

Repeatability of female choice in the guppy: response to live and videotaped males

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Abstract. The degree to which females are consistent in their mate preferences has implications for studies of sexual selection. Because choice of females for particular males may be affected by temporal changes in male characteristics, consistency of mate preferences of individual females of *Poecilia reticulata* was studied by presenting them with the same male pairs in consecutive trials under three experimental procedures: live males behind clear glass, live males behind one-way glass and images of males on videotape. Although females did not habituate to males in any of the experiments, they spent significantly more time in proximity to males behind clear glass than in the video and one-way glass presentations. Females preferred the bright male over the pale one in the video and the clear glass presentations, but not in the one-way glass experiment. Repeatability of preferences by individual females for a male was high in the video and one-way glass presentations but low in the clear-glass experiment. Behavioural interactions with the male in the clear-glass experiment affected both the time that females spent viewing males as well as female visual preferences. Results indicate that the video playback is not only useful for detecting differences between female preferences for morphological traits of male guppies, but is also much more effective in detecting preferences than the other two techniques, because it eliminates temporal variation in male behaviour.

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Most communication systems consist of a complex series of interactions between sender and receiver (Guilford & Dawkins 1991; Harper 1991). Courtship displays of males and female responses to these displays are an example of such a dynamic system. Motivation, reinforcement and facilitation are important in the observed variation in the intensity of a male's display and a female's response to it.

Video playback has been used successfully to study a number of communication systems, such as mate choice (Clark & Uetz 1990, 1992; McKinnon 1995; Rowland et al. 1995a, b; Rowland 1995; Rosenthal et al. 1996), male–male interactions (Macedonia et al. 1994), and anti-predator behaviour (Evans & Marler 1991). The video playback technique has two advantages for

studies of mate choice. It eliminates the problem of temporal variation in male motivational state, appearance and display rate, because one or more females can be repeatedly presented with an identical male image. Video playback also controls the variation in female response due to the interaction between the male and the female. Thus, it is excellent for studying consistency of individual females in their choice of males.

Consistency of female preference is important in studies of sexually selected traits. An underlying assumption of both the good genes and runaway models of sexual selection is that individual females show consistent (repeatable) preferences for particular male phenotypes (Lande 1981; Kirkpatrick 1982; Kodric-Brown & Brown 1984; Pomiankowski 1988). Repeatability is a measure of the consistency of individual females' responses to a particular male trait and is determined from a repeated measures analysis on the same individuals (Boake 1989). Consistency of individual females' responses is difficult to study, because it is

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rarely possible to present a female with identical male signals over time.

Considerable intra- and inter-population variation exists in colours and patterns of the body, ornamentation of the caudal fin and courtship behaviour of male guppies and female preferences for these traits (Farr 1983; Houde 1988, 1994; Houde & Endler 1990). Individual males also show temporal changes in physiological state and motivation, with concomitant variation in behaviour, especially the frequency and intensity of courtship displays (Baerends et al. 1955; Farr 1980; Rodd & Sokolowski 1995). Despite numerous studies on patterns of female choice, little is known about temporal variation in females' criteria for choosing males (but see Godin & Dugatkin 1995).

This study had two aims. First, we evaluated the applicability of the video playback technique to the study of female mate choice in the guppy by comparing the visual responses of females to video images of males and live males. Second, we compared the consistency of females' responses to repeated presentations of video images of males and live males. Only in videotaped presentations can we control both male appearance and behavioural sequences and repeatedly present females with identical male images.

GENERAL METHODS

Fish were reared in the laboratory and were descendants of an introduced population living in a thermal spring in the Jemez Mountains near Albuquerque, New Mexico. Males of this population are colourful, and females show strong preferences for males with large areas of carotenoid pigments, complex colour patterns and high display rates (Nicoletto 1993, 1995).

In all mate-choice trials we used virgin females of similar age (6 months, from litters born within 10 days of each other) and size ($\bar{X} \pm \text{SD} = 2.0 \pm 0.5$ cm). Virgin females were collected as fry from stock tanks and transferred into another aquarium; males were culled as soon as they could be sexed. The virgin females were raised in 75-litre aquaria divided into two compartments by clear glass partitions; females were in one half and males in the other. Thus the females to be tested were raised in visual, but not physical, contact with males. Fish were

maintained in aquaria with undergravel filters, a natural gravel substrate, a water temperature of $28 \pm 2^\circ\text{C}$, and a 16:8 h light:dark photoperiod.

