

ORIGIN AND MAINTENANCE OF A FEMALE MATING PREFERENCE

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Abstract.—We investigated the role of maintenance and origin of female mating preferences in three species of fish. *Poecilia latipinna* and *P. mexicana* are sexual species that hybridized to form the gynogenetic clonal *P. formosa*, which reproduces asexually but requires sperm to initiate embryogenesis. We demonstrate that all three species display almost identical and statistically indistinguishable preferences for large males. Although processes of good genes, runaway sexual selection, and direct selection could maintain preferences in the sexual species, good genes and runaway sexual selection are unlikely to operate in the asexual species. Furthermore, we found that the most likely direct selection benefit, an increase in fecundity, can also be excluded in the gynogens. We conclude that the most parsimonious explanation for this *P. formosa* preference is that it was inherited from the parental species and is maintained without forces generated by good genes, runaway selection, or direct selection for increased fecundity. This preference may be maintained because of pleiotropic effects (e.g., sensory bias) or mate searching costs.

Key words.—Fecundity, gynogenesis, mating preference, *Poecilia formosa*, sexual selection.

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The relative importance of origin and maintenance has been both complicated and controversial in evolutionary biology (e.g., Williams 1966; Gould and Vrba 1982; Harvey and Pagel 1991; Reeve and Sherman 1993), particularly for the evolution of female mating preferences. Most studies have focused on the maintenance of female preferences through sexual selection (Bradbury and Andersson 1987; Kirkpatrick 1987; Kirkpatrick and Ryan 1991; Andersson 1994). Hypotheses explaining how female mating preferences have evolved often center on the genetic consequences of syngamy, suggesting, for example, that females improve the quality of offspring by choosing genetically superior males (good genes hypothesis); or on the idea that genetic correlations exist between female preferences and male traits causing a runaway process (Fisher's runaway sexual selection). Direct benefits (such as increased fecundity or resources) and pleiotropy have also been proposed to explain the maintenance of female preferences (e.g., Kirkpatrick 1987; Ryan 1990; Kirkpatrick and Ryan 1991; Endler 1992). These hypotheses have been difficult to evaluate empirically because many of their predictions are not mutually exclusive (Bradbury and Andersson 1987).

In an attempt to circumvent the above difficulties, we have analyzed female choice in the sexual/asexual complex of poeciliid fish in which the asexual species is gynogenetic (Hubbs and Hubbs 1932). Two of the species are bisexual, the Atlantic molly (*Poecilia mexicana*) and the sailfin molly (*Poecilia latipinna*). These species have presumably hybridized to form the unisexual Amazon molly, *Poecilia formosa* (Hubbs and Hubbs 1932, 1964; Turner 1982; Avise et al. 1991; Scharl et al. 1995). Although the gynogenetic female *P. formosa* reproduce clonally they need to mate with males from closely related species to trigger egg activation and embryonic development. Genetic material from the sperm is generally not incorporated into the progeny's genome (Kallman 1962), although microchromosomes from the males can

be incorporated into the gynogen's genome (Scharl et al. 1995). For example, in 10^{-3} cases offspring will appear with black pigmentation if Amazon mollies are bred with black colored *Poecilia*, known as black mollies. This genetic contribution made by the males is both extremely rare and extremely small. Thus, Amazon mollies differ from the two closely related bisexual species in the genetic contributions made by males to their offspring, but the three species are ecologically similar (Hubbs 1964; Balsano et al. 1981; Balsano et al. 1985; Rasch and Balsano 1989) and are therefore ideal for species comparisons. Most importantly for this study, the peculiarities of this sexual/asexual system virtually eliminate the potential for runaway sexual selection and good genes in maintaining female mating preferences in the gynogenetic species.

In this study we examined a common female preference found in numerous animal taxa: the preference for large males (Ryan and Keddy-Hector 1992). While male size is frequently under sexual selection by female choice, it is again often difficult to distinguish between hypotheses typically proposed to explain such a preference. We addressed two questions. To what extent do the sexual and asexual species differ in their preferences for larger males? And, does this preference result in direct selection on the gynogenetic species through fecundity effects?

