THE INFLUENCE OF SEXUAL AND LARVAL SELECTION ON THE MAINTENANCE OF POLYMORPHISM AT THE SEPIA LOCUS IN *DROSOPHILA MELANOGASTER*

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Manuscript received September 21, 1979
Revised copy received April 14, 1980

ABSTRACT

Sexual selection is measured between two strains of *Drosophila melanogaster*: a wild strain and a strain mutant at the sepia locus. Frequency-dependent male mating was found to be successful, whereas the female genotype exerted no influence. The rarer the male genotype becomes, the greater is its mating success. A selection model is built for this behavior characteristic in which selection operates differently in the two sexes. The genetic consequencies of this model upon the maintenance of genetic polymorphism at the sepia locus are compared to experimental data from previous population cage studies. The fit obtained with this sexual selection model is compared to that of the larval selection model previously investigated. A model composed of both sexual and larval components of fitness is presented. The role that each major selection component is expected to play in experimental populations as the gene frequency changes is discussed. Sexual selection leads to an equilibrium level higher than larval selection, and the combined model is very close to the experimental values.

THIS study deals with the role of a behavioral characteristic in the maintenance of polymorphism in an experimental population of *Drosophila melanogaster*. The existence of sexual selection in Drosophila species was demonstrated many years ago (DOBZHANSKY 1944; DOBZHANSKY and MAYR 1944) and has been found in several instances to depend on the frequency of competing genotypes, where rare types are often at an advantage and common types at a disadvantage in a population (PETIT 1951, 1954, 1958; EHRMAN 1966; EHRMAN *et al.* 1965; EHRMAN and PETIT 1968; SPIESS and SPIESS 1969; EHRMAN and PROBBER 1978). This model of selection is thought to be a possible mechanism for maintaining genetic polymorphisms in nature.

In previous papers (ANXOLABEHERE 1976a,b) I have described the maintenance of genetic polymorphism at the sepia (*se*, 3–26.0) locus in an experimental population of *Drosophila melanogaster*, and more especially the larval component of fitness at this locus. The aim of the present paper is (1) to measure sexual selection between two strains that maintain a balanced polymorphism at the sepia locus when they are in competition in population cages; (2) to compare

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the observed equilibrium level to that expected under either sexual selection or larval selection alone; and (3) to discuss the contribution of both viability and mating success fitness components at the sepia locus in order to see what role each component can be expected to play as the gene frequency changes.

MATERIALS AND METHODS

The two strains of *Drosophila melanogaster* used in this study were Tautavel, a wild strain collected two years previous to experimentation, and sepia, a strain (called sepia-o here) kept in the laboratory for many years. The genetic backgrounds of these strains were radically different.

Two techniques were put to use: (1) the direct observation technique originally devised by ELENS and WATTIAUX (1964), and (2) multiple choice. In the first, males and females, aged separately for at least 3 days, were introduced into a 6×6 inch plexiglas chamber, and the different mating types were recorded during 1 hr at 25° and 70% RH. When 2 genotypes had the same phenotype, the distal margin of 1 wing was clipped in 1 genotype to make that genotype distinguishable through the transparent cover of the observation chamber. This marking was rotated from genotype to genotype so that no 1 genotype in any combination of 2 tested together always had its wings clipped. That such wing clipping does not affect the mating propensities of the marked individuals has been shown before (EHRMAN 1966; EHRMAN and PETIT 1968) and was confirmed by us with the strains we used.

The mating frequencies were observed for each genotype in competition with each of the other 3 genotypes. The 2 heterozygous genotypes *se*/+ and +/*se* were distinguished according to their maternal genotype, *se*/*se* or +/+. For every experiment, 3 proportions were used: (1) 5 males and females of 1 genotype plus 20 males and females of a second genotype, (2) 12 couples from one genotype and 12 from another, and (3) the reciprocal of proportions 1.

In addition, male sexual selection was measured by means of the multiple choice technique. One hundred 3-day-old *se*/*se* virgin females and 100 males of 3 different genotypes, *se*/*se*, *se*/+ (the males of heterozygous genotypes were from +/+ or *se*/*se* maternal genotypes) and +/+, were placed in a jar containing food medium. After 2 hr, each female was isolated and the genotype of the male she mated with was determined by observing the phenotype of more than 50 F_1 progeny. This length of time proved enough to allow all females to be inseminated, but made double mating very unlikely.

