Title

Evolution of Fitness. IV. Genetic Evolution of Interspecific Competitive Ability in Drosophila.

Permalink

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Journal

Genetics, 61(3)

ISSN

0016-6731

Author

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Publication Date

1969-03-01

DOI

10.1093/genetics/61.3.737

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EVOLUTION OF FITNESS. IV. GENETIC EVOLUTION OF INTERSPECIFIC COMPETITIVE ABILITY IN DROSOPHILA[1]

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Received December 13, 1968

ADAPTIVE changes in the genetic constitution of natural populations, caused by natural selection in changing environments, have been recorded in several insect species (DOBZHANSKY 1947a, 1958; FORD 1953; KETTLEWELL 1961). Genetic adaptation to the environment has also been observed and measured in the laboratory (DOBZHANSKY 1947b; DOBZHANSKY and SPASSKY 1947; CARSON 1958; STRICKBERGER 1963, 1965; SPIESS 1966; AYALA 1965a, 1966a, 1968).

MOORE (1952a), studying competition between *Drosophila melanogaster* and *D. simulans*, showed that populations with improved competitive ability can be developed by selection, and that this can be done in relatively few generations. In experiments where the housefly and the blowfly were competing, PIMENTEL *et al.* (1965) observed reversal of dominance: in some instances the blowfly, initially at a disadvantage, ultimately eliminated the housefly. AYALA (1966b) also observed reversal of dominance in experiments where one of the competing species was *D. serrata* and the other was *D. pseudoobscura*, *D. nebulosa*, or *D. melanogaster*. Initially, *D. serrata* was at a disadvantage but eventually it became dominant in each of the three combinations. Apparently, genetic changes occurred in *D. serrata* which enhanced its ability to compete with the other species.

According to PIMENTEL *et al.* (1965) and AYALA (1966b) reversals of dominance should not be a rare occurrence since they are likely to occur given certain conditions. When two species compete with each other for a number of generations, the interspecific competitive ability of the rarer species may evolve since the individuals of that species compete mostly with the other species, while the individuals of the abundant species compete primarily among themselves and are selected for intra- rather than interspecific competitive ability.

Genetic changes enhancing the interspecific competitive ability of *D. serrata* are perhaps the most likely explanation of the reversals of dominance observed by AYALA (1966b). However, it was not demonstrated that genetic changes had in fact occurred; alternative explanations do exist. For instance, it is possible that the competitive ability of the other species might have deteriorated; or it may be that undetected changes in the environment had reversed the relative fitnesses of the two competing species. It is also conceivable that the equilibrium between the two competing species is unstable and chance fluctuations in their numbers resulted in the observed changes of dominance.

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[1] Supported by PHS Research Career Development Award IK3 GM 37265 from the National Institute of General Medical Sciences, and by Contract AT-(30)-3096 U. S. Atomic Energy Commission.

Genetics **61**: 737–747 March 1969.

The experiments reported here were designed to test whether reversals of dominance would occur and whether these are due to genetic changes in the competitive ability of the species.

MATERIALS AND METHODS

The flies used in the experiments come from a strain of *D. serrata* collected in Popondetta, New Guinea, and a strain of *D. nebulosa* collected in Belem, Brazil. Both strains had been kept in the laboratory in single species cultures for several years before the beginning of the experiment.

