Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males

Ingo Schlupp[a,b] and Michael J. Ryan[a]

[a]University of Texas at Austin, Department of Zoology, Austin, Texas 78712, USA and [b]Universität Hamburg, Zoologisches Institut und Zoologisches Museum, Martin-Luther-King Platz 3, D-20146 Hamburg, Germany

Female mate-copying has been shown to occur between heterospecifics: female sailfin mollies *Poecilia latipinna* copy the choice of their gynogenetic associates, Amazon mollies *P. formosa*. Female mate-copying thus contributes to the maintenance of this asexual-sexual species complex by providing an advantage to male sailfin mollies that mate with Amazon females; because of mate-copying these males increase their attractiveness to conspecific females. Here we show that male mate-copying, an unreported phenomenon, also occurs and that it can reverse male preferences for conspecific females. Male mate-copying should also contribute to the maintenance of gynogens and might be advantageous in allowing males a means to rapidly assess female receptivity although sometimes resulting in heterospecific matings. *Key words:* Heterospecific matings, mate choice, mate-copying, Pisces, *Poecilia formosa*, *Poecilia latipinna*, Poeciliidae, Teleostei. [*Behav Ecol 8:104–107 (1997)*]

Mate-copying is an example of non-independent choice in which individuals copy the mate choice of others. Mate-copying should increase the variability in mating success (Wade and Pruett-Jones, 1990) and might therefore have important implications for sexual selection (Gibson and Höglund, 1992; Kirkpatrick and Dugatkin, 1994; Pruett-Jones, 1992). Most studies of copying have investigated females copying conspecific females (Dugatkin, 1992; Dugatkin and Godin, 1993; Höglund et al., 1995).

We have recently shown that female mate-copying can occur among heterospecifics as well as conspecifics and that such mate-copying might contribute to the maintenance of an asexual-sexual species complex of fishes by providing some benefit to males who mate with heterospecific females by increasing their attractiveness to conspecific females (Schlupp et al., 1994).

The purpose of this study is to determine the extent to which male mate-copying, an undescribed phenomenon, might occur and what role it might also play in maintaining an asexual-sexual species complex.

The Amazon molly is a gynogenetic, all-female, live-bearing fish of hybrid origin (Hubbs and Hubbs, 1932; Schartl et al., 1995a; Turner, 1982). As a poeciliid with internal fertilization *Poecilia formosa* needs to be inseminated by males of a "sperm donor" species to initiate embryogenesis. Thus it has to live syntopically with either the sailfin molly *P. latipinna* in southeast Texas or the Atlantic molly *P. mexicana* in northeast Mexico. Inheritance is normally strictly maternal, only rarely a male contribution to the clonal genome occurs (Schartl et al., 1995b).

Sexual males and both conspecific and gynogenetic females can form mixed shoals in nature (Balsano et al., 1989; Hubbs, 1964; Schlupp and Ryan, in press). Thus males of these species frequently face a situation in which they have to choose between a heterospecific and a conspecific female. Males of both species are capable of species recognition and have a preference for conspecific females (Hubbs, 1964; Ryan et al., in press; Schlupp et al., 1991, and references therein for *P. mexicana*).

It has been assumed that gynogenesis is evolutionarily unstable because there should be intense selection on males not to mate with gynogenetic females since this represents only a cost with no perceivable benefits.

By consorting with heterospecifics, however, male *P. latipinna* increase their attractiveness to conspecific females. Thus mate-copying in this species complex shows a potential advantage for male *P. latipinna* mating with *P. formosa* females and is thus implicated in maintaining the species complex (Schlupp et al., 1994). Although male sailfin mollies can discriminate between conspecific and gynogenetic females, they still mate with gynogenetic females, but they might gain some benefit because conspecific females copy the mate choice of gynogenetic females.

In this study we ask whether the male mate preference, like that of the female, is influenced by the mate choice of others, and, more specifically, if mate-copying increases the tendency to mate with heterospecifics thus further contributing to the maintenance of this asexual-sexual species complex.

MATERIAL AND METHODS

All fish were collected in 1993 from a population in central Texas (Martindale, San Marcos River), USA, and maintained in stock tanks in the laboratory or in a large outdoor breeding tank in the Brackenridge Field Laboratory, University of Texas (for housing conditions see Schlupp and Ryan, 1996). Females were matched for size ($\pm$ 1 mm).

