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MEASUREMENT OF FITNESS AND ITS COMPONENTS IN SIX LABORATORY STRAINS OF *DROSOPHILA MELANOGASTER*

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ABSTRACT

Six laboratory strains of *Drosophila melanogaster* were used to measure "net fitness" and its components by interspecific competition with *D. hydei* using 100 experimental populations. The "total competitive ability," an estimate of net fitness measured in these competition experiments, was tightly correlated with another measure of net fitness, the population size, in single-species experiments (phenotypic correlation $r_p = 0.675$ and genotypic correlation $r_g = 0.997$). Other components of fitness were also measured simultaneously, and the correlation with the net fitness was calculated. The very high correlation between two measurements of net fitness and lower correlations between net fitness and components of fitness suggests that these net fitness measures are more reliable estimates of the "real net fitness" than the components of fitness.

THE estimation of fitness is the first step in understanding the adaptive evolution of a population. There have been many attempts to measure the fitness of various genotypes in the study of population genetics. Some of the most frequently used study animals have been the fruit flies of the genus Drosophila, especially *D. melanogaster* (*e.g.*, MUKAI and YAMAZAKI 1971), and *D. pseudoobscura* (*e.g.*, DOBZHANSKY, SPASSKY and TIDWELL 1963). The reason for the popularity of these species in such studies is the availability of balanced marker stocks, making it possible to study single wild chromosomes.

Net fitness comprises various components such as viability, female fecundity, male mating ability, developmental time, longevity, etc. In most studies in which fitness has been measured, only one or a few components of fitness have been measured on the assumption that the components of fitness are positively correlated to net fitness (MUKAI and YAMAGUCHI 1974). There is some experimental evidence for such a positive correlation of fitness components (BONNIER and JONSSON 1957; MUKAI and YAMAZAKI 1971); but there is also experimental evidence of little or negative correlation between fitness components (HIRAIZUMI 1960; SIMMONS, PRESTON and ENGELS 1980).

In this study I measured net fitness both by using population size [carrying capacity, as the term is used in ecology (CARSON 1958; AYALA 1965)] of genotypes in single-species (or strain) experiments and total competitive ability in

interspecific competition experiments (AYALA 1969, 1970). Several components of fitness were also studied, using six different strains of *D. melanogaster* and one strain of *D. hydei* as a standard. In the accompanying paper (YAMAZAKI and HIROSE 1984), the same methodology was applied to a natural population of *D. melanogaster* and the correlation between net fitness and its fitness components was examined.

MATERIALS AND METHODS

Materials

Two species of Drosophila were used in this experiment: *D. melanogaster* and *D. hydei*. The *D. hydei* population was originally derived from ten isofemale lines, each of which had been inseminated in a natural population. A new population was established by placing these ten lines in a population cage. This population had been maintained for about a year previous to the start of the experiment. The heterogeneous *D. hydei* strain was chosen as a control since our preliminary experiments showed that the heterogeneous strains were more stable under various environmental conditions than the isogenic one.

Six different *D. melanogaster* strains were used for these experiments. The description of the strains are as follows.

Katsunuma strain: A wild-type strain that originated from a single female collected at Katsunuma, Japan. It had been maintained in mass culture for a year before the start of this experiment. Therefore, this strain initially contained at least four genomes independently derived from nature. The *D. hydei* strain and the Katsunuma strains were collected from the same locality at the same time.

C-160 strain: *In(2LR)SM1/In(2LR)Pm*, abbreviated as *Cy/Pm* (see MUKAI and BURDICK 1959).

Brown strain: An inbred strain marked by a recessive eye mutant, *bw*, on the second chromosome (2-104.5).

Cinnabar strain: An inbred strain marked by a recessive eye mutant, *cn* on the second chromosome (2-57.5).

Ebony strain: An inbred strain marked by a recessive body mutant, *e*, on the third chromosome (3-70.7).

Vestigial strain: An inbred strain marked by a recessive wing mutant, *vg*, on the second chromosome (2-67.0).

