The influence of experience on mating preferences of the gynogenetic Amazon molly

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Abstract. The role of experience in shaping individual female mating preferences has been relatively neglected. The goal of this study was to examine how female mating preferences are shaped through male–female interactions in the clonally reproducing female gynogenetic fish, *Poecilia formosa*. In visual choice tests, some *P. formosa* preferred *P. latipinna* males and others preferred males of another poeciliid species, *Xiphophorus multilineatus*. After interacting with the same males, but without a transparent barrier between them, females originally preferring *X. multilineatus* switched their preference to *P. latipinna* males. Females can therefore change their preferences based on experience. The degree of male sexual behaviour may contribute to this change in preferences, but the direct cause is unknown. As a control, we examined how experience influenced preferences of *P. latipinna* and *P. formosa* females that had originally preferred *P. latipinna* males. Female preferences of the sexual species *P. latipinna* were statistically indistinguishable from preferences of *P. formosa* with an initial preference for *P. latipinna* males. The preferences of these two female groups were not influenced by interactions with their preferred male (*P. latipinna*). The post-encounter preferences of *P. formosa* females that originally preferred *X. multilineatus* also became statistically indistinguishable from these two groups of females. Female preference changes based on experience may also be generalized to males with similar traits. *Poecilia formosa* initially preferring *X. multilineatus* did not revert back to their original preference when exposed to a new pair of males, but demonstrated a significant decrease in the amount of time spent with *X. multilineatus* males compared with *P. latipinna* males.

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Variation in female mating preferences may be shaped through both heritable influences as well as interactions with the environment (reviews by Hepper 1991; Ritchie 1992). One area receiving considerable attention is the role of social influences, particularly that of mate-copying behaviour (Gibson & Hoglund 1992; Hoglund et al. 1995). A number of studies support the importance of mate-copying behaviour; that is, females of several species copy the mating preferences of other conspecific females. Other interactions are also likely to influence female mating preferences, including individual encounters with males.

Mating preferences can be influenced by experience during development to avoid inbreeding (reviewed in Bateson 1983; Hepper 1991; Brown & Eklund 1994). Males can also form mating preferences for receptive versus non-receptive females based on experience (e.g. Taylor & Dewsbury 1988), and the social environment may impact male sexual behaviour in populations of Trinidadian guppies (Rodd & Sokolowski 1995). Thus experience may influence mating preferences in several ways.

In this study, we examined whether an adult female's visual preferences for a male would be influenced by directly interacting with him. We initially examined this question in a species with female preferences for mates with very different traits, the gynogenetic Amazon molly, *Poecilia formosa*. This all-female species has an unusual mating system; although each offspring is a

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genetic clone of its parent, sperm from a male is required to activate the eggs (Hubbs & Hubbs 1932; Turner 1982; Avise et al. 1991). *Poecilia formosa* is thought to result from hybridization between *P. latipinna* and *P. mexicana*, and *P. formosa* is usually found sympatrically with one of its presumed parental species. Mating complexes between *P. formosa* and its host species have been investigated in several studies under natural conditions (Rasch et al. 1970; Balsano et al. 1972, 1981, 1985; Menzel & Darnell 1973; Rasch & Balsano 1974; Woodhead & Armstrong 1985). The eggs of *P. formosa* have been activated by the sperm of a number of other poeciliid species under laboratory conditions, including *P. sphenops*, *P. vittata* and *Gambusia affinis* (reviewed in Schultz 1989).

