

POPULATION GENETICS OF A POULTRY FLOCK UNDER ARTIFICIAL SELECTION

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THE subject of population genetics first received attention shortly after the rediscovery of MENDEL'S work. In the last thirty years purely deductive studies of the consequences of Mendelian heredity in biological populations have been carried out by many investigators, culminating in the definitive summaries of FISHER (1930) and WRIGHT (1931 and 1942). The principles derived in this fashion are being gradually tested by observations and experiments under both natural and laboratory conditions. Much of this work has been summarized by HUXLEY (1940) and by DOBZHANSKY (1941) with particular reference to the evolutionary aspects of population genetics.

The same principles have been applied to problems of breeding and improvement of domestic animals by WRIGHT (1939) and more particularly by LUSH (1945) and his students. The development of systematic breeding plans designed to control and manipulate the forces acting in population dynamics have proceeded largely on the basis of the deductive studies mentioned above, with but little direct aid from experiments on either laboratory or domestic animals.

Not only are properly designed experiments with animals of economic value expensive to conduct, but the relatively long span between generations places a definite limitation on the study of long-range changes in the genetic makeup of such populations. Most herds and flocks have not been maintained for sufficiently long periods of time, and records generally are not complete enough for a satisfactory study. Suitable material for a study of some of these problems is found in the complete pedigree and production records which have been kept on the production-bred Single Comb White Leghorn flock at the UNIVERSITY OF CALIFORNIA from 1933 to date. Using these records of this flock we compared some of the actual changes which have occurred in the flock with those expected to occur on the basis of current theories of population genetics.

The forces causing genetic changes in biological populations have been identified as selection, migration, chance and mutation. The material at hand permits a thorough study of the first of these. Some information is available on the rôles of migration and of chance. The effects of mutation could not be investigated directly, but these must have been small in view of the low mutation rate commonly observed in laboratory experiments and of the relatively small number of generations. Hence, the specific objectives of the present

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study were to examine the changes which have occurred in our material in relation to the rôles of selection, migration and chance.

FLOCK HISTORY AND THE BREEDING PLAN

The flock originated in 1933 from birds kept for various experimental purposes. At that time and for several years previously the average production in the first laying year per original pullet housed at five months of age fluctuated around an average of 120 eggs, roughly similar to that observed then on commercial egg-production farms in California. The actual averages were 117.5 eggs in 1931, 118.6 eggs in 1932 and 125.6 eggs in 1933, when part of the flock was set aside for selection for high egg production. Thereafter, a systematic plan of family- and progeny-testing in breeding for productive characters was pursued under the direction of DR. LEWIS W. TAYLOR and the senior author.

Several males originating from other flocks were introduced during the course of the years; however, only the introductions made in 1933 and 1934 were incorporated into the flock to any large extent. Females from other groups of birds on the University plant were used as breeders in the production flock occasionally until 1941, since which date the flock has been entirely closed.

The number of pullets each year varied from 402 to 704, except in 1944 when only 260 were retained because about half the flock was diverted to another experiment. The birds were hatched in March and April each year, care being exercised to maintain their pedigree identity throughout life. Pullets were housed at about five months of age and no culling was practiced until the end of the first laying year.

The essential features of the breeding plan were:

- 1) emphasis in selection was largely placed on sister and progeny performance;
- 2) with a few exceptions in the early stages the breeding was from hens two or more years old;
- 3) as already noted, occasional outcrosses were made in the early years of flock formation, the flock being closed after 1941;
- 4) the size of the flock varied from 400 to 700 pullets each year from approximately 11 sires and 85 dams, with the previously noted exception in 1944;
- 5) mating of closely related individuals was consciously avoided.

Breeding plans similar to this appear to be fairly common in the field. The senior author has had occasion to examine the pedigree records of a number of California flocks. Several resembled rather closely those of the flock under study. An additional feature that this flock has in common with commercially bred flocks is the fact that the number of eggs laid was not the sole criterion of selection. Such characters as sexual maturity, egg size, egg quality, hatchability, and viability were also considered. The over-all effect of including these characters was to reduce the selection intensity for egg production. Thus the improvement obtained in egg number is not the maximum but rather that which is feasible under commercial breeding conditions where the number of eggs laid is not the exclusive criterion of worth.

