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Analysis of early growth of guppy strains, *Poecilia reticulata*, with different color patterns

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Summary. The guppy, *Poecilia reticulata,* is economically the most important species of freshwater ornamental fish cultured in Singapore. About 30 strains with different color patterns and fin shapes are reared in guppy farms practising monoculture in Singapore. To compare the growth rates of domesticated strains with different color patterns, newborn fry of 11 strains were obtained on the same day from a single farm in Singapore and were reared experimentally in the laboratory for about 100 days. Each strain was distributed randomly into 4 tanks with 30 fish/tank. Weekly weighings of 10 fish/tank were made from 17 to 100 days of age. Three strains were homozygous for the autosomal recessive blond gene which gives rise to a pale yellow background pigmentation (*bb*). These blond strains had significantly smaller body weights than corresponding ones with the same color pattern but with the wild-type grey-brown background coloration due to the dominant allele (*BB*). The strains with the red tail pattern due to a dominant X-linked gene (*Rdt*) had more rapid growth than those with other tail color patterns including the blue, black, green snakeskin and variegated. However, no significant differences were detected among the other color pattern strains. Thus among the strains studied, the blond strains were associated with slower growth while those with the red tail color were associated with faster growth.

Key words: *Poecilia reticulata* – Guppy strains – Color genes – Growth

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Introduction

The live-bearing teleost, *Poecilia reticulata,* shows striking sexual dimorphism. Adult males are typically smaller than females and exhibit complex polymorphic, secondary sexual coloration. In contrast, females are uniformly grey-brown without color patterns. The guppy, domesticated about 40 years ago, is now economically the most important species of freshwater ornamental fish produced in Singapore mainly for export (Fernando and Phang 1985). Altogether, about 30 strains with different color patterns and fin shapes are currently cultured in farms practising monoculture. Each farm specializes in 8–12 different strains. The strains are reared individually, with the sexes separate, to maintain pure lines.

For ornamental fishes, color and growth could be considered to be two of the most important economic traits. Guppy farmers in Singapore have reported differences in the growth and viability of the different color strains (C. L. Lim, personal communication). Mode of inheritance of the color patterns of a few domesticated strains has been worked out (Dzwillo 1959; Nayudu 1979; Phang et al. 1985, 1988). Growth rates of domesticated guppy strains with different colors or color patterns have not been documented. Hence, the goal of this study on pre-adult growth of 11 domesticated guppy strains with different color patterns was to identify possible relationships between growth and color genes carried by these strains.

In another species of poeciliid fish, *Xiphophorus maculatus,* linkage relationship has been found between the color genes (*Ir* and *Br*) and alleles of the sex-linked locus *P*, which determine growth and the time of sexual maturation (Kallman and Schreibman 1973; Kallman

Table 1. Summary of the color phenotypes of guppy strains

Strain no.	Strain name	Tail color	Tail pattern	Black c.p.	Background color
1	Blue Var	blue	Var	none	*B*
2	Blond Green Ss	yellow	Ss	none	*b*
3	Red Ss	red	Ss	none	*B*
4	Green Ss	green	Ss	none	*B*
5	Red T	red	none	none	*B*
6	Blond Red T	red	none	none	*b*
7	3/4 Black	black	none	present	*B*
8	Tuxedo	red	none	present	*B*
9	Blue T	blue	none	none	*B*
10	Blond Tuxedo	red	none	present	*b*
11	Green Var	green	Var	none	*B*

Var – variegated; Ss – snakeskin; T – tail; Black c.p. – black caudal peduncle; *B* – wild-type background color; *b* – blond background color

found strong positive correlation between size of adult et al. 1973). In a study of *X. variatus*, Borowsky (1973) males and intensity of yellow or red fin coloration. Further investigations of natural populations of *X. maculatus* showed significant differences in growth rates among three tailspot morphs (Borowsky 1978, 1984). However, other studies failed to reveal consistent relationships between the tailspot color morphs, and fitness traits such as growth rate, length, weight and fecundity of females (see review by Borowsky 1984).

