DIRECT AND ASSOCIATE EFFECTS OF BODY WEIGHT AND VIABILITY IN *DROSOPHILA MELANOGASTER*¹

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WHEN genotypes coexist in a common environment, the genotypes interact in a variety of ways. Probably the most frequently observed interaction is that of competition, where the success of some genotypes results in a failure of others. Competition among genotypes in *Drosophila* has been investigated by many workers. For example, DOBZHANSKY (1950) found changes in adaptive values of different chromosome arrangements when the genotypes were reared together in crowded conditions; LEWONTIN (1955) and LEWONTIN and MATSUO (1963) found competition affecting larval viability among different genotypes in *Drosophila melanogaster* and *Drosophila buskii*, respectively; MATHER and COOK (1962) reported competition among different lines of *D. melanogaster* affecting sternopleural chaetae numbers.

Another form of genotypic interaction is known as "facilitation" (LEWONTIN 1955). Here the simultaneous presence of two genotypes is mutually beneficial. In an experiment using *D. melanogaster*, LEWONTIN (*loc. cit.*) showed that larval viabilities of wild-type and white genotypes were both increased when they were reared together at an optimal density.

Apart from competition and facilitation, other forms of interaction are possible; for example, SEATON and ANTONOVICS (1967) found that the success in mixed cultures of one mutant *Drosophila* over another might be dependent on an ability to avoid flies of the other genotype.

Genotypic interactions may change with changing biotic and physical environments. In *Drosophila* the relative viabilities of competing genotypes vary with density. The literature has been reviewed by LEWONTIN and MATSUO (1963), who showed that relative viabilities also change with different larval compositions. MATHER and COOK (1962) found differences in competitive abilities among lines of *D. melanogaster* in different temperatures.

The ability of a genotype to coexist with another may be highly heritable in *Drosophila*. In a selection experiment, SEATON and ANTONOVICS (1967) showed that the ability of dumpy flies to coexist with wild type could be altered rapidly by selection. PIMENTEL *et al.* (1965) showed that in mixtures of house flies and blow flies, the ability of house flies to gain ascendance over blow flies, or *vice versa*, was evolved in a few generations.

It was pointed out by GRIFFING that selection theory could be made more gen-

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eral if effects of interactions among genotypes were incorporated in biological models. In one such model GRIFFING (1967) defined the "direct" effects as those gene effects due to the genes specified by the genotype under consideration, and the "associate" effects as the contributions due to other members of the same group of interacting individuals. The associate effect can be positive or negative so as to account for different forms of interaction.

The present experiment was designed to detect the presence of genotypic interactions and to estimate the sizes of associate effects among five genotypes in *Drosophila*. A range of external and biotic environments was used to observe the change, if any, in interactions as expressed in different regimes.

Two traits were observed in this study: (i) body weight of adult flies, and (ii) viability from first instar larvae to adults. Body weight represents a quantitative character not directly related to fitness, and viability is a component of fitness. In past experiments these two traits have usually been recorded by workers in different aspects of population genetics. However it is possible that findings based on a metric trait might not be applicable to a component of fitness, and *vice versa*. One of the aims in this work was to detect differences between interactions for the two kinds of characters in the same biological group.

MATERIALS AND METHODS

The experimental material included five stocks of *D. melanogaster*: yellow scute(*y sc*), ebony (*e*), giant vermillion (*gt v*), Bar (*B*), and wild-type (+) flies.

Mixtures between genotypes were created by placing an equal number of first instar larvae of two stocks into a shell vial containing 4 cc of standard food. The environmental variables involved were density and temperature. The densities were 8, 16, 32, 64, 128, and 256 larvae per vial and the temperatures used were 16°, 20°, 25°, and 30°C. For each temperature-density regime, the five genotypes were arranged to include all pairwise mixtures as well as pure cultures of each genotype. In this way 15 combinations were established for each regime. Twenty-four replicates, each consisting of the 15 combinations, were established and scored. Due to the large number of replicates required for this experiment, the replicates were initiated in different weeks. In each week combinations involved for each density were synthesized. Parents used for the production of larvae were selected at random from population cages at the beginning of each larval collection period.