We took advantage of the finding that approximately 40% of the *P. formosa* collected from the San Marcos River in Texas prefer *X. multilineatus* over sympatric *P. latipinna* males in visual preference tests (C. A. Marler, C. Foran & M. J. Ryan, unpublished data). This finding provided us with a population of individuals with distinctive variations in preferences. *Xiphophorus multilineatus* is also in the poeciliid family, but is more distantly related to *P. formosa* (Parenti & Rauchenberger 1989) and, to our knowledge, is not sympatric with *P. formosa*. Our first goal was to determine whether female preferences in a visual choice test between two males of different species would change after physically interacting with these males without a barrier between them. Females were allowed to visually choose between male *X. multilineatus* and *P. latipinna*, and females preferring males of one species over the other were identified (see Results). Females were then allowed to interact with the two test males without a barrier between them, after which they received a second visual choice test to test for changes in preference. Next we determined whether a change in preference was generalized to males with similar characteristics. Specifically, we examined whether a species preference would be generalized to a new pair of male *X. multilineatus* and *P. latipinna*. Finally, we examined the rates of attempted copulation by *P. latipinna* and *X. multilineatus* males towards *P. formosa* to test the hypothesis that the behaviour of the males of these two species towards *P. formosa* differs and therefore might provide a potential explanation for changes in female preference.

METHODS AND MATERIALS

Choice tests were performed by placing females in the middle of an aquarium ($45 \times 90 \times 41$ cm) divided into five equal sections with two end sections separated from the middle three by Plexiglas partitions (Ryan et al. 1990). One male was placed in each end section and the test female was placed in a lowered opaque cylinder in the centre section and allowed to acclimate for 10 min. The cylinder was raised and the amount of time the female spent in the sections adjacent to the males and in the middle neutral arena was recorded for 10 min. The female was then placed back in the cylinder, test males were switched to opposite sides of the aquarium, and the procedure was repeated to reveal any side biases.

Choice tests were performed with three groups of females: *P. formosa* that preferred *X. multilineatus* over *P. latipinna* males (M-*formosa*), *P. formosa* that preferred *P. latipinna* over *X. multilineatus* males (L-*formosa*), and *P. latipinna* females. *Poecilia formosa* and *P. latipinna* were collected from the San Marcos river in Texas, where *P. formosa* were introduced from the lower Rio Grande valley (Courtenay & Meffe 1989). All females had the opportunity to be exposed to *P. latipinna* males because they were collected from populations including *P. latipinna* males, but none had been exposed to *X. multilineatus* males. *Xiphophorus multilineatus* were offspring of gravid females collected in the Rio Coy south of Ciudad Valles, San Luis Potosi, Mexico. No male was used more than once for each group of females.

We first tested *P. formosa* and identified nine M-*formosa* females and 10 L-*formosa* females. Ten *P. latipinna* females were also chosen (females from this species prefer *P. latipinna* males over *X. multilineatus* males; C. A. Marler, C. Foran & M. J. Ryan, unpublished data). A female was categorized as preferring a male if she spent more than 50% of her time during the choice test associated with a male. There was no significant difference in the standard body length of M-*formosa* and L-*formosa* females (two-tailed *t*-test, $t_{17}=1.26$, $P=0.22$). Male *P. latipinna* and *X. multilineatus* were matched for size in the preference tests of L-*formosa* ($t_{18}=0.48$, $P=0.64$), M-*formosa* ($t_{16}=-0.17$, $P=0.87$), and *P. latipinna* females ($t_{18}=0.08$, $P=0.98$).

Table I. Results of *t*-tests comparing time (s) spent with *X. multilineatus* and *P. latipinna* males in visual choice tests within each of the three groups of females

	X. multilineatus	*P. latipinna*	*N*	*t*	*P*
M-*formosa*	687 ± 58	329 ± 28	10	4.31	0.002
L-*formosa*	245 ± 43	778 ± 53	10	-2.34	0.04
P. latipinna	351 ± 57	670 ± 82	9	-5.96	0.0003

The number of seconds was the time spent associated with each male during a 10-min trial.

Females within each of the three sets of females received three choice tests. The first choice test was between a pair of *P. latipinna* and *X. multilineatus* males (day 1, 7 June–17 July). We then moved the female to a 20-litre aquarium without barriers and allowed the female to interact with the same pair of males for 3 days (days 2–4). The next day (day 5) females received a second choice between the same pair of males, after which females were isolated. Finally, on the last day (day 6), females received a third choice test between a new pair of *P. latipinna* and *X. multilineatus* males.

