Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*

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Females can choose a male independently of other females' mate preferences, or they can copy the mate choice of other females. Alternatively, mate-choice copying and independent mate choice can interact if females assess male traits when deciding whether or not to copy. We investigated how mate-choice copying interacts with a preference for large males in the sailfin molly (*Poecilia latipinna*). Sailfin molly females exhibited a preference for larger males. They also copied the mate choice of other females when males were of similar body length. Females did not copy, however, when males differed substantially in body length. Our results show that conspecific mate copying occurs in the sailfin molly but does not override a preference for larger males. *Key words:* male body length, mate-choice copying, sailfin molly, *Poecilia latipinna*. *[Behav Ecol 9:534–539 (1998)]*

In many species females exhibit a preference for male traits and thereby potentially influence the evolution of male traits (Andersson, 1994). Females often show a preference for large body length in males, especially in fish. In fishes with paternal care, females gain direct benefits by choosing larger males (Côté and Hunte, 1989; Downhower and Brown, 1980), as these males defend their brood more successfully (Bisazza and Marconato, 1988; Hastings, 1988) or guard the brood for a longer period (Côté and Hunte, 1989). In some species without any parental care, females prefer larger males as well (e.g., Reynolds and Gross, 1992; Ryan and Wagner, 1987; Ryan et al., 1990). This preference can be explained by a Fisherian runaway process, models of good genes, or pleiotropic effects resulting in sensory bias for larger size (Ryan, 1997).

Models of both direct and indirect selection are based on independent mate choice in females. There is evidence, however, for nonindependent mate choice in which females are influenced by the mate preferences of other females and copy their mate choice. Empirical evidence for mate-choice copying exists in polygynous fish species (Dugatkin, 1992, 1996a; Dugatkin and Godin, 1992; Grant and Green, 1996; Schlupp et al., 1994), and birds (Gibson et al., 1991; Höglund et al., 1995). Theoretical studies have investigated how copying could evolve and be maintained in a population (Dugatkin, 1996a; Gibson and Höglund, 1992; Kirkpatrick and Dugatkin, 1994; Losey et al., 1986; Pruett-Jones, 1992; Servedio and Kirkpatrick, 1996). In some situations, females might be confronted with a conflict between nonindependent and independent mate-choice strategies, in which these strategies interact with each other. For example, Dugatkin (1996b) showed that in guppies, mate copying interacts with a female preference for orange coloration in males. Here, we investigated how copying behavior interacts with a preference for larger males in the sailfin molly. Schlupp et al. (1994) and Marler and Ryan (1997) have shown that sailfin molly females exhibit a preference for larger males. We determined if size differences between males influenced mate-choice copying by sailfin molly females. The aim of our study was to understand the condi-

tions under which females copy a choice of another female and how strong copying is in relation to independent choice.

METHODS

We conducted two copying experiments, one with males matched for body length and another with males of quite different body length. Additionally, we performed two different control experiments to test for consistency in female mate preference and for shoaling behavior, as well as a simple mate-choice experiment to test for a preference for larger males among females of our sample.

Study species

The sailfin molly is a live-bearing fish without parental care. Sailfin mollies live in mixed-sex shoals comprising 10–20 individuals within which females may have the opportunity to observe other females during mate choice. Schlupp et al. (1994) have shown that sailfin molly females copy the choice of Amazon molly (*P. formosa*) females. It is therefore likely that sailfin molly females copy the choice of conspecific females as well.

All fish used in the experiments were collected in the San Marcos River in central Texas, USA, in 1996. We maintained the fish in tanks separately by sex and fed them once daily with flake food (TetraMin). All females and males used in the tests were mature. We separated females from males for at least 18 days before testing to ensure that females were not gravid. None of the females exhibited abdominal swellings which could indicate pregnancy. We tested the females independently of their reproductive cycle.

General procedure

We basically followed the procedure of Schlupp et al. (1994). All experiments were performed in the same apparatus: a large tank (70 cm × 30 cm × 40 cm) and four small tanks (each 30 cm × 15 cm × 25 cm) with two standing side by side at each end of the large tank (Figure 1). Before tests started we gently placed a test female in a clear Plexiglas cylinder (8.5 cm diam) in the center of the large tank. One male was placed into each of the two small tanks at each end, so that they were placed diagonally from each other to minimize male-male competition.

