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Behaviour (5170 words)

FEMALE MATE PREFERENCE IS FOR MALE TOTAL LENGTH, NOT TAIL LENGTH IN FERAL GUPPIES

by

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Summary

Exaggerated male traits can evolve either directly by
female choice of males with those traits or indirectly by
female preferences for related traits. In this study, we
tested whether female choice was based upon male tail
length or total length in a feral guppy population in
Okinawa, Japan. In this population, about 30 % of the
males had elongated sword-like tails, and even swordless
males had longer tails than females. A series of
dichotomous female choice experiments revealed that female
guppies chose mates by total length, not by tail length
itself. This is inconsistent with the handicap principle.
Tail elongation of male guppies may have evolved as a male
mating strategy to enhance their attraction to females,
mediated by female preference for longer male total length.
However, only one-third of the males developed pronounced
sword-like tails. This suggests that there are some costs
for tail elongation or trade-offs between multiple sexually
selected traits. Alternatively, tail elongation may be a
deceptive male strategy with frequency-dependent success.

Introduction

Exaggerated male secondary sexual traits are often
considered as a result of sexual selection, i.e.,
intrasexual competition and mate choice (Bradbury &
Andersson, 1987; Andersson, 1994). For example, female
mate choice may have resulted in long and/or elaborate
tails of males in some animals (e.g., the long-tailed
widowbird Euplectes progne, Andersson, 1982; the peacock
Pavo cristatus, Petrie et al., 1991; the barn swallow
Hirundo rustica, Møller, 1994).

It is often thought that females may obtain direct or
indirect benefits by choosing males with long and elaborate
tails (Andersson, 1994; Møller, 1994; Zahavi & Zahavi,
1997). Zahavi (1975), for example, proposed the handicap
principle to explain the evolution of exaggerated male
traits such as long tails. Males having a secondary sexual
trait of greater size may suffer much higher survival costs
and therefore the trait size may be a honest reflection of
the viability of the males. Consequently, females can
obtain indirect benefits by choosing mates using the
magnitude of certain male traits (Zahavi, 1975; Zahavi &
Zahavi, 1997). Møller (1994) documented in the barn
swallow that sons of fathers with longer tails had a
greater viability as shown by their longevity and parasite
resistance. In addition, Rowe et al. (2001) demonstrated
that long tails of male barn swallows decrease flight
performance, and suggested that long male tails are a
costly handicap and probably evolved through female choice.

Preexisting bias model (reviewed by Ryan & Keddy-
Hector, 1992) also explains the evolution of male longer
tails. Basolo (1990a, b) found female preference for male
longer tails (swords) not only in the green swordtail
Xiphophorus helleri but also in the platyfish Xiphophorus
maculatus, even the lack of swords in males of the latter
species. Therefore, Basolo suggested that the preference

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for longer tails results from a preexisting bias in the female visual system and male longer tails then arise that are selected by the female preference.

In the guppy <u>Poecilia reticulata</u>, female preference for males with longer tails has been examined (Bischoff et al., 1985) similar to the green swordtail and the platyfish. Rosenthal & Evans (1998), however, revealed that female green swordtails choose their mates by male total body size rather than sword (tail) length. This result suggests that in a variety of animals, some exaggerated male traits, such as long tails, may have evolved through female mate preference for larger apparent size rather than for size of the trait itself. The purpose of the present study is to examine whether female guppies choose their mates using males' total length or tail length. We discuss the mechanism for the evolution of long tails in male guppies, also considering the frequency of males with elongated tails in a population.

Methods

Study animals

Guppies are live-bearing poeciliid fish native to streams and rivers of Trinidad and adjacent parts of South America (Houde, 1997). Guppies show remarkable sexual polymorphism and dichromatism: males assume bright spots of orange, black or iridescent coloration on their bodies and have long caudal and dorsal fins.

We used guppies from an introduced feral population in Okinawa, a southern island of Japan. It is well known that guppies introduced into new habitats flexibly change the conspicuousness of male traits and female preferences for those male traits. This occurs within several years according to the environment of these new habitats (Endler,

1980; Houde, 1997). They may also alter life history
traits, such as age and size of maturity (Reznick et al.,
1990). Guppies were introduced into Okinawa in 1970s
(Kouchi, 1997), and thus might have been subjected to
natural and sexual selection for a sufficient long period
to adapt to these new habitats. In fact, size of male
sexual secondary traits, such as orange spots and tail
length, are highly variable among individuals within an
Okinawan population (Karino & Haijima, 2001), and degrees
of trait size and individual variation of size of male
traits are similar to those of native populations (cf.
Houde & Endler, 1990; Winemiller et al., 1990).

We collected guppies using hand nets in March 1998
and March 1999 at the Hiji River (26°43'N, 128°11'E)
located in the northern part of Okinawa Island. In this
population, male secondary sexual traits varied
individually as mentioned above, but obviously under
control of genetic factors (Karino & Haijima, 2001).
Collected specimens and their descendants were reared in
40-60 l aquariums with circulated water at 26-28°C with a
12:12 h light:dark regime.

