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Female choice in the guppy (*Poecilia reticulata*): the interaction between male color and display

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Abstract The effect of two components of male courtship, color and display behavior, on female choice of mates was investigated in the guppy (*Poecilia reticulata*). Computer-modified videos were constructed to determine the relative importance of a static trait, the presence or absence of carotenoid pigment (C and NC), and a dynamic trait, high and low display rate (HD and LD), on female response. Females were given a choice between all combinations of male display and color in a binary choice design. Preference was determined by the time females spent visually inspecting the animation. Females preferred animations with high display rates when both animations displayed color (CHD vs CLD), but not in the absence of color (NCHD vs NCLD). Equal numbers of females chose the color/low-display animation and the no-color/high-display animation when the two were paired. Conversely, color became a criterion of choice when both animations showed a low display rate (CLD vs NCLD), but not when both displayed at a high rate (CHD vs NCHD). These results suggest that females use both static and dynamic traits to evaluate males, but their rankings are affected by the choices available. Results of these experiments provide insights into how females use multiple traits to assess males.

Keywords Sexual selection · Static-dynamic traits · Video animations · Guppy · Mate choice

Introduction

Studies of sexual selection have focused on the role of secondary sexual traits, especially morphological ones, in mate choice. This emphasis on relatively static or time-invariant traits, such as bright color patterns and elaborate fins in fish and plumage color and tail length in birds, is partly due to the ease with which they can be studied. Highly variable, dynamic traits, such as courtship behavior, are less tractable, because their expression is often affected by such intervening variables as motivation, female response to male courtship, and the presence of competitors and predators (e.g., Magurran and Seghers 1990; Magnhagen 1991; Rowland 1994). Most of those studies attempting to determine the interacting roles of static and dynamic sexually selected traits in mate choice are correlative rather than manipulative, because it is difficult to control for the variation in male courtship behavior and the feedback effect of female response to display (but see Gerhardt 1991; Rowland et al. 1995; Rosenthal et al. 1996). Emphasis on certain components of secondary sexual traits may introduce a bias into the way the process of sexual selection is viewed, leading to simplistic interpretation of the complex nature of male-female interactions and mate choice. Theoretical models of mate choice integrating both static and dynamic components of male displays are available, but they have yet to be tested empirically (Balmford and Read 1991; Møller and Pomiankowski 1993; Pomiankowski and Iwasa 1993; Andersson 1994). Perhaps most importantly, it is not clear how the static and dynamic components interact.

We approached this problem experimentally in male guppies by manipulating two components of the courtship display: orange color (a static component) and courtship rate (a dynamic component). We created computer animations of males and then presented them to females and observed their visual responses. The advantage of using animations is that both behavior and morphology of males can be precisely controlled and individually manipulated (Clark and Uetz 1990; Evans and

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Marler 1991; Rosenthal et al. 1996). Guppies are an ideal system to test predictions of complex models of sexual selection. Females respond readily to video images of males. They discriminate among these images based on the area of their carotenoid pigment spots (Kodric-Brown and Nicoletto 1997) and both the number of displays and their duration in a courtship sequence (Nicoletto and Kodric-Brown 1999).

Many secondary sexual traits, such as the hue and saturation of carotenoid pigment spots and kinds and intensities of courtship behavior are conditionally expressed, thereby reflecting male health and physical condition (Kodric-Brown 1989; Houde and Torio 1992; Nicoletto 1993, 1995). However, highly changeable (dynamic) components, such as display rate and duration, may be better indicators of a male's current health and condition than more static components, such as body ornamentation, because static traits respond more slowly than dynamic traits to environmental factors, such as changes in diet or presence of parasites. Thus, if the information content of dynamic traits is greater than that of static traits, females might be expected to respond preferentially to variation among males in these traits, and only secondarily to the less variable static ones (Ligon and Zwartjes 1995; but see Møller 1990; Mateos and Carranza 1995 for an alternative view). This is supported by empirical studies (Gerhardt and Watson 1995; Rowland 1995; Rosenthal et al. 1996; Vinnedge and Verrell 1998). We asked the following questions: (1) What is the variation in the strength of preferences for static and dynamic components of male courtship for females expressing such preferences? (2) Is there a consensus among females for particular attributes of a display?

