FITNESS AND DENSITY-DEPENDENT POPULATION GROWTH IN *DROSOPHILA MELANOGASTER*

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ABSTRACT

The density-dependent rates of population growth were determined for 26 populations of *Drosophila melanogaster* maintained in the serial transfer system. Twenty-five populations were homozygous for an entire chromosome *2* sampled from nature; the other was a random heterozygous population. Rates of population growth around the carrying capacity cannot explain the large fitness depression of these lines. However, the homozygous lines show large differences in rates of population growth at low densities relative to the random heterozygous standard. The average relative fitness of the homozygous lines, as determined from the growth rates at the lowest density, is 0.51.

EVOLUTIONARY biologists relate certain biological phenomena with measurements of fitness. Population geneticists call these biological phenomena "components of fitness," which include viability (DOBZHANSKY, SPASSKY and TIDWELL 1963), fecundity (MARINKOVIC 1967), virility (BRITTNACHER 1979), developmental rate (MARINKOVIC 1967) and sperm displacement (PROUT and BUNDGAARD 1977). Population ecologists have examined such traits as the intrinsic rate of increase, r, (DOBZHANSKY, LEWONTIN and PAVLOVSKY 1964), the carrying capacity, K, of a population (CARSON 1961; AYALA 1966, 1968), mate selection (EMLEN and ORING 1977) and foraging behavior (SCHOENER 1971). Particular attention has been paid to the population parameters r and K. Indeed, much of the theory of life-history evolution has assumed that life-history parameters evolve in such a way as to maximize r (HAMILTON 1966; EMLEN 1970).

It is reasonable to assume that all of these biological properties are important in determining the reproductive success of an organism. It is not clear, however, what their relative importance is in determining the net fitness of a genotype and whether one or a few have overwhelming importance. Population geneticists have seen that viability is a poor indicator of net fitness (*e.g.*, SVED and AYALA 1970). It seems that, at least for Drosophila, the adult components of fitness are more important (SVED and AYALA 1970; PROUT 1971; BUNDGAARD and CHRISTIANSEN 1972). It would be of great importance to the theory of ecological genetics to be able to determine the relationship between density-dependent rates of population growth and some independent measure of net fitness.

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Such a comparison is possible for genotypes of *Drosophila melanogaster* homozygous for whole second chromosomes sampled from nature. The net fitness of such genotypes has been determined (SVED 1971; TRACEY and AYALA 1974). These estimates of net fitness were determined from observations of the contribution to successive generations of homozygous genotypes relative to a random heterozygous "wild" genotype. In such experiments, the populations are maintained near their carrying capacity, and the performance of the genotypes is a function of all components of fitness. In the present study, we examine the population dynamics of various genotypes in the serial transfer system. Previous work (MUELLER 1979) has given experimental and statistical procedures for estimating rates of population growth in the serial transfer system. The stability of these populations around their carrying capacity has also been examined (MUELLER 1979).

MATERIALS AND METHODS

Drosophila melanogaster collected in Strawberry Canyon, Berkeley, California, were made homozygous for each of 49 chromosomes by standard procedures involving crosses with a balancer-lethal stock (TRACEY and AYALA 1974). From these 49 populations, 25 nonlethal and nonsterile populations were selected for this study. These 25 populations were intercrossed, and the F_1 progenies were intermixed in order to produce a random heterozygous line.

The density-dependent rates of population growth are determined in the following fashion (MUELLER and AYALA 1981). A specified number of adults, $N,^*$ are allowed to lay eggs for one week in a fresh half-pint culture bottle. The survivors are counted one week later and the adults emerging from this same culture over the following 3 weeks are recorded. N^* consisted of equal numbers of males and females. All flies were raised at the same density as that of the experiment in which they were used. It should be noted that these experiments are similar to the "Type II" experiments conducted by AYALA, GILPIN and EHRENFELD (1973). For each population, $N^* = 10$, 20, 50, 100, 250, 500, 750 and 1000. Six replicates at each density were made for each homozygous line, except at $N^* = 1000$, at which only 3 replicates were made. For the random heterozygous line, 12 replicates at each density were done, except at $N^* = 1000$, at which only 3 experiments were carried out. The experiments were performed at 23° and *ca.* 70% relative humidity.

