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## Estimation of the Number of Loci Controlling the Male Body Size in the Guppy

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### Summary

Comparative growth profiles were investigated for strain difference between F and S3 of the guppy, *Poecilia reticulata*. There was an obvious difference in body length between female and male from Day 60, which became more pronounced with growth to Day 180. Size difference was more apparent in the male body length; F was larger than S3.

Using the strain comparison between F and S3 strains, the heritability of body length at various ages was estimated, and the high heritability was obtained from Day 60 ( $h^2=0.877$ ) to Day 180 ( $h^2=0.912$ ) in the males. The number of loci affecting the male size difference between F and S3 strain was estimated from F1 and F2 generations in the crosses of F and S3, and approximately 9 loci affecting the male body size at Day 180 were computed.

In the breeding process of organisms, many strains have been made by planned and/or unplanned selection. A comparison of genetic changes in the guppy strains showed them to be influenced by the intensity of selection pressure and/or by the history of breeding (1). The genetic differences among guppy strains were demonstrated using electrophoretic markers (2). The strain differences were also reported in four growth-related characters and four reproductive characters in the guppy (3). These strain differences would be caused by the genetic differences among strains.

During the process in establishment of strain, the limitation of population size may have led to a constriction in the gene pool of the cultured species, resulting in strain differences. Nakajima *et al.* (4) reported the fluctuation of gene frequencies among sub-populations made from one guppy pair using electrophoretic markers.

Nakajima and Fujio (5) estimated the heritability of body length at various ages using strain comparison of 8 strains of the guppy. The heritability changed with age, suggesting different genetic control in the three stages for the growth curve.

In our breeding experiments, two guppy strains, Fancy (F) and Standard (S3) displayed significant differences in growth. Size difference between F and S3 is more apparent in male body length, although the same tendency is observed for female body length. F is larger than S3 (1, 5).

The purposes of this study consist of two parts, one of which is to estimate the level of variance within parental F strains and within the subpopulations of F strain. The other is to estimate the heritability of body size in comparison of two strains and the number of loci.

### Materials and Methods

Two guppy strains, F and S3, were used and these were maintained as a closed colony in our laboratory. These were maintained in 60-liter aquaria at densities of 300-500 individuals per aquarium. Three sub-populations (F4, F21, F22) were made from one litter obtained from a gravid female of the F strain. One sub-population (S3HL) was made from one litter obtained from a gravid female of the S3 strain. Sub-populations were used for experiment after three or four generations and their density became the same level as the original population. For the growth profiles, the litter was obtained from the gravid females in each of the strains and sub-populations. Each litter was reared in 2.5-liter aquaria and the density per aquarium was limited to a maximum of 10 individuals. Guppies were maintained at a temperature of  $23 \pm 2^\circ\text{C}$  and fed a ground carp diet twice daily with dried *Daphnia* given as a supplement. Standard body length was measured at 15 day intervals from their birth to Day 180.

Heritability was estimated by standard analysis of variance (6). The expected mean square between strains is equal to  $\sigma_E^2 + k\sigma_G^2$ , where  $\sigma_E^2$  and  $\sigma_G^2$  are the environmental and genetic components of variance, respectively, and  $k$  is the number of individuals measured per strain.

$F_1$  and  $F_2$  generations were obtained from the cross between females of F22 strain and males of S3HL sub-population.

The minimum number of loci affecting the character was estimated from the results of cross experiments. The equation is  $n = (m_1 - m_2)^2 / 8 (V_{F_1} - V_{F_2})$ , where  $m_1$  and  $m_2$  are the means of the parental strains and  $V_{F_1}$  and  $V_{F_2}$  are the computed variance of the  $F_1$  and  $F_2$  generations, respectively.

**Results and Discussion**

Fig. 1 shows the growth curves for female and male of F22 and S3HL subpopulations from Day 0 to Day 180. F22 and S3HL subpopulations were representative for F and S3 strains, respectively, because they were prepared from the F and S3HL strain. Sex differentiation usually occurred between Day 45-60. Growth curves were essentially linear from Day 0 to 60, after which the curves for females gradually decreased in slope, while the curves for males drastically decreased in slope and plateaued. There was an obvious difference in size between female and male in both strains from Day 60, which become more pronounced as growth proceeded to Day 180. The size differences between F22 and S3HL had to be found by comparing the measurements within each sex separately, and a significant difference was observed between F22 and S3HL in the males after Day 60. This profile was the same as that of original F and S3 strains (5).

