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Source: Zoological Science, 23(3) : 255-260

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.23.255>

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Long Tails Affect Swimming Performance and Habitat Choice in the Male Guppy

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Sexual selection often favors male secondary sexual traits, although in some cases the elaborate traits incur costs to the males with respect to natural selection. Males of the guppy *Poecilia reticulata* have longer tails (caudal fins) than females, and the long tails contribute to the mating success of the males through female mate choice. We examined the effect of tail length on the swimming performance of male and female guppies. In a laboratory experiment, males with longer tails exhibited poorer swimming performance than those with shorter tails. However, this effect was not apparent in females. In addition, in a feral population, tail length of males was negatively correlated with water flow velocity in their microhabitats. Although body size of females was negatively correlated with water flow velocity in their microhabitats, tail length of females showed no significant correlation with degree of water flow. These results suggest that the long tail of male guppies incurs costs, such as a decrease in swimming performance, to the males with respect to natural selection and consequently limits their choice of habitats to those with slow water flow.

Key words: microhabitat, natural selection, secondary sexual trait, sexual selection, water flow velocity

INTRODUCTION

The occurrence of exaggerated male traits is often considered to be a result of sexual selection, *i.e.*, female mate choice and male-male competition (Darwin, 1871; Andersson, 1994; Reynolds and Harvey, 1994). Males that develop elaborate traits are often chosen as mates by females or can win in fights with other males to access females (Andersson, 1994; Halliday, 1994; Ryan, 1997). However, these extravagant traits are apparently costly to the males' fitness in terms of natural selection (Zahavi, 1975; Partridge and Endler, 1987; Halliday, 1994; Basolo and Wagner, 2004). For example, long tails decrease the flight performance of male barn swallows, *Hirundo rustica* (Rowe *et al.*, 2001), although females preferentially choose as mates the males with long tails (Møller, 1994). Therefore, the degree of exaggeration of male secondary sexual traits may be determined by a balance between benefits from sexual selection and costs through natural selection (Fisher, 1930; Partridge and Endler, 1987; Andersson, 1994).

In some fishes, males have longer fins than females (Turner, 1993). In some cases, these long fins result from sexual selection; *i.e.*, females preferentially choose males with long fins as mates (Bischoff *et al.*, 1985; Basolo, 1990; Sekiya and Karino, 2004). Although long fins appear costly for males with respect to natural selection, little information is available about the negative association between male long fins and fitness components (Rosenthal *et al.*, 2001; Basolo and Alcaraz, 2003).

The guppy *Poecilia reticulata* is a live-bearing poeciliid fish native to the streams and rivers of Trinidad and adjacent parts of South America (Houde, 1997; Magurran, 2005). It shows remarkable sexual dimorphism and dichromatism; males have longer fins than females and develop brightly colored spots on their bodies. It is well known that females choose their mates on the basis of male secondary sexual traits (Houde, 1997). For instance, female guppies in many populations choose their mates on the basis of orange spot patterns (Houde, 1987; Kodric-Brown, 1989). By doing so, females may be able to obtain indirect benefits through mate choice, such as greater foraging ability of their offspring (Endler, 1980; Karino *et al.*, 2005). Males have longer tails (caudal fins) than females, and male tail length shows high individual variation (Bischoff *et al.*, 1985; Karino and Matsunaga, 2002; Karino and Kobayashi, 2005). Bischoff *et al.* (1985) have documented female mate preference on the basis of male tail size. However, females in a feral population preferred males with larger total lengths (Karino and Matsunaga, 2002); in this case, long tails in males contributed to their mating success as a component of their total length. Therefore, it can be considered that the evolution of long tails in male guppies is caused by female mate preference.