Males and females used in the mate-choice trials were individually placed into one compartment of a 75-litre aquarium that had been subdivided into eight compartments with opaque Plexiglas partitions. They were introduced into the compartments 24 h before the start of the trial and remained there during the trial.

In all experiments, we used pairs of males that were matched for size but that differed in the proportion of the body covered with carotenoid and iridescent spots. After the trials, colour patterns of each pair of males were quantified as follows. Males were anaesthetized with MS222 and photographed with a 50-mm macro lens using Kodachrome 64 DX film. Slides were projected onto a computer digitizing tablet and the area of carotenoid and iridescent spots, as well as total area, was recorded (Kodric-Brown 1989). One male of the pair was ornamented (25–30% of body with carotenoid and iridescent spots) and the other was plain (5–10% of body with carotenoid and iridescent spots). Each female was presented with the same pair of males on four consecutive days. All trials were conducted between 0800 and 1200 hours. We conducted three mate-choice experiments.

Experiment 1: Live Males Confined Behind Clear Glass

In this design, a female could visually interact with one pair of males, and males could respond to the female with courtship displays. We used 25 females and 40 males presented in unique combinations in such a way that females could choose between an ornamented and a pale male. Whenever a male was used again in a mate choice trial he was paired with a different male.

We used a 38-litre aquarium subdivided by two glass partitions into three equal-sized compartments (20.5 × 21 cm). The bottom of the aquarium was covered with natural-coloured gravel. The front of the central compartment was marked in 5-cm increments to facilitate recording the female's position during the trial. Males were introduced into the outside compartments of the test aquarium 30 min before the beginning of a trial. The female was introduced into the central compartment of the test aquarium and allowed to

view the males 10 min before a trial. The female's preference for a male was measured as the amount of time she spent within 5 cm of a male's partition during a 10-min observation period. Time spent by a female near a displaying male is a good predictor of mating preference (Kodric-Brown 1985). The observation period consisted of two 5-min segments with a 1-min pause, during which the males were switched between compartments to control for possible side bias by the female.

Experiment 2: Live Males Confined Behind One-way Glass

This design eliminated interactions between males and females, but retained temporal variation in male behaviour between successive trials. We used the same test aquarium described in experiment 1, but replaced the two clear glass partitions with one-way glass such that females could view males, but males could not view the females. Two 40-watt fluorescent lights were placed over the compartments of the males, but the central compartment of the female was not illuminated. Replicates consisted of 25 females and 40 males presented in unique combinations.

Experiment 3: Videotaped Males

This experiment used video images of swimming males to eliminate interactions between the male and female as well as temporal variation in male behaviour between successive trials. Replicates consisted of 25 females and 10 taped males presented in unique combinations.

We used a small aquarium (20.5 × 21 cm). The bottom of the aquarium was covered with natural-coloured gravel. The front was marked in 5-cm increments to facilitate recording the female's position during the trial. Two 12.5 × 17.5 cm high resolution (450 TV lines) colour Sony monitors (model PVM8044Q) were placed opposite each other, on the right and left side of the aquarium. Females were introduced into the test aquarium 10 min prior to the trial. The trial began with the simultaneous presentation of two videotapes of life-sized images of a bright (colourful) and a pale male. On each tape we recorded the following sequence: 5 min of an empty aquarium, 5 min of the first male (either bright or pale), 1 min of an empty aquarium and 5 min of the second male. On the second tape we

reversed the sequence of presentation of males to control for side bias.

Videotapes of the males were made by recording the behaviour of a single male in a 15 × 10 × 15-cm glass compartment. The rear, bottom and sides of the compartment were covered with flat black plastic to prevent light from reflecting back onto the male and thereby eliminate bleeding of the male's colour pattern on the videotape. The compartment was illuminated with a 150-watt Dolan-Jenner fibre optic illuminator with a 3200°K lamp. The recordings were made on S-VHS tapes with a Panasonic WV-D5100HS camera with a 100-mm macro lens. Tapes were edited using a Panasonic AG-5700 video tape recorder and a Ag-A570 edit control board. Because not all males displayed to the females during a taping sequence, and to produce a consistent behavioural sequence for each pair of males, we used only taped sequences in which the male was vigorously swimming in the front of the aquarium and orienting towards the female. Males were introduced into the taping compartment 10 min prior to recording to permit them to acclimate to the compartment and the light conditions. Two females were introduced into a small tank that was placed at a slight angle to one side of the front of the filming compartment, so that males could see and visually interact with the females. This kept the males in the front of their compartment and in clear focus.