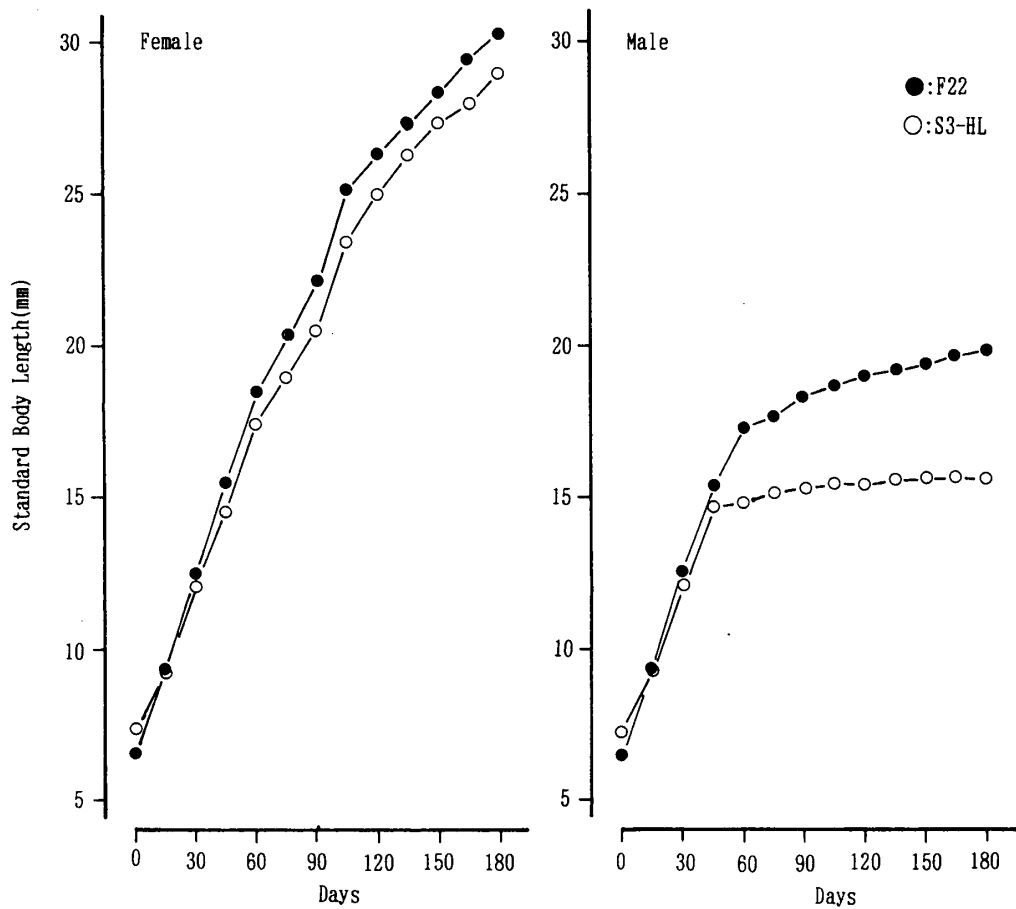


FIG. 1. Comparative growth profiles in females and males of F22 and S3HL sub-populations.

Coefficient of variation (CV) of body length at various ages was computed, and the CV changed with age (Fig. 2). The curves of CV increased from Day 0 to Day 15, after which the curves maintained a high level until Day 90 in female and until Day 45 in male. Then CV decreased and plateaued at around Day 105 in female and around Day 60 in male.

Comparison of CV was done for three categories in the subdivision of a population; original population, sub-population, and litter-population in the F

TABLE 1. *Coefficient of variation (CV) for body length in three categories in the subdivision of F strain population.*