Male sexual selection was measured at 5 different allelic frequencies: 0.20, 0.40, 0.50, 0.70, 0.80. Male proportions agreed with those of the Hardy-Weinberg law. The influence of male or female genotypes in sexual selection was tested by means of a chi-square test for goodness-of-fit to a random mating distribution. The frequency-dependent mating success of males was measured by the regression of the logarithm of the ratio of males that mated on the logarithm of the ratio at which the males were present. This graphical method previously described by DE WIT (1960) was proposed as a test for frequency dependence in sexual selection by AYALA (1972).

RESULTS AND DISCUSSION

Table 1 summarizes the results of the experiments using the direct observation technique. The tests for random mating distribution (χ^2 r.m.) were always significant at the 0.01 level when the *se*/*se* genotype competed. This discrepancy from a panmictic distribution was due to a male sexual selection and not any female sexual selection; in fact, the female chi-square tests (χ^2 ♀) were not significant (2 significant tests out of 18 at the 0.05 level; the probability of obtaining this score is greater than 0.05). By contrast, the male chi-square tests (χ^2 ♂) in which the sepia male genotype competed were all significant. In the three ex-

TABLE 1

Mating observed in chambers at different genotypic proportions†

Genotypes 1	Genotypes 2	Proportions 1	Proportions 2	Mating types 1×1	1×2	2×1	2×2	χ^2 r.m. (3 df)	Mated ♀♀ 1	Mated ♀♀ 2	Mated ♂♂ 1	Mated ♂♂ 2	χ^2 ♀♀ (1 df)	χ^2 ♂♂ (1 df)
se/*se*	+/+	5	20	4	16	43	158	16.84**	47	174	20	201	0.22	16.56**
		12	12	19	18	63	66	51.12**	82	84	37	129	0.02	50.99**
		20	5	78	24	82	29	144.54**	160	53	102	111	3.17	137.28**
se/*se*	*se*/+	5	20	4	11	40	115	17.17**	44	126	15	155	3.67	13.07**
		12	12	16	22	49	54	30.83**	65	76	38	103	0.86	29.96**
		20	5	55	11	46	17	72.03**	101	28	66	63	0.23	67.05**
se/*se*	+/*se*	5	20	2	12	34	106	13.41**	36	118	14	140	1.10	11.45**
		12	12	16	14	72	66	69.90**	89	80	30	139	0.38	70.30**
		20	5	65	5	48	16	71.65**	113	21	70	64	1.57	64.54**
se/+	+/+	5	20	15	32	39	134	5.40	54	166	47	173	2.84	0.26
		12	12	24	18	31	46	14.68**	55	64	42	77	0.68	10.29**
		20	5	94	32	42	10	11.50**	136	42	126	52	1.44	9.44**
+/*se*	+/+	5	20	11	30	27	137	2.48	38	167	41	164	0.27	0.00
		12	12	26	40	48	63	16.20**	74	103	66	111	4.75*	11.44**
		20	5	112	32	32	13	4.78	144	45	144	45	1.71	1.71
se/+	+/*se*	5	20	26	51	52	170	19.44**	78	221	77	222	6.92*	6.18**
		12	12	84	66	84	101	7.31	168	167	150	185	0.00	3.66
		20	5	156	47	50	13	3.47	206	60	203	63	1.09	2.27

† *se*/+ and +/*se* are the heterozygote genotypes from *se*/*se* and +/+ maternal genotypes, respectively.
* Significant at the 0.05 level.
** Significant at the 0.01 level.

periments where only wild phenotypes competed, every significant χ^2 r.m. corresponded to a male selection (the χ^2 ♂ was significant). It seems that there was no significant difference in mating success between the two heterozygotes (from the reciprocal cross) when they were competing with one another. Thus, the direct observation technique shows that: (1) sexual selection exists between the Tautavel strain and the sepia-o strain; and (2) sexual selection at the sepia locus is independent of female genotype, but is due to a lesser mating success of sepia males.

