RELATIVE FITNESS OF POPULATIONS OF *DROSOPHILA SERRATA* AND *DROSOPHILA BIRCHII*[1]

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DOBZHANSKY (1955), in a discussion of evolutionary processes in Mendelian populations, has pointed out that "the work in this field is severely handicapped by lack of reliable methods of comparing the fitness of populations and, of course, by the lack of clarity of the concept of fitness itself." Fitness is a property that can be attributed to an individual, a genotype, a Mendelian population, a species or a higher biological category. At any of these different levels of integration of the biological world, the word "fitness" may be used meaning widely different things, but in all instances "fitness must refer to the ability of an organism to leave surviving offspring" (LERNER 1954).

The fitness of an individual is measured by the mean number of offspring in the next generation (PENROSE 1949; KNIGHT and ROBERTSON 1957; REED 1959). For a higher biological category, fitness may be defined in terms of the descendants left after one or many generations. THODAY (1953, 1958) defines fitness as the probability that a "contemporary group of individuals" will leave descendants after a given long period of time, such as 10^8 years. This kind of definition, whatever its theoretical interest, does not lend itself to an experimental estimation of fitness.

Several attempts have been made to define the fitness of a genotype or of a Mendelian population in quantitative terms, so that it may be experimentally approached. These definitions are given in relation to a certain environment. FISHER (1930) has defined the fitness of a genotype as the "expectation of offspring," that is the contribution of the individuals carrying that genotype to the next generation, and defined the "Malthusian parameter" as the natural logarithm of that quantity. Related concepts are the "intrademic selective value" of a population as defined by WRIGHT (1955) and the "adaptive value" used by population geneticists in their experimental studies (WRIGHT 1931; HALDANE 1932) which involve the relative fitness of different genotypes.

The fitness of a genotype or of a Mendelian population has been frequently discussed in terms of the various components of the life cycle, such as fecundity, hatchability, rate of development of immature stages, differential mortality of immature stages, sterility, sexual activity of adults, longevity of adults, etc. It should be noted that all these are components of a single value of fitness and not alternative estimates of it, as some workers seem to imply. Attempts have been made (e.g. WALLACE 1948) to combine these components into the fitness in the

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sense of WRIGHT, but one can never be sure that all the components have been included.

There have been other attempts to measure the fitness of a Mendelian population. One of them is the "innate rate of increase" (ANDREWARTHA and BIRCH 1954) used by BIRCH, DOBZHANSKY, ELLIOT and LEWONTIN (1963), but this refers to an ideal situation with no competition. CARSON (1957, 1958) proposed the use of *biomass* (the wet weight of hatching adults) produced per unit time in a population at equilibrium with its environment. Other things being equal, a population can be considered better fit than another in reference to a certain environment if the first one is able to exploit better the available resources of space and energy of the environment to produce a greater amount of living matter. In a later paper CARSON (1961a) suggested the use of the average size of a population, when equilibrated over many generations by natural selection in a certain environment, as a measure of the performance or fitness. He referred to this collective measure as the "relative population fitness."

In the experiments to be reported in this paper, a set of environmental conditions has been chosen in which to study the relative performance of several populations of Drosophila coming from geographically widely separated natural habitats. Definite amounts of food and space are provided at fixed intervals, so that the ability of the population to exploit the environmental resources can be measured. The parameters used for this measurement are the biomass, the number of adults produced per food unit, and the average size of the total population. Two temperatures are used throughout the experiment, 25° and 19°C. Furthermore, all possible hybrid populations between pairs of the strains used were made. From this, it was expected to gain some insight on the relative importance of genetic coadaptation and genetic variability in the processes of evolutionary adaptation to the environment.

MATERIALS AND METHODS

Two sibling species, *Drosophila serrata* and *D. birchii* (AYALA 1965), were used. Each strain was derived from several impregnated females collected with banana bait, and had been maintained in the laboratory by mass culture for 1 to 3 years before the beginning of the present experiments. The strains were as follows:

D. serrata. A population was collected from the southernmost known part of the distribution of the species, some 130 miles north of Sydney, at Bulahdelah, New South Wales, Australia (referred to as s-Sydney). Some 1600 miles north of Sydney, the next population was collected near Cooktown, on the East Coast of the Cape York Peninsula, Queensland, Australia (referred to as s-Cooktown). The third population was collected near Popondetta, New Guinea (referred to as s-Popondetta).

D. birchii. Two strains were used. The first one was collected some 100 miles south of Cooktown, at the Crystal Cascade, near Cairns, Queensland (referred to as b-Cairns). This is the only locality of Australia where the species *D. birchii* has been found. The other population was collected in the same locality as the third strain of *D. serrata,* near Popondetta, New Guinea (referred to as b-Popondetta).

The strains s-Sydney and b-Cairns were obtained from PROFESSOR DOBZHANSKY; the other three strains were provided by the Genetics Foundation of the University of Texas and had been collected by DR. M. WASSERMAN. The experimental procedure of maintaining populations is a variant of the technique of BUZZATTI-TRAVERSO (1955) and CARSON (1958), modified by DOBZHANSKY and PAVLOVSKY (1961). The adult flies are maintained in a ½-pint milk bottle, with a ¾-inch high layer of Spassky's cream of wheat-molasses medium. A double piece of toweling paper, 2 × 7 inches, is partially pressed into the medium to provide an extended surface for adult flies and for pupation. No yeast was added to the medium since some of the strains of these species perform better without addition of live yeast.

At 25°C the adult flies are allowed to oviposit in a bottle with fresh medium for two days. They are then transferred, without etherization, into a bottle with fresh food for another two days, after which period they are transferred, again without etherization, to a new bottle where they remain for three days. In this way, a weekly cycle is completed. The adult flies are always kept in a constant temperature room at 25 ± 0.5°C. The bottles with the eggs deposited in them are placed at the same temperature until F_1 flies appear. When emergence begins, the young flies are collected three times a week, on the same days on which the adult population is transferred to a new bottle with fresh food. These young flies are etherized, counted, and added to the adult population immediately before its transfer to the new bottle. The adult ovipositing flies are thus always in a single bottle with fresh food, while some 14 bottles in each series contain eggs, larvae, pupae and newly hatched adults. Every second week, after the first two-day interval, the adult population, before adding the new-born flies of that period, is etherized, counted, weighed and transferred to a fresh bottle, and the new-born flies to be added to the adult population are also weighed after being counted. The weighings are made on a chemical balance with a precision of 0.1 mg. Eclosion of flies begins around the 12th day after oviposition, and mass eclosion between the 13th and the 15th day, and thereafter falls off rapidly. The bottles are discarded on the 28th day.

