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Genetic variation for rate of development in natural populations of *Drosophila melanogaster*

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Abstract

We have sampled wild chromosomes from two natural populations of *Drosophila melanogaster* and obtained flies fully homozygous for the second chromosome, the third chromosome, or both, as well as flies heterozygous for one or both wild chromosomes and balancer chromosomes. Rate of embryogenesis (egg laying to larval hatching) and rate of development from egg to adult are measured, by classifying the individuals into fast, intermediate, and slow developmental classes. The experiments indicate that variation for rate of embryogenesis and for rate of egg-to-adult development is plentiful in the natural populations. Various hypotheses are enunciated to account for the small range of phenotypic variation observed in wild-type individuals with respect to the two parameters (embryogenesis and egg-to-adult development) and for the difficulty in changing the mean rates by artificial selection. Appropriate experiments may decide among the hypotheses, helping us to understand the genetic control of rate of ontogenesis, which is an important fitness component.

Introduction

Rate of ontogenesis, i.e., the time elapsed from the egg to the adult stage, is an important fitness component: the earlier an individual reaches reproductive age, the greater its fitness (Cole, 1954; Lewontin, 1965; Parsons, 1983). Nevertheless, there are physiological constraints that set limits to how fast ontogenesis may be, and this may be a reason why the variance for ontogenetic time is relatively small in many organisms, homeotherms as well as poikilotherms with complex development. The interaction between the fitness gained by faster development and the physiological constraints may also be the reason for the apparent strong homeostatic control of the rate of development. Indeed, most artificial selection experiments attempting to modify the mean rate of development in *Drosophila* are usually unsuccessful for a number of generations, although if the selection is sustained for many generations selection gains are usually obtained (Sang & Clayton, 1957; Marien,

1958; Clarke *et al.*, 1961; Prout, 1962; Dawson, 1966; Tigerstadt, 1969; Cavener, 1983). The persistent selection may eventually overcome the homeostatic control and make possible the expression of underlying genetic variation.

In our laboratories we have been unsuccessful in selection for faster and slower rates of embryogenesis – time from egg laying to larval hatching – in *Drosophila melanogaster* and *D. simulans* (Marinković & Ayala, in press). The experiments suggest, however, that there is genetic variation for embryogenesis time. The present experiments explicitly address the question whether natural populations of *D. melanogaster* store genetic variation for rate of embryogenesis and also for rate of development from egg to adult. The opportunity for the expression of the genetic variation is enhanced by obtaining flies that are fully homozygous for the second and the third chromosomes (which together amount for 80 percent of the genome of *D. melanogaster*), so that recessive genes will be expressed.

Material and methods

The experimental flies are derived from two natural populations of *Drosophila melanogaster*: Tito-va Mitrovica (TM, Yugoslavia, 300 km south of Belgrade) and Furnace Creek (FC, Mojave Desert, California). Large numbers of F_2 progenies from several hundred flies collected in TM were brought to the laboratory at the University of California in Davis and distributed over many culture bottles with standard cornmeal-and-molasses *Drosophila* medium. One hundred F_3 females collected from these cultures were used for the crosses described below. Some 200 wild females were collected in FC and distributed into separate cultures in the laboratory; 100 F_2 females from these cultures were used for the crosses.

Figure 1 outlines the crosses made. The pattern of these crosses is well known (e.g., Ives, 1945). Our pattern differs, however, from previous ones in that in the P and F_1 generations the males (rather than

Fig. 1. The crosses made with *Drosophila melanogaster* in order to obtain four genotypes with none, one, or two chromosomes fully homozygous. II^+ and III^+ represent wild chromosomes; Cy , Pm , Ubx , and Sb symbolize chromosomes with various genetic markers as well as inversions that inhibit recombination in the heterozygotes (see Ives, 1945). In the F_1 , F_2 , and F_3 generation, the wild chromosomes are labeled II^{+1} and III^{+1} to indicate that there is only one wild second chromosome and only one wild third chromosome. The crosses differ from the usual ones of this type in that the males (rather than the females) come from the tester stock in the P and F_1 generation. This ensures that the cytoplasm of the progenies derives from the wild flies.