As described in MUELLER (1979), a general model of the serial transfer system is,

$$N_t = f_1(N_{t-1}) + f_2(N_{t-2}) + f_3(N_{t-3}) + f_4(N_{t-4}) \ , \qquad (1)$$

where N_t is the number of adults in the population at a given time, and $f_i(N_{t-i})$ is an unknown function that relates the number of adults emerging (or surviving, in the case of f_1) from an i-weeks-old culture with the number of individuals that laid eggs in that culture. The experiment described above yields repeated observations of the $f_j(N_{t-j})$ functions. The observations from one experiment may thus be represented as $f_1(N^*)^i, f_2(N^*)^i, f_3(N^*)^i, f_4(N^*)^i$, where the superscript now refers to the ith replicate of the experiment at N^*.

Density-dependent rates of population growth are determined using a linear version of (1).

$$N_t = a_1N_{t-1} + a_2N_{t-2} + a_3N_{t-3} + a_4N_{t-4} \ , \qquad (2)$$

where a_i is a constant per capita output of an i-weeks-old culture that is estimated from the observations at a particular N^*. The estimation of each a_i proceeds directly from the observation as

$$\hat{a}_i = \frac{1}{m}\sum_{j=1}^{m} f_i(N^*)^j/N^* \ ,$$

where m is the total number of replicates (which is 3, 6 or 12 in these experiments). (2) is a fourth-order homogenous and linear difference equation. The largest eigenvalue of (2), λ_{N^*}, is

used as an estimate of the rate population growth for each N^*. Thus at each value of N^*, a different set of observations is made in order to estimate the a_i values in (2), which yield a different per capita rate of increase, λ_{N^*}, for each N^*.

In practice, λ_{N^*} is estimated as the mean of m approximately independent and identically distributed (i.i.d.) random variables obtained from m separate experiments. These m approximately i.i.d. random variables are called pseudovalues, and their method of estimation is called the "jackknife" (MUELLER 1979, also see MILLER 1974 for a review of the jackknife statistic). The pseudovalues are also used for estimating the variance of the largest eigenvalue, as well as in a one-way analysis of variance (ANOVA). The ANOVA gives an indication of the heterogeneity of the λ_{N^*} values among the genetically heterogeneous lines.

RESULTS

The main experimental results are given in Table 1, which shows for each population the mean (with its standard error) of the net productivity expected at each initial density. Table 2 gives for each homozygous line at each density the per capita rate of population growth, λ_{N^*}, as the largest eigenvalue of equation (2). As mentioned in the MATERIALS AND METHODS, this growth rate is estimated by the jackknife technique and is the mean of m pseudovalues. An analysis of variance has been carried out on these pseudovalues at each density to determine whether there are significant differences among the λ_{N^*} for the 25 homozygous lines.

Highly significant differences among the homozygous lines indeed exist at every density. The results of the ANOVA have been summarized in Figure 1. All homozygous lines have been divided into 5 groups according to their value of λ_{10}, and 95% simultaneous confidence intervals (see SCHEFFE 1959, pp. 68–72) have been placed on the mean λ_{N^*} of each of these groups. As can be seen in Figure 1, the magnitude of the difference in λ_{N^*} decreases with increasing density; although highly significant differences still exist at high densities among the λ_{N^*}, these differences are not nearly so great as at lower densities. Moreover, the relative rankings of the growth rates at low densities are only weakly preserved at higher densities; some relative rankings are, in fact, altered at the higher densities.

We are interested in obtaining some measure of relative fitness of the homozygous lines. The estimates of the growth rate per week provide a reasonable statistic to use as a measure of relative fitness. Hence, fitness will be defined herein as the per capita contribution of offspring in one generation. This contribution is standardized relative to the per capita contribution of the random heterozygous line. If $\lambda_{N^*}^{(i,i)}$ is the weekly growth rate of the ith homozygous line and $\lambda_{N^*}^{(i,j)}$ is the same for the random heterozygous line, then, assuming a three-week generation time, relative fitness is estimated by

$$w_{N^*}^{(i,i)} = [\lambda_{N^*}^{(i,i)}/\lambda_{N^*}^{(i,j)}]^3 .$$

A three-week generation time is the same as assumed by TRACEY and AYALA (1974), and allows us to compare the present results with those they obtained.