Comparison of tail lengths between and within sexes

We first examined the difference in tail length compared to
body size (standard length; SL) between and within sexes.
In this population, males can easily be divided in two
types based upon their tail features; males with elongated
sword-shaped tails (hereafter, sworded males) and males
with no sword (swordless males). We measured the maximum
tail length and SL of both sworded and swordless males, as
well as females, to the nearest 0.1 mm using a vernier
caliper. Before measurement, fish were anesthetized using
2-phenoxyethanol solution. Measured specimens were
randomly chosen from stock aquariums in which wild-caught

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guppies and their first or second generation descendants
were reared. All individuals measured were sexually mature.

Because the interaction between SL and the category
(sworded males, swordless males and females) against tail
length was significant (p < 0.001), we could not use ANCOVA
(SAS institute Inc., 1998). Therefore, to analyze the
difference in relative tail length (tail length/SL) among
the category, we conducted one-way ANOVA after arcsin-
transformation of these relative values (Zar, 1999). In
addition, we conducted comparisons of slopes of regressions
between SL and tail length among them (Ichihara, 1990).
All data, both the original and transformed ones, were
normally distributed (Kolmogorov-Smirnov one-sample test, p
> 0.4).

Female choice experiments

<u>Set-up and procedure</u>
In order to establish whether male tail length or total
length is the trait on which female choice is based, we
conducted dichotomous choice experiments. For the testing
apparatus, we divided an aquarium (36 x 22 cm with 25 cm
depth) with a clear glass plate into two major compartments.
One major compartment was then further divided into three
smaller compartments with two opaque plastic plates (Fig.
1). For each trial, we put one test female into the
undivided major compartment and a stimulus male into each
of the two smaller end compartments (Fig. 1). By using
this experimental setup, we could examine female choice
excluding male-male competition, because the test female
could see both males but males could not see each other (cf.
Zuk et al., 1990; Candolin, 1999; Smith et al., 2002). The
small center compartment provided a neutral area and
allowed us to easily judge which male was chosen by the
female. A 5.5 x 11 cm area at the front of each male

compartment was considered as the preference zone (Fig. 1).

We added 2-3 cm gravel on the bottom of the test
aquarium, put opaque boards on three sides of the aquarium
and a dark screen on the fourth side (facing the test
female compartment) to avoid disturbance. Observations
were carried out through a 5 x 10 cm hole in the curtain.
A 15-Watt daylight lamp (Toshiba FL15ex) was placed 10 cm
above the aquarium. Although it has been known that
ultraviolet light influenced female choice in guppies
(Kodric-Brown & Johnson, 2002; Smith et al., 2002), the
wavelength of this lamp did not contain UV (> 390 nm).
Water temperature was maintained between 26-28°C. Trials
were conducted from 1000 to 1800 hours. All test fish were
fed 1 h prior to trials.

We used virgin females, the first or second
generation descendants of wild-caught guppies, for all
experiments, since pregnant females are not receptive to
males (Houde, 1997). These virgin test females were
obtained by rearing them separately from males from 4-5
weeks after birth when secondary sexual traits appeared.
However, it is known that females who have matured without
ever seeing adult males often mate indiscriminately during
their first encounter with males (Houde, 1997). Therefore,
one day prior to the experiment, all test females were
placed individually into a clear cylinder (7 cm in diameter
with 21 cm height) that was subsequently put into an
aquarium which held 50-60 males. These naive virgin
females appeared to be able to discriminate preferable
mates among males by this preparation (cf. Houde, 1997).

Female preference was measured through side-
association data (Houde, 1997). When fish were introduced
into each compartment, they got a 10-min acclimation period
before the start of the trial. After the acclimation
period, we conducted a 10-min observation and measured the
time spent by the test female within the preference zone in
front of each stimulus male compartment. Females usually

oriented toward stimulus males and frequently responded to male displays when they were in the preference zone. To control for side preference, we then switched stimulus male location, and repeated the trial after a 10-min acclimation period. We combined data from both trials to determine female preference for each of the two stimulus males. In order to ensure confidence in our evaluation of female preference, we excluded data from females which did not enter preference zones of both stimulus males. We also excluded data from females that did not show a sexual response (Liley, 1966) toward male displays during the acclimation period and from females that spent less than 5 min in total within the preference zones of both males during the 10-min trial. We tested 6 different females with each pair of subject males to minimize individual variation in female preference and used the averaged value among 6 females for the analysis. In addition to female preference, the frequency of male courtship displays toward the females was recorded during the observation period.

We composed pairs of stimulus males that differed in the desired stimulus (i.e., tail length and/or total length), but that resembled each other in other secondary sexual traits as much as possible. To quantify male traits, we measured SL, tail length, total length, dorsal fin length, and gonopodium (anal fin modified to the intromittent organ) length on each stimulus male. During these measurements, males were anesthetized with 2-phenoxyethanol solution and all data recorded to the nearest 0.1 mm using a vernier caliper. Orange and black spot patterns on their bodies were also quantified from digital video stills that were input into a Macintosh computer using Photoshop 5.0 software. Numbers, absolute and relative areas (spot area/total body area) of orange and black spots were calculated as mean values between the right and left sides of their body. Hue, saturation and brightness of each orange spot were also quantified as the

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mean value of six-point measurements by the software, and the mean value for all orange spots on both body sides was calculated for each male (see Karino & Haijima, 2001 for a detailed method).