the females) come from the laboratory stock. This ensures that the cytoplasm in the F_1 and following generations derives from the wild flies, rather than from the laboratory stock. In the F_3 generation, four kinds of phenotypically distinguishable flies are recovered: doubly heterozygous (i.e., heterozygotes for a wild second chromosome and the balancer second chromosome as well as for a wild third chromosome and the balancer third chromosome); homozygous for the second chromosome and heterozygous for the third; homozygous for the third chromosome and heterozygous for the second; and doubly homozygous (i.e., flies that are fully homozygous for a given wild second chromosome as well as for a given third chromosome). Each balancer chromosome carries a recessive lethal gene, so that no homozygotes for the balancer chromosomes are recovered. Each balancer chromosome also contains inverted segments that completely inhibit recombination in the heterozygotes. In the F_3 , the expected frequencies of the four genotypes are, according to the Mendelian rules of segregation: 44.4, 22.2, 22.2, and 11.1 percent, respectively, for the four kinds of genotypes mentioned. Viability differences result in variable frequencies. The proportion of flies homozygous for the second (or the third) chromosome is 33.3 percent: 11.1 percent doubly homozygous plus 22.2 percent homozygous for only the second (or only the third) chromosome. Whenever the total number of flies homozygous for the second or for the third chromosome was less than 10 percent of the total, the line was eliminated from consideration. The embryogenesis experiments involved 16 lines from the TM population and 14 lines from the FC population. The egg-to-adult experiments used the 14 FC lines plus two others.

Embryogenesis time was determined as follows. Groups of about ten pairs of 5–10 days-old double heterozygotes (F_2 generation in Fig. 1) were placed in half-pint culture bottles that had no food on the bottom. The medium for egg laying was provided in a small Petri dish that snugly fits the top of the bottle and to which it is sealed with external masking tape. A fresh Petri dish was placed at 1 pm on a given day, replaced at 2 pm by another, which was removed one hour later. The removed dishes were covered and the larvae hatching in them removed at two-hour intervals, continuously from the early morning following the day when the eggs were laid.

Larvae started to hatch about 17 h after egg laying and continued to do so somewhat beyond 40 h into the second day after egg laying.

Three classes of larvae were isolated according to the rate of embryonic development: 'fast', those hatching in less than 20 h; 'intermediate', those hatching in 23–26 h; and 'slow', those requiring more than 30 h for hatching. The larvae from each chromosomal line were placed into separate culture bottles with food according to their developmental class. When the imagoes (F_3 in Fig. 1) emerged in these cultures, they were counted according to their genotype.

The egg-to-adult rate of development was determined as follows. Eggs were collected in Petri dishes as described above, except that 20 pairs (rather than 10) of double-heterozygous flies (F_2 in Fig. 1) were introduced in each bottle. Groups of eggs collected at one-hour intervals were placed in separate cultures with food, in uncrowded conditions. The emerging imagoes (F_3 in Fig. 1) were classified according to genotype at 6–8 h intervals as 'fast' (developed in less than 10 days), 'intermediate' (developed in 12 days), and 'slow' (developed in 20–22 days).

All experiments were performed at 23 °C.

Results

Rate of embryogenesis

The eggs laid by the double-heterozygous parents (F_2 generation in Fig. 1) were separated according to their rate of embryonic development into three classes: fast (hatching in less than 20 h), intermediate (hatching in 23–26 h), or slow (hatching in more than 30 h). When the adults emerged within each class, they were classified according to their genotype (F_3 in Fig. 1). Table 1 gives the mean frequency of each genotype within each embryogenesis class for all 30 chromosome lines. The 16 lines from the TM population and the 14 lines from the FC population have been combined because the two sets are not significantly heterogeneous, according to an analysis of variance.

