

FLUCTUATIONS OF SAMPLING IN A MENDELIAN POPULATION¹

J. A. DETLEFSEN
University of Illinois, Urbana, Illinois

[Received June 3, 1918]

In experimental crosses with pedigreed cultures, the observed Mendelian ratios are supposed to be due to the chance combinations of 2^n kinds of gametes (n = number of allelomorphic pairs) occurring in equal numbers. The total or aggregate results may show larger or smaller deviations from the calculated ratios, but these deviations frequently lie within reasonable limits of error on the hypothesis of simple sampling. The aggregate results are obtained by adding subgroups—litters, families, pods, cobs, plants, or the like, in the experiments. The subgroups themselves may show extreme deviations. The theory of simple sampling which underlies strict Mendelism does not preclude such fluctuation in subgroups but calls for fluctuations of various sizes with *expected* frequencies. One could hardly postulate Mendelian inheritance with few or no deviations in subgroups or in totals. However, it is entirely conceivable that the total results in a Mendelian experiment may agree closely with the calculated ratio, and yet pure chance may not be operative, for extreme plus and minus deviations in the subgroups may counterbalance each other. YULE (1914) drew attention to such a case in analyzing LOCK's data on maize, for although the means agree very well with expectation,

“the contrast between DR's selfed and the DR \times RR crosses is curious. The former certainly do not suggest any significant fluctuation; the latter do on the whole suggest some source of disturbance or possibly error.”

Mendel recognized wide fluctuations in the subgroups, and recorded in his original paper four plants which gave dominants to recessives in the ratios of 43 : 2, 32 : 1, 14 : 15, and 20 : 19. While such departures are not utterly impossible, their occurrence should be extremely infrequent. The odds against a ratio of 20:19, for example, are about

¹ Paper No. 8, from the Laboratory of Genetics, Department of Animal Husbandry, ILLINOIS AGRICULTURAL EXPERIMENT STATION.

1600 to 1. As one examines experiments recorded in the literature, one occasionally notes similar cases. HAYES and EAST (1915) record in table 1, a plant which gave 208 corneous to 142 floury kernels where 175 of each kind is the most probable expectation. The other 12 plants and the total in this table agree very well with theory, but the odds against this exceptionally wide deviation are about 2300:1. The fruit fly, *Drosophila*, used so commonly for demonstrating alternative inheritance, gives conspicuously poor ratios and wide deviations in sampling on a Mendelian hypothesis. In fact, it is almost impossible to speak of random sampling in this material. The numbers usually available in experiments with domestic animals are so small as to be misleading. One occasionally finds discrimination against bulls and stallions when a sire produces a large excess of one sex where the other is desired. In such cases the deviation from an approximate equality of both sexes is often very large but probably not impossible in relatively small samples, as fluctuations of sampling.

The object of this study has been to determine how closely deviations of various sizes in the subgroups, litters of mice, approach their expected frequencies in an actual breeding experiment, or whether such fluctuations have any significance other than chance. The results have proved serviceable as concrete illustrations of sampling in a Mendelian population.

The materials used in this study have been described in the preceding paper (DETLEFSEN and ROBERTS 1918). This paper deals only with the offspring of 90 trihybrid F_1 females ($AaDdBb$) bred back to ultimate recessive males ($aaddbb$). There were 561 F_2 litters, of which 361 were classified as undepleted and 170 as depleted. The undepleted are those in which the total number born was classified, but the depleted litters showed some elimination between birth and classification. I have made no attempt to subdivide the depleted litters according to the causes of elimination. Since there are three allelomorphic pairs involved in this cross we expect equal numbers of dominants and recessives with respect to any one pair. The results of the former study on this material agree with such an hypothesis. The chances should be even that any individual in the segregating generation will show agouti (A) or non-agouti (a); similarly black (B) or brown (b); and dark eye (D) or pink eye (d). Hence, we can study (1) the fluctuations of sampling in each one of these pairs separately, and (2) the fluctuations in dominants and recessives by disregarding the particular characters and classifying all characters simply as dominant or recessive.