The influence of male frequency on the male mating success can be observed in the direct observation technique results; yet, for more precise measurement of the frequency influence, it is better estimated from results of the multiple choice experiment, where the three male genotypes competed simultaneously.

Table 2 summarizes the results of experiments using the multiple choice technique. Comparisons to random mating (χ^2 r.m.) were significant for high frequencies of sepia but not for low frequencies. To test for frequency dependence, it seemed more appropriate to study the regression of mating frequencies on the frequencies at which the two types of individuals were present. The regression equation for the ratio +/*se* and +/+ mated males (R_1) on the initial ratio of these

TABLE 2

Relative mating success of males at different genotypic proportions from multiple choice technique

Male frequencies			Number of mated males					$r_1 =$ ♂♂ +/*se* / ♂♂ +/+	$R_1 =$ mated ♂♂ +/*se* / mated ♂♂ +/+	$r_2 =$ ♂♂ *se*/*se* / ♂♂ [+]	$R_2 =$ mated ♂♂ *se*/*se* / mated ♂♂ [+]
se/*se*	*se*/+	+/+	*se*/*se*	*se*/+	+/+	Σ	χ^2 r.m.				
0.04	0.32	0.64	24	199	349	572	2.24	0.50	0.57	0.04	0.04
0.16	0.48	0.36	49	189	142	380	2.73	1.33	1.33	0.19	0.15
0.25	0.50	0.25	83	221	134	438	11.98**	2.	1.65	0.33	0.23
0.49	0.42	0.09	172	266	59	496	41.30**	4.67	4.51	0.96	0.53
0.64	0.32	0.04	203	194	44	441	81.45**	8.	4.41	1.78	0.85

** Significant at the 0.01 level.

Initial ratios of male genotypic frequencies are indicated by r_1 and r_2, while ratios of frequencies of males that mated are indicated by R_1 and R_2.

male genotypes (r_1) was $R_1 = 0.01 + 0.79r_1$. The regression coefficient (0.79 ± 0.09) did not differ significantly from unity ($t_b = 2.33$, $P > 0.10$). Thus, the mating success of $+/se$ and $+/+$ did not differ, and it was possible to pool these genotypes in order to test for frequency dependence in sepia males. The regression equation for the ratio of se/se and [+] mated males (R_2) on the initial ratio of these male genotypes (r_2) was $R_2 = -0.26 + 0.79r_2$. The regression coefficient differed significantly from unit ($t_b = 42.5$, $P < 0.001$). The coefficient of regression being less than unity ($b = 0.79 \pm 0.09$), a frequency-dependent sexual selection therefore exists with a raw-male advantage. These results are plotted in a logarithmic scale in Figure 1.

The regression equation for the ratio of se/se and [+] mated males (R'_2) on the initial ratio of these male genotypes (r'_2) estimated from the direct observation experiments was $R'_2 = -0.51 + 0.84\ r'_2$. The regression coefficient differs significantly from unity ($t_b = 3.3$, $P < 0.01$).