Days after birth	Original Population of F strain	3 Sub-populations of F strain	8 litter populations of F22 sub-population
Female			
0	5.4	6.9 (5.2- 7.8)	6.2 (3.0- 7.5)
15	9.5	9.2 (8.6- 9.6)	5.6 (3.1- 8.5)
30	14.1	9.7 (8.5-10.4)	6.9 (3.6-10.2)
45	15.0	9.6 (8.6-11.1)	7.7 (6.5-10.0)
60	14.9	10.3 (8.6-12.3)	8.7 (6.8-10.6)
75	7.5	11.0 (9.6-12.6)	8.0 (5.6- 9.9)
90	13.1	9.8 (7.1-12.2)	9.2 (4.4-14.5)
105	10.3	9.4 (7.3-10.7)	9.8 (7.9-13.4)
120	11.2	8.5 (5.4-11.0)	9.6 (7.9-13.8)
135	11.4	10.9 (5.5-16.3)	9.5 (6.5-12.0)
150	10.9	7.8 (4.5- 9.7)	8.5 (7.4- 9.8)
165	10.7	8.1 (5.4- 9.7)	8.3 (5.9- 9.9)
180	10.0	8.5 (6.8- 9.8)	8.3 (7.4-10.3)
Male			
0	5.4	6.9 (5.2- 7.8)	6.2 (3.0- 7.5)
15	9.5	9.2 (8.6- 9.6)	5.6 (3.1- 8.5)
30	14.1	9.7 (8.5-10.4)	6.9 (3.6-10.2)
45	15.0	9.6 (8.6-11.1)	7.7 (6.5-10.0)
60	10.0	5.9 (2.1- 7.9)	5.7 (2.4-11.0)
75	5.2	6.0 (3.5- 7.3)	6.9 (2.8-11.0)
90	6.5	6.1 (4.1- 7.3)	6.6 (1.1-11.4)
105	5.2	4.5 (1.1- 6.3)	4.1 (2.9- 6.9)
120	6.3	5.0 (2.6- 6.2)	3.8 (2.1- 5.4)
135	5.9	5.1 (3.3- 6.1)	4.1 (2.6- 7.1)
150	5.8	5.4 (3.9- 6.2)	3.9 (2.0- 7.1)
165	5.8	5.7 (5.0- 6.1)	4.2 (2.4- 5.6)
180	6.5	5.0 (3.9- 6.0)	3.4 (1.3- 6.7)

Numbers in parentheses indicate range. Data include both sexes until Day 45.

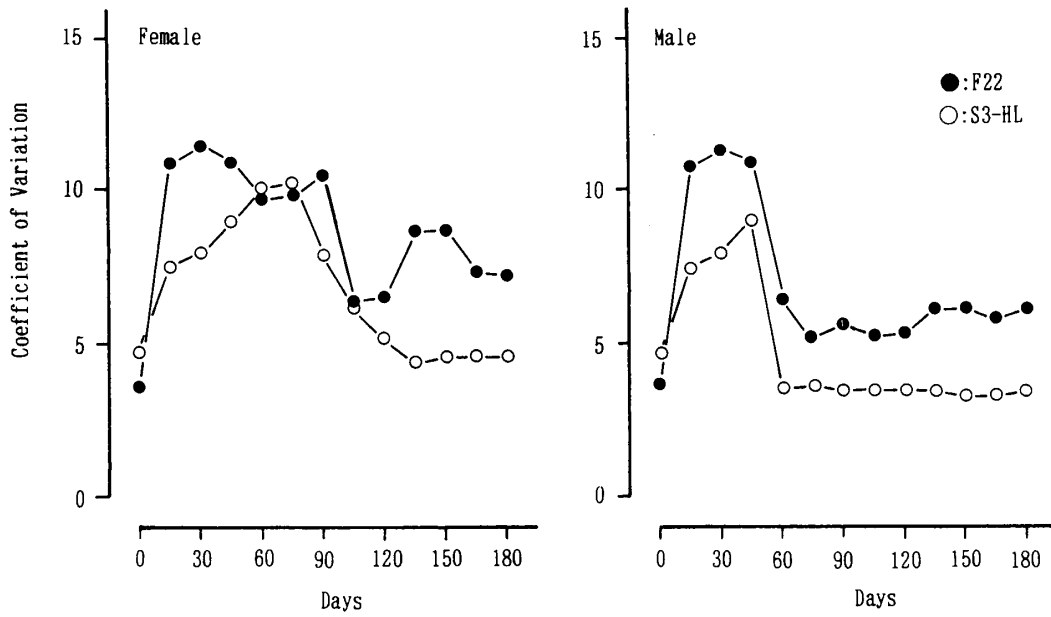


FIG. 2. Coefficient of variation (CV) for body length at various ages in F22 and S3HL sub-populations.

