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Behaviour

MALE ALTERNATIVE MATING BEHAVIOUR DEPENDING ON TAIL LENGTH
OF THE GUPPY, POECILIA RETICULATA

by

KENJI KARINO¹⁾ and MIHO KOBAYASHI²⁾

(Department of Biology, Tokyo Gakugei University, 4-1-1
Nukui-kita, Koganei, Tokyo 184-8501, Japan)

¹⁾ Corresponding author's e-mail address: kkarino@u-gakugei.ac.jp

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Short title: TAIL LENGTH AND MATING BEHAVIOUR IN MALE
GUPPIES

Corresponding author: Kenji Karino, Department of Biology,
Tokyo Gakugei University, 4-1-1 Nukui-kita, Koganei, Tokyo
184-8501, Japan (e-mail: kkarino@u-gakugei.ac.jp, Tel: +81-
42-329-7520, Fax: +81-42-329-7737)

Summary

Male guppies, Poecilia reticulata, exhibit two distinct types of mating behaviour, i.e., courting females for solicited copulation and sneaking behaviour for forced copulation. It is known that the frequency of these alternative mating behaviours is affected by environmental, genetic and morphological factors. We examined the influence of male tail (caudal fin) length on the frequency of these two types of mating behaviour. Female orient responses to courting males increased according to male courtship frequency and did not differ between males with longer and shorter tails. In further mating interactions, however, females showed glide responses much more frequently to displaying males with shorter tails than to those with longer tails. Males with shorter tails performed courtships more frequently than males with longer tails. Males with longer tails attempted sneaking (gonopodial thrusting) more often than those with shorter tails. These results indicate that male tail length determines the frequency of these alternative mating behaviour in the guppy. Assuming male long tails to be a deceptive tactic to attract females, the greater frequency of sneaking behaviour by males with longer tails to unreceptive females should be adaptive.

Introduction

Alternative reproductive behaviours of males are known to occur in a variety of animals and have attracted the interest of many behavioural and evolutionary biologists (Gross, 1996; Taborsky, 1998; Brockmann, 2001; Shuster & Wade, 2003). Male alternative mating behaviour may have evolved not only as a result of male-male competition, such as sneaking or satellite behaviour of subordinate males (Gross, 1996; Brockmann, 2001), but also as a tactic for circumventing female choice (Magurran & Seghers, 1994). In the guppy, Poecilia reticulata, males use two types of distinct mating behaviour for attempting to copulate with females, courtship and sneaking behaviour (Liley, 1966; Houde, 1997). In the former type of mating attempts, the male exhibits courtship displays, such as sigmoid displays, toward females and then copulates with a female with her cooperation when she accepts the male courtship (solicited copulation). In the latter type, on the other hand, the male rapidly approaches a female from behind and attempts a sneak copulation by performing gonopodial thrusting (Liley, 1966; Houde, 1997). Male guppies can transfer their sperm to females by either type of copulations (Matthews & Magurran, 2000; Pilastro et al., 2002). Since the same individual guppy usually exhibits both mating behaviours, there exist alternative reproductive tactics (Reynolds et al., 1993; Houde, 1997; Matthews & Magurran, 2000).

It is well known that several factors influence frequencies of both courtship and sneaking behaviours by male guppies. For example, larger males court females less frequently than smaller males at high light levels, while males with longer gonopodiums perform thrusts with a higher frequency at low light levels (Reynolds et al., 1993). The

frequency of these alternative mating behaviours in male guppies often varies among populations and is genetically based to a certain degree (Luyten & Liley, 1985; Magurran & Seghers, 1994; Evans & Magurran, 1999). In addition, effects of environmental factors such as predation risk on these male behaviours are known (Magurran & Nowak, 1991; Reynolds et al., 1993; Magurran & Seghers, 1994). The alternative mating behaviours of male guppies have attracted much attention in relation to morphological and environmental effects and have been studied in order to reveal the evolutionary implications of male mating behaviour (Magurran & Seghers, 1994; Houde, 1997).