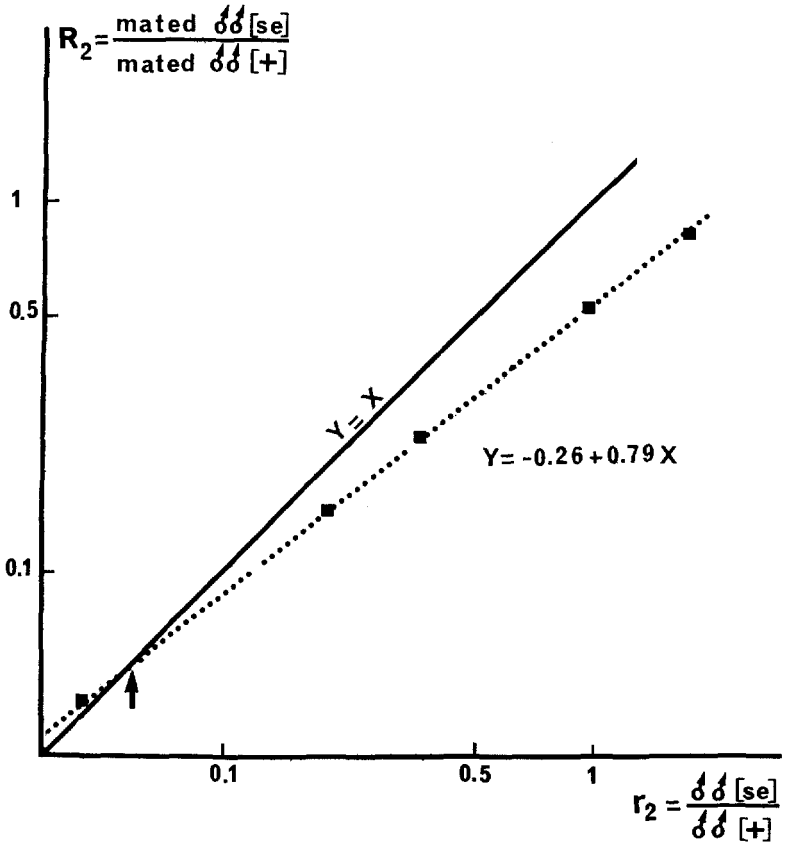


FIGURE 1.—Linear regression of the logarithm of the ratios of males having mated on the logarithm of the ratios at which the males were present. The ratio at which the two types of males have identical mating success is given by $X = Y$.

The results obtained from the two techniques (direct observation and multiple choice) are similar in indicating a frequency-dependent sexual selection, with a rare-male advantage of the Tautavel and sepia-o strain.

Analysis of sexual selection at the sepia locus allows exclusion of any female genotype influence and points out a relationship between male sexual selection and the genotypic composition of the male population. This relationship shows a rare-male advantage; consequently, sexual selection can lead to maintenance of polymorphism at the sepia locus. In a previous paper (ANXOLABEHERE 1976a), the allelic frequency equilibrium level at the sepia locus in experimental populations made up of the two strains used here was studied; the sepia frequency equilibrium in these experimental populations was about 0.27.

The major conclusions of the previous study was that viability selection operated at the sepia locus (or closely linked genes) and that this selection was frequency dependent. Meanwhile, it is shown here that a frequency-dependent sexual selection at the sepia locus also exists. In order to see what role each major component might have played in the previously studied populations as the gene frequency changed, I have calculated the expected changes of the sepia allelic frequency under (1) frequency-dependent sexual selection alone, (2) frequency-dependent larval selection alone, and (3) both 1 and 2.

Allelic variation under sexual selection: To build the algebraic model of sexual selection. the sexual adaptive values of each male genotype can be defined by the

TABLE 3

Sexual adaptive values of males (W) *in the multiple choice experiment*

Male genotypic frequency	$W_{+/+} \pm s$	$W_{+/se} \pm s$	$W_{se/se} \pm s$
$G_{+/+} = 0.64$ $G_{+/se} = 0.32$ $G_{se/se} = 0.04$	0.779 ± 0.037	0.875 ± 0.030	0.917 ± 0.049
$G_{+/+} = 0.36$ $G_{+/se} = 0.48$ $G_{se/se} = 0.16$	0.789 ± 0.077	0.880 ± 0.055	0.703 ± 0.042
$G_{+/+} = 0.25$ $G_{+/se} = 0.50$ $G_{se/se} = 0.25$	1.070 ± 0.10	0.884 ± 0.055	0.664 ± 0.084
$G_{+/+} = 0.09$ $G_{+/se} = 0.42$ $G_{se/se} = 0.49$	1.092 ± 0.044	1.055 ± 0.076	0.585 ± 0.052
$G_{+/+} = 0.04$ $G_{+/se} = 0.32$ $G_{se/se} = 0.64$	1.850 ± 0.232	0.968 ± 0.139	0.528 ± 0.034

W_i is defined as the number of females inseminated by the male of a genotype relative to the number of males of this genotype which were present. (s is the standard error calculated from W_i's obtained in separate experiments.)

number of females inseminated by these males relative to the number of males of this genotype present (ANDERSON 1969). The sexual adaptive values of the three male genotypes measured in the multiple choice experiments are presented in Table 3 and graphed in Figure 2 for various genotype frequencies. For *se/se* and +/+ genotypes, the sexual adaptive values were inversely proportional to the genotype frequency and are represented by $W_i = 1/[aG_i + c]$, where G_i is the genotypic frequency of the male i, and a and c are the selection parameters. The biological meaning of these parameters can be proposed in relation to the following particular conditions: If G_i is very small, $W_i \simeq \frac{1}{c}$ represents the sexual capacity of one sepia male when it is alone; and if $G_i = 1$, $W_i = \frac{1}{a+c}$ represents the sexual capacity of a sepia male when it is competing with other sepia males.