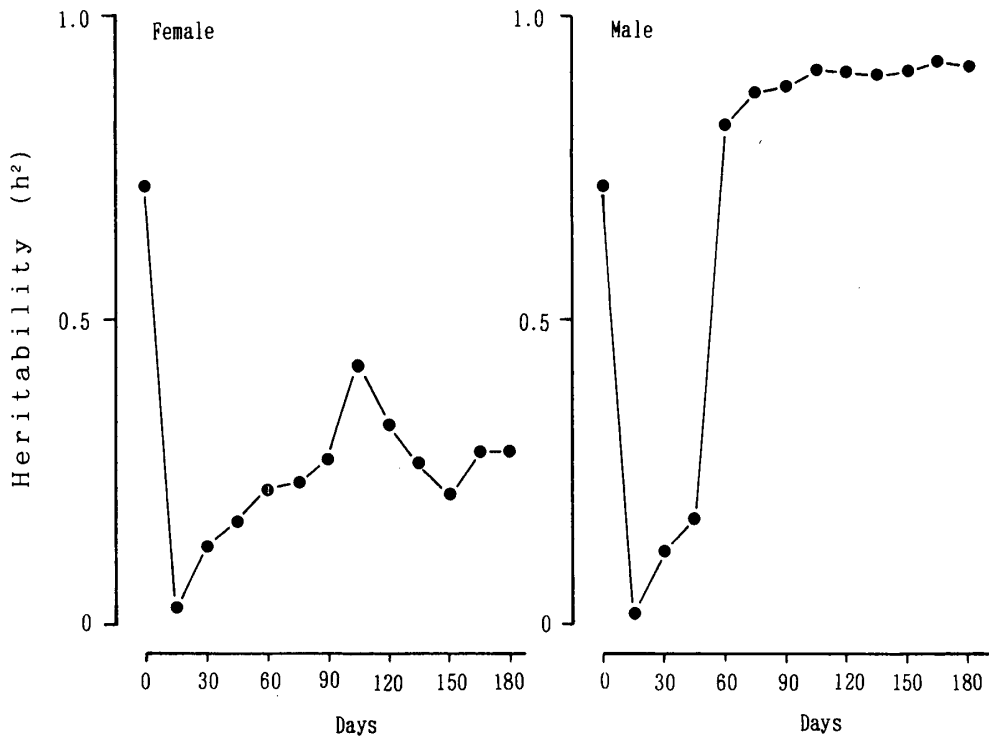


FIG. 3. Change in heritability ( $h^2$ ) estimated by strain comparison with age in the guppy.

strain (Table 1). One of the basic genetic phenomena was that three categories were different in the degree of resemblance between relatives. If genetic variation exists for the growth in original population, the CV would be significantly different among three categories, although the tendency of decrease was observed from original population to litter population. It suggests that a large proportion of the observed variance is caused by environmental variance.

To estimate the proportion of genetic determination for growth at each age, the heritability ( $h^2$ ) was calculated by standard analysis-of-variance techniques. The result is presented in Fig. 3. From a comparison between F22 and S3HL for body length, the heritability was 0.716 at Day 0, 0.020 at Day 15, 0.124 at Day 30, and 0.162 at Day 45. After sexual differentiation (Day 60), the profiles of heritability with age followed different patterns for females and males. With respect