The four genotypes are expected in the proportions 4:2:2:1. The frequencies of the four genotypes averaged over all 30 chromosome lines fit fairly well the expected frequencies in the fast as well as in the intermediate class, but not so in the slow embryogenesis class ($\chi^2 = 7.74$, with 3 d.f.; $P \approx 0.05$). There is an obvious excess of double homozygotes in the slow developmental class, reflecting the com-

Table 1. Frequency of four genotypes among three developmental classes (embryogenesis) of *Drosophila melanogaster*. The values given are the mean and standard error (with the coefficient of variation, in parenthesis) for 30 different lines. The mean time for embryonic development for each genotype is also given.

Genotype	Expected frequency	Observed frequency in each developmental class			Time to embryogenesis (hrs.)
		Fast	Intermediate	Slow	
$\frac{II^+}{Cy} \frac{III^+}{Ubx}$	0.444	0.418 ± 0.029 (37%)	0.438 ± 0.041 (50%)	0.338 ± 0.042 (72%)	26.6 ± 0.2
$\frac{II^+}{II^+} \frac{III^+}{Ubx}$	0.222	0.224 ± 0.024 (58%)	0.184 ± 0.030 (87%)	0.217 ± 0.036 (96%)	27.5 ± 0.2
$\frac{II^+}{Cy} \frac{III^+}{III^+}$	0.222	0.228 ± 0.026 (61%)	0.239 ± 0.029 (65%)	0.264 ± 0.041 (89%)	27.1 ± 0.2
$\frac{II^+}{II^+} \frac{III^+}{III^+}$	0.111	0.129 ± 0.023 (95%)	0.139 ± 0.023 (89%)	0.181 ± 0.031 (94%)	28.2 ± 0.3
χ^2 (3 d.f.)	–	0.46	1.50	7.74*	–

The genotype frequencies have been arcsine transformed in order to calculate the chi-squares.

* $p \approx 0.05$.

mon observation that *Drosophila* flies homozygous for full chromosomes have, on the average, lower fitness than heterozygous flies (review in Dobzhansky, 1970; see Seager, Ayala & Marks, 1982). Consistent with this result is that the double homozygotes have the (significantly) slowest average rate of embryonic development (28.2 hours) and the double heterozygotes have the (significantly) fastest average rate (26.6 hours; see last column in Table 1).

The coefficients of variation (Table 1, in parentheses) indicate that the variation from line to line in the frequency of a given genotype is largest among the double homozygotes (89–95%) and least among the double heterozygotes (37–72%). This is expected, given that recessive alleles become expressed in the homozygotes. There is also greater variation in genotypic frequencies in the slow developmental class, less in the intermediate class, and least in the fastest class. This suggests that different chromosome lines are genetically heterogeneous with respect to the rate of embryonic development, so that the lines 'respond' differently to the classification of individuals into slow, intermediate, or fast.

To ascertain whether the apparent agreement (at least for the fast and intermediate classes) between the observed and expected frequencies of the four genotypes is the result of averaging among the lines, we have examined the fit for each individual line. The results are summarized in Tables 2 and 3. First, we examine the frequencies of the four genotypes within each line to test whether they agree with the expected frequencies (4:2:2:1). Of the 30 chi-squares, 16 are significantly different in the fast class, 21 are so in the intermediate class, and 25 are in the slow class (Table 2). The averages of the 30 chi-squares are also given in this table.

Table 3 gives the results of a somewhat different way of examining the data. We have compared the observed and expected frequencies separately for each genotype in all 30 lines, which gives a chi-squared with 29 degrees of freedom. All chi-squares are statistically significant ($P < 0.001$). The chi-squares are generally larger for the double homozygotes than for the other genotypes; and they are definitely larger for the slow class than for the other two. These results are consistent with the analysis in Table 1 and 2.

The heterogeneity of the genotypic frequencies

Table 2. Average chi-square for all 30 lines and number of lines with significant chi-squares for the difference between the observed and expected frequencies of four genotypes in three developmental classes (time for embryogenesis) of *Drosophila melanogaster*.