Mate-choice experiment stimuli

We examined female preference for male tail length or total length using the following four experiments. For each experiment, we made 15 different pairs of stimulus males. In order to compare data of traits between a given stimulus male pair and that of female preference for each stimulus male, we conducted paired t-tests, because all data showed the normal distribution (Kolmogorov-Smirnov one-sample test, $p > 0.18$).

Experiment 1.

To confirm female preference for male tail length or total length in this population, stimulus male pairs were created such that one (male A) had both longer tail and total lengths than the other (male B). No other traits differed significantly between the two males, including courtship frequency (Table 1).

Experiment 2.

To exclude effect from other traits correlated with tail or total lengths on female preference, tail and total lengths were reversed for males A and B in Experiment 1 via surgical manipulation. Before surgery, males were anesthetized with a 2-phenoxyethanol solution. Tails of both males A and B were surgically shortened to control for the effect of surgical manipulation between the two males. We adjusted the degree of tail shortening to reverse their size order for tail and total lengths. Hence, tail and total lengths of male A both became shorter than those of male B. Soon after the manipulation, males were placed in an isolation tank with methylene blue for 3 days before

test trials were initiated for infection prevention. When females preferred a different male from that in Experiment 1, we assumed that females choose males based upon tail or total lengths and no other factors (Table 2).

All surgically-manipulated males fully recovered and their tails grew out to their original lengths in 1-2 months.

Experiment 3.

To assess the influence of male total length on female preference, we used a pair of two males that differed in total length (male C > male D) but did not differ in tail length. No other quantified traits, as well as courtship frequency, differed significantly between the two males except body size (SL) and dorsal fin length (Table 1).

Experiment 4.

In contrast to Experiment 3, to assess the influence of male tail length on female preference, we used a pair of two males that differed in tail length (male E > male F) but not in total length. Other traits and courtship frequency did not differ between them except SL and dorsal fin length (Table 1).

If female preference is based upon male total length, females should prefer male C over male D in Experiment 3, but the time spent by females between males E and F in Experiment 4 should not differ (Table 2). If females choose their mates by tail length, male E would be preferred over male F, and no difference should be seen between males C and D (Table 2).

The relationship of tail or total length differences to the degree of female preference

When females choose their mates using a given male trait,

it would be expected that the degree of the difference in female preference between two males should increase according to the increment of the difference in the trait's size magnitude between the males. In order to further clarify whether female guppy mate choice is based upon male tail or total lengths, we examined the relationship between the degree of the difference in time spent by females for each male and the difference in tail and total lengths between the stimulus males using data from female choice experiments 1-4 (N = 60 pair males). Because total time spent by females with both males varied individually, the difference between the times spent with each of the males was calculated as a relative value by dividing by the total time spent. These relative values were arcsin-transformed before further analysis (Zar, 1999). We analyzed these data using regression analysis, because all data were normally distributed (Kolmogorov-Smirnov one-sample test, $p > 0.9$).

Results

Comparison of tail lengths between and within sexes

Relative tail length, tail length divided by body size (SL), was significantly different among sworded males, swordless males, and females (ANOVA, $F_{2,322} = 211.2$, $p < 0.001$). The relative tail length of sworded males (mean $\pm$ SD = 0.59 $\pm$ 0.15, N = 53) was greater than that of both swordless males (0.44 $\pm$ 0.03, N = 108) and females (0.38 $\pm$ 0.02, N = 164)(Fisher's Protected Least Significant Difference, $p < 0.001$ for both). The relative tail length of swordless males was also longer than that of females (Fisher's Protected Least Significant Difference, $p < 0.001$).

Sworded males showed a steeper slope for the SL and tail length regression ($y = 0.99x - 7.46$, $r = 0.65$, $p <$

0.001, N = 53) than swordless males (y = 0.48x - 0.88, r = 0.83, p < 0.001, N = 108) and females (y = 0.35x + 0.36, r = 0.97, p < 0.001, N = 164; Fig. 2). In comparing slopes of regressions, the slope of sworded males was significantly different from that of swordless males (t = -4.17, p < 0.001) and females (t = -7.28, p < 0.001). Also, swordless males had steeper slopes than females (t = -4.24, p < 0.001; Fig. 2). These results indicated that males, especially sworded males, had longer tails relative to body size than females and that male tail length greatly increases with body size growth.

Female choice experiments

Experiment 1.
Male A had longer tail (mean ± SD = 8.4 ± 2.3 mm) and total lengths (24.1 ± 2.9 mm) than male B (tail length; 6.2 ± 2.0 mm, total length; 21.7 ± 2.4 mm; Table 1). Females spent considerably more time close to male A than to male B during the observation (paired t-test, t = 7.5, p < 0.001, N = 15; Fig. 3a). This indicates a preference for male A.

