



Benefit to male Sailfin Mollies of Mating with Heterospecific Females

Ingo Schlupp, Cathy Marler, Michael J. Ryan

Science, New Series, Volume 263, Issue 5145 (Jan. 21, 1994), 373-374.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Science is published by The American Association for the Advancement of Science. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aaas.html>.

Science

©1994 The American Association for the Advancement of Science

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2000 JSTOR

Benefit to Male Sailfin Mollies of Mating with Heterospecific Females

Ingo Schlupp,* Cathy Marler, Michael J. Ryan†

Female gynogens reproduce clonally but rely on sperm from heterospecific males to initiate embryogenesis. It has been assumed that males gain no benefit from such matings; thus, selection should favor males that avoid them. Here it is shown that males gain a benefit by mating with female gynogens in an asexual-sexual complex of fish. The sexual females increase their preference for males whom they observe consorting with female gynogens. Thus, gynogenetic species might persist because selection favors males to be sexually parasitized.

An organizing principle for many fields of biology, including aspects of genetics, physiology, behavior, and evolution, is that males should not mate with females of other species because viable offspring usually do not result. Mating with heterospecifics should therefore decrease a male's fitness (1).

Some species, however, can persist only if males of other species mate with their females (2). Such species are all-female and reproduce asexually, but must still mate in order to reproduce. In such gynogenetic systems, reproduction results in the clonal transmission of a completely unreduced female genome, but stimulation from sperm is required to initiate embryogenesis. In all known cases, gynogenetic females acquire sperm from males of closely related species. It has been assumed that the males reduce their fitness (1) by mating with gynogens, making female gynogens sexual parasites. Selection should result in the evolutionary ability of the parasitized males to discriminate against gynogens, and when this discrimination is sufficiently accurate, the gynogenetic species would become extinct. The maintenance of gynogenetic species, therefore, has presented a serious challenge to evolutionary biologists (3).

Explanations for heterospecific matings posit that such interactions result from discrimination errors by parasitized males (4) which allow gynogenetic species to persist in spite of selection to avoid heterospecific matings. Here, we present data that negate that assumption. Our data indicate that males gain a reproductive advantage by mating with heterospecific females because it makes these males more attractive to conspecific females. The mechanism for such an advantage is mate copying (5). Studies have shown that females copy the mate choice of conspecific females; thus, by mating a male increases not only his instan-

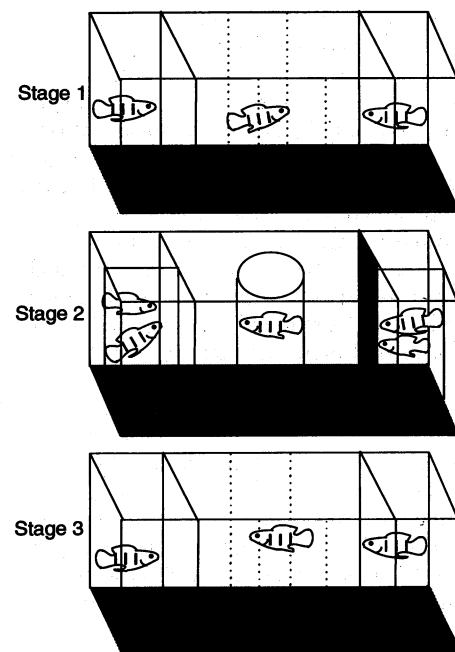
taneous reproductive success but also his future reproductive success, because unmated females will copy the choice of their just-mated female conspecific (5). We show that female sailfin mollies copy the mate choice of gynogenetic Amazon mollies, thus providing a potential benefit to males that engage in heterospecific matings. Although there might be some costs to such matings, it is now clear that there might be a sufficient reproductive advantage to outweigh these

