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Evolution

Interface between culturally based preferences and genetic preferences: Female mate choice in *Poecilia reticulata*

(imitation/mate choice/culture/sociobiology)

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ABSTRACT **The relative contribution of genetic and socio-cultural factors in the shaping of behavior is of fundamental importance to biologists and social scientists, yet it has proven to be extremely difficult to study in a controlled, experimental fashion. Here I describe experiments that examined the strength of genetic and cultural (imitative) factors in determining female mate choice in the guppy, *Poecilia reticulata*. Female guppies from the Paria River in Trinidad have a genetic, heritable preference for the amount of orange body color possessed by males. Female guppies will, however, also copy (imitate) the mate choice of other females in that when two males are matched for orange color, an "observer" female will copy the mate choice of another ("model") female. Three treatments were undertaken in which males differed by an average of 12%, 24%, or 40% of the total orange body color. In all cases, observer females viewed a model female prefer the less colorful male. When males differed by 12% or 24%, observer females preferred the less colorful male and thus copied the mate choice of others, despite a strong heritable preference for orange body color in males. When males differed by 40% orange body color, however, observer females preferred the more colorful male and did not copy the mate choice of the other female. In this system, then, imitation can "override" genetic preferences when the difference between orange body color in males is small or moderate, but genetic factors block out imitation effects when the difference in orange body color in males is large. This experiment provides the first attempt to experimentally examine the relative strength of cultural and genetic preferences for a particular trait and suggests that these two factors moderate one another in shaping social behavior.**

A well-studied suite of behaviors that is almost certainly influenced by cultural as well as innate factors is a female's choice of mates. One way in which cultural selection may manifest itself in female mate choice is via imitation (1). Imitation of the choice of mates is intriguing at the conceptual and theoretical level because genetic models of sexual selection indicate that female mate choice may coevolve with the male trait being chosen (see refs. 2 and 3 for reviews). If, however, imitation plays a role in mate choice, then the dynamics of sexual selection may be influenced by cultural evolution in ways that may be distinct from genetic evolution (4, 5). Furthermore, studying culture in the context of female mate choice may also allow us to experimentally examine the evolution of a trait (female preference) when both innate and cultural factors are operating simultaneously.

Most work on female mate choice, both theoretical and empirical, has assumed that a female's preference for a particular male trait is under some sort of genetic control (sensu ref. 6). The extent to which a female's preference is affected by the preference of other females and how genetic factors and social/cultural factors (such as imitation) interact to affect the dynamics of sexual selection, particularly the coevolution of female mate choice and male traits, has only recently become the subject of study (1, 7–9).

To date, virtually all of the empirical evidence for female mate copying has been anecdotal or lacking the proper control experiments (refs. 10–12; but see refs. 13 and 14 for controlled experimental evidence that female fallow deer, *Dama dama*, do not mate copy). For example, a number of studies of female mate choice in fishes indicate that females prefer to mate with males that already have broods from prior matings (15–19). It has recently been suggested that such preferences are a sign of mate copying (20). However, these experiments are in fact rather ambiguous, as females may prefer nests with eggs, not as a mechanism for mate copying but rather because this dilutes the probability that their own eggs will be taken should a predator attack occur (1, 21, 22).

Recently, the first controlled experimental evidence for female mate copying has been found in the guppy, *Poecilia reticulata* (refs. 23–25; see ref. 1 for a review and ref. 26 for information on copying in sailfin mollies, a related species). Even though female guppies will copy each other's choice of mates, it is well known that in the absence of mate-copying opportunities, female guppies will choose between males on the basis of a number of phenotypic traits, such as size, tail length, and color pattern (refs. 27–32; see ref. 33 for a review). Given this, it seems reasonable to ask if a female's preference for a certain male can be reversed by social cues, such as information on the mate preference of other females.

Dugatkin and Godin (24) addressed this question by using a "reversal" experiment. This study comprised two treatments. In both treatments, "focal" females were allowed individually to choose between two males on two separate occasions. The treatments differed mainly in that treatment II provided the focal female with the opportunity to copy (imitate) the experimentally staged mate preference of another female (the "model"), whereas such an opportunity was not available in treatment I. In treatment I, each trial consisted of paired consecutive preference tests. In the first test, a focal female was allowed to choose between one of two males. Following this, a second preference test was carried out with the same female and the same males to determine whether females are consistent in their choice of mates.