	Fast	Intermediate	Slow
Average χ^2 (3 d.f.)*	14.3	21.7	31.5
Number of significant χ^2 (N = 30)	16	21	25

The genotype frequencies are arcsine-transformed in order to calculate the chi-squares. *With three degrees of freedom, $p < 0.05$ whenever $\chi^2 > 7.81$.

among the three developmental classes is further examined in Tables 4 and 5. First we have compared the observed frequencies for all four genotypes between each pair of developmental classes. All 30 chromosome lines are compared in each case: 20–24 of the 30 comparisons are statistically significant (Table 4). Then we have compared the frequency of a given genotype in any two different classes. We have 30 pairs of frequencies for each genotype, which yields chi-squareds with 29 degrees of freedom. All four genotypes give highly significant chi-squares ($P < 0.001$) for all three pairwise comparisons (Table 5).

Figure 2 illustrates the distribution of genotypic frequencies among the chromosome lines separately

Table 3. Chi-squares for the observed versus expected frequency of each genotype in 30 different chromosome lines of *Drosophila melanogaster*. The three developmental classes (time for embryogenesis) are separately considered.

Genotype	Fast	Intermediate	Slow
$\frac{II^+}{Cy} \frac{III^+}{Ubx}$	62.4	158.5	241.9
$\frac{II^+}{II^+} \frac{III^+}{Ubx}$	112.3	171.9	226.2
$\frac{II^+}{Cy} \frac{III^+}{III^+}$	122.5	138.4	256.9
$\frac{II^+}{II^+} \frac{III^+}{III^+}$	152.2	144.5	302.1

Each chi-square has 29 degrees of freedom; all are statistically significant ($P < 0.001$). The genotypic frequencies are arcsine-transformed in order to calculate the chi-squares.

Table 4. Average chi-squares for all 30 lines and number of lines with significant chi-squares for the heterogeneity between the frequencies of four genotypes observed in any two developmental classes (time for embryogenesis) of *Drosophila melanogaster*.

	F:I	F:S	I:S
Average χ^2 (3 d.f.)*	19.9	32.8	34.7
Number of significant χ^2 (N = 30)	20	24	24

The genotype frequencies are arcsine-transformed in order to calculate the chi-squares. F = fast; I = intermediate; S = slow rate of embryogenesis. *With three degrees of freedom, $P < 0.05$ whenever $\chi^2 > 7.81$.

ly for each developmental class. The three developmental classes have quite differently shaped distributions. Most different is the distribution of the slow class that shows obvious departure from normality and the greatest variance: in all four genotypes, the slow class has the largest numbers of lines at each end of the distribution.

Rate of development from egg to adult

Sixteen chromosome lines from the FC population were used in this experiment. Groups of eggs laid at one-hour intervals by doubly heterozygous

Table 5. Chi-squares for the comparison between the observed frequency of each genotype in two given developmental classes (embryogenesis time) of *Drosophila melanogaster*. There are 30 different chromosomal lines.

Genotype	F:I	F:S	I:S
$\frac{\text{II}^+}{\text{Cy}} \frac{\text{III}^+}{\text{Ubx}}$	124.0	250.6	270.6
$\frac{\text{II}^+}{\text{II}^+} \frac{\text{III}^+}{\text{Ubx}}$	168.7	182.7	245.8
$\frac{\text{II}^+}{\text{Cy}} \frac{\text{III}^+}{\text{III}^+}$	100.8	229.9	215.7
$\frac{\text{II}^+}{\text{II}^+} \frac{\text{III}^+}{\text{III}^+}$	141.3	288.4	290.1

Each chi-squared has 29 degrees of freedom. All chi-squares are statistically significant, $P < 0.001$. The genotypic frequencies are arcsine-transformed in order to calculate the chi-squares.

