

Male Mate Choice in the Guppy (*Poecilia reticulata*): Do Males Prefer Larger Females as Mates?

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Abstract

Although females are the choosier sex in most species, male mate choice is expected to occur under certain conditions. Theoretically, males should prefer larger females as mates in species where female fecundity increases with body size. However, any fecundity-related benefits accruing to a male that has mated with a large female may be offset by an associated fitness cost of shared paternity if large females are more likely to be multiply mated than smaller females in nature. We tested the above hypothesis and assumption using the Trinidadian guppy (*Poecilia reticulata*) by behaviourally testing for male mate choice in the laboratory and by ascertaining (with the use of microsatellite DNA genotyping) patterns of male paternity in wild-caught females. We observed significant positive relationships between female body length and fecundity (brood size) and between body length and level of multiple paternity in the broods of females collected in the Quaré River, Trinidad. In laboratory tests, a preference for the larger of two simultaneously-presented virgin females was clearly expressed only when males were exposed to the full range of natural stimuli from the females, but not when they were limited to visual stimuli alone. However, as suggested by our multiple paternity data, males that choose to mate with large females may incur a larger potential cost of sperm competition and shared paternity compared with males that mate with smaller females on average. Our results thus suggest that male guppies originating from the Quaré River possess mating preferences for relatively large females, but that such preferences are expressed only when males can accurately assess the mating status of encountered females that differ in body size.

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Introduction

Females are generally the choosier sex, because they are relatively less abundant (Emlen & Oring 1977), invest relatively more in reproduction (Trivers 1972), or have

lower potential reproductive rates (Clutton-Brock & Vincent 1991) than males. In polygynous species with conventional sex roles, males should also have mating preferences and exhibit mate choice whenever females vary in quality (Parker 1983), mate searching and mating costs vary among females (Parker 1983; Pomiankowski 1987), the operational sex ratio is female biased (van den Berghe & Warner 1989), males invest in parental care (Sargent et al. 1986), and/or sperm production limits male reproductive success (Nakatsuru & Kramer 1982; Verrell 1982).

Theoretically, males should mate preferentially with larger females in species where female fecundity increases with body size, because male fitness increases with the number of mating and offspring sired (Andersson 1994; Bonduriansky 2001). However, if large females are more likely to be multiply mated than smaller females in nature, then the fecundity-related benefit potentially accruing to a male that has mated with a large female could be offset by an associated fitness cost of sperm competition and shared paternity (Wedell et al. 2002). Consequently, males should assess this fitness-related benefit and cost when choosing to mate with females that vary in body size.

Compared with female mate choice, male mate choice and the factors underlying its evolution have been little studied and are thus poorly understood. Mate choice by males and females is known to operate concurrently in relatively few species (e.g. Kraak & Bakker 1998; Jones & Hunter 1999; Sandvik et al. 2000; see Andersson 1994 for further examples). A candidate species for the study of mutual mate choice is the Trinidadian guppy (*Poecilia reticulata*), a species widely used as a model system for the study of sexual selection (reviewed in Houde 1997).

The guppy is an internally-fertilizing poeciliid that exhibits a non-resource-based, promiscuous mating system in which females mate with numerous males during their lifetimes and apparently only receive sperm from them (Houde 1997). Males and females occur in mixed-sex shoals in nature (Houde 1997), wherein intense sperm competition (Matthews et al. 1997; Pilastro & Bisazza 1999; Matthews & Magurran 2000) and conflict between the sexes over mating decisions (Magurran 2001) occur. Female guppies exert mate choice based on male body colour patterns, as well as other male traits and social cues (Houde 1997). Male guppies have two alternative mating tactics. Individuals may either court (using sigmoid displays) a receptive female prior to attempting to copulate with her or they may attempt a coerced (sneak) copulation. Sneak copulation entails a male approaching a female from behind and thrusting his gonopodium at the female's urogenital pore without first displaying to her, or without a prior receptive response from her. Females typically flee from sneaking males (Houde 1997).

Although male-male competition contributes to male reproductive success in the guppy, it is commonly assumed that such success depends primarily on individual male quality and female mate choice (Houde 1997). However, male mating preferences in this species should also occur because, in nature, male guppies typically encounter multiple females concurrently (Houde 1997), females vary widely in body size and fecundity (Reznick & Endler 1982; Kelly 1999), and sperm production in males requires a refractory period between consecutive ejaculates (Pilastro & Bisazza 1999). In general, males ought to be prudent with

each insemination and preferentially inseminate higher-quality females (Wedell et al. 2002). Thus, male guppies are expected to be selective in their choice of mates and to copulate with the larger and most fecund of available females, so as to maximize their reproductive success (cf. Houde 1997). However, males should be choosy only if they can assess whether individual females have been previously mated by other males, and thereby assess their relative risk of shared paternity.

