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EVIDENCE FOR MATE CHOICE BY MALE GUPPIES (*POECILIA RETICULATA*)

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ABSTRACT

Mate choice by males in organisms that do not make obviously costly contributions to offspring should be expected where sperm production is limited and courtship time is finite. Although male guppies (*Poecilia reticulata*) contribute only sperm to their offspring, preliminary evidence points to male mate choice in this species. Thus, the hypothesis that male guppies choose their mates was investigated. Mate choice was measured by giving males a choice of different-sized females, using only visual cues. The data revealed that males preferred large females over small females whether they were presented singly, in pairs, or with a small female. This preference may arise because large females may produce larger broods.

† † †

Theory and research on mate choice in animals has led to the conclusion that the sex that invests most in offspring production should be the sex that is most discriminating in its choice of mates (Daly and Wilson, 1983). Because females produce larger gametes, often nourish the developing embryo, and spend more time and energy in offspring care, it is not surprising that females are "choosier" about prospective mates than are males (Daly and Wilson, 1983). However, in those species that have extensive male investment in reproduction, males may be as or more discriminating than females. For example, male sticklebacks build nests and care for the eggs and fry and are "choosy" about prospective mates (Li and Owings, 1978).

Males may exhibit mate choice even if they invest relatively little in offspring production or in parental care if their ability to generate sperm is limited, or if courtship time is more profitably directed toward females that will contribute most to male fitness. For example, male red-spotted newts (*Notophthalmus viridescens*) choose to mate with large females (Verrell, 1985). Female body size is positively correlated both with fecundity (number of eggs laid after mating) and with number of yolked oocytes in the ovary (Verrell, 1982). Male red-spotted newts also have severely limited amounts of sperm during the courtship season and invest heavily in courtship behavior and secondary sexual characteristics (Verrell, 1985).

Dewsbury (1982) suggests that the proper unit of evaluation for the costliness of male contribution is the ejaculate rather than the individual spermatozoan. For example, male lemon tetras (*Hyphessobrycon pulchripinnis*) cannot fertilize all the eggs released by a female during spawning (160 eggs released in 23 spawnings) even though males produce enough sperm to fertilize all the eggs if they were released en masse (Nakatsuru and Kramer, 1982). Dewsbury (1982) also notes that male choice should be the rule rather than the exception. Thus, we should expect to see mate choice in both sexes, although it may be more pronounced in the sex that performs most of the parental care.

Female guppies mate preferentially with certain males under several different conditions. For example, females mate preferentially with males whose color pattern is under-represented in the local population. These males are therefore over-represented in the F_1 generation (Farr, 1977; Resnick, 1982). Female guppies also mate preferentially with colorful males over those that are less colorful (Kodric-Brown, 1985). In this case, color serves as an index of the male's foraging ability, as the male can obtain certain pigments (e.g., carotenoids) only from foraging. Thus, the presence of these pigments may indicate male fitness and, indirectly perhaps, the fitness of offspring fathered by him. Finally, female guppies mate preferentially with males that exhibit more vigorous courtship displays (Farr, 1980a, b). This, again, may indicate the nutritional state of the male, as the more vigorous the courtship,

the more energy is used. Courtship vigor may also indicate male fertility, as vigor is significantly correlated with number of offspring produced (Farr, 1980b).

Male guppies should discriminate among potential mates because, for a given amount of courtship effort and gamete cost, they may be reproductively more successful by directing their courtship toward females that are sexually receptive or fecund. We have noticed that male guppies constantly pursue some females but ignore others, suggesting that males are discriminating among females. This study was conducted to investigate the possibility that female size may be an attribute used by males in selecting among potential mates. We hypothesized that male guppies would tend to choose to mate with large females over small females when given an unforced choice between females of different sizes.

METHODS

Subjects

Guppies (*Poecilia reticulata*) were obtained from a local dealer as breeding stock and were kept in two separate populations. One population was kept in two 220-liter aquaria containing adult and juvenile males and females. This stock population provided the males ($n = 60$) used in these experiments.

The guppies were fed once a day at approximately 0830, and were on a light: dark schedule of 14:10, with the lights on between 0600 and 2000. The water was maintained at room temperature (24°C) and was replenished as necessary.

Materials

Virgin females were obtained by collecting fry from the stock-population females, which were place in breeding traps shortly before giving birth. Young males were removed from tanks of fry as soon as the anal fin began differentiation. The mature virgin females were kept in a separate 160-liter tank system to prevent inadvertent fertilization. These virgin females were used as stimuli for male mate-choice. The stimulus females were divided into two dichotomous size classes: Large (L) females were greater than or equal to 20 mm in length, and small (S) females were less than 20 mm in length. In practice, a large female was always at least 5 mm larger than the small female against which she was tested.

The testing apparatus was a transparent plexiglass box subdivided into two end compartments that were 15 × 15 × 10 cm, and a center compartment that measured 15 × 15 × 40 cm. The front of the center compartment was marked off into eight 5-cm-wide sections by scoring the outside. The exterior bottom, back and sides of the box were covered with opaque brown paper to prevent external distractions.