The two original populations, I and II, were started with 200 flies of each species from stock cultures. After a reversal of dominance occurred in population I (see RESULTS), 20 test populations were started as follows: Between weeks 31–33, flies of both species were sampled from each population: 500 *serrata* and 210 *nebulosa* from population I, and 70 *serrata* and 330 *nebulosa* from population II. The larger the sample the more genetic variability is likely to be obtained. However, in order to avoid a serious depletion of *D. serrata* in population II the number sampled was relatively small. The sampled flies were distributed in a number of bottles under relaxed conditions of selection. At the same time a number of cultures were prepared with flies from the single species stocks of *D. serrata* and *D. nebulosa*, which had provided the founder flies for the two original experimental populations. The F_1 progenies of these cultures were used to establish four replicates of each of the five types of test populations: Populations 41–44, *D. serrata* from population I with *nebulosa* from the stocks; 51–54, *serrata* from population II with *nebulosa* from the stocks; 61–64, *serrata* from the stocks with *nebulosa* from the stocks; 71–74, *serrata* from the stocks with *nebulosa* from population I; 81–84, *serrata* from the stocks with *nebulosa* from population II. Comparison among the first three types of populations would indicate whether the competitive ability of *D. serrata* flies from population I was superior to that of *serrata* flies from population II or from the stocks. Comparison among the three last types of populations would indicate whether the competitive ability of *D. nebulosa* had changed by selection in either population I or population II. Each replicate population was started with 300 flies of each species. The 20 test populations are characterized in Table 1.

The populations are cultured in half-pint milk bottles with a 2 cm-high layer of Spassky's cream of wheat and molasses medium. A double piece of towelling paper 5 × 18 cm, partially pressed into the medium, provides an extended surface for adult flies and for pupation. No yeast is added. All the experimental populations are kept in one constant temperature incubator at 19 ± 0.5°C.

The populations are maintained by the serial transfer technique (AYALA 1965b). Adult flies are introduced in one ½-pint milk bottle with food. Every seven days they are etherized, counted, and transferred to a fresh bottle. When emergence of adult flies begins in the bottles where the flies have deposited eggs, the newly emerged flies are etherized, counted, and added to the bottle with the adult population. The adult ovipositing flies are thus in a single bottle while five other bottles for each population contain eggs, larvae, pupae, and young newly emerged adults. The bottles are discarded after 5 weeks; by this time the emergence of first generation progeny has finished while a second generation is avoided.

TABLE 1

Description of the 20 "test" populations

Population number	Origin of *D. serrata*	Origin of *D. nebulosa*
41, 42, 43, 44	Population I	Stocks
51, 52, 53, 54	Population II	Stocks
61, 62, 63, 64	Stocks	Stocks
71, 72, 73, 74	Stocks	Population I
81, 82, 83, 84	Stocks	Population II

The serial transfer technique allows easy measurement of two parameters, i.e., productivity, or number of flies emerged per bottle, and survival, or average longevity. "Total" population is defined as the number of flies surviving from the previous week ("old" flies) plus the number of flies emerged during that week ("newborn" flies). Natural selection in the population is intense, both among the larvae and among the adults, since the populations reach a large size due to the continuous addition of newly emerged flies.

RESULTS

At 19°C the strains of *D. serrata* and *D. nebulosa* used in this experiment reach equilibrium with *serrata* at a frequency around 20% (AYALA 1966b). Two replicate populations, I and II, were started in September 1965, each with 200 flies of each species. By week 11 an equilibrium was reached with a frequency of *D. serrata* around 30% in population I and around 20% in population II. The total population of both species was about 800 flies. On week 22 in population I *D. serrata* started a gradual increase in absolute and relative numbers reaching a frequency of about 90% by week 31 (Figure 1); the frequency of *D. serrata* remained higher than 60% during the following 8 weeks. During this time, the frequency of *D. serrata* remained nearly constant in population II. The reversal of dominance in population I is unlikely to be due to undetected environmental changes since both populations, I and II, are treated similarly and simultaneously.

To test whether genetic improvement has occurred in the interspecific competitive ability of *D. serrata* in population I, and whether any changes have taken place in *D. serrata* in population II and in *D. nebulosa* in either population, 20 test populations were established as described above.