Fig. 1. (Stage 1) A large (122 by 32 by 52 cm) aquarium was divided into five sections of equal size. The sections on each side were partitioned from the rest of the tank with clear plexiglass. These two end sections constituted the two male compartments. The three central sections were delineated by markings on the bottom and sides of the tank. The female was able to move freely among these three central sections. One male sailfin molly (*P. latipinna*; in the figure, all fish of this species are designated by vertical bars) was placed in each of the two male compartments; the males differed slightly in size. A female sailfin molly was placed in the central section and allowed to acclimate for 20 min. The amount of time the female spent in the section adjacent to each male compartment during the next 10 min was quantified. The males were then switched between the two compartments and the experiment was repeated to control for side biases. If a female spent more than 66% of the time with one of the males, she was considered to have shown a preference and was used in the experiments in stages 2 and 3. (Stage 2) The female sailfin molly was placed in a clear container in the center of the tank. Each male compartment was divided in half, parallel to the long end of the tank. A female Amazon molly (*P. formosa*, the gynogenetic species; in the figure, all fish of this species are designated by a lack of vertical bars) was placed in each of the halves of the male compartments without the male; the male was in the adjacent half. Thus, both male sailfin mollies could interact with and be stimulated by a female Amazon molly. The female sailfin molly, in the center of the tank, could observe both males behaving. She could see only one pair interacting, however; an opaque partition prevented her from observing one of the Amazon molly females. In each case, the female could observe the male that was not preferred in the initial experiment consorting with a female. She could also observe the previously preferred male but was prevented from seeing the female that interacted with him. After 20 min, the testing aquarium was returned to its original condition (stage 3) and the preference test was repeated to test the null hypothesis that observing the unpreferred male consorting with a female Amazon molly does not influence the female's initial preference. All fish were from the San Marcos River, Martindale, Texas, where the two species interact continuously, usually forming mixed-species schools.

costs. Thus, the maintenance of gynogenetic species might occur because selection favors males that mate with gynogens.

The Amazon molly (*Poecilia formosa*), named for an all-female tribe in Greek mythology, is a gynogenetic species that resulted from the natural hybridization of two sexual species of mollies, *Poecilia latipinna* and *Poecilia mexicana* (6). In northern Mexico, southeastern Texas, and an isolated population in central Texas, the sailfin molly (*P. latipinna*) and the Amazon molly (*P. formosa*) are sympatric, and female Amazon mollies must obtain sperm from sailfin mollies for successful reproduction. Whereas experiments have shown that male sailfin mollies can discriminate between their own females and the female gynogens (7), in nature heterospecific matings clearly occur; otherwise the gynogenetic Amazon mollies could not persist.

We tested the hypothesis that males gain an advantage through heterospecific matings because female sailfin mollies copy the mate choice of other females, including female gynogens. If this were so, male sailfins would benefit by mating with female Amazon mol-



Department of Zoology, University of Texas, Austin, TX 78712.

*Present address: Zoologisches Institut und Museum der Universität Hamburg, Martin-Luther-King Platz 3, D-20146 Hamburg, Germany.

†To whom correspondence should be addressed.

lies because the males would thus be more attractive to their own females.

Experimental procedures are detailed in Fig. 1. In stage 1, female sailfin mollies were given a choice between two conspecific males differing slightly in body size (mean size difference, 12.7 mm). As with some other poeciliid fishes, females often prefer larger males (8). If a female exhibited a preference, she was subsequently given an opportunity to copy the mate choice of a female Amazon molly (stage 2). In this situation, the same two males each interacted with a female Amazon molly; the female sailfin molly, although she could observe both males, was prevented from seeing the female that interacted with the previously preferred male. In a second preference test (stage 3), the same female was tested for her preference of the same two males as in the original experiment but without the presence of the Amazon molly. The null hypothesis is that the amount of time the female spends associating with the unpreferred male is not influenced by her experience; that is, the time spent with the initially unpreferred male does not differ between experiments (Fig. 1).

In the initial preference tests, the females that exhibited preferences showed a strong preference for larger males (Wilcoxon $\chi = 2.91$, $n = 20$, $P < 0.005$). Thus for a female to copy a mate choice in this experimental paradigm, she must reverse a fairly strong preference for larger males (7). After these females observed the initially unpreferred male consorting with a female gynogen, there was a significant change in preference. The amount of time a female spent associating with the initially unpreferred male exhibited a strong increase in the second preference test ($\chi = 2.99$, $n = 20$, $P < 0.005$) (Fig. 2).

