The relationship between male ornamentation and swimming performance in the guppy, *Poecilia reticulata*

Paul F. Nicoletto

Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

Summary. The objective of this study was to determine if three male ornaments in the guppy (*Poecilia reticulata*) were reliable indicators of swimming performance. Tail shape and dorsal fin length were chosen because they are ornaments that are of primary importance in swimming, which is a major survival component of fitness in fish. The carotenoid pigments and especially their density are ornaments that are hypothesized to be long term indicators of male vigor. Carotenoid pigment density and swimming performance were significantly positively correlated, but there was no relationship between swimming performance and tail shape or dorsal fin length. These results indicate that density of carotenoid pigmentation may function as a male vigor indicator during mate choice. Tail shape and dorsal fin length are not related to swimming performance, and females probably could not use them as vigor indicators during mate choice. The results are discussed in terms of ornament function and adaptive and Fisherian hypotheses of female choice.

Introduction

Male guppies, *Poecilia reticulata,* are highly polymorphic in body coloration and dorsal and caudal fin shape. These polymorphisms are thought to have evolved by female choice (Endler 1980, 1983; Houde 1987, 1988; Kodric-Brown 1985). Female choice is a form of sexual selection that occurs when females exhibit some behavior that causes them to mate nonrandomly with males exhibiting certain traits (Maynard Smith 1985). Our current knowledge of the characteristics that females evaluate during mate choice is quite extensive. Female guppies choose males on the basis of display rate (Farr 1980), color pattern (Houde 1987, 1988; Kodric-Brown 1985, 1989), dorsal and caudal fin size and shape (Bischoff et al. 1985), and color intensity (Kodric-Brown 1989). The idea that these ornaments and displays have evolved by female choice is widely accepted, but how costly these

ornaments are and whether their evolution conforms best to Fisherian or adaptive hypotheses of female choice is unclear (Endler 1983; Houde 1988; Kodric-Brown 1985).

The Fisherian hypothesis of female choice is based on the runaway model of sexual selection developed by R.A. Fisher (1958). Fisher's model has been investigated and modified by numerous researchers using haploid, oligogenic, and quantitative genetic models (Arnold 1985; Heisler 1984, 1985; Kirkpatrick 1982, 1987; Lande 1980, 1981; O'Donald 1980, 1983; Seger 1985). The Fisherian female choice model predicts that: (1) male ornaments are arbitrary, i.e., no relationship exists between the development of the ornament and the male's vigor or fitness, (2) in populations at genetic equilibrium, sexual and natural selection have equal but opposite effects, and (3) no relationship exists between female choice and offspring vigor or fitness (Heisler et al. 1987; Kirkpatrick 1982).

The adaptive female choice hypothesis contends that females choose males in ways that maximize their fitness and that male ornaments are indicators of genetic quality (Andersson 1982, 1986; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Nur and Hasson 1984; Pomiankowski 1987a, b; Zahavi 1975). The adaptive models of female choice predict that: (1) maie ornaments are reliable indicators of age, dominance, parasite load, or vigor, (2) females prefer older, more dominant vigorous males, with low parasite loads, (3) females use these indicators during mate choice, and (4) a positive relationship exists between female choice and offspring vigor or fitness (Heisler et al. 1987; Kodric-Brown and Brown 1984).

The cost of male ornamentation is of great interest to the proponents of both the Fisherian and adaptive models of female choice (Partridge and Endler 1987; Price et al. 1987). The Fisherian model predicts that elaborate male ornaments reduce survivorship, primarily via predation selection, and it is this cost that constrains the continual elaboration of the ornament via female choice (Kirkpatrick 1987). The adaptive model predicts

that ornaments are costly to produce and maintain, which is important in maintaining the honesty of the advertisement, but which may or may not reduce male survivorship (Kodric-Brown and Brown 1984).

This study determines the relationship between three male ornaments (caudal fin shape, dorsal fin length, and carotenoid pigment density) and swimming performance. Its objectives were twofold. The first objective was to test the prediction that ornaments were reliable indicators of vigor. If no relationship or a negative relationship exists between male ornamentation and swimming performance, then these ornaments are probably not vigor indicators. This result would be consistent with the Fisherian view of female choice. If a positive relationship exits between male ornamentation and swimming performance, then these ornaments could function as vigor indicators. This result would be consistent with the adaptive view of female choice. The second objective was to determine if there were locomotory costs associated with elaborate caudal and dorsal fins. If there were locomotory costs, then males with elaborate fins would exhibit reduced swimming performance when compared to males with less elaborate fins.

