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Female mate choice in a mating system dominated by male sexual coercion

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In poeciliid fishes, males can gain copulation either by courting females or through sexual coercion. In some species these two tactics coexist. However, in about half of the poeciliids, males do not display, females never cooperate during copulation and all matings are achieved by thrusting the intromittent organ toward the genital pore of apparently unaware females. In one of these species, the eastern mosquitofish (*Gambusia holbrooki*), the probability of insemination is influenced by the time females are previously deprived of males, suggesting that females exert some control over the occurrence of mating even in a system apparently dominated by sexual coercion. In the present study we investigated the tendency of female mosquitofish to approach males in relation to their reproductive status and the time they were previously deprived of males. The tendency to approach males increased in females that were previously deprived of males and in females that had recently given birth. When allowed to choose between males, male-deprived females preferred larger males and normally pigmented over melanistic males. Females preferred groups of three males over a single male, whereas the preference for three males over a group of one male and two females was only marginally significant. Collectively, these results suggest that, even when coercive mating is the only tactic adopted by males, females may be able to influence the outcome of these attempts, and thus exert some control over the paternity of their offspring. *Key words*: sexual selection, female choice, sexual coercion, *Gambusia holbrooki,* fish, mating tactics. *[Behav Ecol 12:59–64 (2001)]*

Interest in sexual selection has focused principally on two forms of interaction between and within the sexes, namely intrasexual competition for mates and intersexual mate choice (Andersson, 1994). It is increasingly recognized that, in some species, other aspects of intersexual selection, such as sexual coercion, can be equally important in shaping the mating system (Clutton-Brock and Parker, 1995). Theory predicts that conflicts of interest between the sexes are likely to arise when males can obtain coercive matings (Clutton-Brock and Parker, 1995; Parker, 1979; Trivers, 1972). Females may suffer direct costs due to unnecessary multiple mating (e.g., disease transmission, risk of predation), harassment (e.g., reduced feeding efficiency), or physical damage from forced copulation. In addition, if coercive copulation is frequent, this may limit the capacity of females to take advantage of benefits arising from mate selection. If female choice is costly and coercive matings frequent, one may expect that female choice may eventually disappear, being undermined by this male mating tactic.

Poeciliids, namely guppies and swordtails, are favorite subjects of sexual selection studies, in particular those concerning mate choice and its role in the maintenance of male secondary sex traits (Houde, 1997). Because these fishes have internal fertilization, it is important that females, after choosing a mate, cooperate with the males for transferring sperm (Hughes, 1985; Liley, 1966). Poeciliid males usually perform a sigmoid display in front of females to persuade them to mate. A receptive female responds by swimming in a tight circle, exposing her abdomen and facilitating insemination. Then the male introduces his long copulatory organ, the gonopodium (derived from the modified anal fin), into the female's genital pore (Houde, 1997). Yet, this is not the sole mechanism by which males can inseminate a female. Encountering an unreceptive female, the male can circumvent her reluctance to mate by directly inserting his gonopodium into the genital tract of the apparently unaware female. The success of any single coercive mating attempt is exceedingly low (Pilastro et al., 1997; Pilastro and Bisazza, 1999), but males compensate with high frequencies of mating attempts, approximately one per min in the species where it has been measured (Bisazza and Martin, 1995; Godin, 1995; Magurran and Seghers, 1994). Only virgin females and females that have just given birth are usually responsive to male courtship, and a male often has to compete with other males to gain access to females in this stage of their reproductive cycle (Constantz, 1975, 1984). It has been recently demonstrated that female guppies, *Poecilia reticulata,* which have been deprived of males for a long time can also be receptive to males (Pilastro and Bisazza, 1999). In comparison, males can coercively mate at any time with any female in the population. Following copulation with a gravid female, sperm migrate into folds of the ovary and the genital tract where they can survive for months and wait until a new batch of ova can be fertilized (Constantz, 1989).