Guppies are an ideal system to address the questions posed above. Their ecology, life history, genetics, and behavior have been studied intensively (summarized in Houde 1997). Guppies have a promiscuous mating system. Males show conspicuous color patterns consisting of black (melanins), red or orange (carotenoids), and iridescent blue and white (structural pigments). Courtship of male guppies consists of behavioral sequences expressed as a series of S-shaped lateral movements of the body with the caudal and dorsal fins either apposed to the body or fully extended (Baerends et al. 1955; Liley 1966). There is considerable intra- and interpopulation variation in colors and patterns of the body and ornamentation of the caudal fin, in courtship behavior, and in female preferences for these traits (Farr 1980; Endler 1983; Bischoff et al. 1985; Stoner and Breden 1988; Houde and Endler 1990; Brooks and Caithness 1995; Endler and Houde 1995; Nicoletto 1995; Kodric-Brown and Nicoletto 1996). However, in most populations for which female preferences are known, females show a preference for males with carotenoid pigment. In our experiments we used females from a wild population of domestic guppies from the Jemez Mountains of New Mexico.

Methods

We briefly describe the process of filming and creating the digitally modified video animations. A detailed description of the process can be found in Nicoletto and Kodric-Brown (1999). The male that we used to create these animations had a single large orange color spot that covered 19.1% of the body. This color pattern is frequently encountered in the Jemez population. We filmed the male in the presence of a female against a black background in a 15×10×8 cm compartment of a 9.47-l aquarium. Illumination was provided by reflecting the light from two 3,400 K bulbs off two white reflectors placed beside the compartment. We filmed the behavior with a Sony 5100HS, S-VHS video camera and recorded it on a Panasonic AG-5700 video tape recorder. The focal distance of the camera was adjusted so that the male appeared life size on the monitor used to present the animation (standard length=20 mm).

The digitally modified video sequences were produced by capturing single frames of various behavioral sequences using a video Toaster 4000 (Newtek) frame grabber. We captured successive frames where there was significant movement. These frames were rendered into 256-color, 640×400 pixel IFF files with a batch image-processing program (Procontrol; ASDG). The background around the male image was cleared and the position of the image on each frame was adjusted to yield smooth transitions from one behavior to another using Deluxe Paint IV (Electronic Arts).

We created animations with high and low display rates. The two animations were identical in the timing, sequence, and position of the various behaviors, but differed in the rate at which the male displayed. The high-display-rate animation contained three courtship sequences per minute (nine per trial). The low-display-rate animation had one courtship sequence per minute (three per trial). Each courtship sequence consisted of a double-sided open fin sigmoid display. The male shows both sides of his body during a double-sided display. Since females respond more strongly to males courting with fully extended dorsal and caudal fins, we used these in our animation sequences (Baerends et al. 1955). Both the high and low display rates of our animations were well within the range of those seen in the Jemez Mountain population (mean=5.56, SE=0.03, range=1–12 displays/3 min; Kodric-Brown and Nicoletto 1996).

To create animations in which the male lacked the orange spot, we removed the color by adjusting the animation palette. The palette software contains sliders that can be used to adjust the hue, value, and chroma of the colors in the palette. We adjusted the slider for hue to zero and thereby converted all of the colors in the palette into shades of gray. The value and the chroma sliders were not adjusted.

We used all combinations of display rate and color to construct four animations. The animations were: no color, high display (NCHD), no color, low display (NCLD), color, high display (CHD), and color, low display (CLD). Animations were 1 min long and were played three times at 30 frames per second on the computer in the Scala multimedia program (Scala AS) and downloaded onto S-VHS tape using a Panasonic AG-5700 videotape recorder. Each of the tapes consisted of 2 min of SMPTE color bar pattern, 2 min of blank screen showing the black background of the animation, 3 min of the first animation, 1 min of the blank screen with the background, followed by 3 min of the second animation. We used the SMPTE color bars to visually adjust the monitors to the same hue and brightness. The background color was shown to partially acclimate the fish to the background of the animation.

