

Female mate-choice copying in guppies, *Poecilia reticulata*: a re-evaluation

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Abstract. It has been argued that intraspecific mate-choice copying can be adaptive under certain conditions. Dugatkin's (1992, *Am. Nat.*, **139**, 1384–1389) work with guppies, *Poecilia reticulata*, remains the most influential experimental demonstration of this phenomenon. We replicated Dugatkin's work using several choice criteria to ensure that our results were not dependent upon any single method of judging mate choice. We also tested our findings against two null hypotheses of differing stringency. Irrespective of the choice criteria or null hypothesis used, we did not observe any relationship between female mate choice and copying. We conclude that further experimental evidence of female mate-choice copying is required before the existence of this behaviour can be affirmed.

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The two main components of sexual selection are competition between members of the same sex for mating opportunities (intra-sexual selection) and mate preferences for certain traits in members of the opposite sex (epigamic selection; Darwin 1871). In intra-sexual selection, interactions between individuals of one sex are an integral part of the process. In contrast, until very recently, it has been assumed that females always choose mates independently from each other. Recent developments indicate that this assumption may not always be true.

Mate-choice copying occurs if the mate selection by one female, and not the consequences of this choice, affects the mate selection of another female (Pruett-Jones 1992). Recent theoretical models have suggested that mate-choice copying may be an adaptive strategy when there is a cost to choice involving direct assessment, and/or when certain individuals are better judges of mate quality (Losey et al. 1986; Gibson & Höglund 1992; Pruett-Jones 1992; Dugatkin & Höglund 1995). Correlational evidence suggestive of mate-choice copying has been found in two species of lekking grouse (Höglund et al. 1990, 1995; Gibson et al.

1991), some species of fish (Ridley & Rechten 1981; Marconato & Bisazza 1986; Goldschmidt et al. 1993) and one marine isopod, *Paracerceis sculpta* (Shuster & Wade 1991). None of these studies, however, has isolated mate-choice copying from all alternative explanations. So far, only one controlled experimental study has shown intraspecific mate-choice copying (Dugatkin 1992; see Schlupp et al. 1994 for an example of inter-specific mate-choice copying).

Dugatkin performed a series of experiments using female guppies from the Turure River, Trinidad. In these experiments, a confined female (the 'focal' female) was allowed to observe two males, one of which was in the company of another female (the 'model' female). The model female was then removed and the focal female was released and allowed to move freely. In significantly more trials, the focal female spent more time closer to the male that had been with the model female, even when the location of the males was reversed following the 'observation' period. In further experiments, Dugatkin (1992) did not find evidence for alternative explanations, such as the tendency by females to aggregate and female preferences based on changes in male behaviour. Subsequent studies have indicated that the tendency to copy is strong enough to reverse previous mating choices (Dugatkin & Godin 1992), and that females copy larger females, but do not copy smaller ones (Dugatkin & Godin 1993).

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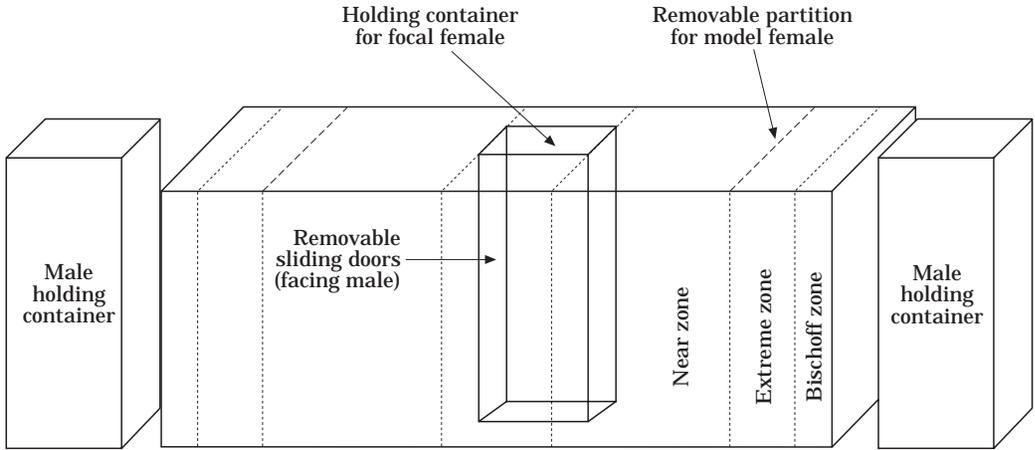


Figure 1. Schematic representation and dimensions of the testing apparatus.

