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EXPERIMENTAL STUDIES OF THE DISTRIBUTION OF GENE
FREQUENCIES IN VERY SMALL POPULATIONS OF
DROSOPHILA MELANOGASTER.
III. ARISTAPEDIA AND SPINELESS

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HISTORY BY GENERATION

This experiment involves the histories of 113 lines, all started from groups of 4 s/a females and 4 s/a males (using s and a for the alleles spineless (ss) and aristapedia (ss^a) for simplicity). These were continued by random selection of 4 females and 4 males for 10 generations, except for 7 lines in which spineless became fixed. An additional line became fixed in this respect in the 10th generation. The distributions of number of aristapedia genes in each set of 8 flies is shown by generation in table 1, together with averages and variances of gene frequencies for each generation, excluding those previously fixed. The small number fixed is in marked contrast with the results with forked and Bar discussed in

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previous papers and is undoubtedly due to strong selection against both homozygous types, relative to the heterozygotes.

The mean gene frequency of aristapedia fell from initial .50 to .3544 in generation 5 among those in which fixation had not occurred but then rose somewhat to an average in the last 3 generations (.4032) which was substantially the same as that in generation 2 (.4043). The variance reached .0235 in 2 generations and fluctuated about this thereafter. A χ^2 test for homogeneity from generation 2 to 10 (excluding previously fixed lines, and grouping frequencies 0 and 1, and 11 to 14) gives $\chi^2 = 61.5$, $n = 80$, probability .94. Practically, we may consider that the distribution reached equilibrium of form in 2 generations with a mean gene frequency of $.3882 \pm .0049$ and a standard deviation of $.1536 \pm .0035$.

SELECTION COEFFICIENTS

If there were no differences in viability, generation 1 should consist of 25% a/a, 50% a/s and 25% s/s. The actual percentages (17.92:56.75:25.33) differ

TABLE 1. *The distribution of numbers of aristapedia genes, represented in each generation among 113 lines, consisting of 4 females, 4 males each. Newly fixed spineless is distinguished from previously fixed spineless.*

		Generation										Total 2-10	
		0	1	2	3	4	5	6	7	8	9		10
Old	0					(1)	(4)	(4)	(4)	(5)	(6)	(7)	
New	0				1	3			1	1	1	1	8
	1			2	3	1	2	2	3	1	3	1	18
	2		1	5	5	4	8	4	0	3	3	5	37
	3		1	6	9	9	10	6	8	6	8	10	72
	4		10	10	8	17	12	13	11	15	12	7	105
	5		11	15	17	13	19	19	17	15	10	13	138
	6		11	17	18	18	18	19	24	14	14	19	161
	7		22	22	21	18	16	16	14	17	18	12	154
	8	113	22	17	12	16	14	12	12	14	14	16	127
	9		20	8	10	6	7	12	9	7	10	10	79
	10		7	3	5	2	1	4	7	9	10	6	47
	11		6	6	3	3	2	1	2	2	2	3	24
	12		1	1	1	0		1	1	2	1	1	8
	13		1	0		1				2	1	2	6
	14			1		1							2
Total		113	113	113	113	112	109	109	109	108	107	106	986
\bar{q}		.5000	.4629	.4043	.3833	.3711	.3544	.3830	.3893	.4051	.4030	.4015	.3882
σ_q^2		0	.01707	.02351	.02333	.02515	.01896	.01932	.02095	.02603	.02677	.02693	.02350

significantly (probability $<.001$) and indicate viabilities of 63% for a/a and 89% for s/s relative to that for a/s. There is probably also a slight difference between males and females (probability about .04) in the viabilities of the homozygotes relative to the heterozygotes of the same sex. The present data give no indication of the true relative viabilities of males and females.