All of these mutant strains had been maintained for many years in the National Institute of Genetics, Japan, when the experiment started, and they were likely to be genetically homogeneous.

Methods

A total of 100 experimental populations were run. The populations were maintained by so-called Pearl's methods (see BUZZATI-TRAVERSO 1947). Each population was composed of seven food vials each containing 11 ml of cornmeal medium; 200 founder flies with a sex ratio of 1:1 were introduced in one vial and kept 4 days so that oviposition could occur. In interspecific competition experiments 100 *D. melanogaster* and 100 *D. hydei* with a sex ratio of 1:1 were put into a vial. These adult flies were collected from a large population cage so that they could be expected to be in equilibrium with respect to age distribution. This process minimized the rapid change of the number of flies due to the effect of nonequilibrium age distribution at the outset of the experiments. Every 4 days the flies were etherized and counted, and all of the adult flies, including newly emerged ones, were moved to a new vial. At this time the oldest vial (28 days) from each population was discarded after the adult flies had been transferred to a new vial. Therefore, each population was maintained in a continuing series of seven vials, none of which were older than 28 days. Within this 28-day period, almost all of the progeny had emerged, and very few second-generation progeny had appeared, since almost all of the food was used up in a single generation. Population size was defined as the number of adult flies transferred from seven old vials to a new vial. In total, 536,000 flies were counted to obtain the data in this paper.

Single-species experiments: The carrying capacity of a population or the population size was measured at steady state in 52 different populations. Actual counting of flies was carried out half

a year after the establishment of populations to avoid the rapid changes of population size at the initial stage. Eight replications were run of each strain of *D. melanogaster* and four of *D. hydei.*

Interspecific competition experiments: In this series of experiments not only total competitive ability but also the components of fitness, such as productivity, adult viability and developmental time, were measured. The frequency changes of *D. melanogaster* against *D. hydei* strains were recorded. Eight replicated populations for each *D. melanogaster* strain, 48 populations in total, were studied for about 400 days, as long as the two species remained coexistent in the population. A species was assumed to be eliminated when five consecutive counts of adult flies yielded only the other species. Since fitness or its components of the *D. melanogaster* strains were measured relative to those of *D. hydei* in the interspecific competition experiments, the effects of population size at any time or the effects of other uncontrolled environments were minimized. On the other hand, no standard strain or comparison species was present in measuring population size in the single-species experiments. Much longer observations, therefore, are necessary to eliminate the effects of temporal change in population density due to other uncontrolled environmental conditions in single-species experiments.

Fitness estimation: Five different indices of fitness or fitness components were measured from these populations. Two of them, total competitive ability and population size, are two different estimates of net fitness. The other three, adult viability, productivity and developmental time, are components of fitness. The total competitive ability and the several components of fitness were measured relative to those of *D. hydei*, in interspecific competition experiments.

1. Population size: Average population size as a net fitness measure was estimated only in single-species populations. Average values of more than 100 days were used, although exact periods differ somewhat depending on the strains. This is equivalent to the carrying capacity of the population. Population sizes were used as an index of net fitness originally by CARSON (1958) and also by AYALA (1965).

2. Total competitive ability: As an alternative measure of net fitness, total competitive ability in *D. melanogaster* against *D. hydei* was measured. It was measured as the regression coefficient of the natural logarithm of *D. melanogaster* frequency on time.