To date, male mate choice has been little studied in the guppy (Houde 1997). A notable exception is the laboratory study of Benz & Leger (1992) using domesticated guppies of unknown origin. They reported some evidence for male mate choice based on female body length, suggesting that this phenomenon may occur in natural populations of this species. To our knowledge, there is presently no evidence for this. Therefore, we investigated the possibility of male mate choice in the guppy, originating from wild populations in Trinidad, by ascertaining the relationship between individual body size and level of multiple paternity in wild-caught females, and by behaviourally testing for male mate choice in the laboratory. More specifically, we tested the predictions that (i) larger females in nature should have more sires contributing to their broods than smaller females, presumably as a result of multiple mating (cf. Wedell et al. 2002) and (ii) males should be selective in their choice of mates and preferentially direct sexual behaviour toward the largest available (virgin) females when given a choice, but only when they can accurately assess whether a female has already been mated; otherwise, males should not be choosy.

Methods

Paternity Assessment

Field collections and DNA genotyping

To determine whether large female guppies are more likely to be multiply mated than smaller females in nature, we collected gravid females of varying body size from each of 10 populations (Table 1) in the Northern Range mountains of Trinidad during the dry season in Apr. to May 1997 and 1998 and genotyped them, and their offspring, to assess multiple paternity. Details of the study river populations and methods of collection are described in Kelly et al. (1999).

To estimate the number of putative sires contributing to individual broods, we genotyped mothers ($n = 253$) and offspring ($n = 1812$) using two highly polymorphic microsatellite DNA markers (GenBank accession numbers AF254116 and AF170707) that are specific to poeciliid fishes, including the guppy. All broods comprised at least three embryos. The detailed characteristics of the two microsatellite loci sampled and the standard genetic analysis procedures followed are provided in Kelly et al. (1999). For each brood, we conservatively estimated multiple paternity by direct observation of the offspring genotypes on the autoradiographed gels. Maternal genotypes were determined directly and observed in the offspring genotypes, whereas paternal genotypes were inferred from the offspring genotypes (cf. Zane et al. 1999).

Table 1: Mean \pm SE and range (brackets) values for the wet body weight, standard body length and brood size of gravid female guppies collected haphazardly from each of 10 river populations in Trinidad and used in our paternity analysis

Population	Number of broods	Brood size	Wet body weight (mg)	Standard body length (mm)
Paria R.	21	7.0 \pm 0.6 (3–12)	340 \pm 22 (171–558)	25.1 \pm 0.5 (20.5–29.0)
Upper Aripo R.	29	4.8 \pm 0.4 (3–14)	320 \pm 19 (156–598)	23.8 \pm 0.5 (19.0–34.0)
Marianne R.	27	8.5 \pm 0.9 (3–20)	217 \pm 21 (109–533)	21.4 \pm 0.6 (17.0–29.0)
Yarra R.	22	5.9 \pm 0.5 (3–12)	232 \pm 14 (157–461)	21.4 \pm 0.4 (19.0–27.0)
Tunapuna R.	25	5.2 \pm 0.4 (3–11)	189 \pm 20 (96–563)	20.6 \pm 0.6 (16.0–28.0)
Oropuche R.	30	8.6 \pm 1.0 (3–28)	203 \pm 17 (78–538)	20.3 \pm 0.5 (15.0–27.0)
Quaré R.	25	6.4 \pm 0.5 (3–12)	296 \pm 13 (138–406)	23.7 \pm 0.4 (19.5–29.0)
Arima R.	25	8.1 \pm 0.9 (3–22)	232 \pm 20 (110–470)	22.5 \pm 0.6 (18.5–29.0)
Guanapo R.	26	8.9 \pm 0.7 (3–18)	264 \pm 19 (115–475)	22.9 \pm 0.6 (17.0–28.0)
Tacarigua R.	23	8.1 \pm 0.8 (3–16)	175 \pm 14 (70–293)	20.4 \pm 0.5 (16.5–25.0)