At 19°C transfers of adult flies and counts of newborn flies are performed twice a week, after alternating periods of three and four days. Counting and weighing of the adult population takes place every two weeks, after a four-day period. All bottles are kept in a constant temperature room at 19 ± 0.5°C. Eclosion starts around the 16th to 17th day, and mass eclosion between the 20th to 24th day. The bottles are discarded after the 38th day.

All populations at both temperatures were started with 150 pairs of founder flies, raised in mass culture bottles from stocks which had a laboratory history of 1 to 3 years at 25°C. Under the conditions of the experiment, the adult populations build up rapidly to a maximum size, and relatively soon come to an equilibrium with the sources of food and space in such a way that the periodic additions from the old bottles approximately equal the amount of dead flies during the same period. After a few weeks the adult population grows to a tremendous number so that the flies become overcrowded and interfere with each other, largely mechanically. The experiment was designed so as to obtain both this strong competition between the adults and a strong natural selection taking place during the immature stages of development.

D. birchii, and to a lesser extent *D. serrata*, are highly sensitive to ether. The etherization was therefore rigidly controlled. Flies were introduced into a chamber free of ether; ether was then applied for 75 seconds, and the flies extracted for counting or weighing. This was enough to maintain the flies etherized for some 3 to 5 minutes.

The counting of newborn flies was always done individually. For the adult population the same was done during the first 20 weeks of the experiment. Thereafter a sample of 300 to 400 flies was counted and weighed, and the rest of the population was weighed, the total number being estimated by a simple proportion.

A list of the 18 populations used in the experiment is given in Table 1.

RESULTS

Production and population size of the strains at 25°C: At this temperature the adult ovipositing flies were transferred three times per week to fresh cultures. Eclosion started during the second week, and rose very rapidly until about the eighth week, when it reached an equilibrium. For the remaining 43 weeks of the

TABLE 1

List and description of the experimental populations

Experimental population number	Geographical origin	Species	Temperature	Start	End
1	Sydney	*D. serrata*	25°C	June 1963	June 1964
2	Cooktown	*D. serrata*	25°C	June 1963	June 1964
3	Popondetta	*D. serrata*	25°C	June 1963	June 1964
4	Cairns	*D. birchii*	25°C	June 1963	March 1964
5	Popondetta	*D. birchii*	25°C	June 1963	June 1964
6	Sydney	*D. serrata*	19°C	June 1963	June 1964
7	Cooktown	*D. serrata*	19°C	June 1963	June 1964
8	Popondetta	*D. serrata*	19°C	June 1963	June 1964
9	Cairns	*D. birchii*	19°C	June 1963	June 1964
10	Popondetta	*D. birchii*	19°C	June 1963	June 1964
11	Sydney × Cooktown	*D. serrata*	25°C	July 1963	June 1964
12	Sydney × Popondetta	*D. serrata*	25°C	July 1963	June 1964
13	Cooktown × Popondetta	*D. serrata*	25°C	July 1963	June 1964
14	Cairns × Popondetta	*D. birchii*	25°C	July 1963	June 1964
15	Sydney × Cooktown	*D. serrata*	19°C	July 1963	June 1964
16	Sydney × Popondetta	*D. serrata*	19°C	July 1963	June 1964
17	Cooktown × Popondetta	*D. serrata*	19°C	July 1963	June 1964
18	Cairns × Popondetta	*D. birchii*	19°C	July 1963	June 1964

experiment there were somewhat irregular oscillations but the mean number of flies produced per week remained at about the same level. Weekly production is presented in graphic form in Figure 1.

Figure 2 presents the total population counts. The adult population increased very rapidly from the original 300 individuals, owing to the continuous addition of newly hatched flies. At the end of the eighth week an equilibrium was reached to be maintained with irregular oscillations for the following 300 days until the end of the experiment. The increase in population size was rather gradual. Unlike the *D. pseudoobscura* populations studied by DOBZHANSKY and PAVLOVSKY (1961), there was no population "explosion" followed by a "crash" before reaching equilibrium.

Table 2 presents the means after equilibrium and their standard errors for the following parameters: number of flies produced per food unit, biomass produced per food unit; individual weight of newborn flies; number of flies in the adult population; individual weight of adult flies. The individual weights are calculated from the collective weighings. The mean number of flies and mean biomass

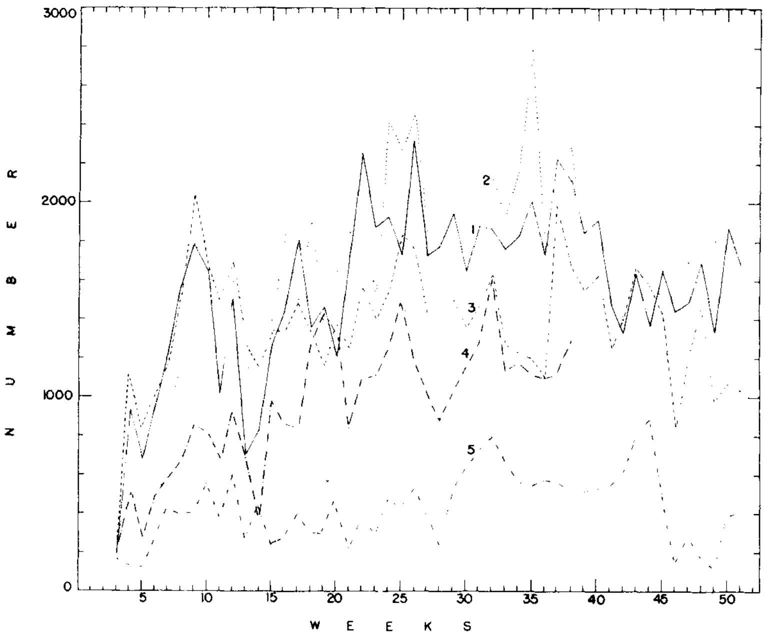

FIGURE 1.—Number of flies produced per week at 25°C by three populations of *Drosophila serrata* and two of *D. birchii*. No. 1 is the population s-Sydney; 2, s-Cooktown; 3, s-Popondetta; 4, b-Cairns; 5, b-Popondetta.