A similar measurement of fitness was carried out by AYALA (1969) who used the ratio of his two study species as a basic statistic, assuming that the number of flies of each species changed independently of the other. In this paper, the percentage of *D. melanogaster* instead of the ratio has been used. This assumes that the total number of adult flies of the two Drosophila species is constant regardless of frequency change, since the amount of space and food per vial is the same throughout the experiments. Total competitive ability was measured after a complete cycle (28 days or seven vial transfers) had been established. By this precaution I could avoid the effects of increasing population size at the initial stage of population. In a few populations involving C-160, *D. melanogaster* was eliminated before a complete cycle had been established. Total competitive ability of these populations was calculated similarly, even though the steady state concerning the population size had not been attained. Since population size often changes drastically in the initial stage before the steady state is attained, it may not be justified to calculate the total competitive ability of these populations from the regression coefficient of *D. melanogaster* frequency. To examine this possibility, I gave -0.4 as the index of total competitive ability to all populations in which *D. melanogaster* was eliminated within 28 days and compared these transformed values with those obtained by the original method. This value, -0.4, was about the lowest regression coefficient obtained for the strains that remained in the population for more than 28 days without being eliminated.

Results were essentially the same as those without transformation. Correlations were $r_p = 0.5949$ (0.6752), $r_g = 0.9951$ (0.9840) between total competitive ability and population size, where the values without parentheses are not transformed, and those within parentheses are transformed, to -0.4.; $r_p = 0.8181$ (0.7280), $r_g = 0.9614$ (0.9779) between total competitive ability and productivity; $r_p = 0.4116$, (0.4844), $r_g = 0.5297$ (0.5148) between total competitive ability and adult viability; $r_p = 0.1210$ (0.0101) between total competitive ability and developmental time. Since no obvious difference was observed between these two different treatments of data, I analyzed the original data without transformation throughout the present study.

3. Adult viability: Four days after the transfer of adult flies from all seven vials to a new vial, the number of surviving adult flies of each species in this 4-day-old vial was counted. The weighted

averages (over the whole period during which populations were maintained) of input flies and surviving flies were calculated in each of the species involved. The index of adult viability was determined as follows.

$$\text{Adult viability} = (N_{ms}/N_{mi})/(N_{hs}/N_{hi})$$

where N_{ms} is the average number of surviving *D. melanogaster* adult flies, N_{hs} is the average number of surviving *D. hydei* adult flies, N_{mi} is the average number of input *D. melanogaster* adult flies collected from seven vials, and N_{hi} is the average number of input *D. hydei* adult flies collected from seven vials.

4. Productivity: Productivity was measured by counting the number of progeny that had emerged during the 28 days after the transfer of adult flies into the new vial. The weighted averages of input flies and output flies were calculated in each of the species involved. The index of productivity was determined as follows.

$$\text{Productivity} = (N_{mp}/N_{mi})/(N_{hp}/N_{hi})$$

where N_{mp} and N_{hp} are the average number of progeny of *D. melanogaster* and *D. hydei*, respectively.

5. Developmental time: Since adult flies were counted and transferred every 4 days, namely, on days 12, 16, 20, 24 and 28, absolute developmental time (ADT) of each species was calculated as follows.

$$\text{ADT} = [(11) \times (n_{12}) + (14) \times (n_{16}) + (18) \times (n_{20}) + (22) \times (n_{24}) + (26) \times (n_{28})]/N$$

where N is the average total number of progeny emerged from one vial; n_a is the average number of flies eclosed on the ath day from the time of transfer of adult flies.

Relative developmental time (RDT) was estimated and used as an index of developmental time as follows.

$$\text{RDT} = \text{ADT of } \textit{D. melanogaster}/\text{ADT of } \textit{D. hydei}$$

A similar developmental time measure was also used in several other studies (MUKAI and YAMAZAKI 1971; YAMAZAKI 1971; YAMAZAKI and HIROSE 1984).

An estimate of the fitness or its components was obtained by counting approximately 10,000 adult flies per population over a period of more than 1 yr. The average of eight of these estimates (obtained from eight replicated populations) is the final estimate of the fitness or its components shown in Table 1.

Correlation analysis: Phenotypic variation of fitness or fitness components are partitioned into two components: error mean square (variance within strain) and between-lines mean square. This between-lines mean square contains both error variance and genotypic variance components. Genotypic variance is solely due to the variation between different strains. The genotypic variance component is separated from the rest of the variance components by the analysis of variance. Phenotypic covariance of fitness or fitness components between strains are similarly partitioned into two components: error covariance and genotypic covariance.

