video Stimuli

We created a video loop of a courting male *X. helleri* with an average sword length for the population. We placed the male into a Plexiglas tank with a female and videotaped courtship behaviour. We then imported clips

of male courtship behaviour, including backward swim, lateral presentation and sigmoid flex behaviour, as well as normal swimming behaviour, to a Macintosh 7600 PowerMac equipped with a Targa 2000 videoboard using Adobe Premiere. We separated the clips into sequences of frames, edited using Adobe Photoshop, and assembled them into a courtship loop using Macromedia Director to produce a Master video of a swimming, courting male; this will be referred to as the normal sword stimulus. Although a number of different sword component combinations could have been tested, we chose to hold length constant, and to manipulate coloration components for this study. Using Photoshop, we digitally manipulated each frame of the normal sword stimulus to produce five additional video stimuli: (1) a sword lacking the upper black stripe; (2) a sword lacking the lower black stripe; (3) a sword lacking black stripes; (4) a sword lacking black stripes and internal yellow coloration; and (5) an entirely black sword. We made the first three stimuli by replacing normal black coloration with caudal fin coloration. We made the fourth stimulus by replacing normal black and yellow coloration with caudal fin coloration. We made the fifth stimulus by replacing all yellow internal coloration with black coloration. We chose stimuli (1), (2) and (5) because our video system allowed the black coloration to be detected by female test subjects, thus colour components were altered, yet sword length was not. In addition, stimulus (5) allowed us to compare the effect of natural sword coloration contrast (e.g. dark–light–dark of the normal sword) to a sword with no contrast. We chose stimulus (4) because if female swordtail vision in the yellow spectrum was accurately measured with our video system, we could test the effect of this colour component alone, holding length constant. We chose stimulus (3) because this manipulation removed all black coloration from the sword, while not altering sword length. We deliberately did not create a stimulus in which the black stripe components remained, but the internal coloration was replaced with caudal fin coloration. Female response to this manipulation would be difficult to interpret because both the caudal fin coloration and internal coloration are relatively light coloured. Nonhuman animals may perceive manipulations of colour in video images differently from humans (Fleishman et al. 1998). It is therefore not known whether female swordtails are able to perceive the internal yellow coloration in its true form on the colour monitor developed for human vision that we used. We constructed a seventh video stimulus of a swimming female. For this video, we videotaped a female swimming alone in the Plexiglas tank and used clips to construct a swimming loop that mimicked the movement (minus courtship behaviours) in the male video stimuli. We transferred all video stimuli to S-video cassette tapes for use in preference tests.

### Measuring Female Response with Video Playback

Our protocol for video presentations has been described in detail elsewhere (Trainor & Basolo 2000), therefore only a brief description is given here. To prime

females prior to testing, we placed each female in a glass tank with a live male for 10 min, separated from the male by a clear divider. Following priming, we transferred each female to a glass test tank with a monitor placed adjacent to each of the two sides. For each trial, we played one of the six male stimuli on one monitor, and played the female stimulus on the other monitor. We used the swimming female video as a control so that schooling behaviour did not confound the data for female preference for male stimuli (Basolo 1995b). It is unlikely that the video stimuli were perceived by the test females as flickering because the flicker fusion frequency of the monitors was 60 Hz, while the maximum critical fusion frequency of green swordtails is 43 Hz (Crozier & Wolf 1939). Following a 10-min acclimation period, we started the two videotapes. We initiated data recording when the test female had entered all three sections. Female response was defined as the time females spent within three body lengths of the video male and orienting towards the video male, and, was recorded for two 10-min observation periods. Between the two periods, we switched the video stimuli to the opposite sides. The two 10-min periods together constituted a single test and the sum time females spent within three body lengths orienting towards males during each test was used as the measure of preference for each video stimulus. We conducted tests between 0800 and 1800 hours and held the time of day constant for each female. We tested each test subject with each of the six test stimuli in random order, with each presentation occurring on successive days. We eliminated three out of the 23 females due to side bias because they remained in the left or the right tank section for more than 960 s (80%) during a test. All tests were observed from outside the test chamber via a remote monitor.

