

THE EFFECTS OF r- AND K-SELECTION ON COMPONENTS OF VARIANCE FOR TWO QUANTITATIVE TRAITS

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ABSTRACT

The genetic and environmental components of variance for two quantitative characters were measured in the descendants of *Drosophila melanogaster* populations which had been grown for several generations at densities of 100, 200, 300, and 400 eggs per vial. Populations subject to intermediate densities had a greater proportion of phenotypic variance available for selection than populations from either extreme. Selection on either character would be least effective under pure r-selection, a frequent attribute of selection programs.

MARGALEF (1958) suggested that the genotypes selected for reproductive rate in the early stages of succession will differ from the genotypes selected for efficiency in utilization of scarce resources in later stages of succession. MACARTHUR and WILSON (1967) called selection for reproductive rate "r-selection" and selection for efficiency in resource utilization "K-selection." Some genetic consequences of the two types of selection were explored with respect to allele frequency at a single locus by KING and ANDERSON (1971). But nearly all characters of practical interest are controlled by the combined effects of alleles at many loci and influenced to some extent by the environment as well. We have therefore chosen to observe the effects of r- and K-selection on two quantitative traits in experimental populations.

We subjected larvae of *Drosophila melanogaster* to four levels of crowding: 100, 200, 300, and 400 eggs per vial. Under conditions of 100 eggs per vial, all the viable larvae formed adults. The likelihood of an individual of the previous generation being represented by offspring was proportional to the number of fertile eggs laid per female, or the number of inseminations per male (high r), since eggs were transferred without regard to genotype. Under conditions of successively higher densities, fewer of the larvae survived the competition for food to emerge as adults. The phenotypes favored at higher densities should be those which were better at exploiting a limited environment (high K). Four selection lines were established, one for each density. Each line was subjected to selection every second generation, with alternate generations being grown in non-competitive conditions (r-selection) so that high-density lines could recover from the stress of food limitation so the different levels of selection would be operating on a comparable group of eggs in each selective generation. The only differences among the selection lines were produced in the selected generations where the

developing larvae were subjected to various degrees of K-selection. The crowded lines were therefore subject to alternate r- and K-selection while the uncrowded lines were subject to continuous r-selection.

Following the fifth generation of selection and the fifth generation in a common, non-competitive environment, estimates were made of the genetic parameters involved in the inheritance of sternopleural bristle number and wing length. These characters were chosen for ease of measurement rather than for any interest in bristle number and wing length as such, in the hope that both would respond similarly to the selective regimes involved in the experiment and thus provide a basis for generalization. The response to crowding of descendants of the selected populations was also measured, providing evidence that populations subject to higher densities produce a greater biomass from a limiting amount of food. The entire experiment was repeated on an independent sample of flies, but both experiments had to be combined in analysis in order to provide statistically significant differences.

MATERIALS AND METHODS

The flies used in each of the two experiments were descended from at least ten inseminated *Drosophila melanogaster* females caught near Chapel Hill in woods where over-ripe fruit was discarded by nearby roadside vendors. The first set of flies was captured in June, 1969, and maintained in the laboratory for about five months before the experiment was initiated. The second set of flies was captured in June 1970 and the first selection was begun one generation later. MITTLER and BENNETT's (1962) medium was used throughout, and the flies were always maintained in a 25° constant temperature incubator with light and a fan.

We began each experiment by distributing eggs among vials at different densities. There were 8 ml of food per vial. 400 eggs were placed in each of two vials, 300 in two vials, 200 in two vials, and 100 in each of four vials. The flies emerging from these vials were treated as four selection lines, one for each density. Table 1 shows the effect of increasing density on emergence and on the weight of emerging males, averaged over the whole experiment. The flies emerging from the more crowded vials were considerably smaller than the uncrowded flies, and laid many fewer eggs than the uncrowded flies. The second generation was therefore raised in uncrowded circumstances. Four hundred eggs were collected from the flies which emerged in each selection lines and 200 were placed in each of two bottles, with 50 ml of food. There was no crowding in these bottles; an average of 76% emerged at an average weight of .89 mg per male. The flies emerging from these uncrowded bottles were collected as virgins. A few days after emergence was complete, males from each selection line were mixed with females of that line, and their eggs were collected over two- or three-hour intervals so that all the eggs in each vial were nearly the same age. Again there were four vials of 100 eggs each and two vials of 200, 300, and 400 eggs each.

