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Strain Differences and Heterotic Effects among Three Strains of the Guppy, *Poecilia reticulata*

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Summary

Three guppy strains, Fancy (F), Mosaic (M), and Standard (S), displayed significant differences in four growth-related traits: survival at Day 0 and Day 60, female and male body length at Day 60; and in four reproductive traits: fertility ratio, age at first parturition, offspring size, and offspring mortality. Hybridization between the three strains, in a total of six reciprocal combinations, resulted in overall trait improvement compared to the parent strains, indicating heterosis. Heterotic effects were measured by the deviation of the reciprocal hybrids from the corresponding mid-parent ([h]/m), where a unidirectional positive deviation for most of the combinations and a tendency for higher average values in reproductive traits were observed. A positive correlation between [h]/m and [d]/m (trait differences between strains), with a tendency toward higher values observed in reproductive traits, suggests that the more divergent the parent strains are, the higher the heterotic effects manifested in the hybrids. The convenience of [h]/m as a general parameter for measuring and comparing heterotic effects among traits and strain combinations was shown.

Introduction

The economic and social importance of heterosis in agricultural breeding cannot be overstated (1). However, in fish species, planned cross for commercial purposes is still a relatively unapplied endeavour. The most studied species, so far, is the common carp, and its genetic improvement by hybridization has been investigated in detail by Moav and Hulata (2), Wohlfarth *et al.* (3, 5) and Hulata *et al.* (4) as well as by Suzuki and Yamaguchi (6). Heterosis for growth, disease resistance, and reproductive performance were also demonstrated in crossbreeds of channel catfish (7). Crossbreeding of rainbow trout strains have demonstrated heterosis for growth and survival (8), for developmental stability measured by symmetry of meristic characters (9), and for hatching rate (10). Moreover, crossing of 5 strains of Atlantic salmon demonstrated significant total heterosis for survival, maturation, and body weight (11). The benefits of strain crossing could be fully realized by quantifying heterotic effects in as many traits and among several strains if possible. A common parameter that could be used to measure and compare these heterotic effects would therefore be convenient and useful.

Strain differences and heterotic effects might be more clearly demonstrated in controlled populations where environmental variation could be minimized. As a model organism for crossbreeding experiments, the guppy, *Poecilia reticulata*, is a suitable fish because of its short life cycle, reproductive capacity, and ease of breeding. Ten strains with varying sizes, fin shapes, and colour patterns have been maintained and/or produced in this laboratory and genetically characterized at several biochemical loci (12). Because of their suitable breeding characteristics, it has been possible to investigate several useful characters related to growth and reproductive capacity. This paper is an account of genetic differences in 3 guppy strains and heterosis in their reciprocal hybrids at 8 quantitative traits. It also reports a general parameter that proved to be an effective measure of heterotic effects in any trait and a comparable index for different traits and strain combinations.

Materials and Methods

A description of the guppy strains, how they were produced and maintained, is given in an earlier paper (12). The 3 strains, Fancy (F), Mosaic (M), and Standard (S) were used in the experiments. F and M belong to Group 1 with larger body size, particularly of the male, compared to Group 2 where S belongs. The experimental breeding scheme is illustrated in Fig. 1. Female and male guppies from the parent stocks are taken at random and pairmated in 2.5 liter aquaria. The litters produced are separated from the parents and designated as the Pl generation for the respective strains. As soon as sex can be differentiated (usually 45-60 days but sometimes as early as 30 days), randomly selected pairs are separated and maintained in 500-ml conical beakers until Day 180 or until first parturition. If possible, half of the offspring are utilized for Fl hybrid production experiments. When males are insufficient, 2-3 females from the same lot are mated to one male ; gravid females are later separated before parturition. The Fl hybrids are designated by letters indicating female parent followed by male parent. The fishes are maintained at a temperature of 23±2°C and fed with ground carp pellets twice a day ; dried Daphnia is given as supplementary diet. Each container is provided with the willow moss, primarily as a hiding place for newborn guppies.