Fig. 2. Rate of embryogenesis. Frequency (number of lines) of four genotypes in the three developmental classes: F, fast; I, intermediate; and S, slow.

parents (F_3 in Fig. 1) were allowed to develop in separate cultures. Three developmental classes were identified among the emerging adults (F_2 in Fig. 1): fast (those completing metamorphosis in 10 days), intermediate (those requiring 12 days), and slow (those requiring 20–22 days). The frequencies of the four genotypes were determined upon emergence, separately for each chromosome line and each developmental class. Table 6 gives the mean frequencies of the four genotypes in each class. The chi-squares in the bottom row of the table indicate that these average frequencies do not significantly

Table 6. Frequency of four genotypes among three developmental classes (egg-to-adult) of *Drosophila melanogaster*. The values given are the mean and standard error (with coefficient of variation, in parenthesis) for 16 different lines. The mean time for egg-to-adult development of each genotype is also given.

Genotype	Expected frequency	Observed frequency in each developmental class			Time from egg to adult (days)
		Fast	Intermediate	Slow	
$\frac{II^+}{Cy} \frac{III^2}{Ubx}$	0.444	0.524 ± 0.043 (32%)	0.286 ± 0.036 (49%)	0.405 ± 0.072 (75%)	14.49 ± 0.12
$\frac{II^+}{II^+} \frac{III^+}{Ubx}$	0.222	0.170 ± 0.028 (66%)	0.287 ± 0.032 (44%)	0.181 ± 0.034 (90%)	14.31 ± 0.15
$\frac{II^+}{Cy} \frac{III^+}{III^+}$	0.222	0.251 ± 0.036 (61%)	0.257 ± 0.027 (40%)	0.259 ± 0.043 (67%)	14.70 ± 0.15
$\frac{II^+}{II^+} \frac{III^+}{III^+}$	0.111	0.055 ± 0.016 -	0.170 ± 0.033 (75%)	0.156 ± 0.062 -	15.46 ± 0.20
χ^2 (3 d.f.)		2.92	4.25	1.39	

The genotypic frequencies have been arcsine transformed in order to calculate the chi squares.

depart from the expected values (4:2:2:1). The mean rate of development is significantly slower in the double homozygotes (15–46 days) than in the other three genotypes (14.31 to 14.70 days), which do not differ among themselves.

Table 6 also gives the coefficient of variation for 10 of the 12 cases. In the case of the double homozygotes within either the fast or the slow class, the coefficient of variation calculated in the usual way ($C.V. = 100 s/\bar{x}$, where s is the standard deviation and $\bar{x}$ is the mean) gives values greater than 100 percent. This occurs because the variances are large and the distributions are not normal (see Fig. 3). Table 6 indicates greater variation in the slow than in the other two developmental classes; and greater among the double homozygotes than among the other three genotypes.

The observed frequencies of the four genotypes significantly depart from the expected frequencies in most of the chromosome lines (13, 9, and 14 in the fast, intermediate, and slow developmental classes, respectively, out of 16 in each case; see Table 7). When the frequency of a given genotype is compared with the expected value in all 16 chromosome lines the chi-square is statistically significant for each one of the four genotypes in each of the three developmental classes (Table 8). These results are analogous to those obtained for the rate of em-

Fig. 3. Rate of egg-to-adult development. Frequency (number of lines) in the three developmental classes: F, fast; I, intermediate; and S, slow.

Table 7. Average chi-squares for all 16 lines and number of lines with significant chi-squares for the agreement between the observed and expected frequencies of four genotypes in three developmental classes (egg to adult time) of *Drosophila melanogaster*.

	Fast	Intermediate	Slow
Average χ^2 (3 d.f.)*	15.1	14.2	34.3
Number of significant χ^2 (N = 16)	13	9	14

The genotype frequencies are arcsine-transformed in order to calculate the chi-squares. *With three degrees of freedom, $P < 0.05$ whenever $\chi^2 > 7.81$.

bryonic development. Also, the heterogeneity between the lines, as in the case for embryonic development, is larger in the slow than in the other two developmental classes, and larger for the double homozygotes than for any of the other three genotypes.

Tables 9 and 10 examine the heterogeneity among the three developmental classes by comparing the observed genotypic frequencies between each two classes. When the frequencies of all four genotypes are jointly considered for each chromosome line, the large majority of the chi-squares are statistically significant (13 or 14 out of 16; Table 9). When the frequency of a given genotype in

Table 8. Chi-squares for the observed versus expected frequency of each genotype in 16 different chromosome lines of *Drosophila melanogaster*. The three developmental classes (egg-to-adult time) are separately considered.