Phenotypic and genotypic correlations were estimated by the following formula.

$$r = \text{Cov}(X,Y)/\sqrt{Vx\ Vy}$$

where Vx, Vy, $\text{Cov}(X,Y)$ are the total variance of X $(=\sigma_G^2 + \sigma_E^2)$, total variance of $Y(=\sigma_{G'}^2 + \sigma_{E'}^2)$ and total covariance between X and Y $(=\sigma_{GG'} + \sigma_{EE'})$, respectively, in cases of phenotypic correlation. In cases of genotypic correlation the genotypic variance of $X(=\sigma_G^2)$, genotypic variance of $Y(=\sigma_{G'}^2)$ and genotypic covariance between X and $Y(=\sigma_{GG'})$ are used.

All of the necessary information for calculating both phenotypic and genotypic correlations is shown in Tables 1 and 2. A similar analysis was performed between larval viability and developmental time by MUKAI and YAMAZAKI (1971).

RESULTS

The average population size of *D. hydei* was 171.1, and no significant increases or decreases in number were observed at equilibrium, despite the fact

TABLE 1

Population sizes, total competitive abilities, adult viabilities, productivities and developmental times of six different strains in D. melanogaster

Strain	Population size	Total competitive ability	Adult viability	Productivity	Developmental time
Katsunuma	445.29 (±15.43)	−0.0075 (±0.0091)	0.9241 (±0.0246)	1.0526 (±0.0112)	0.7176 (±0.0121)
C-160	175.28 (±19.37)	−0.5450 (±0.0371)			
Brown (*bw*)	320.42 (±30.83)	−0.0796 (±0.0342)	0.7310 (±0.0285)	1.1372 (±0.0370)	0.7077 (±0.0138)
Cinnabar (*cn*)	371.26 (±13.00)	−0.0581 (±0.0148)	0.9264 (±0.0214)	0.9909 (±0.0208)	0.6987 (±0.0127)
Ebony (*eb*)	215.71 (±12.28)	−0.3428 (±0.0186)	0.8259 (±0.0601)	0.5831 (±0.1150)	0.6971 (±0.0314)
Vestigial (*vg*)	220.10 (±9.86)	−0.2600 (±0.0361)	0.4438 (±0.0603)	0.8106 (±0.1426)	0.7740 (±0.0336)

The numbers in parentheses indicate the standard errors of means.

that the *D. hydei* strain used was genetically heterogeneous (Figure 1). Since the population size was fairly constant over time, the *D. hydei* strain was used as a standard in interspecific competition experiments.

The average and the change in population sizes of six *D. melanogaster* strains are shown in Table 1 and Figure 1, respectively.

The population size for each strain was fairly constant, although it fluctuated from time to time. The differences in population size between the six strains were highly significant (bottom two rows of Table 2); between-line mean squares were 88318.06 (d.f. = 5) in comparison with the error mean square of 2659.09 (d.f. = 42). The F value was 33.2. The highest population size was obtained from the Katsunuma strain (445.3) and the lowest was obtained from the C-160 strain (175.3). In decreasing order the population sizes were Katsunuma > Cinnabar > Brown > Vestigial > Ebony > C-160.

Interspecific competition experiments: The average frequency changes are shown in Figure 2, together with standard errors of means. C-160 strains were eliminated from populations quickly in all replicates, so that only total competitive ability was estimated. The estimates of net fitness (total competitive ability), components of fitness and population sizes are listed in Table 1. Differences between lines were highly significant in all measures of fitness or fitness components except developmental time (see Table 2).

