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The effect of visual obstructions on the sexual behaviour of guppies: the importance of privacy

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Sexual selection is the outcome of behavioural interactions within and between the sexes. Numerous studies show how individuals modify their sexual behaviour in response to ecological or social conditions, and such changes may therefore affect the evolutionary outcome of sexual selection. Our study examined the effect of habitat structure on the sexual behaviour of male and female guppies, *Poecilia reticulata*. We asked whether the ability of males to observe other courting males would affect the rates of male courtship and courtship interference and the sexual responsiveness of females. Specifically, we manipulated visibility using opaque barriers in laboratory aquaria and found that there was less male interference behaviour in aquaria containing visual obstructions than in aquaria without barriers, regardless of whether the male was courting sexually responsive (virgin) or unresponsive (nonvirgin) females. In addition, sexual responsiveness of virgin females to male displays was significantly increased in aquaria with barriers relative to aquaria without barriers. Finally, the display frequency of males courting virgin females was significantly reduced in aquaria with barriers, probably as a result of the females' increased rate of sexual response. Evidently, the barriers impede visibility enough that males are less likely to observe and interfere with the courtship of other males, and therefore, females are less likely to flee or lose interest in a courting male. Ultimately, characteristics of the visual environment could affect females' ability to choose mates and in turn could potentially affect the evolutionary outcome of sexual selection.

The evolutionary outcome of sexual selection is determined by behavioural interactions within and between the sexes. Numerous studies have shown that individuals modify their sexual behaviour in response to ecological or social conditions, such as predation regime (e.g. Ryan 1985; Endler 1987; Magurran & Seghers 1990; Forsgren & Magnhagen 1993; Hedrick & Dill 1993; Candolin 1997), population density (Rodd & Sokolowski 1995; Hettyey & Pearman 2003), sex ratio (Rodd & Sokolowski 1995) and the visual environment (Endler 1987; Long & Rosenqvist 1998; Candolin 2004). Such changes in individual behaviour may lead to changes in sexual interactions between individuals as well (Evans et al. 2002; Hettyey & Pearman 2003). Ultimately, any variation in these behaviours or interactions between individuals may affect the pattern of sexual selection and its evolutionary consequences. Therefore, in order to gain a better understanding of the evolution of specific, elaborate secondary sexual characteristics, it is important to study the ecological factors and behavioural mechanisms that may influence the outcome of sexual selection (Endler 1993). In this study, we examined the effect of the visual environment on sexual behaviour and interactions of male and female guppies, *Poecilia reticulata*.

Guppies are native to northeastern South America, and are especially abundant and widely studied in Trinidad, West Indies. Males are brightly coloured and vary greatly in their colour patterns within and between populations, whereas females do not have conspicuous colour patterns (Houde 1997). Males in most populations devote much of their time and effort to pursuing females, performing courtship displays and attempting sneak copulations (Houde 1997; Magurran 2005).

The 'sigmoid' courtship display of the male guppy is a conspicuous behaviour in which a male positions himself in front of a female and arches his body into an S-shape, while extending his fins and quivering (Baerends et al. 1955; Liley 1966). Displays are directed towards females by a male attempting to gain the female's attention and eventual copulation. The courtship sequence will not proceed beyond a male's initial displays unless the female makes a characteristic gliding approach to the displaying

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male (Liley 1966; Houde 1997). This glide response clearly indicates the female's sexual interest in that male and has been used to assess female mating preferences (e.g. Houde 1987; Houde & Endler 1990; Reynolds & Gross 1992; Endler & Houde 1995). Such female responsiveness is a necessary step towards copulation and is a prerequisite to mate choice. Hence, any factor that affects female responsiveness, such as courtship disruption, may in turn affect female choice.

