

## Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies

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**Abstract.** Individual male guppies (*Poecilia reticulata*: Poeciliinae) exhibit two distinct types of mating behaviour: sigmoid displays used in courtship, and gonopodial thrusts used in circumventing female choice. To test how these alternatives are influenced by sexual selection and natural selection, ambient light levels were manipulated to vary potential predation risk, and mating behaviour was examined in relation to male morphology. At high light intensity, larger males displayed significantly less often than smaller ones, and did not compensate with increased thrusting. In contrast, at low light, display frequency was unrelated to male morphology, but thrusting behaviour became correlated positively with the length of the male's intromittent organ (the gonopodium). No colour pigment was correlated with either display or thrusting behaviour at either light level when correlations with body size were removed. The decreased courtship by larger males under high light is consistent with individual differences in a trade-off between predation risk and mating success. The correlation between thrusting and gonopodium length parallels an interspecific pattern, and suggests that gonopodium length may be coadapted with male behaviour to circumvent female choice. Thus, covariation between alternative mating behaviour and male morphology is mediated by changing environmental conditions influencing the strengths of sexual and natural selection.

Courtship is a common tactic used to attract mates, but it is by no means universal. In many fishes of the livebearing subfamily Poeciliinae, males use a mixture of courtship displays and direct thrusts to mate with females (reviewed by Farr 1989). Courtship is usually some variant of the 'sigmoid' display, in which males flex their bodies in front of females, giving females the opportunity to choose their mates. When a female is receptive to these displays, the male briefly inserts his gonopodium (modified anal fin) into the female's genital pore for internal fertilization. In contrast, a thrusting male approaches the female from behind and jabs his gonopodium at the urogenital pore without prior display. This behavioural alternative may circumvent female choice, but it carries a low success rate for fertilization owing to female evasiveness and the likelihood of the sperm being displaced by a subsequent full copulation (Clark & Aronson 1951; Liley 1966; Grove 1980).

The presence of these two types of mating behaviour provides an opportunity to study how

individual males resolve trade-offs between mating success and risk of mortality. Guppies, *Poecilia reticulata*, are ideal for such a study because much is known about both forms of selection. Courtship by males encourages female receptivity (Farr 1980; Bischoff et al. 1985). However, in the presence of predators or at high light levels, when predation risk is greatest, courtship decreases (Luyten & Liley 1985; Endler 1987; Magurran & Seghers 1990). Thrusting may increase in frequency or as a proportion of mating behaviour because it is safer for males or because it circumvents female reluctance to mate under the threat of predation. Thus, courtship and gonopodial thrusting appear to have evolved under opposite selection pressures: courtship may attract both females and predators, whereas thrusting may minimize both female choice and predation threat.

Little is known about how individual males resolve such trade-offs. In this paper we test for coadaptation between morphology and mating behaviour of individual male guppies from a single wild population in Trinidad. First, we consider how courtship is related to male body size and

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colour patterns. In particular, we examine whether conspicuous males (large, brightly coloured) are especially sensitive to increased costs of courtship at higher light levels, as might be expected from the previous population-wide comparisons. Second, we consider whether thrusting is a 'best of a bad situation' tactic, used by smaller or unattractive males (Constantz 1975; Gross 1984; Hughes 1985; Farr et al. 1986; Ryan & Causey 1989). Finally, we test for a correlation between thrusting behaviour and the length of the male's gonopodium. An interspecific comparison of poeciliines suggested that species specializing in thrusting have longer gonopodia than species with courtship and female choice (Rosen & Tucker 1961; additional behavioural data in Farr 1989). We examined this relationship on an individual level to test whether similar patterns are evident within species.

## METHODS

### Study Population

The guppies were second and third generation laboratory descendants of approximately 100 fish of mixed sexes and ages, collected from the Quaré River in the Northern Range Mountains, Trinidad. The river drains an area of relatively undisturbed lower montane rainforest. It has an average width of approximately 10 m and depth of 1 m, and high visibility.

In this river most male-female interactions were confined to the stream edges, where the fish grazed in schools of 10-20 individuals of mixed sexes and ages. Edges are partially shaded by the forest canopy and rocky overhangs, but most of the centre of the river receives full sunlight at midday. The most dangerous local predator is the pike cichlid, *Crenicichla alta*, which preys readily on adults (Liley & Seghers 1975; Endler 1978).