All three fish were allowed to acclimatize for 10 min, one male each in one of the two end tanks and a female inside a cylinder in the center of center tank (stage 1 in Figure 1). During this period the test female was able to observe both
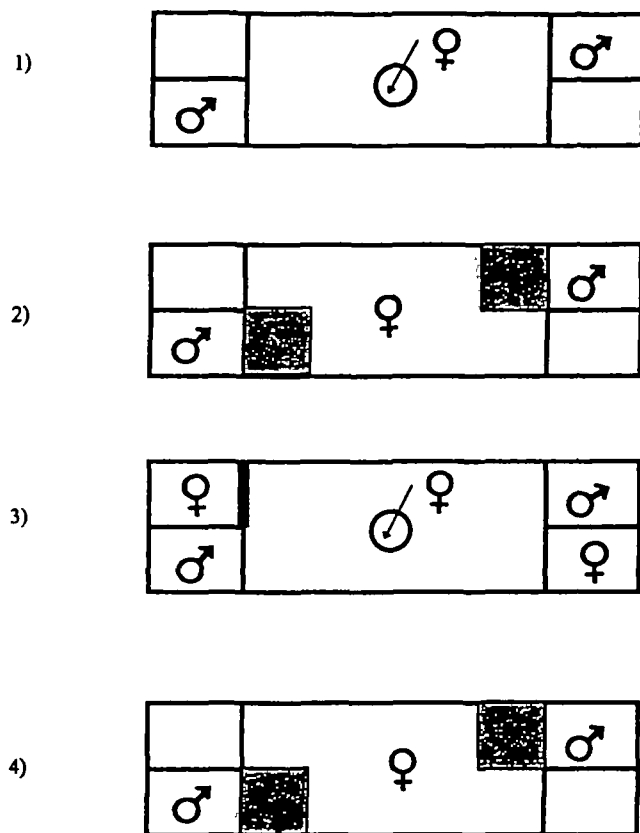
Figure 1
Experimental apparatus: (1) Acclimation period for 10 min. Test female is in the clear Plexiglas cylinder and two males are placed in one of the small tanks on each end of the large test tank. Males are not covered. (2) First preference test: the gray fields show the two preference zones. (3) "Viewing period" for 10 min. A model female is in a separate tank next to the previously nonpreferred male. A pseudo-model female is in a separate tank next to the other male, but behind a black screen and not visible to the test female. (4) Second preference test.

males. After the acclimation period, we removed the cylinder and recorded for 10 min the time the female spent within 20 cm in front of each male tank (i.e., the preference zone; stage 2 in Figure 1). Only her time spent within a preference zone (one preference zone was only 14.28% of the total space of the test tank) was scored as choosing a mate. We then switched the males between the two tanks and repeated the preference trial. The test female was considered to prefer a particular male if she spent more time within the preference zone for that particular male during the two 10-min preference trials. Although time spent is an indirect measurement of female mate preference, Bischoff et al. (1985) and Kodric-Brown (1993) have shown in the guppy that the time a female spends with a male correlates positively with the probability of a copulation with that male. This was found in other species as well (Berglund, 1993; Forsgren, 1992). A female was considered to be side biased if she spent more than 90% of the total time she spent with both males in the same preference zone in both 10-min trials although males had been switched.

When a female was within the preference zone the male swam toward her and followed her movements at the glass wall. Larger males attempted to court the female. They spread their dorsal fins, made zigzag-movements in front of the female, and sometimes flipped the gonopodium. Smaller males just followed the female's movements.

After this first preference test (which comprised two con-

secutive 10-min trials), we allowed females to view the previously nonpreferred male associating with a "model" female. Because males increased activity in the presence of females, however, it was necessary to use both a "model" and a "pseudo-model" female in the "viewing period" of the experiments to control for the stimulatory effect of the model female's presence on the male (see also Schlupp et al., 1994). Therefore, after the first preference test, we placed the test female back into the cylinder and placed a model female next to the previously nonpreferred male and a pseudo-model female next to the preferred male. The compartment with the pseudo-model female was covered with a black screen such that she was visible to the male but not to the test female. Pseudo-model and model females exhibited vertical movements toward the males next to them. The males followed these females' movements, and bigger males showed courtship behavior toward them. All males responded to the presence of a model or pseudo-model female. During a "viewing period" of 10 min (stage 3 in Figure 1), the test female could observe the model female next to the previously nonpreferred male. After this period, we released the test female from the cylinder and recorded the time she spent with both males for 20 min, switching the males after the first 10 min trial as we did in the first preference test (stage 4 in Figure 1).