Genotype	Fast	Intermediate	Slow
<u>II+</u> <u>III+</u> Cy Ubx	45.0	64.2	152.0
<u>II+</u> <u>III+</u> II+ Ubx	59.2	43.4	107.5
<u>II+</u> <u>III+</u> Cy III+	65.0	29.3*	89.4
<u>II+</u> <u>III+</u> II+ III+	82.0	84.3	183.8

Each chi-square has 15 degrees of freedom.

* Statistically significant, $P < 0.05$; for the other 11 chi squares, $P < 0.001$. The genotypic frequencies have been arcsine-transformed in order to calculate the chi-squares.

Table 9. Average chi-squares for all 16 lines and number of lines with significant chi-squares for the heterogeneity between the frequencies of four genotypes in any two developmental classes (egg-to-adult time) of *Drosophila melanogaster*.

	F:I	F:S	I:S
Average χ^2 (3 d.f.)*	45.4	43.2	35.5
Number of significant χ^2 (N = 16)	13	13	14

The genotypic frequencies have been arcsine-transformed in order to calculate the chi-squares. F = fast, I = intermediate, S = slow rate of egg-to-adult development. With three degrees of freedom, $P < 0.05$ whenever $\chi^2 > 7.81$.

Table 10. Chi-squares for the comparison between the observed frequency of each genotype in two given developmental classes (egg-to-adult time) of *Drosophila melanogaster*. There are 16 different chromosome lines.

Genotype	F:I	F:S	I:S
<u>II+</u> <u>III+</u> Cy Ubx	124.6	167.3	323.8
<u>II+</u> <u>III+</u> II+ Ubx	232.6	141.7	127.6
<u>II+</u> <u>III+</u> Cy III+	107.8	145.6	49.0
<u>II+</u> <u>III+</u> II+ III+	169.2	189.5	116.3

Each chi-square has 15 degrees of freedom.

All chi-squares are statistically significant, $P < 0.001$.

The genotypic frequencies have been arcsine-transformed in order to calculate the chi-squares.

all 16 lines is compared between any two developmental classes, all chi-squares are highly significant (Table 10).

Figure 3 illustrates the distribution of genotypic frequencies among the chromosome lines in each developmental class. As it is the case for the rate of embryogenesis (Fig. 2), we see here that the slowest developmental class departs most conspicuously from normality and has the largest variance; we see again that the slow class has the greatest number of chromosome lines at each end of the distribution, for all four genotypes.

Discussion

Artificial selection for fitness components, such as viability or fertility, is often unsuccessful, or yields responses that are far from gradual. An explanation for the lack of additive genetic effects in the determination of fitness components is that these are largely controlled by highly balanced complexes of genes that cannot be easily broken apart (Mather, 1941, 1942, 1943; Mather & Harrison, 1949; Lerner & Dempster, 1951; Gibson & Thoday, 1963; Mather & Jinks, 1982). An alternative explanation, not mutually exclusive with the previous one, is that the mean value of fitness traits is strongly determined by balancing selection, so that the artificial selection is counteracted by natural selection (Schultz & Briles, 1953; Lerner, 1954). Consistent with this theory is the fitness breakdown commonly observed in inbred lines and its restoration in F_1 and F_2 'hybrids' between lines (Thoday, 1953; Mather, 1953; Lewis, 1954; Kidwell & Kidwell, 1966). Heterozygotes would have 'superior homeostasis' due to 'nonspecific effects of heterozygous loci' (Lerner, 1954).

