Transactions of the Illinois State Academy of Science
(1993), Volume 86, 3 and 4, pp. 127 - 132

Effects of Predator Size and Female Receptivity on Courtship Behavior of Captive-Bred Male Guppies

Kristin Braun and R. Given Harper
Department of Biology
Bradley University
Peoria, IL 61625

Present address for RGH:
Department of Biology
Illinois Wesleyan University
P.O. Box 2900
Bloomington, IL 61702

ABSTRACT

The effects of predator size and female receptivity on the courtship behavior of captive-bred male guppies (*Poecilia reticulata*) were investigated. Male guppies exhibited risk-reckless courtship behavior in that they did not decrease the amount of time spent performing visually conspicuous sigmoid displays and increase the frequency of attempted forced copulations when large predatory fish were present. Female receptivity (i.e., virgin or non-virgin females) also had no effect on male courtship behavior.

INTRODUCTION

Predation is a major selective force that has influenced the evolution of life history traits in the guppy (*Poecilia reticulata*) (Farr, 1975; Reznick and Endler, 1982; Reznick et al., 1990), a small, hardy, live-bearing, freshwater fish native to streams in South America (Clark and Aronson, 1951; Houde, 1988). One such trait is male courtship behavior, which represents a balance between natural selection (through predation) and sexual selection. Sexual selection has maximized the rate at which courtship behavior occurs as a result of male-male competition for females (Farr, 1975; Houde, 1988). High levels of courtship behavior increase male mating success (Farr, 1976) but may also increase the risk of predation due to greater visual, and possibly chemical, conspicuousness (Schroder, 1983; Breden and Stoner, 1987).

A male guppy can employ two strategies in order to mate with a female; he can court the female and try to persuade her to mate with him, or he can attempt a forced copulation (Farr, 1980). Courtship behavior consists of sigmoid displays, in which the male bends his body into an "S"-shape with the dorsal and caudal fins either spread fully or closed (Farr, 1976); such displays last up to three seconds (Clark and Aronson, 1951). Forced copulations consist of rapid thrusts of the gonopodium at the genital pore of the female in an attempt to copulate without female consent (Clark and Aronson, 1951).

The results of several studies suggest that predation is an important selective force on reproductive behaviors of male guppies, which can be modified under the threat of predation. Luyten and Liley (1985) found that male guppies from areas with high predation rates by piscivorous fish exhibited low frequencies of sigmoid displays and high frequencies of attempted forced copulations. Endler (1987) documented fewer male guppy sigmoid displays and an increased number of attempted forced copulations in the presence of a predatory fish. Magurran and Seghers (1990) found that in the presence of predatory fish, male guppies from populations experiencing low predation rates exhibited risk-reckless courtship behavior (Fraser and Huntingford, 1986) in that they did not reduce their sigmoid display rate. Conversely, Magurran and Seghers (1990) found that male guppies from populations experiencing high predation rates exhibited risk-sensitive courtship behavior (Fraser and Huntingford, 1986) in the presence of predatory fish by performing fewer sigmoid displays and increasing the number of attempted forced copulations.

Investigators of most studies have not determined whether predator size or female receptivity (i.e., virgin or non-virgin females) affect male guppy courtship behavior. We investigated the effects of predator size and female receptivity on male courtship behavior in a commercially purchased population of guppies. If predation pressure has influenced male courtship behavior, smaller predatory fish that are unable to kill adult guppies should have less of an effect on courtship behavior than larger predatory fish (Schroder, 1983). In addition, because female guppies are most receptive to male sigmoid displays as virgins (e.g., Farr, 1976; Houde, 1988), males should perform more sigmoid displays to virgins than to non-virgins.

METHODS

We obtained the guppies from a stock at a local retail outlet. Seventeen male guppies, ten virgin female and ten non-virgin female guppies were housed in three separate sections (i.e., one section contained only males, one contained only virgin females, and one contained only non-virgin females) of a 50 cm x 26 cm glass aquarium filled to a depth of 20 cm with aged, aerated tap water. A heater maintained the temperature at approximately 25^{o}C, and the aquarium was exposed to dim fluorescent lighting on a 14-h-L:10-h-D cycle. All guppies were fed daily with Tetra-marin flake food.

We used striped convict cichlids (*Cichlasoma nigrofasciatum*) as predators in this experiment. The range of this species overlaps that of the guppy (Axlerod and Vorderwinkler, 1983), and other cichlid species are known guppy predators (e.g., Reznick et al., 1990). In preliminary observations we determined that the two large cichlids, approximately 5 cm in length and 3.3 g in body mass, were capable of preying on adult guppies, whereas two small cichlids, approximately 3.75 cm in length and 1.6 g in body mass, were not capable of preying on adult guppies.