The caudal and dorsal fins and the density of the carotenoid pigments were chosen for the following reasons. Caudal fin shape and dorsal fin length are sexually selected ornaments (Bischoff et al. 1985) that are also of primary importance in swimming (Yates 1983). A vast literature exists on the swimming ability of fish, particularly of game species, and on its physiological and behavioral correlates (see Beamish 1978 for a review). The density of the carotenoid pigments was chosen because, while the location of the pigment on the male's body is under genetic control (Yamamoto 1975), the expression and density of the pigments has a large environmental component (Endler 1983; Kodric-Brown 1989). Males unable to obtain either a sufficient quantity or quality of food obtain fewer carotenoids. Therefore, the density of this pigment may be an indicator of vigor (Endler 1983).

Critical swimming speed was chosen as a measure of vigor. It is defined as the maximum speed that a fish can sustain for a set period of time (Brett 1964). Critical swimming speed is a direct measure of how fast a fish can swim, and it is positively correlated with both active metabolism and endurance (Beamish 1978; Brett 1964; Brett and Glass 1973; Jones et al. 1974; Smit 1965).

Materials and methods

The wild type guppies used in this study were from a third generation laboratory colony derived from a feral population located in the McCauley hot spring in the Jemez Mountains of New Mexico. This population has been there for at least 16 years (R. Thornhill, personal communication). All fish appeared to be in good physical condition.

The three male tail types (Fig. 1) used were upper sword ($N=$ 27), flag ($N=22$), and round ($N=37$). Fish were independently classified into these different tail types by three observers. Any fish not classified unanimously was deleted from the analysis. These three tail types are common in the McCauley springs population
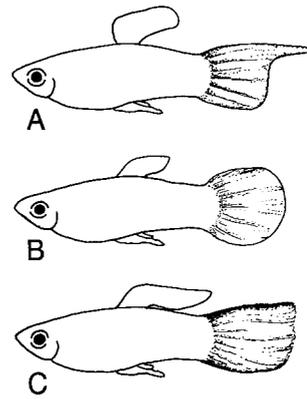

Fig. 1 A–C. Line drawing of the three different tail types used in this study, A upper sword, B round, and C flag. Drawing also depicts variation in dorsal fin length
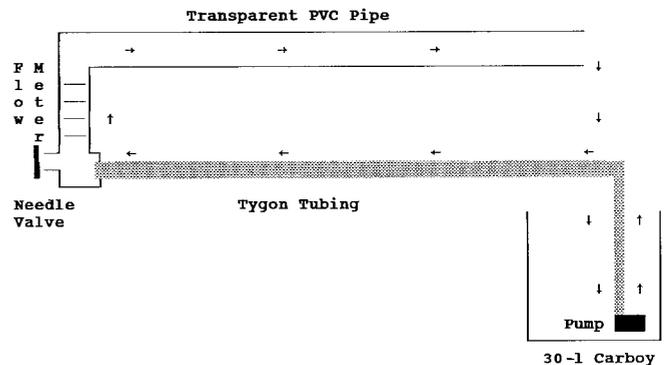

Fig. 2. Diagram of the flow chamber used in this experiment

(personal observation). Fish were kept in 76-l aquaria prior to testing. One to 2 days prior to testing, fish were placed individually in one of four compartments of a 38-l aquarium to standardize their state of rest. All aquaria used in these experiments had undergravel filters, water temperatures of 27°–29° C, and a photoperiod of 16:8 (L:D). Fish were fed Tetramin tropical fish food. One-third of the water in each aquarium was changed weekly with dechlorinated water.