The time from first instar to emergence of adult flies depended largely on temperature. At 25° and 30°C the time period was about 9–10 days while at 16°C the period was as long as 25 days. The flies were weighed as soon as possible, usually within 24 hr after emergence. This procedure was continued until no more flies were found. Each fly was weighed to the nearest .01 mg. For the higher densities, 10 flies of each sex, for each genotype, in every vial were weighed. The total number of imagos in each vial was also recorded. Due to the sex difference in body weight, it was decided to weigh at least one fly of each sex in each genotype in each vial. Thus about 30% of the vials in the lowest density (eight larvae per vial) regimes were repeated. Four vials each containing 16 larvae were also repeated. The above practice tends to bias the viability figures for the low density regimes upwards as any vials with less than four imagos were discarded. However, examination of the data suggested that this bias may be slight. The repeated vials showed a mean viability value only about five percent higher than the discarded vials.

STATISTICAL ANALYSIS

The estimation of direct and associate effects may best be described by using, as an example, a typical set of data from a single temperature-density regime. As mentioned earlier, mixed and

pure cultures of all possible combinations of genotypes were made in each replicate and these cultures yielded 25 means in each set of data. If $\bar{x}_{kl}$ ($k, l=1 \dots 5$) denotes the mean of the k th genotype reared in a mixed culture with the l th genotype, the 25 means may be arranged in a 5×5 matrix.

The direct effect is estimated as

$$\hat{c}_k = \bar{x}_{k.} - \hat{\mu}$$

and the associate effect is

$$\hat{d}_l = \bar{x}_{.l} - \hat{\mu}$$

where $\bar{x}_{k.}$ is the marginal mean of the k th genotype and $\bar{x}_{.l}$ is the marginal mean of the l th associate stock, and $\hat{\mu}$ is the estimated grand mean.

For the total experiment it is assumed that the viability value of a genotype can be described by the model

$$y_{ijkl} = \mu + a_i + b_j + c_k + d_l + ab_{ij} + ac_{ik} + \dots + cd_{kl} \\ + abc_{ijk} + \dots + bcd_{jkl} + e_{ijkl},$$

where μ = general mean viability,

a_i = effect of i th density ($i = 1 \dots 6$),

b_j = effect of j th temperature ($j = 1 \dots 4$),

c_k = direct effect due to the k th genotype ($k = 1 \dots 5$),

d_l = associate effect due to the l th genotype ($l = 1 \dots 5$),

ab_{ij} etc = first-order interaction involving the i th and the j th classifications,

abc_{ijk} = second-order interaction,

e_{ijkl} = residual term.

The analysis of the body weight data is based on means of the two sexes. The model for body weight data is essentially the same except that a covariance term using viability as the independent variable has been included into the model as an additional term. This addition was thought to be necessary since differential viabilities affect body weights.

The analyses of data consist of examinations of marginal means of the main effects as well as estimates of the effects included in the models in the usual way. The means for body weight were first adjusted for viability using the "error" regression coefficient obtained from the covariance analysis (STEEL and TORRIE 1960).

The subclass numbers are unequal, the estimation of a_i , b_j , and ab_{ij} terms is based on unweighted subclass means, and the estimates obtained this way are unbiased because all subclass cells are filled (HENDERSON 1948).

Analyses of variance for viability and covariance for body weight were also carried out. In these analyses it was assumed that all main classifications are fixed and because of unequal subclass numbers, the unweighted means were used (SNEDECOR 1956). Log transformation of body weight and the arcsin square-root transformation of viability data were used.

RESULTS

Main effects: General means for body weight and larval viability together with the marginal means for the main classifications of each trait are listed in Table 1. There is a decline in both body weight and viability with increasing density. As density increases from 8 to 256 larvae per vial, body weight and viability are lowered by 42% and 56%, respectively. The effects of temperature on the two characters are also apparent. In general, body weights are higher at lower temperatures and viability is greatest at the optimal temperature of 25°C. The decline in viability with increasing density is in agreement with the results of LEWONTIN (1955).