If p is the probability that an event (such as the occurrence of a dominant) will happen in a single trial, and $q = 1 - p$ is the probability that it will fail to happen (when the allelomorphic recessive occurs), then ${}_nC_r p^r q^{n-r}$ is the probability that the dominant will happen exactly r times in n trials. The expression ${}_nC_r$ denotes, to be sure, the number of combinations of n things taken r at a time. For example, if we ask ourselves in a concrete case what is the probability of obtaining 4 blacks in a litter of 6, where the probability is $\frac{1}{2}$ that any single individual will be black and $\frac{1}{2}$ that it will be brown, then $p = q = \frac{1}{2}$, $n = 6$, $r = 4$, and ${}_6C_4$

$$\left(\frac{1}{2}\right)^4 \left(\frac{1}{2}\right)^2 = \frac{15}{64}. \quad \text{That is, } \frac{15}{64} \text{ of our litters of 6 should show 4}$$

blacks and 2 browns as the most probable expectation. The relative frequencies with which the dominant will happen r times in n trials, where n = the size of litter and r has all values from 0 to n inclusive, are given by the expansion of $(q + p)^n$. Therefore the several probabilities that the individuals of a litter of any size, n , will show the dominant character 0, 1, 2, 3, n times are $q^n + {}_nC_1 q^{n-1} p + {}_nC_2 q^{n-2} p^2 + \dots + {}_nC_{n-1} q p^{n-1} + {}_nC_n p^n = (q + p)^n = 1$. The calculated mean value of dominants for litters of any size, n , is np and the $\sigma = \sqrt{npq}$. In this paper $p = q = \frac{1}{2}$ in all cases, for the F_1 was always mated back to the recessive type. Hence, the expected proportions of litters of 1 showing 0 and 1 black individual are $\frac{1}{2} + \frac{1}{2}$; of litters of 2 showing 0, 1 and 2 blacks are $\frac{1}{4} + \frac{2}{4} + \frac{1}{4}$; and so on. It is understood that we are making our results a test against a Mendelian or *a priori* probability, a course which is justified by the study of this same material in the previous paper. It would not be justified in monohybrid ratios in which the total results failed to agree with Mendelian expectation, as in the case of waltzing vs. normal gait in DARBISHIRE'S (1904) data. There are several ways in which the data may be treated, but a direct comparison of the experimental results with the calculated binomial distribution is the simplest and, it seems to me, most satisfactory. In all of the tables, the results are given in terms of the dominant character, but the results would be exactly the same if given in terms of recessives.

Table 1 records the frequencies with which the agouti, the dark-eyed, and the black-pigmented individuals occurred 0, 1, 2, n times in undepleted litters of various sizes. The litters ranged from 2 to 10 mice per litter. Italics indicate the calculated frequencies. The tendency for litters of all sizes to conform to expectation is clear in the case of each dominant character studied. It is equally true of their

recessive allelomorphs, since the observed distributions and calculated frequencies in terms of recessives are the same as those given for dominants, except that they stand in a reversed order. For example, in table 1, litters of 3, there are $1 + 5 + 3 + 2$ litters with 0, 1, 2, and 3 dark-eyed, respectively. Stated in terms of the recessive pink-eyed, there are $2 + 3 + 5 + 1$ litters with 0, 1, 2, and 3 pink-eyed, respectively, for manifestly if there are 5 litters of 3 with 1 dark-eyed in each, it follows that these 5 litters have 2 pink-eyed in each. The goodness of fit of the observed to the calculated frequencies is the same irrespective of the way in which the results are stated. In litters of 6, which are the most frequent, the fit is so close in all cases that we can conclude the deviations observed may well have arisen through sampling; for, using PEARSON'S formula for goodness of fit, we find:

$$\text{Agouti, } \chi^2 = 1.8069 \quad P = 0.932;$$

$$\text{Dark eye, } \chi^2 = 5.3856 \quad P = 0.507;$$

$$\text{Black, } \chi^2 = 5.3860 \quad P = 0.507.$$

HARRIS (1912) has shown the use and application of PEARSON'S formula for goodness of fit in the case of Mendelian ratios.