Each fish's critical swimming speed was measured in a laboratory flow chamber (Fig. 2). The flow chamber consisted of a transparent PVC pipe 1.2 m long and 1.8 cm in diameter. The chamber's inflow end was attached to a flow meter (1–7.5 l/min). Immediately below the flow meter was a 1.25 cm needle valve to control flow rate. The needle valve was attached to a submersible pump by 2 m of 1.25-cm diameter Tygon tubing. The pump was submersed in a 30-l carboy. The outflow end of the chamber drained into the carboy containing the pump. A 6-cm-long collimator made of plastic straws was located inside the flow chamber. The function of the collimator was to facilitate rectilinear flow (Vogel 1989).

Critical swimming speed was determined by introducing each fish into the opening at the end of the flow chamber. The initial flow rate was 7.8 cm/s. Guppies can swim for several hours at this flow rate (personal observation). The fish were acclimated to the chamber for 3 min. Thereafter, the flow rate was increased 2.9 cm/s every 3 min until the fish washed out of the chamber. The time that the fish spent at the highest flow rate was recorded and critical swimming speed was calculated after Brett (1964). Critical swimming speed was measured once per fish. The corrected critical swimming speed, the ratio of critical swimming speed and standard length in cm (Stahlberg and Peckmann 1987), was also calculated. Corrected critical swimming speed can be used to compare fish of different sizes and gives the swimming performance per centimeter of fish.

Guppy body size and density of carotenoid pigment were recorded by photographing individual fish in a modified flow

chamber. This chamber was a 2.5-cm transparent acrylic pipe with a 2.2-cm-wide and 10-cm-long gray card placed in the center of the pipe near the flow meter. A transparency of a one-mm grid was positioned along the bottom of the tube in front of the gray card. The gray card provided a standardized background against which to photograph the fish and restricted the fish's movement to one-half of the pipe diameter. The fish were photographed at a flow rate of 7.9 cm/s with a 35-mm camera equipped with a 100-mm or 50-mm macro lens. The film used was Kodak's Kodachrome professional grade, ASA 64. Two 250-watt daylight bulbs (Sylvania, N0 B1 Superflood) provided illumination.

The standard length, dorsal fin length, and tail area of each fish was measured by projecting the photographs onto a computer digitizing tablet. The digitizing tablet was calibrated to the 1-mm grid in the background of each photograph.

The density of the carotenoid color spots was quantified by measuring the photographic slides on a color densitometer (Kodric-Brown 1989). A color densitometer measures the density of color on a photographic slide by projecting white light of known intensity through the slide and then through a color filter. The color filter absorbs all but a given range of wavelengths and permits the wavelength range of interest to pass through. The amount of light that is transmitted through the filter is read by a photocell. The densitometer then subtracts the intensity of the light read by the photocell from the intensity of the light before it passes through the slide and the filter. The difference in light intensities is the amount of light of a given wavelength range that was absorbed by the slide. This unitless density measurement appears on the densitometer display (Wyszecki and Stiles 1967). The densitometer had four narrow pass-band filters, with 10-nm ranges, with peak absorbencies at 410 nm, 450 nm, 520 nm, and 577 nm.

Each carotenoid color spot was measured three different times at each densitometer filter, and the mean was used in the analysis. The densitometer was zeroed on the gray card in the background of each slide at each filter and between each of the three measurements. This gave a measure of color density relative to the gray card and made the photographs of different fish comparable by controlling for differences in the film, developing technique, and light level and quality. This technique did not quantify the true color of the fish, but made all of the photographs relative to each other. A 1-mm aperture was used on the densitometer. Attempting to analyze color spots smaller than the aperture led to inaccurate readings. Therefore, only those fish with color spots greater than 1 mm were used in the color analysis.

Statistical analysis. Differences among the three tail types in tail area and critical swimming speed were analyzed using analysis of covariance. Standard length was used as the covariant to partition the total variance into portions due to tail type and to remove the linear effect of differences in body size from the analysis. Differences among tail types in standard length and corrected critical swimming speed were analyzed with a one-way analysis of variance.

Spearman rank correlation was used to determine the relationship between swimming performance and dorsal fin length. Dorsal fin length is positively related to body size. Therefore, the residuals from the relationship between standard length and dorsal fin length were correlated with critical and corrected swimming speed. This residual analysis provides a value for dorsal fin length that is independent from body size. Spearman rank correlation also was used to determine the relationship between the density of the carotenoid pigments and critical and corrected critical swimming speed. All analyses were done with the SAS statistical package using the Proc GLM and Proc Corr routines (SAS Institute 1982).

