

THE CAPACITY FOR INCREASE IN CHROMOSOMALLY POLYMORPHIC AND MONOMORPHIC POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA*

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1. INTRODUCTION

Most natural populations of *Drosophila pseudoobscura* are chromosomally polymorphic, since they contain two or more, up to eight, variant forms of the third chromosome. The polymorphism is maintained by a strong balancing selection. The intensity of this selection under natural conditions is attested by rapid changes in the relative frequencies of the chromosomal polymorphs which occur in some populations from season to season or from year to year. Experiments on populations kept in laboratory population cages show that the balancing selection operates, usually though not always, because the heterokaryotypes are superior in fitness to the homokaryotypes (a review in Dobzhansky, 1964). Experimental laboratory population cages can, however, be made either chromosomally polymorphic (consisting of heterokaryotypes as well as homokaryotypes), or chromosomally monomorphic, containing homokaryotypes only. The question that naturally arises is in what respects can the polymorphic populations be said to be fitter than, or superior to the monomorphic ones, if, indeed, they are superior at all.

Beardmore, Dobzhansky and Pavlovsky (1960) and Battaglia and Smith (1962) showed that, in experimental population cages, the polymorphic populations produced more individuals, and a greater biomass, than did the monomorphic ones given the same amounts of food. Moreover, the polymorphic populations showed, for several characters, lower variances than the monomorphic ones. Using a rather different technique, Dobzhansky and Pavlovsky (1961) and Strickberger (1963) arrived at a similar conclusion—polymorphic populations yield more flies and a greater biomass than do monomorphic ones.

All the experiments referred to above had in common that the experimental populations were maintained under highly competitive conditions. The size of those populations was limited by the amount of the food given; in the experiments of Beardmore, Dobzhansky and Pavlovsky and in those of Battaglia and Smith (l.c.), the competition

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was most severe in the larval stage, while in those of Dobzhansky and Pavlovsky (l.c.) it was probably more severe in the adult stage. We now wish to enquire whether the polymorphic populations will conserve their superiority should the competition be relaxed. Suppose that these populations are given a supply of food and of other resources and conditions which, for a time, is not limiting; will polymorphic populations increase at rates different from monomorphic ones? What we wish to estimate is the statistic referred to as the "intrinsic rate of natural increase" (Lotka, 1925), "Malthusian parameter" (Fisher, 1930), or "innate capacity for increase" (Andrewartha and Birch, 1954).

Experimentally, this statistic must, working with *Drosophila*, be estimated indirectly, since it is hardly possible to provide an environment for an unimpeded growth of *Drosophila* populations even for a few generations. Birch, Dobzhansky, Elliott and Lewontin (1963) have evolved a technique for the estimation of this statistic in geographic races of the Australian species, *Drosophila serrata*. The following components of the capacity for increase are measured: (a) fecundity of the females at different ages, (b) survival from egg to adult, (c) duration of the development from egg to adult, (d) longevity of the females. The present report concerns the capacity for increase in ten experimental populations of *Drosophila pseudoobscura*, four of them polymorphic and six monomorphic ones. The experiments were conducted at two temperatures, 25° and 16° C.; they were repeated after a time interval of more than one year, in order to see what effects the adaptation to living in the experimental population cages may have.

2. THE EXPERIMENTAL POPULATIONS

Two series of experimental populations were set up, one containing third chromosomes with Arrowhead (AR) and Pikes Peak (PP) gene arrangements derived from wild flies collected at Mather, in the Sierra Nevada of California, in summer of 1959, and the other with AR and Chiricahua (CH) chromosomes from Piñon Flats, Mount San Jacinto, California, collected much earlier, namely in 1949. The manner in which these populations were made is important. We maintain in our laboratory about a dozen strains homozygous for each gene arrangement derived from different wild flies collected in a given locality. The strains are kept in mass cultures, to minimise inbreeding. The founders of each experimental population are always F₁ hybrids between all the available strains containing the desired chromosomes. The experimental populations, whether chromosomally polymorphic or monomorphic ones, are thus always provided with an initial supply of genetic variability, and are never homozygous for the gene complex which was carried in any one ancestral chromosome.

The experimental populations were kept in wooden population cages, with glass tops and wire mesh sides, in incubators or in constant

temperature rooms at 25° C. The populations were started on the following dates:—

No. 183, Polymorphic AR + PP	9th February 1960
No. 204, Polymorphic AR + PP	16th December 1960
No. 205, Monomorphic PP	17th December 1960
No. 206, Monomorphic AR	19th December 1960
No. 207, Polymorphic AR + PP	23rd December 1960
No. 208, Monomorphic PP	23rd December 1960
No. 209, Monomorphic AR	29th December 1960
No. 211, Polymorphic AR + CH	14th March 1961
No. 212, Monomorphic AR	14th March 1961
No. 213, Monomorphic CH	14th March 1961

The relative frequencies of the chromosomes with different gene arrangements in the polymorphic populations underwent changes, as shown in table 1. From time to time a sample of 150 larvæ was taken

TABLE 1
Changes in the frequencies of AR, CH and PP chromosomes in the polymorphic populations (in per cent.)