Treatment II examined whether a female's initial choice of a mate can be altered by an opportunity to copy the mate preference of another female. The protocol of this treatment was similar to that of treatment I, with one major difference. In treatment II, after a focal female initially chose between two males in the first paired preference test, a second female was placed behind a clear Plexiglas partition in the quarter of the experimental tank adjacent to the male not chosen by the focal female in the first preference test. The focal female was then allowed to choose a second time between males, after the model female was removed. In treatment I, females consistently preferred the same male across preference tests, when compared to a null model of random choice [prior work (23)

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ruled out differential male courtship as an explanation for this effect]. When compared with the low frequency of reversals observed in treatment I, however, female guppies in treatment II reversed their initial preference for particular males significantly more often, by copying the mate choice of a nearby (model) female.

The "reversal" experiment shows clearly that social cues can alter female choice, as individual females switched their initial preference for a particular male after they had observed another female choose differently. These results suggest a unique opportunity to examine the relative influence of "innate" vs. "cultural" influences on a specific behavior—namely, female mate choice—if a similar experiment can be undertaken in a population in which females have a known heritable preference for a male trait. Guppies from the Paria River in Trinidad show just such preferences (34–36).

Despite the fact that female preference for male traits varies geographically (32, 33), females from most populations of guppies studied to date prefer orange body color in males (ref. 33; see ref. 37 for more on color vision in guppies). The most thoroughly studied population of guppies are those from the Paria River in Trinidad, West Indies (see ref. 33 for a review). Females from the Paria population prefer orange males as mates, with the strength of preference being positively correlated with the amount of orange color on a male (34, 35). When fourth and fifth generation females from both the Paria and Aripo Rivers were reared in standard laboratory conditions and subject to mate choice tests, interpopulational comparisons suggested that the preference of Paria females for orange body color in males was genetic (34). In addition, orange body color itself is heritable in Paria River males (38), and some evidence indicates that the genetic correlation between these two traits (female preference and male color pattern) in fact exists in the Paria population (36, 39), suggesting a heritable component to female preference for orange (but see ref. 40).

Given the above observations, female guppies from the Paria River population are ideally suited for an experiment in which a heritable preference for a male trait—in this case, orange body color in males—is pitted against a cultural preference in the opposite direction—here, observing other females choosing less orange males. Results can then be interpreted to examine the relative strength of genetic and cultural factors in shaping female mate choice.

MATERIALS AND METHODS

Laboratory-reared males and females descended from individuals captured in the Paria River of Northern Trinidad, West Indies, in 1991, were tested in all treatments and control trials. Because they are very receptive to male courtship, only virgin females were used. A pool of 24 males was employed for all of the trials described here. A week prior to the start of the experiments, these 24 males were anesthetized by using MS 222, and photos of each individual was taken. A Lasico (model 42-P) Planimeter was used to calculate the area of the total body length of each fish (measured from the tip of the nose to the end of the dorsal lobe of caudal fin) and the proportion of total body length covered by orange color ($\bar{x} \pm$ SD% of total body covered with orange = 14.9 ± 5.3%, range = 6.8–24.5%). Results of the experiment are not altered if standard length (measured from the tip of the nose to the end of caudal peduncle) is used in place of total body length. While males were used more than once over the course of the experiment, at least 3 days separated trials using the same individual. New virgin females were used in each trial of each treatment.

In all trials, each pair of males differed in the amount of orange body color (as measured above). Let M denote the proportion of total body length covered by orange color in the more orange of the two males used in a trial, let L denote the proportion of total body length covered by orange color in the less orange male, and let $Q = L/M$. In treatment I, males were matched for body color in that $Q = 4 \pm 2\%$. Q values for treatments II, III, and IV were 12 ± 3% 24 ± 4% and 40 ± 3%, respectively. Males in all trials were matched for total body length (i.e., were within 5% of each other's total length; range of male body sizes = 17.1–19.2 mm). In addition, females in any given trial were also matched for size (range of female body sizes = 20–23.7 mm).

The experimental apparatus is shown in Fig. 1. In each trial, an "observer" female was placed in the central Plexiglas cylinder (section A) and given 30 min to acclimatize, during which time opaque partitions (E) blocked her view into both male chambers (B). After the acclimation period, a second female—the "model" female—was placed behind a clear Plexiglas partition (D) near one of the two males (C). In all treatments, the model female was always placed near the less orange of the two males; hence, if a focal female were imitating the model, less orange males would be preferred by the focal female. [Houde (34) found no correlation between the amount of orange on a male's body and its intensity when courting.]