The average fitness of all 25 homozygous lines relative to the heterozygous line is shown in Figure 2 for each density. A derivation of the approximate

TABLE 1

Net productivity† (with standard error) at various densities in each of 26 experimental populations of Drosophila melanogaster

Population	Density							
	10	20	50	100	250	500	750	1000
H‡	470±12	587±25	665±18	669±20	730±52	260±55	—212±59	—454±72
1	523±44	717±44	685±27	693±42	528±29	425±44	233±61	—408±131
2	336±16	389±33	403±24	468±53	475±20	222±62	105±73	—174±50
3	211±18	318±19	338±25	373±25	452±16	193±15	—187±56	—126±109
6	514±40	541±34	580±34	660±20	722±53	732±61	168±56	328±165
7	156±16	250±22	254±12	227±24	336±40	82±58	— 96±36	—495±151
8	341±35	526±29	634±24	677±25	580±31	482±58	170±79	—184±86
9	298±83	346±42	473±64	455±50	555±17	324±45	192±117	—110±49
13	226±17	267±33	315±48	333±40	358±42	126±35	— 67±21	—684±35
14	441±26	598±37	650±34	587±20	729±17	537±46	317±43	104±55
15	418±30	428±26	565±55	593±33	647±61	494±70	27±91	—551±47
18	427±59	589±47	628±57	706±72	853±48	761±41	479±51	153±18
20	485±44	574±65	685±43	632±20	768±18	557±93	336±108	—225±31
23	186±19	313±31	395±66	416±40	412±70	227±151	— 34±109	—524±32
24	36±12	130±28	158±20	228±22	162±6	*	*	*
25	461±42	643±49	741±41	756±46	853±149	336±48	129±144	—430±22
30	9±5	5±8	96±33	90±31	267±43	198±46	—198±103	—806±31
33	577±27	669±12	783±40	889±51	613±43	228±50	— 89±52	—302±112
36	120±16	155±22	272±28	254±18	274±31	177±21	—161±35	*
37	500±29	483±25	612±25	686±30	685±27	385±92	—258±51	—660±92
40	87±21	190±29	369±19	502±58	329±13	233±26	— 67±94	—366±50
42	439±39	681±42	658±45	551±18	624±42	512±94	172±76	— 7±42
43	389±54	554±18	544±31	720±54	316±65	155±51	—262±56	—423±27
45	336±49	313±84	388±105	306±115	471±37	241±96	—278±45	—484±3
50	288±68	380±42	445±35	447±23	533±11	482±65	70±72	—340±28
52	321±32	517±52	601±21	554±29	333±35	— 87±32	—392±54	—566±51

* No data collected.

† Calculated as $f_1(N^*) + f_2(N^*) + f_3(N^*) + f_4(N^*) - N^*$.

‡ *H* is a random heterozygous population; the other populations are homozygous for different second chromosomes.

sampling variance of these mean fitnesses is given in the APPENDIX. This sampling variance is used to construct the confidence intervals shown in Figure 2. The most striking result is that, at the higher densities, the rates of population growth of the homozygous lines are very nearly the same, on the average, as the rate of population growth of the heterozygous line. On the contrary, the difference between the homozygous lines and the random heterozygous standard is largest at the lowest initial density. This result is particularly interesting because the determination of net fitness in population cages is usually made at densities near the carrying capacity. MOURÃO, AYALA and ANDERSON (1972), studying *Drosophila willistoni* populations homozygous for whole second chromosomes, obtained results similar to the present ones; they observed no correlation between carrying capacity of the populations and the relative fitness of the homozygotes when placed in competition with heterozygous individuals in the same population.