All three females used in one test were matched for body length. Each female was used only once as a test female, but she was used as a model or pseudo-model female in other tests. We measured the body length from the tip of the snout to the end of the caudal peduncle of males and females. We compared the absolute and relative time the test female spent with the previously nonpreferred male in the second preference test (after the viewing period) with the time she spent with the same male in the first preference test (before the viewing period) using a Wilcoxon matched-pairs test. Using a Spearman's rank correlation, we correlated the copying in females with female body length, male body length, the difference in body length of males used in a test, and the total time a female spent with both males. All p values were two-tailed. For each of the five experiments we used new females and males.

Copying experiment with males matched for body length
In our first copying experiment, the males used in each test were matched for body length. The average ($\pm$SD) size difference between males within a pair was 1.4 $\pm$ 1.21 mm. We tested 22 females together with 22 pairs of males. Each male was used in two different tests, but in the second test paired with a different male. The average body length of all males ($n = 11$) used in this experiment was 32.77 $\pm$ 5.39 mm. We defined males that were smaller than the average body length of this sample as "small" males and those larger than the average body length as "large" males. The test female, model female, and pseudo-model female used in any one test were also matched for body length (test females, 43.85 $\pm$ 8.85 mm; model females, 43.74 $\pm$ 8.6 mm; pseudo-model females, 43.46 $\pm$ 8.92 mm).

Control for consistency in mate preference
In this control experiment, we determined if females were consistent in their mate choice when they were not given an opportunity to copy. These experiments were conducted with males matched for body length and with males different in body length. In these controls, both the model female and the pseudo-model female were covered behind a black screen and not visible to the test female but visible to the males during the 10-min viewing period between the first and second preference tests.

In the control with males matched for body length, males

differed on average by 1.91 ± 0.21 mm in body length. We tested 12 females together with 12 pairs of males. Each male was used in two different tests, but with a different male in the second test. We rejected two females because they showed side biases. In the control with males different in body length, we performed 10 tests. The difference in body length of the males within a pair was on average 12.24 ± 3.88 mm.

Simple mate choice test with large and small males

We determined if the sailfin molly females used in our experiments exhibited a preference for larger males as shown in other studies (Marler and Ryan, 1997; Schlupp et al., 1994). We used the same choice apparatus as in the copying experiments. A simple mate choice test lasted 20 min with a 5-min interval; the males were switched after the first 10 min. The males presented to the females differed obviously in body length. The difference was on average 6.5 ± 4.25 mm, with a minimum difference of 2.6 mm and a maximum difference of 14.2 mm. We performed 14 tests with different females and males in each test. Two females showed side biases and were excluded from the analyses.

Copying experiment with males different in body length

In this copying experiment, the males used in each test differed obviously in body length. The average body length of large males was 39.49 ± 4.41 mm and that of small males was 28.44 ± 5.31 mm. Large and small males differed in body length by 11.63 ± 4.39 mm, on average. We performed 17 tests with different females and males in each test. The average body length of females was 37.04 ± 8.83 mm.

Control for shoaling behavior

In a third control experiment, we determined if females showed shoaling behavior; that is, if they preferred to associate with a conspecific that they had seen together with a second conspecific during the 10-min viewing period in the experimental situation. Because shoaling is socially motivated, not sexually motivated, we used only females and tested 10 females by following the same protocol as in the copying experiment. All five females used in one experiment were matched for body length.

RESULTS

Copying experiment with males matched for body length

Although males used in any given test were matched for body length, females did not tend to partition their time evenly between the two males. All test females showed a strong preference for one of the two males in the first test. On average, females spent 8.52 ± 3.93 min with the preferred male and 1.93 ± 1.59 min with the nonpreferred male. After the viewing period, females spent significantly more time with the previously nonpreferred male than before the viewing period, both absolutely ($n = 22$, $z = -3.55$, $p < .001$) and relative to total time spent in preference zones of both males (Figure 2; $n = 22$, $z = -3.29$; $p = .001$). The total time a female spent with both males in a preference test seemed to increase from the first to the second preference test ($n = 22$, $z = -1.7$, $p = .088$). This did not change our result that females spent significantly more time with the previously nonpreferred male in the second preference test than in the first preference test. We therefore conclude that a change in absolute time spent near the nonpreferred male is not due to a change in total time spent near both males.