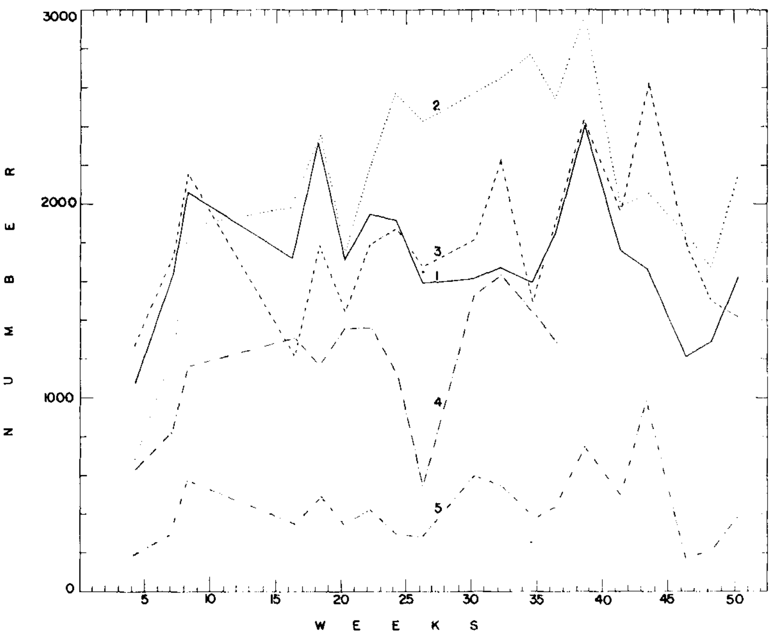

FIGURE 2.—Size at 25° of three experimental populations of *Drosophila serrata* and two of *D. birchii*. No. 1 is the population s-Sydney; 2, s-Cooktown; 3, s-Popondetta; 4, b-Cairns; 5, b-Popondetta.

TABLE 2

Mean production and population size after equilibrium in three experimental populations of D. serrata *and two of* D. birchii *at 25°C*

Population	Individuals produced per food unit	Biomass produced per food unit (mg)	Newborn weight (mg)	Population size	Adult weight (mg)
s-Sydney	$n = 44$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
	550 ± 17	329.0 ± 9.9	0.574 ± 0.011	1782 ± 76	0.715 ± 0.010
s-Cooktown	$n = 40$	$n = 16$	$n = 16$	$n = 16$	$n = 16$
	568 ± 20	334.1 ± 13.2	0.566 ± 0.011	2221 ± 80	0.669 ± 0.007
s-Popondetta	$n = 44$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
	477 ± 13	250.5 ± 7.8	0.531 ± 0.008	1828 ± 90	0.648 ± 0.008
b-Cairns	$n = 31$	$n = 12$	$n = 12$	$n = 12$	$n = 12$
	351 ± 16	199.2 ± 11.0	0.532 ± 0.014	1262 ± 83	0.647 ± 0.012
b-Popondetta	$n = 44$	$n = 16$	$n = 16$	$n = 17$	$n = 17$
	152 ± 9	80.2 ± 6.7	0.506 ± 0.008	469 ± 49	0.596 ± 0.010

n, number of measurements after equilibrium.

per food unit are obtained by dividing the corresponding weekly means by three. The individual weight is greater for the adult flies in the population than for the newly hatched flies at the time they are added. The original data show that this increase in weight is more pronounced for females than for males.

The three populations of *D. serrata* behave similarly, with weekly production of about 1500 individuals, or 500 per food unit, at equilibrium. The mean production of the s-Cooktown population is the highest, very closely followed by s-Sydney, s-Popondetta being the lowest of the three. For adult population size the population s-Cooktown is again the highest, with the s-Sydney and s-Popondetta populations at about the same level. s-Sydney occupies a relatively lower level when the total population is considered than when the weekly production is examined. This must be due to a shorter average longevity of the s-Sydney adult flies (see below). Of the *D. birchii* strains, b-Popondetta is lower and b-Cairns higher, but still considerably below any of the *D. serrata* populations for both measures. The b-Cairns population was discarded after the 38th week owing to a contamination. The differences in mean number of flies produced per food unit and in mean population size between the populations are statistically highly significant ($P < .001$) for all possible comparisons between strains, except for the pair s-Sydney/s-Cooktown if productivity is compared ($P > .40$) and the pair s-Sydney/s-Popondetta if total size is considered ($P > .60$).

The different ability of the strains to exploit the experimental environment is quite striking. But the fact that the populations build up to such tremendous numbers—about 2000 flies living in a ½-pint bottle—requires some explanation. DOBZHANSKY and PAVLOVSKY had used a similar technique with *D. pseudoobscura*, but their populations reached equilibria with a population size of about 300 flies. The imagoes of *D. serrata* and *D. birchii* are less active in crowded cultures than those of most other species of Drosophila. The flies form several layers over the surface of the culture medium, and they do not move as much

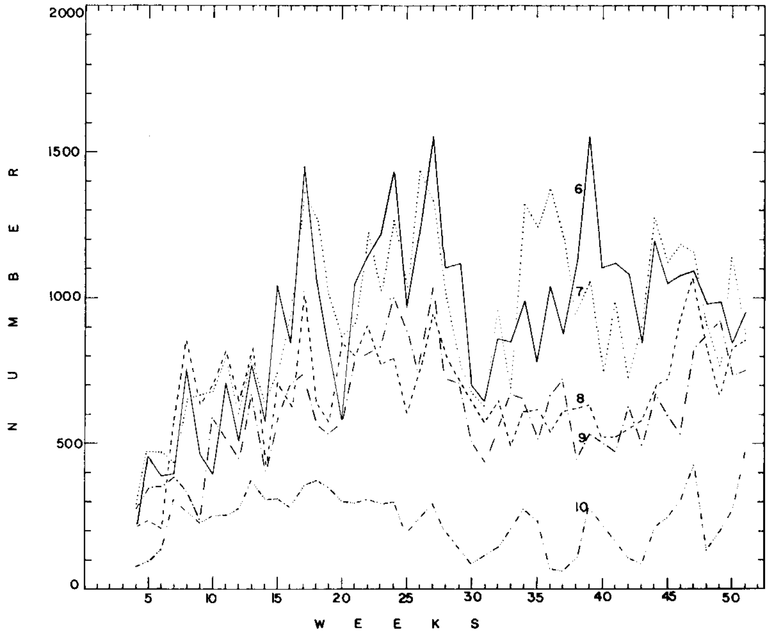

FIGURE 3.—Number of flies produced per week at 19°C by three populations of *Drosophila serrata* and two of *D. birchii*. No. 6 is the population s-Sydney; 7, s-Cooktown; 8, s-Popondetta; 9, b-Cairns; 10, b-Popondetta.