We counted the number of paternal alleles displayed per brood and assigned the number of putative sires to one of three categories: (i) one sire (1+), represented by either one or two paternal alleles, (ii) two sires (2+), represented by three to five paternal alleles, or (iii) three sires (3+), represented by the presence of six or more paternal alleles. This categorization was completed for each population separately. This method is conservative because each paternal allele contributed to a brood could have been donated by a different male, if each male was homozygous for a different allele or alternatively possessing the same di-locus genotype. As a result, the true number of sires per brood may be greater than direct-observation estimates based on the assumption of all sires being heterozygous. There is no a priori reason to suspect that the magnitude of any underestimation of multiple paternity would differ on average between populations in our study. Moreover, estimates of multiple paternity obtained separately by direct observation of genotypes, and by a maximum-likelihood statistical method, have been shown to be closely correlated across populations in a least one fish species (Trexler et al. 1997).

Data analysis

We used the ANCOVA to determine whether the number of sires contributing to a brood was associated with the standard body length of the mother. In the analysis, the putative number of sires (one, two or three) contributing to the brood of each female was the treatment effect, individual female standard length was the dependent variable, and individual female brood size (number of embryos) was the covariate. Because standard body length is a strong predictor of both body weight and fecundity in female guppies (Reznick & Endler 1982; Kelly 1999), we used body length as a proxy for female fecundity as the analysis dependent variable.

In the current study, female body length was positively and significantly correlated with female fecundity for all but one of our 10 sampled populations (regression analysis of \log_{10} female standard length (mm) vs. \log_{10} number of offspring, all $r^2 > 0.31$, nine out of 10 populations $p < 0.05$, Bonferroni corrected).

Mate-Choice Experiments

Fish and holding conditions

Experimental guppies were F_1 and F_2 laboratory-raised offspring of wild guppies collected from the Quaré River, Trinidad ($10^{\circ}41'N$, $61^{\circ}11'W$; map grid reference PS 9780) in Apr. 1998. This population was among the 10 populations which we genotyped (Table 1). We raised the fish in aquaria containing well water at 24–26°C. Aquaria were illuminated overhead with Sun-Glo® fluorescent tubes (R.C. Hagen, Montréal, Canada), which simulate the spectrum of sunlight, on a 12 h L:12 h D illumination cycle. The fish were fed NutraFin flake food ad libitum 2–3 times daily, supplemented with live brine shrimp nauplii (*Artemia salina*).

Females and males were raised separately once the presence of the developing gonopodium (intromittent organ) and colours on males could be detected visually. Both sexes were visually exposed to one another throughout rearing, as they were housed in adjacent aquaria. All females used in this study were virgins and at least 17 mm in standard length, and thus sexually mature (Houde 1997). Female fecundity in this population is positively correlated with body length ($r^2 = 0.589$, $p < 0.001$, $n = 25$). Test males were only used after they had developed normal body coloration and the gonopodium, both indicators of sexual maturity in males (Houde 1997).

Experiment 1: binary mate-choice experiment with visual stimuli only

In this experiment, we tested for male mating preferences by presenting individual males with two sexually-mature, virgin females that were either similar or different in body size, and that were physically separated from the male and each other in small clear containers. Thus, test males received only visual stimuli from the females. We wished to ascertain whether a male mating preference was evident under the latter circumstance of limited information.

We modelled this experiment on the binary mate-choice experimental protocol commonly used in our laboratory (e.g. Dugatkin & Godin 1992; Godin & Briggs 1996) and by others (Houde 1997). The experimental apparatus consisted of a glass aquarium ($40 \times 20 \times 25$ cm; L \times W \times H) and two Plexiglas compartments ($20 \times 5.5 \times 25$ cm) placed at either end of the aquarium. The aquarium and Plexiglas compartments contained aged well water (15 cm depth) maintained at 24–26°C and were illuminated by an overhead Sun-Glo fluorescent tube ($10.0 \mu E/m^2/s$ at the surface). We observed the fish through an angled mirror located above the experimental apparatus. Vertical lines drawn on the front and back of the aquarium, and Plexiglas markers placed on the bottom of the

aquarium, demarcated a 10-cm wide male 'mating preference' zone near each of the Plexiglas end compartments. We covered with tan paper the front and back of the aquarium and the sides and back of the end compartments to minimize external disturbances and to provide a uniform background for male assessment of stimulus females. The bottom of the aquarium was covered with natural gravel substratum (3 cm depth) to simulate natural stream conditions.