We conducted several control experiments to test alternative hypotheses to explain these results. One alternative is that females are more likely to change their preference in subsequent tests independent of copying. We repeated the above experiments, which were identical in all procedures except that no female Amazon mollies were added during the middle stage of the experiments; thus, no copying could take place because the female sailfin molly did not observe males consorting with females. The amount of time spent with the initially unpreferred male did not change ($\chi = -1.27$, $n = 10$, $P = 0.20$) (Fig. 2) between the two preference tests; in fact, there was a trend for the females' initial preference to be strengthened rather than weakened. Another possible explanation for our results is that the apparent copying is due to a schooling effect. For example, the female sailfin mollies might have merely associated with the side of the tank where

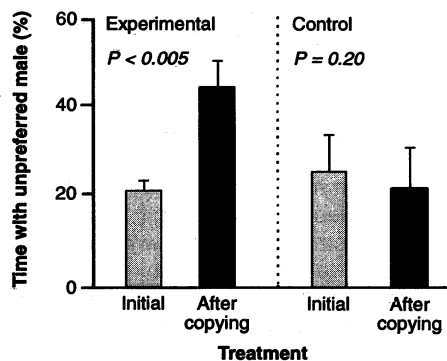


Fig. 2. In the experimental tests, the mean percent of the time (+1 SE) that female sailfin mollies (*P. latipinna*) associated with the unpreferred male in the initial mate preference experiment (initial; also see stage 1, Fig. 1), and the time they associated with initially unpreferred males after they had the opportunity to observe these males consorting with females (after copying; stages 2 and 3, Fig. 1). The control experiments are similar to the experimental tests except that in stage 2 in Fig. 1 no females were placed adjacent to the males; thus, no copying could occur.

they had observed more fish. This is not a valid explanation for these results, however, because in each preference test males are switched between sides of the tank to control for such a side bias (Fig. 1). Schooling effects could also influence our results if the female associated with the individual male she had observed with another fish, independent of any behavior related to mating. To evaluate this effect, we repeated the experiments using female rather than male sailfin mollies. The females' initial preferences were not altered by their observations during the middle stage of the experiments ($\chi = -1.27$, $n = 10$, $P = 0.20$).

In summary, these experiments demonstrate that male sailfin mollies can increase their attractiveness to conspecific females by consorting with gynogenetic Amazon mollies. It is unknown if female sailfin mollies discriminate between conspecific and gynogenetic females and, if so, why they would copy the mate choice of another species. Despite the fact that mate copying might be a widespread phenomenon, it is still not clear why females should engage in this behavior. Although our study resolves the behavioral paradox of gynogenesis for this species complex and perhaps for some other asexual-sexual complexes, many questions remain regarding the coexistence of such species complexes in ecological space (2, 3, 9) and the long-term evolutionary stability of such complexes (10). Nevertheless, our results suggest that even if male sailfin mollies were perfectly capable of discriminating between their own females and female gynogens, they still might be expected to mate with gynogens. And,

more generally, our results challenge the widely held assumption that males derive no benefits from mating with heterospecific females.