TABLE 2

Per capita growth rate (modulus of the largest eigenvalue) with its standard error for each of 26 experimental Drosophila melanogaster *populations at various densities*

Population	Density							
	10	20	50	100	250	500	750	1000
H†	5.0±0.14	4.3±0.11	3.24±0.07	2.60±0.03	1.93±0.07	1.22±0.05	0.88±0.04	0.78±0.02
1	4.5±0.17	3.8±0.06	3.01±0.03	2.43±0.02	1.75±0.03	1.31±0.04	1.13±0.04	0.83±0.07
2	4.1±0.23	3.5±0.30	2.54±0.04	2.18±0.09	1.66±0.02	1.18±0.05	1.04±0.02	0.93±0.02
3	3.4±0.12	3.0±0.12	2.45±0.05	2.09±0.06	1.68±0.02	1.16±0.01	0.86±0.04	0.94±0.06
6	4.7±0.11	3.9±0.15	2.98±0.07	2.55±0.03	1.96±0.05	1.61±0.04	1.09±0.04	1.13±0.06
7	2.9±0.18	2.8±0.06	2.11±0.05	1.71±0.04	1.48±0.04	1.07±0.04	0.95±0.02	0.72±0.10
8	3.9±0.16	3.9±0.17	2.89±0.05	2.35±0.06	1.75±0.02	1.39±0.04	1.10±0.05	0.92±0.04
9	3.8±0.14	3.1±0.12	2.73±0.13	2.14±0.08	1.81±0.02	1.27±0.05	1.12±0.07	0.94±0.03
13	3.4±0.10	2.9±0.09	2.33±0.06	1.94±0.04	1.49±0.05	1.11±0.03	0.96±0.01	0.62±0.06
14	4.2±0.12	4.0±0.10	2.91±0.06	2.38±0.06	1.92±0.01	1.41±0.03	1.14±0.02	1.04±0.02
15	3.8±0.37	3.5±0.15	2.86±0.09	2.46±0.05	1.82±0.09	1.30±0.04	1.01±0.05	0.69±0.05
18	4.2±0.31	4.0±0.25	3.05±0.14	2.57±0.12	2.01±0.03	1.56±0.04	1.25±0.03	1.06±0.01
20	4.5±0.28	3.8±0.21	3.08±0.12	2.44±0.06	1.98±0.02	1.39±0.07	1.16±0.05	0.92±0.01
23	3.5±0.12	3.4±0.14	2.72±0.19	2.17±0.09	1.61±0.09	1.20±0.12	0.97±0.07	0.74±0.03
24	2.2±0.29	2.5±0.12	1.86±0.87	1.74±0.07	1.27±0.01	*	*	*
25	4.8±0.17	4.3±0.30	3.37±0.06	2.72±0.04	1.93±0.15	1.29±0.05	1.06±0.06	0.78±0.01
30	1.4±0.20	1.2±0.24	1.77±0.18	1.46±0.11	1.48±0.06	1.20±0.04	0.85±0.09	0.40±0.06
33	5.1±0.17	4.7±0.29	3.56±0.16	2.77±0.10	1.79±0.03	1.20±0.05	0.94±0.03	0.84±0.06
36	2.7±0.11	2.3±0.11	2.10±0.06	1.75±0.12	1.41±0.04	1.16±0.02	0.90±0.02	*
37	4.4±0.08	3.8±0.11	3.16±0.05	2.64±0.04	1.81±0.03	1.26±0.06	0.84±0.04	0.64±0.10
40	2.9±0.26	2.9±0.13	2.52±0.05	2.33±0.11	1.58±0.02	1.23±0.02	0.95±0.07	0.81±0.03
42	4.3±0.21	3.8±0.13	3.02±0.18	2.27±0.02	1.50±0.08	1.36±0.07	1.09±0.04	1.00±0.02
43	4.1±0.27	4.2±0.11	2.53±0.07	2.56±0.06	1.50±0.08	1.14±0.04	0.81±0.04	0.76±0.008
45	4.6±0.26	3.3±0.15	2.36±0.14	1.84±0.15	1.65±0.04	1.21±0.08	0.80±0.03	0.70±0.001
50	3.6±0.28	3.3±0.14	2.68±0.06	2.25±0.03	1.80±0.02	1.37±0.03	1.04±0.04	0.82±0.02
52	4.4±0.27	4.2±0.09	3.16±0.07	2.28±0.03	1.49±0.03	0.92±0.03	0.72±0.06	0.66±0.05

* No data collected.
† *H* is a random heterozygous population; the other populations are homozygous for different second chromosomes.