Materials and methods

Guppy strains

One-day-old (newborn) fry of 11 guppy strains with different color patterns were obtained on the same morning from a single guppy farm in Singapore. The color patterns of each of these strains are briefly summarized in Table 1. The names of the strains, which reflect to a large extent the color phenotype, are commercial names given by guppy farmers, dealers and hobbyists.

Since guppies are small fish, on the farms, 3–4-month-old breeders are carefully selected from thousands of adult fish for uniformly vivid colors, stream-lined shape and vigor, and then are raised in large, shallow, cement breeding tanks with stocking densities of 100–200 breeders/m^3 water. A sex ratio of one male to three females was used in the guppy farm where the present strains were obtained, while that used in other farms may vary up to a ratio of one male to ten females. Compared to large food fish like salmon or common carp, the guppy is a small ornamental fish. This enables guppy farmers to use large numbers of breeders with high male-to-female ratio and to replace the breeders with a younger batch every 4–6 months. This practise helps minimize inbreeding in the strains. Like all poeciliid fishes, the guppy is viviparous, with females giving birth to the young. Since the adults are carnivorous, newborn fry are collected twice a day from the breeding tanks (in the morning and late afternoon) and are transferred to nursery tanks. Since the strains are raised separately, it was possible to obtain 1-day-old fry of the different strains on the same morning. Details of the commercial culture of the guppy have been documented by Fernando and Phang (1985).

Experimental procedure

To minimize environmental differences and to eliminate farm effects, newborn fry of 11 guppy strains with different color patterns were purchased on the same morning from a single guppy farm in Singapore, and brought to the National University of Singapore where the experiments were conducted. The fish were acclimated for 3 days in large fibreglass tanks. Each strain was randomly divided into 4 groups of 30 fish per group. Each group was held in a plastic tank containing 8 l of dechlorinated water with 0.1 g sea salt/liter water. Altogether, 44 tanks were set up and randomly arranged in the aquarium area. Weekly weighings were taken of ten randomly selected fish from each tank, using an electronic analytical balance (AEL-160, Shimadzu), starting with 17-day-old fish, because young fry were easily killed when handled. The experiment was terminated when the fish were about 100 days old.

From birth to 3 weeks of age, the fry were fed three times daily: in the morning and late afternoon with live brine shrimp, *Artemia* sp., and at noon with powdered Tetramin (a commercial dry fish food). Thereafter, they were fed twice a day with live tubificiid worms in the morning and Tetramin food flakes in the late afternoon. Uneaten food and debris were siphoned off daily. Tanks were washed and the water changed once a week. Throughout the experiment, the fish were held in an aquarium area under a photoperiod of about 12 h of light and at a fairly constant temperature of 28 ± 2 °C.

Analysis of chromatophores

Three of the strains (Blond Green Snakeskin, Blond Red Tail and Blond Tuxedo) have pale yellow background coloration. The other eight strains have the wild-type grey-brown background coloration. The classic study by Goodrich et al. (1947) on the genetics of background coloration of the wild-type, blond, gold and cream strains of the guppy showed that two autosomal gene loci are involved, with the wild-type genes (*B* and *G*) dominant over the mutant blond (*b*) and gold (*g*) genes. The two recessive genes interact to give the cream phenotype (*bb gg*). The four background colors can be identified on basis of number, size and shape of melanophores present on the scales and skin. To check the background colors of the 11 guppy strains used in the present study, 20 females of each strain measuring about 2 cm in length, were subjected to analyses of melanophores using the method of Goodrich et al. (1947). Males were not analyzed due to complications arising from the presence of color patterns.

The background coloration of the three pale yellow-colored strains corresponded to the blond coloration and thus were considered to be homozygous for the recessive blond gene (*bb*). The other eight strains were found to have the dominant wild-type greyish-brown background color (*B*).

