

# Size-Dependent Female Mate Copying in the Guppy (*Poecilia reticulata*): Large Females are Role Models but Small Ones are not

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## Abstract

Previous work on guppies has shown that small females copy the mate-choice decisions of larger females, but not vice versa. We extended this work to ask, when put in a situation where they have little information available to distinguish between males, whether large females will also copy large females, and small females will copy small ones. Using Dugatkin's criteria, our study suggests that large females copy the mate-choice decisions of large females, that small females might copy the decisions of large females, but that neither small nor large females copy small females. Our results provide support for the notion that females are more likely to copy when they perceive that there is an imbalance between their ability to assess a male's quality and the ability of another female to assess that male. However, we did not find evidence of mate copying using criteria used by other researchers.

## Introduction

Female mate-choice preferences were generally assumed to be independent of the preferences of conspecifics. Recently, however, a number of studies have suggested that one form of non-independent mate choice, referred to as mate copying, does occur in a variety of species including fish and birds (e.g. Gibson et al. 1991; Dugatkin 1992; Galef & White 2000; Witte & Ryan 2002). Mate copying is defined as mate choice in which the probability that a female chooses a given male increases if other females have chosen that male and decreases if they have not (Pruett-Jones 1992). This definition separates copying behaviour from other processes because the probability of choice is a direct result of the actions of the other females, and is not the indirect consequence of those actions; for example, if, after a successful copulation, a male displays more vigorously and thus becomes more attractive to females, the increased probability that a female will mate with him is not due to mate-choice copying (Pruett-Jones 1992). Several models of mate-choice copying have suggested

that female copying can be adaptive in some circumstances, depending on the ratio of the costs to the benefits of active mate choice (Dugatkin 1992; Pruett-Jones 1992; Stöhr 1998).

Dugatkin (1992) was the first to perform controlled copying experiments in the laboratory and to show that female mate-choice copying occurs in the guppy (*Poecilia reticulata*). Further studies have shown that females will sometimes reverse their initial mate-choice decisions after observing the choices made by other females (Dugatkin & Godin 1992). Although we are not aware of any studies on mate-choice copying in guppies in the wild, Witte & Ryan (2002) found evidence of copying in natural populations of a related species, the sailfin molly (*Poecilia latipinna*); they controlled for schooling behaviour and found that a female was more likely to associate with a male that already had a female near him, than with a male that was alone.

Theoretical work has suggested that females are likely to copy if they are poor in their ability to discriminate male quality (Dugatkin 1992; Stöhr 1998) and Dugatkin (1992) has proposed that this ability is

directly related to the number of males that a female has observed. Dugatkin & Godin (1993) have shown, in guppies, that smaller females, who are presumably younger and less experienced, copied the mate choices of larger and presumably older and more experienced females, but not vice versa. This suggests that young females are not very good at evaluating male quality and are unsure about their mate-choice decisions, while older females are more 'confident' about their mate-choice decisions simply because, over the course of their lives, they have seen and have been able to compare more males (Dugatkin & Godin 1993). Stöhr's (1998) copying model examined the kinds of errors that can be made in mate-choice decisions and demonstrated that, when the ability to identify high-quality males can be learned, copying may evolve under certain conditions.

Copying is also thought to evolve when the costs of mate choice and of mating are high (Pruett-Jones 1992). In guppies, there are a number of costs associated with mate choice, copulation, and association with males; for example, male sexual behaviour can reduce time available for foraging, increase the risk of attack by a predator (Magurran & Seghers 1994; Godin & McDonough 2003) and lead to parasite and disease transmission (Cable et al. 2002). It might therefore be expected, for example, that all females, when they are unable to identify unhealthy males, would copy the mate choices of older females.

In this study, we test the hypothesis that even large (old) females will copy the mate-choice decisions of other large females in circumstances where they are unable to judge a male's quality. We tested this by asking females to choose between two males with very similar phenotypes. Because some researchers did not find evidence for copying in guppies (Lafleur et al. 1997; Brooks 1999), we repeated Dugatkin & Godin's (1993) experiment and also tested criteria employed by other researchers who found no evidence of mate-choice copying in guppies (Lafleur et al. 1997). We extend the work of Dugatkin & Godin (1993) by asking whether young females copy other young females and whether old females copy other old females. If we can understand when copying occurs, it will help us to understand the mechanisms driving its evolution in natural populations.