The highest total competitive ability was obtained by the Katsunuma strain, and the lowest was obtained by the C-160 strain. The order of competitive ability was the same as that in single-species experiments, namely, Katsunuma

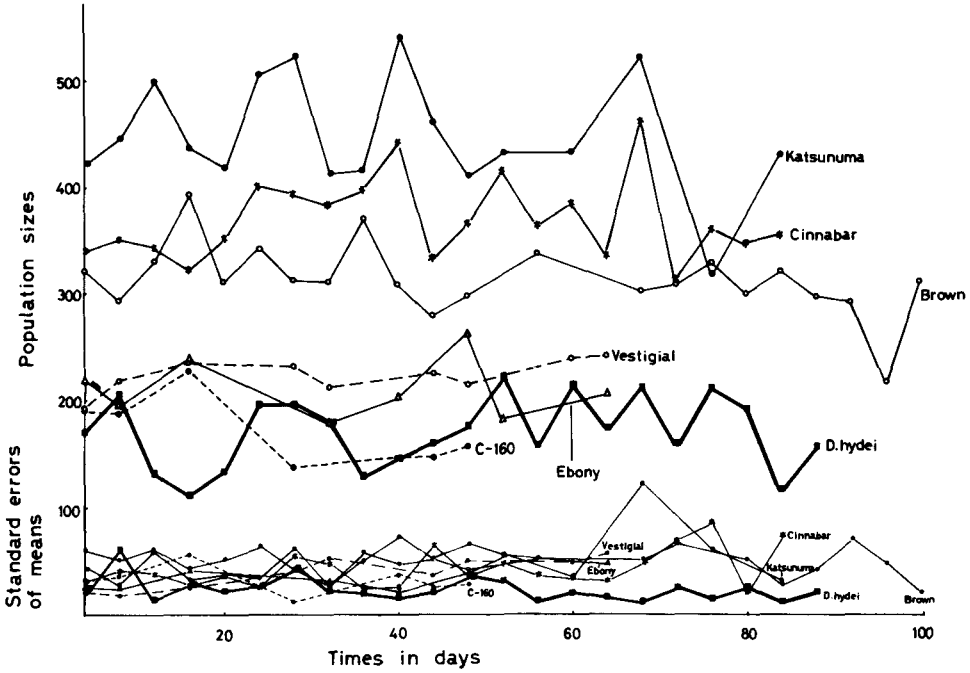

FIGURE 1.—The changes of population size in six laboratory strains of *D. melanogaster* in addition to that of *D. hydei*. At the lower part of the figure the standard errors of the means of each strain are shown.

> Cinnabar > Brown > Vestigial > Ebony > C-160. As far as productivity was concerned, the Brown strain showed the best results followed by Katsunuma > Cinnabar > Vestigial > Ebony.

The adult viabilities were as follows: Cinnabar ≥ Katsunuma > Ebony > Brown > Vestigial. In developmental time the differences between strains were not significant (Table 2), although the order between strains was very different from those of other components of fitness. One of the reasons for the lack of significant differences in developmental time may have been that flies were allowed to lay eggs for 4 days and that the counting and transfer of flies were done once every 4 days. There are, however, several experiments in which highly significant effects in developmental time were observed using the same 4-day oviposition period (MUKAI and YAMAZAKI 1971; YAMAZAKI 1971). It is also possible that little genetic variability with respect to developmental time is left between these populations of *D. melanogaster*, since this component of fitness is a very important component of net fitness (LEWONTIN 1965) and may be under strong directional selection in laboratory cultures.

If the correlation between components of fitness is examined, general features become clearer (Figure 3). Figure 3A shows the phenotypic correlation between population size and total competitive ability (r_p = 0.675); Figure 3B shows correlation between population size and productivity (r_p = 0.350). Figure 3C and D show the relationship between population size and adult viability (r_p = 0.512) and between population size and developmental time (r_p = −0.157).