Results and discussion

Sex determination in *P. reticulata* is basically an X-Y system with heterogametic males (Schmidt 1919; Winge 1922). The color phenotype of guppies consists of a basic background color (wild-type or blond in the strains used in the present study), and in males highly polymorphic color patterns are superimposed on the background coloration. Studies have shown that genes determining background color are autosomal (Goodrich et al. 1944, 1947; Haskins and Haskins 1948), with all known mutant genes recessive to their respective wild-type alleles. In contrast, the color patterns studied so far in both wild-type and selected domesticated stocks are sex-limited to males and controlled by X- or Y-linked genes (Winge 1922, 1927; Winge and Ditlevsen 1974; Kirpichnikov 1981; Phang et al. 1985, 1988). The main aim in this study was to identify possible relationships between specific color genes present in domesticated strains and their growth. There have been reports by some Singapore guppy farmers that strains with blue tail coloration had a lower survival rate and slower growth, thus taking a longer period to reach marketable sizes (S. H. Toh, personal communication).

The body weights of each of the 11 strains were subjected to one-way analyses of variance at 17, 50, 80 and 100 days of age to test for differences among the four subgroups within each strain. Since no significant differences were detected among the subgroups within each strain, the subgroups/strain were pooled and one-way ANOVA was used to test for differences among the 11 strains at different ages. The Student-Neuman-Keuls procedure (Sokal and Rohlf 1981) was carried out for comparison of the strain means and the results are summarized in Table 2. At 17 days old, only the Blue Tail strain showed significantly larger body weight than the other 10 strains. The blue tail color pattern has been shown to be determined by a dominant X-linked gene, *Blt* (Phang et al. 1985).

At 50 days, the mean body weights of the 11 strains fell into 3 sets. The set of strains with the lowest mean weights consisted of the Green and Blue Variegated and also the Blond Red Tail strain. The term variegated is used when more than two colors are present on the tail, and the gene control of the blue variegated tail (blue being the main color) and green variegated tail (green being the dominant color) has not been documented. The red tail coloration of the Red Tail strain is controlled by a dominant X-linked gene, *Rdt* (Phang et al. 1985). The set of strains with intermediate average weights at 50 days of age included 2 strains with blond background (Blond Tuxedo and Blond Green Snakeskin) and strains with blue, green or black tails (Blue Tail, Green Snakeskin and ¾ Black strains, respectively). The Tuxedo and the ¾ Black strains have black caudal peduncle which is controlled by an X- or Y-linked gene (Nayudu 1979). The Tuxedo strain is further characterized by a red tail (*Rdt*) and the ¾ Black by a black tail for which the inheritance is not known. The Green Snakeskin strain has a green tail color due to a dominant X-linked gene (*Grt*) and the snakeskin body and tail patterns are due to the Y-linked *Ssb* and *Sst* genes, respectively (Phang et al. 1989). The set with the largest weights at 50 days of age included 3 strains (Tuxedo, Red Tail and Red Snakeskin) that have the wild-type (*B*) background coloration and red tail color due to the *Rdt* gene. Males of the Red Snakeskin strain in addition to the red tail (*Rdt*) have the snakeskin body and tail patterns (*Ssb* and *Sst*) that are present also in Green Snakeskin males.

The mean body weights of the 11 strains at 80 days of age showed a similar trend to that at 50 days. Strains with wild-type background coloration and red tail color (Tuxedo, Red Snakeskin and Red Tail) had significantly larger body weights than those with either blond background (including strains with red tail) or other tail colors (blue, black and green). At 100 days of age, the Green and Blue Variegated strains continued to have the smallest weights followed by strains homozygous for the blond gene (*bb*) and those with blue, black or green tails. The three strains with wild-type coloration and red tail had the largest body weights. Red color is due to a carotenoid pigment which cannot be synthesized by fishes and must be obtained from the diet. Studies have shown that female guppies favor males with more carotenoid colors (Endler 1983; Kodric-Brown 1985; Houde 1987). Endler (1983) suggested that there was a positive correlation between fitness and the amount of carotenoid pigments present in male guppies since it indicates the foraging ability and nutritional condition of the fish.