## Methods

### The Study Organism

The guppy (*Poecilia reticulata*) is a small, livebearing poeciliid native to Trinidad and Tobago and adjacent

parts of South America. Guppies are sexually dimorphic, with only males expressing polymorphic colour patterns consisting of orange (carotenoid), black, white and other coloured spots. Males vigorously court females and females will mate with several males during their lifetime (Farr 1975; Houde 1997; Kelly et al. 1999). Most inseminations result from cooperative copulations with courting males, although some successful sneaky copulations do occur (Farr 1989; Cheng 2004). In the wild, guppies are found in mixed-sex groups, in which females have the opportunity to view the mate choices of nearby females; however, across populations, there is a range in how aggregated the fish are, ranging from shoals to individuals relatively dispersed across the bottom of shallow streams and rivers (e.g. Seghers 1974; Magurran & Seghers 1991).

### Experimental Apparatus and Procedure

The experimental apparatus (Fig. 1) was similar to the one used by Dugatkin & Godin (1992). To summarize, a focal female was given the opportunity to observe a male in a compartment on one side of her, and, on her other side, a second male and a model female (each in a separate compartment). The model female and the partitions were then removed and the focal female's responses to the two males were recorded.

The experimental apparatus consisted of two 7.6-l tanks (width 15 cm), which housed the males, placed on either side of a 19-l tank (width 40 cm), which contained the focal and model females. One incandescent 60 W light was placed approx. 50 cm above the apparatus. At the start of each trial, opaque partitions (D) were placed between the central

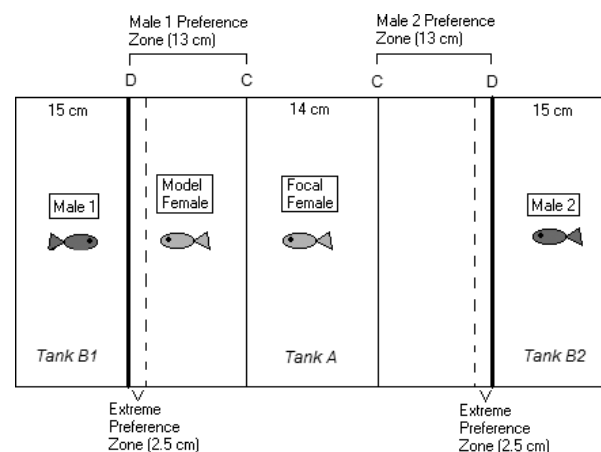


Fig. 1: Experimental set-up

tank (tank A) and the two tanks on the sides (tanks B1 and B2). Removable, perforated, clear Plexiglas partitions (C) divided Tank A into three compartments. One male was placed in each tank B, the focal female was placed in the central chamber and the model female was placed in the preference area of either Male 1 or Male 2. To control for side-biases, the side that the model female was placed in was randomized. The fish were then given 10 min to acclimate. After the acclimation period, the opaque partitions (D) were removed and for 10 min the focal female was able to observe both males and interactions between the model female and the male adjacent to it (Viewing Period). The model female and the partitions (C) were then quickly removed; every effort was made to disturb the focal female as little as possible. The focal female was then observed for 10 min (Data Collection Period). Observations of the focal female were recorded using Observer<sup>®</sup> software (Noldus 1991), with the experimenter (JV) recording approx. 50 cm from the apparatus. All fish were returned to their stock tanks after the completion of the experiment.

Dugatkin (1996) found that when differences in male colouration are large, genetic preferences (independent choice) override imitation factors (copying). Therefore, in this study, to make it difficult for the females to distinguish between the males (and to make copying more likely), the pairs of males used were full-sibling brothers. Because the colouration and size of male guppies in many populations is Y-linked (Haskins et al. 1961; Reznick et al. 1997), the pairs of brothers were of similar size and colouration. Each pair of males was used four to five times over the 2-mo test period.