We used virgin females in our experiments, because they are very receptive to males (Liley 1966). The females were of similar age (6 months±10 days) and similar standard length (range: 16.8–18.4 mm, mean±SE: 17.6±0.54 mm). Fry were reared in 75-l aquaria divided into two compartments by clear glass partitions. Mature males were placed into one compartment of the rearing aquarium and fry were placed into the other compartment. Males were removed from the compartment containing virgin females as soon as they could be sexed. Since rearing conditions may influ-

Table 1 Analysis of side bias, the difference in time females spent between paired male images (Wilcoxon signed-ranks tests), and the number of females preferring each male image. Predicted direction of preference (>). No predicted direction of preference (~)

| Comparison | <i>n</i> | Side bias (right vs left side) | | Difference between pair | | Number of females | |
|------------|----------|--------------------------------|----------|-------------------------|----------|-------------------|----------|
| | | <i>W</i> | <i>P</i> | <i>W</i> | <i>P</i> | χ^2 | <i>P</i> |
| NCHD>NCLD | 27 | 104 | 0.241 | 213 | 0.22 | 4.48 | 0.10 |
| CHD>NCHD | 30 | 17 | 0.830 | 71 | 0.74 | 4.80 | 0.10 |
| CHD>CLD | 25 | 65 | 0.167 | 325 | 0.002 | 25.0 | 0.002 |
| CLD>NCLD | 26 | 20 | 0.773 | 337 | 0.002 | 22.15 | 0.002 |
| CHD>NCLD | 27 | 70 | 0.074 | 368 | 0.002 | 23.15 | 0.002 |
| CLD~NCHD | 24 | 31 | 0.523 | 17 | 0.83 | 0.12 | 0.70 |

ence female mating preferences as adults (Rosenqvist and Houde 1997), virgin females were raised in visual, but not physical, contact with males varying in the area of carotenoid spots on their body from 0.5 to 25%. This coincides with the variation in male ornamentation in Jemez Spring males. Fish were kept in aquaria with undergravel filters, a natural gravel substrate, a water temperature of $28 \pm 2^\circ\text{C}$, and a photoperiod of 16 h:8 h light:dark. Twenty-four hours before a trial, individual females were placed into a compartment of a 75-l aquarium that was divided into eight compartments with opaque plexiglass partitions. A 20-W light strip was attached to the front and back panel of these holding aquaria to illuminate the compartments from the side and to acclimate females to light conditions encountered during presentation of the videotapes.

For the experimental trials, females were placed in a small aquarium (20.5×21 cm). The substrate in the aquarium was natural-colored gravel. The front of the aquarium was marked in 5-cm increments to facilitate recording the female's position during the trial. We placed two 12.5×17.5 cm high resolution (450 TV lines) color Sony monitors (model PVM8044Q) opposite each other, on the right and left side of the test aquarium. The female was introduced into the test aquarium 10 min before the trial. The trial began when we simultaneously presented a pair of tapes. The two test sequences on each tape were presented in reverse order. Thus, for example, the monitor at one end of the tank showed CLD while the other monitor showed NCHD. Then the same sequences were repeated but on the monitors at the opposite ends of the tank. Thus we controlled for a side bias on the part of the female. The behavior of females and their position with respect to the two monitors was recorded during the presentation of the two male images (6 min). All trials were conducted between 0800 and 1200 hours.

To ensure that females were sexually motivated and responded to the male images appropriately, we only counted trials in which a female responded to one of the images with at least one 'gliding motion' (Houde 1997). Sexually receptive females display this behavior in response to male courtship; it is often followed by copulation. We measured female preference as the amount of time she spent within 5 cm of the side of the aquarium nearest to the monitor showing the animation. The screens of the monitors were 2 cm from the glass sides of the aquarium. Thus a female responding to a male would be viewing the male image at a distance of 2–7 cm, well within the range of a courting male. The time a female spends near and viewing a male is a good predictor of mating preference (Kodric-Brown 1993). We discarded trials in which females did not respond to the animations and spent the entire observation period in a corner of the aquarium ($n=5$), or failed to respond to the male animations with a receptive display ('gliding motion', $n=4$). None of the females showed a side bias based on a Wilcoxon signed-ranks test (Table 1).