Nicoletto (1991) did not find a significant association between swimming performance in male guppies and tail shape or dorsal fin length, all of which are aspects of sexual ornamentation. Here we examined the relationship between tail length and swimming performance in male and female guppies in a laboratory experiment. In addition, we conducted a field survey to demonstrate the relationship between tail length of feral guppies and rate of water flow in their microhabitat in the wild. If long tails affect swimming

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doi:10.2108/zsj.23.255

performance in male guppies, we predicted that males possessing long tails would be distributed only in microhabitats with slow water flow velocity.

MATERIALS AND METHODS

Subject animals

We used feral guppies and their descendants from the Hiji River (26°43'N, 128°11'E) located in the northern part of Okinawa Island, southern Japan. Guppies that are introduced into new habitats exhibit flexibility in changing their appearance and life history components to suit their new environments (Endler, 1980; Reznick *et al.*, 1990). Since guppies were introduced into Okinawa in the 1970s, they might have undergone sufficiently strong natural and sexual selection for a sufficiently long period to adapt to the new habitats (Karino and Haijima, 2001). Several potential predators of the guppy were frequently found in the Hiji River, and variation in secondary sexual traits of male guppies appeared to be similar to that in some native populations (Karino and Haijima, 2001).

Laboratory experiments

We used the first- or second-generation descendants of wild-caught guppies to examine the relationship between tail length and swimming performance in a laboratory experiment. The guppies were reared in a laboratory at the Tokyo Gakugei University in 40-liter aquaria with circulated water maintained at 25–28°C with a 12:12 h light:dark photoperiod. They were fed newly hatched brine shrimp nauplii and commercial flake food (TetraMin®; Tetra Werke, Germany) once daily.

We randomly chose from the stock aquaria 36 individual males with tail lengths ranging from 27.4%–85.2% of their standard lengths, and 35 females with tail lengths from 23.2%–51.0% of their standard lengths. Three days prior to the experiment, standard length, total length, tail length, and dorsal fin length of the test fish were measured to the nearest 0.1 mm with a vernier caliper. Dorsal fin length of male guppies also shows high individual variation (Nicoletto, 1991; Karino and Haijima, 2001). Although Nicoletto (1991) documented no significant relationship between male dorsal fin length and swimming performance, we excluded a potential influence of male dorsal fin length on swimming performance by standardizing the dorsal fin lengths of the test males. For the standardization, we surgically shortened the dorsal fin of each test male based on the regression between dorsal fin length and standard length in females (dorsal fin length = $0.023 + 0.205 \times \text{standard length in mm}$; $r^2 = 0.60$, $P < 0.001$, $n = 35$ females). Fish were anesthetized with a 2-phenoxyethanol solution during measurement and surgery, and immediately afterward were placed in an isolation tank containing methylene blue for 3 days until the experiment, to prevent infection.

Critical swimming speed was chosen as a measure of swimming performance. Critical swimming speed is defined as the maximum speed that a fish can sustain for a set period of time (Brett, 1964), and thus is a direct measure of the swimming speed of a fish. Critical swimming speed of each test fish was measured in a laboratory flow chamber (Fig. 1) by the method of Nicoletto (1991). The flow chamber consisted of a transparent acrylic pipe 30 cm long and 1.8

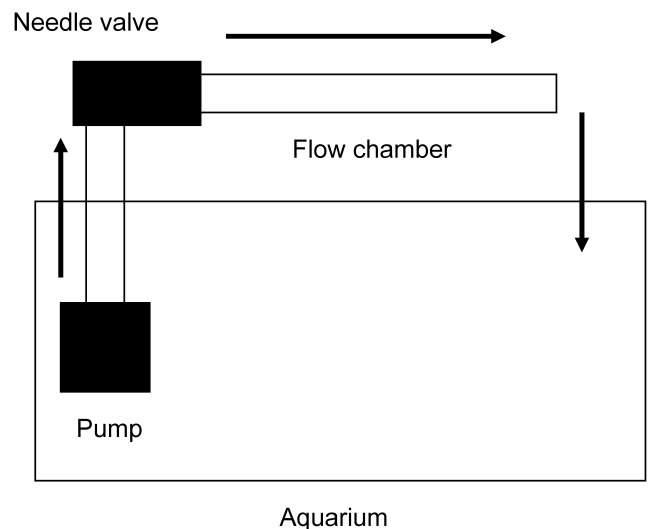


Fig. 1. Scheme of the flow chamber system used in the laboratory experiment. Arrows indicate the direction of water flow.