It is not worth while to calculate the goodness of fit in the case of each litter size, because the total number of litters of the same size is too small in some cases. I have reserved this test to those cases in which the total litters of a given size are about 100 or more. However, we may add in the columns the frequencies of each attribute, and their calculated values, and thereby obtain the distribution of each type of dominant in the whole population. These totals represent the numbers of litters in which the dominants and recessives of the three kinds studied were equal, together with the total litters deviating from the theoretical mid-class value by $+\frac{1}{2}$, $+1$, $+2$ $+5$, and by $-\frac{1}{2}$, -1 , -2 -5 dominants of each particular kind. It will be clear that in $(p+q)^n$ where n is odd, we have two mid-class values equally probable, but we cannot realize litters in such cases with an equal number of dominants and recessives; hence, I have kept these equally probable mid-class values separate where n is odd. The mid-class values in these cases really differ from a theoretical mid-class value or mean by $-\frac{1}{2}$ and $+\frac{1}{2}$. This in no way affects our totals. Applying PEARSON'S test for goodness of fit of the totals observed to the totals calculated, we find that in undepleted litters of all sizes a fit as bad or worse is expected as a fluctuation of sampling 99 times in 100 for agouti, 66 times in 100 for dark eye, and 87 times in 100 for black. Hence we may conclude that our ex-

TABLE I

Undepleted litters; fluctuations in number of agouti, of dark-eyed, and of black individuals in litters of various sizes.²

Size of litter	Classes	Number of agoutis, dark-eyed, and blacks in the litter												Total litters
		-5	-4	-3	-2	-1	Mid-class values		+1	+2	+3	+4	+5	
2	Agouti					1		4		2				7
	Dark eye					1		3		3				
	Black					4		3		0				
	Calculated					1.75		3.5		1.75				
3	Agouti					2		6		0				11
	Dark eye					1		5		2				
	Black					2		1		1				
	Calculated					1.38		4.12		1.37				
4	Agouti				0	9		8		5	1			23
	Dark eye				0	6		7		8	2			
	Black				2	5		9		7	0			
	Calculated				1.44	5.75		8.63		5.75	1.44			
5	Agouti				1	10		17		13	0			65
	Dark eye				1	11		16		8	5			
	Black				4	11		21		10	2			
	Calculated				2.03	10.16		20.31		10.16	2.03			
6	Agouti			1	8	10		28		25	11	1		93
	Dark eye			0	12	27		24		21	7	2		
	Black			0	5	22		28		25	10	3		
	Calculated			1.45	8.72	21.80		29.06		21.80	8.72	1.45		
7	Agouti			1	5	14		27		11	5	0		86
	Dark eye			0	3	21		23		11	4	0		
	Black			0	10	15		22		12	4	0		
	Calculated			0.67	4.70	14.11		23.52		14.11	4.70	0.67		
8	Agouti		0	1	7	10		18		11	5	1	0	53
	Dark eye		0	1	7	11		11		12	9	2	0	
	Black		0	2	5	13		18		7	6	2	0	
	Calculated		0.21	1.66	5.80	11.59		14.49		11.59	5.80	1.66	0.21	
9	Agouti		1	0	1	2		8		2	0	0	0	19
	Dark eye		0	2	0	2		7		2	1	1	0	
	Black		0	1	2	4		4		2	0	0	0	
	Calculated		0.04	0.33	1.34	3.12		4.68		3.12	1.34	0.33	0.04	
10	Agouti	0	0	0	2	1		0		0	0	1	0	4
	Dark eye	0	0	0	1	0		1		0	2	0	0	
	Black	0	0	0	0	1		2		0	0	1	0	
	Calculated	0.00	0.04	0.18	0.47	0.82		0.98		0.82	0.47	0.18	0.04	
Totals	Agouti	0	1	3	24	68		58		69	22	3	0	361
	Dark eye	0	0	3	24	80		57		67	30	5	0	
	Black	0	0	3	28	77		47		64	22	6	0	
	Calculated	0.00	0.28	4.29	24.49	70.47		52.63		70.47	24.49	4.29	0.28	

$$\begin{aligned} \text{Totals } \left\{ \begin{array}{l} \text{Agouti, } \chi^2 = 1.6836, P = 0.986 \\ \text{Dark eye, } \chi^2 = 5.9115, P = 0.657 \\ \text{Black, } \chi^2 = 3.7748, P = 0.875 \end{array} \right. \end{aligned}$$

² In this and subsequent tables, the calculated frequencies were carried out three decimal places in obtaining the totals, and in calculating χ^2 and P .

J. A. DETLEFSEN, FLUCTUATIONS OF SAMPLING IN A MENDELIAN POPULATION

TABLE 2

All litters, undepleted and depleted; fluctuations in number of agouti, of dark-eyed, and of black individuals in litters of various sizes.