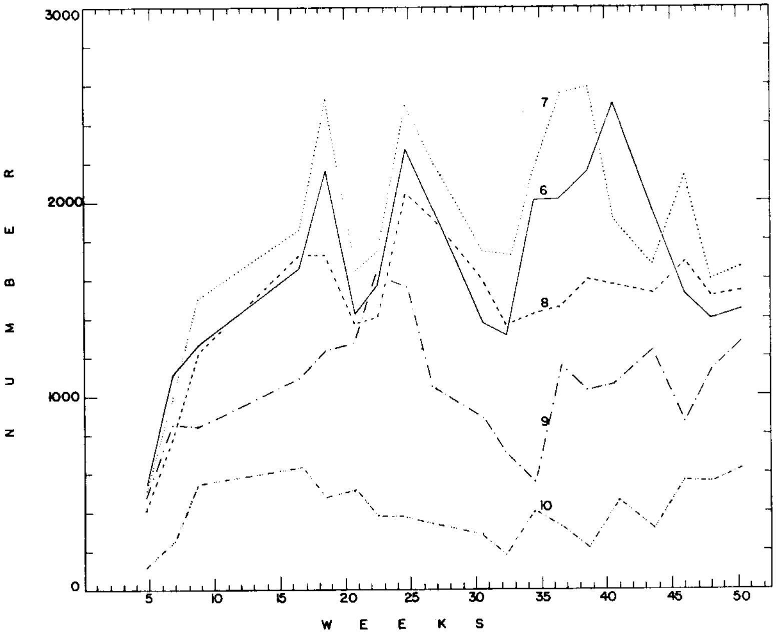

FIGURE 4.—Size at 19°C of three experimental populations of *Drosophila serrata* and two of *D. birchii*. No. 6 is the population s-Sydney; 7, s-Cooktown; 8, s-Popondetta; 9, b-Cairns; 10, b-Popondetta.

as do *D. pseudoobscura* flies (DOBZHANSKY and PAVLOVSKY 1961) under similar conditions. Individuals move slowly in and out of the mass of flies towards the surface of the food in order to feed and to lay eggs. Little activity can be observed in the bottles, except for some walking and mating, usually taking place on the towel paper.

Production and population size of the strains of 19°C: At 19°C the adult ovipositing flies were transferred twice per week to fresh cultures. Production (number of flies hatched and their biomass) increased more slowly than at 25°C, and reached an equilibrium between the 8th and the 15th week. Thereafter the production oscillated around the same level in a rather haphazard fashion, until the end of the experiment. The number of flies produced per week is shown graphically in Figure 3. The total adult population is shown in Figure 4; it reached equilibrium between the 8th and the 16th week. Table 3 presents for the five populations at 19°C the same values as Table 2. The population s-Cooktown reached equilibrium at the highest level followed by s-Sydney while the s-Popondetta population is relatively lower, reaching an equilibrium at a slightly higher level than b-Cairns. b-Popondetta occupies the lowest level of equilibrium and is most irregular. The relatively low level of equilibrium of s-Popondetta at 19°C may be due to the fact that this is the northernmost strain used in this experiment, and is probably adapted to a strictly tropical climate. The differences in mean number of flies produced between populations are highly significant ($P < .001$) except for the pairs s-Sydney/s-Cooktown ($P > .90$) and s-Popondetta/b-Cairns ($P > .10$). The differences in total population size are significant for all possible comparisons.

Production and total size of the hybrid populations at 25°C: Hybrid populations were started by mating the two parental strains in the two possible directions. F_1 individuals from both crosses were taken in equal numbers in order to start the populations with 150 pairs of flies. The population dynamics of the hybrids are

TABLE 3

Mean production and population size after equilibrium in three experimental populations of D. serrata and two of D. birchii at 19°C

Population	Individuals produced per food unit	Biomass produced per food unit (mg)	Newborn weight (mg)	Population size	Adult weight (mg)
s-Sydney	$n = 44$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
	483 ± 13	319.7 ± 13.0	0.643 ± 0.010	1803 ± 87	0.739 ± 0.008
s-Cooktown	$n = 44$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
	486 ± 12	297.7 ± 12.7	0.542 ± 0.012	2017 ± 84	0.671 ± 0.012
s-Popondetta	$n = 44$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
	357 ± 8	199.7 ± 10.9	0.552 ± 0.008	1580 ± 52	0.688 ± 0.007
b-Cairns	$n = 44$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
	324 ± 11	200.7 ± 13.1	0.600 ± 0.009	1091 ± 66	0.719 ± 0.005
b-Popondetta	$n = 44$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
	121 ± 5	68.9 ± 6.3	0.581 ± 0.013	428 ± 33	0.668 ± 0.015

n, number of measurements after equilibrium.

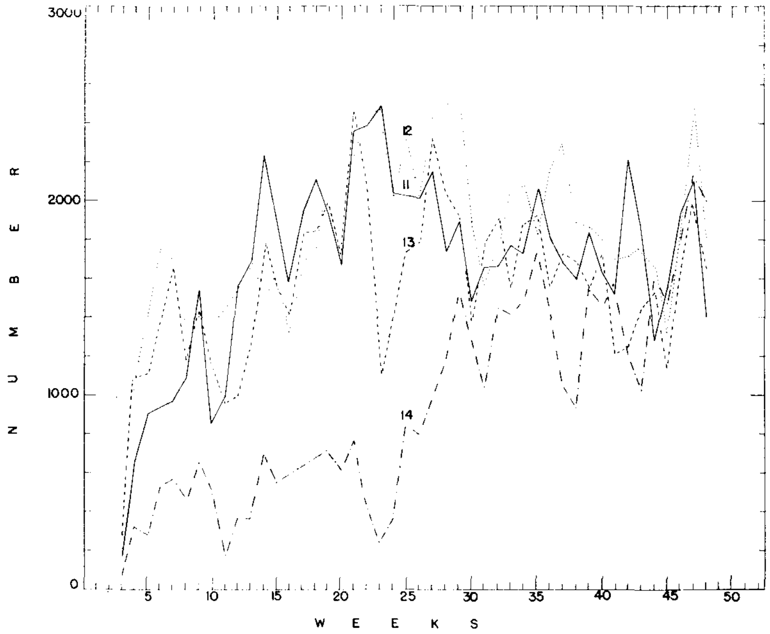

FIGURE 5.—Number of flies produced per week at 25°C by four hybrid populations of Drosophila. No. 11 is the population s-Sydney × s-Cooktown; 12, s-Sydney × s-Popondetta; 13, s-Cooktown × s-Popondetta; 14, b-Cairns × b-Popondetta.