REFERENCES AND NOTES

1. C. Darwin, *The Origin of Species* (Random House, New York, 1859); Th. Dobzhansky, *Genetics and the Origin of Species* (Columbia Univ. Press, New York, 1937); J. A. Coyne, *Nature* **355**, 511 (1992).
2. R. M. Dawley, in *Evolution and Ecology of Unisexual Vertebrates*, R. M. Dawley and J. P. Bogart, Eds. (New York State Museum, Albany, NY, 1989), pp. 1–19.
3. R. J. Schultz, *Am. Zool.* **11**, 351 (1971); G. C. Williams, *Sex and Evolution* (Princeton Univ. Press, Princeton, NJ, 1975); J. Maynard-Smith, *The Evolution of Sex* (Cambridge Univ. Press, Cambridge, 1979); G. Bell, *The Masterpiece of Nature* (Croom, Helm, London, 1982).
4. F. E. McKay, *Ecology* **52**, 778 (1971); J. S. Balsano, K. Kucharski, E. J. Randle, P. J. Monaco, *Environ. Biol. Fishes* **6**, 39 (1981); N. C. Stenseth, L. R. Kirkendall, N. Moran, *Evolution* **39**, 294 (1985); A. D. Woodhead and N. Armstrong, *J. Fish Biol.* **27**, 592 (1985); J. S. Balsano, E. M. Rasch, P. J. Monaco, in *Ecology and Evolution of Livebearing Fishes*, G. K. Meffe and F. F. Snelson Jr., Eds. (Prentice-Hall, Englewood Cliffs, NJ, 1989), pp. 277–287; L. R. Kirkendall and N. C. Stenseth, *Evolution* **44**, 698 (1990).
5. S. G. Pruett-Jones and M. J. Wade, *Proc. Natl. Acad. Sci. U.S.A.* **87**, 5749 (1990); L. A. Dugatkin, *Am. Nat.* **139**, 1384 (1992); ——— and J.-G. J. Godin, *Proc. R. Soc. London Ser. B* **249**, 179 (1992); R. M. Gibson and J. Höglund, *Trends Ecol. Evol.* **7**, 229 (1992); S. G. Pruett-Jones, *Am. Nat.* **140**, 1000 (1992); T. Goldschmidt, T. C. M. Bakker, E. Feuth-de Bruijn, *Anim. Behav.* **45**, 541 (1993); T. Clutton-Brock and K. McComb, *Behav. Ecol.* **4**, 191 (1993).
6. C. L. Hubbs and L. C. Hubbs, *Science* **76**, 628 (1932); K. D. Kallman, *J. Genet.* **59**, 7 (1962); B. J. Turner, in *Mechanisms of Speciation*, C. Barigozzi, Ed. (Liss, New York, 1982), pp. 265–305; J. C. Avise, J. C. Trexler, J. Travis, W. S. Nelson, *Evolution* **45**, 1530 (1991).
7. C. Hubbs, *Bull. Tex. Mem. Mus.* **8**, 1 (1964); I. Schlupp, J. Parzefall, M. Scharl, *Ethology* **88**, 215 (1991); M. J. Ryan and D. M. Hillis, unpublished data.
8. R. J. Bischoff, J. L. Gould, D. I. Rubenstein, *Behav. Ecol. Sociobiol.* **17**, 253 (1985); M. J. Ryan and W. E. Wagner Jr., *Science* **236**, 595 (1987); A. L. Basolo, *Anim. Behav.* **40**, 332 (1990); *Science* **250**, 808 (1990); M. J. Ryan, D. K. Hews, W. E. Wagner Jr., *Behav. Ecol. Sociobiol.* **26**, 231 (1990); M. A. McPeck, *Behav. Ecol.* **3**, 1 (1992).
9. R. C. Vrijenhoek, in *Speciation and Its Consequences*, D. Otte and J. Endler, Eds. (Sinauer, Sunderland, MA, 1989), pp. 386–400.
10. M. Scharl et al., *Proc. Natl. Acad. Sci. U.S.A.* **88**, 8759 (1991); S. B. Hedges, J. P. Bogart, L. M. Maxson, *Nature* **356**, 708 (1992); J. Maynard-Smith, *ibid.*, p. 661; C. M. Spolsky, C. H. Phillips, T. A. Uzzell, *ibid.*, p. 706; J. M. Quattro, J. C. Avise, R. C. Vrijenhoek, *Proc. Natl. Acad. Sci. U.S.A.* **89**, 348 (1992).
11. Funded in part by NSF grant IBN-92-21703 and by a Reeder Fellowship (University of Texas) to M.J.R. I.S. was supported by a German Academic Exchange Fellowship and C.M. by a fellowship from the National Institute of Mental Health (F32 MH10204). We thank K. Yang, A. Schlupp, and W. Wang for assistance with the experiments and J. Bull for comments on the manuscript. We also appreciate the use of facilities at the Brackenridge Field Laboratory, University of Texas. This study is based in part on a doctoral study by I.S. in the Faculty of Biology, University of Hamburg.

7 September 1993; accepted 23 November 1993