Results

The analyses of variance for differences among males with different tail types revealed there were no significant differences among males for standard length (ANOVA,

Table 1. The least squares means and standard errors for guppies of three tail types. There were no significant differences among tail types in any of the variables

Variable	Flag	Round	Upper sword
Standard length	1.75 (0.05)	1.76 (0.04)	1.73 (0.05)
Critical swimming speed	23.7 (0.96)	22.6 (0.79)	21.3 (0.65)
Corrected critical swimming speed	13.7 (0.55)	12.8 (0.42)	12.4 (0.49)
Tail area	0.29 (0.01)	0.29 (0.01)	0.32 (0.01)

Table 2. Spearman rank correlations for the relationship between the residual of dorsal fin length and critical and corrected critical swimming speed

Statistic	Critical swimming speed	Corrected critical swimming speed
Correlation	−0.070	−0.033
P-value	0.508	0.760
N	88	88

Table 3. The results of Spearman rank correlations between the density of the carotinoid pigments at four different densitometer filters and swimming performance. *Asterisks* mark P-values that are significant ($P<0.05$) after a Bonferroni adjustment for that variable

Densitometer filter	Statistic	Critical swimming speed	Corrected critical swimming speed
577	Correlation	0.35	0.45
	P-value	0.023	0.003 *
	N	52	52
520	Correlation	0.23	0.28
	P-Value	0.120	0.042
	N	52	52
450	Correlation	0.27	0.33
	P-Value	0.057	0.012 *
	N	52	52
410	Correlation	0.31	0.38
	P-Value	0.023	0.005 *
	N	52	52

$P>0.79$), tail area (ANACOVA, $P>0.14$), critical swimming speed (ANACOVA, $P>0.09$), and corrected critical swimming speed (ANOVA, $P>0.21$; Table 1).

The regression analyses of dorsal fin length and standard length yielded a significant relationship ($Y=0.052+0.329X$, $P<0.001$, $r^2=0.25$). However, this regression's fit is low, as reflected by the low r^2 value. This indicates that substantial variation exists in dorsal fin length between males. There was no correlation between the residuals of dorsal fin length and critical or corrected critical swimming speed (Table 2).

Fifty-two slides of fish had color spots greater than 1 mm and were analyzed on the densitometer. The correlation coefficients for the relationship between color and corrected critical swimming speed were all positive and three were significant after a Bonferroni adjustment (Table 3; Sokal and Rohlf 1981). A similar trend existed for the relationship between color and critical swimming speed. All of these correlation coefficients were positive and ranged in mangitude from 0.21 to 0.35, but none were significant after a Bonferroni adjustment (Table 3). These correlations indicate that there is a positive relationship between density of the carotenoid pigments and swimming performance.

Discussion

Carotenoid pigment density and swimming performance were positively correlated. This relationship is significant because carotenoid pigments are used by females during mate choice (Houde 1987, 1988; Kodric-Brown 1985, 1989). Swimming performance is also positively correlated with endurance, stamina, and metabolic rate, and is negatively correlated with parasite load in game species (Beamish 1978), and presumably in guppies as well. Thus, the evidence suggests that females use these pigments as indicators of a male's vigor and possibly his suitability as a mate.

A positive relationship between ornament development and condition or vigor has been observed for sticklebacks (McLennan and McPhail 1989; Milinski and Bakker 1990), Jackson's widowbirds (Andersson 1989), jungle fowl (Ligon et al. 1990; Zuk et al. 1990), and house finches (Hill 1990). As one might expect, the correlation coefficients given in these studies were not large (<0.50). This is probably because many variables such as previous activity, pleiotropic genetic effects, food availability and quality, and parasite load influence phenotypic traits such as ornament development, condition, or vigor.

There was no relationship between swimming performance and tail type or dorsal fin length. This suggests that tail type and dorsal fin length are not indicators of a male's condition or vigor. It also suggests that there are no measurable locomotory costs associated with the elaborate fins used in this study. These results do not completely conform to either the Fisherian or adaptive models and can potentially be explained within the framework of either model.