Experiment 2.
Through surgical manipulation, male A that had longer tail and total lengths in Experiment 1 acquired shorter tail (4.9 ± 0.6 mm) and total lengths (20.9 ± 1.3 mm) than male B (tail length; 6.6 ± 0.6 mm, total length; 22.3 ± 1.5 mm; Table 1). After the surgical shortening of tail length, some of the male B had longer tail and total lengths than in Experiment 1, because we conducted Experiment 2 about two months after Experiment 1 in those cases. These grew between the experiments. Courtship frequency of the same males altered between Experiment 1 (mean ± SD = 1.47 ± 2.98/min) and Experiment 2 (3.48 ± 5.07; paired t-test, t =-2.5, p = 0.02), but males courted more frequently after

the surgical manipulation. Therefore, the surgical
manipulation did not appear to negatively affect in the
male courtship frequency. In addition, courtship frequency
and other traits measured did not differ between males A
and B also in Experiment 2 (Table 1).

After this reversal of tail and total lengths of
males, female preference was also reversed; females spent
less time close to male A than to male B (t = -5.2, p <
0.001, N = 15; Fig. 3b).

Experiment 3.
Male C had longer total length (25.5 ± 1.6 mm) than male D
(23.6 ± 1.7 mm), but tail length did not differ between
males C (8.0 ± 1.9 mm) and D (8.0 ± 1.9 mm; Table 1). Thus,
SL of male C (18.4 ± 0.8 mm) was larger than that of male D
(16.6 ± 0.7 mm). Females preferred and spent more time
with the larger male C (t = 6.7, p < 0.001, N = 15; Fig.
3c).

Dorsal fin length, however, also differed
significantly between males C (7.8 ± 1.5 mm) and D (6.6 ±
1.7 mm; Table 1). To evaluate the effect of dorsal fin
lengths on female preference, we re-examined the data from
male pairs according to longer/shorter dorsal fin length.
Time spent by females did not differ between these two male
groups (males with longer dorsal fin, 559.7 ± 177.4 s;
males with shorter dorsal fin, 439.3 ± 176.3 s; t = 1.3, p
> 0.2, N = 15). In addition, we divided the pair-males
into preferred males (females spent more time near them)
and less preferred males, and found that dorsal fin length
did not differ significantly between the two males
(preferred males, 7.6 ± 1.2 mm; less-preferred males, 6.8 ±
2.0 mm; t = 1.4, p > 0.1, N = 15). These results indicate
that dorsal fin length did not noticeably affect female
preference in this experiment.

Experiment 4.

Male E had longer tail length (6.8 ± 1.9 mm) than male F (5.3 ± 2.0mm; Table 1), but their total length did not significantly differ (male E, 22.2 ± 2.3 mm; male F, 22.4 ± 2.3 mm; Table 1). Thus, SL of male E (16.4 ± 0.7 mm) was smaller than that of male F (18.0 ± 0.9 mm; Table 1). Time spent by females did not differ significantly between the males (t = -0.9, p > 0.3, N = 15, Fig. 3d), indicating no preference.

Male E had shorter dorsal fin length (6.1 ± 1.6 mm) than male F (7.3 ± 1.5 mm; Table 1), however. When the pair-males were divided into males with long and short dorsal fins, time spent by females with the former males (489.5 ± 117.4 s) did not differ from that for the latter males (454.4 ± 127.7 s; t = 0.6, p > 0.5, N = 15). Also, when pair-males were divided into preferred and less preferred males, dorsal fin lengths between the two males did not differ (preferred males, 6.8 ± 1.7 mm; less preferred males, 6.7 ± 1.6 mm; t = 0.2, p > 0.8, N = 15).

The relationship of tail or total length differences to the degree of female preference

The difference in relative time spent by females between the two stimulus males significantly increased according to the increment of the difference of total lengths between the pair-males (r = 0.70, p < 0.001; Fig. 4a). Similarly, when the tail length difference increased, the difference of relative time spent by females for each male also increased (r = 0.39, p < 0.01; Fig. 4b). However, the difference of total lengths between pair-males was significantly correlated with that of tail lengths (r = 0.65, p < 0.001, N = 60). The partial correlation coefficient for the difference of relative spent time by females was still significantly positive with the total length difference (0.64, p < 0.001) but not significant

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with the tail length difference (-0.13, p > 0.1). Therefore, the significant relationship between tail length difference and the degree of the difference in female preference (Fig. 4b) is probably an artifact. These results may further support that female choice is based upon male total length, but not upon tail length.

Discussion

This study clearly demonstrates that female guppies choose their mates by male total length, not by tail length. Reynolds & Gross (1992) also found a female preference for longer total length of males in a native guppy population. However, in that study, males with longer total length may also have had longer tails, because male body size (SL) and tail length was significantly correlated (Reynolds & Gross, 1992). Therefore, the relative importance of male tail and total lengths on female preference could not be assessed in that study. In another study, Bischoff et al. (1985) documented female choice based upon male tail size in the guppy. In their female choice experiment, however, two males with different tail sizes were paired but their body sizes were matched (Bischoff et al., 1985). Thus, it seems probable that female preference for males with larger tails in their experiment was a correlated result being mediated by female preference for males with greater 'total length' as in the present study. Similar female preferences for longer male tails associated with longer total length were also found in another poeciliid fish, the green swordtail (Rosenthal & Evans, 1998). Female preference for larger male apparent size may be a general tendency in poeciliid fishes, because it is well reported in other poeciliids such as <u>Gambusia holbrooki</u> (Bisazza et al., 2001), <u>Poecilia latipinna</u> (Schlupp et al., 1994), <u>Xiphophorus nigrensis</u> (Ryan & Wagner, 1987) and <u>Xiphophorus pygmaeus</u> (Morris et

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al., 1996).