There are large differences among genotypes (direct effects) in both body weight and viability. The range of differences, calculated as the difference between the largest and the smallest deviations listed in Table 1 is 0.12 mg in body

TABLE 1

Means and deviations of body weight and larval viability for different sexes, densities, temperatures, genotypes, and associations

		Body weight (mg)		Viability (%)	
		Mean	Deviation	Mean	Deviation
Sex	Male	0.728	-0.109	-	-
	Female	0.946	0.109	-	-
		(adjusted for viability)			
Density	8	1.028	0.191	86.1	21.6
	16	0.932	0.095	77.3	12.9
	32	0.933	0.096	65.1	0.6
	64	0.828	-0.009	63.4	-1.03
	128	0.695	-0.142	56.7	-7.69
	256	0.603	-0.234	38.0	-26.47
Temperature	16°C	0.846	0.009	54.9	-9.5
	20°C	0.906	0.069	66.5	2.0
	25°C	0.832	-0.005	70.4	6.0
	30°C	0.763	-0.074	66.0	1.5
Genotype (Direct effect)	<u>e</u>	0.828	-0.009	64.2	-0.2
	<u>+</u>	0.826	-0.011	74.6	10.2
	<u>gt v</u>	0.909	0.072	58.3	-6.1
	<u>y sc</u>	0.794	-0.042	64.3	-0.2
	<u>B</u>	0.827	-0.010	60.8	-3.6
Associate Effect	<u>e</u>	0.840	0.003	63.7	-0.8
	<u>+</u>	0.825	-0.012	63.0	-1.4
	<u>gt v</u>	0.835	-0.001	64.6	0.2
	<u>y sc</u>	0.840	0.003	65.0	0.6
	<u>B</u>	0.842	0.005	65.8	1.3
Grand Mean		0.837		64.4	

weight between *gt v* and *y sc* flies and the largest difference in viability is 16% between the wild-type and *gt v* flies. The *gt v* genotype, which has the highest mean body weight, is the lowest in viability, while the wild-type stock, with a mean body weight slightly lower than the overall mean, has the highest viability.

The overall differences among genotypes in associate effects are relatively small. In both body weight and viability the range of the associate effects in each trait is much smaller than the range for the direct effects. There are some similarities in overall associate effects for the two traits in different genotypes. The associate effects are positive for both traits in *B* and *y sc* genotypes while the same

effects for wild type are both negative. As indicated under ANALYSIS, the associate effect of a genotype is estimated as the deviation of the mean value of all genotypes reared in mixtures with that genotype from the general mean. A positive or negative estimate of an associate effect indicates whether there is an advantage or disadvantage for other genotypes to be reared with the particular genotype in question. Thus in general there is a disadvantage for genotypes reared in the same vial with the wild-type flies while there is an advantage to be reared together with *B* and *γ sc* genotypes.

The relationships between direct and associate effects may be seen from the deviations for the two effects listed in Table 1. It is apparent that there is no consistent relationship between the two effects in body weight ($r = -0.09$) but the relationship in viability is clearly negative ($r = -0.75$).

The analyses of variance and covariance are summarized in Table 2. With the exception of the associate effects, all the main classifications are very highly sig-

TABLE 2

Analyses of covariance for body weight and variance for larval viability data

Source of variation	Degrees of freedom	Body weight (log transformation)	Larval viability (arcsin square-root transformation)
		Mean squares	Mean squares
Densities (D)	5	0.3268***	5.4634***
Temperatures (T)	3	0.1617***	0.5938***
Genotypes (G)	4	0.0636***	0.5983***
Associations (A)	4	0.0019	0.0316
DT	15	0.0257***	0.3831***
DG	20	0.0045***	0.2125***
DA	20	0.0031*	0.1062*
TG	12	0.0077***	0.0960
TA	12	0.0015	0.0583
GA	16	0.0015	0.1535**
DTG	60	0.0028*	0.0714
DTA	60	0.0027*	0.0646
DGA	80	0.0021	0.0675
TGA	48	0.0019	0.1027**
Residual	239 body wt. 240 viability	0.0019	0.0619