Courtship disruption is important in mating systems of a number of species and may affect the ability of females to exercise mate choice. Specifically, males can interfere in the copulation attempts of other males by attempting to court a female that is being attended by another male or by attempting to drive rival males away. Such courtship interference has been shown to affect the interaction of males and females and the outcome of sexual selection in a number of species including icterid birds (Webster & Robinson 1999), dung flies, *Scathophaga stercoraria* (Borgia 1982; Kraushaar & Blanckenhorn 2002), and the red-spotted newt, *Notophthalmus viridescens* (Gabor et al. 2000). In addition, as is suggested by a study involving sand gobies, *Pomatoschistus minutus* (Kangas & Lindstrom 2001), harassment by intruding males may affect mate choice by females. In guppies, courtship disruption and jockeying for access to females are the most common forms of competition among males, although overt aggression occurs under some conditions (e.g. Houde 1988, 1997; Magurran & Seghers 1991; Rodd & Sokolowski 1995; Kolluru & Grether 2005; Price & Rodd 2005).

Our study examined the influence of habitat structure on the sexual behaviour of male and female guppies in the laboratory. Specifically, we tested whether the ability of males to observe the courtship activities of other males affects the frequency of courtship interference by male guppies, and whether this in turn affects the sexual behaviour of virgin females interacting with these males. We tested these predictions by manipulating the structure of guppy habitats in the laboratory using opaque barriers and observing the effect of such visual obstructions on male courtship and interference behaviour, as well as on female sexual responsiveness to male displays in experimental groups of guppies. We predicted that more male–male competition and interference behaviour would occur in an environment containing fewer visual obstructions relative to an environment with more visual obstructions. We also predicted that increased courtship interruption would decrease the frequency of male courtship sequences leading to a positive response from females. In natural guppy streams, obstructions such as rocks limit visibility to varying degrees in different locations (T. L. Hibler & A. E. Houde, personal observations).

MATERIALS AND METHODS

Experimental Fish

All experimental trials were conducted with descendants of wild guppies collected 4 years (approximately 10 generations) previously from the Paria River of Trinidad. Virgin females were reared in same-sex 40-litre aquaria, while males and nonvirgin females were raised in mixed-sex 40-litre aquaria. All fish used in experiments were between 4 and 8 months of age. Experimental groups consisted of four males and four females arbitrarily chosen from stock tanks; males and nonvirgin females may have been reared in the same or different stock tanks. Males in each group were chosen to have different, individually identifiable colour patterns. Fish were fed twice a day with Tetramin (Tetra, Melle, Germany) flake food in the morning and freshly hatched brine shrimp nauplii in the afternoon, and were kept on a 12:12 h light:dark cycle. Aquarium temperature was maintained between 22°C and 27°C using automatic aquarium heaters. Behavioural observations were conducted within 3 h after the aquarium lights came on in the laboratory each morning.

Observations were conducted in two 38-litre aquaria containing gravel, with tan paper attached to the sides, illuminated with 15-W broad-spectrum fluorescent bulbs. For the 'blank' treatment, the experimental aquarium contained only gravel, and fish could see all other fish in the tank. For the 'barrier' treatment, the experimental aquarium contained four opaque plastic panels placed vertically throughout the tank and extending partially across the aquarium. The barriers created visual obstructions in the tank, in effect dividing it into partially separated 'rooms'. In an aquarium containing barriers, a fish in a given location was in visual contact with other fish only in its immediate vicinity, but its view of fish in other parts of the tank was obstructed by barriers. In contrast, in aquaria without barriers, males had direct and unobstructed visual contact with other courting males.

We observed the behaviour of male guppies in separate trials with virgin females, which are sexually responsive to male displays, and with nonvirgin females, which are generally unresponsive. In all trials, virgin females were introduced to the experimental group the afternoon prior to observing them, and thus, were likely to have mated the day prior to the observations. We refer to these females as 'virgins' for convenience because they continue to be sexually responsive when observed the following day.

A total of 128 males were arbitrarily separated into 32 groups of four males each. In an initial phase of the study, 12 groups of four males were observed with nonvirgin females. Subsequently, another 12 groups of four males were observed with virgin females. Given that these trials were conducted at different times, comparison between results with nonvirgin and virgin females would not have been valid because of the potential for temporal confounding. So, to allow at least a limited valid comparison of male behaviour with virgin versus nonvirgin females, an additional eight groups of four males underwent separate trials with both virgin and nonvirgin females (order of trials randomized). The total sample size for the comparison of aquaria with and without barriers was thus 20 male groups observed with nonvirgins and 20 observed with virgins.