The following traits illustrated in Fig. 1 were considered :

(1) Day 0 survival based on the ratio of survivors to total offspring number ;
(2) Day 60 survival based on the ratio of survivors to the number of Day 0

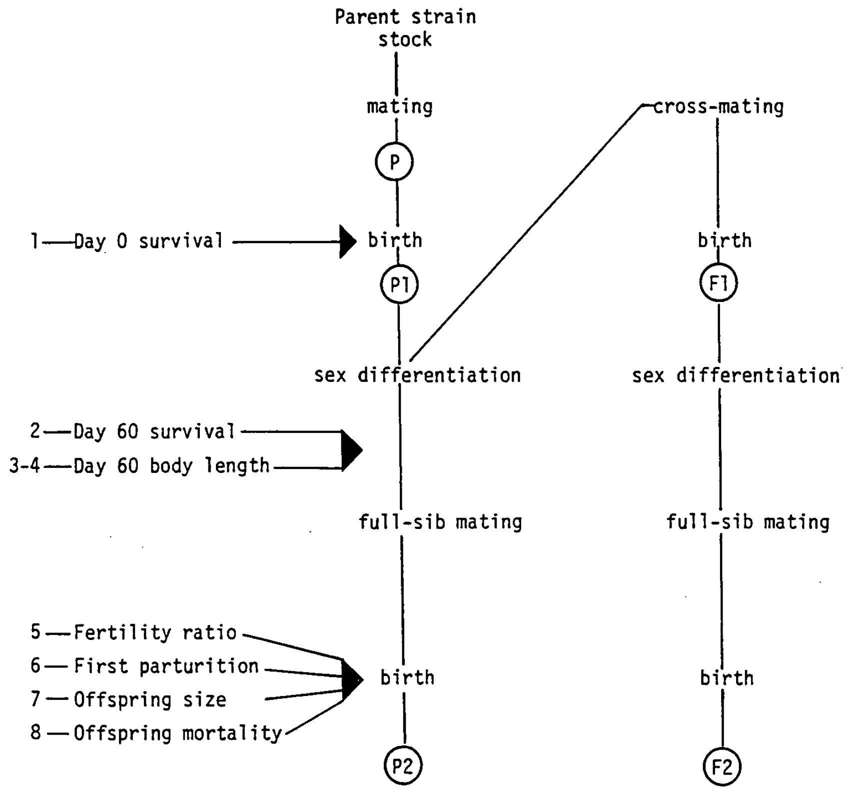

FIG. 1. Breeding schemes used in the measurement of 8 quantitative traits in F, M, S parent strains and their reciprocal hybrids.

survivors ;

(3)-(4) Body length (Standard) of female and male at Day 60 expressed to the nearest hundredth of a mm ;

(5) Fertility ratio based on the number of females which gave birth at or before Day 180, to the total number of females used in the mating experiments ;

(6) Age (Days) at first parturition measured as soon as Pl generation or the Fl hybrid female delivers its offspring ;

(7) Offspring size based on the number of offspring at the P2 or F2 generation for the parent strain and the hybrid respectively and measured simultaneously with age at first parturition ;

(8) Offspring mortality based on the ratio of dead to total number of P2 or F2 offspring and measured simultaneously with age at first parturition. Traits (1)-(4) are growth-related characters and (5)-(8) exhibit the reproductive capacity of the female.

Parent and hybrid values were expressed as the mean and its standard error. The effects of strain crossing on the quantitative traits were expressed as deviations from the mid-parent values. The following estimates, adopted from Jinks (13) were used in this study :

$$m=(Pi+Pj)/2$$
$$[h]=F1-m$$
$$[d]=|Pi-Pj|/2$$

where Pi and Pj are the mean values of the parent strains utilized in the cross, m, the mid-parent value, F1, the hybrid value, and [d], the additive component of variation which also reflects the phenotypic difference between parent strains. The magnitude of improvement of a hybrid compared to its midparent value was expressed as individual heterosis, [h]/m ; in this form, the values become standardized and proportionally estimate what traits are greatly influenced by hybridization. Another expression of heterosis, [h]/[d], termed as potence ratio (14, 15) includes both the dominance and additive components of variation.