TABLE 3
Interaction terms of densities $\times$ direct effects and densities $\times$ associate effects in body weight

	Direct effects (adjusted for viability)				Associate effects (adjusted for viability)			
	$\bar{e}$	+	$\frac{gt}{v}$	$\frac{y}{sc}$	$\bar{B}$	$\bar{e}$	+	$\frac{gt}{v}$
8	-0.005	0.006	-0.024	0.011	0.010	-0.032	-0.002	0.017
16	0.034	0.010	-0.009	-0.022	-0.012	-0.003	0.023	-0.021
32	-0.010	-0.045	0.017	0.038	0.004	0.018	0.016	-0.034
64	0.017	-0.016	0.020	0.006	-0.024	0.056	-0.020	0.009
128	-0.038	0.037	0.021	-0.019	0.000	-0.010	0.004	0.015
256	0.001	0.008	-0.019	-0.016	0.026	-0.024	-0.017	0.014

TABLE 4
Interaction terms of temperatures $\times$ direct effects and temperatures $\times$ associate effects in body weight

	Direct effects (adjusted for viability)				Associate effects (adjusted for viability)			
	$\bar{e}$	+	$\frac{gt}{v}$	$\frac{y}{sc}$	$\bar{B}$	$\bar{e}$	+	$\frac{gt}{v}$
16°C	-0.020	-0.052	0.009	0.040	0.016	-0.014	0.004	-0.002
20°C	0.019	0.000	0.013	-0.007	-0.025	0.012	0.001	-0.001
25°C	0.000	0.024	0.001	-0.041	0.020	0.012	0.005	-0.007
30°C	0.001	0.029	-0.022	0.007	-0.009	-0.008	-0.008	0.010

nificant. The nonsignificant result of the associate effects is not surprising in view of the small differences in mean associate effects shown in Table 1.

Interactions: A striking feature of Table 2 is the large number of highly significant interactions. The effects of density vary with temperature, genotype, and associate genotype. In viability data, interactions involving density are mostly

very highly significant while those involving temperature are nonsignificant. The interactions between direct and associate effects with temperature and density are of particular interest to this study. These interactions have been calculated as deviations and are listed in Tables 3, 4, 5, and 6.

In Tables 3 and 4 it is shown that the wild-type flies are heavier at extreme densities and at higher temperatures. The *gt v* flies are heavier at intermediate densities and lower temperatures, while the *y sc* genotype is lighter at intermediate temperatures. In body weight there is an advantage to be associated with *gt v* and *y sc* flies at extreme densities but a disadvantage to be associated with the *e* flies at the same densities. Differences in associate effects among genotypes in different temperatures can also be found in Table 4.

The viability of the wild-type flies (Tables 5 and 6) are higher at high densities and at 25°C. At extreme densities and temperatures, the *B* stock has relatively lower viability while under the same conditions the *gt v* genotype has higher viability.

The associate effects for the wild-type flies are negative at high densities and positive at low densities while the situation for the Bar stock is reversed.

It is interesting to compare the interaction terms for body weight and viability. It is obvious that a knowledge of the interactions of densities $\times$ direct effects and densities $\times$ associate effects in body weight gives no indication of the same interaction terms with regard to viability (Tables 4 and 6).

Data in Table 2 also indicate that the direct and associate effects in body weight vary with changes in temperature-density combinations but the more complex interactions in viability are small and nonsignificant.