Female preference for a male animation was inferred if she spent at least 70% of the trial with that animation. We chose a 70% response based on the results of binomial tests which indicated that females clearly differentiated between male images at this level of response. We discarded eight females in the NCHD/NCLD trials and two females in the CHD/NCHD trials because they did not meet our criterion of preference. Each female was tested once with a single pair of animations. Females were selected randomly from the virgin female tank and placed into a new tank after a trial.

Statistical analysis

We compared female responses to all six pair-wise presentations of the four animations. The strength of female responses to particular animations was analyzed in two ways: (1) as the difference in the time females viewed each pair of animations and (2) as the number of females showing a preference for an animation.

We tested for differences in the time females spent viewing each animation of a pair (animation 1–animation 2) with a Wilcoxon signed-ranks test. For this analysis we only used trials in which females showed a clear preference (70% of trial) for one of the male images. We predicted that females should show the following preferences: NCHD over NCLD, CHD over NCHD, CHD over CLD, CHD over NCLD, and CLD over NCLD. We could not predict a priori how display and color would interact to affect female choice between the CLD and the NCHD animation. These predictions are based on well-documented patterns of female preferences for males with large areas of carotenoid pigments and high display rates in the Jemez population as well as other guppy populations experiencing low levels of predation (reviewed by Houde 1997). Two-tailed tests were used for all combinations of animations. We used a χ^2 test to determine the distribution of preferences among females for each combination of orange color and display rate. We adjusted the significance level with a Bonferroni inequality for multiple comparisons (Manly 1992).

Results

Females spent more time with one of the animations in three out of six comparisons (Fig. 1). As we predicted, females spent more time viewing the CHD animation when it was paired with the CLD and the NCLD animation. They also spent more time with the CLD animation when it was paired with the NCLD animation (Table 1). However, contrary to our predictions, females did not spend more time viewing the CHD animation when it was paired with the NCHD animation, or the NCHD when it was paired with the NCLD animation. There was also no significant difference in their responses to the CLD and the NCHD animation.

A comparison of the number of females choosing each male image showed a pattern that conformed to our a priori predictions (Table 1, Fig. 2). Females were unanimous in their choice of the CHD over the CLD image. Similarly, all but one of the females chose the CHD over the NCLD image and the CLD over the NCLD image. There was less consensus in the response of females in the NCHD versus NCLD and the CHD versus NCHD trials (Fig. 2). Only in the CLD versus NCHD trials were females clearly divided in their choices of male animations: some preferred one animation and some preferred the other.

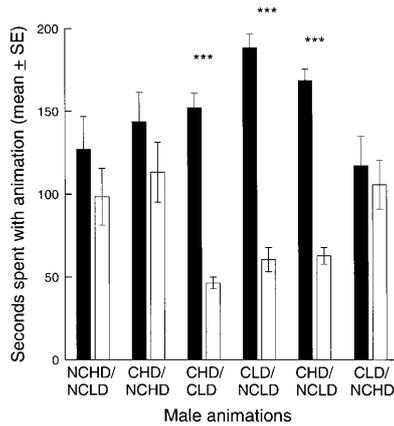


Fig. 1 Pairwise comparisons of the time (mean±SE) females spent with the first male animation of the pair (*filled bar*), and the second animation of the pair (*open bar*). Wilcoxon one-sample test, *** $P < 0.002$. Abbreviations for animations are as follows: no color, high display (NCHD); no color, low display (NCLD); color, high display (CHD); color, low display (CLD)