Statistical Analyses

To compare the overall response of females to taped males with that of live males in the clear glass and the one-way glass experiments, we summed the time that a female spent with both males during each trial, then summed again across all four trials. This gave us a value for the total time a female spent with both males for each of the three experiments. These data were arcsine transformed and compared with a one-way ANOVA.

To determine whether females habituated to males during the four trials, we summed the time that a female spent with both males during each trial. We compared the four trials for each experiment with a repeated measures ANOVA. To test for female preference for the more ornamented (bright) male of the pair, we compared the time that a female spent with the bright versus the pale

male with a repeated measures ANOVA with male coloration (pale, bright) and treatment (clear, one-way, video) as factors. We also calculated the repeatability of the time a female spent with one male of the pair in the four successive replicate trials (Sokal & Rohlf 1981). To do this analysis, we used random numbers to choose which male of a pair was to be used in the analysis. We used a one-way ANOVA to calculate the variance due to differences between females (S^2A) and the error variance, or variance within females across the four trials (S^2), and calculated repeatability after Becker (1992). To determine the consistency of female preferences for one male of the pair, we compared the number of times females chose the same male (two, three or four times) to those expected if females randomly chose males. Expected values were calculated from probabilities of choosing males four of four times ($P=1/8$), three of four times ($P=1/2$) and two of four times ($P=3/8$). We used a chi-square analysis on the combined data from all three experiments.

RESULTS

Did Females Respond Similarly to Males in the Three Experiments?

Females spent significantly more time with males behind clear glass than with males behind one-way glass or with videotaped males, but equal time with males behind one-way glass and videotaped males ($F_{2,71}=17.30$, $P<0.0001$; Duncan's post hoc comparisons: clear versus one-way glass and clear glass versus video $P<0.05$, one-way glass versus video $P>0.05$; Fig. 1). Thus, in the absence of a behavioural interaction between the male and female, females spent less time viewing males.

Did Females Habituate to Males During the Four Consecutive Trials?

Females did not habituate to males in any of the experiments (Table I). There were no significant differences in the time females spent with the males during the four trials.

Did Females Prefer the More Ornamented Male?

Females spent significantly more time with the bright male in the clear glass and video exper-

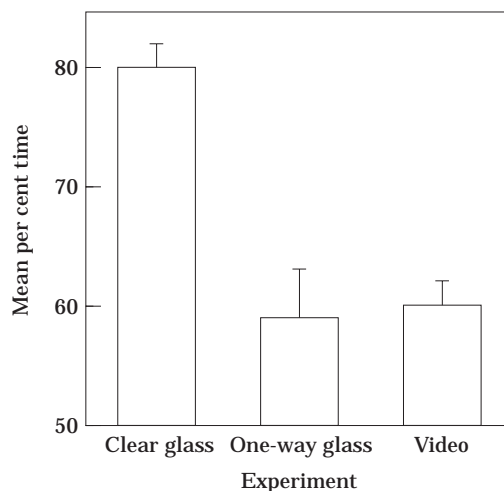


Figure 1. The $\bar{X} \pm SE$ per cent of time female guppies spent viewing both the bright and pale male when these were presented behind clear glass partitions, one-way glass partitions and as videotapes.

iment, but not in the one-way glass experiment ($F_{2,71}=4.22$, $P=0.02$; Duncan's post hoc comparisons: clear versus one-way glass, and video versus one-way glass $P<0.05$, clear glass versus video $P>0.05$). Although females spent a similar amount of time with the bright male in the clear-glass and video experiments, their responses to the pale male differed ($F_{2,71}=6.5$, $P=0.003$; Fig. 2; Duncan's post hoc test: $P<0.05$ for all comparisons). Females spent much less time with the pale male in the video experiment than with the pale male behind clear or one-way glass. Thus