	a/a	a/s	s/s
Males	.525	1	.965
Females	.740	1	.819
Average	.632	1	.893

As these data are from a compact group which may not reflect accurately the situation in later generations, the ratios were obtained from all sets of 8 flies from generations 2 to 10, the parents of which consisted of 4 a/s females and 4 a/s males (table 2). These differed even more from expected 1:2:1 than did generation 1 (viability 47% for a/a and 57% for s/s relative to a:s). The differ-

ence from generation 1 is probably significant (probability .04). Table 2 also shows the ratios from other vials in which gene frequency was .50 in both sets of parents but in which one or both sets consisted of 1 a/a:2 a/s:1 s/s instead of 4 a/s in both sexes. In these cases, deviations from the 1:2:1 ratio among offspring may involve differential productivity of a/a and s/s relative to a/s as well as differential viability among the offspring. There is, however, no significant difference between (121-040) and (040-040) (females first in order a/a, a/s, s/s, males following in the same order) probability .80-.90, or between 121-121 and 040-121 (probability .10-.20) but these two groups differ significantly from each other (probability $<.01$). It appears that there can not be much difference between a/a and s/s females in productivity but that a/a males are much less productive than s/s males under the conditions of these experiments. When the fathers consisted of 1 a/a:2 a/s:1 s/s,

the ratio among the offspring (19 a/a: 146 a/s:67 s/s) includes fewer a/a and more s/s than expected if a/a males were completely nonproductive and s/s males were as productive as a/s males (22.2 a/a:151.8 a/s:58.0 s/s if .50a:50s eggs). These data are not, however, numerous enough for reliable determinations of relative productivities.

The remaining data include so many types of mating with such entanglement of possible differences in productivity of a/a and s/s relative to a/s in both sexes that an analysis of the sort used in the much simpler sex-linked case of Bar did not seem practicable. We have, however, taken out 4 fairly large, moderately homogeneous groups to obtain rough estimates. In group E (table 3) 2 or 3 a/a female parents competed with at least one a/s female, but only one if any a/a male was present in the set of 4 males. Group F gives the same sort of test for an excess of a/a males. In group G, there were 2 or 3 s/s females competing with at least one a/s female while only one if any s/s male and only one if any a/a male were present. The last condition prevents overlap with group F. Group H is similar with reversal of the sexes and thus designed to

test productivity with an excess of s/s males present.

The average gene frequency of arista-pedia is naturally rather high among the parents in E and F (.590, .585 respectively) and much lower in G and H (.346, .345 respectively). The offspring regress strongly toward the population average in all cases (.470 in E, .432 in F, .360 in G, and .400 in H). Using unweighted averages, it appears that the parental difference between the two groups (.242) is reduced to only 29% of its value (.071) in the offspring, indicating an average selection of more than 70% against the homozygotes. The greatest deviation from the parental average is in F, again indicating complete or nearly complete failure of a/a males to produce in competition with a/s males, but the results in E indicate low productivity of a/a females also. The most nearly normal productivity of homozygotes seems to be that of s/s females, in excess in G.

With these indications as a starting point, sets of productivity coefficients were applied to the parental frequencies in E to H and constant viability coefficients were applied to the frequencies of the zygotes from random union of the

TABLE 2. *Offspring from vials in which the parents were of the types indicated at the tops of the columns*

	F ₁ ♀ 040 ♂ 040		F ₂ -F ₁₀ Total		A ♀ 040 ♂ 040		B ♀ 121 ♂ 040		C ♀ 040 ♂ 121		D ♀ 121 ♂ 121		A-D	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
♀ a/a	94	20.8	434	11.0	19	18.3	12	13.6	6	9.4	4	7.7	41	13.3
a/s	254	56.2	2281	57.8	66	63.4	59	67.1	46	71.9	32	61.5	203	65.9
s/s	104	23.0	1229	31.2	19	18.3	17	19.3	12	18.7	16	30.8	64	20.8
♂ a/a	68	15.0	389	9.9	13	12.5	12	13.6	4	6.3	5	9.6	34	11.0
a/s	259	57.3	2198	55.7	71	68.3	59	67.1	42	65.6	26	50.0	198	64.3
s/s	125	27.7	1357	34.4	20	19.2	17	19.3	18	28.1	21	40.4	76	24.7
No.	904		7888		208		176		128		104		616	
q _a ♀		48.9		39.9		50.0		47.2		45.3		38.5		46.3
♂		43.7		37.7		46.6		47.2		39.1		34.6		43.2
Tot.		46.3		38.8		48.3		47.2		42.2		36.5		44.7