Results of the present study also provide evidence that strains with the red tail color pattern (*Rdt*) and wild-type body coloration (*B*) growth better than those with blond coloration (*bb*) or with other tail color patterns.

Among the 11 strains in the present study, three color patterns were represented by strains with either the wild-type (*B*) or the blond (*b*) background color genes (the Red Tail and Blond Red Tail strains; the Green Snakeskin and Blond Green Snakeskin strains; the Tuxedo and Blond Tuxedo strains). Two-way analyses of variance with replication were carried out to test for differences

Table 2. Summary of one-way analyses of variance to compare body weight (mg) among the 11 strains at different ages. The strains are ranked in ascending order of mean weights. Line joining mean weights indicates no significant differences between strains at 0.05 significance

Age (days)		Rank 1	2	3	4	5	6	7	8	9	10	11
17	Strain	Green Var	Blue Var	bTuxedo	Red Ss	bRed T	bGreen Ss	Tuxedo	Green Ss	3/4 Black	Red T	Blue T
	Mean wt. ±s.e.	7.70 ±0.530	9.37 ±0.639	9.77 ±0.839	9.80 ±0.670	10.08 ±0.908	10.22 ±0.791	10.35 ±0.805	10.35 ±0.683	11.63 ±0.794	12.22 ±0.802	17.66 ±2.320
50	Strain	Green Var	Blue Var	bRed T	bTuxedo	Blue T	3/4 Black	Green Ss	bGreen Ss	Tuxedo	Red T	Red Ss
	Mean wt. ±s.e.	80.75 ±4.691	83.48 ±3.879	84.59 ±4.212	94.54 ±5.458	95.14 ±6.573	95.45 ±5.310	101.30 ±5.061	103.29 ±5.567	117.11 ±5.291	118.42 ±6.153	119.61 ±6.641
80	Strain	Green Var	bRed T	3/4 Black	Blue Var	bTuxedo	Green Ss	bGreen Ss	Blue T	Tuxedo	Red Ss	Red T
	Mean wt. ±s.e.	102.03 ±5.395	125.06 ±5.212	126.88 ±4.871	127.53 ±5.624	136.19 ±7.062	141.69 ±4.717	148.88 ±6.924	156.10 ±8.515	163.14 ±7.345	166.89 ±8.469	168.45 ±8.702
100	Strain	Green Var	Blue Var	bRed T	3/4 Black	bTuxedo	Green Ss	bGreen Ss	Blue T	Red Ss	Tuxedo	Red T
	Mean wt. ±s.e.	177.78 ±7.420	197.63 ±7.846	200.43 ±7.026	203.34 ±7.295	218.38 ±10.260	220.38 ±8.869	222.58 ±10.147	229.72 ±11.349	250.34 ±11.593	254.13 ±11.023	257.88 ±11.449

b – blond backround color

Table 3. The results of two-way analyses of variance for differences in body weight between wild-type (*B*) and blond (*b*) strains and among three color phenotypes (red tail, snakeskin and tuxedo) at different ages. Mean weights of the three strains with wild-type background (Red Tail, Green Snakeskin and Tuxedo) and the three strains with blond background (blond Red Tail, blond Green Snakeskin and blond Tuxedo)

Age (days)	Source of var.	d.f.	F-ratio		Mean wt. of strains (± s.e.)	
					B backgr.	*b* backgr.
17	Between background colors	1	2.06	0.15	10.97±0.45	10.02±0.48
	Among color patterns	2	1.01	0.36		
	Interaction	2	0.85	0.43		
	Error	234				
50	Between background colors	1	16.15	0.00	112.27±3.46	94.14±3.01
	Among color patterns	2	0.35	0.71		
	Interaction	2	5.49	0.01		
	Error	234				
100	Between background colors	1	11.47	0.00	244.13±6.63	214.13±5.61
	Among color patterns	2	0.74	0.48		
	Interaction	2	4.76	0.01		
	Error	234				