We report our attempt to replicate Dugatkin's (1992) experiment. We initially conducted preliminary trials as described by Dugatkin (1992). During these trials, it became apparent that several procedural problems could affect the results. Therefore, we modified the testing apparatus and procedures slightly to reduce these potential problems. Our modifications addressed two main concerns: the way the fish were kept and handled before and during the experiment, and the way in which female preference was determined and analysed.

METHODS

The experiment was conducted as described by Dugatkin (1992) except for the following modifications. (1) The sample size was increased by 20% to 24. (2) Potential experimenter effects were reduced by recording the trials on videotape and by using a remote release mechanism, which also decreased handling of the fish. (3) Females were isolated from males for 18 days before the trials to ensure that they were not gravid. Finally, (4) several choice zones, described below, were used in the analysis.

Apparatus

The apparatus consisted of a 6-litre aquarium (30 × 14 × 20 cm high), two clear Plexiglas chambers (14 × 5 × 20 cm high) placed at opposite ends of the aquarium, and one smaller clear Plexiglas

chamber (6 × 5 × 20 cm high) fixed in the centre of the aquarium (Fig. 1). This aquarium was smaller than that used by Dugatkin (10 litres; dimensions not available), but this difference in size is unlikely to reduce mate-choice copying by females. The aquarium was divided into three compartments by two transparent, removable, Plexiglas partitions placed 6.5 cm from each end. To allow water flow between compartments, several small perforations were made in these partitions and in the sides of the central chamber. A 100-W incandescent light bulb, placed 1 m above the central aquarium, was used for illumination. White paper was placed on the back of the aquarium, and on the back and distal side of each Plexiglas end chamber. A video camera placed 1.5 m in front of the apparatus was used to record choice tests. The video camera was linked to a television monitor located out of direct view of the experimental tank. Water in all aquaria and Plexiglas chambers was aerated and maintained at 26°C.

Dugatkin (1992) confined the focal female within a clear Plexiglas canister (5 cm diameter) in the centre of the aquarium. She remained there during the acclimation and observation periods, and then was poured into the aquarium at the start of the choice trial. To reduce potential directional bias and additional handling caused by this pouring procedure, the canister used by Dugatkin was replaced in our study with a clear Plexiglas holding container (6 × 5 × 20 cm high) fixed in the centre of the tank. The container had two removable doors on the sides facing the end chambers. These removable doors could be lifted

remotely by means of a string leading to an adjacent cubicle, out of view of the experimental arena.

Time spent closer to one of two males in choice tests reflects a mating preference of the female for that male (Bischoff et al. 1985). To evaluate female preference, the aquarium was divided into several choice zones (Fig. 1), which allowed comparisons with previous experiments and ensured that the findings were not dependent on an arbitrary choice of zone limits. The first set of zones, called the 'half-and-half' zones, were the two halves of the aquarium, to either side of the centre line, as used by Dugatkin (1992). This division did not include a neutral zone and therefore reflects an assumption that the female was constantly choosing to be closer to one male than the other, even to a slight degree. A second set of zones, called the 'near' zones (Dugatkin & Godin 1992) excluded the 5-cm wide area in the centre of the tank that housed the holding container. This set of zones was based on an assumption of active mate-choice by the female at all times, except when she returned to the area near the holding container. The third set of zones, called 'extreme' zones, consisted of the 6.5-cm areas at the ends of the aquarium. The model female was enclosed in one of these areas. The final set, called 'Bischoff' zones (Bischoff et al. 1985), consisted of the areas 2.5 cm from each end of the aquarium. The preferred male was the one beside the Bischoff zone in which the focal female first spent 15 consecutive seconds. This specific estimate of female mate preference correlates well to subsequent choice of copulation partners in guppies (Bischoff et al. 1985).

Experimental Subjects

Wild-type guppies were obtained from local retail outlets and were descended from unknown, probably varied source populations. Guppies obtained from retail outlets have been used in female mate-preference tests (Farr 1977; Kodric-Brown 1985). Prior to the trials the fish were maintained in aerated aquaria at 26°C on a 12:12 h light:dark photoperiod, and were fed Tetramin flake food daily.