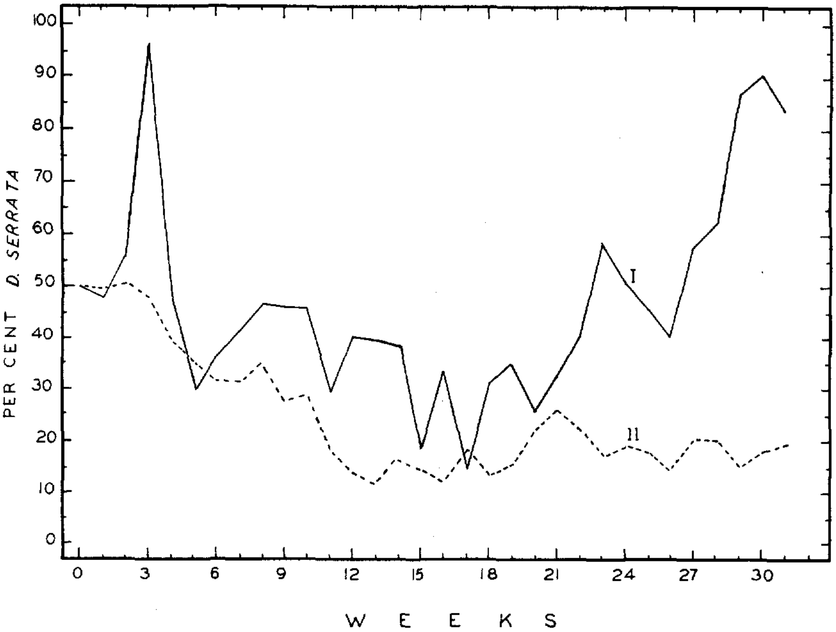

FIGURE 1.—Percent *D. serrata* in two experimental populations.

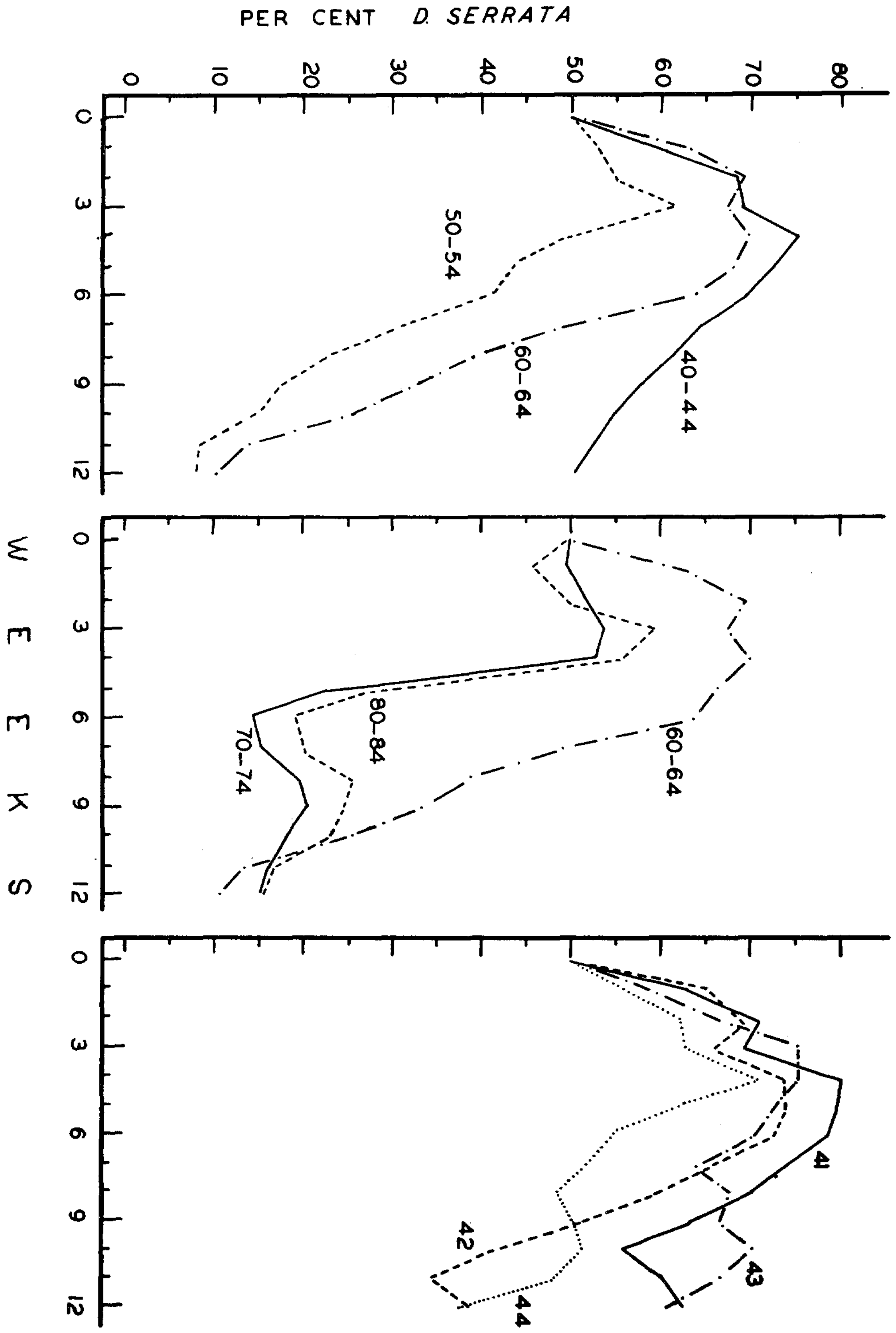
PER CENT D. SERRATA
0
10
20
30
40
50
60
70
80
WEEKS
0
3
6
9
12
50-54
40-44
60-64
80-84
70-74
60-64
41
42
43
44