Mixed and pure cultures: The data also permit an examination of performances of different stocks in mixed and pure cultures. The estimates for direct and associate effects of each genotype presented earlier give quantitative measures of the degree of advantage or disadvantage to be associated with particular genotypes in mixed cultures. The estimates give no indication of the *joint* performance of genotypes in a mixture. In order to examine the joint performance it is necessary to compare the observations in mixed cultures with those obtained in pure cultures. The joint performance of two genotypes in a mixed culture can be classified in four ways. Consider genotypes *A* and *B* in mixed cultures. If we assign a (+) sign for a genotype when its performance in mixture is superior to that in pure culture, and a (—) sign when the situation is reversed, the interactions can be classified in the following straightforward manner:

Performance in mixed culture			
	Genotype <i>A</i>	Genotype <i>B</i>	
(a)	+	+	Facilitation
(b)	+	—	Competition
(c)	—	+	Competition
(d)	—	—	Inhibition

Interaction in cultures of type (a) occurs when both genotypes are mutually

TABLE 5
Interaction terms of densities $\times$ direct effects and densities $\times$ associate effects in larval viability

		Direct effects					Associate effects				
		$\underline{e}$	+	$\underline{gt\ v}$	$\underline{y\ sc}$	$\underline{B}$	$\underline{e}$	+	$\underline{gt\ v}$	$\underline{y\ sc}$	$\underline{B}$
Density	8	1.78	-6.80	7.56	-2.16	-0.37	-1.46	1.76	2.47	2.09	-4.86
	16	-7.78	-13.11	10.75	0.08	10.07	1.28	6.55	5.76	-10.57	-3.02
	32	4.79	-3.24	-6.13	2.25	2.34	7.95	-1.08	-7.32	2.45	-2.01
	64	5.96	4.98	-10.56	-1.54	1.16	3.52	-4.16	3.14	-1.23	-1.29
	128	-10.33	13.54	-4.20	5.83	-4.83	-5.82	-0.50	-2.94	3.33	5.93
	256	5.60	4.62	2.58	-4.45	-8.35	-5.49	-2.57	-1.11	3.91	5.26

TABLE 6
Interaction terms of temperatures $\times$ direct effects and temperatures $\times$ associate effects in larval viability

		Direct effects					Associate effects				
		$\underline{e}$	+	$\underline{gt\ v}$	$\underline{y\ sc}$	$\underline{B}$	$\underline{e}$	+	$\underline{gt\ v}$	$\underline{y\ sc}$	$\underline{B}$
Temperature	16°C	-3.23	1.31	7.95	-5.93	-0.10	0.32	-0.33	3.84	-3.83	0.01
	20°C	-2.05	-1.64	-4.17	5.16	2.71	-2.84	1.38	1.32	-0.79	0.92
	25°C	1.17	0.95	-5.44	1.45	1.87	1.69	-1.96	-5.22	4.67	0.82
	30°C	4.11	-0.61	1.66	-0.68	-4.49	0.83	0.91	0.06	-0.05	-1.75

beneficial. Interactions like (b) and (c) are the usual competition situations where the success of one genotype is accompanied by the failure of another. In type (d) interaction, competition or interaction leads to a mutual deterioration, and for convenience this phenomenon will be termed "inhibition." All four types of interaction exist in the present data for both body weight and

TABLE 7
Mean body weight and viability in pure and mixed cultures*

	Body weight (mg) (adjusted for viability)					Larval viability (%)				
	G_e	G_+	$G_{gt \ v}$	$G_{y \ sc}$	G_B	G_e	G_+	$G_{gt \ v}$	$G_{y \ sc}$	G_B
A_e	0.833	0.844	0.906	0.794	0.832	61.8	73.3	53.8	60.8	68.5
A_+	0.823	0.833	0.892	0.774	0.809	58.0	70.3	63.8	69.7	53.4
$A_{gt \ v}$	0.824	0.814	0.921	0.815	0.811	65.4	79.3	54.7	63.8	60.1
$A_{y \ sc}$	0.820	0.823	0.935	0.790	0.840	68.1	76.8	54.8	59.9	65.5
A_B	0.844	0.820	0.902	0.803	0.849	67.6	73.4	64.3	67.1	56.4

* G = genotype A = association in mixed cultures.