Estimation of these parameters from the multiple-choice experiment data was performed by linear regression on the inverse W_i values (*i.e.*, $\frac{1}{W_i}$ and is as follows:

$$W_{+/+} = 1/[1.02\, G_{+/+} + 0.73] \text{ and } W_{se/se} = 1/[1.27\, G_{se/se} + 1.17].$$

In the multiple-choice experiments used here (see MATERIALS AND METHODS), the heterozygote frequencies varied only from 0.32 to 0.50. It is therefore meaningless to seek a relationship between heterozygote mating success and heterozygote frequencies. The sexual adaptive value of this genotype had to be estimated by its mean fitness over the five tested frequencies: 0.90.

Let D_n, H_n and R_n be the adult frequencies of the +/+, +/*se* and *se/se* genotypes at the emergence of the n^{th} generation, and q_n the sepia allelic frequency of these adults. At the n^{th} generation, the selective model is as follows:

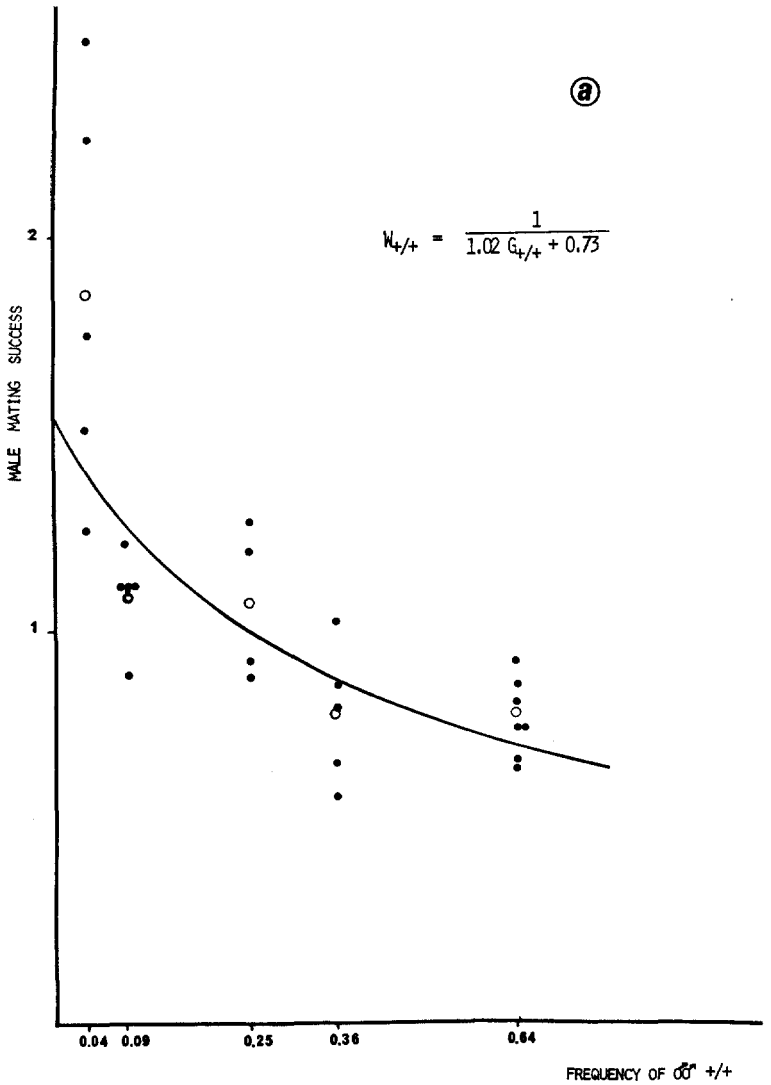
Genotypes	+/+	+/*se*	*se/se*
Frequency of genotypes at emergence	D_n	H_n	R_n
Male sexual component of adaptive value	$\frac{1}{1.02\, D_n + 0.73}$	0.90	$\frac{1}{1.27\, R_n + 1.17}$
Female sexual component of adaptive value	1	1	1