TABLE 2

Basic statistics relating fitness and its components of six laboratory strains: analyses of variances

Fitness or its components	Between-line variance	(d.f.)	Error variance	(d.f.)	*F* value	Genotypic variance
Total competitive ability						
Excluding C-160	0.2201	(4)	0.0121	(35)	18.2**	0.0260
Including C-160	0.3679	(5)	0.0119	(42)	30.9**	0.0445
Adult viability	0.3186	(4)	0.0146	(35)	21.8**	0.0380
Productivity	0.3903	(4)	0.0568	(35)	6.9**	0.0417
Developmental time	0.0081	(4)	0.0042	(35)	1.9	0.0005
Population size						
Excluding C-160	78065.0	(4)	2590.8	(35)	30.1**	9434.3
Including C-160	88318.1	(5)	2659.1	(42)	33.2**	10707.4

** Significant at the 1% level.

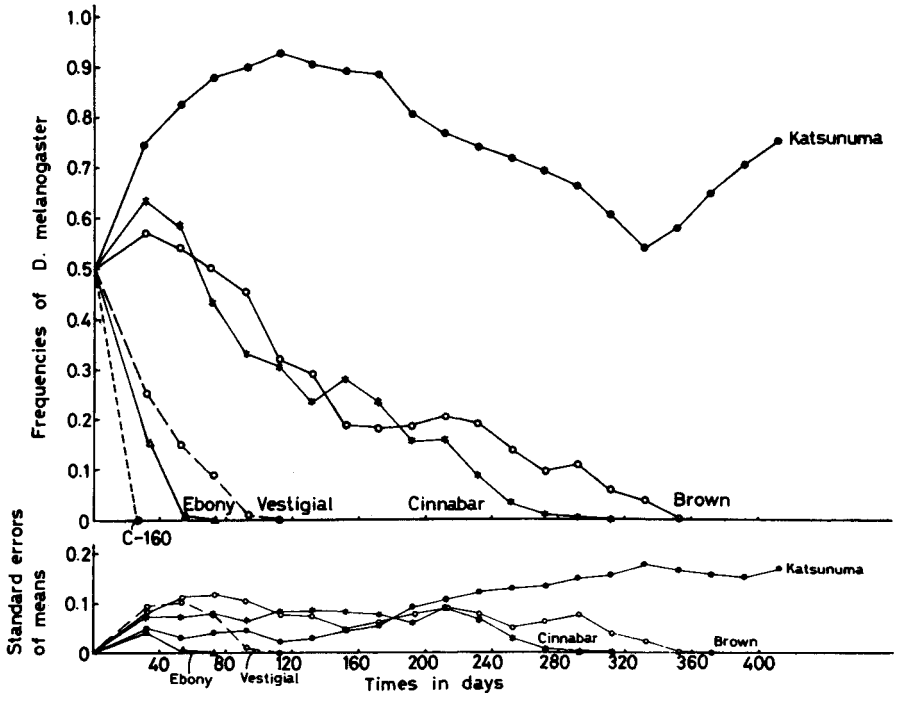

FIGURE 2.—The frequency changes of six laboratory strains of *D. melanogaster* in the competition experiments with *D. hydei*. At the lower part of the figure the standard errors of the means of each strain are shown.