The evolution of female preference for longer male total length in guppies can be explained in two ways. One is a preexisting bias for larger size in the female sensory system (cf. Ryan & Keddy-Hector, 1992). Larger apparent size of male guppies may be favored by females either through a greater stimulation of the female visual system or due to an adaptive reason, e.g., the female sensory system is tuned to greater stimulation by larger animals because of the greater risks from larger predators (Rowland, 1989; Ryan & Keddy-Hector, 1992; Andersson, 1994). After female preference for larger male size was established, the preference will be maintained through the female preexisting bias as well as the Fisherian process (Fisher, 1930). Females that mate with larger, thus, attractive males will obtain an indirect benefit, i.e., enhancing the attractiveness of their sons. Brooks (2000) found that sexual attractiveness in male guppies was heritable and genetically correlated with ornamentation, but male attractiveness showed negative genetic correlation with offspring survival and the number of sons maturing. Brooks (2000) suggested that ornamentation of male guppies will evolve under the balance between the fitness cost of ornamentation and the benefit of attractiveness, as Fisher's prediction.

The other explanation is indirect benefits, not only male attractiveness but also other fitness benefits, for female guppies by choosing larger males. Reynolds & Gross (1992) showed that offspring of males with greater total length grew faster and their daughters had a greater reproductive output. Watt et al. (2001) also found the greater survival rate of offspring of larger males. If this 'good genes' process is operating in our study population, females with a preference for larger male size would have a higher fitness.

According to the handicap principle, exaggerated male

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trait (such as larger or elaborate tails) is a honest
signal of the male viability and females can obtain
indirect and/or direct benefits by choosing mates using the
male trait (Zahavi, 1975; Iwasa et al., 1991; Zahavi &
Zahavi. 1997; Fitzpatrick, 1998). In the present study,
however, female mate choice in this guppy population was
not based upon male tail length itself. That is, female
guppies do not use male tail length as a signal for their
mate choice nor as an indicator of male viability. This
suggests that any mechanisms other than handicap principle
may have operated in the evolution of long male tails in
guppies.

When female preference for greater total length was
established in a guppy population, males should allocate
energy to each body part in order to maximize total length.
Basolo (1998) documented that male green swordtails shifted
energy investment only to tail growth under food-restricted
condition, whereas they invested to both body and tail
growth under condition with unlimited food. This result
suggests different growth costs for body and tail; costs
for tail production may be less than those for body.
Basolo (1998) concluded that males should shift their
investment from a preferred but more costly trait (body
size) to another preferred and less costly trait (tail
length) when the resource is limited. Furthermore, in
guppies, the energetic costs for tail production may be
less than those of body production as tail grew faster than
body in male guppies (our unpublished data). Thus, males
who invest much more energy in tail growth can obtain a
greater total length than males who invest equally in both
tail and body growth. Therefore, the tail elongation in
male guppies may have evolved as a male mating strategy to
improve their attractiveness for females through faster
production of greater total length with lower energy costs.

Even though swordless males had longer tails than
females, only about 30 % (53/161) of males measured in this

study had especially elongated sword-like tails. It is
possible that this frequency might be overestimated,
because we used hand nets to collecting specimen and males
with longer tails may be more vulnerable to the collection
if longer tails would incur swimming cost. Why did not all
males invest more energy towards tail elongation and
produce sword-like tails to attract females? There are
several possible explanations. One possibility is a
reduction in males' fitness by the production of longer
tails through natural selection: long tails may reduce
swimming ability and increase their vulnerability to
predators. Thus, some males might adopt a strategy to
elongate their tails to obtain higher reproductive success
per unit time and experience greater predation risk, but
others do not. It is unknown, however, that the natural
habitat of these fish had enough diversity to maintain a
variety of male tactics. For example, some microhabitats
may have favored vulnerable males with longer tails, but
others favored less attractive males with shorter tails.

Second, trade-offs between multiple preferred traits
may differ among males. It is well known that female
guppies choose their mates not only by male total length
but also by other male traits, e.g., orange spot coloration
or size (Houde, 1987, 1997; Kodric-Brown, 1989) and
courtship frequency (Farr, 1980). Energy allocation among
these preferred traits by males probably differs
individually. So some males may invest more for tails, but
others invest in other traits. Considering the results of
the present study, this is less likely because some paired
males in female choice•experiments had different tail
lengths, but resembled each other in other traits.