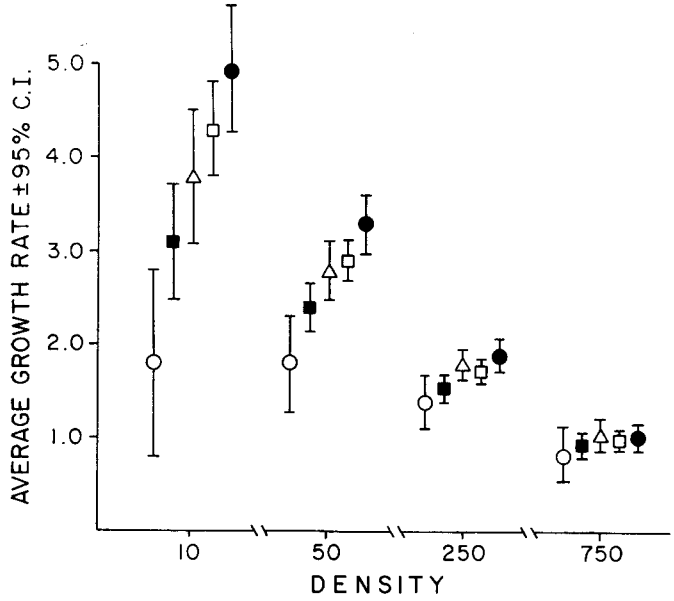

FIGURE 1.—Average λ_{N^*} for five groups of homozygous populations at each of four densities. The homozygous lines included in each group are: ○ lines 24, 30; ■, lines 3, 7, 13, 23, 36, 40; △, lines 8, 9, 15, 50; □, lines 1, 2, 14, 18, 20, 37, 42, 43, 45, 52; ●, lines 6, 25, 33.

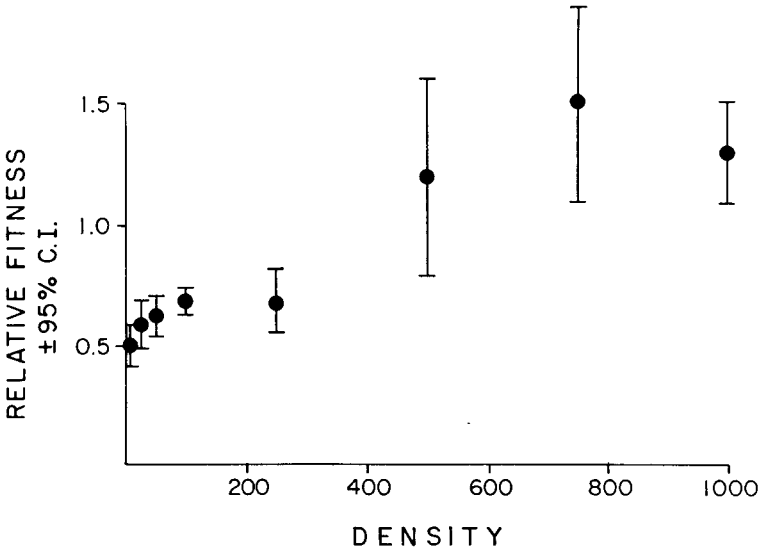

FIGURE 2.—Average fitness of 25 homozygous lines, relative to the fitness of a random heterozygous population, at each of eight densities (10, 20, 50, 100, 250, 500, 750 and 1000).

The carrying capacity of these populations is just the value of N^* where $\lambda_{N^*} = 1$. For most populations used in this study, the carrying capacity was between 750 and 1000 adult flies. As a consequence, there is a high correlation between a population's carrying capacity and its values of λ_{750} and λ_{1000}. Thus, our observation that there is little difference between the growth rates of the average homozygous line and the random heterozygous line at high densities is equivalent to there being little difference between their carrying capacities.