TABLE 2

Mean percent D. serrata ($\bar{y}$) *and coefficient of regression* (b) *of percent* D. serrata *on time, with their standard errors*

Time units for the regression are weeks. Number of measurements = 12 throughout the table

	Newborn		Old		Total	
Population	$\bar{y}$	b	$\bar{y}$	b	$\bar{y}$	b
41	58.4 ± 3.9	−4.2 ± 1.0	71.4 ± 2.9	−1.1 ± 0.8	69.2 ± 2.4	−1.1 ± 0.6
42	47.0 ± 5.0	−4.2 ± 0.8	61.0 ± 4.9	−3.6 ± 0.9	59.7 ± 4.2	−3.4 ± 0.7
43	60.3 ± 2.2	−0.6 ± 0.4	73.2 ± 1.9	0.3 ± 0.6	68.5 ± 1.6	0.2 ± 0.5
44	45.9 ± 2.8	−2.2 ± 0.5	58.1 ± 2.8	−1.7 ± 0.7	54.8 ± 2.6	−1.9 ± 0.5
51	34.7 ± 5.9	−4.5 ± 1.1	45.4 ± 4.4	−3.8 ± 0.6	44.1 ± 4.4	−3.9 ± 0.5
52	18.9 ± 3.8	−3.1 ± 0.6	37.5 ± 6.6	−5.9 ± 0.8	34.0 ± 5.9	−5.4 ± 0.3
53	10.8 ± 3.6	−2.9 ± 0.6	30.1 ± 6.4	−5.7 ± 0.7	26.7 ± 5.9	−5.4 ± 0.5
54	14.2 ± 4.9	−4.0 ± 0.8	33.9 ± 6.8	−6.2 ± 0.7	30.7 ± 6.6	−6.0 ± 0.6
61	28.5 ± 5.9	−4.8 ± 1.0	51.1 ± 5.2	−3.8 ± 1.0	47.2 ± 5.3	−4.4 ± 0.8
62	25.3 ± 5.9	−5.2 ± 0.7	55.0 ± 4.7	−3.7 ± 0.8	48.3 ± 5.4	−4.8 ± 0.7
63	27.1 ± 7.4	−6.6 ± 0.8	48.7 ± 7.5	−6.5 ± 1.0	47.7 ± 7.4	−6.6 ± 0.8
64	24.4 ± 8.5	−7.4 ± 1.1	51.4 ± 8.1	−6.8 ± 1.2	48.3 ± 8.3	−7.3 ± 1.0
71	29.5 ± 4.2	0.2 ± 1.3	43.0 ± 5.6	−2.5 ± 1.5	37.2 ± 4.9	−2.9 ± 1.1
72	19.3 ± 3.2	0.4 ± 1.0	34.9 ± 5.7	−4.5 ± 1.0	31.0 ± 5.8	−4.5 ± 1.1
73	14.8 ± 4.0	−1.3 ± 1.2	29.0 ± 5.3	−4.2 ± 0.9	25.4 ± 5.3	−4.3 ± 0.9
74	14.4 ± 2.6	−0.3 ± 0.8	27.4 ± 4.8	−4.2 ± 0.6	24.0 ± 4.4	−3.8 ± 0.6
81	24.1 ± 3.8	−0.7 ± 1.1	40.8 ± 5.2	−3.4 ± 1.2	36.0 ± 4.8	−3.5 ± 1.0
82	16.0 ± 3.2	−1.0 ± 0.9	31.5 ± 4.1	−3.2 ± 0.7	28.1 ± 4.3	−3.4 ± 0.8
83	17.1 ± 3.8	−1.8 ± 1.0	37.2 ± 5.1	−3.4 ± 1.1	33.0 ± 4.7	−3.5 ± 0.9
84	14.2 ± 3.1	−2.1 ± 0.7	36.1 ± 4.5	−3.5 ± 0.8	31.3 ± 4.6	−3.9 ± 0.7