We used three size categories of stimulus females: small (17–18 mm standard length), medium (21–22 mm), and large (25–26 mm). The size range of the females was chosen to correspond to that found in nature (Reznick & Endler 1982; see also Table 1). We isolated three groups of 6–10 stimulus females (one group per size category) in separate aquaria to provide three pools of stimulus females from which to draw in the experimental trials.

In a typical mate-choice trial, we presented an individual male with a pair of stimulus females to test for his mating preference. The paired females were either both small (control), one small and one medium, one small and one large, or one medium and one large. The females in a given matched pair were placed individually in each of the two end compartments, which were initially shielded from view of the central test aquarium by opaque Plexiglas screens. We randomized the particular compartments in which the stimulus females were placed to control for any potential side bias in male choice. The test male was selected from a pool of 60 males and his standard body length measured. This male was placed in the central aquarium and, with the two stimulus females, were allowed to acclimatize for 1 h before testing. Following this period, we gently dipnetted the male and placed him in a clear Plexiglas cylinder (8.5 cm diameter) in the centre of the aquarium and removed the opaque screens to allow visual contact between the male and the females for 10 min. The opaque screens were replaced and the Plexiglas cylinder was removed and the male allowed to swim freely. We then removed the opaque screens (when the male was in the centre of the aquarium) and recorded from behind a blind the time spent by the male in the preference end zone associated with each female for 10 min. Once this first preference test was completed, the female end compartments were switched and the procedure was repeated for a second 10-min preference test.

Using the above protocol, we tested the mating preferences of each of 40 males ($\bar{x} \pm \text{SE} = 17.6 \pm 0.3$ mm standard length) separately with each of the four experimental categories of stimulus females over a 4-d period. A period of 24-h elapsed between repeated trials for each male. For a given test male, we used different pairs of females to constitute each of the four matched pairs of stimulus females presented sequentially. We randomized the order in which individual males were tested with each of the four pairs of stimulus females.

As a criterion of mating preference, we calculated a preference-difference score for each male by subtracting the total time that the male spent near (≤ 10 cm) and facing ($0 \pm 90^\circ$) the smaller female from the time spent near and facing the larger paired female for each treatment separately. The larger the negative value of this score, the greater the preference for the larger female. Such a mating preference criterion (i.e. time spent near a potential mate) has been used

previously for female guppies, and is a strong predictor of actual mating preference (Bischoff et al. 1985; Dugatkin & Godin 1992; Kodric-Brown 1993). We then analysed these difference scores using the repeated-measures ANOVA to determine if time spent with the larger vs. the smaller paired female varied among the paired-stimulus female treatments.

Experiment 2: binary mate-choice experiment with full range of stimuli

In this experiment, we tested for male mating preferences by presenting individual males with two sexually-mature, virgin females, one smaller (19.6 ± 0.3 mm standard length) than the other (23.3 ± 0.2 mm), that were concurrently free-swimming with the male in a test aquarium. Thus, in contrast with expt 1, both the test male and the stimulus females had full access to each other and to all potential natural stimuli (visual, chemical, tactile) exchanged between them during the behavioural observation period; under this circumstance, males were assumed to be able to accurately assess the reproductive state of paired stimulus females and were thus expected to be choosy.

The test aquarium ($40 \times 20 \times 25$ cm) contained aged well water (15 cm depth) maintained at $24\text{--}26^\circ\text{C}$, and its bottom was covered with natural aquarium gravel (3 cm depth). It was illuminated by an overhead Sun-Glo fluorescent tube ($10.0 \mu\text{E}/\text{m}^2/\text{s}$ at the surface). We covered with tan paper the back and sides of the aquarium to minimize external disturbances and to provide a uniform background for male assessment of females.

At the beginning of a typical mating-preference trial, we divided the aquarium into halves with a clear Plexiglas partition, and placed the two stimulus females into one half and the test male into the other half; the sexes could see each other through the partition. The fish were allowed to acclimatize for 1 h, during which we observed no evidence of female–female competition such as nipping or chasing. Following this period, we removed the Plexiglas partition and thereby allowed the fish to swim and interact freely.