Procedure

The test box was filled with water to a depth of 12 cm. The two end compartments, where the females were placed, were filled with water from a tank that contained only virgin females. The center compartment, where the male was placed, was filled with water from an unpopulated tank that was continually filtered with charcoal, so as to provide no extraneous pheromonal cues.

Males were presented with either zero, one, or two females. This, along with the size classes, set up six conditions: L-L, L-S, L-E (Empty), S-S, S-E, and E-E. Ten trials were conducted for each condition (60 trials total). In those conditions that required two different-sized stimulus-fish, or only one stimulus-fish, the side that the larger (or only) fish was on was counterbalanced across trials.

Trials began by placing the female(s) into the end compartments and allowing them to acclimate until they were actively swimming or had moved into the upper half of the water column. Female acclimation time was the rate-limiting step in all these experiments. (Female acclimation took up to 30 minutes, although most females acclimated in less than 20 minutes. Acclimation seemed to be a function of size, with larger females taking longer to acclimate than smaller ones.) When the females had acclimated, the male was placed in the middle of the center compartment. (Male acclimation never took longer than 10 minutes, and most males acclimated in 2–4 minutes.) After the male had acclimated, the trial began.

Because it took so much time for the females to acclimate, we used each set of stimulus females for either two or three males. Thus the 10 trials that comprised a condition were conducted in four separate blocks. The 24 blocks of this experiment were conducted in random order.

Each trial lasted 10 minutes, during which we instantaneously sampled (Altman, 1974) the male's location by noting which of the eight sectors he occupied at the end of every ten-second period. A male was scored as occupying a sector if his snout was in that sector (Breder, 1948). Each condition consisted of 600 location samples (60 samples per trial × 10 trials).

RESULTS

Male guppies were found significantly more often at the ends of the center compartment than in the middle in the three symmetrical conditions (L-L, S-S,

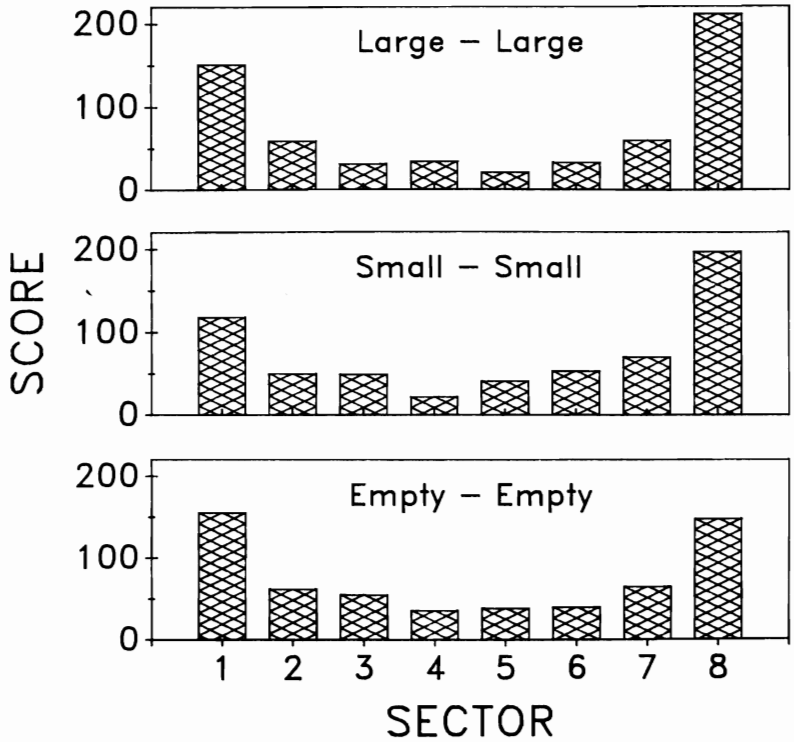

Figure 1. Male proximity to females when presented with a symmetrical condition (two large females, two small females, or empty compartments). The score is the number of instantaneous samples occurring in the sector. There were 600 samples in each condition.