Third, sword-like tail elongation may be a male
deceptive strategy to females to enhance their choice as
mates, mediated by a female preference for longer total
length. In addition, success of this male deception is
frequency-dependent. By mating with these "cheater" males

with long tails but small SL, female fitness enhancement through the choice of apparently larger males (Reynolds and Gross, 1992) is unlikely. This is especially the case if their daughters' reproductive output is related to true paternal body size. In the Reynolds & Gross study (1992), males with greater total length may also have had larger SL as mentioned above, and the larger body size of daughters may be inherited from their fathers. However, body sizes of daughters of "long-tail-small-SL" males may be smaller than those of daughters of "lager-SL" males, even if their fathers have similar total lengths, because females do not elongate their tails. In this situation, if the frequency of deceptive males with sword-like tails increases, counter-tactics of females such as detection of the cheater males should be evolved or female choice based upon male total length may disappear (Johnstone & Grafen, 1993; Kokko, 1997). Therefore, the frequency of sworded males in a population may be restricted.

Although these possibilities may not be mutually exclusive, further research is needed to clarify the evolution of long tails of male guppies. By examining benefits and costs of tail elongation, one might find an explanation for the evolution of tail elongation, even the lack of female preference for male tail length itself. The results of the present study also suggest the need to reevaluate whether female preferences for some male traits are based on the traits themselves, or are mediated by other correlated traits in other animals.

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Legends for figures.

Fig. 1. Apparatus used for dichotomous female choice experiments. Compartments were divided by clear glass between a female and males, and divided by opaque plates between males. Shaded areas indicate preference zones.

Fig. 2. Relationships between body size (SL) and tail length in male and female guppies. Males were divided into two types by their tail features.

Fig. 3. Time spent by female guppies for each stimulus male in Experiments 1 (a), 2 (b), 3 (c) and 4 (d), respectively. Means are given $\pm$ SD.