arrays of eggs and sperms estimated in each case. It appears that the viability coefficients (not distinguishing those of males and females) must be close to .50 for a/a and .75 for s/s to account for the percentages of heterozygotes. These are lower than indicated in F_1 , but not so low as indicated by the progeny of a/s females with a/s males of later generations. The productivity coefficients are easily narrowed by trial to the nearest .05. These indicate relative productivities of a/a, a/s and s/s females of about .40:1: .75 respectively of a/a, a/s and s/s males of 0:1: .25 respectively under the conditions in these groups of parents.

The agreement with observed numbers of offspring (table 4) is not good ($\chi^2 = 13.3$) but from inspection of the differences, it is evident that no single set of productivity and viability coefficients can account well for the results in H and the others. H seems to require lower viability coefficients. Similarly application of the above set of coefficients to groups A to D also gives a poor fit ($\chi^2 = 13.9$) but this is considerably improved

by using .40:1:.60 for the viability coefficients of a/a, a/s and s/s respectively. If the single set of 6 coefficients based on E to H is applied to all 8 groups, $\chi^2 = 27.2$, $n = 10$, probability .001 to .01. This could no doubt be improved a little by deriving the coefficients with maximum probability from all of these data but it is obvious that there must be complications either in assortative mating or heterogeneity.

Possible sex differences in viability, indicated in the data from the first generation, have been ignored above. Groups A to D collectively do not show significant differences in the frequencies of the sexes and the same is true of E to H collectively. In both cases, however, there is a suggestion that aristapedia has somewhat lower viability and spineless somewhat higher viability in males than in females, relative to a/s in both, in agreement with the data from the first generation. Even on combining A to H the distributions of the sexes differ only enough to give $\chi^2 = 4.42$, probability .10 to .20. It is necessary to consider the

TABLE 3. *Offspring from vials in which the parents were in the categories indicated at the tops of the columns. The exact composition of the parental as well as the offspring populations are shown in the columns.*

	E				F				G				H			
	♀: 2,3 a/a, 1,2 a/s ♂: 0,1 a/a				♀: 0,1 a/a ♂: 2,3 a/a, 1,2 a/s				♀: 2,3 s/s, 1,2 a/s ♂: 0,1 s/s, 0,1 a/a				♀: 0,1 s/s, 0,1 a/a ♂: 2,3 s/s, 1,2 a/s			
	Parents		Offspring		Parents		Offspring		Parents		Offspring		Parents		Offspring	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
♀ a/a	171	54.1	57	18.0	21	11.9	29	16.5	24	4.5	38	7.2	45	7.2	57	9.1
a/s	118	37.3	190	60.1	117	66.5	105	59.7	210	39.8	304	57.6	474	76.0	396	63.5
s/s	27	8.6	69	21.8	38	21.6	42	23.9	294	55.7	186	35.2	105	16.8	171	27.4
♂ a/a	46	14.6	48	15.2	92	52.3	24	13.6	39	7.4	40	7.6	26	4.2	56	9.0
a/s	194	61.4	194	61.4	69	39.2	93	52.8	395	74.8	300	56.8	245	39.3	376	60.3
s/s	76	24.0	74	23.4	15	8.5	59	33.5	94	17.8	188	35.6	353	56.6	192	30.8
No.	632		632		352		352		1056		1056		1248		1248	
q _a ♀		72.8		48.1		45.2		46.3		24.4		36.0		45.2		40.9
♂		45.3		45.9		71.9		40.1		44.8		36.0		23.8		39.1
Tot.		59.0		47.0		58.5		43.2		34.6		36.0		34.5		40.0