Gravid females were isolated from the stock population, which consisted of approximately 75 adults at the University of Toronto. After the young were born in 8.5-litre aquaria, they were reared in communal 75-litre tanks at densities of approximately 30 fish/tank, for 4-6 months. The fish were maintained on a 12:12 h light regime (1000 to 2200 hours EST) at 25°C, and fed commercial flake food supplemented weekly with brine shrimp and *Daphnia*.

### Male Morphology

Prior to the behavioural experiments, each of 35 males was weighed on an electronic balance to the nearest mg. Total length was measured from the tip of the snout to the most distal tail fin ray. Males were then photographed individually in a small compartment of an aquarium, without anaesthetic (which alters colour patterns). The photographs were used to measure gonopodium length from the attachment at the body to the tip of the bony elements, not including the small fleshy hood that extends slightly beyond the tip.

A computer digitizing tablet was used to measure body area (not including the fins) and the areas of coloration. Three categories of colour were recognized (Endler 1983): carotenoids, which produce yellow, orange and red; iridescence, produced by guanine crystals, responsible for green and blue (silver was absent from these fish); and melanin, producing black spots. Each male was digitized twice, with the average of the two values of each measurement used in the analyses. Because the tails were not always fully spread in the photographs, percentage tail colours were estimated visually for each fish. Tail colours yielded similar results to those for body colours, so they were combined for all analyses.

### Male Post-maturational Growth

To test whether size variation among males used in the behavioural study might be due to age differences, we measured individual males from another study twice over a 25-week period. The fish had been reared under uniform conditions from birth in 8.5-litre tanks, usually in broods of five. When their gonopodia were nearly fully developed, 21 males from 12 families were transferred to 2.4-litre fine-mesh nylon baskets suspended in water baths. They were then kept at densities of either one or two fish per basket, and weighed when they reached an average ( $\pm$ SD) age of  $12.9 \pm 0.9$  weeks. This is 2-3 weeks less than the minimum age of the fish used in the behavioural experiments. They were returned to their baskets for 25 weeks, after which we reweighed them at an average ( $\pm$ SD) age of  $38.4 \pm 0.9$  weeks. This age was approximately 14 weeks older than the oldest fish used in the behavioural experiment.

At the first weighing, the 21 males averaged ( $\pm$ SD)  $103.7 \pm 17.8$  mg. Twenty-five weeks later they averaged  $109.0 \pm 20.4$  mg (paired *t* on log-transformed

data = 2.64,  $df = 20$ ,  $P = 0.016$ ). Although statistically significant, this change in weight represents only a 5% increase, compared with a coefficient of variation in weights of the males used in the behavioural experiments of 30.9% ( $\bar{X} \pm SD = 139.0 \pm 43.0$  mg) for a narrower age span. This suggests that little of the variation in male size in the behavioural study is due to variation in age.

#### Mating Behaviour

We observed mating behaviour in two 36-litre aquaria, each of which was divided into three equal-sized compartments by opaque partitions. Background colour was controlled with light-brown paper on three sides of the tanks and tan-coloured gravel. Each tank was maintained at the same temperature as the holding tanks, and equipped with water filters and heaters which were removed prior to the experimental trials. A blind was used during observations.

Light was provided by two 100 W incandescent bulbs mounted 25 cm above each tank and 40 cm apart, providing even illumination. Intensities were adjusted with a rheostat and measured with a quantum radiometer, which has a sensitivity directly proportional to the response of guppies' visual receptors (see Endler 1987). Readings were taken just above the water surface. 'High' light intensity was set at  $80 \mu\text{E}/\text{m}^2/\text{s}$  and 'Low' light was  $7 \mu\text{E}/\text{m}^2/\text{s}$ . The Low light was the minimum required to take accurate observations on the fish. Although High light was 11.4 times higher, it remained well below full sunlight, under which courtship drops dramatically (Endler 1987). This light range therefore includes conditions experienced by the fish at dawn and at dusk, when most sexual activity occurs.

The aquarium water was clear and only 22 cm deep. Therefore, little alteration will have occurred to the wavelengths of light reaching the fish (Endler 1991). A more important consideration is the shift of incandescent lighting towards longer wavelengths at low intensities. Thus, under the more reddish light of the Low light treatment, the orange colour spots of the males may have been less distinct to the females. Although we were not concerned with female mate choice in this experiment (see Long & Houde 1989), we cannot rule out the possibility that the males may have altered their behaviour according to shifts in ambient light wavelengths.