Male guppies have longer caudal fins (tails) than females (Bischoff et al., 1985; Karino & Matsunaga, 2002). Bischoff et al. (1985) demonstrated a female mate preference for males with larger tails. However, female guppies did not distinguish between male tail lengths and preferred males with larger total lengths in a feral population, when females were exposed to males through a clear glass partition (Karino & Matsunaga, 2002). Males may be able to elongate their tails with fewer costs than their bodies (cf Basolo, 1998). Reynolds & Gross (1992) documented the indirect benefit of female preference for larger males in terms of faster growth rate of their offspring and higher reproductive output of their daughters. Nevertheless, when females would mate with males having larger total lengths but smaller body sizes and longer tails, it could be expected that their daughters would not grow larger and would have lower reproductive output. Therefore, mating with males with longer tails may reduce the indirect benefit to females. These ideas suggest that longer tails are a deceptive tactic of male guppies to attract females with fewer costs that are associated with

having larger total lengths (Karino & Matsunaga, 2002). The deceptive tactics by males have been predicted theoretically (Johnstone & Grafen, 1993; Kokko, 1997), but only little empirical information is available (Candolin, 1999; Backwell *et al.*, 2000). When costs to females that are deceived by cheater males are high, females may exploit counter-tactics against male deception such as discrimination against cheater males (Weldon & Burghardt, 1984; Johnstone & Grafen, 1993). These female counter-tactics may evoke further adaptation of males in the form of an arms race. Hence, it can be predicted that male guppies with longer tails will adopt sneaking behaviour more frequently than males with shorter tails, when females are unreceptive to males and may possibly discriminate between cheater males with longer tails. The present study aims to examine the hypothesis that the frequency of alternative mating behaviours may differ between male guppies with different tail lengths.

Methods

We collected guppies from the Hiji River (26°43' N, 128°11' E) located in the northern part of Okinawa Island, Japan, in March and July 2002. Females in this population prefer males with larger total lengths and do not distinguish male tail lengths through a clear glass partition as observed in a previous dichotomous choice experiment (Karino & Matsunaga, 2002). The collected specimens and their descendants were reared in 40–60 l aquariums with circulated water at 25–28°C with a 12:12 h light-dark regimen in the laboratory of Tokyo Gakugei University.

We conducted an open aquarium experiment in which a

female and a male directly interacted with each other (Houde, 1997). In the experimental aquarium (23 × 20 cm and 20 cm high), we put 2–3 cm gravel at the bottom and maintained water temperature at 25°C. We also put opaque boards on three sides of the aquarium and a dark screen to cover the entire experimental system to avoid disturbance. We recorded fish behaviour using a digital video camera (Sony DCR-TRV30) fixed within the screen through the fourth open side of the aquarium. A 15-watt daylight lamp was placed 10 cm above the aquarium. Trials were carried out between 0700 to 1000 hours. All test fish were fed 1 hour prior to trials.

We presented two males with different tail lengths to a female. We chose a pair of fully matured males (ca. 5–6 months after birth) having as similar appearances as possible except for tail lengths and standard lengths: One male of the pair had a longer tail (the long-tail male) than the other male (the short-tail male), but they had similar total lengths (Table 1). This was done because females in this population prefer males with larger total lengths (Karino & Matsunaga, 2002). Moreover, Reynolds et al. (1993) documented that male guppies change their courtship frequencies in accordance with their total lengths and environmental light levels. We eliminated these potential influences on the frequency of male mating behaviours by choosing two males with similar total lengths. To quantify male traits, we measured total length, standard length, tail length, dorsal fin length, and gonopodium length of each male before trials. All data were recorded to the nearest 0.1 mm using a vernier calliper. During these measurements, males were anaesthetized with 2-phenoxyethanol solution. Orange spot patterns as well as patterns of black spots on their bodies were quantified

from digital camera stills that were input into a Macintosh computer using Photoshop 6.0 software. Relative areas (spot area/total body area; %) of orange and black spots were calculated as mean values between the right and left sides of fish. We also measured the hue ($^{\circ}$), saturation (%), and brightness (%) of the orange spot coloration, and the brightness (%) of black spot coloration using the software. The hue, saturation, and brightness of each spot were quantified as the mean values of six-point measurements, and the mean values for all orange or black spots on both body sides were calculated for each male (see Karino & Haijima, 2004 for details of the method). These morphological traits, except tail and standard lengths, did not significantly differ between pair-males (Table 1).

We chose pregnant females for the experiment, because pregnant females usually do not respond frequently to displaying males (Liley, 1966). This experimental design may simulate a situation in which females discriminate against cheater males and are unresponsive to them. According to our prediction, long-tail males should perform sneaking behaviour more frequently than short-tail males under this situation. The male and female individuals were used only once for the experiment.

