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Genetic polymorphism and interspecific competitive ability in *Drosophila*

BY FRANCISCO J. AYALA
The Rockefeller University, New York 10021

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1. INTRODUCTION

Chromosomal polymorphisms are widespread in natural populations of many species of *Drosophila*. In *Drosophila pseudoobscura*, polymorphisms for certain chromosome inversions have been shown to be balanced and adaptive both in natural and in experimental populations. Dobzhansky (1948, 1957) and his colleagues have observed that at 25 °C laboratory populations of *D. pseudoobscura* polymorphic for the III-chromosome inversions Arrowhead (AR) and Chiricahua (CH) reach an equilibrium of about 75 % AR and 25 % CH. This indicates that there is heterosis, i.e. that the structural heterozygotes, AR/CH, have higher fitness than either of the two homozygotes, AR/AR and CH/CH.

More recently, Beardmore, Dobzhansky & Pavlovsky (1960) and Dobzhansky & Pavlovsky (1961) have demonstrated that chromosomally polymorphic populations are superior to monomorphic ones. Populations polymorphic for CH and AR produce more flies per food unit and maintain a larger population size than either of the monomorphic populations CH or AR.

The present experiment was designed to compare the performance of polymorphic and monomorphic populations, when *D. pseudoobscura* competes with another species, *D. serrata*, for the available resources of food and space.

2. MATERIALS AND METHODS

Competition between *D. pseudoobscura* and *D. serrata* was studied in three kinds of experimental populations. The same strain of *D. serrata* was present in all populations. It derives from several impregnated females collected in Popondetta, New Guinea, and has been kept in the laboratory in single small mass cultures for several years before the beginning of the experiment.

D. pseudoobscura flies were either monomorphic for the CH or the AR chromosomal arrangements, or polymorphic for CH and AR. The *D. pseudoobscura* populations were established with ten monomorphic AR strains and seven monomorphic CH strains. Each strain derives from a single inseminated female collected by Professor Theodosius Dobzhansky in Mather, California, several years before the beginning of the experiment. Crosses between all the AR strains and between all the CH strains were made to establish the monomorphic populations.

Each AR strain was crossed with one CH strain for the polymorphic populations.

Four replicate populations of each kind were made. Each population was started with 300 flies from each species. The *D. pseudoobscura* flies, F_1 progenies from the crosses mentioned above, were chosen so that the number of founder flies descended from each strain was the same in each population.

The populations are maintained by the serial transfer technique (Ayala, 1965). The founder flies are introduced in a bottle with culture medium. After 7 days they are etherized, counted, and transferred to a fresh bottle. The procedure is repeated every 7 days. When emergence begins in the bottles where the adult flies have deposited eggs, the newly emerged flies are etherized, counted, and added to the bottle with the adult flies. The adult ovipositing flies are, thus, always in a single bottle while five other bottles contain eggs, larvae, pupae, and newly emerged adults. The bottles are discarded after 5 weeks; by this time emergence of the first generation progeny has finished while a second generation is avoided.

The cultures are kept in ½-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. The populations are kept in a constant-temperature incubator at 25 ± 0·5 °C and 85 % relative humidity.

3. RESULTS

(i) *The model*

Let

$$W_s = \frac{s(i+1)}{s(i)} \quad \text{and} \quad W_p = \frac{p(i+1)}{p(i)}, \tag{1}$$

where $s(i)$ is the number of one species, say *D. serrata*, and $p(i)$ the number of a second species, say *D. pseudoobscura*, at time i. W_s and W_p measure the change in numbers between times i and $i+1$. W_s and W_p will be constant for any i if the rate of change in numbers is constant for any fixed interval of time. The relative fitness of *D. serrata* with respect to *D. pseudoobscura* can then be defined as

$$W_{sp} = W_s/W_p. \tag{2}$$

An alternative measure of fitness is

$$m_{sp} = \log W_{sp}. \tag{3}$$

The ranges of variation of relative fitness so defined are

$$0 \leqslant W_{sp} \leqslant \infty, \tag{4}$$

$$-\infty \leqslant m_{sp} \leqslant \infty. \tag{5}$$

W_{sp} equals one and m_{sp} equals zero, when the populations of both species increase or decrease in numbers at equal rate.

From equations (1) and (2):

$$\frac{s(i+1)}{p(i+1)} = \frac{W_s}{W_p}\,\frac{s(i)}{p(i)} = W_{sp}\,\frac{s(i)}{p(i)} = W_{sp}^{i}\,\frac{s(1)}{p(1)}, \tag{6}$$

$$\log\frac{s(i+1)}{p(i+1)} = i\log W_{sp} + \log\frac{s(1)}{p(1)} = im_{sp} + \log\frac{s(1)}{p(1)}. \tag{7}$$

The regression coefficient of $\log s(i)/p(i)$ on time is then an estimate of m_{sp}.