Each of the 35 males was observed courting three consecutive females between 1700 and 2100 hours EST. Six gravid females were used, matched for size (total length  $\bar{X} \pm SD = 34.4 \pm 3.1$  mm; weight  $560 \pm 160$  mg). Repeated use of the same females is justified because in the wild (and in the holding tanks prior to the experiments), individual females typically receive this much attention from males (personal observations; see also Luyten & Liley 1985). No copulations occurred during the observation sessions, as is typical for the wild, where females reject nearly all male overtures by ignoring them or swimming away, and female behaviour did not change noticeably during the experiment.

On the morning of an observation session, three males and three females were removed from a holding tank containing all of the experimental fish and acclimated together in an observation tank for approximately 10 h. Then the partitions were added, with one pair of fish in each of the three compartments. After the fish began swimming around the tank 'calmly', usually within 2 min, each pair of fish was observed in turn for 10 min. Then the males were caught with a dip-net and exchanged between compartments, exposing them to different females. The observations were repeated after the fish began swimming naturally, 1–2 min later. Each male was tested on 2 consecutive days, one designated a High light day, the other a Low light day. The order of presentation of light levels was randomized among males.

The following male behaviour patterns were recorded during each trial: number of sigmoid displays (including caudal and dorsal fins opened or closed); time spent displaying; and number of gonopodial thrusts.

#### Statistical Analyses

Although 35 males were used initially in the behavioural experiment, some behavioural data are missing for three males that jumped from their holding tanks. We were able to measure the gonopodia of 21 males from the photographs.

Since male weight, area and length were highly correlated with one another, they were combined into a single 'size' variable using a principal component analysis that accounted for 93.4% of the original variation (eigenvalue = 2.802).

Each male's behaviour was averaged for the three females he courted at each light level. There

**Table I.** Correlations ( $r$ ) between morphology and mating behaviour of male guppies

Variable	High light		Low light	
	Displays	Thrusts	Displays	Thrusts
Body size	-0.54**	-0.04	-0.28	0.21
Gonopodium length	-0.26	-0.18	-0.29	0.66*
Carotenoid area†	0.08	-0.14	0.23	0.19
Iridescence area†	0.07	-0.11	0.06	-0.16
Melanin area†	0.16	0.03	0.37	0.28

$N = 33$  at High light and 32 at Low light except gonopodium length ( $N = 21$  and 20 for High and Low light).

†Colour areas controlled for body area.

\* $P < 0.005$ ; \*\* $P < 0.001$ . Bonferroni-adjusted critical  $P$  level = 0.0125 (see text).

were strong correlations between the frequency and total time spent displaying ( $r = 0.97$  in each light level,  $P < 0.001$ ), so we present only the frequency of this behaviour. The two types of mating behaviour were analysed both as absolute frequencies of occurrence and as 'proportions' of behaviour, in which each was controlled for the frequency of the other in least-squares regressions. The two methods yielded similar results, so we present only the absolute frequencies of each behaviour.

All data were log-transformed for the analyses, with behavioural data calculated as  $\log(\text{frequency} + 1)$ . Means of raw data are given  $\pm 1$  SD. Pearson correlation coefficients were used for correlations of morphology and behaviour. Four behavioural comparisons were made for each morphological trait (courtship and thrusting at two light levels). To avoid an inflated type I error rate, we therefore used sequential Bonferroni adjustments (Rice 1989) where the significance level for rejecting the null hypothesis of 'no relationship' was set to  $0.05/4 = 0.0125$  for the most significant relationship with each morphological variable.

To control for relationships between gonopodium length and body length in some analyses (noted in the text), we used standardized residuals from least-squares regressions of  $\log(\text{gonopodium})$  against  $\log(\text{total length})$ . Similar analyses controlled for body area when analysing areas of colour. This regression method is more effective and robust statistically than the use of ratios for scaling size (Jackson et al. 1990).