Experimental Trials

Throughout the study, trials consisted of a 10-min focal observation on each of the four males in an experimental group in random order. In the initial phase of the study, each group of four males and four nonvirgin females was observed in the blank treatment for one trial and in the barrier treatment for another trial. The initial treatment, either blank or barrier, was alternated between experimental groups to ensure that time of observation and order of treatments encountered for each group would not bias the results. In order to ensure that any unperceived difference between experimental tanks would not bias the results, barriers were switched between the two tanks for each group of four males. Small amounts of flake food were given to all experimental groups before timed observations to ensure maximum sexual behaviour.

For trials involving nonvirgin females, males and females were introduced to treatment aquaria the afternoon before an observation session. The following morning, fish were observed in the initial treatment and males and females were then immediately moved into the second treatment where they were given 10 min to adjust to the new surroundings before the second set of observations began. For trials involving virgin females, males and females were introduced to the treatment aquaria 24 h before trials to allow time for adjustment to the surroundings, and initial mating of the new females. Immediately following the trial, males were removed from the initial treatment and placed in the second treatment with a new group of four virgin females, then tested again 24 h after introduction. Therefore, only one trial was performed each day for male groups being observed with virgins. As was done for nonvirgin trials, the order of initial treatment, either blank or barrier, was alternated for each experimental group of four males paired with virgin females. It was necessary to use a new set of virgin females for each treatment to ensure that all females had similar levels of receptivity and responsiveness to males (once introduced to males, receptivity of virgin females declines day by day; Liley 1966). The nonvirgin females were uniformly unresponsive to males, so the same set of nonvirgins could be used for both treatments.

Behaviour Data and Statistical Analysis

Each male was observed for 10 min during a given observation session, during which we recorded occurrences of sigmoid displays and male interference behaviour for each male. Female responsiveness to each male's courtship displays was recorded for trials involving virgin females only. None of the nonvirgin females showed a sexual response during the trials, thus female responsiveness to male courtship displays was not analysed for nonvirgin trials.

We scored the responsiveness of females to each male courtship display using criteria described by Liley (1966) and Houde (1997). We recorded a sexual response if the female oriented towards the male and glided smoothly towards the male as he displayed. If the female did not show a glide behaviour we recorded no response.

Following Houde (1988, 1997), we scored interference behaviours as either 'fend-offs' or 'chases'. A fend-off occurs when an intruding male attempts to court a female that is already attended by a male and thus elicits a defensive response from the original male. The original male then moves between the female and the other male and attempts to fend off the intruding male by whipping his tail at the other male. Original males remain with the female in the majority of fend-offs. In the instance of a 'chase', a second male intrudes on the courtship of another male, but instead of being fended off, both males pursue the female for several seconds, each attempting to remain with the female and to exclude the other male as she darts away and swims evasively. Under the experimental conditions of this study, too few sneak copulation attempts or gonopodial thrusts were observed for statistical analysis.

Given that the behaviour data depend on interactions of individuals within groups, mean rates of behaviour per trial (rather than per male) were used as the unit of analysis, thus ensuring independence and avoiding pseudoreplication. Shapiro–Wilk tests and plots of residuals showed no deviations from normality, therefore we used parametric statistical methods on untransformed data. Rates of interference behaviours and sigmoid displays for each group of males, as well as responsiveness of females to sigmoid displays in trials involving virgins were compared between the blank versus barrier tank treatments using paired *t* tests. Data for male groups that were tested with both virgin and nonvirgin females were analysed using ANOVA to determine the effect of both treatment and reproductive status (virgin versus nonvirgin) on male display and interference behaviours with male group as a blocking factor. For trials involving nonvirgin females, ANOVAs containing an order effect (first time tested or second time tested) were also carried out for chases, fend-offs and displays.