From behind a blind, we recorded for 15 min the number of approaches, nips, sigmoid displays, copulation attempts, and post-copulatory jerks (sensu Houde 1997) of the male directed towards either the large or small female. We defined an approach as an unambiguous directed movement of the male towards a female. After approaching a female, the male often engages in nipping behaviour directed at her gonopore (Houde 1997; personal observation). A sigmoid courtship display involves the male arching his body into an S-shape and quivering near a female (Houde 1997). A male copulation attempt involves the male approaching the female laterally and attempting to insert his gonopodium into her gonopore (Houde 1997). If the male's copulation attempt is successful, he typically performs post-copulatory jerks, which are short bursts of full-body shakes (Houde 1997). During the 15-min trial, we also recorded the number of times each female performed gliding behaviour (a female sexual response, Houde 1997) toward the male, regardless of whether he was courting or not. The female gliding response consists of the female orienting herself toward a male and gliding towards him while maintaining a rigid body

posture and only utilizing paired fins for propulsion (Houde 1997). We replicated such a trial 30 times, each with a different male (17.5 ± 0.2 mm) and a different pair of stimulus females. Each type of male sexual behaviour (described above) was tested separately using the paired t-test (Bonferroni corrected) to determine whether male sexual behaviour directed at the small and large females differed. We also tested, using the paired t-test (Bonferroni corrected), whether the sexual responses of the paired stimulus females toward the male differed.

Results

Paternity Analysis

Because the standard length of females within each of our three defined categories of putative sires (i.e. 1+, 2+, 3+ sires) did not vary significantly

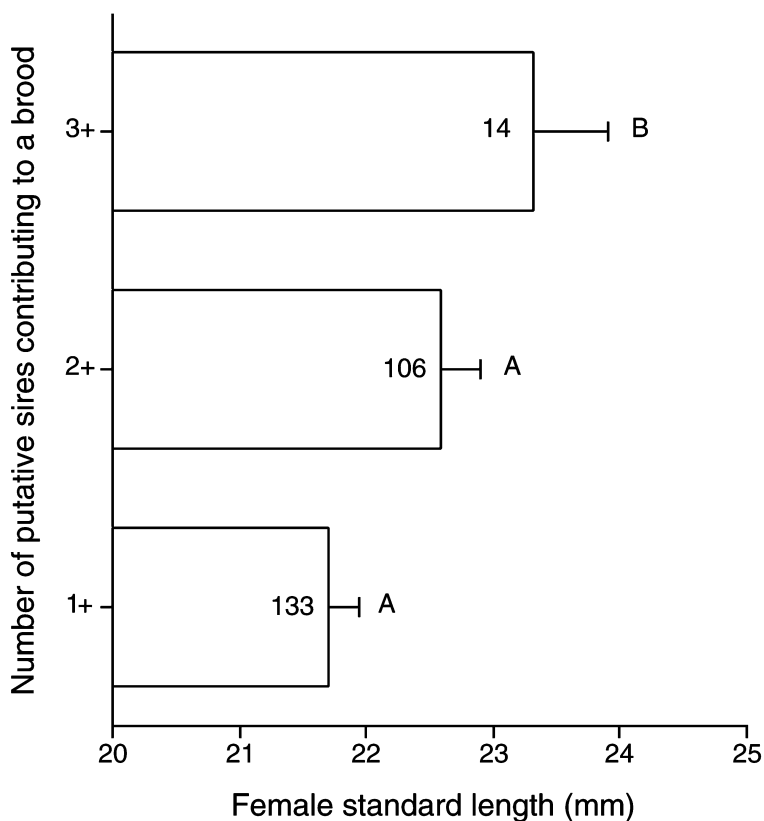


Fig. 1: Mean (\pm SE) standard length of female guppies with one, two or three putative sires contributing to their broods (females pooled across all 10 study populations). Numbers inside the bars denote numbers of females and bars with same letters are not significantly different (Tukey test, $p > 0.05$)

among our study populations (brood size as covariate, nested ANCOVA, $F_{9,239} = 1.35$, $p = 0.18$), we pooled the data across the 10 populations for each sire category separately. Larger females had, on average, significantly more sires contributing to their broods than smaller females (ANCOVA, $F_{2,249} = 5.09$, $p = 0.007$; Fig. 1). Females having broods with 1+ sire or 2+ sires were on average significantly (Tukey's HSD test, $p < 0.05$) smaller than females with 3+ sires contributing to their broods.