The relative fitnesses of two or more populations of one species, say *D. pseudoobscura*, competing independently with the other species, *D. serrata*, can be compared if the rate of change in numbers of *D. serrata* is the same in the various populations. Let

$$W_{sp_i} = \frac{W_s}{W_{p_i}}, \quad W_{sp_j} = \frac{W_s}{W_{p_j}}, \tag{8}$$

and

$$W_{p_ip_j} = \frac{W_{pi}}{W_{pj}}. \tag{9}$$

Then

$$W_{p_ip_j} = \frac{W_s/W_{spi}}{W_s/W_{sp_j}} = \frac{W_{spj}}{W_{sp_i}}, \tag{10}$$

$$m_{p_ip_j} = \log W_{p_ip_j} = \log W_{sp_j} - \log W_{sp_i} = m_{sp_j} - m_{sp_i}. \tag{11}$$

The relative fitness of one population of *D. pseudoobscura* to another can be estimated as the difference between two coefficients of regression. The standard statistical tests for a difference between two regression coefficients can be used as tests of significance. The ranges of variation of $W_{p_ip_j}$ and $m_{p_ip_j}$ are the same as the ranges of variations of W_{sp} and m_{sp}, given in equations (4) and (5).

(ii) *The populations*

In competition with *D. serrata* at 25 °C, *D. pseudoobscura* decreases rapidly in numbers from the initial 300. The population dynamics of both species can be seen in Fig. 1, for one typical population of each kind. In the CH populations, *D. pseudoobscura* became extinct on week 9 in one population, on week 10 in two others, and on week 12 in the fourth one. In the AR populations, *D. pseudoobscura* became extinct on week 9 in one population, on week 10 in a second, and on week 12 in a third replicate. In the four polymorphic and in one of the AR populations, *D. pseudoobscura* flies persisted beyond week 12. It appears, then, that the polymorphic populations of *D. pseudoobscura* are superior to either of the monomorphic populations as competitors with *D. serrata*.

The relative fitnesses of *D. serrata* with respect to *D. pseudoobscura* are given in Table 1. The m_{sp}'s are the regression coefficients on time of the natural logarithms of the ratio of *D. serrata* numbers to *D. pseudoobscura* numbers. W_{sp} is the antilogarithm of m_{sp}. Time units for the regression are weeks, although the estimates of relative fitness are valid for time intervals of any length. The regression coefficients are calculated for measurements from weeks 1 to 12, or from week 1 until

D. pseudoobscura became extinct. The relative small variances of the m_{sp}'s indicate that the assumptions of the model probably hold in these populations. Mean fitnesses and variances are also given in Table 1. However, these variances cannot be used to compare mean fitnesses, since the analysis of variance indicates that

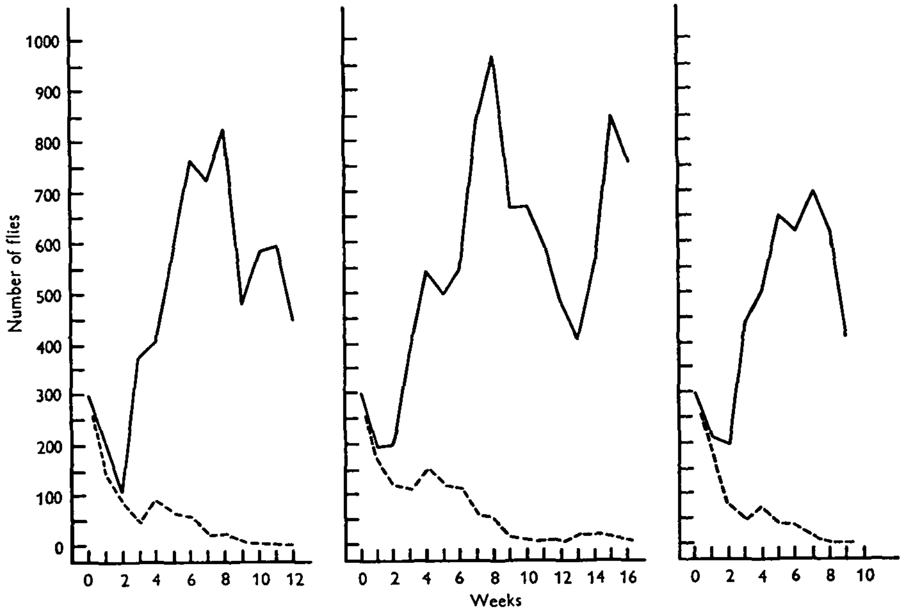

Fig. 1. Numbers of *Drosophila serrata* (——) and *D. pseudoobscura* (– – –) in three experimental populations. The genetic constitution of *D. pseudoobscura* is AR (left), CH and AR (centre), and CH (right).