DISCUSSION

Population biologists have related ecological properties such as the carrying capacity (CARSON 1961; AYALA 1966, 1968) and the maximum rate of population growth (DOBZHANSKY 1968; HAMILTON 1966; CROW and KIMURA 1970) to the fitness of a population. The relative fitness of *D. melanogaster* homozygous for second chromosomes is known through a variety of experiments (SVED 1971; TRACEY and AYALA 1974; SEAGER 1979). These results show that the net fitness of nonlethal, nonsterile individuals homozygous for second chromosomes sampled from nature relative to random heterozygotes is very low (about 0.23, for example, in the experiment of TRACEY and AYALA). It should be noted that these measurements of net fitness are carried out at high densities, and that the different genotypes compete for food, oviposition sites and mates.

The results of the present study show that population growth rates at high densities do not explain the observed differences in fitness between average homozygous individuals and random heterozygotes. However, at low densities, the growth rates of homozygous populations reveal large heterogeneity among these populations. These two sets of results are not necessarily contradictory, but may be understood in terms of models recently developed by PROUT (1980). In such models, the life history of an organism is analyzed in terms of several stages. PROUT assumes that density-dependent regulation acts at a certain stage of the life cycle; whereas, in a similar fashion, density-independent selection operates at a different stage. If the density-dependent regulation happens after the occurrence of density-independent selection, but before the population is counted, then evolution will have little effect on the carrying capacity of the censused stage. Moreover, populations that may, for instance, have large differences in fecundity may show little or no difference in the adult carrying capacity.

The hyperbolic model of PROUT (1980), for example, gives the number of adults N_{t+1} at a certain time as

$$N_{t+1} = [\tilde{S}/(1 + sFN_t)]FN_t ,$$

where F is the per capita fecundity and $\tilde{S}$ and s are parameters of the density-regulating function. The carrying capacity, $N_{t+1} = N_t = K$, is given by $K = (\tilde{S}F - 1)/(sF)$. When $\tilde{S}F >> 1$, then $K \cong \tilde{S}/s$; that is, the carrying capacity is independent of the per capita fecundity. Under this sort of model, genotypes

showing large differences in fecundity would also show large differences in net fitness as measured in competition with other genotypes in population cages, large differences in rates of population growth at low densities, but little or no difference in their carrying capacity or population growth rates near the equilibrium density.

Differences in development time might also lead to the differences observed above. In population cages, overlapping generations are present, and genotypes with a shorter development time would have higher relative fitness even at the carrying capacity. These same genotypes should also have greater per capita growth rates at low densities, although they need not show greater carrying capacities.

The mean relative fitness of the homozygous lines is, at the lowest density, approximately 0.50 (and greater than that at all other densities). This value is considerably higher than the average fitness obtained when *D. melanogaster* homozygous for a second chromosome compete with heterozygous individuals in the same population cage; the values obtained in two experiments are 0.15 (SVED 1971) and 0.23 (TRACEY and AYALA 1974). The reason for this difference is that important fitness components contribute to the performance of a genotype when in competition with other genotypes, but not when grown in pure culture even at low density. These fitness components include larval competitive ability (BAKKER 1969) and male mating advantage (including mating capacity or "virility"; BRITTNACHER 1979). Assume that males with a certain genotype, A_1, mate faster than males of genotype A_2, with both types of females, A_1 and A_2 (that is, they are preferred by either kind of female). This difference would lower the fitness of the A_2 genotype when both genotypes exist together, but not when the two genotypes are grown in pure culture (assuming, of course, that A_2 males are able to inseminate all the available A_2 females).

The points made in the previous paragraphs corroborate the conclusion reached by other authors (*e.g.*, DOBZHANSKY 1970; WALLACE 1970; MOURÃO, AYALA and ANDERSON 1972) that net fitness and genetic load, as measured when alternative genotypes compete with each other, are not good indices of how the genotypes will do in isolation. *Drosophila melanogaster* homozygous for second chromosomes are effectively semilethal (fitness below 0.25) when they compete with heterozygotes, but perform as well as the heterozygotes when grown in pure cultures at high densities (see Figure 2).