The test populations were studied for 12 weeks or about 3–4 generations. The results are summarized in Figure 2 where the percent of *D. serrata* for total number of flies is plotted against time. In the left and center graphs each point represents the average of four replicate populations. The averages for the four populations where both species come from the stocks are plotted in both graphs, since these populations are the control in both cases. In the right graph populations 41, 42, 43 and 44 have been plotted separately to illustrate the amount of variation among replicates.

A more detailed account of the results is given in Table 2. Mean percent *D. serrata* and regression coefficient of percent *D. serrata* on time are given for the 20 populations. Measurements of "newborn" flies are from week 4 to 15; measurements of "old" and "total" are from week 1 to 12. The means of absolute numbers of both species together are given in Table 3.

FIGURE 2.—Percent *D. serrata* in competition with *D. nebulosa*. Left, comparison of two selected populations of *D. serrata* (40–44 and 50–54) with the control (60–64). Center, comparison of two selected populations of *D. nebulosa* (70–74 and 80–84) with the control. Right, four replicate populations. At left and center each point represents an average of four replicate populations.

TABLE 3

Mean number of flies and standard error of D. serrata *and* D. nebulosa *in the populations. Number of measurements* = *12 throughout the table*

Population	Newborn	Old	Total
41	262 ± 22	451 ± 49	663 ± 76
42	311 ± 21	464 ± 41	689 ± 62
43	381 ± 25	460 ± 43	726 ± 76
44	349 ± 23	521 ± 49	777 ± 79
51	356 ± 37	452 ± 46	719 ± 78
52	363 ± 28	438 ± 56	713 ± 87
53	399 ± 45	452 ± 37	756 ± 81
54	467 ± 39	503 ± 56	850 ± 112
61	389 ± 43	493 ± 53	794 ± 85
62	491 ± 38	563 ± 56	912 ± 105
63	326 ± 64	434 ± 38	698 ± 90
64	300 ± 35	532 ± 52	788 ± 84
71	319 ± 43	328 ± 51	566 ± 71
72	302 ± 48	500 ± 60	758 ± 101
73	286 ± 41	459 ± 51	687 ± 81
74	300 ± 42	484 ± 54	746 ± 87
81	308 ± 34	495 ± 45	740 ± 76
82	277 ± 43	449 ± 35	669 ± 66
83	330 ± 39	528 ± 42	802 ± 81
84	338 ± 54	506 ± 35	759 ± 86