TABLE 1
Effects of K-selection procedure

Eggs per vial	Percent emerging	Competitive mortality	Weight of males, mg.	Weight decrease
100	75	..	.81	..
200	69	9%	.77	5%
300	59	22%	.70	15%
400	52	30%	.63	23%

After the relaxed generation following the fifth generation of selection (the ninth generation of the experiment), the sternopleural bristle numbers of males and virgin females were counted and twenty pair matings were made at random. After four or five days, the parents were removed from the vials and their wings mounted on slides for later measurement. A profile projector (Ehrenreich Photo-Optical Industries LP-2) was used to magnify the wings fifty-fold, so they could be measured with a centimeter rule to the closest half-centimeter. The measure used was the distance from the intersection of the anterior crossvein with the fourth longitudinal vein to the intersection of the third longitudinal vein with the marginal vein. Twelve days after the matings, the bristle numbers of five male and five female progeny from each mating were counted, and single wings from three males and three females from each mating were mounted for later measurement. Four replicate sets of twenty matings were made for each selection line in each experiment, providing eight estimates of each parameter.

From the bristle and wing measurements of parents and offspring, we were able to estimate three variance components for each set of matings. The additive genetic variance was estimated as twice the covariance of offspring and midparent. The component of variance due to differences between right and left sides of individual flies was estimated from the parent flies alone. This has been called asymmetry variance, but we follow REEVE (1960) in calling it "chance variance." The chance variance was calculated as the variation of right and left sides about their mean. As a component of variance it contributes only half this value to the total phenotypic variance, since the values for each fly were based on the average of both sides. Means and standard errors of variance components were calculated under the square root transformation, which makes the distribution of estimates more nearly normal. Estimates of the additive genetic variance (from comparison of parents and offspring) and chance variance (within parents) were subtracted from the total phenotypic variance of the parent flies to provide an estimate of the remaining components of variance, primarily non-additive genetic variance and environmental variance, in the parents.

The flies which were not used for estimating components of variance were mated at random to produce eggs for testing response to crowding for each selection line. Four hundred eggs were again collected during a three- or four-hour period after mating and placed in a vial with 8 ml of food. The adult flies which emerged were counted and the males weighed. An estimate of the biomass produced in each vial was obtained by multiplying the number of flies emerging by the average weight of male flies.

RESULTS

Means and estimated components of variance for the four selection lines are set out in Tables 2 and 3. Inspection of the composition of the total phenotypic variance (V_p) graphically (Figures 1 and 2) shows no striking similarities. Some-

TABLE 2

Bristle number: components of variance and means

	Selection lines				s.e.*
	100	200	300	400	
Additive genetic variance	1.19	2.09	2.42	1.26	.46
Environmental and non-additive genetic variance	.65	.76	1.09	1.47	.26
Chance variance	.73	.85	.89	.84	.06
Heritability	.53	.63	.57	.41	.077
Mean	28.3	28.9	29.8	29.4	0.3

* Average standard error, based on 28 degrees of freedom.

TABLE 3

Wing lengths: components of variance and means

	100	200	Selection lines 300	400	s.e.*
Additive genetic variance	131	147	192	126	34
Environmental and non-additive genetic variance	150	95	109	151	18
Chance variance	22	24	20	23	2.5
Heritability	.45	.57	.60	.43	.064
Mean (2×10^{-3} mm)	728	728	731	743	3.6

* Average standard error, based on 28 degrees of freedom.