Experiment 1: binary mate-choice experiment with visual stimuli only

Although there was a tendency for males to spend more time near the larger of the paired stimulus females, the preference-difference behavioural scores of males did not vary significantly among the paired stimulus female treatments (one-way repeated-measures ANOVA, $F_{3,37} = 0.96$, $p = 0.42$, Fig. 2). Therefore, on average, males did not clearly prefer the larger over the smaller female. Similarly, male sexual motivation did not appear to vary among the treatments, as all test males courted (with sigmoid displays) the paired stimulus females and the amount of time individual males spent in the central 'no-choice' zone of the aquarium did not differ significantly among the four treatments (one-way repeated-measures ANOVA, $F_{3,37} = 0.11$, $p = 0.96$).

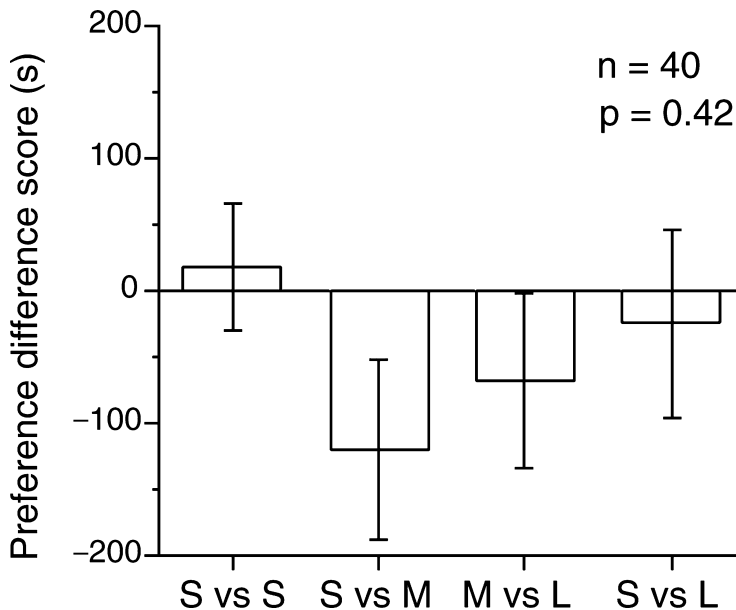


Fig. 2: Mean (\pm SE) difference score in time (s) spent near the paired smaller or larger females for Quaré River males tested in binary-mate choice trials (expt 1). The statistical significance level shown was determined using the one-way repeated-measures ANOVA. S, small female; M, medium female; L, large female

Experiment 2: binary mate-choice experiment with full range of stimuli

Overall, males directed significantly more sexual acts (paired $t_{39} = 3.52$, $p = 0.001$), including approaches, nips, sigmoid displays, copulation attempts and post-copulatory jerks, towards the larger ($\bar{x} \pm SE = 21.6 \pm 2.9$ acts/15 min) than the smaller (15.7 ± 1.8 acts/15 min) of the paired stimulus females. This difference can be attributed mainly to the significantly larger numbers of approaches and nips directed towards the larger female (Fig. 3). Paired small and large females did not differ significantly in the frequency of their sexual gliding behaviour directed towards males overall or that directed towards courting vs. non-courting males (Fig. 4). So, the observed male preference for large over small females cannot be attributed simply to larger females behaving differently towards males compared with smaller females.

