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Female Size Influences Mate Preferences of Male Guppies

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Abstract

Guppies (*Poecilia reticulata*) have a promiscuous mating system in which female choice for brightly coloured males plays an important role. Consequently, much research on guppies has examined how mate choice by females has lead to the evolution of male colour patterns. Much less attention has been devoted to mate choice by males in this species. In this study, we show that male guppies are choosy when selecting a female to associate with, significantly preferring the larger female when presented with two females that differed by ≥2 mm in standard length (SL). The strength of their preference for each female increased with absolute female size. The relative sizes of the females, however, also influenced male mating preferences: males showed stronger preferences for the larger female as the difference in SL between the two females increased. Such a preference for larger females is not unexpected as fecundity generally increases with body size in female fish. Thus, males choosing to mate with the larger female should have higher reproductive success. An apparent, but non-significant anomaly, whereby males appear to prefer the smaller of the two females when the difference between female SL was < 4 mm, deserves further investigation.

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Introduction

Theory predicts that females, often investing more time and energy in offspring than males, have been selected to maximize their reproductive success by choosing mates that provide the best resources and/or genes for their offspring (Trivers 1972). Males, however, have generally been selected to maximize their reproductive success by mating with as many females as possible, and are thus expected to be less 'choosy' than females. Andersson (1994), however, argued that male choosiness should be expected to evolve whenever (i) males have more than one female from which to choose, (ii) males can adequately discriminate among females that differ noticeably in quality (e.g. fecundity, egg size, or parental

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abilities), and (iii) mating with any one female depletes sperm reserves, thereby reducing a male's chance of fertilizing other females. Thus, active mate choice by males should be favoured by selection if mating with higher quality, more fecund females results in higher reproductive success for the male (Bonduriansky 2001). Indeed, males of several species, especially fish, have been shown to discriminate among females that differ visibly in quality (e.g. Rowland 1982; Sargent et al. 1986; Côte & Hunte 1989; Nuttall & Keenleyside 1993; Grant et al. 1995; Verrell 1995; Ptacek & Travis 1997; Kraak & Bakker 1998; Werner & Lotem 2003; Wong & Jennions 2003).

Although male mate choice is probably more common than previously thought (Bonduriansky 2001), it has received much less attention than female choice in fishes, particularly in species in which females show strong preferences for males with conspicuous ornaments (Houde 2001). The guppy (*Poecilia reticulata*), for example, is one of the best-studied species with respect to colour pattern evolution in males and mate choice evolution in females (Houde 2001). Studies examining male mate choice in this species, however, have lagged far behind, with the only published evidence so far being a brief account in Houde (1997). Given that female guppies do vary in fecundity and that males may be sperm-limited (males often refrain from courting females for 1 h after a successful copulation; Pilastro and Bisazza 1999), males should exhibit some degree of discrimination when selecting a female to mate with.

In this study, we examined the mating preferences of male guppies for females that differed in apparent quality. Female body size [standard length (SL)] was used as an indicator of quality because fecundity generally increases with body length in female fishes (Hagen 1967; Bagenal & Braum 1978). In addition, we predicted that male choosiness would increase with male size and coloration because more attractive males usually have more mating opportunities than less attractive males (Johnstone et al. 1996). Thus, smaller, less colourful males should be less discriminatory in their mate choices (Burley 1977).

Methods

We obtained guppies from a breeder in Florida who was raising them as food for the pet store trade. These fish were bred from a stock originally taken from Trinidad and maintained in large 15 m × 30 m breeding ponds. Because these guppies had not been artificially selected for colour or fin size and shape, they were similar to wild-caught guppies from both natural and feral populations. The average SL of guppies used in our experiments was 16.2 mm (±0.18, 14.6–18.4, 27) (±SE, range, n) for the males and 23.0 mm (±0.52, 17.41–29.31) for the females. The average SL of male guppies from natural populations in Trinidad varied from 13.0 to 18.5 mm, depending upon predation pressure. Females in the largest size class varied from 22.8 to 32.2 mm in the dry season (Reznick & Endler 1982).