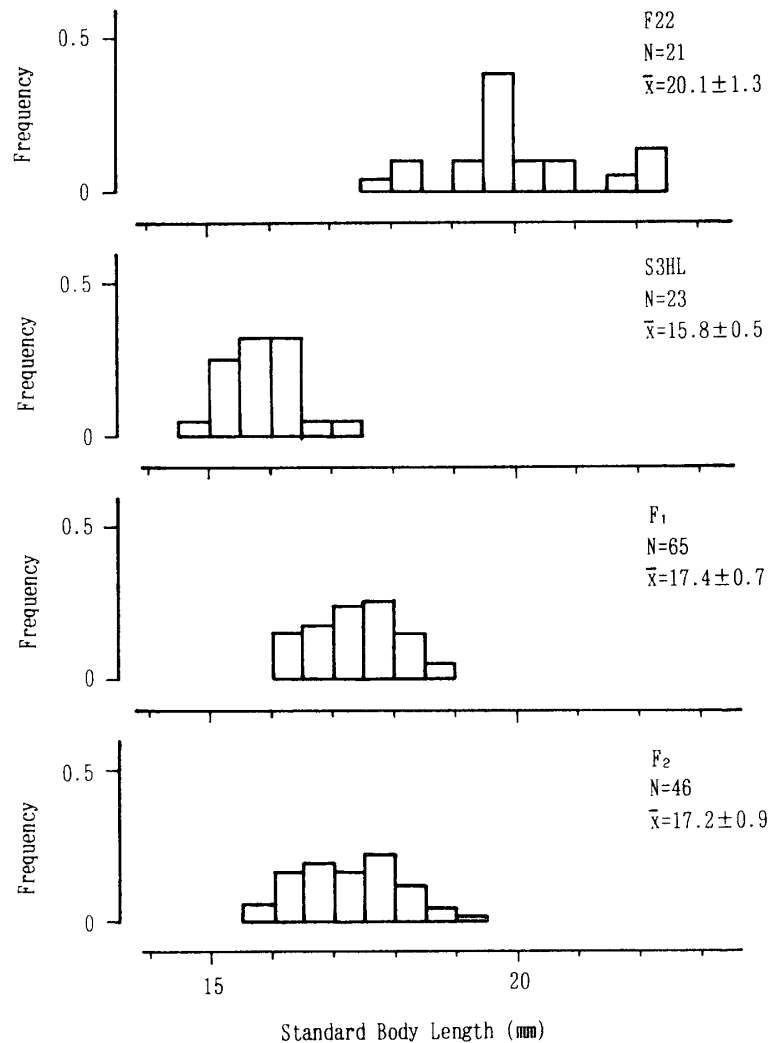


FIG. 4. The distribution of body length at Day 180 in P, F<sub>1</sub> and F<sub>2</sub> generations in the males of the guppy.

to female body length from Day 60 to 180, heritability ranged between 0.206 and 0.437 with an average of 0.276, indicating the stable level. On the other hand, the heritability from Day 60 to Day 180 in males ranged between 0.825 and 0.923 with an average of 0.896, this stable level being higher than in females. This profile was the same as the result reported previously (5). The change of heritability with age suggests three different genetic controls in three stages for the growth curve. The high heritability ( $h^2=0.716$ ) showed a significant difference between F and S3 strain, suggesting maternal genotypic effects. Low heritability at the growing stage showed a few difference between F and S3. The high values ( $h^2=0.896$ ), obtained from Day 60 to Day 180 in males, suggests that the final body size is induced by a major gene with major effects. This assumption was supported by the argument that heritability is inversely proportional to the number of loci controlling variance to the character (7). This high value also suggests a significant difference between F and S3 strain and the existence of inhibitory gene(s) due to the final body size of males.

The following experiment was focused on the strain difference in the final body size of males and was made to estimate the number of loci affecting the final body size of males. For the male body length at Day 180, the distribution of the proportion of individuals falling in each class for the P,  $F_1$  and  $F_2$  generations was shown in Fig. 4. The guppies were grouped in classes, each covering a range of 0.5 mm, but body length varied continuously. In the P generation, no overlap in distribution was observed between parental F22 and S3HL. The F22 and S3HL had average body length 20.1 mm and 15.8 mm, respectively. The  $F_1$  was intermediate in body length between parental strains and the  $F_2$  had broader distribution than the  $F_1$ . With one pair of genes, the expected classification of  $F_2$  individuals was not observed. It can be concluded that more than one pair are involved in the male size difference between two parental strains.

The number of loci affecting the male body length at Day 180 was estimated at 9. This value is calculated based up on the polygenic model. The effect of polygenes are additive because the effects of the alleles having an identical effect are cumulative. Falconer (8) found 35 loci affecting 6-week body weight of mice, the heritability being 0.232. However, it is not always that all alleles have an identical effect and some may have greater effect than others at different loci. In this connection, Fujio and Nakajima (9) estimated the heritability for dwarf body length at Day 60 as 0.880 in normal females and 0.845 in normal males, and demonstrated that dwarfism was induced by a single recessive gene from the segregation of the dwarf in some of the litter of inbred pedigree. Nevertheless, it can be concluded that the number of loci affecting the final male body size is few.



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