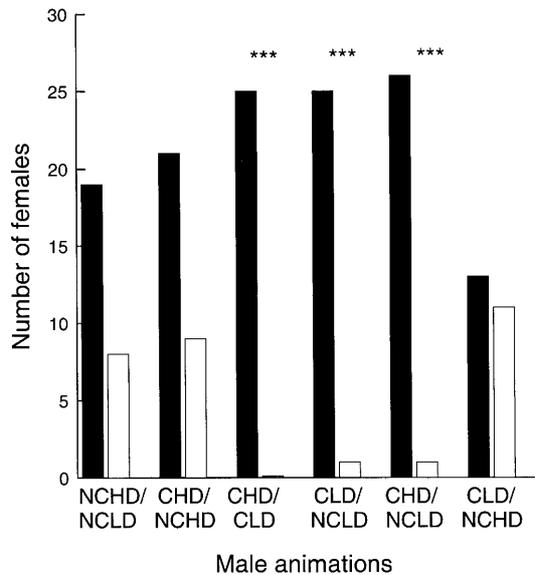


Fig. 2 Number of females preferring the first male animation of the pair (*filled bar*), and number of females preferring the second animation of the pair (*open bar*). χ^2 test, *** $P < 0.002$. Abbreviations for animations are as in Fig. 1

Discussion

Female guppies respond differentially to the dynamic and static components of male courtship. Our results show that female responses to male courtship varied depending on the attractiveness of each component of the signal and the combinations which were presented. Females discriminated most strongly when presented with paired images providing the maximum contrast in both dynamic and static traits (CHD vs NCLD). These results are consistent with previous findings and suggest that the most effective courtship signals are those incorporating

orange (carotenoid) color patterns and high display rate (Houde 1997).

When females were presented with ‘mixed signals,’ namely dull males courting intensely, and males with orange coloration and low levels of courtship, there was no significant difference in the time they spent with each image, because females varied in their preferences for each image (CLD vs NCHD; Fig. 1). These results are consistent with the interpretation that the dynamic (courtship display) and the static signals (orange color) are equally attractive. Our results also support an alternative interpretation, namely that females of this population show individual preferences in the relative ranking of these two traits: some may show a preference for orange color, while others may base their preference on display rate (Fig. 2). The observed patterns are also consistent with those found in a previous study of Jemez guppies using live males, where females differed in their preferences for male ornaments (carotenoid and iridescent spots: Kodric-Brown and Nicoletto 1996).

We also investigated the relative importance of each male trait. If females respond primarily to display rate, then we would expect significant differences in those pairwise comparisons where we manipulated display rate but controlled for color (CHD vs CLD and NCHD vs NCLD). Females did indeed respond to display rate, because we found significant differences in female response when we controlled for the presence of orange color (CHD vs CLD). However, in the absence of color, the animation with the higher display rate was less effective in eliciting a strong response in most females (NCHD vs NCLD, Figs. 1, 2). Thus, female preference for the dynamic trait (display rate) is much weaker in the absence of the static trait (color). These results should be interpreted with caution, since the two treatments (CHD vs CLD and NCHD vs NCLD) are not strictly comparable. Although the display rates of our animations were within the range encountered by females of this population, the manipulation of color is not. In the first treatment, we provided females with two male traits (orange color and courtship display) normally encountered in males of this population, while in the latter, females were presented with entirely novel images with only one trait (courtship) and entirely lacking in color (grey scale). Thus the eight females in the NCHD versus NCLD treatment that were discarded because they did not express a preference for either male image may have had difficulty in discriminating between them in the absence of the color cue. In the Jemez population, females do encounter dull males with few color spots and devoid of orange coloration. Such males, if they court at all, have low display rates and are not attractive to females. Thus, we had to create colorless males with high display rates since this combination normally is not encountered in nature.

If female choice of males is based primarily on orange coloration, a static trait, then females should prefer male images with orange coloration over those without color when both images display at the same rate (CLD over NCLD and CHD over NCHD). Females responded

to the presence of orange color, but only at low display rates (CLD over NCLD). Although a greater number of females preferred the CHD over the NCHD image (Fig. 2), there was no significant difference in the time spent with these two images, because females varied in attentiveness (Fig. 1). Clearly, orange coloration is less effective in attracting females at a high display rate than it is at a low display rate.