The sexual dimorphism of guppies is extreme: males display bright multicoloured patterns, and females are larger than males and drab. Fertilization is internal and females give birth to live

young. Males attempt to obtain copulations by courting females or by sneak copulations (Liley 1966). Owing to the relatively low success of sneak copulations (Liley 1966), female cooperation is important to successful insemination (Baerends et al. 1955). Living in mixed-sex shoals, females can observe and copy the choices of other females.

Females were obtained from mixed sex stock tanks so they were probably non-virgins. Because gravid females are not sexually receptive (Liley 1966), only non-gravid females were used (as in Dugatkin 1992). To ensure that they were not gravid, females were kept in isolation from males for at least 18 days before being tested. This corresponds to the period of embryonic development at 26°C (Liley 1966) and exceeds the 10-day minimum isolation period used by Bischoff et al. (1985). Bischoff et al. found that females not showing visible signs of pregnancy after 10 days of isolation did not subsequently have offspring if maintained in isolation. After this isolation period, females were also inspected for abdominal swelling that would indicate gravidity (Dugatkin 1992). Males born to the females in the isolation tank were removed when they began to develop secondary sexual coloration, which coincides with their sexual maturation (Houde 1992). All females used exceeded 15 mm total body length, which is the best indicator of sexual maturity (Houde 1987). The sexual receptivity of non-gravid, non-virgin females fluctuates substantially within the 21-day brood cycle (Liley 1966; Houde 1987), but such females are still suitable subjects for mate-choice experiments (see Bischoff et al. 1985; Luyten & Liley 1991; Dugatkin 1992).

Only sexually mature males with fully developed secondary coloration were used in these experiments.

Development of the Null Hypothesis

In controlled female mate-choice experiments, the receptive behaviour of females is sometimes used as the criterion of mate-choice (e.g. Ligon & Zwartjes 1995; Mateos & Carranza 1995), but often the criterion used to establish female preference is the proximity to, or time spent with, a male (e.g. Dugatkin 1992; Houtman & Falls 1994; Collins 1995). In the latter case, results are then compared against the null hypothesis of equal time with all males. This null hypothesis may be too liberal, however, because, even in the absence

of males, females moving about randomly may spend more time at one end of the apparatus. Therefore, we developed an empirically derived null hypothesis, based on quantification of female movements within the choice arena in the absence of males.

In each of 24 trials a female was picked from the stock tank and placed in the holding container. The female was left in the holding container for 10 min to acclimate. Following this acclimation period, a dip-net was swept through one of the end compartments in the aquarium to simulate the removal of the 'model' female in the subsequent experiment. The end of the aquarium that was swept was alternated between each trial. The end partitions were then gently raised out of the aquarium and video recording was started. After removal of the end partitions, both doors of the holding container were slowly lifted simultaneously. Each 10-min trial began when the focal female vacated the holding container. At the end of the trial, the female was transferred to a new holding tank. Each female was used only once.

Replication of Dugatkin's Experiment

Opaque barriers were placed between the choice tank and the two end chambers before each trial (Fig. 1). Two males were selected from all available males, matched for total body length (within 5%), tail length (within 1 mm), overall brightness, and area of carotenoid (red, orange and yellow) and structural (blue-green, white and iridescent) pigments (Dugatkin 1992). One male was placed in each of the end chambers. Two females, matched for total body length (within 5%) were also selected. One female (the model) was placed into one end compartment and the other (the focal female) was placed into the holding container. Placement of the model female on the left or right end of the aquarium was alternated between trials. Each fish was used only once in this experiment.

The fish were allowed to acclimate for 10 min. Subsequently, the opaque barriers were removed. During the next 10 min the focal female observed a single male at one end of the set-up, and a male and female at the other end. The model female was then removed with a dip net and the end partitions were gently removed. Video recording was started and both doors of the holding container were slowly lifted simultaneously. The female's movements within the aquarium were

recorded for 10 min after she left the holding container.