IMPROVEMENT IN EGG PRODUCTION

The average annual hen-housed egg production of the flock from 1933 to 1944 is shown in figure 1. The decrease during the period from 1937 to 1939 which gives the appearance of a cyclic trend was caused by increased mortality from lymphomatosis (TAYLOR, LERNER, DEOME and BEACH 1943), presumably due to greater exposure to the disease. This factor and a consequent reduction in selection for egg production due to additional emphasis on resistance to lymphomatosis may account for the considerable drop in the production index in 1938. The slope of a linear regression fitted to the data indicated an annual change in production of 5.6 eggs per year. Although the trend is not

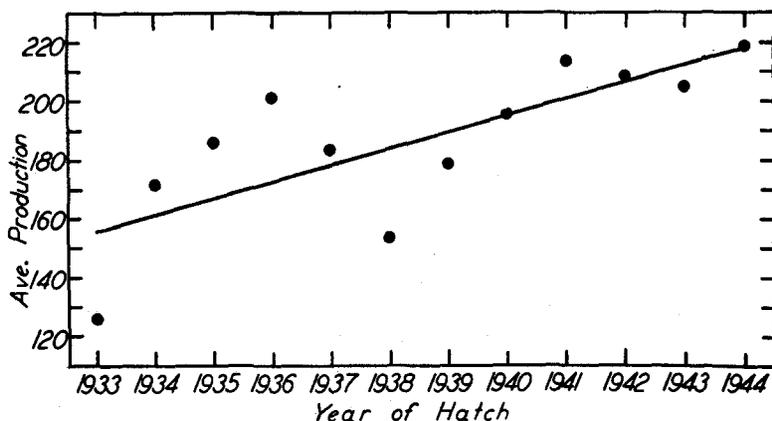


FIGURE 1.—Average production index by years in the UNIVERSITY OF CALIFORNIA production-bred flock. The flock had an increase in incidence of lymphomatosis in 1937-38. The slope of the least squares' regression line is 5.6 eggs per year.

necessarily uniform throughout the twelve years, this figure may be accepted as the average increase in egg number per year.

It is possible to compare the observed rate of improvement with the rate expected on the basis of *a priori* information in this population. The agreement between the actual and the expected rates would partially test whether or not the genetic principles of breeding for egg production are correctly understood. The expected rate of improvement depends on the 1) intensity of selection; 2) accuracy of selection, i.e., heritability; and 3) interval between generations which is measurable in terms of the age of parents (DICKERSON and HAZEL 1944). Estimates of all three of these factors were available in this population, and from them the expected rate of improvement was computed.

Selection intensity can be expressed in terms of the selection differential (the average of the selected birds minus the average of the whole group in which they were hatched). Selection was based chiefly on three criteria: individual performance, records of sisters, and records of progeny. The first two were applied to hens when first selected for mating (since nearly all dams had completed a year of laying before being mated), and the third to hens which were

remated after their progeny had been tested. Sires were first used for breeding when one year old, their selection being based primarily on the incomplete records of their sisters, while older sires were selected on basis of their progeny tests.

TABLE I
Selection differentials, heritabilities and expected genetic gains from the three stages of selection.

STATISTIC	BASIS FOR SELECTION	SIRES	DAMS
Selection differential	Individual performance	—	99.1
	Sisters' record	26.0	39.8
	First-year progeny record	24.4	29.0
Heritability	Individual performance	—	0.045
	Sisters' record	0.155	0.138
	First-year progeny record	0.452	0.155
Expected genetic gain	Individual performance	—	4.46
	Sisters' record	4.03	5.49
	First-year progeny record	11.03	4.50

Table 1 presents in its first part the average selection differentials for four years (1935, 1937, 1939 and 1941) used as a sample representative of the whole period. It may be seen that selection differentials based on sisters' records were greater for dams than for sires. Although the number of dams was nearly eight times as great as that of sires, the completed records of sisters were available for them as against incomplete records for the sisters of sires mated for the first time. The selection differentials for the breeding birds selected on the basis of progeny records were also higher for the dams than for sires (29.0 vs. 24.4 eggs). This presumably is due to the fact that a smaller number of offspring was obtained from dams than from sires. In consequence of this smaller number, the variation in progeny averages was much wider for dams than for sires and the same percentage of culling on progeny-test information gave a larger selection differential (in actual units) for the dams than for the sires.