Fish were maintained at 24–25°C on a 12.00 : 12.00 hours light : dark photoperiod with lights on at 8.00 hours Eastern daylight Savings Time (EDST), and were fed commercial flake food (Hartz Wardley Total Colour, Hartz

Mountain Corp. Secaucus, NJ, USA) twice a day. Test males were housed separately from females and were placed in a different holding tank after testing to ensure that each male was tested only once. All females used in the experiment were housed with non-test males and were thus gravid and sexually unreceptive (female guppies are most responsive to male courtship when they are virgins or shortly after parturition; Liley 1966; Lutyen & Liley 1985). Following Ptacek & Travis (1997), we used only gravid females, to reduce variation in male behaviour caused by differences in female reproductive status and to ensure that male choice would not be confounded by female choice. After females were used in a trial, they were placed in a separate holding tank.

Our experimental apparatus (hereafter 'test tank') was a 60 cm × 32 cm × 32 cm glass aquarium, divided into three 20 cm × 31 cm × 32 cm compartments by solid Plexiglas partitions to prevent water or chemical flow between compartments. Thus males could not detect the reproductive status of females by pheromonal cues. Each test male was placed in the middle compartment and one female in each of the two end compartments. We drew vertical lines on the glass of the middle compartment to divide it into three 6.7-cm-wide zones so that we could record the location of the male. When a male was in one of the zones adjacent to a female compartment, we considered that he had made a choice whereas the central zone was considered 'no choice'.

We used beige-coloured gravel and beige paper covering both ends and the back of the test tank to provide a uniform background colour for male assessment of females and we illuminated the aquarium from 15 cm above with a 15-W full spectrum Sun–Glo fluorescent tube (R.C. Hagen, Montreal, Canada). There was no other lighting in the room. The test tank was maintained at the same temperature as the holding tanks.

Experiments were conducted from 08.30 to 13.00 hours EDST to control somewhat for any variation in male sexual behaviour through the day (Baerends et al. 1955; Liley 1966). All fish were fed to satiation before experiments commenced. To conduct an experimental trial, we chose a male haphazardly and placed him in a black plastic cylinder outside the test tank for 10 min. At the same time, we chose two females that were different by ≥2 mm SL, placed them randomly (with respect to their size) in either end of the test tank, and allowed them to acclimate for 10 min. We chose females such that the largest female was no bigger than twice the SL of the test male to ensure that he would not be intimidated by the size of the female (Houde 1997).

After this initial acclimation period for the females, the male was taken from his cylinder (outside the test tank), placed in the central compartment of the test tank, and allowed to observe the females for 10 min. Following this acclimation period for the male, we observed a 10-min 'test' during which the amount of time the male spent in each of the three zones of the central compartment and the number of displays the male directed towards each female were recorded. We used the amount of time that a male spent in each of the 'choice' zones of the test tank during this 10-min 'test' as a measure of the strength of his preference for each of the females. In total, we performed 27 trials, testing each male once. Because only

33 healthy females of suitable size were available, some females were used in more than one trial but the same dyad of females was never used more than once.

We also calculated a male preference score as the amount of time each male spent in the 'choice' zone near the larger female minus the time spent near the smaller female (Nuttall & Keenleyside 1993; Ptacek & Travis 1997). This male preference score gives the relative strength of preference for the larger female and controls somewhat for variation in the amount of time spent in the central 'no choice' zone of the test tank.

To test for any side bias, the females were switched after the first 10-min test, and all three fish were allowed to acclimate for 10 min before the male's location and courtship displays were recorded for another 10 min. Following Schlupp & Ryan (1997), we considered males to have a side bias if they spent more than 80% of the total test time (20 min) in one of the 'choice' zones, but no males did this.