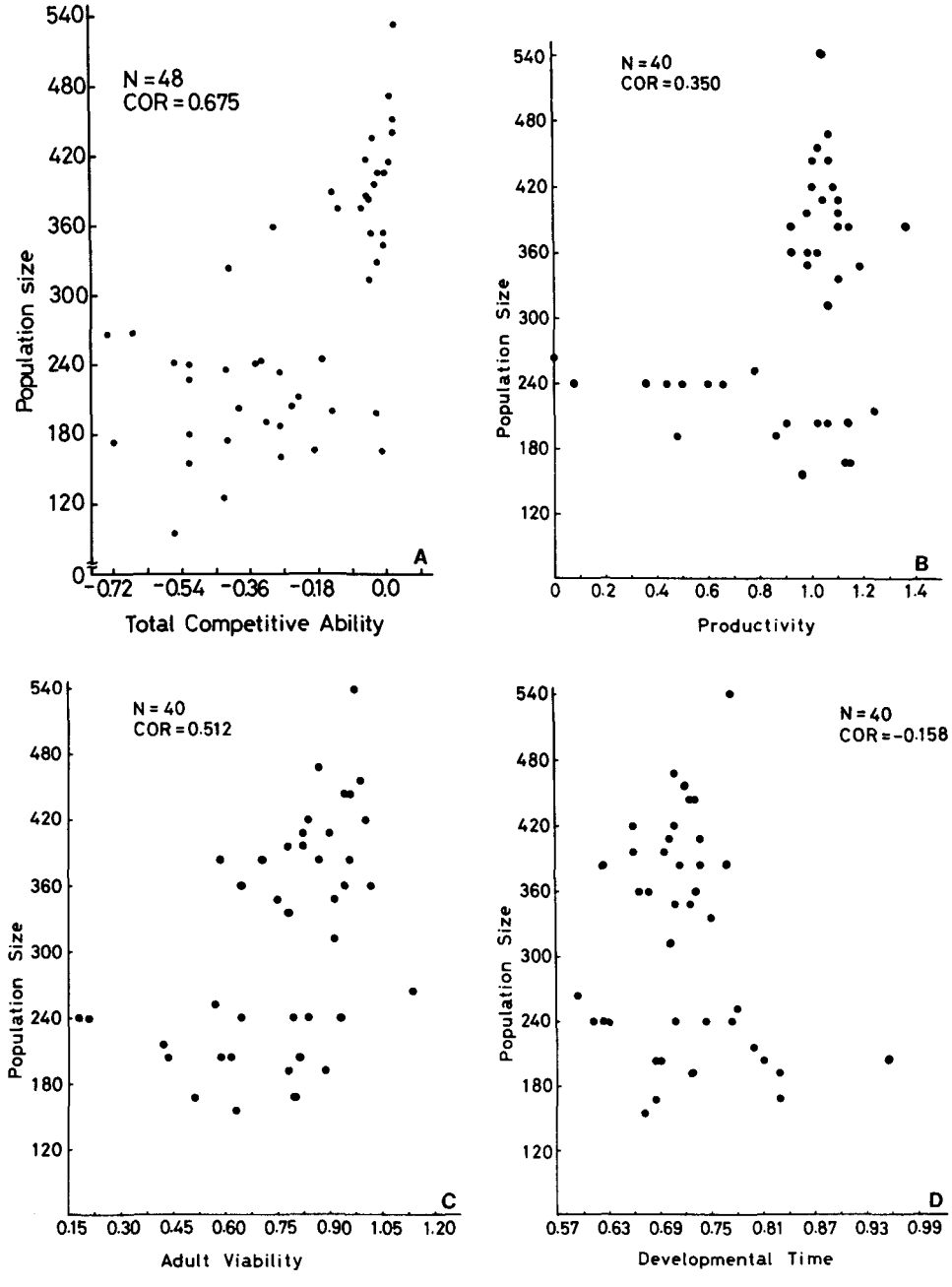

FIGURE 3.—Phenotypic correlations between population size and several fitness components: A, between population size and total competitive ability; B, between population size and productivity; C, between population size and adult viability; D, between population size and developmental time.

To determine whether these correlations are determined genetically or not, genotypic correlations between them were calculated (Table 3).

The results were qualitatively the same as the phenotypic correlations de-

TABLE 3

Basic statistics relating to fitness and its components of six laboratory strains: analyses of covariances, and phenotypic and genotypic correlations