MATERIALS AND METHODS

To examine the size preferences of females of each species, we gave females a choice between two males differing in standard body length by an average of 10.0 ± 0.7 mm. *P. formosa* ($N = 13$, mean standard length \pm SE = 45.9 ± 1.9 mm, range = 34.8–54.4 mm) and *P. latipinna* ($N = 13$, mean standard length \pm SE = 38.04 ± 1.3 mm, range = 28.4–44.3 mm) were caught in the San Marcos River in Texas where both species have been introduced (and where *P. mexicana* is absent, Courtenay and Meffe 1989); and *P. mexicana* ($N = 16$, mean standard length \pm SE = 34.64 ± 0.97 mm, range = 27.7–39.5 mm) were acquired from a stock origi-

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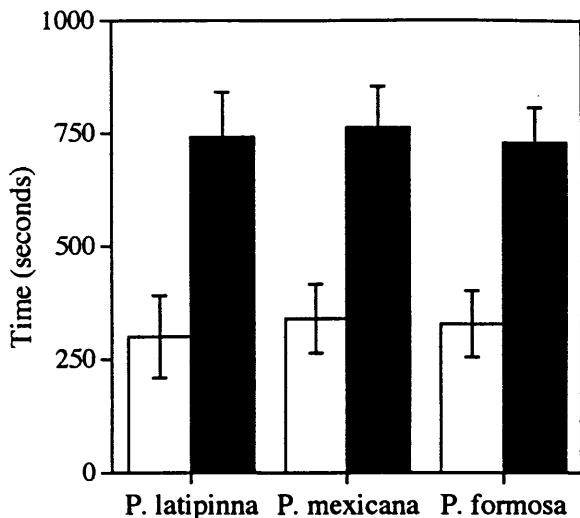


FIG. 1. Preferences of *Poecilia latipinna*, *P. mexicana*, and *P. formosa* for large versus small males. The Y-axis represents the amount of time (out of a total of 1200 min, 600 min. per side) females spent associated with each size class of males when presented with a choice between large (closed bars) and small (open bars) male *P. latipinna*.

nating in the Rio Soto la Marina basin in Mexico. Females were placed in the middle of an aquarium (45 × 90 × 41 cm) divided into five equal sections with two end sections separated from the middle three by a plexiglass partition. One test male was placed in each end section and the test female was placed in a lowered opaque cylinder in the center 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 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. Female *P. latipinna* and *P. formosa* were given a choice between large and small *P. latipinna* males and *P. mexicana* females were given a choice between large and small *P. mexicana* males. Paired t-tests were used to compare amount of time females spent with large and small males; in the choice tests females can occupy the middle section of the test aquarium, therefore making the times spent with each male independent of each other.

To examine whether these choice tests represent mating preferences we also used the above procedures to allow females to choose between a male and female. The reasoning is that if the preference is a schooling preference and not a mating preference, then females are not predicted to preferentially associate with males. In addition, females of *P. latipinna* and *P. formosa* both school with conspecific females in the field and laboratory (Schlupp and Ryan, 1996).

We determined whether fecundity advantages maintain this preference for large males in the asexual gynogens by comparing the number of offspring produced by females mated to large versus small males. We paired 20 mature virgin females with 10 large (mean standard length ± SE = 41.06 ± 1.75 mm, range = 36.35–47.8 mm) and 10 small *P. latipinna* males (mean standard length ± SE = 23.38 ± 0.82, range

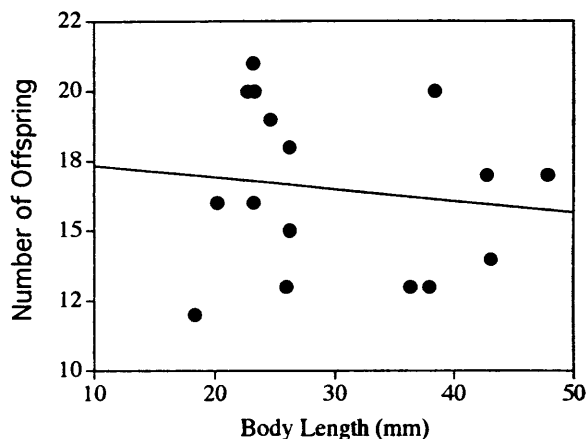


FIG. 2. Number of offspring produced by female *P. formosa* when mated to either small or large males. There was no significant difference in the number of offspring produced by small versus large males in the first brood.

= 18.31–26.2 mm) in 25 × 40 × 20 cm aquaria. There was no difference in size of females mated with large (mean standard length = 32.47 ± 0.63 mm) and small males (mean standard length ± SE = 31.86 ± 0.43 mm, Mann-Whitney U-test, U = 21.0, P = 0.37). Males were removed from the tanks before females gave birth. Females were checked at least once per day for offspring.