TABLE 4. The observed numbers of offspring of genotypes a/a, a/s and s/s in groups A to H and the expected number, assuming productivity in females of genotypes a/a, a/s and s/s in the ratio .40:1:.75 respectively, productivity of males of 0:1:.25 in the same order, and viability coefficients in both sexes of .50 for a/a:1 for a/s: .75 for s/s

		o	c	o-c	$\frac{(o-c)^2}{c}$			o	c	o-c	$\frac{(o-c)^2}{c}$
E	a/a	105	109.9	- 4.9	.22	A	a/a	32	32.0	0	0
	a/s	384	399.5	-15.5	.60		a/s	137	128.0	+ 9.0	.63
	s/s	143	122.6	+20.4	3.39		s/s	39	48.0	- 9.0	1.69
F	a/a	53	44.1	+ 8.9	1.80	B	a/a	24	23.9	+ 0.1	0
	a/s	198	212.5	-14.5	.99		a/s	118	107.4	+10.6	1.05
	s/s	101	95.4	+ 5.6	.32		s/s	34	44.7	-10.7	2.56
G	a/a	78	77.2	+ 0.8	.01	C	a/a	10	17.4	- 7.4	3.15
	a/s	604	610.9	- 6.9	.08		a/s	88	78.1	+ 9.9	1.25
	s/s	374	367.9	+ 6.1	.10		s/s	30	32.5	- 2.5	.19
H	a/a	113	123.4	-10.4	.88	D	a/a	9	12.5	- 3.5	.98
	a/s	772	730.2	+41.8	2.39		a/s	58	62.3	- 4.3	.30
	s/s	363	394.4	-31.4	2.50		s/s	37	29.2	+ 7.8	2.08
Total		3288	3288.0	0	13.28'	Total		616	616.0	0	13.88
Total	a/a	349	354.6	- 5.6	.09	Total	a/a	75	85.8	-10.8	1.36
	a/s	1958	1953.2	+ 4.8	.01		a/s	401	375.8	+25.2	1.69
	s/s	981	980.3	+ 0.7	0		s/s	140	154.4	-14.4	1.34

total distribution from generations 2 to 10 to obtain a significant difference (probability .01 to .02). These data are too heterogeneous for more than rough estimates. Assume that the zygotic frequencies $f_{aa(Z)}$, $f_{as(Z)}$ and $f_{ss(Z)}$ are the same in the sexes. Let $f_{aa(F)}$ and $f_{aa(M)}$ be the observed frequencies of a/a females and males respectively and similarly for a/s and s/s.

$$\frac{f_{aa(F)}}{f_{as(F)}} = \frac{f_{aa(Z)}V_{aa(F)}}{f_{as(Z)}}, \quad \frac{f_{aa(M)}}{f_{as(M)}} = \frac{f_{aa(Z)}V_{aa(M)}}{f_{as(Z)}}$$

The ratio $R_{aa} = V_{aa(M)}/V_{aa(F)}$ can now be obtained.

$$R_{aa} = \frac{V_{aa(M)}}{V_{aa(F)}} = \frac{f_{aa(M)}f_{as(F)}}{f_{as(M)}f_{aa(F)}}$$

$$R_{ss} = \frac{V_{ss(M)}}{V_{ss(F)}} = \frac{f_{ss(M)}f_{as(F)}}{f_{as(M)}f_{ss(F)}}$$

For F_2 to F_{10} , $R_{aa} = .930$, $R_{ss} = 1.146$. Letting

$$\bar{V}_{aa} = \frac{1}{2}(V_{aa(F)} + V_{aa(M)})$$

$$V_{aa(F)} = 2\bar{V}_{aa}/(1 + R_{aa})$$

$$V_{aa(M)} = 2\bar{V}_{aa} - V_{aa(F)}$$

Adopting

$$\bar{V}_{aa} = .50$$

$$V_{aa(F)} = .52, \quad V_{aa(M)} = .48$$

Similarly if

$$\bar{V}_{ss} = .75$$

$$V_{ss(F)} = .70, \quad V_{ss(M)} = .80$$

THE DISTRIBUTION OF GENE FREQUENCIES

In cases in which viability differences are small, in which the productivity coefficients of the various genotypes are sufficiently similar in males and females to be averaged without important errors, and in which mating is random, the average rate of change of gene frequency (Δq) can be expressed as a simple function of the gene frequency and the selection coefficients (Wright and Dobzhansky, 1946).