Analysis

First, the results were tested against the null hypothesis of equal time spent with each male. However, this null hypothesis does not take into account that, even in the absence of males, females may not divide their time equally between the two sides of the apparatus. Therefore, if a significant effect of model female position was found, the results were then analysed against the empirically derived values based on female movements in the absence of males. Tests were conducted using *G* and paired *t*-tests (Zar 1984). The *G*-test is preferable to the chi-square test when the absolute difference between the observed and expected frequencies is less than the expected frequency for any of the categories used in the analysis (Williams 1976).

Equal time with both males as the null hypothesis

Dugatkin (1992) and Dugatkin & Godin (1992, 1993) considered the focal female to have copied if she spent more time on the side on which the model had been than on the other side. Following Dugatkin (1992), four *G*-tests were performed, one for each set of choice zones. In addition, preference was assessed using paired *t*-tests on the difference between the time spent on the model's side and the time spent at the other side. Both tests were also conducted to test for preferences for either side of the apparatus.

Female movements in the absence of males as the null hypothesis

The appropriate null hypothesis was determined by examining female movements within the choice arena in the absence of males. First, the effects of the dip-net sweep on female movements were tested. For each of the four choice zones, *G*-tests and paired *t*-tests were performed to evaluate the side ('swept' or 'not swept') in which females spent more time. These analyses were repeated to test for side preferences.

RESULTS

In the absence of males, the number of trials in which the female spent more time on the swept

Table I. The effect of dip-net sweep on the movements of females in the mate-choice apparatus, in the absence of males as stimuli

Choice zone	Frequency swept side	G^*	P	Mean difference (s)	t_{23}^\dagger	P
Half	9	1.52	>0.10	94	1.523	0.141
Near	9	1.52	>0.10	95	1.534	0.139
Extreme	10	0.67	>0.10	91	1.554	0.134
Bischoff	9	1.52	>0.10	—	—	—

Four choice zones were used.

* G -tests were conducted on the number of females that spent more time on the swept side than the other side.

†Paired t -test comparing the time spent by each female on the swept side to the time spent on the other side.

Table II. Side preferences by female guppies in the absence of males as stimuli

Choice zone	Frequency left side	G^*	P	Mean difference (s)	t_{23}^\dagger	P
Half	10	0.67	>0.10	76	1.22	0.235
Near	10	0.67	>0.10	83	1.32	0.200
Extreme	9	1.52	>0.10	86	1.48	0.154
Bischoff	12	0.00	1.000	—	—	—

* G -tests were conducted on the number of females that spent more time on the left side than the right side.

†Paired t -test comparing the time spent by each female on the left side to the time spent on the right side.

side was not significantly different from the number of trials in which she spent more time on the other side (Table I). The conclusion was the same when compared in terms of the number of trials in which either side was chosen by the Bischoff criterion (Table I). No preference for either side was observed when compared in terms of time spent (Table I). Similarly, in the absence of males, there was no significant preference for either side of the apparatus, either in terms of the side in which more time was spent, the Bischoff criterion, or the actual amount of time spent on either side (Table II).

Females did not copy the mate choices of each other, either when preference was compared in terms of number of trials in which more time was spent with one male, or when a comparison was made of differences in time spent with the two males. Neither the different choice zones, nor the use of the Bischoff criterion, affected these

conclusions (Table III). The mean \pm SE time spent close to the model-side male was variable (half-and-half: 317 ± 37 s; near: 304 ± 38 ; extreme: 264 ± 39 s). Also, we found no bias in the side of the apparatus on which the female spent more time, or in the amount of time spent on either side of the apparatus, regardless of the choice zone or statistical test used (Table IV).

DISCUSSION

No evidence of mate-choice copying by female guppies was observed in this study. This conclusion remained the same regardless of the choice zone used. We failed to find mate-choice copying even when testing the results against the less rigorous null hypothesis, that of equal time at both sides. Such a null hypothesis may not be adequate in mate-choice studies, because a female

Table III. Mate-choice copying by female guppies

Choice zone	Number 'copying'	G^*	P	Mean difference (s)	t_{23}^\dagger	P
Half	12	0	1.000	35	0.464	0.647
Near	12	0	1.000	36	0.489	0.629
Extreme	12	0	1.000	53	0.763	0.453
Bischoff	11	0.168	>0.50	—	—	—

* G -tests were conducted on the number of females that spent more time on the model's side than the other side.

† Paired t -test comparing the time spent by each female on the model's side to the time spent on the other side.