cm in diameter, with a collimator to ensure that the water velocity profile was rectilinear (Nicoletto 1991). A needle valve at the inflow end of the chamber controlled the flow rate. The needle valve was attached with plastic tubing to a submersible pump (10 watt; Tomofuji, Japan) within a 40-liter aquarium. A screen of 1-mm-square mesh was set at the outflow end of the chamber, which drained back into the 40-liter aquarium.

We measured critical swimming speed by introducing each test fish into the opening at the end of the flow chamber. We set the initial flow rate as 7.3 cm/s; preliminary observations showed that guppies could swim for more than 3 h at this rate ($n = 30$ individuals). We acclimated the test fish to the chamber for 3 min, then increased the flow rate by 1.4 cm/s every 3 min, until the fish could not swim and was swept to the screen at the outflow end of the chamber. We recorded the time that the test fish spent swimming at the highest flow rate. Finally, we calculated the critical swimming speed by the method of Brett (1964), and also the corrected critical swimming speed, which is the ratio of critical swimming speed to the total length of the test fish (Stahlberg and Peckmann, 1987). The experiment did not appear to affect the health of any of the test fish.

In order to examine the relationship between tail length and swimming performance of male and female guppies, we calculated Pearson's correlation coefficients. Tail length was significantly correlated with standard length in female test fish ($r = 0.68$, $P < 0.001$, $n = 35$) but not in males ($r = 0.21$, $P = 0.23$, $n = 36$). Therefore, the residual tail lengths from the regression between standard length and tail length were also calculated (Reist, 1985) for both females and males. We analyzed the relationship between residual tail length and swimming performance also using Pearson's correlation coefficient. All data showed a normal distribution (Kolmogorov-Smirnov one-sample test, $P > 0.4$).

Field survey

To demonstrate the relationship between the tail length of feral guppies and the degree of water flow in their natural

habitats, we set up 10 study sites with differing water flow rates in a 30-m stretch along the middle of the Hiji River. Within this stretch were several small islets, and the river showed high topographical heterogeneity, varying from riffles to pools. The study was conducted from 1100–1600 h on 30 October and 1 November 2004, which was within the reproductive season of this population. In fact, courting males and pregnant females were frequently observed. The region around the Hiji River received no heavy rain for several days prior to the field survey or during the survey, so the water conditions at the study sites appeared to be normal.

We determined the flow velocity at each study site by measuring the distance black ink traveled per unit time, as described by Takegaki and Nakazono (2000). With a 5-ml pipet, we injected a drop of black ink into approximately the middle of the river near the surface, where we found abundant guppies engaged in foraging and courting and collected specimens, and measured the distance the ink flowed in 10 s. We repeated this measurement 6 times for each study site and calculated the mean water velocity in cm/s.

We collected at least three adults of each sex at each study site, using hand nets and a bait trap (Purasu-mondori; Johshuya, Japan). Immediately after collection, we measured standard length and tail length of the guppies to the nearest 0.1 mm with a vernier caliper. During measurement, the fish were anesthetized with 2-phenoxyethanol.