Days	211		183		204		207	
	AR	CH	AR	PP	AR	PP	AR	PP
0	50.0	50.0	50.0	50.0	50.0	50.0	50.0	50.0
35	60.3	39.7	57.0	43.0	59.7	40.3	59.0	41.0
70	68.7	31.3	75.3	24.7	63.3	36.7	69.3	30.7
105	69.3	30.7	83.7	16.3	74.7	25.3	75.7	24.3
140	70.7	29.3	89.0	11.0	81.0	19.0	77.3	22.7
210	68.7	31.3	—	—	82.0	18.0	86.7	13.3
280	68.3	31.7	85.3	14.7	89.3	10.7	86.3	13.7
365	71.3	28.7	85.7	14.3	90.0	10.0	91.0	9.0
427	—	—	—	—	93.7	6.3	90.0	10.0
455	75.7	24.3	91.7	8.3	—	—	—	—
545	80.0	20.0	—	—	94.0	6.0	93.3	6.7
572	—	—	96.0	4.0	—	—	—	—
635	77.3	22.7	—	—	95.7	4.3	91.7	8.3
730	80.3	19.7	95.3	4.7	96.3	3.7	97.3	2.7
815	—	—	—	—	96.3	3.7	98.0	2.0
845	—	—	100.0	0	—	—	—	—
905	78.3	21.7	—	—	98.7	1.3	—	—

in every population, and the gene arrangements were scored in 300 chromosomes per sample. In population No. 211, a stable equilibrium has apparently been reached, with AR chromosomes at a frequency between 75 and 80 per cent., and CH between 20 and 25 per cent. In contrast to this, no equilibria were established in the populations 183, 204 and 207; the PP chromosomes were eliminated or were close to elimination, and the populations became monomorphic for AR. This outcome is not surprising; PP is a relatively rare chromosome in California populations (Dobzhansky, 1963), and it appears to form

heterotic combinations with some, but not with all, types of chromosomes found there. This situation will be dealt with in more detail in another publication.

The first series of observations on the longevity and fecundity was started with flies hatching in the population cages Nos. 183 and 204-209 in January and February of 1961, and with the populations Nos. 211-213 in April and May of the same year. The populations (excepting No. 183) were at these times between one and two months old, and the flies used belonged to the first or to the second generation developing in the population cages. The chromosomes in the polymorphic populations were far from having reached their equilibrium frequencies. The second series of observations was started with the flies hatching in the population cages 12 to 17 months later, in 1962. The polymorphic populations were then approaching, although they had not quite reached, the equilibria, and the populations Nos. 183, 204 and 207 still had some PP chromosomes left. The two series were intended to represent the populations at the times when the selectional processes were operating in them and when these processes were close to completion.

3. THE CAPACITY FOR INCREASE

Although the estimates of the value r_m , the "innate capacity for increase", are derived from the data on the fecundity, longevity, viability and the development rate of the flies, it is convenient to begin our presentation with a consideration of this derived value. Lotka showed (1925) that a population growing with unlimited resources would approach a stable distribution of ages of individuals. When such a stable age distribution is reached, the population as a whole will grow at a constant geometric rate satisfying the differential equation:

$$\frac{dN}{dt} = r_m N \quad (1)$$

where N is the size of the population at any instant of time and r is the "rate of increase".

Lotka further showed that the rate of increase, r , in a population with a stable age distribution will be related to the age specific fecundity and mortality schedules by the following expression

$$\int_0^{\infty} e^{-r_m x} l_x m_x dx = 1 \quad (2)$$

where 0 to ∞ is the range of possible ages, l_x is the probability at birth of being alive at age x , and m_x is the number of female offspring produced per unit time at age x . This latter quantity is taken as half the number of eggs laid per unit time.

We use expression (2) to estimate r_m in our experiments by replacing the integration over continuous time by a summation over discrete

time intervals. The exact form of the expression used to estimate r_m is

$$a \sum_0^t e^{-r_m(x+F)} l_x m_x = 1 \quad (3)$$

where

a = proportion of eggs surviving to adults

t = observed maximum life span of our experimental animals

l_x = probability of survival of adults from hatching from the pupal case to age x

m_x = one half the number of eggs laid by a female of age x

x = age, in days, of an adult calculated from date of hatching from the pupal case

F = number of days from egg to pupal hatching

r_m = intrinsic rate of increase.

The value of r_m satisfying this expression is obtained by Newton's iterative method accurate to three decimal places. As expression (3) is written, it can be seen to be a function of four measurable quantities: development time from egg to adult (F), egg, larval and pupal survival (a), the proportion of adults still alive at age x (l_x), and the number of eggs laid by a female on day x of her adult life (m_x). We have made independent replicated estimates of each of these quantities and then combined these quantities to calculate r_m . Birch, Dobzhansky, Elliot and Lewontin (1963) have discussed the statistical problems involved in combining these independent estimates. In essence, we have calculated r_m for every possible combination of replicated values of a , F , l_x schedule and m_x schedule, and used the mean and variance of these combinations as an estimate of the mean r_m and variance of r_m . This, of course, is done separately for each population in each year. If there are 10 replicates of each of the four measurements then there will be 10,000 separate values of r_m calculated from which the variance of r_m is derived. However, these 10,000 values are not all independent so that the degrees of freedom associated with such a variance in statistical tests will be very much smaller than 9999. We take as a conservative value for degrees of freedom $\Sigma(n_i - 1)$ where n_i is the number of replicates of the i th component of the rate of increase. In the case where each component is measured in 10 replicates, there would then be 36 degrees of freedom associated with each variance in any test of significance.