D. serrata flies derived from population I are better competitors than those from population II or from the stocks as shown by both measures, mean percent and coefficient of regression. The coefficients of regression are generally negative, indicating that the frequency of *D. serrata* is decreasing in all populations. The rate of decrease, however, is smaller in populations 41 to 44 than in populations 51 to 54 and 61 to 64. This is more clearly seen in Table 4, where the given statistics have been calculated as follows: The averages for the four replicate populations are calculated for each week and the relevant differences between averages are obtained. The mean differences and the coefficient of regression of the differences on time are given. A positive mean difference indicates a greater average percent of *D. serrata*; a positive coefficient of regression indicates that the difference is increasing with time, while a negative coefficient of regression indicates that the difference is gradually decreasing. The tests of significance are predicated on the assumption that for each week the four replicates represent independent observations of the population. For purposes of comparison, a different approach was also used, namely to consider the coefficients of regression given in Table 4 for the four replicates as independent estimates of a true regression coefficient for the population and ignore their standard errors. The mean regression coefficient and standard error were then calculated for each four replicates and the significant comparisons between mean regression coefficients were made. These tests

TABLE 4

Mean difference (d_y) *and coefficient of regression of the differences* (b_d) *between the averages of various populations.*

The parameters are expressed in percent D. serrata; t *indicates the significance*

Populations compared		$\bar{d}_y$	t	b_d	t
41–44 minus 61–64	Newborn	26.6 ± 4.2	6.3***	3.7 ± 0.5	6.7***
	Old	14.3 ± 4.1	3.5**	3.7 ± 0.4	8.4***
	Total	15.2 ± 4.4	3.5**	4.1 ± 0.3	12.0***
41–44 minus 51–54	Newborn	33.2 ± 2.2	15.0***	1.3 ± 0.5	2.5*
	Old	29.2 ± 4.3	6.8***	3.9 ± 0.4	8.6***
	Total	29.2 ± 3.9	7.5***	3.5 ± 0.4	8.5***
61–64 minus 51–54	Newborn	6.7 ± 3.1	2.2	—2.4 ± 0.6	4.1**
	Old	14.8 ± 4.5	3.3**	0.1 ± 1.4	0.1
	Total	14.0 ± 2.1	6.6***	—0.6 ± 0.6	1.0
61–64 minus 71–74	Newborn	6.8 ± 6.6	1.0	—5.5 ± 1.0	5.6***
	Old	18.0 ± 5.1	3.5**	—1.4 ± 1.5	1.0
	Total	18.5 ± 4.9	3.8**	—1.9 ± 1.4	1.4
61–64 minus 81–84	Newborn	8.5 ± 5.6	1.5	—4.5 ± 1.0	4.7***
	Old	15.1 ± 5.1	3.0**	—1.9 ± 1.4	1.3
	Total	15.8 ± 4.7	3.4**	—2.2 ± 1.2	1.8

* Statistically significant $P < .05$.
** Statistically significant $P < .01$.
*** Statistically significant $P < .001$.

of significance do not differ meaningfully from those given in Table 4, although the level of significance was slightly different in several cases.

The performance of *D. serrata* flies derived from population I is compared with that of the flies derived from the stocks and from population II in the upper part of Table 4. For the three parameters: newly emerged flies, surviving flies, and total number, *D. serrata* from population I has a significantly greater mean percent, and the difference is greater with time at a rate that is statistically significant.

It was not expected that *D. serrata* flies derived from stocks would be better competitors than those derived from population II, as can be seen both in Figure 2 and Table 4. The average difference between both, however, gradually decreased. Apparently the competitive ability of *D. serrata* deteriorated in population II. Conceivably, this may be due to inbreeding, although this explanation seems unlikely since the average number of *D. serrata* flies in population II from the beginning of the experiment until the sample was taken was somewhat over 150; nor is the sample of 70 flies small enough to warrant such an explanation. Perhaps the adaptation in this relatively small population may have been to compete with the specific population of *D. nebulosa* which evolved with it. Still other explanations are possible, but there is no way of deciding among the alternatives.