The experiments took place in March and April, 1992. We conducted all observations during early morning (2-5 hours after first light) because most courtship occurs at this time (Endler, 1987). The experimental apparatus was an aquarium with conditions identical to that of the aquarium in which all guppies were housed (described above), but it was divided in half by a clear plexiglass divider which had two, screen-covered holes (approximately 5 cm in diameter) that permitted water to pass between the adjacent chambers. Coarse gravel was placed at the bottom of the tank and the tank sides were covered (except for the observation side) to minimize disturbance to the fish. We conducted trials in the following manner. Four male guppies, which could be identified by their natural coloration, were placed in the test aquarium. One female guppy (either virgin or non-virgin) was immediately placed in the test aquarium with the males. After 7 min, either two small predators, two large predators, or two male guppies (controls) were placed in the opposite chamber of the test aquarium. We then allowed the fish to acclimate for another 8 min. Similar acclimation periods have been used in other studies of guppy courtship behavior (e.g., Breden and Stoner, 1987). After the acclimation period, we observed one of the four male guppies for 10 min and recorded the length of time spent sigmoid curving and the number of attempted forced copulations. After the 10 min observation period all fish were returned to their respective aquariums. We repeated this process for each of the 17 individual male guppies in six treatments, which were performed in random order: virgin female/control (male guppies present) (CV), virgin female/small predator (SV), virgin female/large predator (LV), non-virgin female/control (CN), non-virgin female/small predator (SN), non-virgin female/large predator (LN).

The effect of predator size and female virginity on the duration of sigmoid curving and frequency of attempted forced copulations were analyzed with t-tests (Univariate procedure; SAS Institute, 1987) on combinations of treatments to test the null hypothesis that the difference in such combinations equals zero. The treatment combinations were: (1) determining the effect of predator size by subtracting the weighted, summed values for the small predator treatments from the weighted, summed values for the large predator treatments (i.e., H_o: 0.5(LV + LN) - 0.5(SV + SN)=0; see above for abbreviations); (2) determining the effect of female receptivity by subtracting the weighted, summed values for the virgin treatments from the weighted, summed values for the non-virgin treatments (i.e., H_o: 0.33(CN + LN + SN) - 0.33(CV + LV + SV)=0); (3) determining the effect of the presence of predatory fish by subtracting the weighted, summed values for the experimental treatments from the weighted, summed values for the controls (i.e., H_o: 0.5(CV + CN) - 0.25(LV + LN + SV + SN)=0). Because we used multiple t-tests, we controlled for the experiment-wise error rate by using an alpha of 0.008 (alpha=0.05/6 tests).

RESULTS

The size of the predatory fish had no effect on the duration of sigmoid displays (t=1.70, df=15, p=0.11) or on the frequency of attempted forced copulations (t=0.84, df=15, p=0.41) (Fig. 1). Female receptivity (i.e., virgin or non-virgin females) also had no effect on the duration of sigmoid displays (t=-1.27, df=15, p=0.22) or on the frequency of attempted forced copulations (t=-1.16, df=15, p=0.26) (Fig. 1). In addition, the presence a predatory fish had no effect on the duration of sigmoid displays (t=-0.01, df=15, p=0.99) or on the frequency of attempted forced copulations (t=0.99, df=15, p=0.34).

DISCUSSION

This study shows that the captive-bred male guppies in our experiment demonstrated risk-reckless courtship behavior in that they did not decrease the amount of time they spent performing visually conspicuous sigmoid displays when either large or small predatory fish were present. These guppies were bred in captivity in large, outdoor ponds, and the stock from which these originated had not been exposed to predatory fish for approximately 25 years (S. Hennessy, personal communication). The lack of exposure to predatory fish over such a time-scale may have been sufficient to select for risk-reckless behavior. Similar time-scales have been cited for the inheritance and selection of other guppy life history traits (e.g., Luyten and Liley, 1985; Houde, 1988; Magurran and Seghers, 1990; Reznick et al., 1990). The decrease in predation pressure may have increased the courtship behavior by favoring sexual selection over natural selection (e.g., Magurran and Seghers, 1990). However, we have no data on the predation levels to which the stock from which our guppies originated had been exposed.