RESULTS

In the visual choice tests, *P. formosa* females spent significantly more time associated with male *P. latipinna* (605.9 ± 66.6 sec) than with female *P. latipinna* (294.1 ± 66.6 sec). This validates our measure of association because it measures mating preferences. When females from the sexual species, *P. latipinna* and *P. mexicana*, were given a choice between large and small males, they spent twice as much time with large males as compared to small males (see Fig. 1, paired t-test, *P. latipinna*: $t = 2.361$, $N = 13$, $P = 0.04$; *P. mexicana*: $t = 2.534$, $N = 16$, $P = 0.02$). Remarkably, the hybrid gynogens, *P. formosa* also spent twice as much time with large males (see Fig. 1, $t = 2.660$, $N = 13$, $P = 0.02$). The degree of preference for large males is essentially identical among the three species: there were no statistically distinguishable differences in the amount of time females from the three species spent with large males (analysis of variance, $F = 0.063$, $P = 0.93$) or with small males ($F = 0.039$, $P = 0.96$).

Poecilia formosa mated with large males did not produce significantly more offspring in the first brood ($X = 15.7 ± 1.67$) than those mated with smaller males ($X = 17.0 ± 0.98$, Mann-Whitney U-test, U = 23.0, P = 0.49), nor was there any correlation between male body size and number of offspring (see Fig. 2). When the second brood was included in the analysis, there was again no significant difference in the number of offspring produced by *P. formosa* mated with large males ($X = 19.0 ± 4.21$) compared to small males ($X = 24 ± 4.3$, U = 17.0, P = 0.18). Moreover, on an individual basis, large males were no more successful at producing offspring than smaller males in the first brood (6/10 successful matings in large males, vs. 10/10 successful in small males).

In fact, the small males were significantly more likely to produce a brood than the larger males (Fisher exact p test, $p = 0.04$).

DISCUSSION

Hypotheses explaining preferences for larger males have been difficult to exclude in many studies. We approached this problem by combining the use of phylogenetic constraints with studies of trait maintenance. We also use the unusual characteristics of the gynogenetic/sexual complex of poeciliid fish to exclude several potential hypotheses for the current maintenance of the traits. This allows us to elucidate several aspects of the evolution of mating preferences within the gynogenetic fish, *P. formosa*.

Female preference for larger males was also found in all three species of this gynogenetic/sexual complex of poeciliid fish using visual choice tests. We found a significant preference for larger males in the sexual species *P. latipinna* and *P. mexicana*, as well as in the asexual gynogen, *P. formosa*. That such choice tests provide an accurate indication of mating preference has been previously documented (Ryan et al. 1990a; McPeck 1992) and further validated in this study by showing that *P. formosa* displayed a preference for males over females using the same protocol.

What selection pressures might maintain this preference for large males? Commonly invoked explanations for preferences for large males are, as previously noted, good genes, Fisher's runaway sexual selection, direct selection for increased fecundity (e.g., Reynolds and Gross 1990; Kirkpatrick and Ryan 1991) and pleiotropic effects such as sensory biases (Kirkpatrick 1987; Ryan 1990; Kirkpatrick and Ryan 1991; Endler 1992). For both the sexual and the asexual species, direct selection mechanisms influencing fecundity can be relatively easily tested. We found no significant difference in the number of offspring produced by large versus small males when mated to *P. formosa*. Although not measured, it is unlikely that a difference in the size of the offspring existed; as previously mentioned, in this system males do not generally contribute genetic material to the offspring. This is unlike sexually reproducing species of fish (reviews by Reznick and Miles 1989; Travis 1989; Trexler 1989) or the clonal *Poeciliopsis* (reproduces via genome exclusion) in which syngamy occurs (Miller and Schultz 1959; Weeks and Gaggioti 1993).

Findings from other studies also provide little evidence supporting a direct fecundity advantage; for example, there are no differences in sperm production between large and small *P. mexicana* (Monaco et al. 1981). Males do not provide any obvious resources for females; these females are live-bearing, thus no nesting sites are needed (Parenti and Rauchenberger 1989). Females do not appear to gain access to foraging areas by mating with males (Baird 1968). Thus, to our knowledge, males cannot provide any material benefits that influence female size preferences. There are direct selection benefits that are less likely to influence preference, but cannot be eliminated, such as size-related predation (e.g., Reznick and Endler 1982). It is unlikely, however, that predation would be similar in all populations examined (i.e.,

most predators targeting small males) and result in these statistically indistinguishable preferences.