Table 2 gives the means and variances of r_m calculated in this way for each of the populations in each year and temperature, together with the number of degrees of freedom to be associated with each variance. The numbers of replicates of each component which contribute to these degrees of freedom are given in the discussions of each type

of measurement below. Inspection of table 2 shows that at 16° the values of r_m are all considerably lower than at 25° as might be expected; the average r_m at 16° is almost exactly one-half of that at 25°. More

TABLE 2

The mean values of r , the "innate capacity for increase", variances, s_r^2 , and their degrees of freedom for the populations studied

Population	Chromosomes		25°		16°	
			1961	1962	1961	1962
211	AR + CH	\bar{r}	0.217	0.222	0.104	0.096
		s_r^2	0.0001161	0.0005819	0.0000586	0.0000442
		d.f.	26	36	26	36
212	AR	\bar{r}	0.198	0.215	0.097	0.098
		s_r^2	0.0002430	0.0007639	0.0000690	0.0000765
		d.f.	26	36	26	36
213	CH	\bar{r}	0.200	0.185	0.101	0.091
		s_r^2	0.0003579	0.0005056	0.0000247	0.0000438
		d.f.	26	36	25	36
183	AR + PP	\bar{r}	0.226	0.226	0.120	0.112
		s_r^2	0.0004959	0.0002234	0.0000554	0.0000993
		d.f.	26	35	26	36
204	AR + PP	\bar{r}	0.209	0.210	0.106	0.108
		s_r^2	0.0008084	0.0004043	0.0001543	0.0000545
		d.f.	26	36	26	36
207	AR + PP	\bar{r}	0.196	0.220	0.093	0.122
		s_r^2	0.0008984	0.0002186	0.0002066	0.0000722
		d.f.	26	36	26	36
206	AR	\bar{r}	0.205	0.197	0.114	0.108
		s_r^2	0.0007512	0.0007953	0.0000537	0.0001365
		d.f.	26	36	26	36
209	AR	\bar{r}	0.198	0.220	0.102	0.106
		s_r^2	0.0007670	0.0002381	0.0002275	0.0001333
		d.f.	27	36	27	36
205	PP	\bar{r}	0.158	0.177	0.090	0.098
		s_r^2	0.0007067	0.0006312	0.0002694	0.0000736
		d.f.	26	36	26	36
208	PP	\bar{r}	0.149	0.197	0.087	0.104
		s_r^2	0.0052889	0.0005548	0.0004681	0.0001429
		d.f.	26	36	26	36

important and interesting is the difference between genotypes. It is immediately obvious that at both temperatures the polymorphic populations and the pure AR populations have the highest r_m ; pure

PP populations have the lowest and pure CH populations are intermediate. This can be seen better in table 3, where the genotypes are arranged in descending order. In these tabulations the replicate populations of AR + PP, AR and PP have been averaged together

TABLE 3
Ordered comparisons of rates of increases, r_m , for different genotypes. Order is based on averages over the two years

Genotype	At 25°		Mean	Genotype	At 16°		Mean
	1961	1962			1961	1962	
AR + CH .	0·217	0·222	0·220	AR + PP .	0·106	0·114	0·110
AR + PP .	0·209	0·219	0·214	AR (Piñon) .	0·108	0·107	0·108
AR (Mather) .	0·198	0·215	0·207	AR + CH .	0·104	0·096	0·100
AR (Piñon) .	0·202	0·208	0·205	AR (Mather) .	0·097	0·098	0·098
CH .	0·200	0·185	0·192	CH .	0·101	0·091	0·096
PP .	0·154	0·187	0·170	PP .	0·088	0·101	0·094

although population 212 AR is not pooled together with the other two AR populations since it is of a different geographical origin. At 25° the polymorphic populations are higher than the monomorphic populations, and among the monomorphics AR is best, CH next and

TABLE 4
Analysis of variance for the data in table 3

Source	At 25°		M.S.	F	At 16°		M.S.	F
	S.S.	d.f.			S.S.	d.f.		
Years .	0·013065	1	0·013065	17·3 P < 0·001	0·000004	1	0·000004	0·025 P > 0·9
Genotypes	0·155935	5	0·031187	41·4 P < 0·001	0·020370	5	0·004074	26·8 P < 0·001
Interaction	0·031035	5	0·006207	8·2 P < 0·001	0·009950	5	0·001990	13·1 P < 0·001
Error .	0·474448	630	0·000754		0·096006	629	0·000152	

PP poorest. There is no appreciable difference between the Arrowhead populations of different geographical origin.

At 16° the picture is less clear. The differences among the genotypes are not as great, and while CH and PP monomorphic populations are still the poorest, there is no consistent superiority of polymorphic populations over monomorphic Arrowhead.