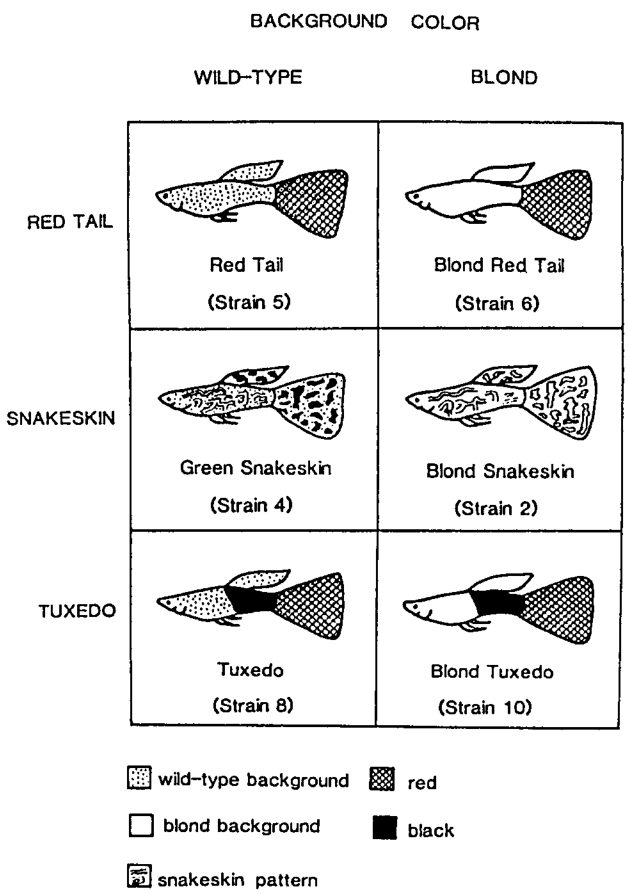

Fig. 1. Pictorial representation of the two-way analysis of variance to compare the weights between strains with the wild-type background color gene (*B*) and corresponding ones with the blond color gene (*b*) and for differences among three color patterns (red tail, snakeskin and tuxedo)

between strains with wild-type background and corresponding ones with blond background color genes, as well as among the three different color patterns (red tail, green snakeskin and tuxedo) (Fig. 1). The results are summarized in Table 3. At the first weighing (17 days old), there were no significant differences between wild-type background strains and blond strains and also no differences among the three color patterns (red tail, snakeskin body and tail and tuxedo pattern, which consisted of red tail and black caudal peduncle).

At 50 and 100 days old, results of the two-way ANOVA showed highly significant differences between strains with the wild-type coloration and corresponding ones with blond coloration, but there were no significant differences between the three color patterns (wild-type and blond combined for each color pattern). The mean body weights of the three strains with wild-type background were significantly larger than those with the blond background (Table 3). Interaction between color pattern and background coloration was also significant at 50 and 100 days.

Thus, results from this study provide evidence that guppy strains with red tail coloration due to the dominant X-linked *Rdt* gene had better growth than strains with other tail color patterns and that strains homozygous for the autosomal recessive background coloration gene (*bb*) had slower growth than those with the wild-type background coloration (*B*).

Farr (1983) reported the influence in the guppy of *r*, an autosomal recessive background color gene, on certain quantitative sexual characters, where males that are *rr* homozygotes exhibited fewer sexual displays with close fins but more with open fins than the *Rr* heterozygotes. Nayudu (1979) found that domesticated guppy varieties carrying the Y-linked *NiII* gene which causes the posterior half of the body to be black had decreased viability. Correlations between the color phenotype and other traits could be due to a few causes including pleiotropic effects of the color genes themselves, linkage of the color genes to those controlling other traits or to genetic drift occurring in the different guppy stocks during domestication. However the present experiment is not capable of determining which of these potential causes is responsible for the observed results.

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