The advantages shown in the records of selected birds were in part due to differences in environment, exposure to disease, or other intangible but non-hereditary factors. The regression expected to occur must be considered in computing the genetic gain accomplished by selection. The fractions of the selection differentials supposed to represent heritable differences are given in the second part of table 1. The following considerations led to their formulation. LERNER and TAYLOR (1943), using records chiefly from this flock, estimated that the heritability of differences in the production index between families averaging eight daughters was 0.155. This figure is equal to

$$\frac{nr G}{1 + (n-1)r G}$$

where n is the number of sisters in a family (in this case 8), r the genetic correlation between them (in this case 0.5), and G the heritability between individuals (see LUSH 1945). Solving the above equation for G , the heritability of individual records is found to be 0.045. In the present case, the sisters' records of sires and dams were averages of eight and seven pullet records respectively, while the first-year progeny records were averages of 36 pullet records for sires and eight for dams. With these figures as a basis, the respective heritabilities for each of the selection differentials in table 1 can be similarly computed.

The genetic gain which theoretically should have resulted from the selection practiced was then computed as the product of each selection differential and its corresponding estimate of heritability. These figures, given in the third part of table 1, represent the genetic gain expected by selection of the parents at the various stages when selection was practiced. It is noteworthy that early selection was considerably more effective in dams than in sires, whereas the reverse was true of later selection. The first selection of dams was based on both individual performance and completed sisters' records, whereas in sires it was of necessity based only on incomplete sisters' records. This type of selection required two years in the case of the dams and only one in the case of the sires. Progeny-testing was approximately 2.5 times as effective in sires as in dams, the difference being due to the greater accuracy attained by having 4.7 times as many progeny per sire as per dam.

All of the birds in a given year were from sires and dams upon which the first selection had been practiced, while 46 and 32 percent were from progeny-tested sires and dams, respectively. Hence, the average genetic gain of the offspring over the genetic merit of the parental generations may be written as follows

$$\begin{array}{r} \text{gain from sires} = [4.03 + 0.46 (11.03)]/2 = 4.55 \\ \text{gain from dams} = [4.46 + 5.49 + 0.32 (4.50)]/2 = 5.70 \\ \hline \text{gain from both parents} \qquad \qquad \qquad 10.25 \end{array}$$

The gain of 10.25 eggs represents the improvement expected during the period from the hatching of the parents to the hatching of the offspring, which corresponds to the average age of parents. As shown later, the average age of parents was 1.94 years. Thus the ratio $10.25/1.94 = 5.28$ represents the annual gain in production which should have resulted from the selection practiced.

The agreement with the actual gain of 5.6 eggs per year is as close as could reasonably be expected. The heritabilities used in the computations are based on an estimate intended by LERNER and TAYLOR (1943) as a minimum figure and some selection not included in the selection differentials which were used in the computations may have been practiced. This study provides good evidence that a knowledge of selection intensity, heritability and inter-generation span actually enables a breeder to predict the rate of improvement expected from selection (DICKERSON and HAZEL 1944).

EFFECTIVENESS OF PROGENY TESTING

At one time it was considered that the use of progeny-tested parents would

prove an effective tool in promoting genetic improvement which would be applicable to all kinds of livestock and for all economic characters. This belief developed because attention had been centered on the greater accuracy of progeny-test information as compared with that obtained from individual performance or from collateral relatives. Deductive research has indicated more recently that the use of progeny-tested parents may actually result in decreasing the rate of progress as compared with that attainable by earlier selection (DICKERSON and HAZEL 1944). This seems to be particularly true where (1) the length of generation is increased considerably by requiring that the parents be progeny-tested before use, (2) the reproductive rate is high, and (3) the basis for making early selections is relatively accurate. It can be inferred from these conditions that progeny-testing is likely to be more effective for some kinds of animals and for some traits than for others, since these conditions are largely beyond artificial control or manipulation

TABLE 2
Increases in average production of the offspring of part-tested and progeny-tested parents over that from untested parents.

	UNTESTED SIREs		PART-TESTED SIREs		TESTED SIREs		TOTAL	
	NUMBER	EGGS	NUMBER	EGGS	NUMBER	EGGS	NUMBER	EGGS
Untested dams	619	0	344	1.5	118	1.3	1081	0.3
Part-tested dams	191	10.1	132	-2.4	59	11.6	382	6.0
Tested dams	42	9.5	29	11.6	50	22.2	121	8.7
Total	852	1.8	505	1.1	227	7.2	1584	2.3

The data from the present flock afforded an opportunity for investigating experimentally the effectiveness of progeny testing for egg production. Matings were made between untested, partially tested, and fully progeny-tested sires and dams in most of the years. The years 1935, 1937, 1939 and 1941 were again chosen for study. Weighted differences between the progeny from each type of mating and those from untested parents were calculated for each of the four years and combined as shown in table 2. Although the figures appearing therein are not wholly consistent, apparently due to the small numbers of offspring involved, they show that in general the offspring from tested and partially tested parents tended to have higher production than the progeny of untested parents. Thus the progeny from partially tested sires averaged 1.1 eggs and those from partially tested dams 6.0 eggs more than those from untested parents, while those from tested sires and dams, respectively, averaged 7.2 and 8.7 eggs higher. The advantages of the older parents are based on the performance of progeny hatched *after* the parents were promoted to tested ratings, as compared with the performance of progeny hatched in the same years from younger parents which had not yet been tested. These figures are not large in themselves, but when they are compared with the annual rate of gain (5.6 eggs) they show distinct advantages for the progeny of tested parents.