Number classified in a litter	Classes	-5	-4	-3	-2	-1	Mid-class values			+1	+2	+3	+4	+5	Total litters
1	Agouti						6		4						10
	Dark eye						5		5						
	Black						4		6						
	Calculated						5.00		5.00						
2	Agouti					2		9		6					17
	Dark eye					2		9		6					
	Black					7		5		5					
	Calculated					4.25		8.50		4.25					
3	Agouti					4	11		11	3					29
	Dark eye					5	10		11	3					
	Black					4	11		11	3					
	Calculated					3.63	10.87		10.88	3.62					
4	Agouti				1	17		17		14	2				51
	Dark eye				1	10		22		14	4				
	Black				4	12		25		8	2				
	Calculated				3.19	12.75		19.13		12.75	3.19				
5	Agouti				1	18	34		34	21	2				110
	Dark eye				1	16	38		30	16	9				
	Black				7	13	34		39	14	3				
	Calculated				3.44	17.19	34.37		34.38	17.19	3.44				
6	Agouti			1	9	30		33		38	14	2			127
	Dark eye			0	16	39		32		27	10	3			
	Black			2	7	30		36		33	16	3			
	Calculated			1.98	11.91	29.77		39.69		29.77	11.91	1.98			
7	Agouti			1	16	26	25		30	16	6	1			103
	Dark eye			0	6	22	27		28	16	4	0			
	Black			1	10	17	26		27	16	6	0			
	Calculated			0.80	5.63	16.90	28.16		28.16	16.90	5.63	0.80			
8	Agouti		0	1	7	10		21		12	6	2	0		59
	Dark eye		1	1	7	12		14		13	9	2	0		
	Black		0	2	6	15		19		9	6	2	0		
	Calculated		0.23	1.84	6.45	12.91		16.13		12.91	6.45	1.84	0.23		
9	Agouti		1	0	1	2	5		8	3	0	0	0		20
	Dark eye		0	2	1	2	4		7	2	1	1	0		
	Black		0	1	2	4	7		4	2	0	0	0		
	Calculated		0.04	0.35	1.41	3.28	4.92		4.92	3.28	1.41	0.35	0.04		
10	Agouti	0	0	0	2	1		0		0	1	1	0	0	5
	Dark eye	0	0	0	1	0		1		1	2	0	0	0	
	Black	0	0	0	0	2		2		0	0	1	0	0	
	Calculated	0.00	0.05	0.22	0.59	1.03		1.23		1.03	0.59	0.22	0.05	0.00	
Totals	Agouti	0	1	3	28	100	82	80	87	113	31	6	0	0	531
	Dark eye	0	1	3	33	108	84	78	81	98	39	6	0	0	
	Black	0	0	6	36	104	82	87	87	90	33	6	0	0	
	Calculated	0.00	0.32	5.20	32.61	101.69	83.34	84.68	83.34	101.69	32.61	5.20	0.32	0.00	

$$\begin{aligned} \text{Totals } \left\{ \begin{array}{l} \text{Agouti, } \chi^2 = 2.9205, P = 0.938 \\ \text{Dark eye, } \chi^2 = 2.8431, P = 0.942 \\ \text{Black, } \chi^2 = 2.0802, P = 0.977 \end{array} \right. \end{aligned}$$

perimental results are consistent with an hypothesis that litters are random samples of two kinds of zygotes of equal frequency in the case of each one of three allelomorphic pairs. Furthermore, since this is a back cross to the ultimate recessive, we may conclude that the gametes functioning at any ovulation are likewise random samples of two kinds in equal numbers, when we deal with a single allelomorphic pair.