Before any discussion of the biological significance of these differences is possible, it is necessary to test whether the differences among the genotypes are in fact real. Table 4 shows the results of

two separate analyses of variance, one for each temperature, of the data in table 3. The within genotype sum of squares has been obtained by combining the within population variances given in table 2 with the between population variances where there is more than one population of a given genotype. The total sum of squares thus obtained is divided by the total of all the degrees of freedom in table 2, plus the extra degrees of freedom introduced from replicate populations. Since different numbers of degrees of freedom are involved for the within genotype variances in different populations, the harmonic mean of the different numbers is used in the analysis. The tests of main effects and interactions use the error mean square since the model is a fixed factor design.

The analysis of variance shows that the genotypes differ significantly from each other at both temperatures; at 25°, but not at 16°, there is a difference between years, the value of r_m having increased with the life of the populations.

4. THE COMPONENTS OF r_m

Before discussing the differences in the various components of r_m , the relationship of the components to r_m itself needs to be considered.

TABLE 5
Number of eggs per female per life

Population	Chromosomes	Eggs at 25° C.		Eggs at 16° C.	
		1961	1962	1961	1962
211	AR+CH	431.3	322.7	374.0	629.5
212	AR	282.9	239.6	307.5	524.6
213	CH	316.4	182.1	319.9	420.0
183	AR+PP	248.2	276.2	418.1	744.4
204	AR+PP	202.4	285.6	315.6	622.4
207	AR+PP	218.2	275.8	333.6	725.3
206	AR	334.7	176.5	401.6	531.6
209	AR	215.1	334.1	273.4	569.8
205	PP	81.5	140.9	238.6	428.6
208	PP	82.3	168.7	206.7	472.9

In general, an increase in total fecundity, or average longevity will increase r_m but not in any simple way. Equation (3) shows that the contribution of eggs laid at time x to r_m is proportional to e^{-rx} . Thus, eggs laid late in life make very little contribution. For example, if $r_m = 0.25$, each egg laid on day 1 makes a contribution to the summation in equation (3) of 0.78, while each egg on the 10th day makes a contribution of only 0.08. The same is true for added longevity. In addition, small decreases in development time (F) count heavily in increasing r . In our data, for example, a 1-day decrease in development time has the same effect as increasing the egg laying rate or larval viability by one-third. For this reason, mean fecundities or mean

longevities are not really good indices of population performance. This is shown clearly in our data. Taking total lifetime fecundities (table 5), the order of populations at 25° is:

$$AR + CH \gg AR \text{ (Mather)} > AR \text{ (Piñon)} > AR + PP = CH \gg PP$$

which does not correspond to the ordering of r_m values in table 2. If only the fecundities during the first 10 days of egg laying are taken (table 6), the order is:

$$AR + CH > AR + PP > AR \text{ (Mather)} = AR \text{ (Piñon)} > CH > PP$$

which is in excellent agreement with the ordering of r_m values in table 2.

TABLE 6
Mean number of eggs per female per day at 25°

Population		Year	Interval (days)		
			3-6	7-12	13+
211	AR + CH	1961	18.1 ± 2.2	18.2 ± 1.9	6.2 ± 0.9
212	AR	1961	13.3 ± 1.7	11.1 ± 1.1	2.3 ± 0.4
213	CH	1961	16.7 ± 1.7	11.8 ± 1.2	4.6 ± 0.7
211	AR + CH	1962	25.9 ± 2.6	12.2 ± 1.0	4.6 ± 0.5
212	AR	1962	23.3 ± 2.3	15.6 ± 1.4	5.0 ± 1.0
213	CH	1962	13.8 ± 1.1	7.3 ± 0.8	2.5 ± 0.5
183	AR + PP	1961	20.0 ± 1.6	12.8 ± 1.6	5.5 ± 1.4
204	AR + PP	1961	17.6 ± 1.5	9.7 ± 1.3	4.0 ± 0.7
207	AR + PP	1961	17.6 ± 1.5	10.3 ± 1.8	5.7 ± 1.0
206	AR	1961	20.8 ± 1.2	11.1 ± 0.5	5.1 ± 0.7
209	AR	1961	13.9 ± 1.3	8.8 ± 1.1	6.6 ± 0.8
205	PP	1961	8.3 ± 1.5	5.1 ± 0.9	5.2 ± 0.9
208	PP	1961	9.5 ± 1.1	2.0 ± 0.6	0
183	AR + PP	1962	22.3 ± 1.3	9.4 ± 1.0	2.4 ± 0.6
204	AR + PP	1962	19.1 ± 1.7	12.2 ± 1.3	3.8 ± 0.7
207	AR + PP	1962	19.7 ± 1.5	12.2 ± 1.0	3.4 ± 0.5
206	AR	1962	17.3 ± 1.6	9.3 ± 1.2	2.6 ± 0.8
209	AR	1962	20.6 ± 1.3	16.5 ± 0.8	4.4 ± 0.6
205	PP	1962	12.4 ± 1.0	5.5 ± 0.6	1.4 ± 0.3
208	PP	1962	15.0 ± 1.3	8.9 ± 1.2	0.6 ± 0.5

Such a consideration may, in fact, lie at the basis of discrepancies between intra-population fitness and fitness as measured by r_m .

The variables which make little contribution to r_m may nevertheless be important in population fitness. It is, for example, conceivable that under some environmental conditions it is the fecundity of the most long-lived 1 per cent. of the population that enables the population to survive instead of becoming extinct. We have, therefore, examined the components of r_m in detail.