In order to exclude the effect of male-male competition, the two males were sequentially presented to the female. In addition, we presented the two males to the female twice in different orders to minimize the effect of the presentation order of males. First, we put the female into the experimental aquarium. After a 20-min acclimation period, we introduced one of the two males into the aquarium and recorded interactions between the female and the male using a digital video camera for 10 min. Then, the male was removed from the aquarium and another male was

put into the aquarium after a 10-min acclimation period. We recorded fish behaviour for 10 min and subsequently removed the male from the aquarium. The female was left in the experimental aquarium and was given a 20-min interval period. Then, we presented the same two males to the female in accordance with the above-mentioned method but in the reverse order. We combined data from both trials to evaluate the behaviour of the two males and the female.

From the video tapes we counted the frequency of courtship behaviour (sigmoid display) and that of sneaking behaviour (gonopodial thrusting; Liley, 1966; Luyten & Liley, 1985) of males. To ensure confidence in the data, we excluded data obtained from males that did not exhibit these reproductive behaviours during the trials. We also recorded the frequency of female responses to courting males. In general, female guppies respond to male courtships in a sequence of behavioural patterns (Baerends et al., 1955; Brooks & Caithness, 1995). First, females ignore displaying males, or respond to males by ceasing their activity and orienting toward males (orient response). In the next step, females swim toward displaying males with a smooth gliding motion using their pectoral fins (glide response). Finally, females cooperatively copulate with males. We also recorded the frequency of these female behaviours to courting males.

Since some behavioural data did not show the normal distribution (Kolmogorov-Smirnov one-sample test, $p < 0.05$), these data were log-transformed after adding 1 to the frequency and subsequently analysed by ANCOVA.

Results

During observations, females frequently exhibited orient behaviour toward courting males (Fig. 1a). The relationship between the frequency of female orient responses and that of male courtships was significantly positive (ANCOVA; $F_{1,187} = 307.0$, $p < 0.001$; Fig. 1a). In most cases (94.7%), however, females did not proceed to the next step (glide responses) and never attempted to cooperatively copulate with the males. Only one long-tail male could succeed in copulating with a female by sneaking.

In order to analyse the influence of tail length on the courtship frequency of males, an ANCOVA was done with the frequency of male courtships as the dependent variable and that of female orient responses as a covariate. Short-tail males courted females more frequently than long-tail males ($F_{1,187} = 22.1$, $p < 0.001$; Fig. 1a). In addition, we excluded a possibility of acceleration of male courting behaviour by further female responses by deleting the data of females whose responses proceeded to gliding behaviour. Even when the possibility was excluded, the difference in courtship frequency between males of different tail lengths still remained (ANCOVA, female orient response; $F_{1,87} = 144.3$, $p < 0.001$, tail length; $F_{1,87} = 20.1$, $p < 0.001$).

The frequency of male sneaking behaviour was not significantly influenced by that of female orient responses (ANCOVA; $F_{1,187} = 0.01$, $p = 0.92$; Fig. 1b). In contrast to courtship behaviour, long-tail males exhibited sneaking behaviour more often than short-tail males (ANCOVA, $F_{1,187} = 11.7$, $p < 0.001$; Fig. 1b). Even when the data of females that performed gliding behaviour were excluded, the frequency of female orient responses did not influence male sneaking frequency (ANCOVA, $F_{1,87} = 0.2$, $p = 0.69$), and long-tail males also exhibited sneaking behaviour more frequently than short-tail males (ANCOVA, $F_{1,87} = 12.0$, $p <$

0.001).

The frequency of male courtship behaviour did not significantly influence that of sneaking behaviour (ANCOVA, $F_{1,187} = 0.8$, $p = 0.38$), *i.e.*, a trade-off between frequencies of these two mating behaviours was not found. Long-tail males performed sneaking behaviour with a higher frequency than short-tail males, as revealed by the ANCOVA conducted with male courtship frequency as a covariate ($F_{1,187} = 7.9$, $p < 0.01$). A similar tendency was found even when the data of females that exhibited glide responses were removed (ANCOVA, courtship frequency; $F_{1,87} = 0.7$, $p = 0.41$, tail length; $F_{1,87} = 8.1$, $p < 0.01$).

When an ANCOVA was conducted with the frequency of female orient responses as the dependent variable and that of male courtships as a covariate, there was no significant difference in females' orient responses between long-tail and short-tail males ($F_{1,187} < 0.01$, $p > 0.99$). Since females exhibited only a few gliding behaviours toward males, the frequency of female glide responses was not normally distributed even after the log-transformation (Kolmogorov-Smirnov one sample test, $p < 0.05$). Therefore, we could not apply ANCOVA to female gliding behaviour. Instead, we compared the ratio (%) of the frequency of female glide responses to courtship frequency by males. The ratio of female glide responses to the courtship frequency of short-tail males was significantly greater than that of long-tail males (Wilcoxon signed-ranks tests, $Z = -2.86$, $p < 0.01$; Fig. 2).