	<i>f</i> (frequency) <i>W</i> (selection value)		
<i>a/a</i>	q^2	$1 - s$	$\bar{W} = 1 - sq^2 - t(1 - q)^2$
<i>a/s</i>	$2q(1 - q)$	1	$\Delta q = \frac{q(1 - q)}{2\bar{W}} \frac{d\bar{W}}{dq} = - (s + t)q(1 - q)(q - \hat{q})/\bar{W}$
<i>s/s</i>	$(1 - q)^2$	$1 - t$	$\hat{q} = t/(s + t)$

The distribution of gene frequencies at equilibrium is (Wright, 1937):

$$\varphi(q) = (C/\sigma_{\delta q}^2) \exp [2 \int (\Delta q/\sigma_{\delta q}^2) dq]$$

If random drift is due solely to accidents of sampling

$$\sigma_{\delta q}^2 = q(1 - q)/(2N)$$

$$\varphi(q) = C\bar{W}^{2N}/q(1 - q) \\ = C[1 - sq^2 - t(1 - q)^2]^{2N}/q(1 - q)$$

In the present data, the situation is obviously much more complicated. The genetic arrays of the sexes differ systematically because of the differences in productivity and to a minor extent viability coefficients. Thus systematic departures from the binomial square law are to

be expected among zygotic frequencies even if mating is assumed to be at random. These departures could be ignored in obtaining rough approximations by use of the averages of the coefficients for the sexes (cf. Wright and Dobzhansky, 1946) if it were possible to deal collectively with all populations of the same zygotic gene frequencies. The most serious difficulty arises from the fact that the frequencies of genotypes are determinable only after large but undoubtedly varying proportions of the homozygotes have died. Letting $W_{aa} = V_{aa}U_{aa}$, $W_{ss} = V_{ss}U_{ss}$, $s = 1 - W_{aa}$, $t = 1 - W_{ss}$, where the *U*'s are productivity coefficients.

<i>Zygote</i>	<i>Imago</i>	<i>Gamete</i>
<i>a/a</i> : q^2	$V_{aa}q^2/D$	$a: (q - sq^2)/\bar{W}$
<i>a/s</i> : $2q(1 - q)$	$2q(1 - q)/D$	$s: [1 - q - t(1 - q)^2]/\bar{W}$
<i>s/s</i> : $(1 - q)^2$	$V_{ss}(1 - q)^2/D$	

$$D = 1 - (1 - V_{aa})q^2 - (1 - V_{ss})(1 - q)^2 \qquad \bar{W} = 1 - sq^2 - t(1 - q)^2$$

The change of gene frequency from zygote to zygote and the distribution of zygotic gene frequencies are (approximately) as given above but the change of gene frequency from imago to imago and the distribution of the gene frequencies in imagoes can not be expressed in simple form. The zygotic *q* is here a quadratic function of the imaginal *q*.

We may, however, as in the case of Bar (Part II of this series), find an empirical relation between imaginal gene frequency and the change in the following generation. Table 5 shows the mean change in gene frequency in the offspring for each class of parental gene frequencies

(generations 1 to 9), the variance of these changes ($\sigma_{\delta q}^2$) and the ratio $q(1 - q)/\sigma_{\delta q}^2$ which would indicate effective $2N_e$ if zygotic gene frequencies were in question and variability were due only to accidents of sampling.