Results

The means and standard errors for 4 growth-related and 4 reproductive traits measured in the 3 strains, F, M, and S, and their F1 hybrids are presented in Tables 1 and 2, respectively. As shown in Table 1, significant strain differences for Day 0 survival were observed between F and M ($.025<P.050$), F and S ($P<.005$), but not between M and S, while Day 60 survival rates were significantly

TABLE 1. *Means ± SE for 8 quantitative traits in the 3 strains of the guppy,* P. reticulata

TRAITS	STRAINS		
	F	M	S
Growth-related traits			
(1) Survival at Day 0	0.970±0.006 [795(51)]	0.936±0.014 [311(33)]	0.946±0.005 [1772(212)]
(2) Survival at Day 60	0.934±0.021 [137(10)]	0.694±0.042 [121(16)]	0.800±0.023 [305(31)]
(3) Body length at Day 60 (♀), mm	17.95±0.37 [55]	16.68±0.32 [58]	18.47±0.44 [34]
(4) Body length at Day 60 (♂), mm	17.61±0.31 [33]	16.88±0.39 [34]	15.52±0.18 [32]
Reproductive traits			
(5) Fertility ratio	0.954±0.045 [22]	0.540±0.082 [37]	0.915±0.029 [94]
(6) Age (Days) at first parturition	111.35±6.02 [20]	113.90±4.02 [21]	103.61±2.98 [88]
(7) Offspring size	10.60±1.06 (20)	7.43±0.93 (21)	8.04±0.55 (88)
(8) Offspring mortality at birth	0.136±0.023 [214(21)]	0.019±0.011 [156(21)]	0.085±0.010 [708(88)]

Number of lots are enclose in ( ) while number of individuals are enclosed in [ ].

different between all strains; F displayed the highest, and M the lowest values. Day 60 female body lengths were significantly different between M and F ($.010 < P < .025$), M and S ($P < .005$), but not between F and S. On the other hand, Day 60 male body lengths significantly differed for F and S ($P < .005$), M and S ($P < .005$), but not for M and F. Fertility ratios were significantly different for M and F ($P < .005$), M and S ($P < .055$), but not for F and S; M displayed the lowest fertility rate and F, the highest. For age at first parturition, only M and S showed a significant diference ($.025 < P < .050$). Offspring size differed between F and S ($P < .050$) and between F and M ($.025 < P < .050$) but not between M and S. Significant differences were observed between the 3 strains for offspring mortality, where M displayed the lowest, and F the highest value. As an overall result, significant differences were observed in 6 out of 8 traits between F and M, in 5 out of 8 traits between F and S, and in 6 out of 8 traits between M and S, indicating divergence in both growth-related and reproductive traits in the 3 strains.

Table 2 presents the means and standard errors for the same traits as determined in the parent strains, of the reciprocal hybrids between, F, M, and S. Significant differences between reciprocal hydrids were observed only in body lengths of female and male, offspring size, and mortality at Day 0 of M×S hybrids, and in female body length of F×M hybrids. Comparisons of the hybrid and corresponding parent values in each of the 8 traits revealed the following results:

Only in M×S hybrids were lower values observed for offspring size and mortality compared to both parents. Intermediate values between parents were observed at Day 60 survival in F×S/S×F, at Day 60 female body length in M×S, at Day 60 male body length in S×M, at fertility ratio in S×F, and at age of first parturition in S×F hybrids. Forty out of 48 comparisons showed higher values for reciprocal hybrids over both parents, indicating heterosis.