Males of *P. latipinna* (standard length: 37.29 mm $\pm$ 2.5 mm SE) were given a choice between one conspecific and one *P. formosa* female, following the experimental methods used in Schlupp et al. (1994) (Figure 1). Each male was used as a test fish only once; some of the model fishes were used more than once. After the experiment the fish were returned to new breeding tanks.

The experimental tank (1.22 $\times$ 32 $\times$ 52 cm) was divided into five sections. The sections on each side were partitioned from the rest of the tank by Plexiglas dividers; thus water and chemical flow between the sections was absent or at least very limited. The central compartment was divided into three sections by markings drawn on the sides and bottom of the tank. Two sections were adjacent to another section containing the model female, the middle section was a neutral zone. The
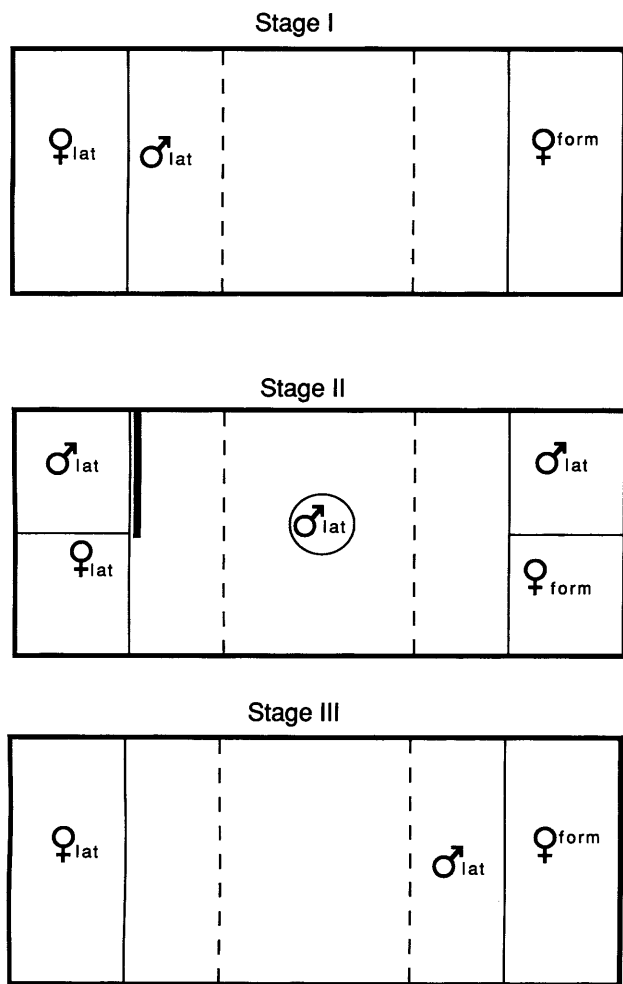
Stage I

Stage II

Stage III

Figure 1
Top view of the experimental setup, depicting the three subsequent experimental stages. lat refers to *P. latipinna*; form refers to *P. formosa*.

Figure 2
Box plot showing the preference of male sailfin mollies for conspecific females. The line in the box indicates the median, the lower end of the box the 25% value, the upper end of the box the 75% value and the two whiskers the 10% and 90% value, respectively.

male was able to move freely among these three central sections.

A complete experimental trial consisted of three subsequent stages.

Stage 1: After an acclimation period of 20 min the males were observed for 10 min and the time spent in each of the three compartments was recorded. The model females were then switched between the end compartments of the tank and the experiment was repeated to control for a potential side bias. We decided a priori that a side bias occurred when a male spent more than 80% of his time on the same side for both trials; such trials were not included in the analysis. If a male spent more than 66% of the time with one of the females he was considered to have shown a preference and was used in the experiments in Stages 2 and 3. Trials in which males had a less strong preference were terminated after Stage 1.