YULE (1914) has studied the fluctuations of sampling in DARBISHIRE'S (1904) data on color and albinism in mice. There were 121 litters of various sizes in which $p = \frac{3}{4}$ and 132 litters in which $p = \frac{1}{2}$. Although the numbers in the few litters of each size are too small for an adequate test against (or close agreement with) the binomial distribution, the total populations agree very well in these two cases studied. YULE has so tabulated his data that litters of all sizes with the same number of albinos fall into columns and may be added. My data can be arranged in this form, if desired, directly from the tables presented. Nevertheless, there is an advantage in arranging the frequencies of litters of each individual size as in our tables so that the mid-class values, the deviations above, and the deviations below may be added separately. Even if there is only a slight tendency to intrafraternal correlation, good mean values or Mendelian ratios are obtained, but in the total population the ends of the frequency distribution are quite properly exaggerated. One can thus more easily recognize the cumulative effect of increased values above and below the mid-class value. I cannot imagine any force that would exaggerate the mid-class values themselves. In YULE'S tabulation the entire distributions of the smaller litters are included in the totals with the lower half of the larger litters. Furthermore, with YULE'S tabulation we obtain one set of values for χ^2 and P when the experimental results are given in terms of albinos, but a different set of values for χ^2 and P when the same experimental results are given in terms of colored individuals. For example, in YULE'S table A, $P = 0.94$, but given in terms of colored individuals, $P = 0.48$. That is, the total frequencies do not admit a reversed order. If we tabulate his table A as I have tabulated my results, $P = 0.77$, and this value is the same in terms of colored or albino individuals. The goodness-of-fit values in such a Mendelian population should be identical irrespective of whether we state our results in terms of the dominant or the recessive allelomorph.

Table 2 is the same as table 1, except that 170 depleted litters have been added to table 1, making a total of 531 litters which is a complete record of the entire experiment. The addition of depleted litters does

not modify our conclusions. The agreement in the totals between hypothesis and experiment is in fact remarkably close as is shown by the values of χ^2 and P for all three characters studied. The litters of 5, 6, and 7 occur over 100 times in each case, hence I have calculated χ^2 and P for each distribution separately (see table 2 A). On the whole, the values of P are as good as could be expected. The distribution of dark eye in litters of 5 shows the poorest agreement ($P = 0.038$), but does not show a very improbable set of deviations from the calculated, for such would occur about once in 25 times as a result of sampling. The small value of P is due in a large measure to 9 litters of 5 all of which showed dark eye, when only 3.44 were expected. Both the depleted and undepleted litters of 5 showed a slight excess in this case; but in view of the close agreement for dark eye in litters of 6 and 7, it is safe to regard this particular case as without significance other than a wide set of deviations due to sampling. The exceedingly close fit for agouti in litters of 7 is noteworthy ($P = 0.996$).

TABLE 2 A

The values of χ^2 and P in measuring the goodness of fit for litters of 5, 6, and 7 in table 2.

Number classified in a litter	Character	χ^2	P
5	Agouti	3.2217	0.667
	Dark eye	11.8361	0.038
	Black	5.9837	0.308
6	Agouti	4.9723	0.547
	Dark eye	4.9884	0.289
	Black	4.6457	0.591
7	Agouti	0.8315	0.996
	Dark eye	2.5903	0.761
	Black	3.5252	0.621

Each litter produced by an F_1 trihybrid female gave data on sampling with respect to three allelomorphous pairs. Each allelomorphous pair was treated separately in tables 1 and 2 in a test against calculated binomial distributions. By disregarding the particular characters and classifying a visible character as dominant or recessive, each litter becomes three separate samples of dominants and recessives. Treating the data in this way we obtain three times as many samples of an attribute in tables 3

J. A. DETLEFSEN, FLUCTUATIONS OF SAMPLING IN A MENDELIAN POPULATION

TABLE 3
Undepleted litters; frequencies with which a dominant allelomorph occurred 0, 1, 2 - - - n times in the litters of various sizes. Calculated frequencies in italics.

Size of litter	Number of dominants in the litter												Total samples	Mean		Standard deviation	
	-5	-4	-3	-2	-1	Mid-class values		+1	+2	+3	+4	+5		Observed	Calculated	Observed	Calculated
2					6 5.25	10 10.50		5 5.25					21	0.95	1.00	0.72	0.71
3					5 4.13	12 12.37	13 12.38	3 4.12					33	1.42	1.50	0.85	0.87
4				2 4.31	20 17.25	24 25.88		20 17.25	3 4.31				69	2.03	2.00	0.93	1.00
5				6 6.09	32 30.47	65 60.94	54 60.94	31 30.47	7 6.09				195	2.48	2.50	1.14	1.12
6			1 4.36	25 26.16	68 65.39	80 87.19		71 65.39	28 26.16	6 4.36			279	3.09	3.00	1.22	1.23
7			1 2.02	18 14.11	50 42.33	70 70.55	72 70.55	34 42.33	13 14.11	0 2.02			258	3.35	3.50	1.28	1.32
8		0 0.62	4 4.97	19 17.39	34 34.78	47 43.48		30 34.78	20 17.39	5 4.97	0 0.62		159	4.00	4.00	1.38	1.41
9		1 0.11	3 1.00	3 4.01	8 9.35	15 14.03	19 14.03	6 9.35	1 4.01	1 1.00	0 0.11		57	4.19	4.50	1.50	1.50
10	0 0.01	0 0.12	0 0.53	3 1.41	2 2.46		3 2.95	0 2.46	2 1.41	2 0.53	0 0.12	0 0.01	12	5.17	5.00	1.82	1.58
Total Observed Calculated	0 0.01	1 0.85	9 12.87	76 73.48	225 211.41	162 157.89	164 169.99	158 157.89	200 211.41	74 73.48	14 12.87	0 0.85	1083	3.10	3.13	1.24	1.25