D. nebulosa flies from population I and from population II perform equally well in competition with *D. serrata,* but both are better competitors than *D. nebulosa* from the stocks. Table 4 shows that the proportion of *D. serrata* is smaller in the two selected populations of *D. nebulosa* and, therefore, the proportion of *D. nebulosa* greater than in the control unselected population. The regressions of the differences are, however, negative indicating that the difference in performance between selected and unselected *D. nebulosa* decreases with time, as is also apparent in Figure 2.

DISCUSSION

STRICKBERGER (1963) has shown in *D. pseudoobscura* that genetic changes which increase their adaptedness to the experimental environment may occur in experimental populations. The degree of fitness evolved is greater when the initial amount of genetic variability is larger (STRICKBERGER 1965).

In experimental populations of *D. serrata* AYALA (1965a, 1968) observed the evolution of genetic fitness which gradually enhanced the adaptedness of the populations to the experimental environment. Genetic improvements for food utilization occurred readily during the first few generations of selection, while genetic changes increasing the average longevity of the adults occurred more gradually through a greater number of generations (AYALA 1968). The rate of evolution was greater in the populations with larger initial genetic variability (AYALA 1965a, 1966a, 1968).

MOORE (1952b) studied experimentally the competition between *D. melanogaster* and *D. simulans. D. melanogaster* was the superior species and in 19 of 20 cases it eliminated *simulans* in about 100 days. In the exceptional case, however, *D. simulans* increased gradually in frequency from days 73 to 218, although eventually it was also eliminated by *melanogaster*. By successively selecting *D. simulans* populations that had competed with *melanogaster* up to 500 days, MOORE (1952a) demonstrated that flies with improved competitive ability can be developed by selection.

Similar results were observed by PIMENTEL *et al.* (1965) in an experimental study of competition between the housefly, *Musca domestica,* and the blowfly, *Phenicia sericata.* In a 16-cell population system the housefly was dominant during the first 50 weeks of the experiment. From week 50 on the blowfly increased in numbers rather sharply, and it became clearly dominant from week 57 until week 65 when the housefly went to extinction. According to PIMENTEL *et al.*, in a two species system the sparse species is at an evolutionary advantage because selective pressure on such species is mostly for interspecific competitive ability. The dominant species is at an evolutionary disadvantage because intraspecific competition is the main selective force working on it. Genetic tests indicated that the interspecific competitive ability of the blowfly was enhanced after a number of generations of selection during which it was the sparse species. Reversals of dominance have also been observed by AYALA (1966b) studying interspecific competition between various combinations of two species of Drosophila.

The present experiments confirm and extend these results under carefully controlled conditions. A reversal of dominance was observed in one but not in the other of two experimental populations. It is thus unlikely that the improved performance of *D. serrata* in population I is due to uncontrolled environmental changes since both populations are treated identically and simultaneously. That a genetic improvement in competitive ability has in fact occurred is demonstrated by the genetic tests. *D. serrata* flies derived from population I are better competitors than *D. serrata* from population II or from the unselected stocks. The genetic tests indicate that *D. nebulosa* has also improved its competitive ability. This is hardly unexpected since natural selection for interspecific competitive ability is operative in both competing species, although its intensity might be greater in the sparse than in the dominant species.

It is worth speculating about the selective mechanisms involved in the observed reversals of dominance. If two species coexist in a limited environment both may share some of the available resources of food and space, while each species may exploit resources that the other species is not able to use. In the Drosophila populations both species may share some food resources, like carbohydrates and certain yeast species, and they also share the available space. But it is likely that larvae of one species eat some yeast or mold species which are not exploited by the other species and vice versa (DA CUNHA, DOBZHANSKY and SOKOLOFF 1951). Similarly, adult flies of the two species may utilize differentially certain components of the available space, and show preferences for certain oviposition sites (MOORE 1952b; DEL SOLAR 1968). It is also possible for one species to utilize catabolites produced by, and useless to, the other species. In the extreme situation, each species may live on the metabolites of the other species, as in the phenomenon of symbiotic mutualism.