We examined the residuals from the raw data to verify the assumptions for parametric tests (Sokal & Rohlf 1981). We square-root transformed female response to male stimuli data to homogenize variance among treatments (Hartley's  $F_{\max(1,18)}=3.4, P>0.05$ ). Female response to the female video stimulus did not violate any of the assumptions of parametric tests. We first analysed transformed female response to male stimuli using a within-subjects analysis of variance (ANOVA) testing for order of presentation, and this was found to be nonsignificant ( $F_{5,18}=1.58, P=0.17$ ). We then analysed female response to male stimuli in a second within-subjects ANOVA testing for differences among sword stimuli. We used post hoc Tukey tests to separate means between sword stimulus treatments.

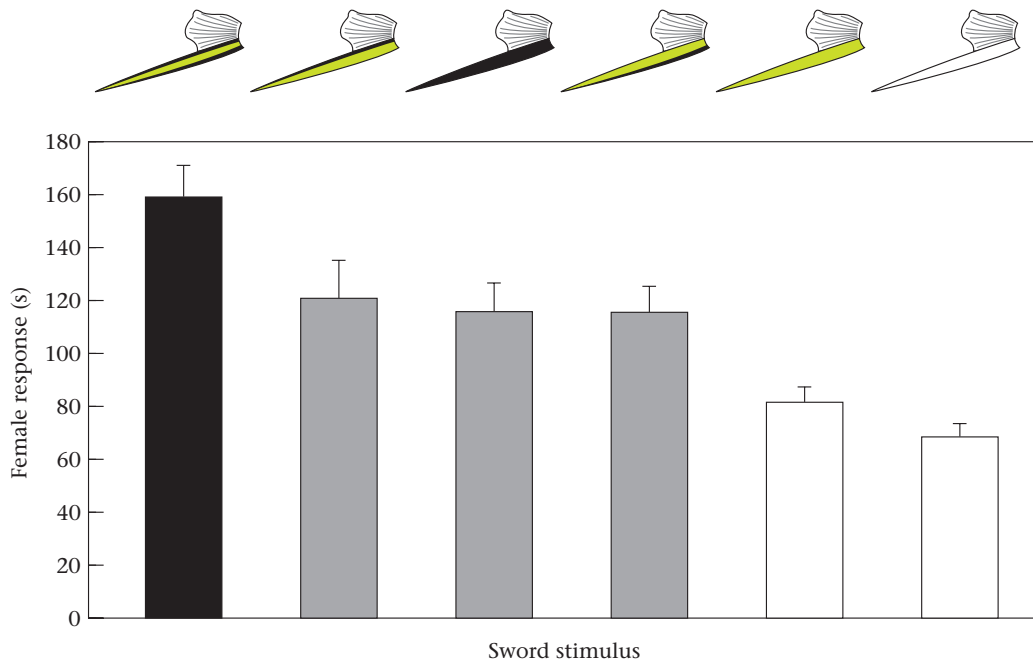
We estimated the effects of sword components by using female response to the different male video stimuli. To determine the effect of the lower stripe on female response, we subtracted each female's response to the stimulus lacking the lower stripe from her response to the normal stimulus. To determine the effect of the upper stripe, we subtracted each female's response to the stimulus lacking an upper stripe from her response to the normal stimulus. To determine the effect of the internal yellow coloration, we subtracted each female's response to the stimulus lacking black stripes and internal yellow

coloration from her response to the stimulus lacking black stripes. We used the stimulus lacking both black stripes and internal yellow coloration to determine a baseline female response attributable to all male traits other than the coloured components of the sword (e.g. elongation sword component, courtship behaviour, male morphology, etc). We summed the average of the effects of the lower stripe, upper stripe, internal yellow coloration, and all other male traits to estimate the response to a male with a normal sword. We compared this sum to the actual female response to the normal sword with a paired  $t$  test. A difference between this sum and the response to the complete sword would indicate that the effects of sword components on female response were not additive. Results are given as  $\bar{X} \pm SE$ .