Fig. 4. The degree of difference of relative time spent by females for each stimulus male (arcsin-transformed) in relation to the differences of total lengths (a) and tail lengths (b) between the pair males.
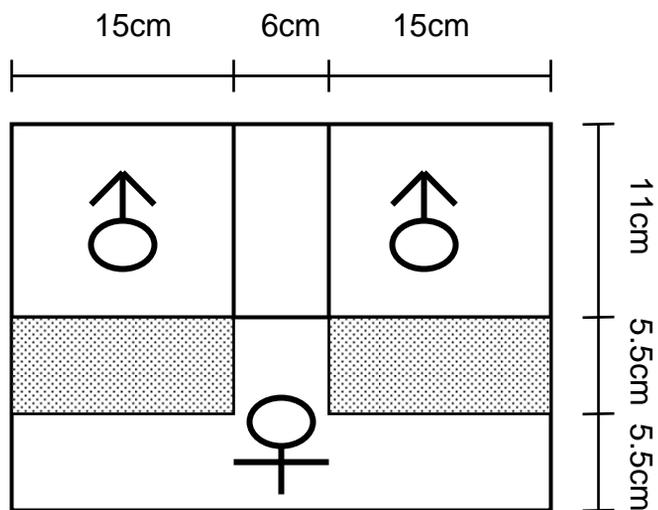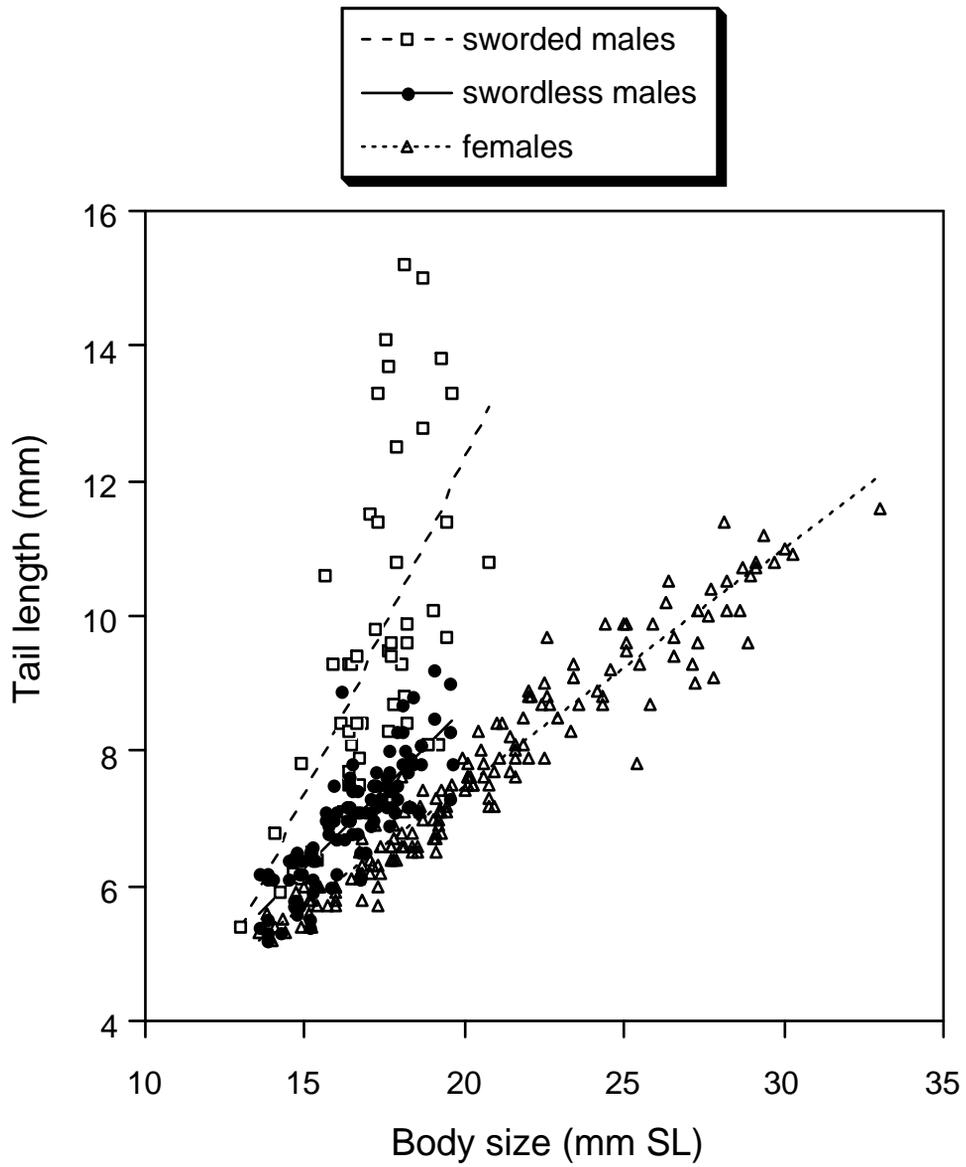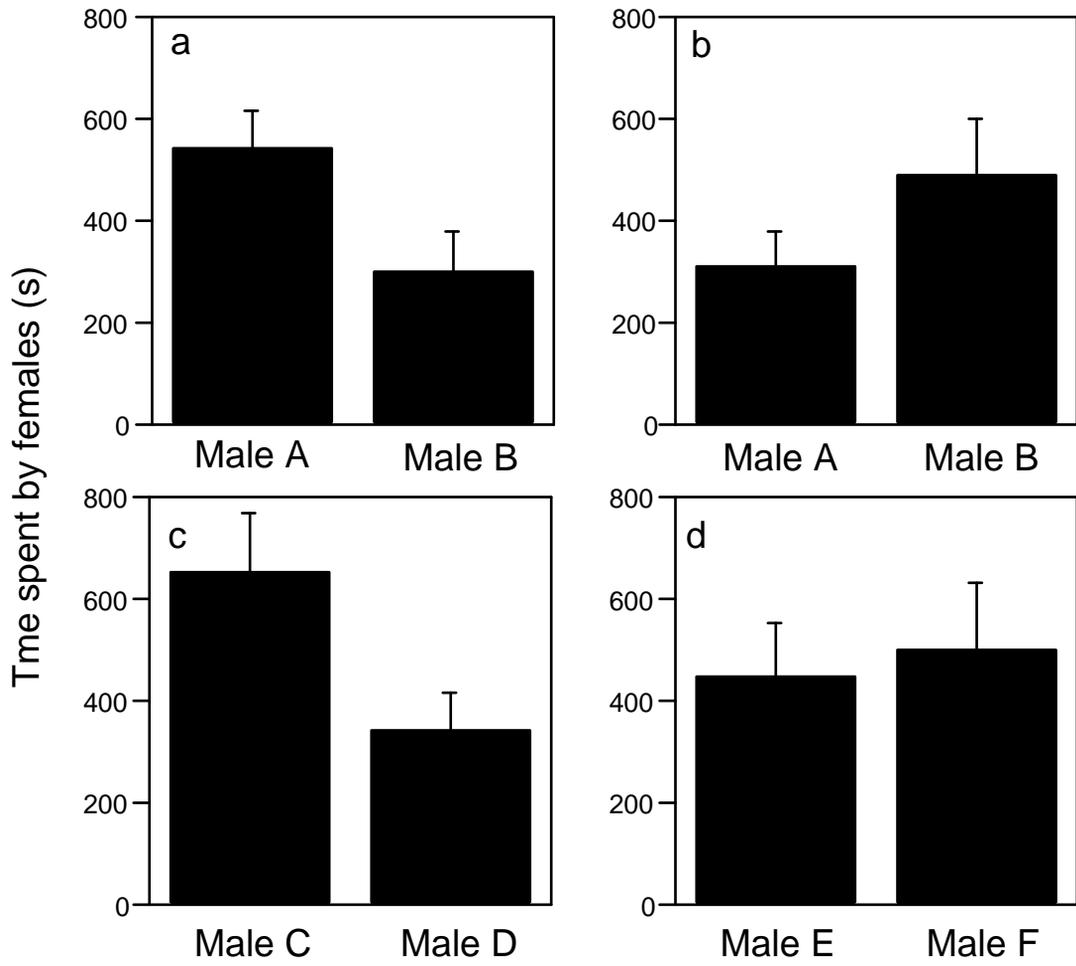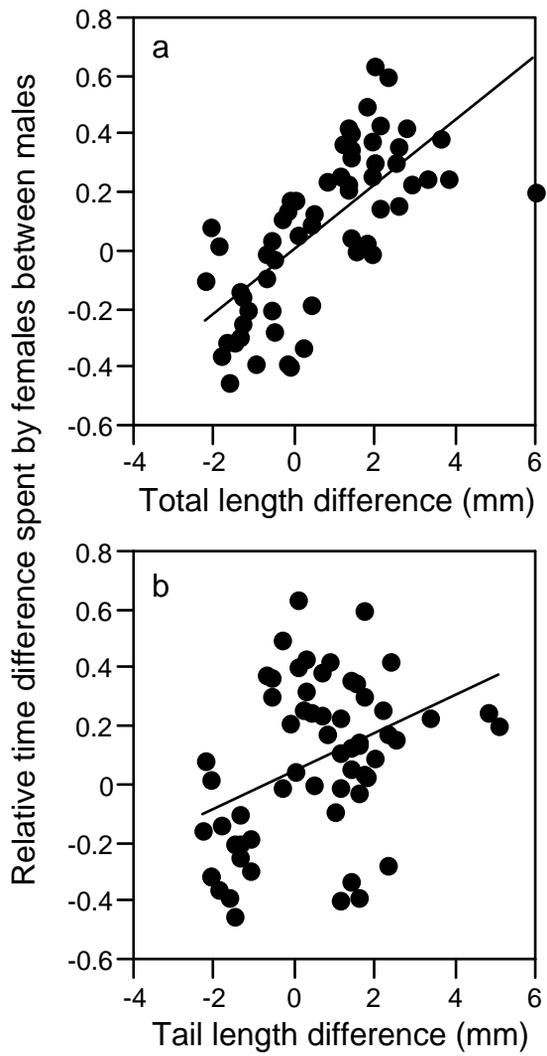
Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