TABLE 3

Average age of parents (in years) for the entire flock and for the families in the upper and lower quartiles of the egg production frequency distribution.

YEAR OF HATCH	POPULATION	SIREs	DAMS	AVERAGE
1935	Upper quartile	1.42	2.50	1.96
	Lower quartile	1.58	2.08	1.83
	Whole flock	1.63	2.51	2.07
1936	Upper quartile	1.90	2.30	2.10
	Lower quartile	1.30	1.80	1.65
	Whole flock	1.53	2.08	1.81
1937	Upper quartile	1.76	2.41	2.09
	Lower quartile	1.71	2.24	1.98
	Whole flock	1.73	2.39	2.06
1938	Upper quartile	1.27	2.20	1.74
	Lower quartile	1.27	2.20	1.74
	Whole flock	1.30	2.20	1.75
1939	Upper quartile	1.50	2.70	2.10
	Lower quartile	1.20	2.40	1.80
	Whole flock	1.52	2.62	2.07
1940	Upper quartile	1.57	2.14	1.86
	Lower quartile	1.29	2.14	1.72
	Whole flock	1.48	2.37	1.93
1941	Upper quartile	1.46	2.08	1.77
	Lower quartile	1.46	2.17	1.82
	Whole flock	1.54	2.21	1.88
Average	Upper quartile	1.55	2.33	1.94
	Lower quartile	1.40	2.15	1.78
	Whole flock	1.53	2.34	1.94

INTERVAL BETWEEN GENERATIONS

The average age of parents is a matter of primary concern in planning breeding programs because it represents the rate at which older generations are being replaced by succeeding ones. Because of the high reproductive capacity of poultry, the interval between generations can be varied considerably depending upon the proportions of old and young parents used for breeding. Table 3 shows the average ages for the sires and dams of the birds hatched from 1935 through 1941. The average ages varied irregularly from year to year, as might be expected where primary emphasis was placed on selecting the apparently superior breeding animals. The figures show no apparent trend either toward younger or older parents as would have been the case if there had been a consistent tendency toward greater use of untested or tested parents. The average age was 1.53 years for sires, 2.34 years for dams, and 1.94 years for both parents.

It may be noted that the sires and dams of the full sister families in the upper quartiles of the frequency distribution of egg production did not average consistently older than those in the lower quartile. Great consistency in this respect is not to be expected, since the heritabilities of the information upon which the parents were selected indicate that many mistakes must have been made in selection. However, the average age of the parents of families in the upper quartile was greater than that of the parents of families in the lower quartile, as might be expected from the conclusion reached concerning the effectiveness of progeny-testing in the preceding section (Table 2). It may also be noted that the parents of families in the lower quartile were consistently younger than the average of all parents.

INTRODUCTION OF BREEDING STOCK

The introduction of breeding stock into herds and flocks of domestic animals corresponds to migration between partially isolated populations. WRIGHT (1940) has shown that partial isolation with limited migration provides a basis for the inter-group selection of genetic systems which is important for the

TABLE 4.
Representation of introduced males in the 1941 flock.

YEAR	MALE	REPRESENTATION IN
		1941 FLOCK
		Percent
1933	G62	53
1933	G65	96
1934	H90	100
1934	H91	0
1936	K99	5
1938	M88	2
1941	S37	5

evolution of the species as a whole. It should be even more effective in herds and flocks of domestic animals, where the multiplication or elimination of genes from introduced stock can be rigidly controlled by the breeder. LUSH (1946), in summarizing investigations on breeds of domestic animals, found that some degree of subdivision existed in about half of the breeds which have been studied.