The deviations of the reciprocal hybrids from the corresponding mid-parent are expressed as ratios of [h]/m (Table 3). Higher [h]/m values mean higher heterotic effects because these values are the resulting rates of increase over the mid-parent (which is the expected hybrid value based on an additive mode of inheritance). For the age at first parturition, the actual age was deducted from 180 (which is the limiting age for the criterion of fertility) to produce a measure that would give a plus deviation if the age at first birth becomes earlier. The same treatment was done on offspring mortality, which value was deducted from 1.000. Thus, for all the traits studied, a plus deviation would mean increased survival rates, body size, fecundity, and fertility, earlier maturity, and decreased mortality. Individual [h]/m values for each reciprocal hybrid presented in Table 3 show opposing effects only for female body length, offspring size, and mortality in S×M/M×S hybrids and for fertility ratio in F×S/S×F hybrids, and a unidirectional positive deviation for all the other combinations. These values were distributed over a wide range from -0.232 to $+0.364$ where the

Table 2. *Means ± SE for 8 qkantitative traits of*

TRAITS	F×M	M×F
Growth-related traits		
(1) Survival at Day 0	1.000±0 [69(7)]	1.000±0 [69(5)]
(2) Survival at Day 60	0.942±0.028 [69(7)]	0.986±0.014 [69(5)]
(3) Body length at Day 60 (♀), mm	20.22±0.23 [33]	18.97±0.22 [40]
(4) Body length at Day 60 (♂), mm	18.02±0.15 [29]	18.16±0.16 [27]
Reproductive traits		
(5) Fertility ratio	1.000±0 [33]	0.970±0.076 [34]
(6) Age (Days) at first parturition	104.84±3.16 [32]	103.45±1.74 [33]
(7) Offspring size	11.03±0.012 (32)	12.30±1.29 (33)
(8) Offspring mortality at birth	0 [353(32)]	0.002±0.002 [406(33)]

Number of lots are enclosed in ( ) while number of

highest average [h]/m ratios observed were for fertility ratio (+0.220), offspring size (+0.207), and survival at Day 60 (+0.165). A tendency for higher average [h]/m ratios in reproductive traits was observed.

The phenotypic difference [d] between parent strains involved in hybridization, expressed as [d]/m ratios, are also shown in Table 3 for 8 quantitative traits. As in [h]/m, the [d]/m values were distributed over a broad range from 0.005 to 0.277, with the highest mean ratios obtained for fertility ratio (0.185), offspring size (0.117), and survival at Day 60 (0.098). A congruence for high [h]/m in high [d]/m strain combinations was observed for the 3 traits-fertility ratio, offspring size, and survival at Day 60, with higher levels in the 2 reproductive traits. Moreover, a positive correlation (r=0.698) between [h]/m and [d]/m was noted over all traits (Fig. 2), indicating that the more divergent the parent strains are, the higher the heterotic effects manifested in the F1 hybrids. A higher correlation coefficient was observed in the 4 reproductive traits (r=0.739) compared to the 4 growth related traits (r=0.430).

The ratio of both values, [h]/[d], which is a measure of the relative potence of the gene sets, is shown at each of the 8 quantitative traits in all of the hybrids. The general condition for heterosis is that the absolute value of the potence ratio should be more than 1. Most of the combinations and traits showed heterosis.

riciprocal hybrids between 3 strains of the guppy, P. reticulata

F1 HYBRIDS			
F×S	S×F	S×M	M×S
0.978±0.012 [137(7)]	0.993±0.007 [148(11)]	1.000±0 [79(9)]	1.000±0 [78(9)]
0.921±0.024 [127(7)]	0.893±0.026 [140(11)]	0.936±0.028 [78(9)]	0.953±0.023 [85(5)]
21.16±0.26 [58]	20.87±0.37 [44]	19.12±0.25 [47]	16.91±0.44 [21]
17.78±0.22 [46]	17.86±0.20 [37]	16.22±0.16 [21]	17.29±0.32 [17]
1.000±0 [52]	0.927±0.041 [41]	0.935±0.036 [46]	0.970±0.030 [33]
98.02±3.07 [52]	106.38±3.50 [39]	102.80±2.45 [43]	100.70±3.89 [32]
12.19±0.95 (52)	12.05±0.98 (39)	9.95±1.11 (43)	5.94±0.62 (32)
0.030±0.007 [634(52)]	0.045±0.010 [446(37)]	0.014±0.006 [428(43)]	0.095±0.021 [190(32)]

individuals are enclosed in [ ].