An additional characteristic of the male guppies in this study was their failure to distinguish between receptive (virgin) and unreceptive (non-virgin) females. A possible explanation may be that guppies with the highest courtship rates acquire the most copulations (e.g., Farr, 1980; but see Houde, 1988), regardless of whether the females are virgins or non-virgins. This behavior may be important in such a short-lived, r-selected species. At a high density of female guppies, males may be unable to determine if females are virgin or non-virgin, and it may be to their advantage to use sigmoid displays rather than attempt forced copulations. Matings resulting from forced copulations are of shorter duration than those associated with sigmoid displays, and hence may result in the formation of fewer zygotes (Endler, 1987).

Other factors may have affected the results of our study. Although we did not quantify the activities of the predators, we believe it unlikely that their behavior could have influenced our results. The small predators were fairly active and spent much time swimming after each other; however, they spent most of their time on the far end of the tank away from the divider. In contrast, the large predators spent much more time swimming near the plexiglass divider, and they even bumped aggressively into it, often causing the guppies in the adjacent chamber to dart away. Another factor that may have influenced our results is the possibility that our guppies were inbred, which could have affected their courtship behavior. However, we do not know the breeding histories of the guppy stock from which our guppies originated.

The results of our experiment using captive-bred guppies have some practical implications. Fish hatcheries commonly use breeding stock bred in captivity for several generations, and such practices have adverse effects (e.g., the fish have no fear of humans) (S. Krueger, personal communication). Effects on courtship behavior are unknown, but if fish in hatcheries are not exposed to predators for several generations, or are inbred, both they and their progeny may exhibit abnormal courtship and other behaviors. The effects on behavioral life history characteristics of using captive-bred stock in fish hatcheries should be investigated.

ACKNOWLEDGMENTS

We thank C. Thompson and I. Welsford for their constructive comments on this manuscript, and S. Juliano for his statistical advice.

LITERATURE CITED

Axelrod, H.R. and W. Vorderwinkler. 1983. Encyclopedia of tropical fishes with special emphasis on techniques of breeding. T.F.H. Publications, Hong Kong.

Breden, F. and G. Stoner 1987. Male predation risk determines female preference in the Trinidad guppy. Nature 329:831-833.

Clark, E. and L.R. Aronson. 1951. Sexual behavior in the guppy, *Lebistes reticulatus* (Peters). Zoologica 36:49-66.

Endler, J.A. 1987. Predation, light intensity, and courtship behaviour in *Poecilia reticulata* (Pisces:Poeciliidae). Anim. Behav. 35:1376-1385.

Farr, J.A. 1975. The role of predation in the evolution of social behavior of natural populations of the guppy, *Poecilia reticulata* (Pisces:Poeciliidae). Evolution 29:151-158.

Farr, J.A. 1976. Social facilitation of male sexual behavior, intrasexual competition, and sexual selection in the guppy, *Poecilia reticulata* (Pisces:Poeciliidae). Evolution 30:707-717.

Farr, J.A. 1980. The effects of sexual experience and female receptivity on courtship-rape decisions in male guppies, *Poecilia reticulata* (Pisces:Poeciliidae). Anim. Behav. 28:1195-1201.

Fraser, D.F. and F.A. Huntingford. 1980. Feeding and avoiding predation hazard: the behavioural response of the prey. Ethology 73:56-68.

Houde, A.E. 1988. The effects of female choice and male-male competition on the mating success of male guppies. Anim. Behav. 36:888-896.

Luyten, P.H., and N.R. Liley. 1985. Geographic variation in the sexual behavior of the guppy, *Poecilia reticulata* (Peters). Behaviour 95:164-179.

Magurran, A.E. and B.H. Seghers. 1990. Risk sensitive courtship in the guppy (*Poecilia reticulata*). Behaviour 112:194-201.

Reznick, D.A., Bryga, H. and J.A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature 346:357-359.

Reznick, D. and J.A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36:160-177.

SAS Institute. 1987. SAS/STAT guide for personal computers, version 6 ed. Cary, North Carolina: SAS Institute, Inc.

Schroder, J. H. 1983. The guppy (*Poecilia reticulata* Peters) as a model for evolutionary study in genetics, behavior, and ecology. Ber. nat.-med. 70:249-279.

Figure 1. Mean (+SE) duration of sigmoid displays and mean (+SE) frequency of attempted forced copulations by male guppies in each treatment. Treatments are: CN (non-virgin female/control), CV (virgin female/control), LN (non-virgin female/large predator), LV (virgin female/large predator), SN (non-virgin female/small predator), SV (virgin female/small predator).

Sorry, figure not available for this volume's on-line version. Contact library or author for reproduction of Figure 1.