After each trial, all three fish were anaesthetized in a clove oil bath (40 mg/l; Anderson et al. 1997) and their SL measured to the nearest 0.01 mm using digital calipers. We also photographed the right side of each male's body and digitized the photographs. We used the public domain program ImageJ (version 1.30, available at http://rsb.info.nih.gov/ij) to measure on the digitized photos the total surface area of the fish and the proportion of its body covered by carotenoid and melanin spots.

All descriptive statistics are reported as mean (±SE, range, n) and all analyses were checked to ensure that they met the assumptions of parametric statistics. Although some females were used in more than one trial, each trial involved a different male and a different dyad of females, so we consider these trials and the trial-females to be independent. To control for any potential bias caused by pseudoreplication, we re-ran all analyses using only the first trial that each female was involved in, but the results remained significant.

Results

The average SL of males was 16.2 mm (±0.18, 14.6–18.4, 27), whereas those designated as the larger females in paired trials averaged 25.3 mm (±0.57, 20.9–29.3, 16) and those designated as the smaller females averaged 20.9 mm (±0.45, 17.4–23.5, 17). The average difference between the larger and smaller females SL in a given trial was 4.8 mm (±0.35, 1.83–8.89, 27 trials). The percentage of body area (not including tail and fins) covered by carotenoid and melanin spots on the males was 7.4% (±0.7, 1.4–15.7, 27) and 8.3% (±0.8, 1.5–21.3, 27), respectively. This is comparable with males inhabiting a low-predation stream in Trinidad where Houde (1987) reported that the average proportion of orange colouration on the body of males (including tails and fins) was 8.7%.

Male guppies spent most of their 'test' time (83 ± 2.0%, 56–98, 27) in one of the two 'choice' zones of the test tank and significantly more of their time associating with the larger of the two females (paired t-test: $t = 2.6$, $p = 0.02$, $n = 27$ trials; Fig. 1). There was no significant difference between the number of displays that males directed towards the larger and smaller females (Wilcoxon

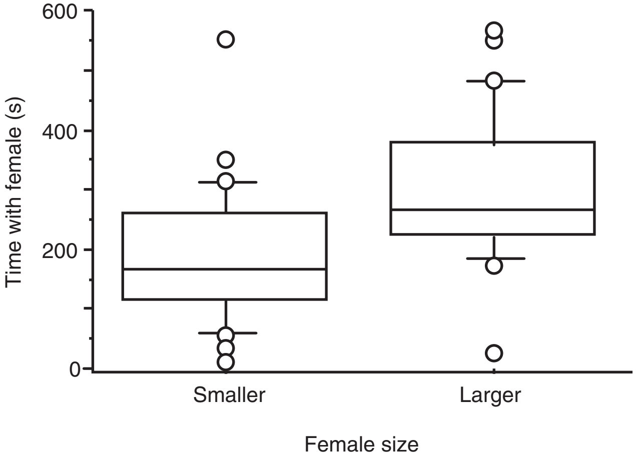

Fig. 1: Male guppies spent significantly more time associating with the larger of two females in a simultaneous choice experiment. Box plots show 10th, 25th, 50th (median), 75th and 90th percentiles with horizontal lines, and all data points outside this range

test, $T_+ = 22.50$, $z = -0.94$, $p = 0.35$, $n = 27$ trials), but only 11 of the 27 males tested actually displayed to any female. There was also no significant difference in the amount of time a male spent with the larger female when comparing those 11 males that did display to those 16 that did not (t-test: $t = 0.40$, $p = 0.7$, $n = 27$). To examine whether time-of-day might have influenced male sexual behaviour, we quantified male displays into three 90-min blocks during the period of our experiments (08.30–13.00 hours) but there was no significant variation in number of displays among time blocks (Kruskal–Wallis test, $\chi^2 = 1.6$, $p = 0.45$, $n = 10$, 6, 11 trials per block).