Discussion

Heterosis has been reported in some fish species for several traits, e.g. for viability (3) and for growth rate and sexual maturity in hybrids between the European and Chinese carp races (4) ; for growth rate, survival, and feed conversion efficiency in crosses between Yamato (Japanese) and mirror (European) carp strains (6) ; for survival, growth, and maturity in crosses between 5 Norwegian strains of Atlantic salmon (11). However, the studied traits have been considered separately and the overall performance of the hybrids with respect to all the traits, as well as what traits demonstrated higher heterotic effects could not be assessed because no common parameter with a comparable weight for each trait was used. Presently, there are not many reports on the heterotic effects of strain crossing in fish species. The study of heterotic effects necessitates the survey of many traits in a systematic combination of parent strains and the use of a general parameter for expressing the results. Although potence ratio ([h]/[d]) is convenient for expressing heterosis (14, 15), the weight of this parameter would vary among different traits, thus making comparisons of heterotic effects among strain combinations and among several traits impossible. The deviation of the hybrids from the corresponding mid-parent ([h]/m) could be considered as a common parameter which can measure the degree of increase or decrease from the mid-parent

TABLE 3. *Measures of heterosis in reciprocal hybrids between F, M, and S strains of the guppy,* P. reticulata

TRAIT	HYBRID	[h]/m	[d]/m	Potence ratio	
				[h]/[d]	Mean
Growth-related traits					
(1) Survival at Day 0	F×M	+0.049	0.018	2.722	2.722
	M×F	+0.049		2.722	
	F×S	+0.021	0.013	1.615	2.231
	S×F	+0.037		2.846	
	S×M	+0.063	0.005	12.600	12.600
	M×S	+0.063		12.600	
(2) Survival at Day 60	F×M	+0.157	0.147	1.068	1.252
	M×F	+0.211		1.435	
	F×S	+0.062	0.077	0.805	0.597
	S×F	+0.030		0.390	
	S×M	+0.253	0.071	3.563	3.725
	M×S	+0.276		3.887	
(3) Body length (♀) at Day 60	F×M	+0.168	0.037	4.541	3.568
	M×F	+0.096		2.595	
	F×S	+0.162	0.014	11.571	11.000
	S×F	+0.146		10.429	
	S×M	+0.088	0.051	1.725	0.490
	M×S	−0.038		−0.745	
(4) Body length (♂) at Day 60	M×F	+0.045	0.021	2.143	2.333
	F×M	+0.053		2.524	
	F×S	+0.073	0.063	1.159	1.198
	S×F	+0.078		1.238	
	S×M	+0.001	0.042	0.024	0.810
	M×S	+0.067		1.595	
Reproductive traits					
(5) Fertility ratio	F×M	+0.339	0.277	1.224	1.152
	M×F	+0.299		1.079	
	F×S	+0.070	0.021	3.333	1.476
	S×+	−0.008		−0.381	
	S×M	+0.285	0.258	1.105	1.198
	M×S	+0.333		1.291	
(6) *Age at first parturition	M×F	+0.116	0.019	6.105	6.632
	F×M	+0.136		7.158	
	F×S	+0.130	0.053	2.453	1.368
	S×F	+0.015		0.283	
	S×M	+0.084	0.072	1.167	1.368
	M×S	+0.113		1.569	
(7) Offspring size	F×M	+0.224	0.176	1.273	1.673
	M×F	+0.364		2.074	
	F×S	+0.308	0.137	2.248	2.193
	S×F	+0.293		2.139	
	S×M	+0.286	0.039	7.333	0.692
	M×S	−0.232		−5.949	
(8) *Offspring mortality at birth	F×M	+0.084	0.063	1.333	1.317
	M×F	+0.082		1.302	
	F×S	+0.091	0.029	3.138	2.845
	S×F	+0.074		2.552	
	S×M	+0.040	0.035	1.143	−0.071
	M×S	−0.045		−1.286	