## RESULTS

### Courtship Displays

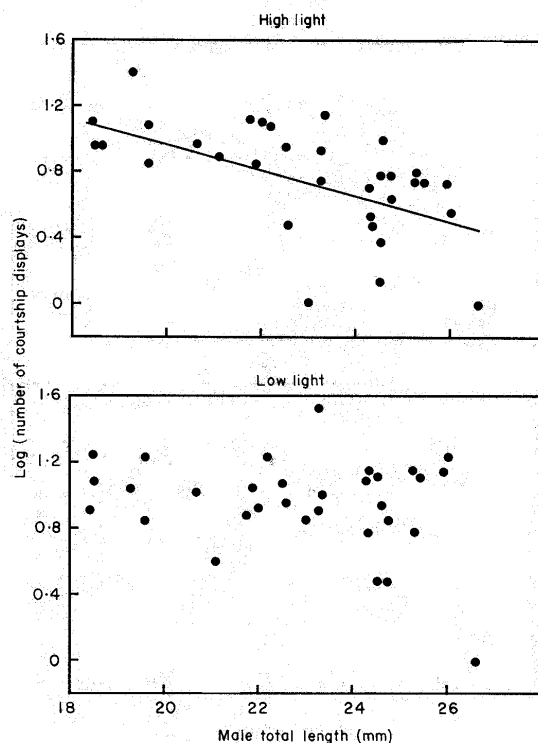
Males displayed to females more frequently in Low than High light (Low  $\bar{X} = 9.7 \pm 6.1$ , High  $\bar{X} = 6.5 \pm 5.0$ ; paired  $t = 2.59$ ,  $df = 31$ ,  $P = 0.014$ ). At Low light there was no relationship between display frequency and male size (Table I). However, at High light smaller males displayed significantly more often than larger ones (Table I, Fig. 1).

No colour pigment area was correlated significantly with courtship when controlled for body area (Table I). Conversely, body size remained negatively correlated at High light in partial correlations with each colour pigment (all  $P$ -values  $\leq 0.002$ ). Thus, larger males courted less often than smaller ones at High light intensity, regardless of their colour patterns.

### Gonopodial Thrusts

The total number of thrusts observed was not affected significantly by light level, though the tendency was for a higher frequency at High light, which is opposite to the finding for courtship behaviour (Low  $\bar{X}$  thrusts =  $8.4 \pm 6.0$ , High  $\bar{X} = 10.6 \pm 8.5$ ; paired  $t = 1.16$ ,  $df = 31$ ,  $P = 0.255$ ). Thrusts were not correlated with courtship displays at either light level (Low light:  $r = -0.02$ ,  $P = 0.904$ ; High light:  $r = -0.12$ ,  $P = 0.500$ ).

At High light, neither size nor any colour variable was correlated with thrusting behaviour (Table I). However, at Low light, males with longer gonopodia thrust significantly more often than



**Figure 1.** Relationship between male total length and sigmoid courtship displays, at two light levels. Behavioural data are log-transformed frequencies averaged over three 10-min trials. Male length is not log-transformed, to facilitate visual presentation. High light:  $F_{1,31} = 15.638$ ,  $r^2 = 0.34$ ,  $P < 0.001$ ; the equation is  $C = 2.611 - 0.080L$ , where  $C = \log(\text{courtship} + 1)$  and  $L = \text{untransformed male length}$ . Low light:  $F_{1,30} = 1.876$ ,  $r^2 = 0.06$ ,  $P = 0.181$ .

males with shorter gonopodia (Table I). To control for body size, we examined residuals of gonopodium length regressed on total length (Fig. 2). Relative gonopodium length remained significantly correlated with thrusting behaviour. When gonopodium length was controlled for composite body size, any size component, or colour pigment, the positive relationship with thrusting at Low light remained (partial correlations: all  $P < 0.02$ ). Conversely, none of the other morphological variables was related to thrusting when gonopodium length was controlled. These results show that gonopodium length, and no other measured variable, was correlated positively with thrusting behaviour at Low light.

## DISCUSSION

By manipulating conspicuousness (light level), we have shown that different individuals resolve the trade-off between natural selection and sexual selection in different ways. The expression of alternative types of mating behaviour depends on both male morphology and the environment.

The decrease in courtship by larger males under a high light intensity, when predation risk is greatest (Ender 1987), suggests that larger males may become particularly vulnerable, perhaps because size per se causes greater conspicuousness to predators (see Winemiller et al. 1990). Alternatively, since larger males were preferred by females in this