Different fitness components are relevant under different conditions. One way of quantifying the effects of the relevant fitness components under different conditions is to express fitness differences in terms of lethal equivalents (MORTON, CROW and MULLER 1956). A lethal equivalent is defined as the number of lethal recessives necessary to explain the decrease in mean fitness of a certain genotype when it is homozygous. If certain assumptions hold (BRITTNACHER 1979), the lethal equivalents for various components of fitness should add up to the lethal equivalents for the net fitness observed in competition; the most restrictive condition is that the fitness components are independent. On the average, 1.47 lethal equivalents are necessary to explain the reduction in net fitness of the chromo-

some 2 homozygotes in the experiments of TRACEY and AYALA (1974). According to the results of the present experiment, 0.67 lethal equivalents are necessary to explain the decrease in growth rates at low densities; and at high densities the number of lethal equivalents is zero. Hence, about 0.80 lethal equivalents might be due to intergenotypic interactions, and about 0.67 lethal equivalents might be due to fecundity and developmental rate differences. BRITTNACHER (1979) has estimated that differential male mating success can account for 0.57 lethal equivalents in *Drosophila melanogaster*; this fitness component may, therefore, be a major contributor to net fitness differences observed in competition.

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APPENDIX

Let the estimated rates of population growth $\lambda_{N^*}{}^{(i,i)} = X_i$ and $\lambda_{N^*}{}^{(i,j)} = Y$. Set $W_i = (X_i/Y)^3$, $\mathrm{E}(X_i) = \mu_{X_i}$ and $\mathrm{E}(Y) = \mu_Y$. Expanding W_i in a Taylor series about (μ_{X_i}, μ_Y) and dropping all terms of second order and higher, we obtain

$$W_i \simeq (\mu_{X_i}/\mu_Y)^3 - 3(Y-\mu_Y)(\mu_{X_i}/\mu_Y)^2(\mu_{X_i}/\mu_Y^2) + 3(X_i-\mu_{X_i})(\mu_{X_i}/\mu_Y)^2(1/\mu_Y). \quad (1A)$$

Using (1A) we derive an expression for the sampling variance of W_i as

$$\mathrm{E}\{[W_i-\mathrm{E}(W_i)]^2\} = 9(\mu_{X_i}/\mu_Y)^6\left[\frac{\mathrm{Var}(Y)}{\mu_Y^2} + \frac{\mathrm{Var}(X_i)}{\mu_{X_i}^2}\right]. \quad (2A)$$

Let the mean fitness of all homozygous lines be $\bar{W} = \frac{1}{n}\Sigma_i W_i$. Then,

$$\begin{aligned}\mathrm{Var}(\bar{W}) &= \frac{1}{n^2}\mathrm{Var}(\Sigma_i W_i) \\ &= \frac{1}{n^2}\left[\Sigma_i \mathrm{Var}(W_i) + 2\sum_{i=1}^{n-1}\sum_{j=i+1}^{n}\mathrm{Cov}(W_i, W_j)\right] . \qquad (3A)\end{aligned}$$

Since the relative fitness of each line uses the same random variable, Y, in the denominator, the W_i values will not be independent. Thus,

$$\mathrm{Cov}(W_i, W_j) = \mathrm{E}\{[W_i - \mathrm{E}(W_i)]\,[W_j - \mathrm{E}(W_j)]\} \simeq 9\mathrm{Var}(Y)\frac{\mu_{X_i}^3 \mu_{X_j}^3}{\mu_Y^8} , \qquad (4A)$$

assuming $\mathrm{Cov}(Y, X_j) = \mathrm{Cov}(X_i, X_j) = 0$. Substituting (2A) and (4A) into (3A), we obtain the final expression:

$$\begin{aligned}\mathrm{Var}(\bar{W}) \simeq \frac{1}{n^2}\Bigg\{\frac{9}{\mu_Y^6}\Bigg[\frac{\mathrm{Var}(Y)}{\mu_Y^2}\Sigma_i \mu_{X_i}^6 + \Sigma_i \mathrm{Var}(X_i)\mu_{X_i}^4\Bigg] \\ + \Bigg(\frac{18\mathrm{Var}(Y)}{\mu_Y^8}\sum_{i=1}^{n-1}\sum_{j=i+1}^{n}\mu_{X_i}^3 \mu_{X_j}^3\Bigg)\Bigg\} .\end{aligned}$$

In practice, we estimate Var $(\bar{W})$ by replacing the population quantities $\mathrm{Var}(Y)$, μ_Y, etc., by their sample analogs $\hat{\mathrm{Var}}(Y)$, Y, *etc.*