Table 1. *Relative fitness* (W_{sp}) *and logarithm relative fitness* (m_{sp}) *of* Drosophila serrata *with respect to* D. pseudoobscura *in twelve experimental populations, the standard errors for* m_{sp} *are also given*

Population	m_{sp} ± S.E.	Variance m_{sp}	W_{sp}	D.F.
AR, 41	0·416 ± 0·033	0·0011	1·52	10
AR, 42	0·649 ± 0·035	0·0012	1·91	8
AR, 43	0·557 ± 0·058	0·0033	1·75	6
AR, 44	0·590 ± 0·051	0·0025	1·80	9
AR, mean	0·5530 ± 0·0226	0·00051	1·739	33
AR, CH, 51	0·441 ± 0·024	0·0005	1·55	10
AR, CH, 52	0·381 ± 0·056	0·0030	1·46	10
AR, CH, 53	0·547 ± 0·032	0·0010	1·73	10
AR, CH, 54	0·562 ± 0·026	0·0007	1·75	10
AR, CH, mean	0·4827 ± 0·0176	0·00031	1·620	40
CH, 61	0·660 ± 0·055	0·0030	1·93	9
CH, 62	0·662 ± 0·070	0·0048	1·94	7
CH, 63	0·721 ± 0·083	0·0068	2·06	7
CH, 64	0·631 ± 0·073	0·0053	1·88	6
CH, Mean	0·6685 ± 0·0352	0·00124	1·952	29

there is significant heterogeneity among the m_{sp}'s of the AR and of the polymorphic populations, although not among the CH populations.

The analysis of variance indicates that there is significant heterogeneity among the three types of populations. The relative fitnesses of *D. pseudoobscura* in the various populations are compared in Table 2. $m_{p_ip_j}$ is the difference between the mean m_{sp_i} and m_{sp_j}. The standard error to compare the mean m_{sp_i}'s has been calculated from mean square error (variance among replicates) of the analysis of variance. The $m_{p_ip_j}$'s are significant for the comparisons between the polymorphic and the CH populations and between the AR and the CH populations, but not between the polymorphic and the AR populations. If the fitness of the CH populations is taken to be one, the relative fitnesses of the AR and the polymorphic populations are, respectively, 1·12 and 1·20.

Table 2. *Relative fitness* ($W_{p_ip_j}$) *and logarithm relative fitness* (m_{p_ip}) *of the* Drosophila pseudoobscura *populations; t and P for the significance of the differences*

Comparison	$m_{p_ip_j}$ ± S.E.	$W_{p_ip_j}$	D.F.	t	P
Polymorphic/monomorphic CH	0·186 ± 0·039	1·204	6	4·70	$<0·01$
Monomorphic AR/monomorphic CH	0·116 ± 0·039	1·123	6	2·92	$<0·05$
Polymorphic/monomorphic AR	0·070 ± 0·039	1·072	6	1·78	$>0·1$

Table 3. *Mean fitness and standard error of* Drosophila serrata *in twelve experimental populations*

Populations	$\overline{W}_s$	Populations	$\overline{W}_s$	Populations	$\overline{W}_s$
41	1·13 ± 0·23	51	1·10 ± 0·11	61	1·31 ± 0·27
42	1·20 ± 0·20	52	1·22 ± 0·19	62	1·10 ± 0·10
43	1·08 ± 0·09	53	1·19 ± 0·12	63	1·30 ± 0·34
44	1·24 ± 0·25	54	1·21 ± 0·22	64	1·11 ± 0·13
Mean	1·162 ± 0·107	Mean	1·183 ± 0·087	Mean	1·202 ± 0·122

D. pseudoobscura was eliminated before the 12th week in three AR and four CH populations. When only *D. serrata* flies are present the ratio of *serrata* to *pseudoobscura* is infinity; it cannot be used for estimation of the regression coefficients. For purpose of comparison the m_{sp}'s were recalculated assuming that the number of *D. pseudoobscura* flies was half in those samples where none was found. The new m_{sp}'s are 0·416, 0·672, 0·753, and 0·606 for the AR populations; and 0·696, 0·745, 0·761 and 0·694 for the CH populations. The mean m_{sp} is now 0·6118 for the AR populations, and the variance 0·00051 (same as in Table 1); for CH the mean is 0·7240 and the variance 0·00063 (smaller than in Table 1). There is, as before, significant heterogeneity among AR but not among CH replicates. The comparison between the polymorphic and the AR populations, however, becomes statistically significant ($m_{p_ip_j} = 0{\cdot}1291 \pm 0{\cdot}0494$, $t = 2{\cdot}61$ with 6 degrees of freedom). If fitness of the CH populations is taken as one, the relative fitnesses of the AR and polymorphic populations are now 1·12 and 1·27 respectively.