Display rates enhance the attractiveness of males, either by drawing the attention of females to male color patterns or, alternatively, the color patterns may enhance the effectiveness of the courtship displays (Endler 1992). The pairwise design of our experiment did not allow us to quantify the interaction between dynamic and static components of courtship on female responses. Nevertheless, our results suggest that females use both dynamic and static traits to evaluate males, but the relative importance of each is determined by the choices available.

Both display rate and carotenoid pigmentation are considered to be honest signals of male condition and genetic quality because they may be energetically expensive (display rate) and reflect access to high-quality carotenoid-rich food resources (orange coloration). Displays are dynamic signals that can be turned on or off instantaneously and indicate not only a male's current physical condition, but also his motivational level and sexual interest. Although the intensity of carotenoid pigmentation also varies somewhat over time and reflects a male's current condition, there is a greater time lag and less temporal variation in its expression. For example, in birds, carotenoids are deposited in feathers at the time of the molt, and thus reflect the bird's physical condition at that time and not necessarily when it is breeding (Hill and Montgomerie 1994). Although the intensity of carotenoid pigment in the spots of a male guppy changes over time, it does so on the order of days or even weeks, not minutes, the time scale over which displays change (Kodric-Brown 1989). Thus, females should primarily evaluate the quality and quantity of male courtship displays, and only secondarily, the quality and quantity of their body ornamentation.

So far there is no consensus regarding the relative importance of behavioral and morphological traits in female mate choice (Zuk 1991; see Houde 1997 for a summary of the relevant literature). Previous studies of mate preferences of Jemez guppies showed that females preferred males with high display rates. Color patterns, and especially the area of orange spots, were of secondary importance (Nicoletto 1993, 1995; Kodric-Brown and Nicoletto 1996; Nicoletto and Kodric-Brown 1999). Further experiments are needed to determine how females evaluate prospective mates and the relative importance of static and dynamic components of male secondary sexual traits in this evaluation process.

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References

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ
- Baerends GP, Brouwer R, Waterbolk HT (1955) Ethological studies on *Lebistes reticulatus* (Peters). I. An analysis of the male courtship pattern. *Behaviour* 8:249–334
- Balmford A, Read AF (1991) Testing alternative models of sexual selection through female choice. *Trends Ecol Evol* 6:274–276
- Bischoff RJ, Gould JL, Rubenstein DI (1985) Tail size and female choice in the guppy (*Poecilia reticulata*). *Behav Ecol Sociobiol* 17:253–255
- Brooks R, Caithness N (1995) Female choice in a feral guppy population: are there multiple cues? *Anim Behav* 50:301–307
- Clark DL, Uetz GW (1990) Video image recognition by the jumping spider, *Maevia inclemens* (Araneae: Salticidae). *Anim Behav* 40:884–890
- Endler JA (1983) Natural and sexual selection on color patterns in poeciliid fishes. *Environ Biol Fish* 9:173–190
- Endler JA (1992) Signals, signal conditions, and the direction of evolution. *Am Nat* 139:S25–S153
- Endler JA, Houde AE (1995) Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* 49:456–468
- Evans CS, Marler P (1991) On the use of video images as social stimuli in birds: audience effects on alarm calling. *Anim Behav* 41:17–26
- Farr JA (1980) Social behavior patterns as determinants of reproductive success in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae): an experimental study of the effects of intermale competition, female choice, and sexual selection. *Behaviour* 74:38–91
- Gerhardt HC (1991) Female mate choice in treefrogs: static and dynamic acoustic criteria. *Anim Behav* 42:615–635
- Gerhardt HC, Watson GF (1995) Within-male variability in call properties and female preference in the grey treefrog. *Anim Behav* 50:1187–1191
- Hill GE, Montgomerie R (1994) Plumage color signals nutritional condition in the house finch. *Proc R Soc Lond B* 258:47–52
- Houde E (1997) Sex, color, and mate choice in guppies. Princeton University Press, Princeton, NJ
- Houde E, Endler JA (1990) Correlated evolution of female mating preferences and male color patterns in the guppy *Poecilia reticulata*. *Science* 248:1405–1408
- Houde E, Torio AJ (1992) Effect of parasitic infection on male color pattern and female choice in guppies. *Behav Ecol* 3:346–351
- Kodric-Brown A (1989) Dietary carotenoids and male mating success: an environmental component of female choice. *Behav Ecol Sociobiol* 25:393–401
- Kodric-Brown A (1993) Female choice of multiple male criteria in guppies: interacting effects of dominance, coloration and courtship. *Behav Ecol Sociobiol* 32:415–420
- Kodric-Brown A, Nicoletto PF (1996) Consensus among females in their choice of males in the guppy *Poecilia reticulata*. *Behav Ecol Sociobiol* 39:395–400
- Kodric-Brown A, Nicoletto PF (1997) Repeatability of female choice in the guppy: response to live and videotaped males. *Anim Behav* 54:369–376
- Ligon JD, Zwartjes PW (1995) Ornate plumage of male red junglefowl does not influence mate choice by females. *Anim Behav* 49:117–125
- Liley NR (1966) Ethological isolating mechanisms in four sympatric species of poeciliid fishes. *Behaviour (Suppl)* 13:1–197