In many poeciliids, the two male mating tactics coexist and are often associated with genetically determined morphological differences. Large males court females to gain matings while small males sneak copulations (Zimmerer and Kallman, 1989). Receptive females usually show a preference for males with large size, large ornaments, and high courtship activity, as in the guppy (Houde, 1997). For reasons that are not yet fully understood, in approximately half of the species, males never court, females never cooperate and coercive mating is the only way males achieve fertilization (Bisazza, 1993; Farr, 1989). It is generally believed that female mate choice plays little or no role in the mating system of these species (Bisazza and Martin, 1995; Farr, 1989; Kolluru and Joyner, 1997).

One of these species is the eastern mosquitofish, *Gambusia holbrooki.* Male mosquitofish do not court and copulations result exclusively from males forcibly inseminating females (Bis-

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azza and Martin, 1995; McPeek, 1992). Males are much smaller than females and they are particularly keen in approaching them without being detected. Though most copulatory attempts are unsuccessful, the estimated number of coercive inseminations received by a female probably exceed 0.5 per day (Giacomello, 1995; Pilastro et al., 1997). Previous studies have tended to dismiss the role of female mate choice in this species. Bisazza and Martin (1991) found no significant preference for large males by postpartum, male-deprived, or virgin females using a classical binary choice apparatus. With a similar setup, Taylor et al. (1996) found no preference for the body coloration of males (melanistic vs. normally pigmented males). McPeek (1992) reported female preference for large males in a *G. holbrooki* population from Florida (USA), but he failed to control for the natural tendency of mosquitofish to shoal (preferably with conspecifics of similar size) especially after being transferred to a novel place.

More recent studies have opened new perspectives on the role of female preference in the mating system of poeciliids. First, it has been shown that female selectivity for mates strongly depends on external factors, such as the presence of a predator, that influence her perceived risks associated with choice (Godin and Briggs, 1996). From this point of view, the experimental set up adopted in the previous studies (Bisazza and Martin, 1991; Taylor et al., 1996) may not be optimal, because females were tested soon after being introduced into a novel environment, and risks perceived by the female were not controlled for. Second, recent studies on the copulatory success of males in relation to male and female body sizes have shown that the probability that a female is coercively inseminated is positively affected by the time she has been previously deprived of males (Pilastro et al., 1997). Nonetheless, all females, irrespective of their prior male deprivation period, attempted to avoid the mating attempts of males. Observations of male–female pairs did not reveal any significant behavioral difference between short- and long-time male-deprived females, or any form of explicit cooperation between male and female.

These results suggest that females can influence the probability of success of male coercive mating attempts, even when they do not obviously cooperate with males. This may be done, for instance, by staying close to a particular male, rather than fleeing or hiding immediately when approached by him. If so, females may exert a form of mate choice by favoring (or by not disfavoring) some male phenotypes over others. The possibility that females can control, at least to some extent, the outcome of sexual coercion opens a new perspective in our understanding of the dynamics of sexual conflicts. However, it is necessary to rule out other possible, non-adaptive explanations. For example, long-time deprived females may simply be less prompt to escape males.

The objective of the present study is to determine if female mosquitofish exert some control over the coercive mating attempts of males and influence the probability of being inseminated by a particular male. First, we studied female proximity preferences in a choice apparatus designed to control for possible social effects. In particular, we tested the hypothesis that females show an increased tendency to stay close to males when deprived of males for a long time. We also compared their approaching behavior with that of postpartum females kept with males, which are inseminated by males with a frequency similar to that of long-time deprived females (Giacomello, 1995). Second, we investigated whether male-deprived females had preferences for particular types of males. Three preferences were tested: between males belonging to their population and males with a new phenotype (melanistic males), between large and small males, and between groups and single males. This last experiment was repeated using females as stimulus fish in order to distinguish social factors (e.g., a safety-in-group effect) from sexual motivation in determining apparent preferences.