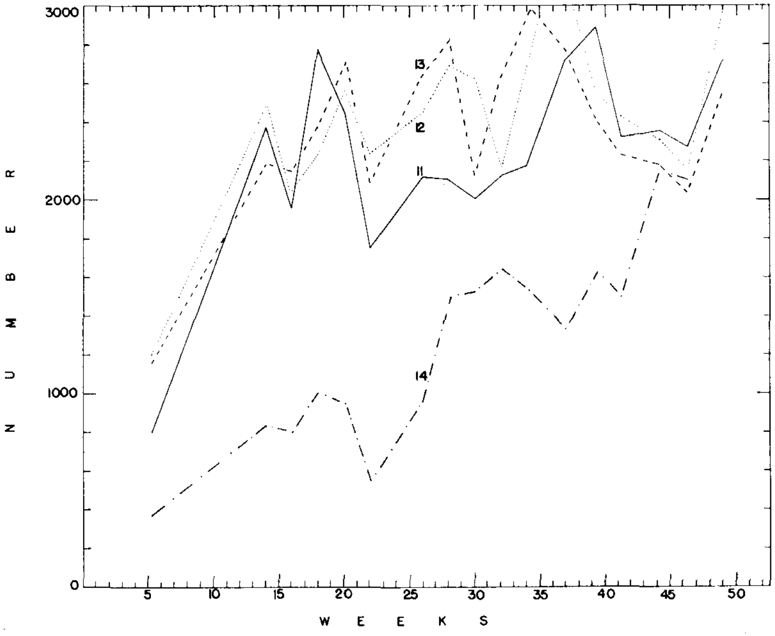

FIGURE 6.—Size at 25°C of four hybrid populations of Drosophila. No. 11 is the population s-Sydney × s-Cooktown; 12, s-Sydney × s-Popondetta; 13, s-Cooktown × s-Popondetta; 14, b-Cairns × b-Popondetta.

similar, in general, to the population dynamics of the parental strains. An equilibrium is reached after a few weeks and the populations oscillate around it thereafter. Figure 5 shows graphically the number of flies produced per week, and Figure 6, the counts of total number of adult flies during the complete experiment. For the *D. serrata* hybrid populations the level of equilibrium is, in general, slightly higher than for the parental strains. The *D. birchii* hybrid population was at the beginning intermediate between the two parental strains, and closer to the lower one, b-Popondetta. Between weeks 23 and 29 a sharp improvement occurred, and production rose to a level almost three times higher than before that period. Table 4 presents the mean values of the four hybrid populations from weeks 8 to 48. Population 14, the *D. birchii* hybrid, appears three times in the table. The first means are calculated for the total experimental period, from weeks 8 to 48. The other two entries, b-Cairns × b-Popondetta (1) and b-Cairns × b-Popondetta (2) give the means calculated for weeks 8 to 26 and 27 to 48 respectively. The differences between the two periods are statistically significant ($P < .001$) for all measures.

The hybrid *D. serrata* populations are superior to the parental strains. The differences are statistically significant in all cases except for the comparison of the s-Sydney/s-Cooktown hybrid with the s-Cooktown parent.

Production and total size of hybrid populations at 19°C: The situation at 19°C is similar to that at 25°C. The production of the *D. serrata* hybrid populations is slightly higher than that of the parental strains. The *D. birchii* hybrid is intermediate between the two parental strains, but considerably closer to the higher one, namely b-Cairns. Figure 7 presents the number of flies produced per week during the total experimental period, and Figure 8, the total population counts. The mean values from the eighth week to the end of the experiment are given in

TABLE 4

Mean production and population size after equilibrium in three hybrid populations of D. serrata *and one of* D. birchii *at 25°C*

Population	Individuals produced per food unit	Biomass produced per food unit (mg)	Newborn weight (mg)	Population size	Adult weight (mg)
s-Sydney ×	$n = 41$	$n = 16$	$n = 16$	$n = 16$	$n = 16$
s-Cooktown	593 ± 16	341.0 ± 13.2	0.556 ± 0.011	2360 ± 74	0.640 ± 0.008
s-Sydney ×	$n = 41$	$n = 16$	$n = 16$	$n = 16$	$n = 16$
s-Popondetta	622 ± 18	330.4 ± 11.5	0.517 ± 0.009	2541 ± 117	0.597 ± 0.007
s-Cooktown ×	$n = 41$	$n = 16$	$n = 16$	$n = 16$	$n = 16$
s-Popondetta	540 ± 18	307.4 ± 9.5	0.545 ± 0.013	2419 ± 76	0.635 ± 0.010
b-Cairns ×	$n = 41$	$n = 15$	$n = 15$	$n = 15$	$n = 15$
b-Popondetta	342 ± 26	191.1 ± 23.0	0.514 ± 0.014	1331 ± 123	0.622 ± 0.014
b-Cairns ×	$n = 19$	$n = 6$	$n = 6$	$n = 6$	$n = 6$
b-Popondetta (1)	187 ± 14	120.3 ± 34.3	0.561 ± 0.020	845 ± 67	0.681 ± 0.011
b-Cairns ×	$n = 22$	$n = 9$	$n = 9$	$n = 9$	$n = 9$
b-Popondetta (2)	475 ± 23	238.3 ± 12.0	0.483 ± 0.011	1655 ± 96	0.584 ± 0.008

n, number of measurements after equilibrium.

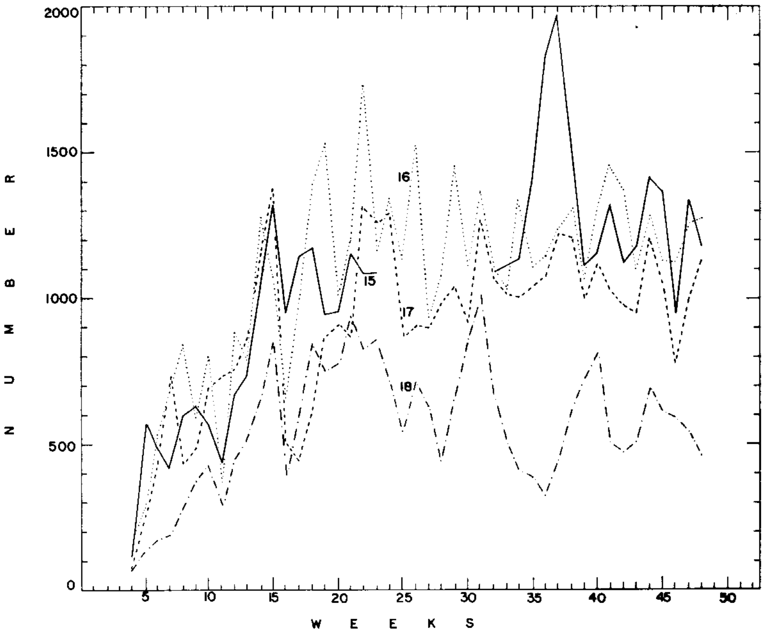

FIGURE 7.—Number of flies produced per week at 19°C by four hybrid populations of Drosophila. No. 15 is the population s-Sydney × s-Cooktown; 16, s-Sydney × s-Popondetta; 17, s-Cooktown × s-Popondetta; 18, b-Cairns × b-Popondetta.