5. FECUNDITY

Cups were taken from the population cages when pupæ were forming in them, provided with transparent plastic "chimneys", and the flies were collected daily when they hatched. Groups of 4 females

and equal or greater numbers of males were placed in glass tubes with cotton plugs, and given paper spoons with a nutrient medium for oviposition. The medium devised by Kalmus, to which carbon black was added to make the eggs more conspicuous, was used, its surface being lightly smeared with a suspension of Fleishmann's yeast. The eggs were counted, and spoons with fresh medium were substituted daily at 25°, and on alternate days at 16° C.

The mean lifetime egg production per female is reported in table 5. The fecundity in our experiments was much lower than that observed by Tantawy and Vetukhiv (1960) and Tantawy (1961). The difference is due to the techniques used. In our experiments, the ovipositing females were raised in overcrowded cups in the population cages, while in those of the authors just quoted they were raised under more nearly optimal conditions. This was planned deliberately, to observe the capacity for increase in populations developed under crowding and competition for food, when this competition is suddenly removed. Moreover, the Kalmus medium seems to be less favourable for oviposition than the regular Spassky culture medium used in our laboratory. It must, then, be stressed that the r_m values which we have obtained are certainly not the maximal which the species is capable of developing.

The population No. 211, polymorphic for AR and CH, showed a higher total fecundity than the monomorphic AR or CH (Nos. 212 and 213). The monomorphic PP populations are consistently below the monomorphic AR or the polymorphic AR + PP, but the latter give variable and inconsistent results. At 25°, AR No. 206 had the highest fecundity in 1961 and one of the lowest in 1962, while AR No. 209 was most fecund in 1962 but only moderately so in 1961. In general, the flies were more fecund in 1962 than in 1961 (in 16 out of the 20 paired comparisons listed in table 5). There were, however, some exceptions, the two most striking ones being populations Nos. 213 and 206 at 25°. Several generations in a population cage lead to an "improvement" in that environment.

In *Drosophila pseudoobscura*, the oviposition starts within a few days after the hatching from the pupa, rapidly increases to a maximum and then declines slowly until death. We have made daily counts of the eggs at 25°, and on alternate days at 16°. The numbers of eggs deposited by a female on successive days are highly variable. It appears that a crop of eggs mature in the ovaries, are deposited within a few hours and then it takes a day or two for a new crop of eggs to be ready for deposition. For statistical purposes, we have rather arbitrarily divided the oviposition period in three parts at 25°, and in five parts at 16°, and then computed the mean numbers of eggs per day deposited by a female in the ten replicate cultures of each population (each containing initially 4 females and about 6 males). The first two days of life at 25°, and the first three at 16°, are disregarded, since very few eggs are produced by immature females.

Although the experimental errors are large, it is clear enough that the females from the polymorphic populations tend to be more fecund at 25° than those from the monomorphic ones (table 6), especially during the early part of the oviposition period. The AR+CH population produced more eggs than AR or CH; the AR+PP populations were clearly more fecund than PP, but about equal to AR. At 16° (table 7) the situation is less clear. The polymorphic AR+CH was

TABLE 7
Mean number of eggs per female per day at 16°

Population		Year	Interval (days)				
			4-6	7-12	13-24	25-36	37+
211	AR+CH	1961	10.3±2.9	10.6±1.0	6.7±0.7	4.2±0.6	3.1±0.4
212	AR	1961	7.6±1.5	8.3±1.3	4.3±0.6	2.8±0.4	3.1±0.6
213	CH	1961	10.4±1.4	8.9±0.9	4.9±0.4	2.2±0.3	1.0±0.2
211	AR+CH	1962	11.8±1.9	17.1±0.9	13.6±0.7	8.1±0.9	8.2±1.3
212	AR	1962	10.2±1.3	14.5±1.0	10.6±0.7	6.1±0.6	4.1±0.5
213	CH	1962	8.4±1.3	11.8±0.8	10.6±0.6	4.5±0.5	1.7±0.3
183	AR+PP	1961	11.3±1.0	13.3±1.2	8.4±0.7	5.3±0.6	1.6±0.5
204	AR+PP	1961	11.3±1.2	9.5±0.9	7.8±1.0	5.1±0.8	0.5±0.2
207	AR+PP	1961	9.5±1.2	8.0±0.9	5.9±0.5	1.4±0.3	1.1±0.3
206	AR	1961	13.5±1.0	7.5±0.7	7.8±0.6	5.6±0.6	1.3±0.4
209	AR	1961	8.5±1.1	5.1±0.7	7.8±0.4	3.2±0.6	—
205	PP	1961	4.7±0.8	6.1±0.7	7.6±0.7	3.53±0.5	0
208	AR	1961	7.9±1.4	5.1±0.7	9.7±0.9	5.6±0.6	1.3±0.4
183	AR+PP	1962	14.0±1.3	17.5±1.1	11.1±0.6	7.8±0.7	6.5±0.8
204	AR+PP	1962	14.9±1.5	17.1±1.2	11.4±0.6	5.6±0.6	4.3±0.6
207	AR+PP	1962	15.8±1.2	18.0±1.3	14.1±0.9	7.7±0.7	4.0±0.8
206	AR	1962	13.4±1.4	14.1±0.9	11.0±0.7	8.0±0.6	2.4±0.3
209	AR	1962	10.1±1.2	13.2±0.8	10.5±0.6	6.8±0.5	2.8±0.3
205	PP	1962	12.1±1.2	12.2±0.7	8.8±0.5	4.3±0.4	0.9±0.8
208	PP	1962	12.6±1.2	12.6±0.8	10.0±0.5	5.2±0.5	1.2±0.9