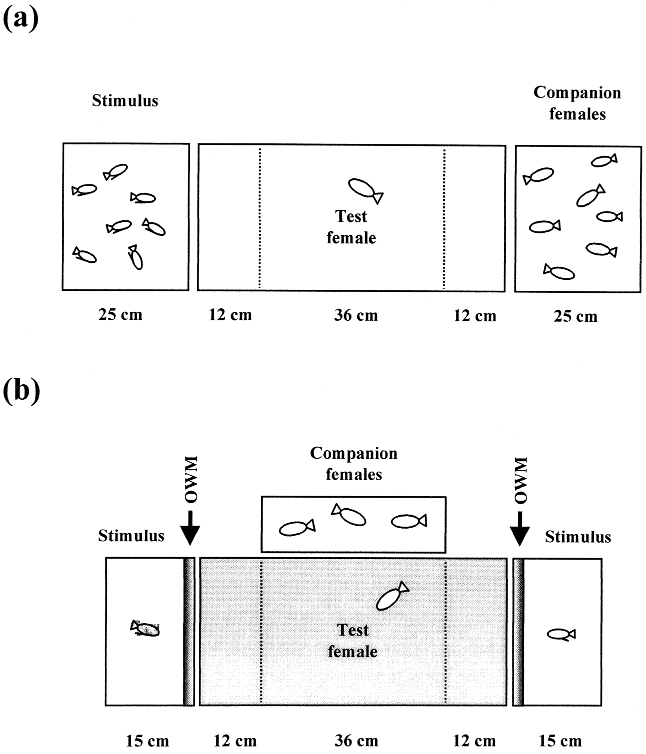

Figure 1
Choice apparatus used for testing (a) the proximity of females to males according to female breeding status, and (b) the female preference for different characteristics or number of males. Compartments were illuminated by a neon light suspended about 25 cm above the water surface (white areas in the figure) or received only indirect light laterally from the nearby illuminated compartments (grey areas), making the fish in these latter compartments able to see the fish in the well illuminated ones, but not vice versa, by means of a one-way mirror (OWM).

MATERIALS AND METHODS

Mosquitofish used in this study originated from a feral population in a stream near Padova (Idrovia Padova—Venezia, Camin), Italy. They were maintained in heterosexual groups of 20–25 individuals in 150 l aquaria (temperature: 24–26°C; photoperiod: 0500–2100 h), and fed brine shrimps and commercial food flakes (SERA GVG mix, Heinsberg, Germany).

Proximity to males in relation to female reproductive condition

In this experiment, we quantified the tendency of females to approach males according to their prior male-deprivation time and breeding status. One female was introduced into the test compartment and seven companion females in one side compartment and allowed to acclimatise for 12 h (Figure 1a). The test compartment was divided into three virtual sectors by vertical lines onto the outside front. The test female could freely swim throughout the test compartment and the observer was not visible to the experimental fish. Seven males were then introduced in the stimulus compartment at the opposite end from a lateral door that was opened remotely by the observer. In this experiment, companion females, stimulus males, and the test female could see each other. Stimulus fish as well as companion females were chosen without a known bias from a large stock aquarium. It is therefore possible that the same stimulus fish has been used more than once. Companion females and stimulus males were placed, alternatively, on the left and right side of the choice apparatus.

Three groups of females were tested: (1) non-deprived females ($n = 12$), which had been kept in aquaria with males at a 1:1 sex ratio for at least 2 months; (2) long time male-deprived females ($n = 12$), which had been kept in aquaria with only females for at least 2 months before being tested; and (3) postpartum females ($n = 10$), which had been previously kept with males and tested within 3 days after parturition. Two observation periods were carried out: before releasing the males into the stimulus compartment, the test female was observed for three bouts of 10 min, each separated by 20 min (pre-test). After a pause of 20 min, the males were then released into the stimulus compartment and the test female was observed for 30 min. During observations, we recorded every 15 s whether the test female was within 12 cm from the males' compartment. To control for possible side preferences, we used as a variable the difference between the times the test female was observed in the sector near the males' compartment before and after their introduction in the statistical analyses.

In order to exclude the possibility that male-deprived females approached the stimulus males just because they were attracted by the appearance of a novel group of fish (i.e., to discriminate between exploratory and sexual motivation), we carried out another 24 control replicates (12 with 2 months male-deprived female and 12 with non-deprived females) using seven females instead of the males. Proximity to the stimulus females' compartment was calculated as above.