Male preference score (i.e. difference between time spent with each female) was positively correlated with the difference between the larger and smaller females' SL ($r = 0.64$, $p = 0.0003$, $n = 27$; Fig. 2). Thus, as the difference between the two females' SL increased, the strength of the male's preference for the larger of the two females increased. Notice, however, that when the difference in female SL was < 4 mm, males spent slightly more time with the smaller female in seven of 10 trials (Fig. 2), although this ratio is not significantly different from 50 : 50 (binomial test, $p = 0.17$).

To examine the independent influence of the sizes of each female on male choice, we also performed a multiple regression analysis with male preference score as the dependent variable and the sizes of both females in each trial as independent variables. Male preference score was significantly related to the absolute size of both the large (standardized beta = 0.73, $F_{1,23} = 14.9$, $p = 0.0008$) and small female (standardized beta = −0.79, $F_{1,23} = 20.5$, $p = 0.0002$) presented in a trial (multiple regression, $R^2 = 0.51$, $F_{1,23} = 8.1$, $p = 0.0008$; interaction term not significant, $F_{1,23} = 1.6$, $p = 0.22$). A contour plot reveals the general relationship between male preference and female size (Fig. 3), showing that males spent more time with the

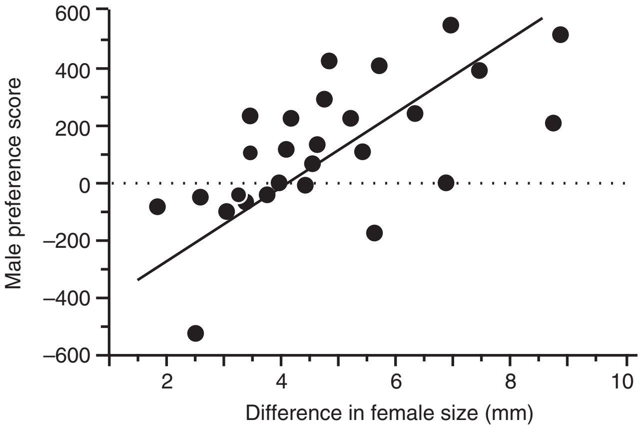

Fig. 2: Male guppy preference score (time spent with larger minus time with smaller female) in relation to the difference between female sizes. Model II regression line is shown ($y = -507 + 130x$, $r^2 = 0.41$, $p = 0.0003$, $n = 27$ trials)

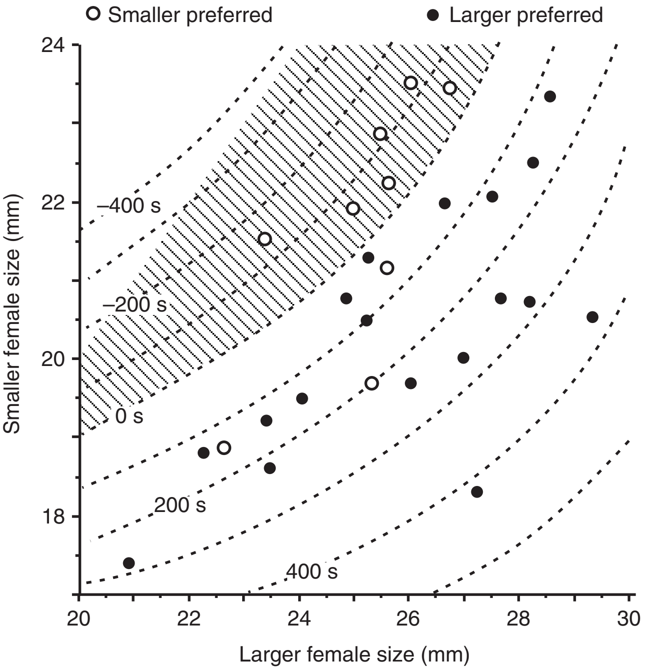

Fig. 3: Contour plot showing male preference score in relation to the sizes of larger and smaller females in a simultaneous choice experiment. Contour lines (shown in 100 s increments) are based on a multiple regression predicting male preference score during a trial from smaller and larger female sizes (including the interaction term). The shaded area indicates the range of female sizes where a preference for the smaller female is predicted by the model. The sizes of the larger and smaller females used in each trial are superimposed on this plot to indicate which female the model predicts the male would choose in each trial