Stage 2: A male sailfin molly that showed a preference in Stage 1 was placed in a clear Plexiglas tube in the center of the tank. Each female compartment was divided in half, parallel to the long end of the tank. A male *P. latipinna* was placed in each of the halves of the female compartments without the female; the female was in the adjacent half. Thus both females could interact with and be stimulated by a male. The choosing male sailfin molly, in the center of the tank, could observe both females behaving. He could only see one pair
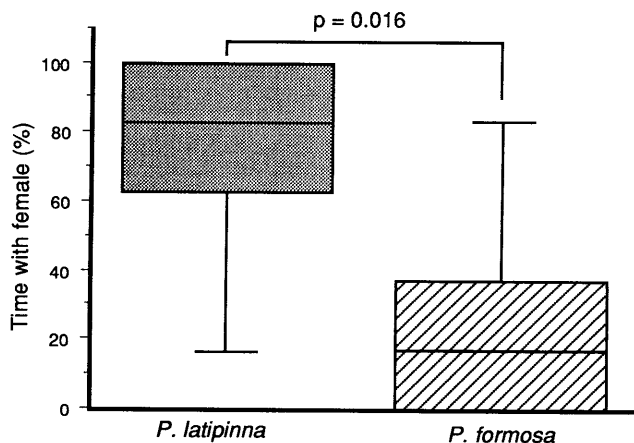
interacting, however; an opaque partition restricted him from observing one of the *P. latipinna* males. In each case the male could observe the female that was not preferred in the initial experiment consorting with a male. He could observe the previously preferred female but was restricted from seeing the male that interacted with her. This presentation stage lasted for 20 min.

Stage 3: After 20 min, the testing aquarium was returned to the original condition, and the preference test was repeated as in Stage 1 to test the null hypothesis that observing the unpreferred female consorting with a male *P. latipinna* does not influence his initial preference. Percentages were calculated from the time in the sections adjacent to a female, the time in the neutral zone was not counted.

As a control we repeated the above experiment, but in Stage 2 no *P. latipinna* males were used. In this situation no opportunity for copying was given. All *p* values are two-tailed.

RESULTS

In the first part of the experiment in which the initial preference was determined, male *P. latipinna* showed a strong preference for conspecific females (Wilcoxon test, $z = -2.39$, $p = 0.016$, $n = 17$) (Figure 2). After the opportunity to copy (Stage 2) in the mate-copying experiment, the *P. latipinna* males spent significantly more time with the heterospecific *P. formosa* females (Wilcoxon test, $z = -3.006$, $p = 0.0028$, $n = 17$) (Figure 3 A).

The control experiment with no opportunity to copy, i.e., no model males were present, revealed no differences (Wilcoxon test, $z = -0.42$, $p = 0.674$, $n = 8$) (Figure 3 B).

During the presentation in Stage 2 the choosing male saw two fishes on one side and only one on the other. However, because of the switching of sides, individuals with a shoaling tendency would have been detected as showing a side bias and thus excluded from the dataset. This is further supported by the finding that female *P. latipinna* show no shoaling behavior in comparable situations (Schlupp and Ryan, 1996).