## RESULTS

There was significant variation in female responses to the six video stimuli ( $F_{5,90}=17.48, P<0.0001$ ). Tukey tests revealed three different sword stimulus groupings (Fig. 1). Female response to the normal sword was significantly greater than to the stimulus lacking the lower stripe ( $P<0.05$ ), the stimulus that was completely black ( $P<0.01$ ), the stimulus lacking the upper stripe ( $P<0.01$ ), the stimulus lacking both black stripes ( $P<0.01$ ), and the stimulus lacking black stripes and internal yellow coloration ( $P<0.01$ ). Female response to the stimulus lacking the lower black stripe was significantly greater than to the stimulus lacking both black stripes ( $P<0.05$ ) and the stimulus lacking both black stripes and internal yellow coloration ( $P<0.01$ ) stimuli. Female response to the completely black stimulus was significantly greater than to the stimulus lacking both black stripes ( $P<0.05$ ) and the stimulus lacking black stripes and internal yellow coloration ( $P<0.01$ ). Female response to the stimulus lacking the upper black stripe was significantly greater than to the stimulus lacking both stripes ( $P<0.05$ ) and the stimulus lacking black stripes and internal yellow coloration ( $P<0.05$ ). Female response to the stimulus lacking both black stripes and the stimulus lacking black stripes and internal yellow coloration were not significantly different from one another. The sum of female response to the coloured components of the sword and the stimulus lacking the black stripes and the internal yellow coloration component stimulus was not significantly different from the actual response to the normal sword video stimulus (paired  $t$  test:  $t_{18}=0.11, P=0.90$ ).

Female response averaged across all six male stimuli was significantly greater than female response to the swimming female stimulus averaged across all six presentations (paired  $t$  test:  $t_{18}=17.1, P<0.001$ ). In addition, female response to both the stimulus lacking both black stripes and the stimulus lacking black stripes and internal yellow coloration was significantly greater than female response to the swimming female stimulus (paired  $t$  test:  $t_{18}=2.1, P<0.0001$ ;  $t_{18}=2.1, P<0.0001$ ). Female response to the female stimulus did not differ across sword video treatments ( $F_{5,90}=0.94, P=0.46$ ).



**Figure 1.** Female response to the six male video stimuli. Bars with the same colour pattern were not significantly different. ■: the results for the normal sword stimulus. □: the results for the three stimuli that lacked one sword component, either the lower stripe, yellow internal coloration, or the upper stripe. □: the results for the stimuli lacking black coloration, either the stimulus that was coloured yellow or the stimulus that was coloured to match caudal fin.

## DISCUSSION

The results from these video presentations suggest that the complete sword is most attractive to females. Although female response was strongest to the complete sword, females did respond differently to male stimuli when sword components were manipulated. The four male stimuli with black sword coloration were the same apparent length as a complete sword, yet females preferred the male stimuli with a complete sword to the other three. This result suggests that a preference for sword length cannot explain the female preference for sword length in green swordtails, as previously suggested (Basolo 1990b; Rosenthal & Evans 1998). Despite the black stripe response, increasing the amount of black did not necessarily affect female response; the response of females to the solid black stimulus did not differ from the response to a single stripe, while the stimulus with two black stripes separated by yellow elicited the strongest female response. Lythgoe (1979) proposed that animals have mechanisms to 'detect edges formed between areas of different colour'; thus the internal yellow coloration layered between the black stripes could enhance response to the sword due to increased stimulation of female horizontal edge detectors. Although females did not discriminate between the three different stimuli with a black component, these three stimuli were preferred over both the stimulus lacking black and the stimulus lacking black and yellow internal coloration. Females showed the lowest response to the two stimuli lacking black coloration, but they did not discriminate between the stimulus lacking black and the stimulus lacking both black and yellow. The results, however, do not necessarily indicate

that yellow internal coloration is not important to mate choice. It could be that the internal coloration component is important in terms of enhancing female response only when it is contrasted against black. Or, it could be that females did not perceive a difference between the two stimuli. One drawback of video playback is that colours displayed by monitors designed for human colour vision may be perceived differently by other organisms. Because of this, it is unclear whether female swordtails perceived the internal yellow coloration in its true form. If not, females could possess a response specific for an internal yellow component that our methodology precluded from detection. Despite this potential problem, however, it is clear that females prefer swords in which the black stripes are contrasted against a lighter coloration to stimuli lacking black coloration.