Table I. Results of a repeated measures ANOVA testing for the presence of habituation, using the $\bar{X} \pm SE$ amount of time female guppies spent with both males during each of four consecutive trials ($N=25$ females in each experiment)

Trial	Experiment		
	Clear glass	One-way glass	Video
1	501 ± 10	397 ± 20	380 ± 18
2	461 ± 22	316 ± 27	394 ± 17
3	478 ± 16	352 ± 25	335 ± 25
4	460 ± 12	362 ± 29	329 ± 19
<i>F</i>	0.89	0.79	0.91
<i>df</i>	3	3	3
<i>P</i>	0.466	0.513	0.559

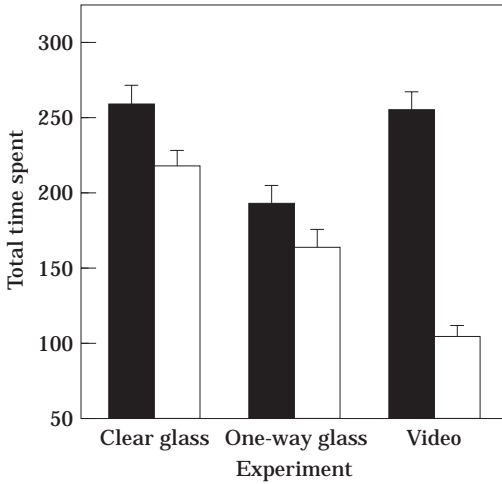


Figure 2. Visual preferences of female guppies expressed as time, summed over four trials, that they spent viewing the bright (■) and pale male (□), respectively, when males were presented behind clear partitions, one-way glass partitions and as videotapes.

the greater total time that females spent with males behind clear glass detected in the analyses of overall female response was due to the increased time spent with the pale male.

How Repeatable Were Female Preferences?

Females spent a similar amount of time with the same male between the four trials in the one-way glass and video experiments, but not in the clear glass experiment. Again, females responded very differently in the experiment where they could interact behaviourally with males (Table II).

The experimental regimes differed in the number of times a female visually preferred the same male during the four consecutive trials ($\chi^2_3=48.34, P<0.0001$; Fig. 3). In the clear glass

Table II. Repeatability of the amount of time an individual female guppy spent with a male between the four trials ($N=25$ females per experiment)

	Experiment		
	Clear glass	One-way glass	Video
<i>R</i>	0.05	0.40	0.47
SE	0.093	0.110	0.106

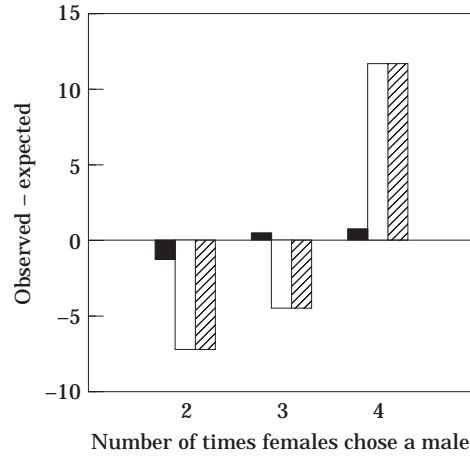


Figure 3. Consistency of visual preferences of female guppies, expressed as the difference in the number of times an individual female repeatedly chose a male, compared to the expected probability, in the clear glass (■), one-way glass (□) and videotape (▨) experiments.

experiment, the number of times that females chose a particular male did not differ from random. In both the one-way glass and video experiments, however, females were much more consistent; they chose the same male during all four trials more often than expected.

DISCUSSION

This study demonstrates the utility of the video playback technique in studying mate choice in the guppy. A comparison of the time that females spent with the bright and pale male, respectively, in the clear glass and video experiments, showed that the video technique gave more repeatable results and was much more effective in detecting female preference for the brighter male than was the technique using a live male behind clear glass. The results of the one-way glass experiment differed from the other two, since females did not show a preference for the more ornamented male (Fig. 2). The error variance, owing to temporal variation in behaviour among males and between trials, may have been great enough to obscure the preference for the more ornamented male.