Fitness combination	Covariance			Correlation	
	Between line	Error	Genotypic	Phenotypic	Genotypic
Population size: Total competitive ability					
Excluding C-160	122.9380 (4)	−1.7441 (35)	15.5853	0.5949**	0.9951 ±0.0482
Including C-160	168.7997 (5)	−1.8054 (42)	21.3256	0.6750**	0.9970 ±0.0445
Population size: Productivity	132.5361 (4)	−3.2057 (35)	16.9677	0.3495*	0.8556 ±0.2021
Population size: Adult viability	108.1534 (4)	0.0576 (35)	13.5120	0.5123**	0.7136 ±0.2664
Total competitive ability: Productivity	0.2724 (4)	0.0192 (35)	0.0317	0.8181**	0.9614 ±0.0630
Total competitive ability: Adult viability	0.1356 (4)	0.0024 (35)	0.0167	0.4116**	0.5297 ±0.3839
Population size: Developmental time	−8.8736 (4)	−0.1933 (35)	−1.0850	−0.1572	
Total competitive ability: Developmental time	−0.0113 (4)	0.0030 (35)	−0.0018	0.1210	
Productivity: Developmental time	−0.0055 (4)	0.0097 (35)	−0.0019	−0.3959**	
Adult viability: Developmental time	−0.0442 (4)	−0.0014 (35)	−0.0054	−0.3996**	

Numbers after ± indicate the standard deviation. Numbers in parentheses indicate the degree of freedom.

* Significant at the 5% level.

**Significant at the 1% level.

scribed earlier: 0.997 (including C-160) or 0.995 (excluding C-160) between total competitive ability and population size, 0.856 between productivity and population size; 0.714 between adult viability and population size. Standard deviations of the estimates were calculated by the method of TALLIS (1959). It is clear from these results that population size is highly correlated with total competitive ability.

DISCUSSION

There have been many attempts to measure "fitness" of a genotype, a chromosome, a strain or a population. In this study population size of a strain was measured as an index of fitness. The use of population size as a measure of fitness was pioneered by CARSON (1958, 1961) in Drosophila. It is not known how appropriate this is as an estimate of fitness in natural populations.

Population size as a statistic contains all of the components of fitness encountered during a life cycle of Drosophila. The components of interaction between species is necessarily absent in single-species experiments. In addition,

the population sizes are easily affected by fluctuations in the natural environment such as temperature, the amount and quality of food available, humidity, etc. Therefore, the average population sizes must be determined using data based on long observations of equilibrium populations.

Interspecific competitive ability contains both the interspecific and intraspecific components. If interspecific components hold substantial components of fitness, the correlation between interspecific competitive ability and population size, which has only intraspecific components, is expected to be low. High correlation means that either the intraspecific component is important in determining fitness or that similar selection takes place in both intra- and interspecific competition. In interspecific competition experiments, total competitive ability was measured by the relative performance of *D. melanogaster* and *D. hydei*. The results of competition between *D. melanogaster* and *D. hydei* are almost the same as those obtained between *D. melanogaster* and *D. virilis* (YAMAZAKI 1978). AYALA's (1969) experiment showed that the results of interspecific competition between *D. serrata* and several other species of Drosophila were almost the same. These results support the idea that the results of competition experiments between *D. melanogaster* and *D. hydei* might be extended to fitness estimation generally.

In this experiment the population size and total competitive ability were tightly correlated: $r_g = 0.997$, $r_p = 0.675$. Correlations among other combinations of fitness and fitness components were lower. Moreover, total competitive ability is better than population size as an estimate of net fitness, since the former estimate is less influenced by culture conditions, due to the presence of a standard within the population. Total competitive ability is, therefore, the best among several measurements that can be used as an index of net fitness. These findings are essentially the same as those obtained by AYALA (1970). AYALA also found that fitness of three strains of *D. serrata* estimated in single-species experiments were quite similar to those obtained in interspecific competition experiments. The fact that such close agreement was observed between two different experiments, by different investigators, with different species may indicate that these results show a general phenomenon. HAYMER and HARTL (1982) reported that little correlation was obtained between the fitness estimated by interspecific competition and those by intraspecific competition. It is likely, however, that the results were obtained mainly due to the difference in experimental conditions (single generation *vs.* multigeneration experiments) rather than due to intraspecific *vs.* interspecific competitions). In the present study all of the estimates of fitness were obtained from multigeneration experiments. The relatively low genotypic correlation between net fitness and components of fitness or between fitness components may indicate that fitness and fitness components are not always positively correlated.

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