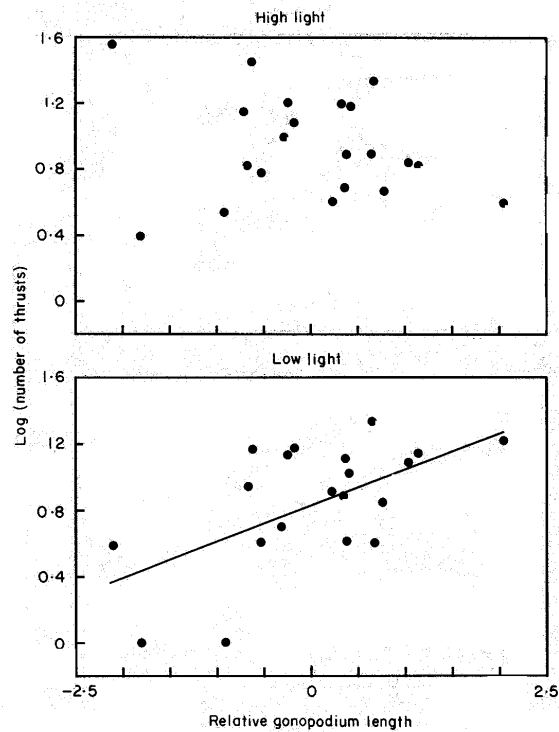


Figure 2. Relationship between male gonopodium length and thrusting behaviour, at two light levels. Thrusts are log-transformed frequencies averaged over three 10-min trials. Gonopodium lengths are standardized residuals of  $\log(\text{gonopodium length})$  versus  $\log(\text{total body length})$ . High light:  $F_{1,19} = 0.868$ ,  $r^2 = 0.04$ ,  $P = 0.363$ . Low light:  $F_{1,18} = 10.121$ ,  $r^2 = 0.36$ ,  $P = 0.005$ ; the regression equation is  $T = 0.849 + 0.227G$ , where  $T = \log(\text{thrusts} + 1)$  and  $G = \log(\text{gonopodium})$  residual from  $\log(\text{body length})$ .

population when tested under a light intensity intermediate to the two studied here (Reynolds & Goss 1992), they may not need to court as vigorously as smaller males (see Houde 1988 for another possible example). Furthermore, female receptivity may change with light levels if conspicuous males attract predators. Male size is controlled by both genetic (Reynolds & Goss 1992) and environmental (Reznick 1990) components and, as we have shown here, is nearly fixed at maturity. Adult males are thus 'locked' into a body size which, depending on environmental conditions (e.g. light level), determines their mating tactic. If decreased courtship by larger males hampers mating success, this

could select for the smaller size found in populations with high predation pressure on adults (e.g. Reznick & Endler 1982; Winemiller et al. 1990). Thus, the threat of predation may select against size through its negative effects on mating success, without larger males actually dying at a higher rate.

In contrast to body size, colour patterns had no relationship with male mating behaviour, despite their population-wide responsiveness to predation risk (Endler 1978, 1980, 1983; Winemiller et al. 1990). If brightly coloured males are more at risk to predators, the effect may occur under different light conditions than those studied here. Endler (1991) has shown that guppies are least conspicuous to

*Crenicichla*, the main predator in this population, under dawn/dusk light levels such as those used here. Subtle variation in light quality could therefore affect predation risk, particularly if predators are sensitive to variations in colour intensity (and not just area), as has been shown for females choosing mates (Kodric-Brown 1989).

Unlike the typical poeciliine pattern, smaller male guppies did not specialize in gonopodial thrusting. In four other species in three tribes (*Poeciliopsis occidentalis*, *Gambusia affinis*, *Poecilia latipinna* and *Xiphophorus nigrensis*), smaller males are less preferred by females (as in guppies) and they are subordinate to larger males, which court more often (unlike guppies) (Constantz 1975; Hughes 1985; Farr et al. 1986; Ryan & Causey 1989; Travis & Woodward 1989; Zimmerer & Kallman 1989; Ryan et al. 1990). Thrusting by guppies therefore does not fit into the typical 'best of a bad situation' tactic, whereby subordinate individuals emphasize stealth (Dunbar 1982; Arak 1984). This may be due to low levels of aggression compared with other poeciliines: fights or other forms of dominance are rare in most guppy populations both in the wild and in the laboratory under natural sex ratios (personal observations). Thus, smaller males may be able to compensate for their unattractiveness by increasing courtship without interference from other males.

The higher frequency of thrusting behaviour by males with longer gonopodia is consistent with the hypothesis that gonopodium length is under selection for circumventing female choice. The numerous bony hooks and grapples found on the gonopodia of many poeciliine species probably also serve this function, as well as aiding in sperm competition (Constantz 1984). Furthermore, our finding provides a within-species confirmation of a correlation across species between gonopodium length and the use of thrusts rather than courtship displays (Rosen & Tucker 1961). This suggests that selective processes occurring within guppy populations may be similar to those that have produced interspecific variation in mating behaviour and morphology.

Thus, this study highlights the importance of environmental conditions in alternative types of mating behaviour. As in many other species mating behaviour in guppies is related to male morphology. Large males court less often, and those with long gonopodia are more likely to use thrusts. The first relationship, however, occurs only

under a high light level and the second is restricted to low light. Alternative types of mating behaviour may help different individuals resolve the demands of sexual and natural selection according to both their own morphology and the environmental conditions they face.

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