Since the ratio of tail length to body size differed between male and female guppies (Karino and Matsunaga, 2002), we calculated the mean standard length and tail length of both males and females from each study site. We analyzed the relationships between mean water velocity and mean standard length as well as mean tail length by Pearson's correlation coefficient, because all data showed a normal distribution (Kolmogorov-Smirnov one-sample test, $P>0.8$). We found a significant correlation between standard length and tail length in females ($r=0.83$, $P<0.001$, $n=46$), although no significant relationship was observed in males ($r=0.06$, $P=0.62$, $n=64$). Therefore, we also calculated the residual tail lengths of females and males based on the regression between their standard length and tail length. The relationship between water velocity and mean residual tail length of males and females at each study site was also analyzed by Pearson's correlation coefficient.

RESULTS

Laboratory experiments

For guppies used in the laboratory experiment, males had smaller standard lengths and longer tails than females (Table 1). The coefficient of variation in standard length was smaller for males (13.1%) than for females (24.6%), whereas the coefficient of variation in tail length was greater for males (29.3%) than for females (20.9%). Females showed greater swimming performance than males, *i.e.*, both critical swimming speed and corrected critical swimming speed were significantly greater in females than in males (Table 1).

In males, standard length was positively correlated with critical swimming speed, although it was not significantly correlated with corrected critical swimming speed (Table 2). The relationships between male tail length and both critical

Table 1. Mean \pm SE (range) of morphological traits and swimming performance of male and female guppies in the laboratory experiment. Significant difference was analyzed by t-test.

	Males (n=36)	Females (n=35)	<i>P</i>
Standard length (mm)	15.64 \pm 0.34 (11.80–20.40)	20.70 \pm 0.86 (14.85–30.65)	<0.001
Tail length (mm)	7.76 \pm 0.38 (4.20–12.45)	6.74 \pm 0.24 (4.85–9.65)	0.03
Residual tail length	0.004 \pm 0.371 (–4.234–4.801)	0.002 \pm 0.174 (–1.676–2.995)	0.97
Critical swimming speed	13.58 \pm 0.46 (7.40–19.25)	18.50 \pm 0.32 (15.15–21.55)	<0.001
Corrected critical swimming speed	0.59 \pm 0.02 (0.26–0.83)	0.71 \pm 0.03 (0.40–0.97)	0.002

Table 2. Pearson's correlation coefficients between swimming performance and morphological traits of male and female guppies in the laboratory experiment. Numerals in parentheses indicate *P*-values.

Traits	Critical swimming speed	Corrected critical swimming speed
Males (n=36)		
Standard length	0.35 (0.04)	–0.02 (0.91)
Tail length	–0.45 (0.002)	–0.68 (<0.001)
Residual tail length	–0.39 (0.02)	–0.69 (<0.001)
Females (n=35)		
Standard length	–0.01 (0.97)	–0.85 (<0.001)
Tail length	–0.19 (0.28)	–0.81 (<0.001)
Residual tail length	–0.25 (0.15)	–0.32 (0.07)

and corrected critical swimming speed were significantly negative (Table 2). Residual tail length of males was also negatively correlated with both critical and corrected critical swimming speed (Table 2). These results indicated that males with longer tails exhibit lower swimming performance.

Critical swimming speed of females was not significantly correlated with standard length, tail length, or residual tail length (Table 2). However, the corrected critical swimming speed of females was negatively correlated with both standard length and tail length (Table 2). Residual tail length also showed a negative association with corrected critical swimming speed in females, but the association was not significant (Table 2). Therefore, tail length alone appears to have no apparent effect on swimming performance in the females.

Field survey

Water flow velocities varied from 0.8 to 9.8 cm/s (mean \pm SE=3.9 \pm 0.8 cm/s) among the 10 study sites in the Hiji River. Mean standard length of males did not correlate with water velocity at the collection sites ($r=0.21$, $P=0.56$, $n=10$), whereas both mean ($r=-0.86$, $P=0.001$, $n=10$; Fig. 2a) and mean residual ($r=-0.88$, $P<0.001$, $n=10$) tail length of males showed a significantly negative relationship with water velocity. This indicated that males having longer tails