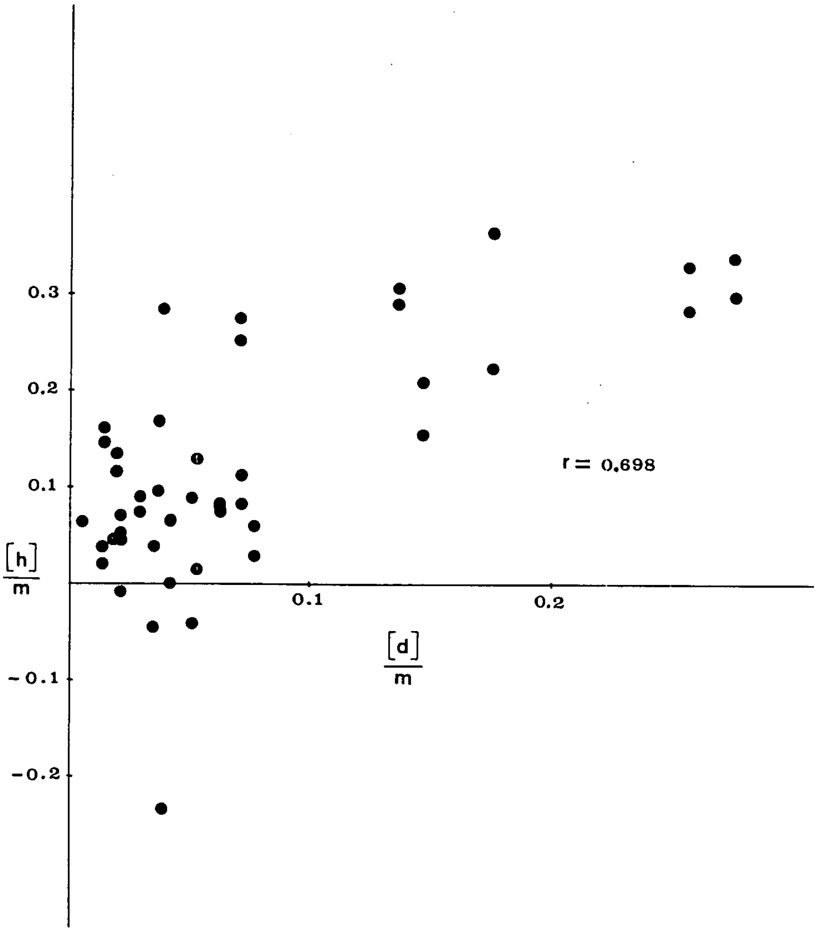

FIG. 2. Correlation between dominance deviation [h]/m and additive deviation [d]/m, expressed as ratios over the mid-parent means.

value or the expected hybrid performance based on additive inheritance. Using [h]/m, a quantitative comparison of heterotic effects could be done among several traits and among strain combinations.

Although heterosis has become synonymous with heterozygote superiority, the causal factors and mechanism remain obscure. What was clearly revealed in the present study was the correlation between the deviation of the hybrid from the mid-parent value (=heterotic effect) and the additive component of variation (= phenotypic difference) of a trait. This strongly suggests that the levels of heterosis observed in hybrids depend on the magnitude of difference in the traits between strains ; thus, higher heterotic effects can be expected in strain combinations with more divergent traits.

In the present study, the traits that seemed to be most affected are the traits related to fitness, namely, survival at Day 60, fertility ratio, and offspring size, with more pronounced effects in the reproductive traits. Results of an earlier work by Sasaki and Fujio (16) on the effects of inbreeding on propagation in guppies are the reverse of the results of this paper ; just as inbreeding depression was highly manifested in reproductive traits, heterotic effects caused remarkable improvement in the same traits. Thus, that heterosis could be "inbreeding depression in reverse" is exemplified here.

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