Prior to the choice tests, we quantified the number of mating attempts made by male *P. latipinna* and *X. multilineatus* towards *P. formosa*. Fertilization in these species is internal, and the male intromittent organ is the gonopodium. A male swims to the side of the female and attempts to insert his gonopodium into the gonopore of the female (gonopodial thrust). To measure the frequency of gonopodial thrusts, a male, either a *P. latipinna* or *X. multilineatus*, and a female *P. formosa* were placed in a tank ($41 \times 20 \times 25$ cm) in which the two fish were separated by a clear plastic barrier. The pair was permitted to interact visually for 30 min. The barrier was then removed and the number of gonopodial thrusts was recorded for 10 min. Males and females were housed separately for over 1 week prior to the test. Females used to document frequency of male mating attempts were not used in the choice tests.

We used parametric statistics to describe the initial preferences in the visual choice tests; thereafter, we used non-parametric statistics to compare ratios of time spent with *X. multilineatus* and *P. latipinna* males between different choice tests and between groups of females.

RESULTS

Initial Female Preferences (Choice Test 1)

Female preferences were examined in three groups of females (Table I). M-*formosa* females spent significantly more time with *X. multilineatus* than with *P. latipinna* males. In contrast, L-*formosa* spent significantly more time with *P. latipinna* than *X. multilineatus* males, as did the *P. latipinna* females. Thus one group of females originally preferred *X. multilineatus* males in visual choice tests (M-*formosa* females), and two groups of females originally preferred *P. latipinna* males (L-*formosa* and *P. latipinna* females).

Effect of Experience (Choice Tests 1 and 2)

Ratios of time spent with *X. multilineatus* and *P. latipinna* males were compared before and after physical encounters with the males for each of the three groups of females described above (Fig. 1). M-*formosa* females displayed a significant decrease in the ratio of time spent with *X. multilineatus* males to *P. latipinna* males after the physical encounter (Wilcoxon matched-pairs signed-ranks test: $Z=2.8$, $P=0.005$). In contrast, L-*formosa* females did not show a significant change in preference after the encounter ($Z=1.72$, $P=0.09$), nor did *P. latipinna* females ($Z=0.26$, $P=0.80$).

Pre- and post-encounter comparisons were also made between the three groups of females. Prior to the encounter, there was a significant difference between the three groups in the ratio of time spent with *X. multilineatus* and *P. latipinna* males (Kruskal–Wallis ANOVA by ranks: $H_2=17.63$, $N=29$, $P=0.001$), but this statistical difference disappeared after the encounter ($H_2=2.04$, $N=29$,
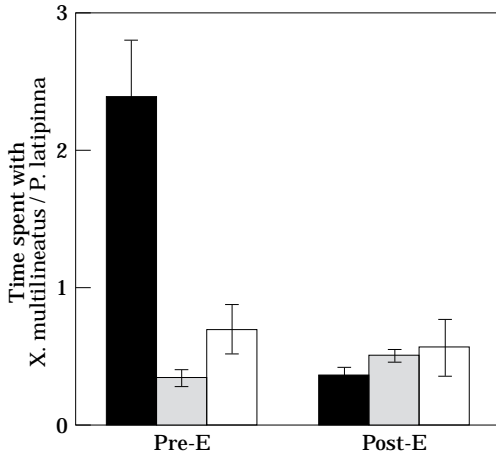
Figure 1. Ratio of time spent associated with *X. multi-lineatus* to time spent with *P. latipinna* in visual choice tests before (Pre-E) and after (Post-E) interacting with the same males without a barrier present. The three groups shown are *P. formosa* females with an initial preference for *X. multilineatus* males (■, M-*formosa*), *P. formosa* females with an initial preference for *X. multilineatus* males (▨, L-*formosa*), and *P. latipinna* females (□).