Following the placement of the model into the experiment tank, the opaque partitions (sections E in Fig. 1) were removed (by using a motorized pulley system that did not appear to disturb the fish), and the two males and the model female were in view of the observer female for a period of 10 min. Although the model female was not allowed to freely choose between the

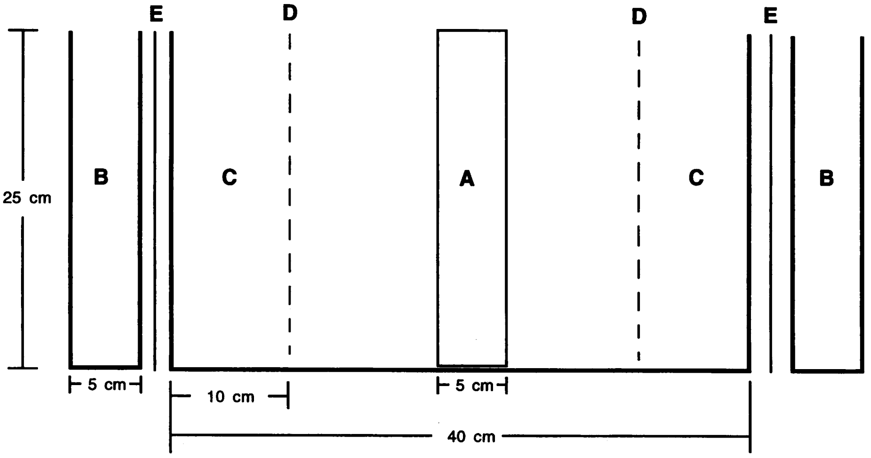

FIG. 1. Side view of the experimental apparatus, consisting of a rectangular aquarium (40 × 20 × 25, L × W × H) with a clear Plexiglas rectangular container juxtaposed against each of its ends. Sections: A, central Plexiglas cylinder; B, male chambers; C, area into which model was placed; D, clear Plexiglas partition; and E, opaque partitions.

males (as she was always placed in an area near the less orange male), the courtship behavior displayed by the model female and the male nearest her was stereotypical guppy courting behavior (41) and thus provided an opportunity for the focal female to see the model apparently "choose" a male. After this "viewing period," the model female was taken from the arena and motorized pulleys removed both the Plexiglas partition that kept her near one of the two males (D) and the Plexiglas cylinder that housed the observer female (A). Fish behavior was viewed by using a video camera (coupled to a television monitor) mounted behind a black curtain 91.5 cm from the apparatus.

The amount of time the observer female then spent in the preference zone (area C) associated with each male (Fig. 1) was recorded for 10 min. During this period, both males and females displayed typical courtship activities (41, 42), with males exhibiting sigmoid displays to females and females showing the "gliding" motion typically associated with courtship. [Houde (34) found no correlation between male courtship behavior and position relative to the female during the first part of a trial.] The focal female was classified as "preferring" a particular male if over the course of the test she spent more time in the preference zone of that male compared with the other male (i.e., time spent outside both preference zones was not used to determine female choice). The mate choice of individual female guppies determined by such a preference test is known to correlate well with their choice of mate when actual mating is allowed (25, 28).

Controls for each treatment were run in which the protocol was identical to that of the given treatment, except that no model female was present. The same pairs of males tested in the treatment were tested in the controls, but new females were used.

RESULTS

In the control for treatment I ($Q = 4 \pm 2\%$), females randomly chose between males: females preferred more orange males in 9 of 20 trials (*G*-test, adjusted *G* value = 0.2, df = 1, $P > 0.5$). In the controls for treatments II, III, and IV, females consistently preferred males with more orange body color; in the control for treatment II, females preferred more orange males in 17 of 20 trials (adjusted *G* value = 10.6, df = 1, $P < 0.005$); in the control for treatment III, females preferred more orange males in 18 of 20 trials (adjusted *G* value = 14.4, df = 1, $P < 0.001$); and in the control for treatment IV, females preferred more orange males in 18 of 20 trials (adjusted *G* value = 14.4, df = 1, $P < 0.001$; see Fig. 2).