smaller females only under a limited range of female size combinations. Although absolute female size explained only 51% of the variation in the amount of time that a male spent with each female, this model correctly predicted which female the male preferred in all but three of the 27 trials we conducted (Fig. 3).

Neither the male preference score nor the amount of time a male spent with the larger female was correlated with male traits that have been shown to be attractive to females in this species. Thus, a male's preference score was not significantly related to his SL (partial $r = 0.10$, $p = 0.63$ $n = 27$), the proportion of his body covered by carotenoid or melanin spots (partial $r = 0.16$ and -0.19, $p = 0.45$ and 0.36, respectively, $n = 27$), or the proportion of total colour (carotenoid plus melanin) covering his body (partial $r = -0.04$, $p = 0.85$, $n = 27$). We used partial correlation for these analyses to hold the difference between small and large female sizes constant, as this difference strongly influenced male mating preferences (Fig. 2). Partial correlations between the amount of time a male spent with the larger females and these male traits (proportions of carotenoid, melanin, and total colour) were similarly non-significant ($p > 0.35$ in each case).

Discussion

The results of this study demonstrate that the male guppies in our captive-bred population were able to assess the relative sizes of females and make seemingly adaptive mate choices based on that assessment. When males were simultaneously presented with two females of unequal size, they spent significantly more time associating with the larger female. This result is similar to those of other studies examining male choice for female size in fish (Rowland 1982; Sargent et al. 1986; Nuttall & Keenleyside 1993; Grant et al. 1995; Ptacek & Travis 1997; Beeching & Hopp 1999; Werner & Lotem 2003; Wong & Jennions 2003). Thus, by preferentially associating with and courting larger, more fecund females, male guppies can potentially maximize their reproductive success.

Because males preferred the larger and more fecund females, we conclude that they made a choice that would be adaptive in the sense that it would maximize their own reproductive success, everything else being equal. Because female guppies mate multiply, however, it is possible that a male's actual reproductive success could be higher if he chose to mate with the smaller female, but only if she had not already mated or had mated with proportionally fewer males than the larger female. Under such a scenario an ideal free distribution of male matings is expected and neither female should be preferred by any one male. In the apparent absence of male rivals, as in our experiments, however, males would obtain a clear reproductive benefit from mating with the larger female.

Although we did not find a significant difference between the number of courtship displays directed towards smaller and larger females, we also found no significant difference in the strength of the male's preference for the larger female when comparing males that displayed with those that did not display at all. This suggests that male display behaviour was not a good indicator of the strength of a male's preference in our experiment, although Baerends et al.

(1955) found that larger females elicited higher rates of male display behaviour in guppies. However, in addition to female size, male display behaviour is also affected by the behaviour and reproductive status of females (Houde 1997). Because the females used in our experiment were gravid and thus unreceptive, they probably did not show any interest in the male's courtship attempts, reducing the benefits of engaging in such costly behaviour. It is also unknown what determines the extent to which a male will display to a female under a controlled mate-choice setup compared with a natural situation. Amundsen & Forsgren (2003) report similar findings in their study on male mating preferences in the two-spotted goby (*Gobinsculus flaviscens*), where only 18 of the 31 males tested performed clear courtship displays to one or both females.