The sepia allelic frequency of the effective sperm bringing about the next generation is given by:

$$q'_{\delta n} = \left[\frac{R_n}{1.27\, R_n + 1.17} + \frac{0.90\, H_n}{2}\right] \Big/ \overline{W}_n \,. \qquad (1)$$

where,

$$\overline{W}_n = \frac{D_n}{1.020\, D_n + 0.73} + 0.90\, H_n + \frac{R_n}{1.27\, R_n + 1.17} \,.$$



The sepia allelic frequency of the effective ova giving the next generation is identical to that of adults, as here there is no sexual selection among the females. Thus, $q'_{\varphi n} = R_n + H_n/2 = q_n$.

As selection pressure exists only during mating competition and not during other times of the life cycle, the genotypic frequencies of the adults at the emergence of the $n + 1$ generation are as follows:

$$D_{n+1} = (1 - q'_{\delta n})(1 - q_n)$$
$$H_{n+1} = (1 - q_n)q'_{\delta n} + (1 - q'_{\delta n})q_n$$
$$R_{n+1} = q'_{\delta n} \cdot q_n$$

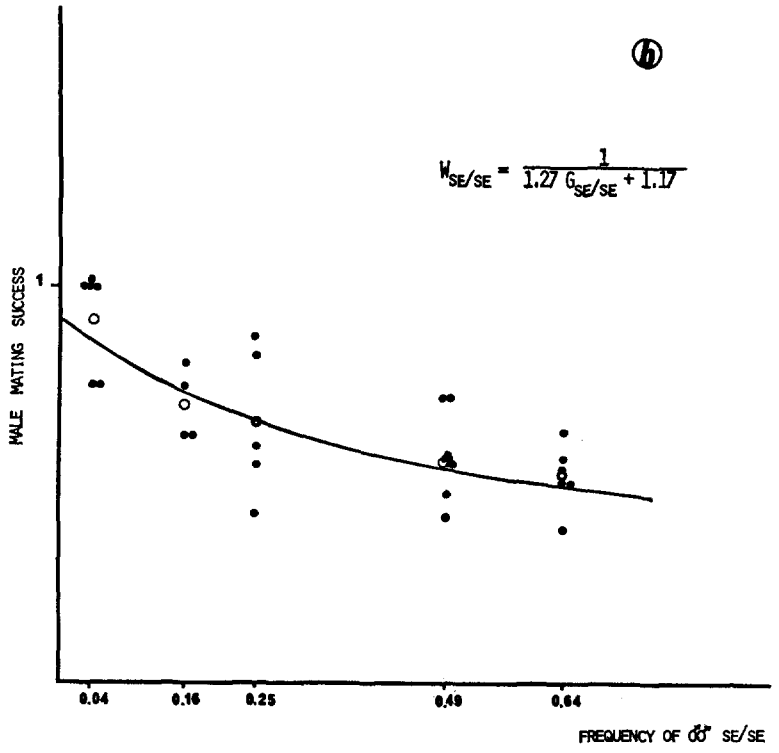


FIGURE 2.—Male mating success as a function of male genotypic frequency in the multiple choice experiment. (Means are represented by open circles.) (a) +/+ males. (b) *se/se* males.

and the sepia allelic frequency is given by:

$$q_{n+1} = (q'\delta_n + q_n)/2$$

or, with substitution of $q'\delta_n$ by its value in (1):

$$q_{n+1} = \frac{1}{2}\left[(1+q_n)\left(\frac{R_n}{1.27R_n + 1.17} + \frac{0.90H_n}{2}\right) + q_n\left(\frac{D_n}{1.02D_n + 0.73} + \frac{0.90H_n}{2}\right)\right]\Big/\bar{W} \quad (2)$$