Figure 2. Stereotyping of visual preferences formed by interacting with males without a barrier present. Ratios of time spent associated with *X. multilineatus* to time spent with *P. latipinna* in visual choice tests are shown before (Pre-E) and after (Post-E) interacting with the same males without a barrier present and when presented with a new pair of males (new pair). The three groups are a subset of the females shown in Fig. 1 and again include *P. formosa* females with an initial preference for *X. multilineatus* males (■, M-*formosa*), *P. formosa* females with an initial preference for *X. multilineatus* males (▨, L-*formosa*), and *P. latipinna* females (□).

$P=0.36$). Prior to the encounter, the ratio of time spent with *X. multilineatus* to *P. formosa* was significantly greater in M-*formosa* than in L-*formosa* females (Mann–Whitney *U*-test: $U=0.00$, $N_1=10$, $N_2=9$, $P=0.0002$) or *P. latipinna* females ($U=7.0$, $N_1=10$, $N_2=10$, $P=0.001$), and there was no significant difference between the preferences of L-*formosa* and *P. latipinna* females ($U=27.0$, $N_1=10$, $N_2=9$, $P=0.14$).

Generalized Preferences (Choice Tests 1 and 3; Choice Tests 2 and 3)

To examine whether females generalized the change in preference for males shown after a physical encounter, a subset of the above females ($N=5$ per group) was tested in a third visual choice test with a new pair of males with similar traits; that is of the same species (Fig. 2). Comparisons were made between (1) the first (pre-encounter) and third choice tests and then (2) the second (post-encounter) and third choice tests. The ratio of time that M-*formosa* females spent with *X. multilineatus* to *P. latipinna* males was significantly decreased when they received a choice between a new pair of *X. multilineatus* and
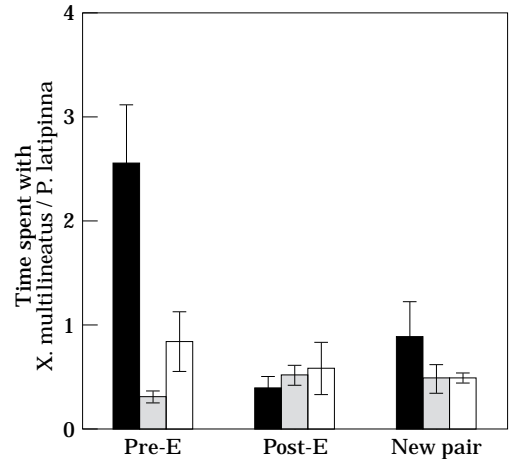
P. latipinna males, compared with the initial preference test ($Z=2.02$, $P=0.04$); thus, they did not revert back to their original preference. The ratio of time spent with *X. multilineatus* to *P. latipinna* did not change when the M-*formosa* females were able to choose between males with which they had previously interacted versus a new pair of males ($Z=1.75$, $P=0.08$). In other words, after interacting with one set of males without a barrier present, their preferences did not differ depending on whether they chose between the same set of males, or males with similar characteristics (but see discussion for potential effects of the small sample size).

We also made the same comparisons for L-*formosa* and *P. latipinna* females. In the L-*formosa* females, there was no significant difference in the ratios of time spent with *X. multilineatus* and *P. latipinna* males in either the first and third choice tests ($Z=1.21$, $P=0.25$) or the second and third choice tests ($Z=0.13$, $P=0.89$). This pattern also occurred in the

P. latipinna females, because there was again no difference between the first and third choice tests ($Z=1.21$, $P=0.25$) or the second and third choice tests ($Z=0.41$, $P=0.69$).

Copulation Attempts

We determined whether there was a difference in the sexual response of male *P. latipinna* and *X. multilineatus* towards *P. formosa* by recording the frequency of gonopodial thrusts. *Poecilia latipinna* males performed significantly more gonopodial thrusts towards *P. formosa* females ($N=6$, 7.27 ± 3.36/min) than did *X. multilineatus* males, which performed no gonopodial thrusts ($U=4.0$, $N=8$, $P=0.01$).