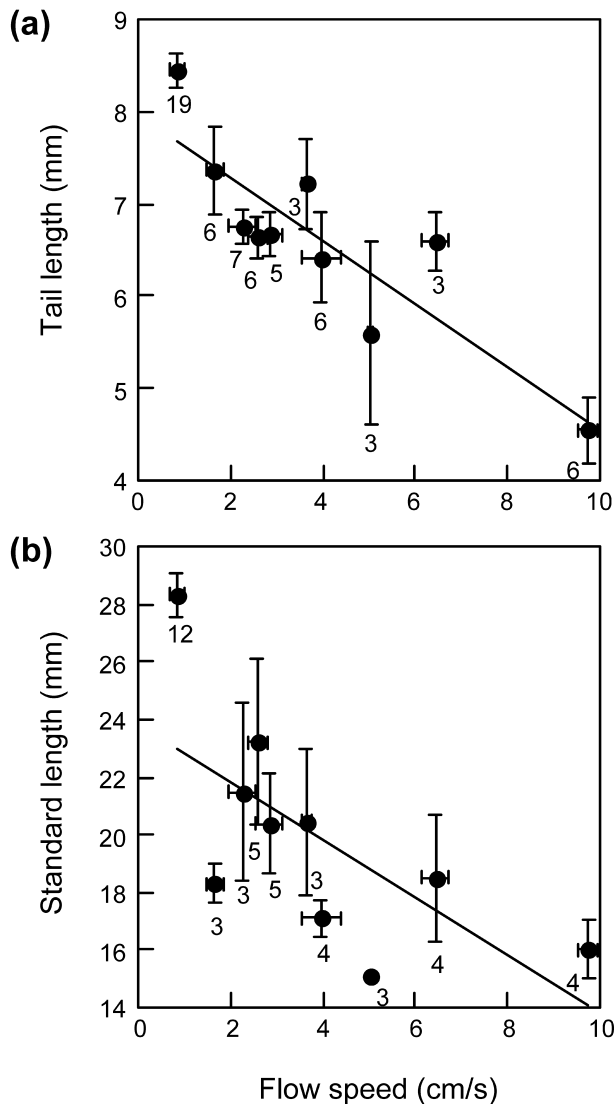


Fig. 2. The relationships (a) between mean tail length of male guppies and water flow velocity and (b) between mean standard length of female guppies and water flow velocity at their collection sites. The solid line indicates the regression line. Bars indicate SE. Numerals are sample sizes.

generally live within microhabitats with slower water flow velocity.

In females, mean standard length showed a significant and negative correlation with water flow velocity at the collection sites ($r = -0.68$, $P = 0.03$, $n = 10$; Fig. 2b), but neither mean ($r = -0.39$, $P = 0.27$, $n = 10$) nor residual ($r = -0.19$, $P = 0.61$, $n = 10$) tail length showed a significant correlation with water velocity. Thus, body size rather than tail length influences the choice of microhabitat by the female guppies.

DISCUSSION

Results of the laboratory experiment clearly indicate a negative relationship between male tail length and swimming performance. Males having longer tails showed lower critical and corrected critical swimming speeds. In addition, under natural conditions, male guppies with long tails were found to be distributed within microhabitats with low water

flow velocity. These results suggest that the long tails restrict the distribution of males to habitats with low water velocity in which they can swim effectively, considering their low swimming performance. Moreover, it is possible that long tails increase the predation risk for the males by reducing their ability to escape from predators (Godin, 1997; Basolo and Wagner, 2004). Therefore, male guppies appear to incur costs in terms of natural selection on account of their long tails.

The long tails of male guppies may have either evolved directly due to female preference for mates with longer tails (Bischoff *et al.*, 1985) or indirectly through their preference for mates with greater total lengths (Karino and Matsunaga, 2002). Basolo (1998) suggested that the cost of tail production may be less than that of body production in male green swordtails, *Xiphophorus helleri*. In male guppies, the growth cost for tail elongation is probably also lower than that for body production, and thus they can more efficiently achieve a larger total length by tail elongation. By producing long tails, males may obtain benefits with regard to sexual selection, *i.e.*, being preferred by females as their mates. Ultimately, tail length of male guppies may be determined by the balance between benefit from sexual selection (female mate choice) and cost from natural selection due to decreased swimming performance.