Looking at the positive relation between male preference score and the difference between female sizes (Fig. 2), it is tempting to conclude that male preferences are influenced solely by the disparity in female size, as others have done (Nuttall & Keenleyside 1993). Our analyses suggest, however, that male guppies simply apportion the amount of time they spend with each female in relation to a female's absolute size (Fig. 3), the apparent response to a difference in female sizes possibly being an artifact of this relationship and the experimental design. Similarly, Sargent et al. (1986) found that male threespine sticklebacks (*Gasterosteus aculeatus*) divided their courtship attempts between females in a manner that matched the females' expected fecundities. We caution future workers to be aware of this alternative explanation for male association patterns when males are faced with two females to choose between. Determining whether absolute or relative sizes of females is a more important determinant of male preferences will require an experimental design that is different than the one we have used here.

We also show that, in some circumstances, male guppies spent slightly more time with the smaller of the two females, most often (seven of 10 cases) when the differences between the sizes of the females were small (<4 mm; Fig. 2). A similar pattern has previously been reported in convict cichlids (*Cichlasoma nigrofasciatum*; Nuttall & Keenleyside 1993) where males seemed to prefer the smaller female most often when the difference in size was <5 mm. In our study, the pattern was not statistically significant and further work will be needed to determine if it is real and why such a male preference may exist. Male guppies, for example, may have relied on other cues (such as the apparent reproductive condition of a female) to assess female quality when they had difficulty discriminating such a small size difference between the females. The abdominal distension of gravid female guppies increases as the brood develops and a pigmented spot near the female's anus becomes largest shortly before parturition (Constantz 1989). Neither the degree of abdominal distension, nor the size of the female's pigmented spot, were controlled in our experiments. Thus those few males that did show increased preferences for the smaller female may have done so because the smaller female actually appeared to be further along in the development of a brood than the larger female. Because ovulation immediately precedes birth, female guppies are most receptive sexually for a brief period immediately following parturition (Constantz 1989). Thus, it would be clearly advantageous for males to allocate more of their time to the most gravid female as she would soon give birth and be sexually receptive again.

An important direction for future studies is to determine if the degree of female abdominal distension, or the size of pigmentation in the female's anal region, influences male mate choice decisions in the guppy. It would also be interesting to determine if male guppies show an increased ability to discriminate among females that are similar in size when they are placed side-by-side rather than at opposite ends of the test tank. In the wild, guppies often exhibit schooling behaviour such that females are close together, presumably making the discrimination of smaller differences in body size easier for males than in our experiments.

In contrast to male sticklebacks (Bakker & Rowland 1995; Kraak & Bakker 1998), sailfin mollies (*P. latipinna*; Ptacek & Travis 1997), and two-spotted gobies (Amundsen & Forsgren 2003), more attractive (i.e. larger, more colourful) male guppies did not exhibit stronger preferences for more attractive (i.e. larger, more fecund) females. This result may have been a consequence of using gravid, and thus unreceptive, females in our experiment, compared with Kraak & Bakker (1998) and Amundsen & Forsgren (2003) who used receptive females. As we noted in the 'Methods' section, however, the use of sexually receptive females can potentially influence male choice via female behaviour. In addition, because the main purpose of our experiment was not to look for a correlation between male attractiveness and mating preference, we did not select males that necessarily varied greatly in coloration or body size. Thus, the variation in attractiveness of the males used may have been too subtle to reveal such a correlation.

Our results contribute to the increasing number of studies demonstrating that male mate choice does indeed occur, even in promiscuous mating systems where males do not invest in parental care. Male guppies prefer to associate with larger, more fecund females and show discriminatory abilities with respect to female size that are similar to those of male Japanese medaka (*Oryzias latipes*; Grant et al. 1995), sailfin mollies (Ptacek & Travis 1997), and haplochromine cichlids (*Astatotilapia flaviijosephi*; Werner & Lotem 2003). Although under certain conditions, male guppies appeared to show slightly stronger preferences for the smaller of the two females presented, a carefully designed experiment that controls for female reproductive condition may provide more insight into this apparent anomaly.

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