Change of gene frequency is plotted against parental gene frequency in figure 1. From the form it appears that the formula, applicable to zygotic frequencies may give an adequate empirical fit. A rough evaluation of the coefficients can be obtained as described previously (Wright and Dobzhansky, 1946) from the regression of Δq on *q* in the nearly straight middle portion of the

curve.

$$\frac{1}{\bar{W}} = 2 \left(1 + \frac{\Delta q}{\bar{q}} \right) \left(1 - \frac{\Delta q}{1 - \bar{q}} \right) - 1 - b_{\Delta q, q}$$

$$s = \frac{1}{\bar{q}} \left[1 - \left(1 + \frac{\Delta q}{\bar{q}} \right) \bar{W} \right]$$

$$t = \frac{1}{1 - \bar{q}} \left[1 - \left(1 - \frac{\Delta q}{1 - \bar{q}} \right) \bar{W} \right]$$

In the present case, the entries from $q = 5/16$ to $q = 12/16$ yield $\bar{q} = .452$, $\Delta q = -.0331$, $b_{\Delta q, q} = -.568$, $\bar{W} = .652$, $s = .875$, $t = .563$, $\hat{q} = .392$. If parental generation 1 is omitted, s comes out .878 and t .582.

The ratio $q(1 - q)/\sigma_{\delta q}^2$ varies irregularly but there is no clear trend except perhaps for small values between $q = 1/16$ to $4/16$. The indicated estimate for $2N_e$ is 13.0 (instead of 16). Even this, however, is undoubtedly too high, since it is based on the variability after the frequencies of homozygotes have been cut down severely by selective viability (a complication that was absent or unimportant in the case of Bar).

If Δq and $\sigma_{\delta q}^2$ for imaginal gene frequencies may be taken as approximating empirically the same functions as for the

TABLE 5. The observed changes per generation (Δq) in relation to gene frequency of parental populations of generations 1 to 9, the calculated values from the formula

$$\Delta q = - (s+t)q(1-q)(q-\hat{q})/[1-sq^2 - t(1-q)^2], \quad s = .86, \quad t = .60, \quad \hat{q} = t/(s+t),$$

the variance of changes, $\sigma_{\delta q}^2$, and the ratio $q(1-q)/\sigma_{\delta q}^2$

$16q$	t	q	Δq		$\sigma_{\delta q}^2$	$\frac{q(1-q)}{\sigma_{\delta q}^2}$
			obs.	calc.		
1	17	.0625	+.0882	+.0635	.0127	4.6
2	33	.1250	+.0511	+.0866	.0106	10.3
3	63	.1875	+.0972	+.0867	.0165	9.2
4	108	.2500	+.0689	+.0724	.0192	9.8
5	136	.3125	+.0533	+.0489	.0131	16.5
6	153	.3750	+.0049	+.0191	.0174	13.5
7	164	.4375	-.0312	-.0147	.0165	14.9
8	133	.5000	-.0536	-.0512	.0162	15.4
9	89	.5625	-.1088	-.0888	.0237	10.4
10	48	.6250	-.0950	-.1263	.0233	10.1
11	27	.6875	-.1574	-.1621	.0151	14.2
12	8	.7500	-.2969	-.1938	.0131	14.3
13	5	.8125	-.1750	-.2172	.0147	10.4
14	2	.8750	-.2500	-.2231	.0078	14.0
15	0	.9375	—	-.1863	—	—
986						13.03

zygotic frequencies, the distribution of imaginal gene frequencies should be approximated by the formula cited except