RESULTS

All experimental groups showed active courtship behaviour, with the exception of one of the 20 groups tested with nonvirgin females, in which males did not interact, interfere, or court, suggesting that these fish may have been sick. Therefore, only 19 groups were included in the statistical analysis for nonvirgin comparisons.

Our prediction that interference behaviour would be reduced when visual obstructions were present was supported by the results involving both virgin and nonvirgin females. The frequency of chases and fend-offs differed markedly between the two treatments, with significantly more chases and fend-offs occurring in blank tanks than in barrier tanks (chases: nonvirgin trials: $t_{18} = 5.73$, $P < 0.001$; virgin trials: $t_{19} = 2.49$, $P = 0.022$; Fig. 1a; fend-offs: nonvirgin trials: $t_{18} = 4.58$, $P < 0.001$; virgin trials: $t_{19} = 3.69$, $P = 0.0016$; Fig. 1b).

Of the 19 groups of males observed with nonvirgin females, 18 showed an increase in the frequency of interference behaviour (total number of chases and fend-offs combined) in the blank treatment relative to the

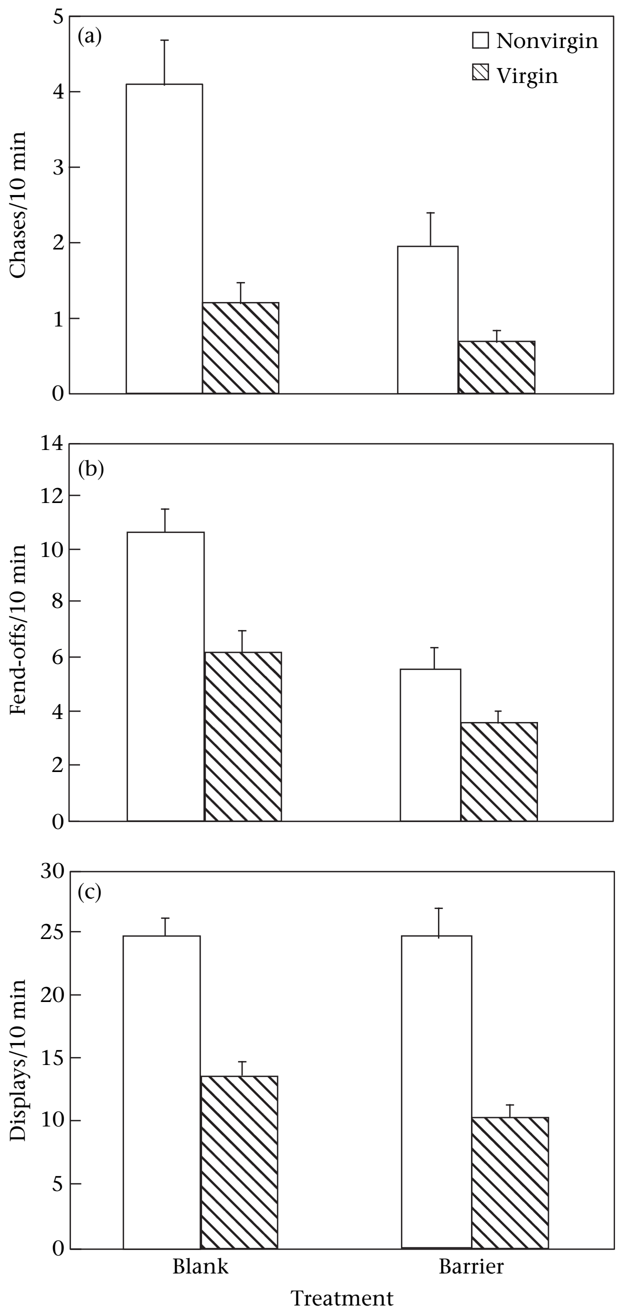

Figure 1. Sexual behaviour of male guppies in blank and barrier tanks. (a) Number of 'chase' interactions between males per 10 min. (b) Number of 'fend-off' interactions between males per 10 min. (c) Number of male displays per 10 min. Data for virgin and nonvirgin females were analysed separately. Values are means ± SE.

barrier treatment (binomial test: $P < 0.001$). Only one group did not follow this trend, showing no difference in interference behaviour between treatments. Eighteen of the 20 groups of males observed with virgin females showed more interference behaviour in the blank treatment relative to the barrier treatment (binomial test: $P < 0.001$). In this case, two groups did not follow the trend, showing more interference behaviour in the barrier treatment than in the blank treatment. In the subset of eight trials involving male groups that were tested with both virgin and nonvirgin females, there were significantly fewer chases involving virgin females relative to nonvirgin females but there was not a significant effect of female receptivity on the frequency of fend-offs (Table 1).