The comparisons between fitnesses of the *D. pseudoobscura* populations are based on the assumption that the rate of change in numbers of *D. serrata* is the same in the three types of populations. One may argue, however, that if two species compete for the same resources, the fitness of one species may be inversely correlated with the fitness of the other one. If the argument is valid the relative fitnesses of the monomorphic AR and of the polymorphic population are overestimated in Table 3. This objection is not serious. It implies the assumption that there are real differences in competitive ability among the *D. pseudoobscura* populations, and that the differences are of the same sign as observed.

In any case, the mean relative fitnesses of *D. serrata* in the populations are given in Table 3. They are calculated as the mean s_{i+1}/s_i, as in equation (1). There are no significant differences in mean fitness among the populations. The assumption of equal fitness is presumably warranted.

The frequency of each karyotype in the *D. pseudoobscura* polymorphic populations was 50 % at the beginning of the experiment. On week 10, egg samples were taken from three of the polymorphic populations. Salivary gland squashes were prepared from the larvae to estimate the karyotypic frequencies. The frequency of the CH karyotype, based on a sample of about 100 chromosomes per population, was 38·7, 37·2 and 36·7 % in populations 51, 52 and 53 respectively. The frequency of the CH chromosomal arrangement has decreased, but the populations are definitely polymorphic.

4. DISCUSSION

Experimental populations of *D. pseudoobscura* polymorphic for the two chromosomal inversions CH and AR reach at 25 °C an equilibrium of about 70–75 % AR and 25–30 % CH (Dobzhansky 1948, 1957; Levine 1955; Levene, Pavlovsky & Dobzhansky 1954). The relative fitnesses of the three genotypes present in the populations vary in different experiments, but the heterokaryotype AR/CH is always highest, the homokaryotype AR/AR next, and the homokaryotype CH/CH is lowest.

Polymorphisms for certain inversions of the third chromosome are widespread in natural populations of *D. pseudoobscura*. The natural polymorphisms appear to be balanced owing to higher fitness of the heterokaryotypes. The heterosis must be due to greater efficiency of the heterozygote individuals in the exploitation of the environmental resources. A direct comparison of polymorphic and monomorphic populations in their efficiency to exploit the environment can be made in the laboratory at least in two ways. First, the biomass produced and/or the average size of the populations when the available resources of food and space are limited can be compared. Second, one may compare the performance of the populations when they compete for available resources with another species. Both approaches attempt to measure the ability of the populations to survive under certain environmental conditions.

Beardmore *et al.* (1960) studied at 25 °C seven population cages of *D. pseudoobscura*, four polymorphic for CH and AR, two monomorphic AR and two monomorphic CH. The polymorphic populations produced 15–60 % more flies per food unit than the monomorphic ones. In another study, Dobzhansky & Pavlovsky (1961) measured the average size of the populations and observed again a clear superiority of the polymorphic populations.

The present experiments demonstrate the superiority of polymorphic populations over monomorphic ones when *D. pseudoobscura* competes with *D. serrata* at 25 °C. Strickberger (1963) studied the competition between *D. pseudoobscura* and *D. melanogaster* at 25 °C. One population monomorphic CH was superior, although a second was not, to the polymorphic populations for CH and AR. The discrepancy between Strickberger's results and the present experiment may be due to one or more of the following differences. First, Strickberger's experiments were made on population cages, which provide considerably different environmental conditions than the serial transfer technique. Secondly, the geographic origin, and therefore the genetic composition, of the strains of *D. pseudoobscura* was different in both experiments; in Strickberger's studies they were derived from flies collected in Piñon Flats, San Jacinto Mountains, California. Thirdly, the polymorphic populations may be superior in competition with *D. serrata* but not with *D. melanogaster*.

Populations will remain polymorphic in nature if the heterozygotes are on the average superior to the homozygous individuals, in over-all performance. Given the complexity of natural environments, where the populations face a variety of food resources, competions, predators, etc., the over-all superiority of the heterozygotes need not imply that they are superior to the homozygotes with respect to every component of the environment.

SUMMARY

A simple method is given to compare the relative fitnesses of various populations of one species when they compete with another species. Populations of *Drosophila pseudoobscura* polymorphic for the chromosomal inversions CH and AR are superior to monomorphic populations CH or AR when they compete for the available resources with *D. serrata*.

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