rather consistently above AR or CH in 1962, but not in 1961. Among the polymorphic AR+PP, the population No. 207 was below the other two (Nos. 183 and 204) in 1961, but above in 1962. The monomorphic PP tended to be low in fecundity, but not consistently so. At 16°, the fecundity was quite consistently higher in 1962 than in 1961, while at 25° it was sometimes higher and sometimes lower. An "improvement" at the lower temperature was actually unexpected, because the populations from which the material came were kept at the higher temperature, 25°.

6. LONGEVITY

The flies for measurements of the longevity were obtained from the same source as those used in the fecundity tests, *i.e.*, from the cups withdrawn from the population cages. However, to study the longevity

groups of 10 females and 10 males were placed in half-pint bottles with Kalmus medium to which no carbon black was added. A drop of yeast suspension and a loose strip of sterilised white paper towelling were placed in each bottle. For each population, 10 replicate bottles were kept at 25° and an equal number at 16°. The flies were transferred, without etherisation, to fresh culture bottles at 2-day intervals

TABLE 8

Mean longevity, in days, in females and in males

Population	Chromosomes	25°		16°	
		1961	1962	1961	1962
Females					
211	AR+CH	38.09±1.21	29.09±0.83	88.55±3.18	56.09±1.81
212	AR	37.51±1.24	25.81±0.86	89.44±3.56	62.30±1.95
213	CH	31.28±1.10	25.08±0.67	77.27±2.47	55.45±1.73
183	AR+PP	26.09±1.03	27.16±0.78	66.38±2.75	55.05±1.54
204	AR+PP	26.96±1.20	25.83±0.77	53.55±2.53	53.38±1.27
207	AR+PP	26.02±0.97	24.15±0.71	40.44±2.68	54.44±1.37
206	AR	38.10±1.57	25.47±0.76	60.37±2.23	47.74±1.38
209	AR	29.36±1.51	25.96±0.77	68.26±2.70	49.29±1.20
205	PP	18.89±0.88	20.05±0.68	47.78±2.93	48.84±1.61
208	PP	15.61±0.82	24.81±0.73	33.95±2.01	48.29±1.27
Males					
211	AR+CH	22.65±0.88	16.35±0.44	53.52±1.75	27.30±0.92
212	AR	22.90±1.00	14.82±0.43	51.96±2.57	28.86±0.87
213	CH	21.95±0.76	14.98±0.31	44.93±1.50	26.44±0.76
183	AR+PP	17.12±0.60	20.43±0.58	30.52±0.95	37.03±1.01
204	AR+PP	17.37±0.71	19.26±0.59	30.63±0.96	28.88±0.76
207	AR+PP	19.88±0.58	16.65±0.54	19.91±0.79	31.03±0.82
206	AR	19.91±0.60	17.20±0.56	33.66±0.98	30.92±0.75
209	AR	16.51±0.57	19.14±0.60	31.23±1.38	30.09±0.81
205	PP	14.85±0.58	13.74±0.47	26.17±0.91	24.49±0.74
208	PP	10.69±0.35	14.90±0.56	20.32±0.77	21.94±0.61

at 25°, and twice per week at 16°. The remains of dead flies, easily visible on the transparent medium, were counted. The results are reported in table 8. Each mean value is, thus, based on observation of 100 flies.

The results were different in 1961 and in 1962. In 1961, the females from the monomorphic CH population (No. 213) had a significantly shorter life duration than those from the monomorphic AR (No. 212) or from the polymorphic AR+CH population (No. 211). The same was true of the males at 16°, but at 25° there was no significant difference. The polymorphic and the monomorphic AR populations did not differ in longevity. The monomorphic PP populations (Nos. 205 and

208) were inferior in longevity to the corresponding monomorphic AR (Mather, Nos. 206 and 209), but there was no consistent difference between the latter and the polymorphic AR + PP. At 16°, the polymorphic population No. 207 showed actually the lowest longevity.

In 1962, the longevity was more nearly uniform in all populations than it was in 1961. At 25°, but not at 16°, the polymorphic AR + CH was superior to the monomorphic AR (No. 212) and CH. Monomorphic PP was no longer consistently inferior to AR and to AR + PP—the inferiority seemed to persist in males but not in females. The polymorphic AR + PP lived longer than the monomorphic AR and PP at 16° but not at 25°, and even then only as females but not as males. The striking and unexpected change was, however, that the mean longevity actually *decreased* in 1962 as compared with 1961 in most populations. While, as we have seen above, these populations improved with time with respect to the fecundity, they rather deteriorated with respect to longevity. Only the monomorphic PP populations (Nos. 205 and 206), which had the lowest longevity in 1961, did not change or even improve in 1962. This is the main reason why the longevity of all populations was more uniform in 1962 than in 1961.