Guppies used in this experiment were sexually mature and descended from guppies from several natural populations in Trinidad. The focal females, the model females and the males all came from different tanks and therefore had no previous experience with each other. The fact that the females had never seen these males before also meant that they might be more likely to rely on the mate-choice decisions of other females. All females were from mixed-sex tanks, where they had been exposed to approx. 10–20 males, and were not virgins. The females did not show signs of approaching parturition, such as distended abdomens. Most females were used once as the focal female and once as the model female (always focal first); 12 females were used only once. All fish were maintained at 12L:12D, at  $25 \pm 2^\circ\text{C}$ , and fed twice a day.

There were four treatments in the experiment. Using size as an indication of age, females were classified as either small ('young') or large ('old'). Small females were 14–18 mm in total length, while large females were 24–30 mm in total length. The large difference between the two groups of females was selected so that there would be a clear distinction between large and small females. All females came from tanks that contained both classes of females and all tanks were maintained identically in the same room. The four treatments were: *Treatment 1*: small focal female/large model female; *Treatment 2*: large focal female/large model female; *Treatment 3*: small focal female/small model female; and *Treatment 4*: large focal female/small model female.

Fifteen trials were conducted for each treatment in Feb. and Mar. 2003. All trials were conducted in the morning (7:00–11:00 a.m.), when guppy sexual activity is generally at its peak (Endler 1987). One trial was re-run because one male did not display. Data collected during four trials were not used in any analyses because the focal female spent the majority of the Data Collection period in the central, neutral area or was generally unresponsive to male displays. Depending on the selection criteria that were used (see below), a number of other trials were also excluded from a specific analysis because the mate choice of the focal female was ambiguous; in these cases, the focal female did not prefer either male as defined by the relevant preference criteria. For example, following the Dugatkin criteria, if a female did not spend at least 300 s in the preference zone of either male, there was no clear preference and the trial could not be used in the analysis. Female preference was evaluated as the proportion of time spent in the area adjacent to each male's tank. Several studies have shown that such preference tests are consistent with the results of more direct measures of female choice in the same type of experiment (Bischoff et al. 1985; Kodric-Brown 1992; reviewed in Houde 1997).

#### *Dugatkin criteria*

Preference was first measured using Dugatkin's (1992) criteria. The Preference Zones were delineated by lines on the walls of the female tank and corresponded to the positions of the partitions (C), which were used to contain the focal female during the Viewing Period (Fig. 1). These zones encompassed the area within 13 cm of each male. During the 10-min interaction period, a female

was said to prefer a male if she spent over half of the interaction period (>300 s) in the preference zone of that male.

#### *Lafleur criteria*

Lafleur et al. (1997) expressed concerns that the preference zones used by Dugatkin (1992) were too large and were arbitrarily chosen. They contended that the presence of a focal female within such a large zone might not in fact reflect preference, but simply random movement within the tank. Although Lafleur et al. (1997) used a series of increasingly smaller preference zones, we chose, as a second preference criteria, the smallest zone that they suggested (referred to as the 'Bischoff zone' by Lafleur et al. (1997)). These Extreme Preference Zones were delineated by lines on the front wall of the female tank (Tank A, Fig. 1) and included the area within 2.5 cm of each male. Using Lafleur et al.'s (1997) criteria, a focal female was said to prefer the male in whose Extreme Preference Zone she first spent 15 consecutive seconds.

We modified the Lafleur criteria and added a third set of preference criteria. Based on our preliminary observations, we thought that the 15 s used by Lafleur et al. (1997) might not be a long enough to indicate preference by a female, because this might be too short a time for courtship behaviour to commence, and for the female to assess the male and make a preference decision. Therefore, for our third preference criterion, we modified the Lafleur criteria such that a female was said to prefer the male in whose Extreme Preference Zone she first spent 25 consecutive seconds. We used the G-test (Sokal & Rohlf 1995) to determine whether a significant number of females in each treatment copied the model female, tested against a null hypothesis of random choice (expected frequency = 0.5) (Dugatkin & Godin 1993).

#### **Assessment of Males**

We also asked whether females differed in their assessments of the two males. Using the Lafleur criteria of 15 consecutive seconds in the Extreme Preference Zone as an indication of assessment, we asked whether females assessed both males, i.e. did they spend 15 consecutive seconds in the Extreme Preference Zones of both the preferred and the non-preferred males. A second analysis was also performed using the modified 25 consecutive second criteria. The data were analysed using a chi-square

contingency table test for partial independence (Sokal & Rohlf 1995).