In the present study, tail length did not appear to affect female swimming performance. However, body size (standard length) of females negatively influenced the corrected critical swimming speed. In addition, under natural conditions, larger females were limited to habitats with lower water flow velocity. In adult guppies, most females are generally pregnant and rear offspring within their bodies (Houde, 1997). The clutch size of individual females appears to increase with the female body size (Reznick, 1989; Abrahams, 1993). Therefore, it is possible that larger females, in general, carried a greater number of offspring in their bodies, and thus a greater load was exerted on their swimming ability due to increased resistance of their cross sectional area against the water current. Since female guppies showed less individual variation in tail length than males, female body size may be a more important factor in swimming performance than tail length. Indeed, the cross sectional area of female guppies in this population was about 10–120% greater than that of males of similar total length, and the cross sectional area of females increased with body size (our unpublished data).

To explain the evolution of exaggerated male traits through female mate choice, Zahavi (1975) proposed the handicap principle. Since exaggerated male traits incur some costs to males, the degree of the exaggeration of the traits is a reliable indicator of male viability, and females can obtain indirect and/or direct benefits by choosing males on the basis of these traits (Zahavi, 1975; Andersson, 1994; Fitzpatrick, 1998). For example, female barn swallows prefer males with long tails as mates (Møller, 1994), but long tails in males decrease their flight performance (Rowe *et al.*, 2001). Rowe *et al.* (2001) suggested that the long tails of male barn swallows are a costly handicap and have evolved through female choice in accordance with the handicap principle.

In male guppies, long tails contribute to the males' mat-

ing success through attractiveness to females (Bischoff *et al.*, 1985; Karino and Matsunaga, 2002). On the other hand, as demonstrated in this study, the long tails hamper the swimming performance of the males. The handicap principle appears relevant to long tails in male guppies. However, female guppies in this population choose their mates on the basis of male total length rather than on the basis of tail length itself (Karino and Matsunaga, 2002). Therefore, the females do not use male tail length to select a mate, nor as an indicator of male viability. This suggests that some mechanism other than the handicap principle, such as a preexisting bias of female preference (Ryan and Keddy-Hector, 1992; Endler and Basolo, 1998) or a male deceptive tactic to attract females (Karino and Matsunaga, 2002), may have worked in the evolution of long tails in male guppies. In addition, tail length of male guppies shows high variation even within a single population (Brooks, 2002; Karino and Matsunaga, 2002). Karino and Matsunaga (2002) suggested that the high variation in male tail length reflects heterogeneity of benefits and costs across various microhabitats.

The results of the present study indicate that the cost of a long tail to male guppies is a decrease in swimming performance, and suggest that there is a relationship between the males' lower swimming performance and the degree of water flow in their microhabitats. The effect of the water flow velocity on female mate preference in the guppy is still unclear, although it is possible that female guppies assess the body condition or viability of males on the basis of male courtship intensity at high water velocity (cf. Takahashi and Kohda, 2001). Further study is required to clarify the benefits and costs of long tails in male guppies among various microhabitats, and it will provide insight into the mechanism underlying the maintenance of polymorphism within male guppies (Brooks, 2002).

ACKNOWLEDGMENTS

We are grateful to R. Aihara, M. Kobayashi, A. Sasaki, S. Shinjo, and C. Someya for help with data collection and culture maintenance, and to two anonymous reviewers for their helpful suggestions. This work was supported by a Grant-in-Aid (#16570012) to KK from the Japan Society for the Promotion of Science.

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(Received October 18, 2005 / Accepted December 8, 2005)