TABLE 1.   Differences of traits between pairs of stimulus males used in each experiment (N = 15)

Trait	Experiment 1 Mean ± SD (male A minus male B)	Experiment 2 Mean ± SD (male A minus male B)	Experiment 3 Mean ± SD (male C minus male D)	Experiment 4 Mean ± SD (male E minus male F)
Total length (mm)	2.32 ± 1.30***	-1.37 ± 0.64***	1.95 ± 0.71***	-0.18 ± 0.38
Standard length (mm)	0.17 ± 0.38	0.27 ± 0.50	1.87 ± 0.60***	-1.59 ± 0.50***
Tail length (mm)	2.19 ± 1.31***	-1.70 ± 0.40***	0.00 ± 0.43	1.49 ± 0.45***
Dorsal fin length (mm)	0.45 ± 1.15	0.42 ± 1.52	1.23 ± 2.02*	-1.18 ± 1.65*
Gonopodium length (mm)	0.09 ± 0.25	-0.02 ± 0.22	0.16 ± 0.31	-0.04 ± 0.20
No. of orange spots	0.00 ± 0.42	-0.13 ± 0.72	0.27 ± 0.70	-0.17 ± 0.56
No. of black spots	-0.03 ± 0.48	-0.17 ± 0.49	0.23 ± 0.62	0.10 ± 0.54
Absolute orange spot area (mm^2)	-0.40 ± 1.22	-0.61 ± 1.68	0.09 ± 1.39	0.74 ± 1.70
Absolute black spot area (mm^2)	-0.09 ± 4.07	1.20 ± 2.35	0.07 ± 0.51	0.14 ± 0.48
Relative orange spot area (%)	-1.29 ± 3.02	-1.15 ± 2.94	-1.11 ± 2.39	1.21 ± 3.03
Relative black spot area (%)	-0.06 ± 0.78	-0.13 ± 1.13	-0.17 ± 0.88	-0.11 ± 1.08
Hue of orange spots (˚)	3.03 ± 17.73	1.01 ± 11.50	-0.80 ± 17.22	-2.93 ± 16.68
Saturation of orange spots (%)	1.99 ± 12.47	4.72 ± 12.90	4.37 ± 8.98	-5.51 ± 11.14
Brightness of orange spots (%)	-1.29 ± 3.02	0.79 ± 8.78	-3.06 ± 7.25	0.18 ± 6.61
No. of courtship displays (/min)	0.05 ± 0.34	-0.19 ± 0.51	-0.15 ± 0.40	0.06 ± 0.20

*$p < 0.05$, ***$p < 0.001$ (paired t-test).

Percent data indicated untransformed values, but statistical analysis was done for arcsine-transformed data.

TABLE 2.   Summary of predicted results of four female chocie experiments

	Female mate preference based upon	
	tail length	total length (TL)
Experiment 1	Male A having longer tail & TL was preferred	Male A having longer tail & TL was preferred
Experiment 2	Male B having longer tail & TL was preferred	Male B having longer tail & TL was preferred
Experiment 3	No difference between males C and D	Male C having longer TL was preferred
Experiment 4	Male E having longer tail was preferred	No difference between males E and F