DISCUSSION

Our results demonstrate that experience can influence a female's mating preference. *Poecilia formosa* with an original visual preference for *X. multilineatus* males over *P. latipinna* males (M-*formosa*) switched their preference to *P. latipinna* after interacting with these males when no physical barriers were placed between them. Thus, this study provides evidence that sexually mature females may switch their preferences because of individual interactions with males. Individual interactions may not only influence the likelihood of future matings with the same males, but these mating preferences may also be generalized to males with similar traits, in this particular case, a preference for males of a particular species. The females appear to 'stereotype' potential mating partners based on past experience. It is not clear how long these preferences might endure. When tested with a new pair of males after the encounter, M-*formosa* females did not revert back to their original perference for *X. multilineatus*, but there was a non-significant trend for the preference for *X. multilineatus* to be greater than when measured with the original pair after the encounter. A significant difference might not have been found because of the small sample size of new pairs used in the tests. Therefore, we can not rule out a weakening over time of the preferences formed via experience.

In general, female preferences appear to be relatively consistent. Thus, there were no significant changes in female preferences between the three choice tests in either the *P. latipinna* females or the *P. formosa* females which preferred *P. latipinna* males (L-*formosa*). Individual female mating preferences for brightly coloured males in the Trinidadian guppy, *P. reticulata*, a species that has female mate-copying behaviour, are also repeatable and consistent (Dugatkin 1992; Godin & Dugatkin 1995). What male traits could affect a female enough to cause a change in her preferences? One potential trait is simply whether a male is likely to mate with a female. Our results are consistent with this hypothesis: male *P. latipinna* were more likely to attempt copulation with *P. formosa* than were female *X. multilineatus*. The lack of response of the *X. multilineatus* males may, however, have been a result of a fear response to the larger females of a species they had not previously encountered. Other studies will need to determine whether individual female preferences are influenced by the willingness of males to mate, as well as determine whether female *P. formosa* preferences differ in response to individual interactions with potential mates compared with bisexual species such as *P. latipinna*. An increased flexibility in mate choice would be advantageous for *P. formosa* because of the necessity of mating with males from other species. At minimum, they have formed natural mating complexes with *P. latipinna* and *P. mexicana* (Rasch et al. 1970; Balsano et al. 1972, 1985, 1981; Menzel & Darnell 1973; Rasch & Balsano 1974; Woodhead & Armstrong 1985).

Potential confounding factors could have influenced the results discussed above. The change in response to the *X. multilineatus* could potentially have been a response to repeated exposure to the same pair of males. This was not the case, because no changes in preferences occurred in L-*formosa* or *P. latipinna* females after interacting with the same pair of males without a barrier or when exposed to a new pair of males (of the same species). This result is consistent with the findings of Schlupp et al. (1994), who also found no significant change in preference between two visual choice tests using the same individuals. It is unknown whether experience is more likely to influence the preferences of *P. formosa* compared to *P. latipinna*.

The original preference for *X. multilineatus* could also have been a general response to males with novel characteristics. Females from some species will respond to novel characteristics

and show preferences for rare males (i.e. Farr 1977; Partridge 1983). Because L-*formosa* and *P. latipinna* females did not change their preferences for *P. latipinna* males over the series of choice tests, it is unlikely that this is a general response to a novel male.

Do these visual choice tests examine female mating preferences or schooling preferences? Schlupp et al. (1994) found that the visual preferences of *P. latipinna* females in the same type of laboratory set-up were not a result of schooling behaviour. Other studies within the poeciliid family also show that these visual preferences in choice tests are representative of actual mating preferences (Bischoff et al. 1985; Ryan et al. 1990; Dugatkin & Godin 1992; McPeek 1992).

This study adds to our understanding of how female preferences are formed in the gynogenetic species *P. formosa*, not only on an individual level, but also how general preferences for traits can potentially be formed through experience. Social encounters may influence female responses to males with similar characteristics and result in stereotyping. If females from other species also display this ability to modify their preferences based on male behaviour, it may provide a mechanism to avoid males with characteristics such as being energetically unable or unwilling to court females.

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