7. VIABILITY AND DEVELOPMENT RATE

Females developed in the population cages were allowed to oviposit on paper spoons with the Kalmus synthetic medium, to which carbon black was added for easier visibility. Samples of 50 eggs were taken and transferred, on excised blocks of food (so that the eggs themselves were not distributed), to bottles with the ordinary culture medium. Ten such samples were taken from each population in 1961, and another ten in 1962. The adult flies hatching from these samples were counted; the results are summarised in table 9. The egg to adult survival was between 71 and 96 per cent., with no consistent differences between the populations or between years.

Rather unexpected technical difficulties arose in the study of the length of the development from egg to adult. The flies hatched in the population cages were transferred at daily intervals to fresh culture bottles, to ensure that the females were active egg layers and did not have developing eggs in their vaginæ (as happens with females which withhold their eggs because of unfavourable conditions). When the females were near the peak of their egg laying, they were transferred several times to fresh culture bottles, at intervals no more than 3 hours at 25° and at most 6 hours at 16°, to obtain cultures with eggs deposited at a known time. Always more than 10 replicate cultures were obtained for each series, because only the cultures in which more than 25 but fewer than 100 adult flies hatched were utilised, and those underpopulated and overpopulated were ignored. The counts of the hatching flies were made twice daily in the 1961 series, and once daily in 1962. As a rule, the hatching extended from about the 12th to the

17th day at 25°, and from the 25th to the 38th day after the egg laying at 16°. Despite all the precautions, there was some heterogeneity among the replicate cultures, some developing faster and others slower than the rest. No relation was found between the development

TABLE 9
Viability—per cent. survival from egg to adult

Population	Chromosomes	25° C.		16° C.	
		1961	1962	1961	1962
211	AR+CH	90.6	88.4	96.2	88.0
212	AR	87.2	90.8	91.6	87.2
213	CH	71.6	87.2	77.6	88.6
183	AR+PP	84.8	92.1	93.6	89.8
204	AR+PP	79.2	92.4	86.8	88.8
207	AR+PP	81.2	88.3	90.0	89.0
206	AR	90.0	89.4	96.0	92.4
209	AR	89.2	93.3	94.8	87.6
205	PP	83.2	83.0	90.0	82.0
208	PP	75.2	82.9	75.3	81.8

TABLE 10
Rate of development from egg to adult in days (females)

Population	Chromosomes	25°		16°	
		1961	1962	1961	1962
211	AR+CH	13.73±0.17	14.52±0.34	31.56±1.05	38.90±0.89
212	AR	13.85±0.27	14.89±0.22	31.35±1.06	36.51±0.62
213	CH	14.44±0.22	14.23±0.39	30.40±0.61	37.02±1.03
183	AR+PP	13.74±0.17	13.94±0.24	29.68±0.39	34.47±0.79
204	AR+PP	13.72±0.26	14.16±0.22	29.34±0.70	33.39±0.42
207	AR+PP	13.37±0.17	13.51±0.22	31.29±0.86	30.72±0.51
206	AR	13.40±0.17	16.46±0.35	30.81±0.84	33.02±0.74
209	AR	13.66±0.16	13.93±0.36	30.31±1.41	39.73±0.69
205	PP	13.79±0.45	14.32±0.23	28.22±0.55	32.91±0.94
208	PP	13.50±0.09	13.50±0.27	31.50±1.11	37.01±0.53

time and the number of the flies hatching in a culture. None of the cultures utilised was overcrowded. We suspected that there may be temperature variations between the cultures standing on the front part and in the rear of the shelves in the constant temperature room. The whole experiment was repeated in 1961, the cultures being moved daily from the front to the rear on the shelves, and *vice versa*. The heterogeneity between the replicating did not disappear. Evidently there were some environmental variations between the replicate cultures which we did not succeed in detecting and eliminating.

As table 10 shows, the standard errors for development time are quite large, sometimes as great as 1 day, because of the relatively large differences between replicates. Thus, the observed differences between mean development times for the different populations cannot be given any significant biological interpretation.

8. DISCUSSION

Beardmore, Dobzhansky and Pavlovsky (1960), Dobzhansky and Pavlovsky (1961), and Battaglia and Smith (1962) have shown that under competitive conditions the chromosomally polymorphic populations of *Drosophila pseudoobscura* are superior to the monomorphic populations. Both when the competition was due to a crowding in the larval stage and when the adults were crowded, the polymorphic populations produced more individuals and a greater biomass than did the monomorphic ones given the same amount of food. In the present investigation, a quite different measure of the population fitness is introduced. The competition by crowding is eliminated; we estimate the value r_m , which measures essentially the capacity of the population to increase in numbers of individuals under a certain set of environmental conditions.

As expected, the populations are more fit at 25° than at 16° C. (table 3). This does not mean, of course, that a higher temperature will always increase the r_m values; *D. pseudoobscura* populations can be maintained in the laboratory with some difficulty at 27°, but as a rule not at 27½°. The higher values of r_m at 25° than at 16° are due to the more rapid development, and to the at least equal egg laying rate during the early part of the adult life at the higher temperature. More interesting is the increase with time of the r_m values in most of the populations at 25°. This must be ascribed to the adaptation of the populations to the environment of the population cages, rather than to the attainment of the equilibrium frequencies of the chromosomal polymorphs. In fact, the increase in r_m was more prominent in the chromosomally monomorphic than in the polymorphic populations (tables 2 and 3). Particularly noticeable is the improvement in the monomorphic PP populations, which had originally the lowest fitness. This improvement has occurred both at 25° and at 16°, although the population cages were maintained at the former temperature.