Total, $\chi^2 = 2.9187$ $P = 0.938$

TABLE 4

All litters, undepleted and depleted; frequencies with which a dominant allelomorph occurred 0, 1, 2 - - - n times in the litters of various sizes. Calculated frequencies in italics.

Number classified in a litter	Number of dominants in the litter												Total samples	Mean		Standard deviation		
	-5	-4	-3	-2	-1	Mid-class values		+1	+2	+3	+4	+5		Observed	Calculated	Observed	Calculated	
1						15 15.00		15 15.00					30	0.50	0.50	0.50	0.50	
2					11 12.75		23 25.50		17 12.75				51	1.12	1.00	0.72	0.71	
3					13 10.87	32 32.63		33 32.62	9 10.88				87	1.44	1.50	0.87	0.87	
4				6 9.56	39 38.25		64 57.37		36 38.25	8 9.56			153	2.00	2.00	0.93	1.00	
5				9 10.31	47 51.56	106 103.13		103 103.12	51 51.56	14 10.31			330	2.55	2.50	1.08	1.12	
6			3 5.95	32 35.72	99 89.30		101 119.06		98 89.30	40 35.72	8 5.95		381	3.08	3.00	1.24	1.23	
7			2 2.41	23 16.90	55 50.70	79 84.49		85 84.49	48 50.70	16 16.90	1 2.41		309	3.41	3.50	1.34	1.32	
8		1 0.69	4 5.53	20 19.36	37 38.72		54 48.40		34 38.72	21 19.36	6 5.53	0 0.69	177	4.01	4.00	1.39	1.41	
9		1 0.12	3 1.05	4 4.22	8 9.84	16 14.77		19 14.77	7 9.84	1 4.22	1 1.05	0 0.12	60	4.18	4.50	1.51	1.50	
10	0 0.01	0 0.15	0 0.66	3 1.76	3 3.08		3 3.69		1 3.08	3 1.76	2 0.66	0 0.15	0 0.01	15	5.27	5.00	1.73	1.58
Total Observed Calculated	0 0.01	2 0.95	12 15.61	97 97.83	312 305.07	248 250.01	245 245.03	255 250.01	301 305.07	103 97.83	18 15.61	0 0.95	0 0.01	1593	2.89	2.89	1.18	1.20

$$\text{Total, } \chi^2 = 1.4517 \quad P = 0.990$$

and 4 as are found in tables 1 and 2 respectively, and we have what is tantamount to 1083 and 1593 litters in tables 3 and 4 respectively. The procedure is quite comparable to throwing simultaneously n coins of each denomination, a , b , and c , N times; in which we first measure the agreement between observed and calculated distributions for each denomination separately, and later pool the results as $3N$ samples of n coins regardless of denomination.

In table 3 are given the frequencies with which a dominant allelomorph occurred 0, 1, 2 n times in undepleted litters of various sizes. Table 4 is similar to table 3, except that both depleted and undepleted litters are included in table 4 and this table describes the entire experiment. In both of these tables it is clear that the experimental results agree closely with the calculated values, both in the case of the individual litter sizes and in the total populations, as is shown by the values of χ^2 and P .

The goodness of fit was calculated for the distributions of the more numerous litters of an individual size. The constants are recorded in table 5. The distribution of a dominant allelomorph in samples of 4,

TABLE 5
The values of χ^2 and P in measuring the goodness of fit for litters of 4, 5, 6, 7, and 8 in tables 3 and 4.