Control for consistency in mate preference

To determine if the increase in absolute and relative time spent with the previously nonpreferred male is due to copying
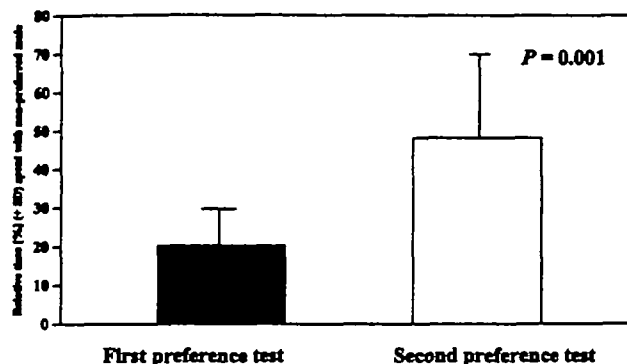

P = 0.001

First preference test   Second preference test

Figure 2
Copying experiment with males matched for body length. Relative time (% ± SD) the test female spent with the nonpreferred male in the first preference test (before the viewing period) and in the second preference test (after the viewing period).

or due to inconsistency in mate choice, we repeated the previous experiment with no opportunity to copy (both model female and pseudo-model female were covered during the 10-min viewing period). In this situation, females did not significantly increase the absolute and relative time spent in front of the previously nonpreferred male in either the control with males matched for body length (absolute change in time spent: $n = 10$, $z = -1.54$, $p = .1235$; relative change in time spent: $n = 10$, $z = -1.68$, $p = .093$) or in the control with males differing in body length (absolute change in time spent: $n = 10$, $z = -0.15$, $p = .878$; relative change in time spent: $n = 10$, $z = -0.866$, $p = .386$). The total time a female spent near both males did not change between the first and second preference tests in both the control experiment with males matched for body length ($n = 10$, $z = -0.84$, $p = .40$) and the control experiment with males differing in body length ($n = 10$, $z = -1.274$, $p = .20$). Therefore, females were consistent in their choice in the absence of any opportunity to copy, and the increase in time spent in the copying experiment with males matched for body length cannot be explained by inconsistency in female mate choice.

Do females prefer larger males?

In a simple mate-choice test, females ($n = 12$) spent significantly more time with the larger of the paired males (Wilcoxon matched-pairs test: $n = 12$, $z = -2.91$, $p = .003$). Thus sailfin molly females used in our study showed a preference for larger males.

Copying experiment with males different in body length

In the first preference test of this copying experiment, females showed a clear preference for the larger of the two males (binomial test: $n = 17$, $p = .002$). Females also spent on average significantly more time with larger males (10.57 ± 4.37 min versus 2.91 ± 1.61 min with smaller males; $n = 17$, $z = -3.4$, $p < .001$). Two of 17 females preferred the smaller male in the first preference test. In these cases, the model female was placed next to the larger male in the viewing period of the experiments. After the viewing period both females changed their mate preferences and preferred the larger male.

The 15 females that preferred the larger male in the first preference test did not change their mate preference after observing a model female next to the smaller male (binomial test: $n = 15$, $p = .03$) and did not spend more time with the smaller male ($n = 15$, $z = -1.09$, $p = .27$). In this experiment, the total time spent near both males in the second preference test was lower than in the first preference test ($n = 15$, $z =$
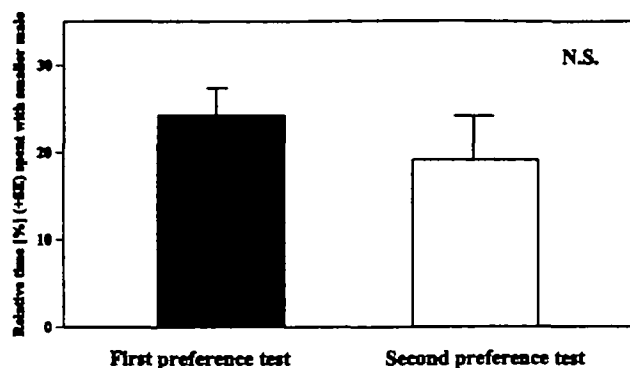
Figure 3
Copying experiment with males different in body length. Relative time (% ± SD) the test female spent with the smaller male in the first preference test (before the viewing period) and in the second preference test (after the viewing period).
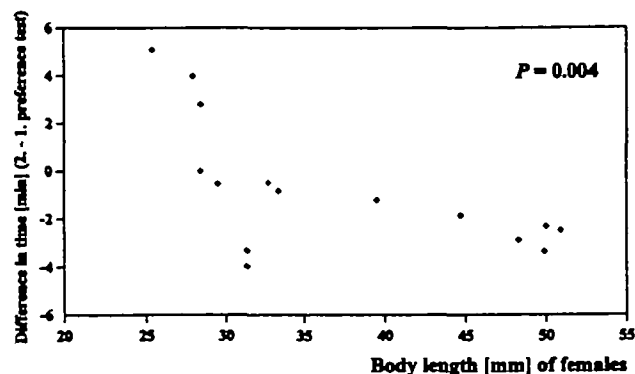