Selection for interspecific competitive ability may, then, occur in two different ways. First, selection may improve the ability of one species to exploit the resources also exploited by the second species. This may be called selection for "positive competitive ability" or, simply, selection for competitive ability proper. Second, genotypes may be selectively favored which allow the population to exploit resources not utilized by the competing species. This second process may be called selection for "avoidance of competition" since it tends towards decreasing the intensity of the competition. Obviously, intermediate situations can exist like in the case of improvement of the ability of one species to exploit one resource which the other species exploits inefficiently or to a limited extent.

If two coexisting species exploit mostly the same limited resources, it is likely that one or the other species will eventually become extinct. However, selection for avoidance of competition increases the probability of coexistence by leading the two species towards ecological differentiation. Therefore, selection for avoidance of competition operates as a positive feedback mechanism. The longer it proceeds the more likely are the two species to coexist, and therefore the greater the probability that the selection will continue. From the evolutionary point of view only selection for avoidance of competition is likely to continue for a large number of generations. If this reasoning is correct, one can make the prediction that populations of two species in localities where the two species coexist will be ecologically more divergent than populations of the two species which do not coexist.

Selection for competitive ability, i.e. selection for exploitation of the resources utilized by both species will affect the two species independently of their relative frequencies. If the same yeast species is equally eaten by larvae of two Drosophila species, selection for intraspecific competition will be equivalent to selection for interspecific competition. The intensity of the selection will depend on the absolute numbers of both species together and not on their relative frequencies. On the contrary, selection towards avoidance of competition will preferentially occur in the sparse species. If one species is more efficient in the exploitation of the resources shared by both, those genotypes of the other species will be favored which allow the flies to exploit resources not utilized by the dominant species. Reversals of dominance are likely to be the result of selection for avoidance of competition.

From the experiments reported here, it is not possible to decide whether the observed improvement in the performance of *D. serrata* in one of the two replicate experimental populations is the result of evolution towards improved competitive ability, or towards avoidance of competition. Most likely it is the result of both processes to different degrees. Nevertheless, it is important to emphasize that the two types of selection can be distinguished by appropriate experiments. If selection for avoidance of competition occurs the increase in numbers of one species will take place without a proportionate decrease in the numbers of the competing species. Both processes, however, are likely to occur at the same time. If the competition goes on for a large number of generations, it is still possible to test whether selection for avoidance of competition has occurred at all, since it should result in a gradual increase of the biomass of both species together. Experiments are in progress to test this hypothesis.

I have greatly profited from many discussions with Professor THEODOSIUS DOBZHANSKY. I am also indebted to PROFESSOR HOWARD LEVENE and DR. JOHN SVED for statistical advice. MRS. M. K. GILES did most of the calculations with great care and dedication.

SUMMARY

Evolution of interspecific competitive ability in Drosophila is demonstrated in a study of competition between *D. serrata* and *D. nebulosa*. Two populations were started each with 50% flies of each species. An equilibrium was reached with *D. serrata* at 20–30% frequency. Between weeks 22 to 31 a gradual increase in the frequency of *D. serrata* was observed in one of the populations. Genetic tests demonstrate that the interspecific competitive ability of *D. serrata* in this population has been greatly increased by natural selection. The competitive ability of *D. nebulosa* has also increased in both populations.—When two species compete for certain limited resources, natural selection may produce genotypes which are better competitors. Selection may also be for avoidance of competition, i.e., for genotypes which allow the species to exploit resources not utilized by the competing species. Selection for avoidance of competition increases the probability of coexistence and leads to ecological divergence of two coexisting species.

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