In the trials in the barrier tank, the fish seemed to be well dispersed throughout the tank and thus somewhat visually isolated from other males as predicted, however, quantitative data on dispersion of fish were not recorded. Cases in which individual males showed more interference in the aquarium with barriers or no difference between treatments (3 of the 39 groups of males included in the results) might be attributable to the occasional grouping of many fish in one area of the tank divided by barriers.

When courtship data for all trials were analysed separately for virgin and nonvirgin females, males reduced their rate of displays in barrier treatments relative to blank treatments in trials involving virgin females ($t_{19} = 3.10$, $P = 0.0059$; Fig. 1c), however, there was no significant effect of barriers on rates of courtship displays in trials involving nonvirgin females ($t_{19} = 0.096$, $P = 0.923$; Fig. 1c). In the subset of eight trials involving male groups that were tested during the same time period with both virgin and nonvirgin females, males displayed significantly less often to virgins than to nonvirgins overall (significant receptivity effect), and males displayed significantly less often overall when barriers were present than when barriers were absent (significant treatment effect), but there was no significant interaction between receptivity and treatment (Table 1). The P value for the interaction term was low enough to hint that the effect of barriers on display rate might in fact be stronger with virgin than nonvirgin females, however, as is suggested by Fig. 1c.

The fact that we used the same nonvirgin females in each treatment, but different virgin females suggests a potential for bias in the above analysis if the behaviour of nonvirgins differed between the first and second test. An ANOVA including this order effect indicated no significant difference in the behaviour of males towards

Table 1. ANOVAs testing effects of female receptivity (virgin versus nonvirgin) and treatment (blank versus barrier) on male sexual behaviours for the subset of eight male groups tested with both virgins and nonvirgins. Male group is entered as a blocking factor

	df	*F*	*P*
Fend-offs			
Receptivity	1, 21	1.11	0.3038
Treatment	1, 21	17.17	0.0005
Receptivity*treatment	1, 21	2.44	0.1330
Group	7, 21	2.76	0.0337
Chases			
Receptivity	1, 21	7.03	0.0149
Treatment	1, 21	18.15	0.0003
Receptivity*treatment	1, 21	5.16	0.0337
Group	7, 21	8.64	<0.0001
Displays			
Receptivity	1, 21	49.89	<0.0001
Treatment	1, 21	13.78	0.0013
Receptivity*treatment	1, 21	2.95	0.1007
Group	7, 21	2.50	0.0492

nonvirgin females between the first and second tests, once treatment effects were taken into account (order effects in ANOVAs: chases: $P = 0.54$; $P = 0.91$; fend-offs: displays: $P = 0.57$).

Our prediction that female responsiveness to male courtship displays (recorded for virgin trials only) would increase when visual obstructions were present was also supported by the results. Specifically, females that were courted by males in the barrier treatment responded to a significantly greater mean ± SE fraction of displays (58.1 ± 4.3%) than in the blank treatment (36.3 ± 2.9%; $t_{19} = 5.19$, $P < 0.0001$). In trials with nonvirgins, no sexual responses were noted in any trials.

DISCUSSION

The results of this study support our predictions that visual obstructions reduce male interference behaviour and increase female responsiveness to male displays in tanks with visual obstructions relative to tanks with unobstructed visibility. On average, males engaged in fewer chase and fend-off interactions when barriers were present than when barriers were absent. The likely explanation for this change in behaviour, and the basis for our initial prediction, is that males intrude on the courtship activity of other males when they see a courting pair, then approach and attempt to court and monopolize the female themselves. Evidently, the barriers impede visibility enough that privacy is permitted and males are less likely to see and respond to the courtship activity of other males in this way.