Discussion

The results of this study clearly indicate that male

guppies adopt each of the two mating behaviours, i.e., courting and sneaking, with different frequencies depending on their tail lengths. Consistent with our hypothesis, males with longer tails exhibited sneaking behaviour more frequently than males having shorter tails. On the contrary, males with shorter tails courted females more frequently than males with longer tails. If long tails of male guppies would have evolved for deceiving females (Karino & Matsunaga, 2002), the higher frequency of sneaking behaviour by cheater males with longer tails toward unreceptive females that could possibly discern the male deception should be adaptive. Since tail length of the guppy is a heritable trait (Brooks & Endler, 2001; Karino & Haijima, 2001), the different adoption rate of these two mating behaviours among males with different tail lengths may be genetically determined as other morphological or behavioural traits (Farr, 1983; Luyten & Liley, 1985; Brooks & Endler, 2001). Alternatively, it is also plausible that male guppies can monitor their own tail lengths and adjust their mating behaviour in accordance with their tail lengths (Bischoff et al., 1985).

It is expected that males may incur some costs for the elongation of their tails in terms of natural selection. For example, long tails in male barn swallows decrease flight performance (Rowe et al., 2001). Therefore, another explanation for the different adoption rate of alternative mating behaviours between male guppies with different tail lengths can be considered. If long tails affect swimming performance in guppies, males with longer tails might incur more costs for performing courtship displays than males with shorter tails. Thus, males with longer tails would not be able to exhibit courtship with a high frequency; and therefore, they would need to increase their sneaking

behaviour to compensate for the loss of their mating opportunity. However, Nicoletto (1991) documented that tail shape as well as dorsal fin length did not influence swimming performance in male guppies. Moreover, assuming that long tails affect swimming performance of males, it is still unclear whether or not courtship behaviour requires greater swimming ability of male guppies than sneaking behaviour, because males have to rapidly approach females from behind for sneaking. Indeed, the frequency of courtship behaviour toward females through a clear partition did not differ between males with longer and shorter tails in this guppy population (Karino & Matsunaga, 2002). It seems unlikely, therefore, that males with longer tails performed courtship displays less often due to their lower swimming ability.

Female guppies in this population did not distinguish tail lengths of males when they had no physical contact with males (Karino & Matsunaga, 2002). In the present study, the frequency of female orient responses also did not differ between males with different tail lengths. However, females exhibited gliding behaviour toward males with shorter tails with a higher ratio than toward males with longer tails. This may imply that females can discriminate between male tail lengths during direct interactions involving physical contact with males and that they may be unresponsive to males with longer tails. However, since we used pregnant females for the experiment in this study, the females did not proceed to gliding behaviour in most cases and never attempted to copulate with males cooperatively. Thus, it will be necessary to further confirm female discrimination between male tail lengths through direct interactions using receptive females such as virgin females.

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TABLE 1. Comparison of male traits measured between short-tail and long-tail males
(N = 95 pairs)

Traits	Short-tail males median (range)	Long-tail males median (range)	p
Total length (mm)	21.4 (18.1-26.4)	21.6 (18.0-27.8)	0.31
Standard length (mm)	16.8 (13.0-19.6)	14.7 (11.7-17.8)	<0.001
Tail length (mm)	4.4 (2.8-8.3)	7.0 (5.2-12.2)	<0.001
Dorsal fin length (mm)	3.8 (2.9-6.6)	3.9 (3.1-5.8)	0.20
Gonopodium length (mm)	3.8 (2.4-5.1)	3.8 (3.0-4.9)	0.35
Orange spots			
Relative area (%)	5.9 (2.3-10.1)	5.4 (2.3-9.3)	0.19
Hue (°)	25.0 (13.7-38.4)	25.0 (13.9-38.4)	0.70
Saturation (%)	58.3 (32.5-92.3)	59.4 (32.5-93.3)	0.21
Brightness (%)	73.0 (53.0-87.3)	73.0 (53.0-87.1)	0.42
Black spots			
Relative area (%)	1.3 (0.7-3.2)	1.3 (0.7-2.9)	0.54
Brightness (%)	25.0 (3.7-34.0)	25.1 (3.7-34.5)	0.82

Statistical analysis was conducted by Wilcoxon signed-ranks test.