Mate choice in male-deprived females

The following experiments were designed to quantify the female choice between two stimulus fish presented simultaneously to her. Female mosquitofish are gregarious. To make the test female perceive the aquarium as a safe environment, we used a choice apparatus wherein three companion females were always visible to the test female, in the rear of the test compartment (Figure 1b). By means of one-way mirrors and differential illumination, stimulus males were prevented from seeing test and companion females. Stimulus males were simultaneously presented to the test female on either side of the test compartment, by allowing them to enter the stimulus compartment through a door opened remotely by the observer.

All the test females used in this and the subsequent experiments were deprived of males for at least 2 months. We used male-deprived females because they showed a similar proximity preference for males to that of postpartum females (see results below), and are more easily obtained in the lab. Prior to testing, stimulus males were kept for some days in aquaria with a one-way mirror on one side to acclimatize them with their reflected image. Test females were introduced into the test compartment about 24 h before being tested. Twenty min before the test began, males were introduced into the end compartments and the test female was subsequently observed for 40 min. The position of the test female was registered every 15 s, and her preference was expressed as percentage of the time spent in the 12 cm sector near either male compartment out of the total time spent in sectors near both male compartments (Figure 1b).

To test preference for males of different body coloration, females were allowed to choose between three normally pigmented males and three melanistic males, belonging to a stock of melanistic eastern mosquitofish originally from Florida (USA) and maintained in our laboratory. We carried out 20 replicates with different fish. The size of the males ranged between 22 and 27 mm, SL. Within each replicate, males in the melanistic group were size-matched (± 0.5 mm) to the males in the wild type group. The two phenotypes were presented alternatively on the right and the left stimulus compartment. To test female preference for male size, three large (range: 27–29 mm) and three small males (range: 19–20 mm SL) were simultaneously presented to the female ($n = 12$). The stimulus males used in this and the following experiments were all normally pigmented. To study preference between different numbers of males, we allowed females to choose between a single male and a group of three males. Overall, the size of the males used ranged between 25 and 29 mm, but all males were of similar size (difference ± 0.5 mm SL, $n = 10$) within replicate.

Additional experiments were carried out to investigate the causes of preference for groups of males. For these experiments we used the same apparatus (Figure 1b), but we adopted a slightly different procedure that allowed us to reduce the duration of each replicate. In particular, the test females were introduced into the test compartment to acclimatize for 1 h before being tested. Then, stimulus fish were introduced into the two end compartments and the position of the females was recorded, every 15 s, for 30 min. Female preference was expressed as described before. We used three experimental arrangements: (1) a single male vs. a group of three males ($n = 12$); (2) a group of three males vs. a group of one male and two females ($n = 12$), and (3) one single male vs. a group of one male and two females ($n = 12$). The first experimental setup (one male vs. three males) was the same as in the previous experiment and was repeated in order to control that the shorter acclimation time did not affect the direction of the female preference. In the mixed stimulus groups containing one male and two females, the females were always larger than the male. Overall, all males had similar size within replicates, ranging between 26 and 28 mm, and differing less than 1 mm.

Where not otherwise stated, means ± SD are presented. Data from all the experiments were tested for deviance from normality (all experiments, Kolmogorov-Smirnov one sample test) and for the homogeneity of variance (first experiment, Levene test). Since these assumptions were met in all cases ($p > .05$), we used parametric tests (one-sample t test and one-way ANOVA). Post-hoc comparison was done using Ryan's Q test (Day and Quinn, 1989). All probabilities are two-tailed. Statistical test were performed using SPSS 8.0.

Results

Proximity to males in relation to female reproductive condition

Male-deprived and postpartum females did not differ from each other in the time spent close to the males' compartment and both differed significantly from non-deprived females (one-way ANOVA, $F_{2,31} = 4.815$, $p = .015$; Ryan's Q post-hoc comparison, $p < .05$; Figure 2). When females, instead of males, were presented to the test female, we found no significant difference between deprived (X ± SD = 35.2 ± 7.1) and non-deprived females (X ± SD = 42.9 ± 8.7) in the time they spent near the stimulus females ($t_{22} = 0.69$, NS).