A Fisherian explanation is that tail shape and dorsal fin length in guppies may be examples of traits whose evolution is affected by the opposing effects of sexual and natural selection. The evolution of tail shape and dorsal fin length might be constrained by natural selection that maintains swimming performance. Sexual selection apparently favors elaborate fins as evidenced by the tendency for fancy females to choose males on the basis of fin size and shape (Bischoff et al. 1985). The only evidence supporting this explanation is the lack of significant differences in tail area among the three tail types in this study. This indicates that, within certain limits, sexual selection on tail shape can give rise to

phenotypic variation that does not affect tail size and swimming performance.

An equally possible adaptive explanation for the lack of both a locomotory cost and a relationship between fin elaboration and swimming performance is that elaborate fins are handicaps that reveal male vigor (Nur and Hasson 1984; Zeh and Zeh 1988). Males with elaborate fins might compensate for the handicapping effect of the fins by being in superior physical condition. This hypothesis can only be tested by measuring male vigor in a way that is independent of any handicapping effect. This could be done by determining if fish with elaborate fins have larger condition factors (Milinski and Bakker 1990) than fish with unelaborated fins.

The lack of locomotor costs to elaborate fins does not preclude other costs for these ornaments (Price et al. 1987). The elaboration of fins might be constrained by predation intensity. Flag tail males are more conspicuous than round tail males, at least to the human observer. The elongated dorsal fin is probably more costly to produce than the unmodified fin simply because it is larger.

Results of this and other studies on guppies support predictions of both the Fisherian and adaptive models of female choice. The Fisherian model contends that ornaments are arbitrary and the female gains no information about a male's condition or vigor. The lack of a relationship between tail shape, dorsal fin length, and swimming performance is consistent with this prediction. This model also predicts that sexual and natural selection are opposed in populations at genetic equilibrium (Kirkpatrick 1987). Other studies on the conspicuousness of guppy color patterns (Endler 1983) and male display rates (Fraser and Gilliam 1987) in high and low predation environments support this prediction.

Evidence supporting the adaptive hypothesis also exists. This study found a positive relationship between the density of the carotenoid pigments and swimming performance. Other studies have shown a negative relationship between male sigmoid display rate and parasite load (Kennedy et al. 1987; McMinn 1990). Thus, the carotenoid pigments and sigmoid display rate fit two predictions of adaptive female choice (Heisler et al. 1987); male ornaments are reliable indicators of vigor or health, and females use the ornaments during mate choice (Houde 1988; Kodric-Brown 1985, 1989).

The sexually selected traits examined in this study appear to be traits within a continuum. At one end are traits that, once expressed, do not vary within an individual's lifetime. Their environmental sensitivity occurs during ontogeny. Examples of these kinds of traits in guppies may be tail shape, dorsal fin length, and elements of the color pattern, such as spot location. These traits are probably not reliable indicators of male vigor because they do not vary within an individual's lifetime. These traits may evolve by the dual action of natural selection and sexual selection (Endler 1980, 1983) or by the classic Fisherian runaway process (Kirkpatrick 1987).

Within the continuum are traits that vary within an individual's lifetime, i.e., over a period of days, weeks,

or months. Their expression may depend upon the male's physical condition and his recent feeding history (Endler 1983; Kodric-Brown and Brown 1984). An example of this kind of trait in guppies is carotenoid pigment density. These traits are probably reliable vigor indicators because they reflect a male's ability to exploit the current environment. Faking these traits may be difficult because they are probably costly to produce and maintain (Kodric-Brown and Brown 1984).

At the other end of the continuum are traits whose expression can change in response to immediate social circumstances. Their expression may depend upon male sexual interest and female receptivity. Display rate is an example of this kind of trait (Farr 1980). Display rate is probably a reliable indicator of vigor, but is probably tied to immediate physical condition and may not accurately reflect long term health or vigor. Thus traits that vary over the long or short term provide the female with partially redundant information on a male's physical condition.

The empirical evidence on mate choice in the guppy does not clearly support either the Fisherian or the adaptive hypothesis of female choice. Components of Fisherian and adaptive female choice apparently coexist in the guppy. Final resolution of this controversy awaits empirical studies that examine the relationship between female choice and offspring fitness or vigor.

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