#### **Results**

In most trials, the male adjacent to the model female spent the 10-min Viewing Period courting the model female, and the model female was generally attentive and responsive to the adjacent male, i.e. the female was oriented towards him and would move towards him as he displayed. Generally, during the Viewing Period, the focal female was relatively inactive and observed the model female and the adjacent male, and sometimes the other male as well.

During the Data Collection Period, for the most part, both males were at the ends of their tanks closest to the female, displaying vigorously. When the focal females were given a chance to interact with the two males, the females were responsive to them (data for the four unresponsive focal females were excluded from the analyses).

#### **Size-Dependent Effects on Mate-Choice Copying**

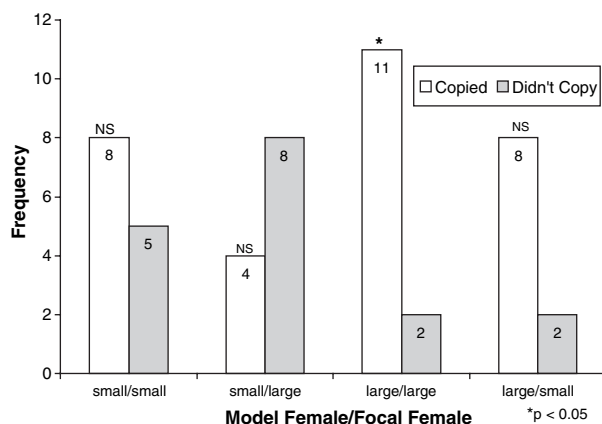
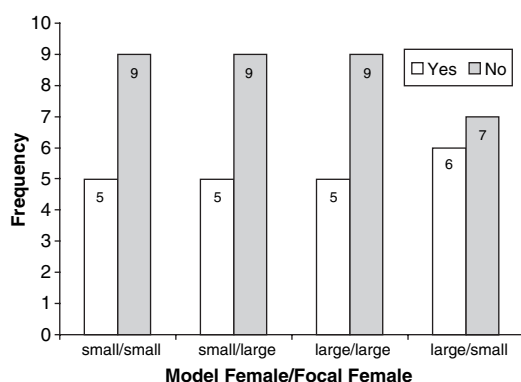
We found, using the Dugatkin criteria, that large females copied large model females. We also found weak (statistically non-significant) evidence, after the Williams' correction (Sokal & Rohlf 1995), that small females copied large females, but we found no evidence, statistically, that females of either size copied small model females (Table 1, Fig. 2). Using the Lafleur et al. criteria and our modified Lafleur et al. criteria, we found no evidence for copying in any of the four treatments (Table 1). If anything, the trend for all three criteria was for large females to avoid the male near the small model.

#### **Assessment of Males**

We asked whether female propensity to assess both males for at least 15 s in the Extreme Preference Zone was related to the size of either the focal or the model female. Of the females that showed a preference for one male (according to the appropriate Lafleur criteria), there was not a significant difference among treatments in whether or not the focal females assessed the non-preferred male ( $\chi^2_{0.05,3} = 0.45$ ,  $p > 0.9$ ). On average, only 34% of the females assessed the non-preferred male for at least 15 consecutive seconds (Fig. 3). Results using the 25-s criteria test were similar but slightly lower (27% of the females assessed the non-preferred male for at least

**Table 1:** Evidence for copying behaviour in female guppies. Number of trials in which the focal female copied the apparent mate choice of the model female

	Treatment	Focal female	Model female	No. trials focal female copied (%)	No. trials analysed	G value	p
Dugatkin criteria	1	Small	Small	8 (62)	13	0.699	>0.10
	2	Large	Small	4 (33)	12	1.359	>0.10
	3	Large	Large	11 (85)	13	6.41 <sup>a</sup>	<0.05*
	4	Small	Large	8 (80)	10	3.55 <sup>a</sup>	0.05–0.1
Lafleur criteria (15 s)	1	Small	Small	9 (64)	14	1.16	>0.10
	2	Large	Small	4 (28)	14	2.658	>0.10
	3	Large	Large	10 (71)	14	2.657	>0.10
	4	Small	Large	9 (69)	13	1.972	>0.10
Modified Lafleur criteria (25 s)	1	Small	Small	9 (64)	14	1.16	>0.10
	2	Large	Small	5 (36)	14	1.16	>0.10
	3	Large	Large	9 (64)	14	1.16	>0.10
	4	Small	Large	8 (67)	12	1.359	>0.10