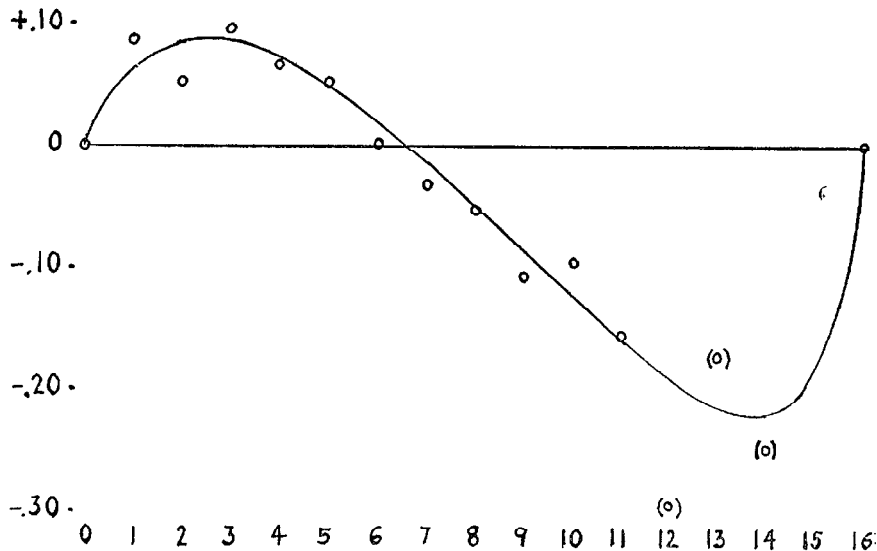


FIG. 1. Observed mean changes of gene frequency in relation to numbers of aristapedia genes in populations of eight flies (small circles) in comparison with those expected from the formula

$$\Delta q = - (s + t)q(1 - q)(q - \hat{q})/[1 - sq^2 - t(1 - q)^2];$$

$$s = .86, \quad t = .60, \quad \hat{q} = .411.$$

for the usual inaccuracy near the extremes in applying a formula based on large $2N$ to populations with small $2N$. The low rate of fixation is ignored.

It turns out that the values $s = .88$, $t = .58$ give too small a mean and $2N_e = 13$ gives, as expected, too small a variance. It was found by trial that the values $s = .86$, $t = .60$, $2N_e = 10.7$ give the best fit without going to a larger number of decimal places. Figure 1 shows how well the values of Δq calculated from these estimates of s and t fit the observed values of Δq . Table 6 and figure 2 show the agreement between the observed and calculated frequencies of the gene frequencies. $\chi^2 = 5.38$, $n = 9$ (on grouping the small classes 12 to 14), probability .80.

We take this opportunity to correct a typographical error and a confusion between two modes of presentation of certain equations in part II of this series (Evolution VIII, p. 235, right side)

In line 8:

– $4Ns$ instead of – $4N$ at beginning

TABLE 6. *The observed frequencies of aristapedia genes in sets of 8 flies (generations 2 to 10) from unfixed parental populations, in comparison with frequencies calculated from $s = .86$, $t = .60$, $2N_e = 10.7$*

$16q$	frequency		$(o-c)$	$\frac{(o-c)^2}{c}$
	o	c		
0	8	10.4	–2.4	.55
1	18	20.9	–2.9	.40
2	37	38.8	–1.8	.08
3	72	68.9	+3.1	.14
4	105	105.7	–0.7	0
5	138	138.8	–0.8	0
6	161	156.3	+4.7	.14
7	154	151.0	+3.0	.06
8	127	124.6	+2.4	.05
9	79	86.9	–7.9	.72
10	47	50.1	–3.1	.19
11	24	23.2	+0.8	.03
12	8	8.1	+5.6	3.02
13	6	2.0		
14	2	0.3		
15	0	0		
16	0	0	5.38	
	986	986.0		

In line 9:

$$q(1 - q)\phi(q) = e^{2Ns}\chi(q)$$

In line 13:

$$\chi(q) = Cq(1 - q)[1 + C_1q(1 - q)]$$

DISCUSSION

In natural panmictic populations of ordinary size, genes subject to such enormous selection, as that against Bar in the second paper of this series, would be eliminated too rapidly for random drift from inbreeding to be of appreciable importance. The same is probably true of forked (in the first paper) even though the selection against it was hardly detectible in the small experimental populations. In the case of aristapedia and spineless, the enormous selection against both homozygotes would keep a large population very close to the equilibrium point (about 40% *ss*^a). We may, however, consider the experimental populations as models, on exaggerated scales with respect to the effects of inbreeding and, in two cases, of selection, of situations that might occur in isolated local populations in nature with respect to a pair of isoalleles or of alleles with primary effects on multifactorial quantitative variability.