- Magnhagen C (1991) Predation risk as a cost of reproduction. *Trends Ecol Evol* 6:183–186
- Magurran AE, Seghers BH (1990) Risk sensitive courtship in the guppy (*Poecilia reticulata*). *Behaviour* 112:194–201
- Manly BF (1992) The design and analysis of research studies. Cambridge University Press, Cambridge, UK
- Mateos C, Carranza J (1995) Female choice on morphological features of male ring necked pheasants. *Anim Behav* 49:737–748
- Møller AP (1990) Male tail length and female mate choice in the monogamous swallow *Hirundo rustica*. *Anim Behav* 39:458–465
- Møller AP, Pomiankowski AN (1993) Why have birds got multiple sexual ornaments? *Behav Ecol Sociobiol* 32:167–176
- Nicoletto PF (1993) Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. *Anim Behav* 46:441–450
- Nicoletto PF (1995) Offspring quality and female choice in the guppy, *Poecilia reticulata*. *Anim Behav* 49:377–387
- Nicoletto PF, Kodric-Brown A (1999) The use of digitally-modified videos to study the function of ornamentation and courtship in the guppy, *Poecilia reticulata*. *Environ Biol Fish* 56:333–341
- Pomiankowski AN, Iwasa I (1993) Evolution of multiple sexual preferences by Fisher's runaway process of sexual selection. *Proc R Soc Lond B* 253:173–181
- Rosenqvist G, Houde A (1997) Prior exposure to male phenotypes influences mate choice in the guppy, *Poecilia reticulata*. *Behav Ecol* 8:194–198
- Rosenthal GG, Evans CS, Miller WL (1996) Female preference for a dynamic trait in the green swordtail, *Xiphophorus helleri*: attractive males swim backwards. *Anim Behav* 51:811–820
- Rowland WJ (1994) Proximate determinants of stickleback behavior: an evolutionary perspective. In: Bell MA Foster SA (eds) *The evolutionary biology of the threespine stickleback*. Oxford University Press, Oxford, pp 297–344
- Rowland WJ (1995) Do female stickleback care about male courtship vigour? Manipulation of display tempo using video playback. *Behaviour* 132:951–961
- Rowland WJ, Bolyard KJ, Jenkins JJ, Fowler J (1995) Video playback experiments on stickleback mate choice: female motivation and attentiveness to male colour cues. *Anim Behav* 49:1559–1567
- Stoner G, Breden F (1988) Phenotypic differentiation in female preference related to geographic variation in male predation risk in the Trinidad guppy (*Poecilia reticulata*). *Behav Ecol Sociobiol* 22:285–291
- Vinnedge B, Verrell P (1998) Variance in male mating success and female choice for persuasive courtship displays. *Anim Behav* 56:443–448
- Zuk M (1991) Sexual ornaments as animal signals. *Trends Ecol Evol* 6:228–231