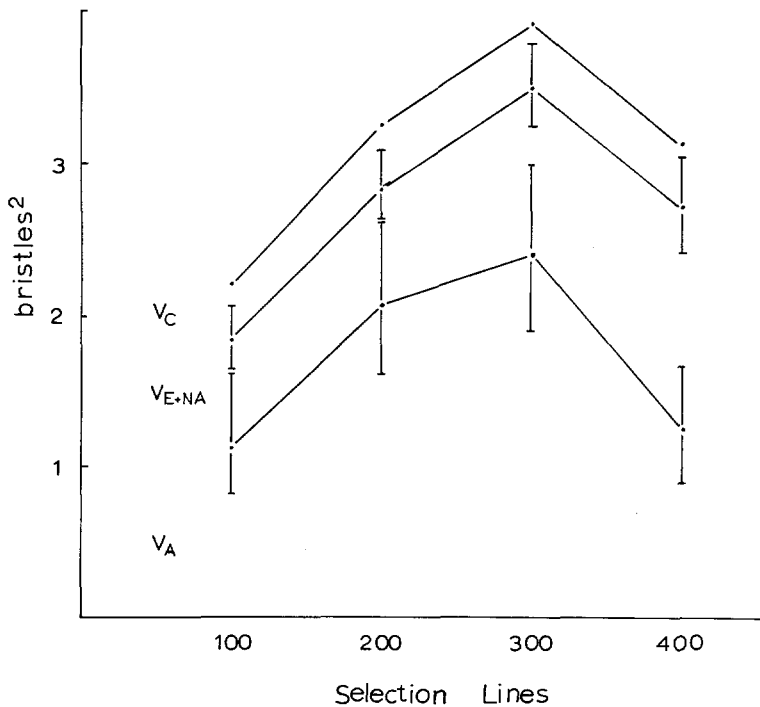


FIGURE 1.—Components of variance for sternopleural bristle number, as a function of K-selection density. The components are additive genetic variance (V_A) between abscissa and lower line, environmental and non-additive genetic variance (V_{E+NA}) between lower and middle lines, and chance variance (V_C) between middle and upper line. The phenotypic variance is roughly equal to the sum of estimates of individual components, here represented by the upper line. Standard errors of the first two components of variance are indicated.

what surprisingly, the additive genetic variance for bristle number is nearly twice as great in the 200- and 300-egg lines as in the 100- and 400-egg lines. Student's t for this difference is 2.25, significant at the 5% level. Conversely, the nonadditive genetic and environmental component of variance (V_{E+NA}) for wing length is significantly less in the 200- and 300-egg lines than in the 100- and

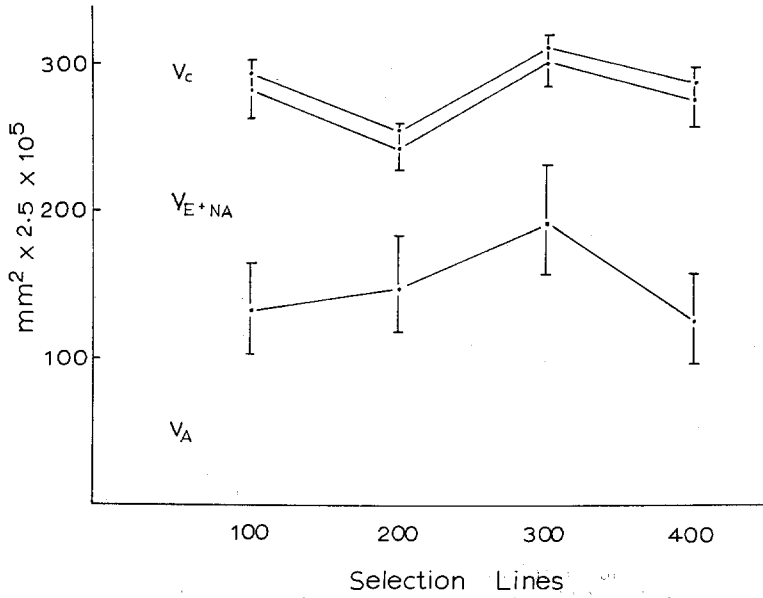


FIGURE 2.—Components of variance for wing length, as a function of K-selection density. Arrangement and abbreviations as in Figure 1.