DISCUSSION

A strong male preference for conspecific females has been well-documented in the *P. latipinna* / *P. formosa* mating complex and also in the related *P. mexicana* / *P. formosa* mating
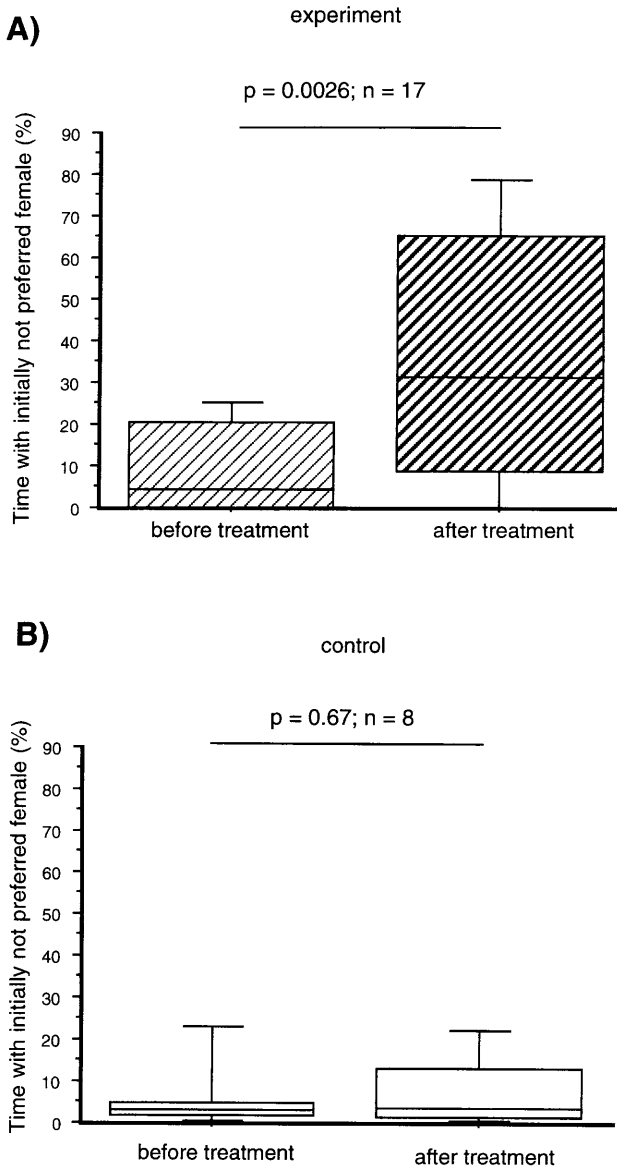
A)

B)

Figure 3
Box plot showing percentages of time male sailfin mollies have spent with the initially not preferred female before and after opportunity to copy. A: experiment, B: control. The line in the box indicates the median, the lower end of the box the 25% value, the upper end of the box the 75% value and the two whiskers the 10% and 90% value, respectively.

complex. This preference can be altered by mate-copying. If a male observes another male interact with a female, he will subsequently spend more time with her, even if it is a heterospecific female. If no opportunity for copying is provided, the preference remains unaltered. This indicates that mate-copying is exhibited by both females and males in the sailfin molly. It also indicates that just as female mate-copying contributes to the maintenance of gynogenesis, by providing a potential advantage to male mating with gynogens, male mate-copying also helps maintain gynogenesis by overriding the male's preference for conspecific females.

Currently two non-exclusive models for the adaptive significance of mate-copying are discussed (Gibson and Höglund, 1992; Höglund and Alatalo, 1995): One hypothesis is that mate-copying increases the accuracy of mate choice via a pro-

cess called the informational cascade (Bikchandani et al., 1992), the other hypothesis is that the cost of finding a mate is reduced. (Both models predict occasional mismatings.) In our study mate-copying leads to mismatings but may significantly reduce search costs, thus lending some support to the latter hypothesis.

Studies of female mate-copying, including our own, have not demonstrated any clear advantage to females. Dugatkin and Godin (1993) suggested that younger females might selectively copy older, more experienced females, presumably to avoid errors.

Potential advantages in this case of mate-copying are easier to imagine. As in most vertebrate mating systems, molly females are sexually active for shorter periods of time than males (Constantz, 1989), leading to a highly skewed operational sex ratio and thus intense mating competition among males (Emlen and Oring, 1977). Since males and the females of both species reside in shoals, males are faced with the constant need to evaluate not only the female's species but her receptivity. This is less of a problem in species that gather at a site for the sole purpose of mating, as with some birds and most frogs (Höglund and Alatalo, 1995). In such systems the operational sex ratio is also skewed, but females at the breeding site are usually ready to mate.

In mollies, a female being actively courted by a male might indicate that she is receptive, and it would behoove an unoccupied male to join others in their attempt to mate this female. Thus it is probably mate-copying that leads to the mating frenzies in mollies in which several males attempt to copulate with a female (Balsano et al., 1985; Schlupp I, personal observation). Although males can discriminate between conspecific and gynogenetic females, the cost of a mating with a heterospecific will be lower if a male does not forsake a conspecific mating to do so, a possibility that is more likely with a more skewed operational sex ratio. One corollary of this behavior is an increased potential for sperm competition.