Individual components of composite traits may affect female response in an iterative (redundant) manner, in an antagonistic manner, or they may act synergistically in either an additive or multiplicative manner. Based on the results, it appears that sword components have independent effects on the sword preference, thus components do not appear to be iterative. If the preference for a sword is the result of a simple additive effect, we would expect that the summed preferences for the components would not differ from the preference for the composite sword. The sum of the estimated effects of the upper stripe, lower stripe, internal yellow coloration, and other male traits (morphological and behavioural) influencing female response was not significantly different from female response to the normal male stimulus with the composite sword. These results suggest that the multiple components of the sword operate in conjunction to make the

sword structure more attractive to females in an additive manner.

Female response was greatest to the four stimuli with black sword coloration. Preferences for black melanistic pigmentation have been found in other poeciliids. In some populations of guppies (*Poecilia reticulata*), females prefer males with a greater number of black spots (Endler & Houde 1995) and the removal of black reduces the attractiveness of males to females (Brooks & Caithness 1995). A preference for a lower caudal black stripe occurs in southern platyfish, *X. maculatus* (Basolo 1995a). Although Rosenthal & Evans (1998) concluded that female preference for black stripes was relatively weak in *X. helleri*, sword length was a confounding factor on female response to stripes in this study. In the present study, elongation is held constant, revealing a female preference for both the upper and lower black stripes. Preference for black coloration in males is not universal in poeciliids; female mosquitofish, *Gambusia affinis*, discriminate against males with black mottled coloration (Taylor et al. 1996). For *X. helleri*, however, black coloration appears to contribute to the preference for sworded males, and a sword with two black stripes elicited the strongest female response.

Numerous hypotheses have been proposed for the evolution of mating preferences (e.g. Fisherian selection: Fisher 1958; Lande 1981; direct benefits: Trivers 1972; good genes: Williams 1966; Hamilton & Zuk 1982; correlated effects: Darwin 1871; Lande & Arnold 1985; and pre-existing biases: Barlow 1977; West-Eberhard 1984; Basolo 1990b). In considering the evolution of single versus multiple male traits via female preferences, researchers have suggested that multiple signals can evolve under stable conditions via Fisherian selection (Pomiankowski & Iwasa 1993; Moller & Pomiankowski 1993), while good genes mechanisms should lead to the evolution of preferences for single male traits (Moller & Pomiankowski 1993). Schluter & Price (1993) suggest that preferences should evolve for individual male traits that honestly indicate male quality and that are easier to detect; quality indicators could evolve via either direct benefits or good genes mechanisms, while traits improving delectability result from direct benefits mechanisms. Multiple male traits may also arise in populations in which females have different preferences (Schluter & Price 1993; Iwasa & Pomiankowski 1995), however, a second possibility is that individual females could possess multiple preferences. Based on female swordtail responses to sword components, it is possible that there are multiple sensory or cognitive biases contributing to the female sword response, and thus that different inputs are synthesized to produce the female preference favouring the sword. In terms of sword evolution, the pre-existing bias model for the evolution of a female bias favouring a sword has been experimentally supported (Basolo 1990a, b; Haines & Gould 1994; Basolo 1995b). Whether other mechanisms work in conjunction with the female bias for swords is yet to be tested. But regardless of which mechanism(s) contributed to the evolution of the preference favouring a composite sword in green swordtails, it is clear that sword components presently act jointly to

achieve an effect on female response that each individually does not produce.

The results from these experiments provide new insight concerning the nature of female responses to multi-component traits. While numerous studies have shown that females prefer some trait variants over others, few have examined the conformation of a mating preference for a composite male trait. Although a trilayer array consisting of two black stripes contrasted against a lighter colour was found to be the most stimulatory to *X. helleri* females, some subset combinations were more stimulatory than others. These results provide greater knowledge concerning the preference favouring the sword, yet many questions remain to be answered. Future examination of female preference for components of the sword both within swordtails as well as in other poeciliid fish may provide clues to aid in determining whether the sword preference actually results from several biases rather than one, and, should lead to a better understanding of the mechanisms underlying the evolution of the female preference favouring a sword.

### Acknowledgments

The authors thank J. Johnson, C. Marler, L. Moscovice and W. Wagner for critical input on this manuscript; J. Wise for sharing his knowledge of the animation programs; and W. Feeney for developing illustrations for a figure. This research was supported by a Grant-in-aid from Sigma Xi to B.C.T and an UNL Layman grant, NSF grant RPG 9309211, NSF grant IBN9629318, and NIH grant MH55288-01 to A.L.B. This research was conducted under the guideline of the Institutional Animal Care and Use Committee of the University of Nebraska-Lincoln (Protocol No. 97-09-056).