The results of the treatments themselves are clear (Fig. 2). Treatment I shows that when males are matched for orange color, females imitate one another: treatment I females preferred more orange males in only 3 of 20 trials vs. 9 of 20 trials in the control (adjusted *G* value = 8.0, df = 1, $P < 0.005$). When males differ in orange body color by an average of 12% or 24% (treatments II and III, respectively), females consistently prefer the less orange of the two males: treatment II females preferred more orange males in 3 of 20 trials vs. 17 of 20 trials in the control (adjusted *G* value = 47.4, df = 1, $P < 0.001$), whereas treatment III females preferred more orange males in 4 of 20 trials vs. 18 of 20 trials in the control (adjusted *G* value = 51.2, df = 1, $P < 0.001$); hence, imitation overrides a female's genetic preference for male orange body color. However, when male orange body color differs by an average of 40% (treatment IV), females consistently prefer the more orange of the two males, thus overriding any effects of imitation: treatment IV females preferred more orange males in 16 of 20 vs. 18 of 20 in the control (*G*-test, adjusted *G* value = 1.73, df = 1, $P > 0.1$). Prior work (23) has shown that neither activity patterns of males nor spatial position of males relative to the female can explain any of the results outlined above.

DISCUSSION

It has been notoriously difficult for behavioral ecologists and evolutionary biologists to experimentally examine the relative

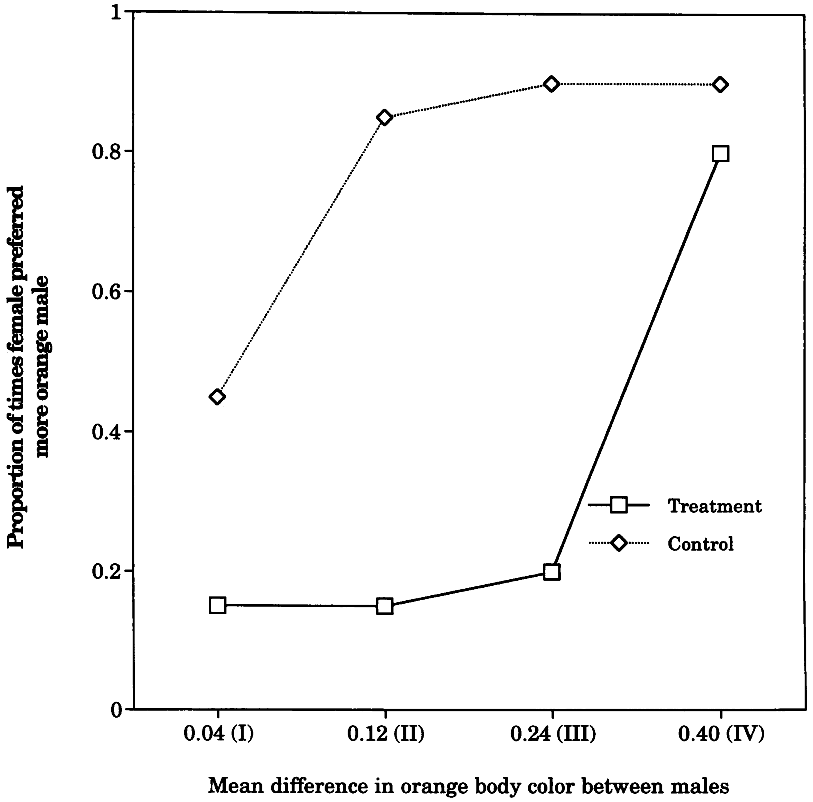

FIG. 2. The proportion of times females preferred the more orange of the two males. "Treatment" refers to cases in which an observer female saw the less orange male adjacent to the model female, and "Control" refers to the trials in which a female did not observe the mate choice of any other individuals.

effect of genetic and cultural elements on the manifestation of behavior. However, the results presented here indicate that for at least some sexually selected traits, it may be possible to experimentally examine the relative strength of both cultural (here imitative) and genetic effects on female mate choice. In the case of female mate preference for orange color in male guppies, cultural cues via imitation can "override" genetic preferences for more orange males, when males differ by small (12%) or moderate (24%) amounts. When the difference between males in orange body color is great (40%), however, imitation effects are blocked and females consistently prefer more orange males. It thus appears that a threshold difference in male orange body color exists below which imitative effects are predominant and above which genetic preferences mask any cultural effects. Although some models have examined the relationship between cultural and genetic preferences in the context of mate copying (5, 7, 9), none of these models has examined the phenomenon outlined here.

The protocol developed here, though specific to guppies, could be modified to examine the relative strength of genetic and nongenetic factors on the expression of a variety of traits in species in which at least a baseline level of information is available about each factor.

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