Figure 4
Copying experiment with males different in body length. Relationship between female body length (mm) and mate-copying tendency measured as the difference in absolute time (min) the test female spent with the smaller male in the second preference test and the time she spent with that male in the first preference test (=after-before the viewing period). Only the three smallest females of our sample ($n = 15$) copied the mate choice of the model female.

-2.38; $p = .001$). We therefore compared the percentage of time (time spent with both males was 100%) a female spent with the smaller male in the first preference test with the time she spent with the same male in the second preference test, but this did not change our result (Figure 3, $n = 15$, $z = -1.09$; $p = .21$). Thus, sailfin molly females did not copy an apparent preference for small males.

We found a significant negative relationship between female body length and copying tendency (i.e., the difference in absolute time spent in front of the smaller male before and after the viewing period; Figure 4, Spearman's rank correlation $n = 15$, $r = -.69$, $p = .004$). Female body length was the only variable that showed a significant relationship with copying tendency. We found no significant relationship between male body length of the smaller male and copying tendency ($n = 15$, $r = 0.2$, $p = .45$), between the difference in size of both males presented in a test and copying tendency ($n = 15$, $r = 0.13$, $p = .62$), and between the total time spent in front of both males in the first preference test) and copying tendency ($n = 15$, $r = 0.42$, $p = .11$). Three out of 15 females that had preferred the larger male in the first preference test copied a preference for smaller males (Figure 4). These females were the smallest females in our sample. When we excluded these females from the analysis, we found no significant relationship between female body length and copying tendency ($n = 12$, $r = -0.41$, $p = .19$).

To investigate whether the absolute body length or the difference in body length between males used together in a test influences copying behavior in females, we examined female choice between two small males (average ± SD body length of small males: 26.46 ± 6.61 mm, $n = 10$), two large males (average ± SD) body length of large males: 37.1 ± 2.68 mm, $n = 12$), and when females could choose between a large and a small male (average ± SD body length of large males: 39.49 ± 4.41 mm, $n = 15$). The mean (±SD) absolute body length of large males in the copying experiment with two large males did not differ from the absolute body length of large males in the copying experiment with males different in body length (Mann-Whitney U test: $z = -1.58$, $p = .113$). The difference in body length between males in a test differed significantly from those two groups of males (average ± SD difference in body length in large males): in the copying experiment with males matched for body length, 1.44 ± 1.33 mm; in the copying experiment with males different in body length, 11.63±4.39 mm (Mann-Whitney U test: $n_1 = 15$, $n_2 = 12$, $z = -4.34$, $p < .001$).

When females could choose between two small males, all

10 females copied the choice of the model female. When females could choose between two large males in the copying experiment with males matched for body length, 10 out of 12 females copied the choice of the model female (Fisher's Exact test: $p = .48$). In the copying experiment with males differing in body length, however, only 3 out of 15 females, which had preferred the larger male in the first preference test, copied the choice of the model female (Fisher's Exact test: $p < .002$). Thus females behaved differently when males were matched for body size or not.

The absolute body length of large males in both copying experiments was similar, but the difference in body length was significantly different between males of both groups. We therefore conclude that the difference in body length of males influenced copying behavior in females. Additionally, we found a significant difference in the strength of copying in females (measured as the average ± SE change in absolute time spent near the previously nonpreferred male before and after the viewing period) between copying experiments with two large males and copying experiments with one large and one small male (Figure 5; Mann-Whitney U test: $n_1 = 15$, $n_2 = 12$, $z = -2.53$, $p = .011$). We also found a significantly
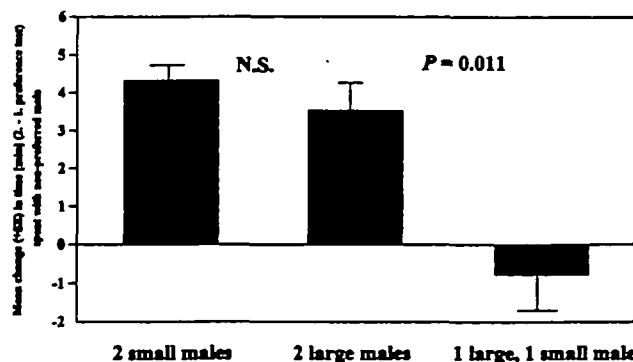