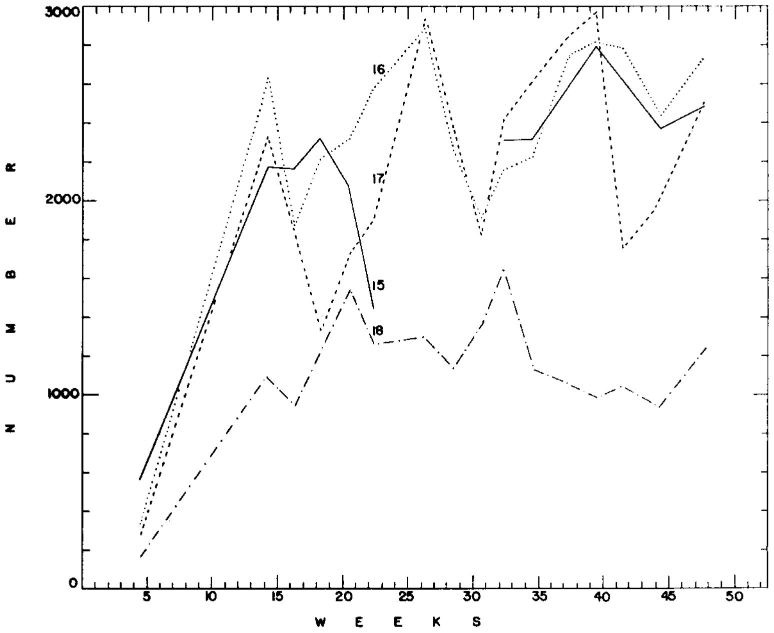

FIGURE 8.—Size at 19°C of four hybrid populations of Drosophila. No. 15 is the population s-Sydney × s-Cooktown; 16, s-Sydney × s-Popondetta; 17, s-Cooktown × s-Popondetta; 18, b-Cairns × b-Popondetta.

TABLE 5

Mean production and population size after equilibrium in three hybrid populations of D. serrata *and one of* D. birchii *at 19°C*

Population	Individuals produced per food unit	Biomass produced per food unit (mg)	Newborn weight (mg)	Population size	Adult weight (mg)
s-Sydney ×	$n = 33$	$n = 12$	$n = 12$	$n = 12$	$n = 12$
s-Cooktown	554 ± 19	376.3 ± 14.1	0.611 ± 0.012	2418 ± 171	0.663 ± 0.012
s-Sydney ×	$n = 41$	$n = 14$	$n = 14$	$n = 14$	$n = 14$
s-Popondetta	572 ± 14	364.7 ± 17.1	0.582 ± 0.011	2448 ± 86	0.666 ± 0.008
s-Cooktown ×	$n = 41$	$n = 15$	$n = 15$	$n = 15$	$n = 15$
s-Popondetta	479 ±12	294.0 ± 12.3	0.590 ± 0.013	2227 ± 172	0.663 ± 0.011
b-Cairns ×	$n = 41$	$n = 15$	$n = 15$	$n = 15$	$n = 15$
b-Popondetta	303 ± 10	186.4 ± 10.9	0.562 ± 0.013	1203 ± 55	0.673 ± 0.006

n, number of measurements after equilibrium.

Table 5. All the hybrid populations of both *D. serrata* and *D. birchii* have larger mean total population values than their parental strains, and the differences are statistically significant except for the comparison of the s-Cooktown × s-Popondetta hybrid and the s-Cooktown parent and the comparison of the *D. birchii* hybrid with the Cairns parent.

Longevity of adult flies: In a population at equilibrium the mean number of births and of deaths per unit time are equal. The mean numbers of the adult flies in the populations, and the mean numbers of the flies born per unit time being known, the mean longevity of the flies in the experimental populations can be calculated. If birth and death both occur continuously at a constant rate, the mean longevity, m, is equal to the mean number of living individuals, N, divided by the mean number born per unit interval of time, B. In the present experiment, the death process may be considered approximately continuous. The birth process, however, is essentially discrete, since "birth" in the present conditions is not the time of biological birth but the time at which the individual enters the population. This takes place after intervals of two or three days at 25°C, and after intervals of three or four days at 19°C. A correction factor is, therefore, necessary to account for this discrete character of births, and $a = N/B$ is only the crude estimate of longevity.

PROFESSOR HOWARD LEVENE has kindly developed a correction formula for the conditions of the present experiment. The correction formula for a situation in which flies are added after three periods of arbitrary length, t_1, t_2, t_3, and with population size counted after the period of length t_3 before adding the newborn flies is, as derived by PROFESSOR LEVENE (personal communication; see also DOBZHANSKY and PAVLOVSKY 1961, Appendix).

$$a = \frac{N}{B} = \frac{t_3 e^{-(t_1+t_2+t_3)/m} + t_1 e^{-(t_2+t_3)/m} + t_2 e^{-t_3/m}}{1 - e^{-(t_1+t_2+t_3)/m}} \tag{1}$$

In the present case, at 25°C, counts of the adult population were made on Wednesday, and the other additions of newborn flies were made on Friday and

Monday. Then $t_1 = 2$ days, $t_2 = 3$ days, $t_3 = 2$ days. Therefore formula (1) becomes:

$$a = \frac{N}{B} = \frac{2e^{-7/m} + 2e^{-5/m} + 3e^{-2/m}}{1 - e^{-7/m}}$$

If arbitrary values of m are chosen, corresponding values of a are obtained from the formula, and $m - a$ can be calculated for each value of a. Several values of m conveniently spaced may be chosen, and the obtained values of $m - a$ can be plotted in a graph as a function of the corresponding a values. Then, for any value of a the corresponding value of $m - a$ may be read from the graph. At 25°C the corrected estimates of longevity, m, range from 7.95 to 10.29, with the correction term, $m - a$, nearly constant.