Females were more responsive to courting males in the treatment containing visual barriers. In the absence of frequent interruptions by intruding males, females may have more opportunity to respond to male courtship than when they are frequently interrupted. In guppy courtship, the first few displays by the male often do not receive a response from the female even if the female is receptive, so they may be performed only to gain the female's attention. If intruding males are frequently breaking up a courting pair, then the courting male may not get the chance to perform a complete display and/or the female may not get to the point of responding to the male's displays and ultimately may not mate cooperatively with her preferred male.

Although the barriers we used were artificial and the fish were observed in laboratory aquaria, the structure of Trinidad streams containing guppies varies from location to location so that visibility varies in a way comparable to that seen in our experiment (T. L. Hibler & A. E. Houde, personal observations). In some locations, wide, deep pools have relatively long unobstructed views, while in others, shallower water is broken into many small pools by rocks and other obstructions that limit visibility. Thus, differences in the visual structure of the habitat may influence patterns of sexual behaviour in wild populations.

Our comparison of male display rates between trials involving virgin and nonvirgin females revealed that males displayed significantly less frequently to virgin females than to nonvirgin females. Similarly, Houde (1988) found a negative correlation between frequency of courtship displays and frequency of female responses and suggested that once a female responds to a male's display, the male follows that female more closely and displays to her more selectively, waiting until no other fish are in the vicinity and the female is in a position to view the display. This has the effect of reducing the number of male displays performed towards receptive females. Therefore, while males generally appear to pursue receptive females more persistently (Houde 1997), they do so with a lower total rate of display than they do to unresponsive females.

This lower display rate to virgin females appeared to be exaggerated even more when barriers were present and when less male interference was occurring. A possible explanation is that the greater frequency of sexual responses by virgin females in the barrier treatment may itself have resulted in a reduced frequency of courtship as discussed above. The data are less clear, however, as to whether this effect of barriers applies to male displays towards nonvirgins, possibly because nonvirgin females do not respond to males, regardless of the visual structure of the habitat. On the other hand, increased visual contact with other males and females could plausibly lead to increased courtship as well as increased interference (e.g. Farr 1976).

Several other studies indicate that the visual environment can affect the sexual behaviour of males, and of females. Reynolds et al. (1992) and Long & Rosenqvist (1998) found effects of light level on several aspects of sexual behaviour in guppies. In sand gobies, Kangas & Lindstrom (2001) found that when males were placed in visual contact with one another there was increased aggression between males, decreased duration of courtship and decreased consistency of female choice. Finally, Wong (2004) demonstrated that aggressive interactions between male Pacific blue-eyes, *Pseudomugil signifer*, resulted in shorter courtship bouts when males were able to interact visually or physically than when male interaction and competition were absent. On the other hand, interactions between males in three-spined sticklebacks, *Gasterosteus aculeatus*, may enhance females' ability to exercise choice (Candolin 2004). Candolin (2004) found that habitats with increased vegetation and reduced visual contact between individuals tend to reduce the encounter rate of males and females at a nesting site, possibly reducing the ability of females to compare males.

The decrease in female responsiveness with increased male interference in our study suggests that the ability of females to assess or mate with their preferred males could be reduced as a consequence. In extreme cases of male−male competition and harassment, as in water striders, *Aquarius remigis*, females may be unable to avoid unwanted copulations by harassing males, thus undermining female mate choice (Watson et al. 1998). Indeed, any increase in levels of harassment and interference by males could constrain the ability of females to exercise mating preferences, and hence may alter the pattern of mating success in the population (Houde 1997). The studies by Kangas & Lindstrom (2001), Wong (2004) and Candolin (2004) discussed above suggest that changes in male interference resulting from differences in visual environment similar to those in our study could affect patterns of mate choice. Further research is needed to examine how visual environments affect patterns of mating success and the outcome of sexual selection.

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