<sup>a</sup>Adjusted G value (Sokal & Rohlf 1995).\*Significant at  $p < 0.05$ **Fig. 2:** Incidences of mate-choice copying (Dugatkin criteria)**Fig. 3:** Assessment of non-preferred males by focal females according to the Lafleur criteria (15 s assessment)

25 s) and are not shown. Therefore, we did not detect an effect of the size of the focal or the model female on her propensity to assess both males or just one male using these criteria.

## Discussion

The main findings of this study, based on Dugatkin's (1992) criteria, suggest that large females copy the mate-choice decisions of large females and that small females might copy the decisions of large females, but that neither small nor large females copy small females. These results corroborate and extend the results of Dugatkin & Godin (1993) and Amlacher & Dugatkin (2005). This evidence provides support for the notion that females are more likely to copy when they perceive that there is an imbalance between their assessment ability and that of another female. The fact that we obtained this result, by presenting females with two unfamiliar males that were very similar in appearance, lends support for the idea that copying is due to an information asymmetry. Because few females copied the apparent mate choices of small model females, it suggests that young, presumably less experienced, females are unlikely to have reliable information about a male.

In natural populations, what kinds of information might a large, presumably older, female have that a smaller, younger one would not? Dugatkin & Godin (1993) suggest that older females have more experience choosing mates; however, it is difficult to know how females would evaluate the quality of males in a non-resource-based mating system like guppies. It is possible that the size of the model does not (only) indicate age, but it could also indicate something about the competitive or foraging ability of the female, as size is also influenced by food intake. There may, however, be direct benefit(s) to the choice of a 'good' mate; the fact that a larger female is alive and healthy is an indication that she has

avoided the costs of mate choice in the past. One such cost is disease and parasite transmission. Based on the hypothesis that females should copy when there are costs of mating and when they lack experience/information about these costs, we propose that female guppies copy to avoid transmission of diseases/parasites during copulation. *Gyrodactylus turnbulli*, an external parasite that commonly infects guppies in natural populations, is a particularly good candidate for this hypothesis (Lyles 1990; Cable et al. 2002; Kolluru et al., 2006). It moves between guppies when they come into close contact, such as during sexual behaviour (Harris 1988), especially copulation (B. Bridges & A. E. Houde, pers. comm.). This parasite can kill a guppy in a few days (Lyles 1990) and, in the laboratory, it kills 50% of the fish it infects (Houde 1997). Two of the male traits that females use to select mates, 'brightness' (chroma) of orange spots and courtship display rates (reviewed in Houde 1997), are reduced when males have moderate-to-heavy loads of this parasite (Kennedy et al. 1987; Houde & Torio 1992). However, individuals that are lightly infected (less than 20 *G. turnbulli*) do not always appear sick (Houde 1997) and inexperienced females may be unable to discriminate between these lightly infected males and healthy individuals. An error could be lethal and therefore parasite avoidance could be a factor maintaining copying behaviour. We feel that further study of mate-choice decisions in light of parasite infections is warranted. A critical assumption of all copying models is that females differ in their ability to discriminate between males and that they are able to improve this ability (Stöhr 1998). Do females differ in their ability to distinguish parasitized from non-parasitized males? Can females learn to identify parasitized males? Is it a matter of being exposed to a wide range of male phenotypes, including males with bright orange spots that are presumably healthy and males with pale orange spots that are presumably ill, or do they actually need to be infected to learn to avoid parasitized males?