The recurrence relation is not easily solved, but the successive values of q obtained by iteration are given in Figure 3, as well as the sepia allelic frequency variations observed in four experimental populations (L_1, L_2, H_1 and H_2) described in a previous study (ANXOLABEHERE 1976a). The equilibrium frequency given by equation (2) is $\bar{q}_s = 0.325$. The difference between the equilibrium frequency ($\bar{q}_s$) caused by sexual selection pressure and that observed in experimental populations (0.293 or 0.257, respectively, for populations beginning with low or high frequencies of the sepia allele) is insignificant. However, the observed approach towards equilibrium varies from that predicted on the sole basis

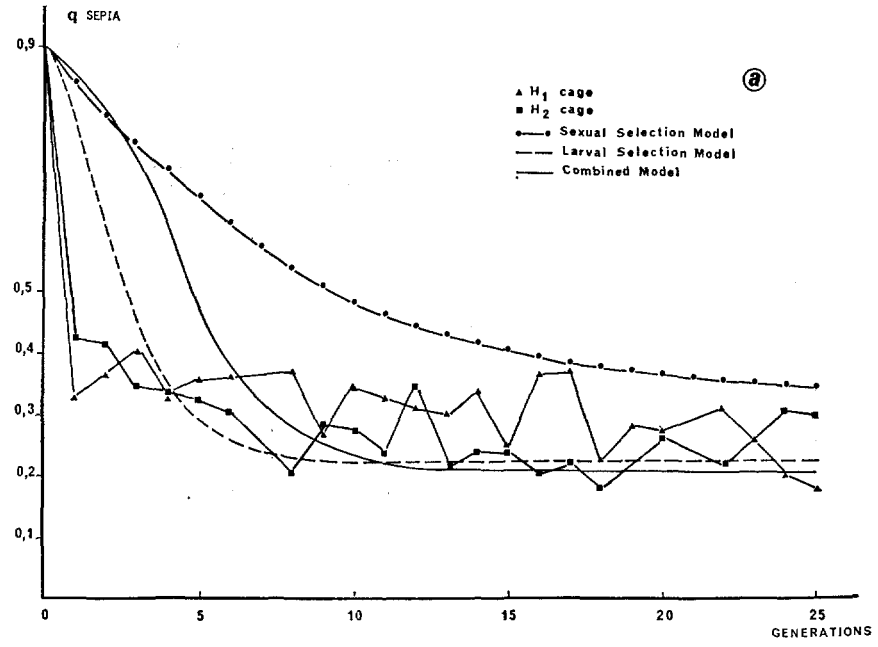


FIGURE 3.—Comparison between sepia allelic frequencies in the experimental populations and sexual selection model, larval selection or combined model. (a) Experimental populations H_1 and H_2 began with a high frequency of sepia allele; the observed equilibrium level are 0.234 and 0.281, respectively. (b) Experimental populations L_1 and L_2 began with a low frequency of the sepia allele; the observed equilibrium levels are 0.314 and 0.273, respectively. The equilibrium level is 0.325 with the sexual selection model, 0.205 with the larval selection model and 0.221 with the combined model.

of male mating differences. The poorness of this fit may be due to the role of frequency-dependent larval selection observed previously in experimental populations.

Allelic variation under larval selection: In a previous study (ANXOLABEHERE 1976a), the larval components of fitness were measured under these conditions: (a) during evolution of the population while the sepia allelic frequency and genetic background changed, and (b) in synthetic populations composed of different frequencies of the sepia allele, using either the original strains or strains extracted from a population cage after 30 generations. In the three kinds of experiments, it was demonstrated that (1) larval sepia homozygote viability compared to that of the heterozygote is independent of sepia allelic frequency, but depends upon genetic background, and (2) larval wild homozygote viability compared to that of the heterozygote is frequency dependent. As sexual selection was not measured during evolution of the populations, but rather with the original strains used to establish the populations, the larval selection measurements on the original strains should be used to compare the role that each major fitness component plays as gene frequency changes.