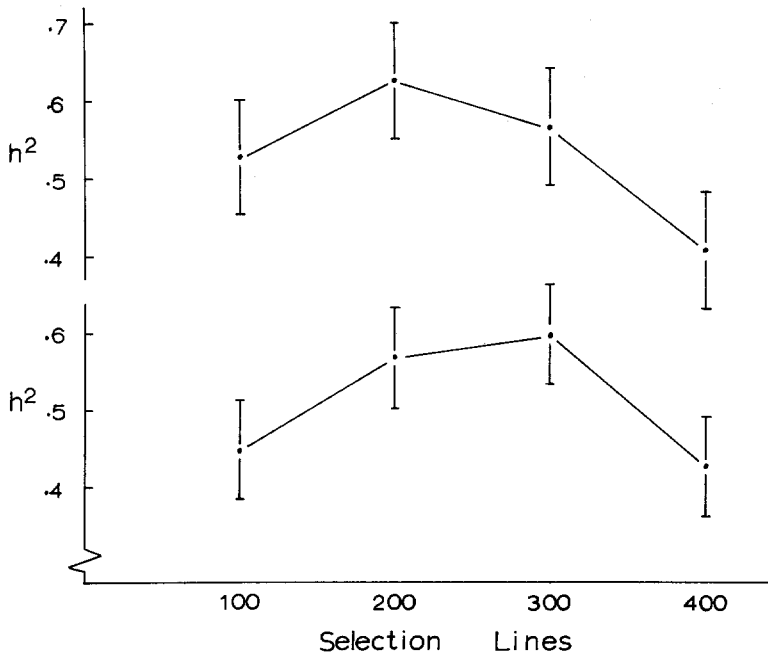


FIGURE 3.—Heritability as a function of K-selection density. Upper line, sternopleural bristle number. Lower line, wing length. Standard errors of the estimates are indicated.

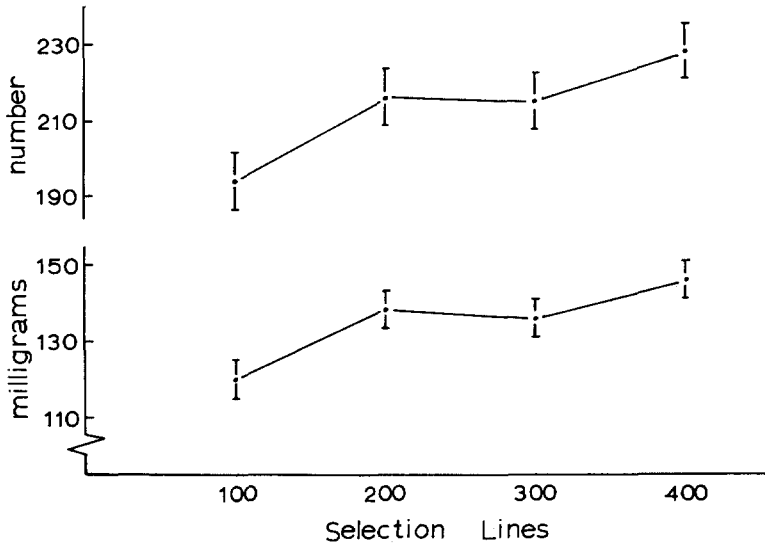


FIGURE 4.—Response to a density of 400 eggs per vial, as a function of K-selection density. Upper line, total number of flies emerging as adults. Lower line, biomass of emerging flies in milligrams. Standard errors of the estimates are indicated.

400-egg lines ($t = 2.62$). This suggests that the heritability may vary similarly in the two characters as a function of larval density.

Figure 3 shows that the intermediate densities do have higher heritability for both characters than the extreme densities, the difference being significant in the case of wing length ($t = 2.27$).

Figure 4 shows that the selection lines did respond to differential selection for ability to utilize a limiting resource. When tested after a generation in a common environment, the number of individuals emerging and the biomass produced under a density of 400 eggs per vial is found to be highest in the 400-egg selection line and lowest in the 100-egg selection line.

DISCUSSION

The differences observed in this study are most likely genetic, since the measurements were made on flies raised in a common environment. There is, nevertheless, the possibility that environmentally-produced effects were carried over from previous K-selection generations.

It appears that pure r-selection and intense K-selection both reduce the proportion of additive genetic variance relative to the total phenotypic variance. Were selection for bristle number or wing length to be made on the experimental populations, the heritability estimates indicate that more progress would be made (for a given intensity of selection) in populations with a history of mild r- and K-selection than in populations with a history of strong r- or K-selection. This result implies further that genetic flexibility is maintained when two forms of selection are pitted against one another, thus preventing a strong directional selection response.

While selection for bristle number or wing length is less efficient at high densities, it may well be more effective because the greater selection intensity possible with higher numbers of eggs offsets the lower heritability. Selection would be least effective, under the conditions of this experiment, for populations subject only to r-selection. Simultaneous r-selection is nevertheless a frequent feature of selection programs. For instance, densities are often controlled by culling some number of individuals without regard for numbers per parent. This practice is a form of r-selection, since the likelihood of individuals leaving offspring is proportional to their fecundity.

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