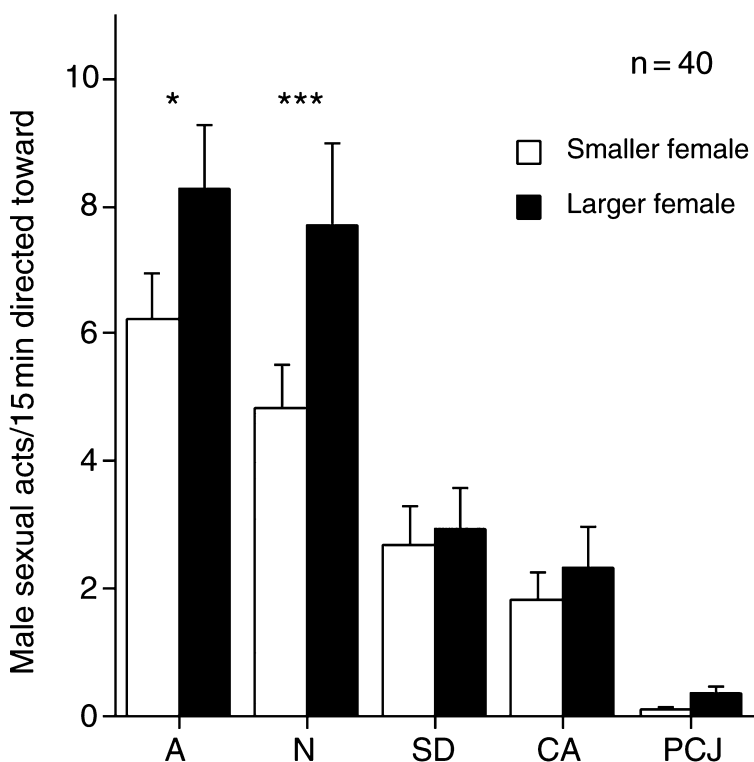


Fig. 3: Mean (+SE) number of male approaches (A), gonopodial nips (N), sigmoid courtship displays (SD), copulation attempts (CA), and post-copulatory jerks (PCJ) directed towards the larger or smaller paired females per 15 min in free-swimming mate-choice trials (expt 2). * $p < 0.05$, *** $p < 0.005$ (paired t-test with sequential Bonferroni correction)

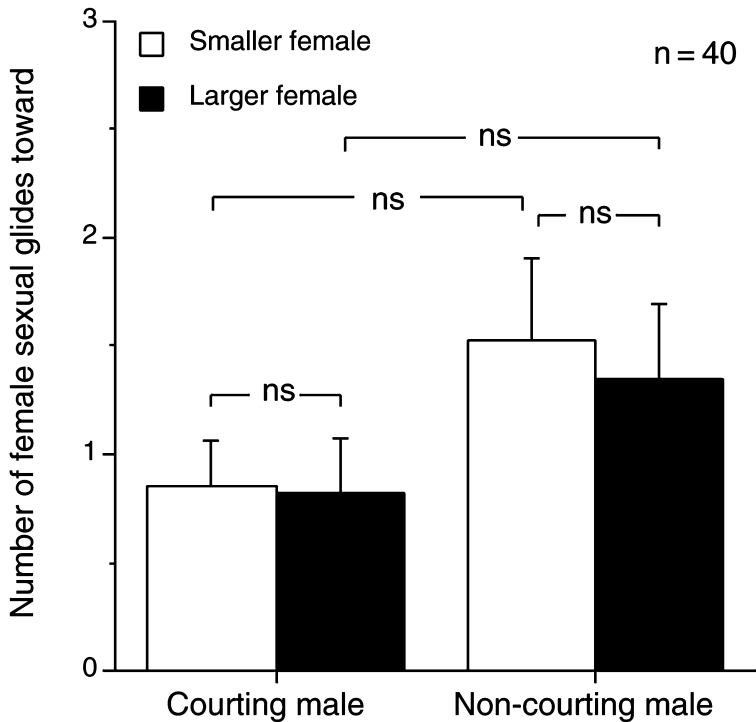


Fig. 4: Mean (+SE) number of female glides/15 min directed at non-courting and courting males by the smaller and larger females in free-swimming mate-choice trials (expt 2). p-value obtained using the paired t-test

Discussion

Our experimental results provide evidence for male mating preferences in the Trinidadian guppy. In laboratory tests, a preference for the larger of two simultaneously-presented virgin females was clearly expressed only when males were exposed to the full range of natural stimuli from the females, but not when they were limited to visual stimuli alone. However, as suggested by our multiple paternity data, males that choose to mate with large females may incur a larger potential cost of sperm competition and shared paternity compared with males that mate with smaller females on average.

The paternity analysis on wild-caught females revealed a positive, significant relationship between the number of putative sires per brood and female body length. A similar multiple paternity – female size pattern has been previously reported for the sailfin molly, *Poecilia latipinna*, another internally-fertilizing poeciliid fish species (Travis et al. 1990). Our data demonstrate that female guppies engage in multiple mating in nature (see also Kelly et al. 1999) and that large females have broods with more sires on average compared with smaller females. This pattern may be owing to large females being either more sexually

attractive to males, visually encountered more frequently by males in nature, and/or are more easily inseminated than smaller females. Irrespective of the mechanism(s) underlying this relationship, the fecundity-related benefit potentially accruing to a male that has mated with a large female could be offset by an associated fitness cost of sperm competition and shared paternity (Wedell et al. 2002). Importantly, this potential cost should select for accurate male assessment of female mating status in species wherein females vary in fecundity and level of multiple paternity, both of which are correlated with female body length in the guppy (this study; Reznick & Endler 1982; Kelly et al. 1999).