The low cost of mating with a heterospecific, because of the skewed operational sex ratio, combined with the possibility of discrimination error as well as the potential advantage of increasing one's attractiveness to conspecifics, all might interact to promote the frequency of heterospecific matings. Thus male mate-copying, even though it might lead to heterospecific matings, might be favored by selection because it increases male mating success, but a consequence of male mate-copying might be that of promoting the continued maintenance of the gynogenetic *P. formosa*.

REFERENCES

Balsano JS, Randle EJ, Rasch EM, Monaco,PJ., 1985. Reproductive behavior and the maintenance of all-female *Poecilia*. Env Biol Fish 12:251–263.

Balsano JS, Rasch E.M, Monaco PJ, 1989. The evolutionary ecology of *Poecilia formosa* and its triploid associate. In: Ecology and evolution of livebearing fishes (Poeciliidae). (Meffe GK, Snelson FFjr, eds). New Jersey, Prentice Hall; 277–298.

Bikchandani S, Hirshleifer D, Welch I, 1992. A theory of fads, fashion, custom and cultural change as information cascades. J Polit Econ 100:992–1026.

Constantz GD, 1989. Reproductive biology of poeciliid fishes. In: Ecology and evolution of livebearing fishes (Poeciliidae). (Meffe GK, Snelson FFjr, eds). New Jersey, Prentice Hall; 277–298.

Dugatkin LA, 1992 Sexual selection and imitation: Females copy the mate choice of others. Am Nat 139:1384–1389.

Dugatkin LA, Godin J-G J, 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). Proc R Soc Lond B 249: 179–184.

Dugatkin LA, Godin J-G J, 1993. Female mate-copying in the guppy (*Poecilia reticulata*): age-dependent effects. Behav Ecol 4:289–292.

Emlen ST, Oring LW, 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215–223.

Gibson RM, Höglund J. 1992. Copying and sexual selection. Trends Ecol Evol 7:229–232.

Höglund J, Alatalo RV, Gibson RM, Lundberg A, 1995. Mate-choice copying in black grouse. Anim Behav 49:1627–1633.

Höglund J, Alatalo RV, 1995. Leks. Princeton, New Jersey: Princeton University Press.

Hubbs C, 1964. Interactions between bisexual fish species and its gynogenetic sexual parasite. Bull Tex Mem Mus 8:1–72.

Hubbs CL, Hubbs LC, 1932. Apparent parthenogenesis in nature in a form of fish of hybrid origin. Science 76:628–630.

Kirkpatrick M, Dugatkin LA, 1994. Sexual selection and the evolutionary effects of copying mate choice. Behav Ecol Sociobiol 34: 443–449.

Pruett-Jones SG, 1992. Independent versus non independent mate choice: do females copy each other? Am Nat 140:1000–1009.

Ryan MJ, Dries, L, Batra P, Hillis DM. Male mate preferences in a gynogenetic species complex (*Poecilia latipinna—P. mexicana—P. formosa*). Anim Behav, in press.

Schartl M, Wilde B, Schlupp I, Parzefall J, 1995a. Evolutionary origin of a parthenoform, the Amazon molly, *P. formosa*, on the basis of a molecular genealogy. Evolution 49:827–835.

Schartl M, Nanda I, Schlupp I, Wilde B, Epplen JT, Schmid M, Parzefall J. 1995b. Incorporation of subgenomic amounts of DNA as compensation for mutational load in a gynogenetic fish. Nature 373:68–71.

Schlupp I, Parzefall J, Schartl M, 1991. Male mate choice in mixed bisexual/unisexual breeding complexes of *Poecilia* (Teleostei; Poeciliidae). Ethology 88:215–222.

Schlupp I, Marler C, Ryan MJ, 1994. Benefit to male sailfin mollies of mating with heterospecific females. Science 263:373–374.

Schlupp I, Ryan MJ, 1996. Mixed species shoals and the maintenance of a sexual-asexual mating system in two species of mollies, *Poecilia latipinna* and *P. formosa*. Anim Behav 52:885–890.

Turner BJ, 1982. The evolutionary genetics of a unisexual fish, *Poecilia formosa*. In: Mechanisms of speciation. Barigozzi C (ed). New York: Alan R. Liss.

Wade MJ, Pruett-Jones SG, 1990. Female copying increases the variance in male mating success. Proc Natl Acad Sci USA 87:5749–5753.