At 19°C the newborn flies were added twice a week, on Monday and Friday, the counting of the adult flies being done on Friday, after the 4-day period. The correction formula takes the form,

$$a = \frac{4e^{-7/m} + 3e^{-4/m}}{1 - e^{-7/m}}$$

The corrected estimates of longevity, m, at this temperature range from 13.85 to 18.43.

Table 6 lists the values of a, $m - a$, and m. It should be noted that the longevities, as given in the table, are measured from the time the flies are placed in the crowded cultures. On the average, flies when added to the total population are 1.17 days old at 25°C and 1.75 days old at 19°C. It should also be noted that these estimates assume that, in the relatively uncrowded conditions of the culture bottles where the flies are born, the death rate is practically zero, except for the few exceptional flies which die immediately after eclosion. This assumption seems to be safe. The data for two of the populations at each temperature were examined and it was observed that roughly the mean number of flies added after the 2-day periods at 25°C (3-day periods at 19°C) was ⅔ (¾ at 19°C) the mean

TABLE 6

Estimated mean longevity, in days, of the adult flies in the population

Population	Mean longevity at 25°C			Mean longevity at 19°C		
	a	*m—a*	*m*	*a*	*m—a*	*m*
s-Sydney	7.55	0.73	8.28	13.07	2.14	15.21
s-Cooktown	9.14	0.74	9.88	14.51	2.15	16.66
s-Popondetta	8.39	0.73	9.12	15.49	2.16	17.65
b-Cairns	8.36	0.73	9.09	11.73	2.12	13.85
b-Popondetta	7.22	0.73	7.95	12.11	2.13	14.24
s-Sydney × s-Cooktown	9.29	0.74	10.03	15.30	2.16	17.46
s-Sydney × s-Popondetta	9.55	0.74	10.29	15.01	2.15	17.16
s-Cooktown × s-Popondetta	9.30	0.74	10.04	16.26	2.17	18.43
b-Cairns × b-Popondetta	9.06	0.74	9.80	13.83	2.14	15.97

a, crude estimate of longevity; *m—a*, correction factor; *m*, corrected mean longevity.

number of flies added after the 3-day periods (4-day periods at 19°C). For example, for the hybrid population s-Sydney × s-Cooktown, the mean number of flies added after the 2-day periods was 552, and after the 3-day periods was 779. The ratio between these two means is 0.71, while the expected ratio is 0.67. It seems, therefore, that mortality in the culture bottles where the flies are born is small enough to be ignored in the estimation of longevity.

Generation time: A crude estimate of the mean generation time under the present experimental conditions can be obtained in the following way. At 25°C, mass hatching of flies occurs between the 13th and 15th day after the adult flies were first exposed to the food in the bottles. Probably more than 90% of the flies are born during this period. Since adults oviposit for two or three days, the mean time from laying to hatching is about 13 days, and this figure can be taken as the mean development time for immature stages. Mean longevity of adults being about 9 days, we obtain 22 days as a rough estimate of generation time at 25°C. At 19°C the corresponding figures are 20 days for development of immature stages, and 16 days for adult longevity, giving a crude estimate of generation time of 36 days.

The above estimates of generation time are given merely as crude approximations. The value to be added to mean development time of immature stages in order to obtain mean generation time is not mean longevity of adults, but the mean age of parents at the time the mean number of eggs are laid. This value is probably not greatly different, under the present conditions, from the mean longevity of adults.

DISCUSSION

To measure differences between populations of *D. serrata* and *D. birchii* from different geographic regions, Birch, Dobzhansky, Elliot and Lewontin (1963) used the statistic r_m, or innate capacity for increase in numbers. They concluded that, under laboratory conditions, r_m is a satisfactory ecological statistic characterizing geographic races of the same species. In the present work the same problem has been approached using a different experimental method. Carson (1957, 1961a) used production and the total population size at equilibrium to estimate relative population fitness. I have used a similar technique to measure small differences between strains of the same or different species. The differences in mean number of flies produced and in mean population size between the strains are, at both 25° and 19°C, in most cases highly significant. Production and population size appear, therefore, as satisfactory statistics to estimate small differences in fitness in experimental environments between different strains of Drosophila.

Some interesting observations emerge from the study of the hybrid populations. Extensive work on the genetics of natural populations has shown that the gene pool of a Mendelian population contains a variety of coadapted gene complexes maintained mostly in heterozygous condition. Natural selection does not, however, coadapt the gene complexes of different geographic populations, because the latter interbreed rarely or not at all. Vetukhiv (1953, 1954) studied the viability of five geographically separated populations of *D. pseudoobscura*, three populations of *D. willistoni*, three populations of *D. paulistorum*, and their F_1

and F_2 hybrids. He found that in *D. pseudoobscura* and *D. willistoni* (and in only one of three crosses of *D. paulistorum*), the F_1 hybrids were superior in viability to the parental populations. The F_2 hybrids, however, not only lost the heterosis present in the F_1, but in fact were usually inferior to the parental populations. He concluded that the loss of viability in the F_2 hybrids showed that the genotype of each of these populations represented a coherent system evolved under the control of natural selection. The gene recombination which occurs in the offspring of the hybrids between the populations results in a breakdown of such naturally coadapted systems.

Carson (1961b), using a technique somewhat similar to that employed in the present work, studied the performance of populations of hybrids between geographic strains of *D. robusta*. When a relatively low-fitness marginal population was hybridized with a relatively high-fitness central population, the resulting hybrid population was intermediate, but not significantly different in fitness from the high-fitness parental population. Carson proposed that the populations of central origin are already carrying a high degree of heterozygous balance and may be very nearly saturated in the sense that little improvement is possible by increasing the amount of heterotic buffering.

In the present experiments, hybrid populations derived from widely separated geographic strains were made to study their performance over a number of generations. The environmental conditions of the experiment, with very strong competition at both immature and adult stages of the life cycle, are in many respects different from the environments to which the populations had been exposed previous to the experiment. Natural selection is expected to operate producing adaptations to the new conditions. The hybrid populations offer a greater genetic variability for the operation of natural selection, with the possibility of producing, at least in some cases, a highly fit genotype.

The results show that, in general, the performance of the hybrid populations of *D. serrata* is better than that of the parental strains. At 25°C the differences in productivity and in size between the three hybrid populations and their parental strains are significantly in favor of the hybrid populations, except for the comparison between the s-Sydney/s-Cooktown hybrid with the s-Cooktown parent where differences are not significant. At 19°C the performance of hybrid populations are again significantly superior, except for the comparison of the s-Cooktown/s-Popondetta hybrid with the s-Cooktown parent where differences are not significant. Whether the superior performance of the hybrid populations is due to natural selection operating on a larger genetic variability is a question not fully answered by the present experiments. No progressive increase in adaptation to the environment is safely established after the first few weeks of population growth. Perhaps that period of time, during which at least three generations have elapsed, has been sufficient for the selection of better fit genotypes, given the highly competitive conditions in this experiment. There is no way of telling whether there was any hybrid breakdown in the F_2, which was the first generation to appear in the experimental population, at a time when numbers always increase rapidly.