The results of our behavioural mate-choice experiments suggest that male guppies assess the mating status of females when choosing among them as mates. When presented with paired stimulus females in binary-choice trials in expt 1 (female visual stimuli available only), males did not show any significant behavioural preference for either one or the other of the females. In comparison, when males were given access to free-swimming females (i.e. potential visual, chemical and tactile stimuli from them available) in expt 2, they directed significantly more sexual acts (particularly more approaches and gonopodial nips) towards the larger of the paired females. Based on these behavioural assays, we conclude that male guppies originating from the Quaré River possess mating preferences for relatively large females, but that such preferences are expressed only when males concurrently encounter females of different body size and have access to the full natural range of stimuli from them. Our results further suggest that the expression of directional male mate choice in the guppy specifically requires the presence of chemical and/or tactile information from females that is correlated with their body size. Because access to all of this information was not available to the males in expt 1, they presumably were unable to accurately assess whether or not the paired stimulus females had previously mated with other males and consequently they did not choose between them. Male mating preferences for the larger of available females in behavioural assays has been previously reported for the one-sided livebearer, *Jenynsia multidentata* (Bisazza et al. 2000), and Japanese medaka, *Oryzias latipes* (Grant et al. 1995); in both these studies, males were given access to freely-swimming females during behavioural assays, as was the case for our expt 2.

Limitation in male production of ejaculate should favour differential male mating behaviour towards higher-quality females (Wedell et al. 2002). However, for this to occur, males must be able to assess differences in female quality. Because production of ejaculates in male guppies is rate limited (Pilastro & Bisazza 1999), they are thus expected to be discriminating in their choice of mates. We observed, in our expt 2, that male guppies approached and nipped (at the gonopore) at significantly higher rates the larger of the two free-swimming stimulus females. This apparent male mate choice for larger females cannot be attributed to differential female behaviour, because paired small and large females did not differ in their sexual behavioural responses towards the test males. We suggest that male guppies use gonopore nipping behaviour to olfactorily assess at closer range the quantity and/or quality of sexual pheromones produced by the females; these pheromones are excreted through the gonopore and are known to

stimulate increased courtship rate in male guppies (Crow & Liley 1979). Further study is required to ascertain conclusively the role of pheromones in male assessment of female quality and mating status in the guppy.

For mate choice to evolve and be maintained in a population, its fitness-associated benefits must equal or exceed its costs (Parker 1983; Pomiankowski 1987). The benefits of male mate choice are associated with the qualities of preferred females (Parker 1983). In the guppy, larger females produce larger broods (Reznick & Endler 1982; this study). While there appear to be fecundity-related reproductive benefits accruing to males in preferring larger females, mate choice is not without potential costs (Pomiankowski 1987). Although very little is known about such costs in male guppies, differential predation risk may be one of them. Because fish predators prefer female guppies over males as prey (Pocklington & Dill 1995), males that associate sexually with larger females may be more likely to attract predator attention and thereby face a greater risk of predation than otherwise. This remains to be determined. Given that large female guppies have a greater likelihood of being multiply mated than smaller ones (this study), another potential cost to males of choosing larger females as mates is increased risk of sperm competition and shared paternity (Wedell et al. 2002). Therefore, sperm competition should become more intense as females become more attractive to males (Wedell et al. 2002). Consequently, as female size increases in the guppy, males are more likely to share paternity than if they had inseminated a small female, resulting in decreased male reproductive success per brood (4.69 offspring/male/brood for multiply-sired broods vs. 5.65 offspring/male/brood for singly-sired broods in the guppy, Kelly 1999). Thus, when sperm competition reaches a particular intensity, it should be more beneficial for males to allocate mating resources to smaller and less fecund females (Wedell et al. 2002). However, this may result in the loss of other potential benefits of mating with larger females, such as increased quality of offspring for example (Bisazza et al. 1989; Wedell et al. 2002). Even when sperm competition is intense, males may still benefit from competing for access to larger females.

To our knowledge, our study represents the most comprehensive attempt at investigating male mate choice in the Trinidadian guppy to date. Our behavioural assay and paternity results suggest that male guppies preferentially direct their mating behaviour toward and mate with the larger of available females under natural conditions. Male mate choice may thus play an important, yet relatively unexplored, role in the guppy mating system. In particular, mutual male and female mate choice, and the implications for sexual selection, in this system warrant further study.

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