Table IV. Tests for side biases in the mate-choice copying experiment. All tests are as in Table II

Choice zone	Frequency left side	G	P	Mean difference (s)	t_{23}	P
Half	13	0.168	>0.50	85	1.17	0.256
Near	13	0.168	>0.50	83	1.14	0.268
Extreme	13	0.168	>0.50	83	1.14	0.268
Bischoff	10	0.670	>0.10	—	—	—

is unlikely to spend equal time on each side of the enclosure, even in the absence of males. Therefore, clear preferences can be concluded only if the time a female spends near a male is greater than the time spent on any one side in the absence of males.

We see no reason why mate-choice copying would occur only in fish derived from the Turure River, Trinidad (Dugatkin 1992), given that all guppies live in conditions under which mate-choice copying would be theoretically advantageous. Population differences have been documented in mate preferences (Endler 1983; Breden & Stoner 1987; Houde 1988; Houde & Endler 1990; Reynolds et al. 1993) and other behavioural features (Magurran et al. 1995). Therefore, it is difficult to speculate how widespread mate-choice copying is among guppies.

Dugatkin (1992) carried out a series of experiments, subsequent to the mate-choice copying experiment, in which he investigated alternative explanations for his results. The results of these experiments failed to support alternative explanations. Dugatkin interpreted these results as support for his conclusion that mate-choice copying

had occurred in the first experiment. In one of these experiments, no evidence of copying was observed when the model female and the adjacent male were prevented from interacting visually. However, the failure to find mate-choice copying in this experiment can also be viewed as evidence that mate-choice copying did not occur in the first experiment, but rather that focal females chose males that courted more intensively during the observation period. The result of this experiment failed to provide support for a related, but not necessarily alternative, explanation.

To date, most laboratory-based experiments on female mate-choice copying have failed to measure or account for differences in male courtship (but see Grant & Green 1996). Courtship displays in guppies vary in duration, general activity level, distance from the female, degree of curvature of the sigmoidal displays and the frequency of the displays (Liley 1966; Farr 1976). This high variability made it difficult to quantify courtship rates reliably, as we had first intended. Had we found evidence of mate-choice copying, we would have been unable to eliminate changes in male courtship as an alternative explanation.

There may have been some important procedural differences between our study and Dugatkin's (1992). We kept females isolated from males for at least 18 days before the trials in an attempt to reduce possible effects of preference due to prior association (Dugatkin & Alfieri 1991; Magurran et al. 1994). We also recorded the trials using a remotely controlled video camera, which allowed us to remain outside the view of the experimental arena during the trials, and thus eliminated the potential effect of the observers' movements on the behaviour of the fish. No details are provided by Dugatkin (1992) on how his fish were kept or how female movements were scored, so it is difficult to make comparisons.

A clear difference between our study and Dugatkin's is the way in which the focal female was handled. After 10 min of acclimation and 10 min of observation, Dugatkin (1992) released the focal female 'by gently pouring the water from the canister into the centre of the aquarium (this procedure did not seem to disturb the fish)' (page 1385, his parentheses). We reduced potential handling effects by using a fixed central chamber with remotely removable side doors.

One problem common to many laboratory-based mate-choice experiments is the use of a two-way choice apparatus. An alternative approach is to use a three-way choice apparatus but only two males, whereby a female can 'choose' (i.e. spend more time near) one of the two males or an empty holding area (e.g. Houtman & Falls 1994). Had we found evidence of mate-choice copying, we were planning to expand this procedure to a multi-way choice apparatus, in which we would have tested all of Dugatkin's (1992) alternative explanations simultaneously.

It is important to replicate experiments that offer novel insights to verify results, obtain new perspectives and alternative explanations, and establish the extent to which findings can be generalized. Given our failure to replicate his work, Dugatkin (1992) remains for now the only experimental study that suggests the occurrence of intraspecific mate-choice copying. More evidence of mate-choice copying is needed before we venture further in the development of models that incorporate genetic and cultural effects on the evolution of female mate-choice. Although we have raised several alternative explanations for Dugatkin's findings, the possibility remains that mate-choice copying occurs only in some popula-

tions. If this is the case, then our task is clear yet daunting, for neither do we have a way of predicting when mate-choice copying should occur, nor do we know the pervasiveness of this behaviour, two issues that must be settled if we are to understand the role of mate-choice copying in sexual selection.

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