### References

- Adret, P. 1997. Discrimination of video images by zebra finches (*Taeniopygia guttata*): direct evidence from song performance. *Journal of Comparative Psychology*, **111**, 115–125.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Balshine-Earn, S. & Lotem, A. 1998. Individual recognition in a cooperatively breeding cichlid: evidence from video playback experiments. *Behaviour*, **135**, 369–386.
- Barlow, G. W. 1977. Model action patterns. In: *How Animals Communicate* (Ed. by T. A. Sebeok), pp. 98–134. Bloomington, Indiana: Indiana University Press.
- Basolo, A. L. 1990a. Female preference for male sword length in the green swordtail, *Xiphophorus helleri* (Pisces: Poeciliidae). *Animal Behaviour*, **40**, 332–338.
- Basolo, A. L. 1990b. Female preference predates the evolution of the sword in swordtail fish. *Science*, **250**, 808–810.
- Basolo, A. L. 1995a. A further examination of a pre-existing bias favouring a sword in the genus *Xiphophorus*. *Animal Behaviour*, **50**, 365–375.
- Basolo, A. L. 1995b. Phylogenetic evidence for the role of a pre-existing bias in sexual selection. *Proceedings of the Royal Society of London, Series B*, **259**, 307–311.

- Bischoff, R. J., Gould, J. L. & Rubenstein, D. I. 1985. Tail size and female choice in the guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, **17**, 253–355.
- Brooks, R. & Caithness, N. 1995. Female choice in a feral guppy population: are there multiple cues? *Animal Behaviour*, **50**, 301–307.
- Brooks, R. & Coudridge, V. 1999. Multiple sexual ornaments coevolve with multiple mating preferences. *American Naturalist*, **154**, 37–45.
- Burley, N. 1981. Mate choice by multiple criteria in a monogamous species. *American Naturalist*, **117**, 515–528.
- Clark, D. L. & Uetz, G. W. 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour*, **43**, 247–254.
- Crozier, W. J. & Wolf, E. 1939. The flicker response contours for genetically related fishes. II. *Journal of General Physiology*, **22**, 463–485.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: J. Murray.
- Endler, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes*, **190**, 173–190.
- Endler, J. A. & Houde, A. E. 1995. Geographic variation in female preference for male traits. *Evolution*, **49**, 456–468.
- Evans, C. S. & Marler, P. 1990. On the use of video images as social stimuli in birds: audience effect on alarm calling. *Animal Behaviour*, **41**, 17–26.
- Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*. Oxford: Clarendon.
- Fleishman, L. J., McClintock, W. J., D'Eath, R. B., Brainard, D. H. & Endler, J. A. 1998. Colour perception and the use of video playback experiments in animal behaviour. *Animal Behaviour*, **56**, 1035–1040.
- Goncalves, D. M., Oliveira, R. F., Korner, K., Poschadel, J. R. & Schlupp, I. 2000. Using video playback to study visual communication in a marine fish, *Salarias pavo*. *Animal Behaviour*, **60**, 351–357.
- Haines, S. & Gould, J. 1994. Female platys prefer long tails. *Nature*, **370**, 512.
- Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218**, 384–387.
- Houde, A. E. 1987. Mate choice based upon naturally occurring color-pattern variation in a guppy population. *Evolution*, **41**, 1–10.
- Iwasa, Y. & Pomiankowski, A. 1995. Continual change in mate preferences. *Nature*, **377**, 420–422.
- Kallman, K. D. & Bao, I. Y. 1987. Female heterogamety in the swordtail, *Xiphophorus helleri* Rosen (Pisces, Poeciliidae), with comments on a natural polymorphism affecting sword coloration. *Journal of Experimental Zoology*, **243**, 93–102.
- Kilner, R. M., Noble, D. G. & Davies, N. B. 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, **397**, 667–672.
- Lande, R. M. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences, U.S.A.*, **78**, 3721–3725.
- Lande, R. M. & Arnold, S. J. 1985. Evolution of mating preferences and sexual dimorphism. *Journal of Theoretical Biology*, **117**, 651–664.