In arrays of such populations with effective size one thousand times as great as in the experimental populations, the random drift and ultimate fixation due to inbreeding would occur at only one-thousandth of the rates observed here. The forms of the distributions after approximate stability has been reached (in one thousand times the observed periods) would, however, be nearly the same as observed if selective disadvantage in all cases is only one-tenth of a percent of those in the experiments. Such coefficients are reasonable enough for isoalleles or alleles with primary effects on quantitative variability (Wright, 1952).

The experiments with forked may be considered as giving a model of the inbreeding effect in almost pure form. Those with Bar give a model of the case in which an allele tends toward fixation

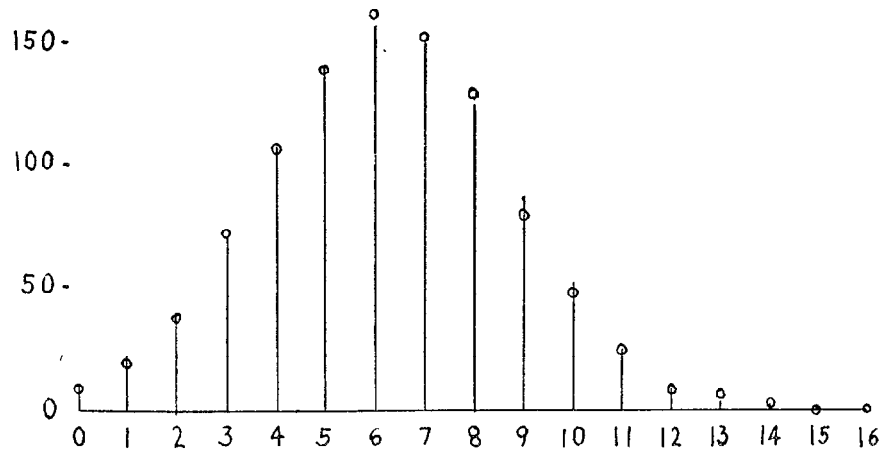


FIG. 2. The observed frequencies of each type of population according to number of aristapedia genes (small circles). These are compared with the theoretical frequencies in an array of populations in which a stable state has been reached with 86% selection against homozygous aristapedia, 60% against homozygous spineless, relative to heterozygotes, and with effective $2N$ of 10.7.

but not so decisively as to prevent the unfavorable allele from occasionally drifting into fixation against the pressure of selection. Those with aristapedia and spineless illustrate an approach to equilibrium between alleles because of selection against both homozygotes, but balancing of these selection pressures against random drift from inbreeding in such a way that gene frequency varies almost from one extreme to the other among the populations and one at least of the alleles may occasionally drift into fixation.

It should be recognized that in natural populations with effective size in the thousands, all other types of steady and random drift are likely to be present. Isolation from the rest of the species is not likely to be so complete that immigration can be neglected. Recurrent mutation may have to be considered. With respect to random drift it becomes necessary to take account of fluctuations in the coefficients pertaining to selection and amount and quality of immigration. In a broad sense, however, the experimental arrays may still be considered as exaggerated models of certain patterns of interplay of the directed and random processes which must be taken into account in the study of natural populations.

SUMMARY

Among 113 lines, each starting from four ss^a/ss females and four ss^a/ss males and continued to fixation or to ten generations by random selection of four females and four males in each generation, there was rapid attainment of a nearly stable distribution of gene frequencies. Spineless, however, drifted into fixation in eight lines. Aristapedia reached a maximum gene frequency of 87.5%. The mean gene frequency of aristapedia came to be 38.8%.

Analysis indicated very strong selection against both homozygotes in both viability and productivity. The viability coefficients were approximately in the ratio .50:1:.75 for ss^a/ss^a , ss^a/ss and ss/ss respectively with only slight differences in the sexes. The productivity coefficients were approximately in the ratio .40:1:.75 for these genotypes in females and 0:1:.25 in males.

A relatively simple empirical formula was obtained for the net rate of change of gene frequency per generation (net selective values in the ratio .14:1:.40). The observed distribution of gene frequencies agreed closely with that expected from those values among populations with effective $2N_e$ of 10.7.

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