One important fitness component is rate of development (Cole, 1954; Dobzhansky *et al.*, 1964). Artificial selection experiments attempting to change the rate of development in *Drosophila* (as well as in other organisms) are often unsuccessful, or succeed only after very many generations (Sang & Clayton, 1957; Marien, 1958; Clarke *et al.*, 1961; Prout, 1962; Dawson, 1966; Tigerstadt, 1969). A critical period of development is embryogenesis: the stage from egg to larval hatching. There are apparently no reports of successful modification of the rate of embryogenesis by artificial selection. We have ourselves failed to obtain divergence between lines of *D. melanogaster* (and *D. simulans*) intensively selected for fast and slow rate of embryogenesis (Marinković & Ayala, in press). This lack of success may be due to the counteracting effects of natural selection just mentioned. There must certainly be physiological constraints that set lower bounds to the time required for embryogenesis. But it is not clear why the rate of embryogenesis could not be lengthened under conditions of artificial selection.

One possibility is that natural populations do not harbor any genetic variance for rate of embryogenesis. This is not altogether implausible: natural selection might conceivably have achieved the phys-

iologically fastest possible rate of embryogenesis, given that this is such an important fitness component. The experiments reported here indicate that natural populations of *D. melanogaster* possess sizeable stores of genetic variation for rate of embryogenesis and egg-to-adult development.

In our experiments, the progenies (F_3 generation in Fig. 1) of any one chromosome line consist of only four genotypes (there is only one wild chromosome and only one balancer chromosome and there can be no recombination between them, for the second as well as for the third chromosome). In addition, the cytoplasm of all individuals is derived from the wild flies. When the progenies of a given cross are classified according to their rate of development, not all four genotypes are equally represented in the developmental classes. This is not surprising given the large genetic differences among the four genotypes. More relevant for our purposes is that distribution of the four genotypes among the developmental classes varies from line to line. This reflects genetic heterogeneity among the wild chromosomes sampled from the natural populations: homozygous effects as well as interactions with the balancer chromosomes may be involved.

Our experiments show greater variation (from line to line) among the double homozygotes than among any one of the other four genotypes. This may be due to the loss of homeostatic balance that has been associated with overall increased homozygosity (Lerner, 1954). But it may also be due to the fact that recessive alleles become expressed only in the homozygotes. However, we have also observed greater variation between lines in the slow developmental class than in the other two (for embryogenesis as well as for egg-to-adult development). This suggests that fitness reductions due to lengthened development are due in part to the loss of homeostatic balance: the increased variance associated with the slow developmental class occurs for each one of the four kinds of genotypes.

If there is genetic variance for rate of embryogenesis, why does artificial selection fail to obtain divergence between lines selected for slow and for fast development? One possibility is that the genetic factors determining embryogenesis time have low penetrance, so that the phenotype of an individual is a poor index of its genetic composition with respect to this trait. Another possibility, not mutually

exclusive with the previous one, is that the genetic factors for mean embryogenesis time are strongly balanced so that the artificially imposed selection is counteracted by natural selection. If the first alternative is correct, artificial selection might never be successful no matter how long continued, or the response could be very slow but gradual. If the second alternative prevails, artificial selection might, more or less suddenly, start to become effective after a number of generations, once the balanced gene complexes are broken up. This seems to be the predominant experience of the studies in which artificial selection for rate of development has been continued for very many generations (*e.g.*, Tigerstadt, 1969).

The common lack of success of artificial selection for divergent rates of development might also be explained in terms of Lerner's (1954) concept of genetic homeostasis. Individuals with fast rates of development (hence, higher fitness) might be heterozygous at many loci, whereas individuals with slow rates of development would be largely homozygous. But different homozygotes would carry different alleles. The two groups (fast = heterozygotes, and slow = homozygotes for different sets of alleles) would, then, generate every generation similar genotypic arrays consisting of both, heterozygotes and homozygotes, which would defeat the selection efforts (Marinković, 1977). This hypothesis is favored by the large variance observed in the slow developmental classes. The hypothesis could be directly tested by using multiple selection sublines, each generated by very few parents (preferably, a single pair). The fast individuals, because they are largely heterozygotes, would produce progenies with diversified genotypes and the average rate of development; the slow individuals, on the contrary, would produce largely homozygous individuals (for different alleles in different sublines) that would mostly be slow in development.

Explicit consideration of these alternatives may facilitate the design of experiments that might eventually yield a better understanding of the genetic control of rate of development.

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