Although the responses of females to video images of males were qualitatively similar to those to live males behind clear glass, there were

important quantitative differences. Females spent less time viewing both males and were more consistent in their preference for a male in the video experiment. We did not record the behaviour of females toward males, but in all three experiments females responded to males, or images of males, with 'orientations' and occasionally, 'glides'. These behaviours indicate sexual interest by females, and in the field, or aquaria, where males and females are in physical contact, usually are followed by copulations (Clark & Aronsen 1951; Liley 1966; Houde 1988).

Comparisons between these three approaches indicate the importance of visual interactions between a male and a female. In video and one-way glass experiments, where behavioural interactions were not possible, females were highly consistent in their choice of males ($r=0.47$ and $r=0.40$, respectively). Repeatability in the amount of time a female spent viewing a male was low for the clear glass experiment, however ($r=0.05$). A male's behavioural response to the presence of a female not only increases her attentiveness, but also may influence her response to subsequent presentations of the same male. A male's behaviour may also change with subsequent presentations of a female (Rodd & Sokolowski 1995). A female can elicit interactive courtship from initially less preferred (duller) males. Thus the behaviour of the male, and visual interactions between a male and female, affect the consistency of female choice. Although we did not record the behaviour of males in the clear glass experiment, studies have shown that males vary temporally in their display behaviour, and female preferences are strongly biased by a male's display rate, which often override her preference for body ornamentation (Farr 1989; Kodric-Brown 1993; Nicoletto 1993).

An assumption of sexual selection models is that there is heritable variation in female preferences for male secondary sexual traits, such as showy colour patterns (Andersson 1994). If there is a genetic basis for female mating preferences, then individual females should show consistent preferences when repeatedly presented with the same choice of males.

Studies attempting to determine whether females show constancy in their criteria for choosing males have produced equivocal results. When female red jungle fowl, *Gallus gallus*, were repeatedly presented with two males differing in

plumage colour, they switched their preferences between them over time (Ligon & Zwartjes 1995). Repeatabilities of mating preferences vary widely, from $r=0.00$ in flour beetles, *Tribolium castaneum* (Boake 1989), $r=0.50-0.59$ in crickets, *Gryllus integer* (Wagner et al. 1995), to $r=0.65$ in sticklebacks, *Gasterosteus aculeatus* (Bakker 1993). Female preferences for orange spots of males and the heritability of these colour spots, have been shown for Trinidadian guppies (Houde 1988, 1992, 1994; Houde & Endler 1990). Heritability for display rates also has been shown (Farr 1983). Endler & Houde (1995) also showed that populations of Trinidad guppies vary both in female preferences for different types of male traits and in male behaviour. Godin & Dugatkin (1995) estimated a repeatability of $r=0.58$ for female preferences for males with more carotenoid spots for a population of guppies from the Quare River in Trinidad. This estimate is somewhat higher than the repeatability estimate in our study when Jemez Springs females were presented with video images of males ($r=0.47$), but the standard errors from these two analyses overlap. The repeatability of Jemez Springs females was very low when they were presented with males behind clear glass ($r=0.05$). These differences in repeatability estimates probably reflect differences in predation regimes and their effect on male courtship behaviour. The Quare population is under intermediate to heavy predation by piscivores, but the Jemez Springs population is not. In a predator-free environment, males should court more vigorously, and females should respond to the courtship behaviour more strongly, than they do in populations with many predators. Thus male behaviour may override female preferences for male morphological traits. Our results suggest that the repeatability estimate obtained from the video image analysis may be based on male colour pattern, and the repeatability estimate from the clear glass experiment may be based on a complex set of traits, including morphological and behavioural components. Our results suggest caution in interpreting repeatability estimates, especially if only one trait is measured, yet the estimates are based on a suite of traits and the correlation between these traits is low.

Our comparative approach also provides insight into the function of ornamentation and courtship displays in female mate choice. In guppies, male ornamentation captures the

attention of females and results in an initial assessment of male breeding colours and patterns and their conspicuousness against a background (Endler 1983, 1995). In most populations studied to date, where predation pressure on adults is low, females preferentially respond to males with large, conspicuous carotenoid spots (Houde 1987; Endler & Houde 1995). Male displays, however, may reinforce or reverse this visual assessment of a male. The importance of courtship displays on female mate choice is well known (e.g. Baerends et al. 1955; Farr 1980; Kodric-Brown 1993), but their interactions with morphological traits are relatively poorly understood.

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