Figure legends

Fig. 1. Relationships between frequencies of female orient responses and male courtship behaviour (a) and male sneaking behaviour (gonopodial thrusting; b). Data before log-transformation are shown.

Fig. 2. The ratios of female glide responses to courtship displays of males with different tail lengths. Box shows 95 and 5 percentiles, and a broken line indicates 75 percentile. $N = 95$ male pairs.

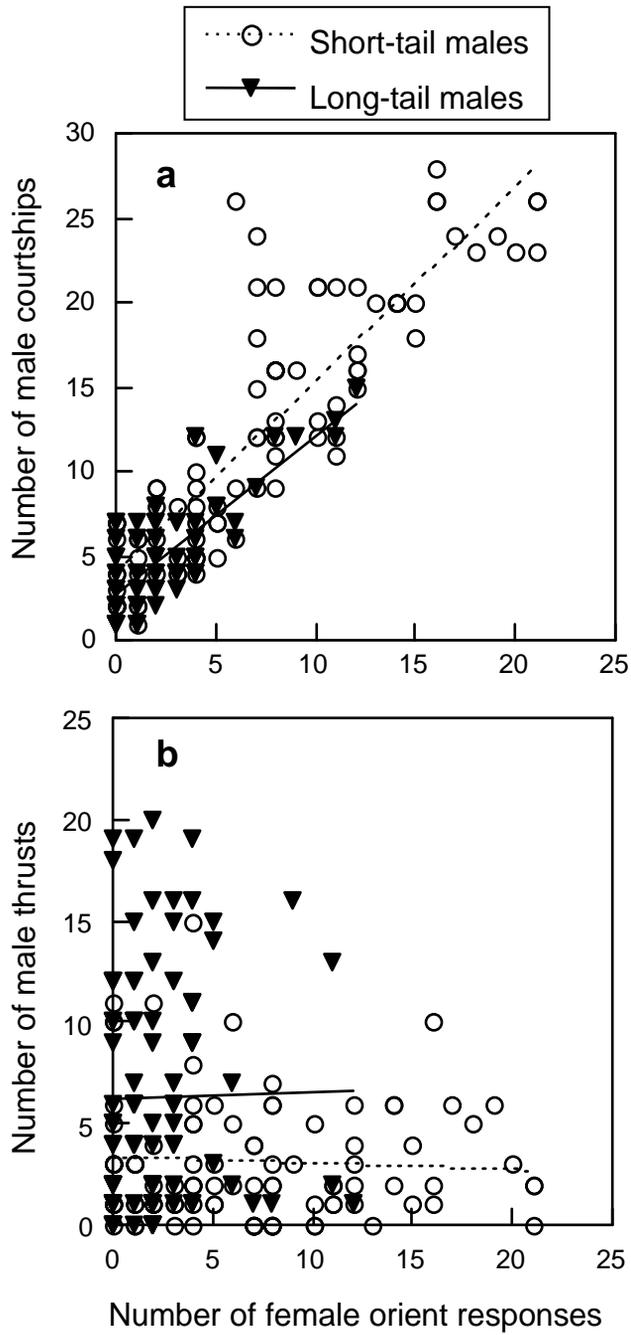


Fig. 1. (Karino & Kobayashi)

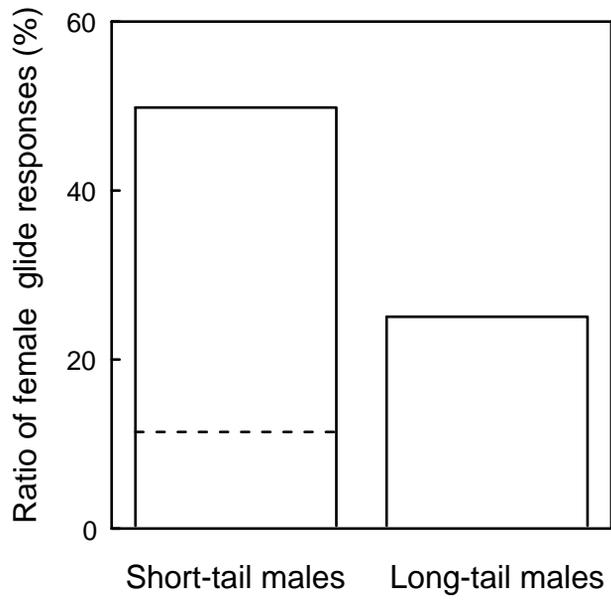


Fig. 2. (Karino & Kobayashi)