Mate preferences in male-deprived females

When presented to paired melanistic and wild-type males, females spent significantly more time near wild-type males than expected by chance (one-sample t test, $t_{19} = 2.43$, $p = .025$, Figure 3a). When females were allowed to choose between large and small males, they spent significantly more time near the group of large males (one-sample t test: $t_{11} = 2.59$, $p = .025$, Figure 3b). Females that were presented to a single male and a group of three males, preferred the larger group over

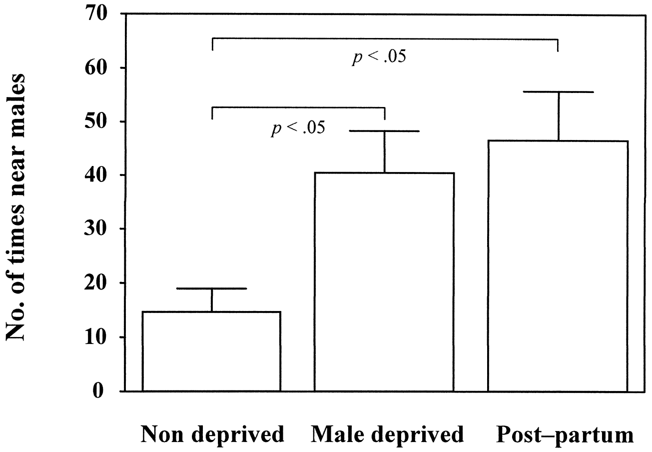

Figure 2
Proximity to males in relation to female breeding condition (non-deprived = mid-cycle females previously kept with males; male-deprived = mid-cycle females deprived of males for 2 months; postpartum = females tested 2–3 days after parturition and previously kept with males). Proximity to males is expressed as the mean (± SE) number of times the test female was observed in the 12-cm sector near the stimulus compartment after the males were introduced, minus the times she was in the same sector before males' introduction.

the single male (one-sample *t* test: $t_9 = 2.51$, $p = .033$, Figure 3c).

In the corollary experiment with the shorter acclimation time, females confirmed their preference for a group of three males over a single male ($t_{11} = 2.21$, $p = .049$; Figure 4a). The preference for trios of males was confirmed also in the second experiment of this series, where test females preferred trios of males over trios composed by one male and two females ($t_{11} = 2.60$, $p = .025$, Figure 4b). In the third experiment (Figure 4c), test females spent more time near the compartment containing two females and one male than near that containing only one male, although the difference was marginally nonsignificant (one-sample *t* test, $t_{11} = 2.08$, $p = .06$). This result was strongly influenced by a single female that spent all her time near the single male compartment. The other 11 females spent 69.7% (± 11.9 SD, range 53–94%) of their time near the compartment containing the group of one male and two females.

DISCUSSION

In those species in which males provide nothing but sperm, a female's reproductive success is unlikely to increase with the number of males she mates with, since each copulation involves several potential costs, for example, transmission of diseases, visibility to predators, or reduction of foraging efficiency (but see Zeh and Zeh, 1997, for possible advantages of multiple inseminations). Consequently, the best strategy for females in such a mating system is usually to mate with the highest quality available partner(s) a minimum number of times that will ensure the fertilization of all her eggs and then to refuse further copulations. Coercive mating is believed to evolve in males to obtain copulations when they are not chosen by females, and resistance in females is seen as the attempt to avoid the costs associated with unnecessary copulations (Clutton-Brock and Parker, 1995).

In practical terms, however, it is not always simple to distinguish female effort to avoid unwanted copulation from mate assessment, since the female can selectively resist copulatory attempts in order to select the most vigorous or most persistent males, which are able to overcome their resistance (Allen and Simmons, 1996; Arnqvist, 1992; Thornhill, 1980). Some of these studies also showed that the different mechanisms of sexual selection can be so tightly intermingled that it can be very difficult, and sometimes impossible, to clearly separate them into well defined female choice, male competition and coercive mating.