Figure 5
The difference in male body length and the strength of female copying measured as the mean (± SE) change in absolute time (min) spent with the nonpreferred male before and after the viewing period when females could choose between two small males, two large males, or one large and one small male.

negative correlation (Spearman rank correlation, $n = 27$, $r = -.46$, $p = .015$) between the strength of copying and the difference in body length between males used together in tests. In this analysis, we included all males of both copying experiments. This shows that the difference in body length between males determined the strength of copying in females.

Control for shoaling behavior
In these tests females did not increase their time spent with the female that was together with a second female during the viewing period ($n = 10$, $z = -0.46$, $p = .646$). Thus we conclude that females' preference is not due to shoaling per se in our experimental design.

DISCUSSION

Our results show that conspecific mate-choice copying occurs in female sailfin mollies. Females copied the mate choice of another female when both males presented in a test were matched for body length. Females, however, did not copy as often when males presented in a test differed in body length. Comparison of the results of both copying experiments indicates that the difference in body length of the paired males influenced copying behavior in females and determined the strength of their copying response; when the difference in male body length was large, females did not copy. Thus copying interacted with, but did not override, a preference for large males.

In several species of poeciliids, such as mollies (Farr et al., 1986) and swordtails (Ryan and Causey, 1989), male mating strategy is influenced by body length (Farr, 1989). Bigger males show courtship behavior to females, whereas smaller males try to sneak copulations without displaying any courtship. Because male mating behavior correlates with male body length, we cannot distinguish whether body length or male behavior was more important for the female mate-copying behavior. This can be tested in copying experiments using videotapes instead of real fish in which body length or mating behavior can be held constant.

Schlupp et al. (1994) performed a heterospecific copying experiment in which sailfin molly females had the opportunity to copy a mate choice of the Amazon molly *P. formosa*, the gynogenetic hybrid species. In their copying experiment, the average length difference between males used in a test (mean: 12.7 mm) was similar to the average length difference in our copying experiment with males differing in body length (11.65 ± 4.39 mm). Although sailfin molly females preferred the larger male in their experiment, females copied the mate choice of the Amazon molly females next to the smaller male. This is in contrast to what we found. We compared the change in time a female spent with the smaller male as a measure of the strength of mate-choice copying in both studies and found that our result is significantly different from the heterospecific copying experiment (Mann-Whitney U test $n_{1(Schlupp\ et\ al.)} = 16$, $n_{2(our\ experiment)} = 15$, $z = -2.629$, $p = .009$). In the heterospecific copying experiment, the viewing period lasted 20 min, whereas this period was 10 min in our copying experiment. It is possible that the longer viewing period in the heterospecific copying experiment led to a higher probability of females copying. Dugatkin (1998) showed that the duration of the viewing period in a copying experiment influences copying behavior of females in guppies *P. reticulata*.

Our result, that females did not copy when given a choice between males differing in a preferred trait (i.e., body length), is similar to what Dugatkin (1996b) found in copying experiments in the guppy. Dugatkin tested a genetically based preference for orange coloration in males against a culturally based preference. Female guppies copied the choice of model

females when the males differed in the amount of orange by 24% or less, but they did not copy when males differed in the amount of orange by 40%. Thus, imitation could not override a genetically based preference for orange coloration in male guppies when the difference in color between males was large.

In our experiments, female sailfin mollies did not copy when they could choose between a large and a small male. The three females in our experiment that did copy a mate choice for small males were the smallest females in our sample. This is congruent with what Dugatkin and Godin (1993) found in another copying experiment. In their study, only small and possibly young females, which might be inexperienced in mate choice, copied the choice of large model females, which were older and presumably more experienced in mate choice. This shows that copying is an optional mate-choice strategy which females use only in specific situations. Our results suggest that copying interacts with a preference for larger males. Further experiments are necessary to investigate in which situations females copy and which fitness advantages they gain by copying.

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