Number classified in each litter	Undepleted litters (table 3)		Undepleted and depleted litters (table 4)	
	χ^2	P	χ^2	P
4	2.6523	0.620	2.4944	0.648
5	1.2828	0.930	1.9753	0.852
6	4.5651	0.602	7.7116	0.262
7	6.7515	0.456	4.0193	0.777
8	1.5590	0.949	2.5600	0.955

5, 6, 7, and 8 agree as well with the calculated values as could be expected in a coin-tossing experiment or the like. Furthermore, the mean number of dominants in all samples of a given size (tables 3 and 4) shows close agreement with the calculated mean of the most probable distribution on the hypothesis of simple sampling. Although the probable errors of these means are not given, it is perfectly obvious that the difference between the observed and calculated means is small compared with the probable error of such a difference. Calculations were made in several cases and they agreed with this statement. The standard deviations of the distribution of litters of each individual size are likewise

given in tables 3 and 4. Like the means, the observed standard deviations agree closely with the calculated, and the difference between the observed and calculated values is exceedingly small compared with the probable error in every case. We may therefore conclude that fluctuations of a dominant zygote in litters of any size agree with our conception of sampling in a Mendelian population. It is also clear that the dominant and recessive gametes functioning at an ovulation are random samples of two kinds occurring in equal numbers. In Mendelian experiments we usually pool all samples and present observed ratios in totals, but if a more detailed analysis of our data is made, the subgroups agree with the theory of simple sampling of attributes which underlies strict Mendelism, for the fluctuations of various sizes approach closely their expected frequencies.

It has been shown (DETLEFSEN and ROBERTS 1918) that there is little or no evidence in our data, of selective elimination of recessives, particularly if our calculated values are based upon an *a priori* (Mendelian) probability. The fluctuations of sampling for dominants in *depleted* litters agree with this conclusion. I have given no table for this case, but one can be constructed readily from the data presented by subtracting table 3 from table 4, cell for cell. Such a table gives excellent agreement with the calculated values both in the individual litter distributions and in the total population. The goodness of fit for the distribution of dominants in depleted litters in the total population is shown by the value of $P = 0.850$.

It would be both interesting and valuable to examine the fluctuations of sampling in litters with respect to two or more allelomorphic pairs considered simultaneously, but sufficient data are not easily obtained; and, even if obtained, it is almost impossible to present them in satisfactory form. The number of possible types of litters is too large for tabulation. If, for example, we deal with two allelomorphic pairs, the relative frequencies with which segregating F_2 litters of any size, n , will show any one or any combination of the four zygotic types, AB , Ab , aB or ab , are given by $(p + q + r + s = 1)^n$ where p , q , r and s are the probabilities that AB , Ab , aB and ab , respectively, will happen in a single trial. The number of possible types of a given-sized litter is therefore $2^{a+n-1}C_n$, where a = number of allelomorphic pairs, 2^a = number of zygotic classes, C stands for combinations of, and n = size of litter. This is, simply stated, the number of combinations of 2^a kinds of different things taken n at a time, with repetition allowed. In this particular problem we require the number of terms in a complete homo-

geneous polynomial of the n th degree in 2^n variables. For example, in our experiment, litters of 6 were the most frequent, occurring 127 times. If we study the fluctuations of sampling for two allelomorphic pairs in such litters of 6, these litters may be distributed among 84 possible types, each type of litter being a different combination of the four zygotic classes. Not all types occur with equal probability, to be sure. With three allelomorphic pairs, these litters of 6 would show 1716 types. It will therefore be clear that a continuation of this study with two or more allelomorphic pairs is hardly possible with the numbers usually available.

LITERATURE CITED

- DARBISHIRE, A. D., 1904 On the result of crossing Japanese waltzing with albino mice. *Biometrika* **3**: 1-51.
- DETLEFSEN, J. A., and ROBERTS, E., 1918 On a back cross in mice involving three allelomorphic pairs of characters. *Genetics* **3**: 573-598.
- HARRIS, J. A., 1912 A simple test of the goodness of fit of Mendelian ratios. *Amer. Nat.* **46**: 741-745.
- HAYES, H. K., and EAST, E. M., 1915 Further experiments on inheritance in maize. *Bull. Conn. Agr. Exp. Sta.* 188, pp. 1-31, 7 *pl.*
- YULE, G. U., 1914 Fluctuations of sampling in Mendelian ratios. *Proc. Cambridge Phil. Soc.* **27**: 425-432.