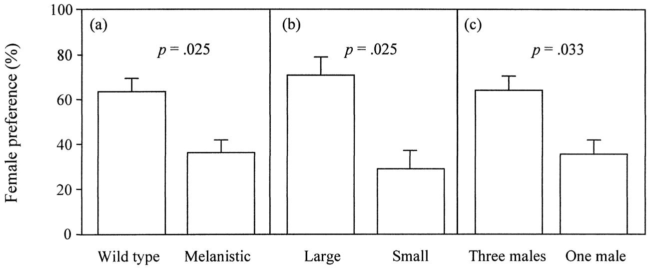

Figure 3
Mean (± SE) percentage of the time spent by the test female near each of the two end compartments containing males differing in: (a) body coloration, (b) body size, and (c) number.

Mechanisms of sexual selection in the eastern mosquitofish, especially those acting on body size, have been described previously (Bisazza et al., 1989, 1996; Bisazza and Martin, 1991, 1995; Bisazza and Pilastro, 1997). In brief, small males had a strong advantage in coercive copulation because they are less conspicuous when approaching the female from behind and maneuver better when inserting the gonopodium. Male size relative to female size explains nearly 77% of the variance of sneaking mating success. Males showed a preference for large females or for those that recently delivered young. Large males tended to be dominant and to outcompete small ones for access to these high-quality females, especially at high population densities and male-biased sex ratios. To simulate the effect of sexual selection, Bisazza and Martin (1995) ran a computer simulation using behavioral and demographic data from a wild population. The analysis suggested that a small male mating advantage is expected to occur for 4/5 of the breeding season in the population considered. As females never cooperate with males during copulation, the above study credits only a marginal role to female choice—females may under some circumstances indirectly favor dominant males as mates (Bisazza and Martin, 1991; McPeek, 1992). The results of the present study, however, suggest that the picture may be more complex than previously thought.

The first part of this study shows that, when deprived of males for a long time (and probably under the risk of depleting their sperm stores) or close to the fertilization of a

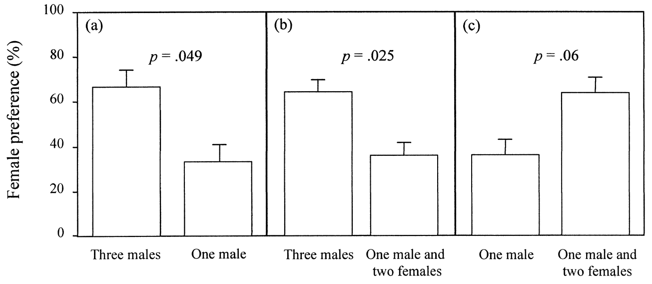

Figure 4
Mean (± SE) percentage of the time spent by the test female near each of the two end compartments containing groups of fish differing in: (a) number of males, (b) sex ratio, and (c) number of females.

new batch of ova, female mosquitofish show a clear tendency to approach males. The increased insemination frequency in male-deprived females observed in a previous study (Pilastro et al., 1997) may be simply explained by females progressively losing their ability to escape coercive mating, for example by being less trained in burst swimming or in detecting approaching males. In this study, however, the behavior of deprived females was indiscernible from that of postpartum females kept with males until a few min before being tested, thus suggesting that females seek the proximity of males when sperm obtained by copulation is likely to be used briefly after in next reproductive bout.

This interpretation also emerges from studies investigating the lateralization of the central nervous system. Male mosquitofish that are required to circumvent a barrier in order to reach females, tend to turn around the barrier on the left and thereby observe the females with the right eye. This preference disappears when there are males or no fish beyond the barrier. The turning direction depends on motivational state, because males that are not sexually motivated do not show such tendency (Bisazza et al., 1997). In another study, females were tested using males as targets: They turned more frequently to the left to circumvent the barrier after 2 months of deprivation, but not if deprived only for 3 weeks or kept with males (Bisazza et al., 1998). This suggests an increased sexual motivation of females that are deprived of males for a long time.

In the second part of the current study, we demonstrated that approaches to males were not random. Females choose to approach large males more often than small ones, wild type more often than melanistic males, and group of males more often than single individuals. Do these preferences result in a real mating advantage for males whose characteristics match females' choice criteria? Mating success of males was not measured in this study. Nonetheless, possible indications can be derived extrapolating from the results of previous studies (Giacomello, 1995; Pilastri et al., 1997). In particular, it has been shown that males kept with unreceptive females for 48 h were able to inseminate about 90% of females that were previously male-deprived for 2 months. When female deprivation time was shorter (15–30 days), insemination frequency dropped to 35%. These results suggest that, even if all females tried to avoid male coercive copulation attempts, variation in male insemination success is likely to be influenced by female behavior. Females' proximity preference may have an important influence on the mating success of males with different phenotypes. A conclusive support to this hypothesis could be obtained only through field experiments and paternity tests.