While testing direct mechanisms for female choice can be relatively straightforward, testing indirect mechanisms, such as good genes and runaway sexual selection, has been difficult, especially in sexual species such as *P. latipinna* and *P. mexicana*. However, the special features of the asexual *P. formosa* system make it possible to exclude the good genes hypothesis because males make at most only an extremely small genetic contribution to the offspring and then only rarely (Schartl et al. 1995). Runaway selection can also be excluded because it requires a genetic correlation between male display traits and mating preference, yet there are no male *P. formosa*. Thus while good genes and runaway selection may still explain large-male preferences in the sexual species, it is unlikely that these mechanisms continue to operate in the asexual species (Hubbs 1964; Balsano et al. 1981; Balsano et al. 1985; Rasch and Balsano 1989).

What, then, is the basis for the size preference of *P. formosa*? The preference does not appear to be a result of mate copying behavior among species (e.g., Schlupp et al. 1994) or experience with males from other species (e.g., Marler and Ryan 1997) because lab-reared fish raised apart from other species display similar preferences (J. Travis, pers. comm. 1996). The simplest, most parsimonious explanation is that the size preference was inherited from *P. latipinna* and *P. mexicana*, the ancestors of *P. formosa*, just as testosterone-dependent traits have also been inherited by these gynogenetic females (Turner and Steeves 1989; Schartl et al. 1995). As we have shown, the three species display a statistically indistinguishable preference for large males. Females of *P. mexicana* collected in Mexico and *P. latipinna* collected from an introduced population in Texas do not differ in their preferences; females of *P. formosa* formed by a hybridization event 10,000 to 100,000 years ago (Darnell and Abramoff 1968; Avise et al. 1991) do not differ from the two parental species, *P. latipinna* and *P. mexicana*. The preference for large males may even have originated in the ancestors of the poeciliids because the preference for large males is also characteristic of other species in this family (Hughes 1985; Zimmerer and Kallman 1989; Ryan et al. 1990a; McPeck 1992), although it is not known if these preferences are statistically indistinguishable from those tested in this study. Other studies suggest that mating preferences can be inherited within a species (review by Ritchie 1992). Our data suggest that some mating preferences can also be strongly conserved between closely related species.

Given that the hybrid *P. formosa* originated 10,000–100,000 years ago (Darnell and Abramoff 1968; Avise et al. 1991; Schartl et al. 1995), why has preference for large size been maintained over 30,000–300,000 generations if good genes, runaway selection, and selection for increased fecundity are not operating? Experience from quantitative genetics suggests that this is ample time for mutations for small male preference to appear (Hill 1982a,b; Hill and Rasbash 1986). For example, there is empirical evidence that mutations have resulted in considerable genetic variation in the clonal killifish *Rivulus marmoratus* and that divergence between clones may potentially have been mediated by natural selection (Turner et al. 1992). Thus it appears likely that there has been

sufficient time for natural selection to alter female preference for large males.

What potential mechanisms could maintain this preference? Selection would favor preference for more visually conspicuous males if this preference reduces search costs for the females (Reynolds and Gross 1990; Kirkpatrick and Ryan 1991). As mentioned earlier, some direct selection benefit of preference for large males may exist that we have not identified, but that would somehow result in the same levels of preference among the different species. The female preference might also be maintained because of pleiotropic effects; that is, there may have been selection for a greater response to larger objects in contexts other than mating (e.g., predation or foraging, Ryan 1990; Kirkpatrick and Ryan 1991; Endler 1992). This possibility of a sensory bias is especially intriguing because if the bias arose in the ancestors of the poeciliids, then sensory exploitation (Ryan 1990; Ryan et al. 1990b) may explain the origin of a preference for large males, setting in motion the evolution of larger male morphs in some species. This hypothesis is supported by the lack of a statistical difference in preferences between species in this study, evidence of preferences for larger males in other species in the family Poeciliidae (Hughes 1985; Zimmerer and Kallman 1989; Ryan et al. 1990a; McPeck 1992), and evidence from another population of *P. latipinna* demonstrating a preference for larger males (Schlupp et al. 1994).

A final possibility is that the costs of mating with large males may be so small that insufficient time has passed to result in loss of the trait. However, it is important to note for all of these hypotheses that selection against a preference for large males could potentially be strong because females mated to large males were less likely to produce offspring than those mated to small males (perhaps indicating that large males may be more discriminating in mate choice than smaller males). We suggest that this inherited female mating preference for large males in Amazon mollies is not maintained by runaway sexual selection, good genes, or direct selection for increased fecundity, but that it could be maintained by pleiotropic effects or mate searching costs.

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