- Lythgoe, J. N. 1979. *The Ecology of Vision*. Oxford: Clarendon.
- Macedonia, J. M. & Stamps, J. A. 1994. Species recognition in *Anolis grahami* (Sauria, Iguanidae): evidence from responses to video playbacks of conspecific and heterospecific displays. *Ethology*, **98**, 246–264.
- McKinnon, J. S. 1995. Video mate preferences of female three-spined sticklebacks from populations with divergent male coloration. *Animal Behaviour*, **50**, 1645–1655.
- Marchetti, K. 1998. The evolution of multiple male traits in the yellow-browed leaf warbler. *Animal Behaviour*, **55**, 361–376.
- Marler, P. 1965. Communication in monkeys and apes. In: *Primate Behavior* (Ed. by I. DeVore), pp. 544–584. New York: Rinehart & Winston.
- Møller, A. P. & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology Sociobiology*, **32**, 167–176.
- Omland, K. E. 1996. Female mallard mating preferences for multiple male ornaments. II. Experimental variation. *Behavioral Ecology and Sociobiology*, **39**, 361–366.
- Parenti, L. R. & Rauchenberger, M. 1989. Systematic overview of the poeciliines. In: *Ecology and Evolution of Livebearing Fishes (Poeciliidae)* (Ed. by G. K. Meffe & F. F. Snelson, Jr), pp. 3–12. Englewood Cliffs, New Jersey: Prentice Hall.
- Petrie, M. & Halliday, T. 1994. Experimental and natural changes in the peacock's (*Pavo cristatus*) train can affect mating success. *Behavioral Ecology and Sociobiology*, **35**, 213–217.
- Plimpton, E. H., Swartz, K. B. & Rosenblum, L. A. 1981. Responses of juvenile bonnet macaques to social stimuli presented through color videotapes. *Developmental Psychology*, **14**, 109–115.
- Pomiankowski, A. & Iwasa, Y. 1993. Evolution of multiple sexual preferences by Fisher runaway process of sexual selection. *Proceedings of the Royal Society of London, Series B*, **253**, 173–181.
- Rosenthal, G. G. & Evans, C. S. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proceedings of the National Academy of Sciences U.S.A.*, **95**, 4431–4436.
- Roster, N. O., Clark, D. L. & Gillingham, J. C. 1995. Prey catching behaviour in frogs and toads using video-simulated prey. *Copeia*, **2**, 496–498.
- Rowe, C. & Guilford, T. 1996. Hidden colour aversion in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature*, **383**, 520–522.
- Schluter, D. & Price, T. 1993. Honesty, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society of London, Series B*, **253**, 117–122.
- Sokal, R. R. & Rohlf, J. 1981. *Biometry*. 2nd edn. San Francisco: W. H. Freeman.
- Taylor, S. A., Burt, A., Hammond, G. & Relyea, K. 1996. Female mosquitofish (*Gambusia affinis holbrooki*) prefer normally pigmented males to melanistic males. *Journal of Comparative Psychology*, **110**, 260–266.
- Trainor, B. C. & Basolo, A. L. 2000. An evaluation of video playback using *Xiphophorus helleri*. *Animal Behaviour*, **59**, 83–89.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.
- West-Eberhard, M. 1984. Sexual selection, competitive communication and species-specific signals in insects. In: *Insect Communication* (Ed. by T. Lewis), pp. 283–384. Toronto: Academic Press.
- Wickler, W. 1978. A special constraint on the evolution of composite signals. *Zeitschrift für Tierpsychologie*, **48**, 345–348.
- Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, New Jersey: Princeton University Press.
- Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990a. Mechanisms of mate choice in red jungle fowl. *Evolution*, **44**, 477–485.
- Zuk, M., Thornhill, R., Ligon, J. D., Johnson, K., Austad, S., Ligon, S., Thornhill, N. & Costin, C. 1990b. The role of male ornaments and courtship behavior in female choice of red jungle fowl. *American Naturalist*, **136**, 459–473.
- Zuk, M., Ligon, J. D. & Thornhill, R. 1992. Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. *Animal Behaviour*, **44**, 999–1006.