An exhaustive analysis of the selective advantages of mate preferences shown by female mosquitofish is beyond the scope of this study. Female preferences for larger males in particular appear widespread in various taxa (Andersson, 1994) and has been reported for other poeciliid fishes (Hughes, 1985; Ptacek and Travis, 1997; Reynolds and Gross, 1992; Ryan and Wagner, 1987).

The presence of melanistic males, in spite of their reduced crypsis, has raised the question of whether color polymorphism in mosquitofish populations can be maintained through female mate choice. Previous studies on mosquitofish have generally failed to show female preferences for particular male color morphs or to clearly distinguish female mate choice from male competition or shoaling behavior (Karplus and Algom, 1996; Martin, 1977; Nelson and Planes, 1993; Taylor et al., 1996). In the current study, females spent more time near normally pigmented males. Females may be avoiding the more conspicuous melanistic morph because the latter may attract predators more readily, as is the case for female guppies from populations with high predation pressure, which tend to avoid brightly colored males because they attract more predators and expose them to a greater risk (Breden and Stoner, 1987; Pocklington and Dill, 1995).

When given a choice, females prefer the vicinity of a group of males to a single male. This experiment did not clarify if the preference served to promote competition among rival males or to ensure a safer condition during mating. Both aerial and aquatic predators of poeciliids prefer to catch females (Pocklington and Dill, 1995; Trexler et al., 1995); therefore, a "safety in group" hypothesis would predict that females would prefer groups containing more females. An additional experiment on group size indicated that females look for groups containing more males rather than simply looking for groups of fish, although the preference in this case was less pronounced.

One may wonder, then, why mosquitofish females do not simply cooperate directly with males, as some other poeciliid species do, with overt female choice and male courting behavior, since the latter strategy is likely to be more efficient in determining the paternity of the offspring and probably is not associated with much greater costs. One reason may simply be that females adopt a strategy of indirect mate choice (Wiley and Poston, 1996) when they cannot avoid sneaky inseminations by males. By using the selective approach to males outlined in this study (i.e., discriminating between different male phenotypes), females may ensure for their offspring both preferred characteristics (e.g., a large body size) and the ability to obtain sneaky copulations. Benefits associated with one phenotype may be extremely variable. For instance, at the beginning of the breeding season, when population density is low and sex ratio is female biased, groups are small and composed largely of females and sneaking efficiency is probably the best predictor of male mating success (Bisazza and Martin, 1995). In contrast, at the end of the breeding season, population density is higher (Zulian et al., 1995), many males compete for females and a large body size increases the chances for a male to obtain mates. At the time of insemination, probably females cannot predict what situation their male offspring will face at maturity, and both large size and sneaking ability are likely to increase the future reproductive success of their male offspring.

In addition, in order to have a high probability of inseminating females, sneakers must perform about one mating attempt per min throughout the day, and only vigorous males in optimal conditions can probably afford such a task (Blanckenhorn et al., 1995). Sneaking copulation through gonopodial thrusting requires a highly precise coordination of sensory and motor organs and a rapidity of execution certainly similar, if not greater, to that necessary for a male performing an elaborate courting display. A female who stays close to males, but does not allow them to easily inseminate her, adopts a mate selection strategy that is different from that of typically receptive females choosing between displaying males. Nonetheless, this strategy may confer to females the same advantages, immediate and future, that have been proposed to explain the evolution of the overt mate choice, such as access to parasite-free males with high foraging and metabolic efficiency, and a high mating success of the offspring (Andersson, 1994). Given that the success of sneaky mating attempts increases exponentially with decreasing size of the male (Bisazza and Martin, 1995), females that stay close to large males (or to group of males) may be indeed selecting males with a higher-than-average sneaky copulation ability, and not simply selecting the smallest males in the population.

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