Although we did find evidence of mate copying, this was only true when we used the Dugatkin (1992) criteria; i.e. over 300 s in the preference zone of a male indicated a female preference for that male. We did not find evidence for copying based on Lafleur et al.'s (1997) criteria or on our modified version of Lafleur et al.'s criteria. However, we feel that we were more likely to detect copying behaviour than Lafleur et al. (1997) for two reasons. First, we feel that their criteria are too stringent because they allow the female so little time to make

her decision apparent and because it is also possible that females continue to assess males during this period. Also, our assessment analysis suggests that females may be making a decision about a male without being within 2.5 cm of him. As shown in Fig. 3, the majority of focal females did not assess the non-preferred male according to the Lafleur criteria (15 s), suggesting that assessment of males might be performed, and subsequent mate-choice decisions might be determined, from a considerable distance. In fact, a female might be reluctant to assess a male at such close proximity because of the increased risk of sneaky copulations and parasite transmission. Also, we might be more likely than others to reveal copying because we intentionally used pairs of males that were similar in appearance, perhaps making it more likely for females to rely on the mate-choice decisions of other females.

There are several, alternative, non-copying explanations for the behaviour we observed. Dugatkin (1992) did test for and eliminate several possibilities including a shoaling response to the model female. However, it is possible that the focal females in our study were not copying the mate-choice decisions of the model females but, rather, that the focal females were responding directly to subtle differences in the behaviour of the two males. Dugatkin (1992) did test for behavioural (or physiological) changes in the male near the model female, to which the focal female might be responding, by using a naïve female. However, he added the naïve female after the model and focal females were removed, so any differences in male behaviour that only occurred while the model female was present would be gone or reduced. Nevertheless, it is possible, in our study, that there were subtle differences between the behaviours of the males with the small model and those with the large model and this could have affected the focal female's willingness to copy the choice of the model female. Several studies have shown that male guppies prefer larger females (Abrahams 1993; Dosen & Montgomerie 2004; Herdman et al. 2004). Male preference for larger females is not unexpected because larger female guppies generally have higher fecundity (Reznick 1989). Abrahams (1993) found that more males courted large females than small females. Dosen & Montgomerie (2004) showed that, in a divided tank, males spent more time with the larger female, but that there was no difference, for the males that did display, in the number of displays directed towards large vs. small females. Herdman et al. (2004) showed that, in a free-swim situation, male guppies

directed more approaches and gonopodial nips, but not more sigmoid displays, at larger females. In our experiment, we did observe that both males were actively responding to the model and/or the focal females in the tests. Unfortunately we did not make detailed observations of male behaviour, but even if we had, it is unlikely that we would be able to measure all the subtle differences in their behaviour; for example, it is possible that the males did not court the large model females at a higher rate, but that their displays or another component of their repertoire (Rodd & Sokolowski 1995) were longer or more intense. Differences between the pair of males presented to the focal female might be especially exaggerated when the model female is large. This could make a focal female more likely to 'select' the male near the large model female simply because he appeared to be more 'sexy' in some way. Alternatively, females might have been attracted to the side of the tank with the larger model female because large models are easier to observe and hence attract more attention. Or, there might be differences in the behaviours of the small vs. small model females towards the males (e.g. the large females were more receptive to the male displays), and this could also have influenced the focal females' responses.

Regardless of whether females were responding to subtle differences in the males' behaviour or directly copying the model females' mate choice, the results of this experiment have implications for guppies in natural populations. Females were apparently assessing males based on their interactions with other females. This suggests that a male should invest heavily in courtship, even of non-receptive females, because other females may be observing him and basing their future mate-choice decisions on his performance. Males do spend a great deal of time in the natural populations courting females [display rates of over 2.74 times a minute have been recorded (Farr 1975)].

Using Dugatkin's criteria, we found that large females will copy the mate-choice decisions of large females, but that all females are unlikely to copy small females. This suggests that females are copying when they feel that they are less able to assess a male than another female who, based on her size, apparently has greater knowledge/experience. We suggest several possible reasons why this information asymmetry might exist, including experience with parasites. We did not find evidence for copying using the Lafleur et al. (1997) criteria. We offer some explanations for the differences in these results, but whether or not copying really is occurring, we, like

Dugatkin and colleagues, have identified some differences in the behaviour of female guppies selecting their mates. These differences in behaviour have implications for guppies in natural populations and may help to explain the extremely high courtship rates of male guppies in those populations.

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