The considerable difference in performance between the Cairns and Popondetta strains of *D. birchii* indicates the existence of notable genetic differences between these populations. This conclusion is also suggested by the relative poor performance of the hybrid population at 25°C during the first 23 weeks of the experiment. The two gene pools not being mutually coadapted may account for this result. The size of the hybrid population was, during this period, intermediate between the two parental strains, and the productivity was closer to that of the lower one, b-Popondetta. Between weeks 23 and 29, however, the level of productivity becomes almost three times higher and the mean population size goes well above that of either parental strain. A possible interpretation is that a highly successful gene combination has been produced, and multiplied by natural selection in two generations, greatly improving the general performance of the population in this environment. During the course of these evolutionary changes, this population has also developed some incipient sexual isolation with respect to the parental strains, as shown by results to be reported elsewhere.

The events in the *D. birchii* hybrid population at 19°C proceeded smoothly, without any sharp increase in fitness during the experiment. The performance of this population is not significantly different from that of Cairns, the parental strain of higher fitness. This result parallels that obtained by CARSON (1961b) with the central Steelville and the marginal Chadron populations. But in the present case we must look for a different explanation. The Cairns strain may represent an isolated population of *D. birchii* in Australia; the Popondetta strain comes from an island where the species is relatively more abundant. As in the case of *D. serrata* no information is available concerning the genetic make-up of these natural populations. A possible explanation is that the range of genotypes selected during the first few weeks of the experiment are basically those of the Cairns strain. The genetic variability contributed by the Popondetta strain has been either eliminated or, whatever may still be present in the hybrid population, natural selection has been unable to use to produce new highly adapted genetic combinations. Tests made at the end of the experiment show that this population is more sexually isolated from the Popondetta than from the Cairns parental strain.

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SUMMARY

The relative fitness of three strains of *D. serrata* and two strains of *D. birchii* and of their intraspecific hybrids was studied at two temperatures, 25° and 19°C. Constant amounts of food and space were provided at fixed intervals, so that the ability of the populations to exploit the environmental resources could be measured. The experimental design was such as to provide strong competition

both between the adults and during the immature stages of development. The parameters estimated were the biomass, the number of flies produced per food unit, and the total population size, measured after the attainment of an equilibrium with the environment.

Both production and total population size increase rapidly during the first few weeks, and reach an equilibrium between the 8th and the 15th week. The number of flies per culture bottle was about 2000 for the *D. serrata* populations, and considerably lower for the *D. birchii* strains. The differences between the strains in productivity and in population size were, in general, highly significant. Production and population size appear, then, as satisfactory statistics for characterization of strains of the same or different species.

The hybrid populations of *D. serrata* performed, in general, better than their parental strains at either temperature. This may be due to a greater genetic variability offered to the action of natural selection by the hybrid populations. The *D. birchii* hybrid was, at 19°C, intermediate between the two parental strains. At 25°C, the *D. birchii* hybrid was intermediate between the parental strains during the first 27 weeks of the experiment. Thereafter a sharp improvement occurred, and the equilibrium level increased by a factor between two and three, making the hybrid population superior to both parental strains.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch, 1954 *The Distribution and Abundance of Animals.* University of Chicago Press, Chicago, Illinois.

Ayala, F. J., 1965 Sibling species of the *Drosophila serrata* group. Evolution (in press).

Birch, L. C., Th. Dobzhansky, P. O. Elliot, and R. C. Lewontin, 1963 Relative fitness of geographic races of *Drosophila serrata.* Evolution **17**: 72–83.

Buzzati-Traverso, A. A., 1955 Evolutionary changes in components of fitness and other polygenic traits in *Drosophila melanogaster* populations. Heredity **9**: 153–186.

Carson, H. L., 1957 Production of biomass as a measure of fitness of experimental populations of Drosophila. Genetics **42**: 363–364. —— 1958 Increase in fitness in experimental populations resulting from heterosis. Proc. Natl. Acad. Sci. U.S. **44**: 1136–1141. —— 1961a Heterosis and fitness in experimental populations of *Drosophila melanogaster.* Evolution **15**: 496–509. —— 1961b Relative fitness of genetically open and closed experimental populations of *Drosophila robusta.* Genetics **46**: 553–567.

Dobzhansky, Th., 1955 A review of some fundamental concepts and problems of population genetics. Cold Spring Harbor Symp. Quant. Biol. **20**: 1–15.

Dobzhansky, Th., and O. Pavlovsky, 1961 A further study of fitness of chromosomally polymorphic and monomorphic populations of *Drosophila pseudoobscura.* Heredity **16**: 169–179.

Fisher, R. A., 1930 *The Genetical Theory of Natural Selection.* Oxford University Press.

Haldane, J. B. S., 1932 *The Causes of Evolution.* Harper, London.

Knight, G. R., and A. Robertson, 1957 Fitness as a measurable character in Drosophila. Genetics **42**: 524–530.

Lerner, I. M., 1954 *Genetic Homeostasis.* Oliver and Boyd.

Penrose, L. S., 1949 The meaning of "fitness" in human populations. Ann. Eugen. **14**: 301–304.

Reed, T. E., 1959 The definition of relative fitness of individuals with specific genetic traits. Am. J. Human Genet. **11**: 137–155.

Thoday, J. M., 1953 Components of fitness. Symp. Soc. Exptl. Biol. **7**: 96–113. —— 1958 Natural selection and biological progress. pp. 313–333. *A Century of Darwin*, Edited by S. A. Barnett. Heinemann, London.

Vetukhiv, M., 1953 Viability of hybrids between local populations of *Drosophila pseudoobscura*. Proc. Natl. Acad. Sci. U.S. **39**: 30–34. —— 1954 Integration of the genotype in local populations of three species of Drosophila. Evolution **8**: 241–251.

Wallace, B., 1948 Studies on "sex ratio" in *Drosophila pseudoobscura*. I. Selection and sex ratio. Evolution **2**: 189–217.

Wright, S., 1931 Evolution in Mendelian populations. Genetics **16**: 97–159. —— 1955 Classification of the factors of evolution. Cold Spring Harbor Symp. Quant. Biol. **20**: 16–24.