For example, the value $G_e A_+ = 0.823$ is the mean body weight of the ebony genotype when it is reared together with the wild-type stock.

viability. The subclass means for genotypes and associate effects, averaged over all densities and temperatures, are presented in Table 7. Since each item in Table 7 represents a mean value over 24 subclass means (four temperatures in combination with six densities), the values in the table are less subject to sampling

variations and indeed the direct $\times$ associations term in viability is statistically highly significant (Table 2).

In Table 7 the diagonal values represent means in pure culture while off-diagonal values are the means in mixtures. Thus G_iA_j values represent the performance of the i th genotype reared in a mixture with the j th stock. For example, the G_+A_e value represents the mean of the wild-type genotype reared in association with the ebony stock. Examination of Table 7 reveals an important difference between body weight and viability data. In body weight, interactions between genotypes are frequently of the inhibition type. For example, body weights of the genotypes in the combinations of ($e, gt\ v$), ($+, gt\ v$), ($+, \gamma\ sc$), and ($+, B$) are inferior to their respective means in pure cultures. In all combinations only one case of facilitation was found ($gt\ v, \gamma\ sc$); however, these interactions are not significant. On the other hand, facilitation in viability occurred in many mixed cultures. The viability means of genotypes in the mixtures of ($e, \gamma\ sc$), (e, B), ($+, gt\ v$), ($+, \gamma\ sc$), ($gt\ v, B$), and ($\gamma\ sc, B$) are all superior to those in pure cultures. While competition for viability frequently occurred, inhibition was never found.

The differences in interactions for body weight and viability indicate that there is a difference in the average performance of the two traits in mixed and pure cultures. The means of all genotypes in mixed and pure cultures were calculated and are listed in Table 8.

The mean body weight averaged over all genotypes is higher in pure than in mixed cultures, while the mean viability is higher in mixed cultures. Table 8 also shows the consistency of the differences between cultures over various temperatures and densities.

Analysis of covariance and variance, using the log transformation for body weight data and the arcsin square-root transformation for viability data, were carried out. In the covariance analysis for body weight data the viability value was again used as the independent variable. In each analysis the three main effects (cultures, temperatures, and densities), as well as the appropriate interaction terms, were tested for significance. The results (not presented in detail here) showed that for body weight, mean difference between cultures was non-significant, while the mean difference between cultures for viability was significant at the five percent level. The first-order interaction terms involving cultures were all nonsignificant with each F ratio close to unity. The latter is not surprising in view of the consistent differences found between cultures in various temperatures and densities (Table 8).

DISCUSSION

The data in this study show that overall associate effects between genotypes are small and nonsignificant. However, in both body weight and viability the associate effects change with changing densities and these interactions are statistically significant. In viability the interaction terms involving direct and associate effects are large and highly significant.

TABLE 8

Mean body weight and viability over all genotypes in mixed and pure cultures

	Body weight (mg) (adjusted for viability)		Viability (%)		
	Pure	Mixed	Pure	Mixed	
Density	8	1.038	1.027	79.8	87.5
	16	0.953	0.925	69.2	79.3
	32	0.921	0.935	61.5	66.3
	64	0.830	0.828	65.8	62.8
	128	0.695	0.697	56.0	56.8
	256	0.633	0.594	31.3	39.5
Temperature	16°	0.847	0.845	48.8	56.3
	20°	0.914	0.903	63.8	67.2
	25°	0.845	0.829	65.2	71.7
	30°	0.773	0.761	64.5	66.2
Overall	0.845	0.834	60.5	65.3	

Interactions between the same genotypes affect body weight and viability in different ways. From the present data several differences can be summarized:

1. There is a strong negative relationship between the overall mean direct and associate effects in viability, but the same relationship is not apparent in body weight data.

2. The direct effects in body weight interact with temperatures while the interaction terms involving temperatures in the viability analysis are small and nonsignificant.