The larval adaptive values of +/+ (WL_1) and sepia (WL_3) genotypes from the Tautavel or sepia-o strains, which were used for the experimental populations study, are $WL_1 = 0.39 + 2.72q$ and $WL_3 = 0.80$, respectively, the corresponding adaptive value of the heterozygous genotype being fixed at unity. The expected allelic variation under these larval adaptive values is compared in Figure 3 with the experimental data from the four experimental populations. The expected equilibrium of the sepia allelic frequency (0.205) does not greatly differ from the observed frequency (about 0.293) in the experimental populations begun with a low frequency of the sepia allele (L_1 and L_2 cages), nor from that (about 0.257) found in experimental populations begun with a high frequency of this allele (H_1 and H_2 cages). Hence, relative to the equilibrium frequency, measurements of both frequency-dependent viability alone and frequency-dependent sexual selection give a good fit; but with regard to the approach toward equilibrium, the fit is better with larval selection model. With this model, the speed at which the equilibrium level is reached is faster than with the sexual selection model; nevertheless, the approach toward equilibrium with larval selection alone is slower than that observed in the experimental populations.

To build a comprehensive selection model at the sepia locus from separate measurements of frequency-dependent male mating success and frequency-dependent larval viability, these two fitness components must be combined and the predictions from this model compared with the experimental results.

Allelic variation under larval and sexual selection model: Among the mature adults of generation n, let D_n, H_n and R_n be the genotype frequencies of +/+, +/*se* and *se*/*se*, respectively. Let q_n and p_n represent the allelic frequencies with $q_n = R_n + 1/2H_n$. The sexual adaptive values already given allow calculation with the formula (2) of the allelic frequencies $q'_{\varphi n}$ and $p'_{\varphi n}$ among the ova and $q'_{\sigma n}$, $p'_{\sigma n}$ among the sperm. Random association of gametes produces the newly formed zygotes of generation $n + 1$. Let D'_{n+1}, H'_{n+1} and R'_{n+1} be the genotypic frequencies among the newly formed zygotes.

The larval viabilities presented previously modify the genotypic frequencies and give the adult proportions of generation $n + 1$: D_{n+1}, H_{n+1} and R_{n+1}. The new allelic frequencies among the adults are:

$$q_{n+1} = R_{n+1} + 1/2\, H_{n+1} \quad \text{and} \quad p_{n+1} = 1 - q_{n+1} \ .$$

The generational sequence of sexual selection (S.S.) and larval selection (L.S.) can be shown by:

$$q_n \ldots\ldots \text{S.S.} \ldots\ldots q'_n \ldots\ldots LS \ldots\ldots q_{n+1} \ldots\ldots \text{S.S.} \ldots\ldots q'_{n+1}$$

and at equilibrium:

$$q_{n+1} = q_n \text{ and } q'_{n+1} = q'_n \ .$$

The successive values of q obtained by iteration are given in Figure 3 (dashed lines). In this combined model, the sepia allelic equilibrium frequency among adults is 0.221; in comparison with the observed equilibrium, the fit is better than with the larval selection model alone. The goodness of fit is also clearly

improved with regard to the approach toward equilibrium. The greatest departure of predicted frequencies from the observed ones comes in the first few generations, which is just the time when experimental conditions might be expected to affect selection most in a population cage; change in environment may have a large effect here because selection is more powerful and because gene frequencies are rather far from equilibrium. Another cause of divergence between the predicted and observed gene frequencies is the greater influence of genetic background during the first few generations when there is maximum genetic revolution. This is the reason that population cage analysis gives more precise information about equilibrium points than about the time course of frequencies. It is clear that the sexual selection model leads to an equilibrium level higher than that of larval selection and that the equilibrium level produced by the combined model is very close to the experimental value. However, without other factors of variation, relatively great sexual selection must continue to exist in balanced populations since the experimental population becomes stable at frequencies distant from the frequency level that corresponds to sexual selective neutrality. Of course, other components of selection besides viability and male mating success may operate in experimental populations, but these two probably account for the greater part of total selection at the sepia locus. The experiments reported here do not show whether or not the measured sexual and larval selections are due to the sepia locus or to other genetic differences between the two strains used; the results of previous studies (ANXOLABEHERE 1976a,b), however, suggest a role of the sepia locus itself or of closely linked genes.

I am grateful to W. W. ANDERSON for his help on improving this manuscript.

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Corresponding editor: W. W. ANDERSON