Comparison of the r_m values in the different populations shows that the polymorphic populations are usually superior to the monomorphic ones with similar histories and tested simultaneously (tables 2 and 3). This is consistent with the behaviour of the chromosomes with different gene arrangements within the populations kept at 25°. The heterokaryotypes usually exhibit, at that temperature, heterosis, and consequently a population which includes heterokaryotypes may be expected to be fitter than the one consisting entirely of homokaryotypes. At 16° the heterotic advantage of the heterokaryotypes over

the homokaryotypes is, however, weak or absent (Wright and Dobzhansky, 1946). In agreement with this, the polymorphic AR+CH populations are not superior to the monomorphic AR (Piñon) populations (table 3).

A closer analysis discloses, however, several facts which could not have been predicted from the known behaviour of the chromosomes within the populations. As shown in table 1, the PP chromosomes are eventually eliminated in competition with AR. This confirms the observations on the same chromosomes made earlier by Dobzhansky (1957) and by Lewontin (1958). The AR/PP heterokaryotype should accordingly not be superior to the AR/AR homokaryotype, even at 25°. Nevertheless, the polymorphic AR+PP populations have, both at 25° and at 16°, higher r_m values than the monomorphic AR, and these latter higher than the monomorphic PP. Thus, the effect of the natural selection on the karyotype frequencies in the polymorphic AR+PP populations is to make those populations evolve towards a composition with a lower r_m value. This can be seen most clearly in table 3. In 1961, when the frequency of PP chromosomes in the polymorphic populations was high, the r_m value for these populations was 0.209, and for AR (Mather) populations 0.198 (table 3). A year later, in 1962, the frequency of PP in the polymorphic populations was low (about 5 per cent.), but the r_m rose to 0.219, while in the monomorphic AR populations it rose to 0.215. The net superiority of the polymorphic populations was, hence, 0.011 in 1961 and only 0.004 in 1962. With the loss of PP chromosomes, the r_m s in the polymorphic and the monomorphic populations converge, as expected. A similar phenomenon was observed by Lewontin and Matsuo (1963), in *Drosophila busckii*, where a genotype which was superior in mixed cultures had a lower viability in pure cultures.

Our conclusion must be that, although in broad outline there is a correspondence between the relative fitness of the karyotypes within the populations and the population fitness as measured by the r_m , there may be, in particular cases, no relation or even an inverse relation between these measurements. This may indicate that the value r_m is unduly influenced by variables which do not have a proportionate ecological importance in nature. As pointed out above, in our experiments the r_m is correlated with the rate of egg laying during the early part of the adult life, less so with the longevity or with rates of egg laying at older ages, and very little, at a given temperature, with the development rate and with the viability. Similarly, in the experiments of Beardmore, Dobzhansky and Pavlovsky (1960) and Dobzhansky and Pavlovsky (1961), there was no indication of heterosis in polymorphic populations with respect to the mean body size or body weight of the adult flies, but a clear heterosis in the numbers of individuals and in the biomass produced.

The relative fitness of populations, like that of genotypes within a population, is not the same in different environments. Comparisons

of fitness should, ideally, be made over the entire range of the environments to which the populations, or the genotypes, are exposed, and should also take into account the incidence of these environments in the natural habitats of the species. This ideal is hardly ever attainable; working with *Drosophila*, the experiments are made in environments which are not exactly like any that the flies inhabit in nature. It is, then, rather remarkable that in almost all the environments in which the chromosomally polymorphic and monomorphic populations were compared in the experiments of Beardmore, Dobzhansky and Pavlovsky (see above), as well as in the present ones, the results showed as consistently as they did that the polymorphic populations were superior to the monomorphic ones.

9. SUMMARY

Ten experimental laboratory populations of *Drosophila pseudoobscura*, four of them polymorphic and six monomorphic for gene arrangements in the third chromosomes, were examined for the rates of survival and the duration of the development from egg to adult, and for the longevity and the fecundity of the females at different ages. These observations were used to compute the value r_m , the innate capacity for increase, of the populations examined. The observations were run at two temperatures, 25° and 16° C., and were repeated in 1961 and in 1962, when the populations were only beginning, and after they had had some time to adapt to the living conditions in the population cages.

By and large, the r_m was higher in the polymorphic than in the corresponding monomorphic populations, the superiority of the polymorphic ones being generally more pronounced at 25° than at 16°. This superiority did not depend equally on all the components of the r_m , but chiefly on a greater fecundity of the females from the polymorphic populations. The r_m value has increased in most populations between 1961 and 1962, the increase being especially striking in the populations which had the lowest r_m in 1961. The increase depended again chiefly on a higher fecundity, while the duration of life has, on the contrary, declined in at least some of the populations. As a measure of the fitness of a population, the r_m value has both virtues and limitations.

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