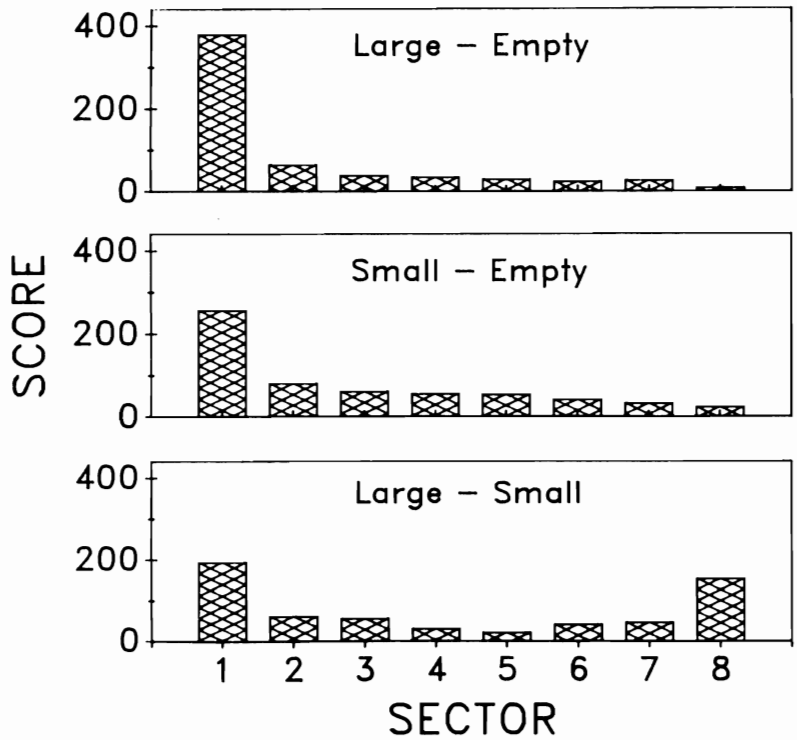

Figure 2. Male proximity to females when presented with an asymmetrical condition (one large female, one small female, or one large female versus one small female). The score is the number of instantaneous samples occurring in the sector. There were 600 samples in each condition.

and E-E) (see Figure 1). We compared the number of samples in the two ends (sectors 1, 2, 7, and 8 combined) with the number of samples in the middle (sectors 3, 4, 5, and 6 combined) using chi-square goodness-of-fit tests. Males were closer to the ends in all three symmetrical conditions (L-L: $\chi^2(1) = 218.411, p < 0.001$; S-S: $\chi^2(1) = 121.50, p < 0.001$; E-E: $\chi^2(1) = 112.67, p < 0.001$).

Male guppies were found significantly closer to the ends when the stimulus compartments contained large females than when they were empty or when they contained small females. However, males were not significantly closer to the ends when the stimulus compartments contained small females than when they were empty. We compared the number of samples in the end sectors (sectors 1, 2, 7, and 8 combined) and the middle sectors (sectors 3, 4, 5, and 6 combined) across symmetrical conditions using chi-square contingency tests (L-L vs. S-S, L-L vs. E-E, and S-S vs. E-E). We found that the L-L condition was significantly different from the S-S condition, and from the E-E condition. However, the S-S condition was not significantly different from the E-E condition (L-L vs S-S: $\chi^2(1) = 9.34, p < 0.005$; L-L vs. E-E: $\chi^2(1) = 11.40, p < 0.001$; S-S vs. E-E: $\chi^2(1) = 0.066, p > 0.1$; all using Yates correction for 2×2 contingency tables). Thus, although male guppies remained closer to the ends of the compartment than to the middle in all conditions, they spent significantly more time at the ends when large females were present.

When only one female was present (L-E and S-E), the male spent most of his time near her. Although this is obvious from Figure 2, we also tested for statistical significance by comparing the number of samples in the four sectors closest to the female against the four sectors farthest from the female, using chi-square goodness-of-fit tests (L-E; $\chi^2(1) = 305.31$, $p < 0.001$; S-E; $\chi^2(1) = 152.01, p < 0.001$).

Males spent more time near the end compartment with the female in it when the female was large than when the female was small. We compared the first sector from the L-E condition against the first sector from the S-E condition, using a chi-square goodness-of-fit test. We discovered that males were found more often near the large female than near the small female (L-E vs. S-E; $\chi^2(1) = 23.48, p < 0.01$).

The final condition consisted of a direct comparison of large and small females. We found that males were in the half of the compartment nearest the large female more often than in the half nearest the small female ($\chi^2(1) = 10.14, p < 0.01$). Males were found more often in the sector next to the large female than in the sector next to the small female ($\chi^2(1) = 4.62, p < 0.05$). There was no significant difference for any other pair of sectors at equal distances from the stimulus females.

DISCUSSION

Males spent significantly more time near large than small females, regardless of whether large females were presented singly, in pairs, or with a small female. Further, males performed courtship displays (sigmoid displays; Liley, 1966) and swam in parallel with the movements of the female when they were in the sector closest to the female, regardless of the female's size. Thus, although there is conspecific affiliation in this species regardless of gender (Liley, 1966), the fact that the males "courted" females than were unreachable, and spent more time near larger females, tends to exclude simple affiliation as an explanation of the males' behavior.

Male guppies clearly "prefer" large females over small ones, although the reason for this preference is not yet known. Some preliminary work done in our lab, however, indicates that larger females produce larger broods than do smaller females. This is true for at least one other species in this family, the least killifish, *Heterandria formosa* (Cheong et al., 1984). Larger broods from larger females might explain, in an ultimate sense, why the males choose larger females over smaller ones.

In conclusion, we have shown that male mate-choice occurs in a species in which males contribute nothing except sperm to their offspring. Consequently, we believe that it behooves us to examine more carefully those species in which female choice is thought to be the only form of sexual selection.

ACKNOWLEDGMENTS

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