3. In body weight data inhibition is the mode of genotypic interaction. In contrast, facilitation is commonly found in the viability data.

4. Mean body weight is higher in pure than in mixed cultures while the mean viability is higher in mixed than in pure cultures.

It may be concluded therefore that findings concerning genotypic interactions, based on quantitative traits not directly related to fitness, may not be applicable to components of fitness or *vice versa*.

The relative importance of associate effects should be evaluated not only by their presence but also by their magnitudes. One method to assess the size of the associate effects is to compare the range of these effects with that of the direct effects.

TABLE 9
Relative range of direct and associate effects in different environments

Environment		Body weight (mg) (adjusted for viability)			Viability (%)		
		Range of Direct Effect	Range of Associate Effect	Ratio Associate/ Direct	Range of Direct Effect	Range of Associate Effect	Ratio Associate/ Direct
Density	8	0.035	0.049	1.4	14.36	7.33	0.51
	16	0.056	0.044	0.79	23.86	17.12	0.72
	32	0.083	0.052	0.63	10.92	15.27	1.40
	64	0.044	0.084	1.91	16.52	7.68	0.46
	128	0.075	0.025	0.33	23.87	11.75	0.49
	256	0.045	0.046	1.02	13.95	10.75	0.77
Temperature	16°	0.092	0.022	0.24	13.88	7.67	0.55
	20°	0.044	0.026	0.59	9.33	4.22	0.45
	25°	0.065	0.019	0.29	7.31	9.89	1.35
	30°	0.051	0.025	0.49	8.60	2.66	0.31

As mentioned earlier the associate effects, when averaged over all environments, are relatively small, with a range of about one-sixth that of direct effects for the two traits. However individual associate effects in different environments can be sizeable. The ratios of the relative sizes of associate to direct effects over all genotypes have been calculated and are shown in Table 9. Individual asso-

ciate effects are mostly about one-half the size of the direct effects, but in some circumstances the associate effects can be as large or larger than direct effects.

Differences in associate effects among genotypes are also of interest. In general, flies exhibit an advantage when associated with the Bar genotype but a distinct disadvantage when associated with the wild-type genotype. In terms of competition, wild type is the most successful all-round competitor. The *B* flies are poor competitors, while the other three genotypes are intermediate between these extremes. It is interesting to compare the associate effects of the extreme genotypes at different temperatures and densities. The body weights of wild-type flies are low at 30°C, while those for *B* flies are high in extreme temperatures. With regard to viability, wild type tends to be highly competitive when the densities are high (32 or higher), and when the temperature is at the optimal value of 25°C. On the other hand the *B* genotype is competitive only at low densities (64 or lower) and at 30°C. Since it has been shown by LEWONTIN (1955) that larval viability tends to be low when the total density is less than optimal, the ability for wild type to coexist at low densities and to compete successfully at high densities may partly explain the higher adaptability of the wild genotype.

The present investigation shows that interactions between environments and genotypes and among genotypes affect both the body weight and viability of coexisting genotypes. It also shows that the associate effects are in general small but the sizes and signs of the effects can vary with differing physical and biotic environments. Therefore, it seems reasonable to speculate that if the differences in associate effects are partly due to additive genetic differences between genotypes, directional selection for a greater or lesser ability of a genotype to coexist or to compete with another would be effective only if selection is carried out under a suitable environment and if the environment is kept constant.

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SUMMARY

Genotypic interactions affecting body weight and larval viability among five genotypes in *Drosophila melanogaster* were investigated. The associate effect of a genotype measures the influence of that genotype on another when the genotypes are reared together. It was found that the overall associate effects among genotypes for both traits were small and nonsignificant. However, individual associate effects among genotypes in certain specific physical and biotic environments can be large and significant.——The direct and associate effects of various genotypes for body weight are frequently different from the same effects for viability. It was concluded that a knowledge of genotypic interactions in a quantitative trait, not directly associated with fitness, may not be applicable to interactions in fitness characters.

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