Breeding stock was introduced into the production-bred University flock at various times between 1933 and 1941, since which time the flock has been completely closed. The history of the introduced males seemed worth considering in some detail. They are shown in table 4 along with the percentages of the birds in the 1941 flock which trace to them at least once. Males G62 and G65 were half brothers which were first used in 1933. In 1941 53 percent of the birds were descendants of G62 in at least one line, while 96 percent were descendants of G65. The two males imported in 1934 show an even more striking

difference in the extent to which their genes have spread through the flock) H90 being represented in the pedigrees of all of the 1941 flock and H91 in none. Additional introductions of one male each in 1936, 1938 and 1941 were made but these had little effect upon the genetic composition of the present flock. The genes of M88 and S37, which probably were present in low frequency in 1941 (table 4), have since been eliminated entirely, so that they are absent from the 1945 flock, while those of K99 are still present in low frequency. Thus genes from two of the introduced males have been disseminated widely through the flock while those from three others have been eliminated entirely.

Females have been introduced into the production-bred flock from experimental groups on the University farm from time to time. However, it does not seem likely that they could have had much influence in changing the genetic composition of the flock, particularly since they were from the same foundation stock as the original production-bred flock or from families removed from that flock for other studies.

INBREEDING AND RELATIONSHIP

The average coefficients of inbreeding (WRIGHT 1923) are given in table 5 for 1935, 1937, 1939 and 1941, calculated from 1931 as the base year. These coefficients represent the expected average percentage loss or "decay" in heterozygosis since 1931 as a result of gene segregation and subsequent sampling between generations where the effective number of breeding animals is

TABLE 5

Production, inbreeding and relationship data on full-sister families containing five or more birds in relation to the family's position in the flock with respect to egg production.

YEAR OF HATCH	POPULATION	TOTAL NUMBER IN FLOCK	BIRDS INCLUDED		AVERAGE PRODUCTION	AVERAGE INBREEDING COEFFICIENT
			FULL-SISTER FAMILIES NO.	PULLETS NO.		
1935	Upper quartile		12	90	241.1	2.0
	Lower quartile	485	12	87	134.7	2.6
	Whole flock		49	391	190.7	1.5
1937	Upper quartile		17	133	224.3	4.1
	Lower quartile	592	17	126	143.8	3.0
	Whole flock		66	510	185.3	3.4
1939	Upper quartile		10	70	238.8	3.8
	Lower quartile	465	10	82	124.3	9.3
	Whole flock		39	293	184.2	7.0
1941	Upper quartile		13	106	269.8	8.9
	Lower quartile		13	98	166.0	8.1
	Whole flock	638	52	390	219.6	8.1

finite. Changes in heterozygosis which may have occurred due to mutation or selection *per se* are not included in these estimates.

The average inbreeding in 1935 was 1.5 percent, after which it rose to 8.1 percent in 1941. This corresponds to an average increase of about 1.1 percent per year or 2.1 percent per generation. From nine to 14 sires were used in the flock each year, the average number being about 11. The number per generation would be somewhat larger than 11, but would not be more than 17, since about half of the offspring were from sires used more than one year. The number of hens used each year was from about 60 to 90. According to WRIGHT's approximate formula (1931), the rate of inbreeding expected per generation is $100/8M$ percent in a random mated population consisting of a large number of females and M equally used sires. The actual increase of 2.1 percent per generation corresponds to $M = 100/8 (2.1) = 5.95$ or approximately 6 as the effective number of sires per generation in the University flock.

Several factors in the mating system tended to make the actual inbreeding differ from that expected on the basis of WRIGHT's formula. Close inbreeding was avoided in most cases by mating birds which had no parents or grandparents in common. Some males and females were introduced after 1931 so that the flock was not strictly closed. These factors would tend to reduce the inbreeding and make the effective number of males larger than the actual number. Family selection was practiced rather intensively (table 1) and required the use of larger numbers of full brothers and sisters as breeders than would have been the case if males had been chosen at random or without reference to the performance of their sibs or parents. In addition, the intensive use of progeny-tested parents made large families of closely related birds available for use as parents. Thus the actual situation in any year was that the males used for breeding consisted of a few sires and their sons (and occasionally grandsons), while many of the females were daughters of the older sires and full sisters of the younger ones. The net result was that the effective number of sires was distinctly smaller than the actual number.

Another aspect of the inbreeding picture is shown by the *inter se* relationship between families. If matings were made at random (except for avoiding full siblings) the inbreeding coefficient would be $R/(2 - R)$, where R is the *inter se* relationship between families. The relationships between families in the upper quartile of the egg-production frequency distribution are shown in table 6 for each of four years. The actual inbreeding coefficient is smaller than the coefficient expected on the basis of random mating among non-siblings in each case. This shows that closely related individuals were mated together less frequently than would have occurred under random mating. The two practices followed in the breeding plan, intense family selection and deliberate avoidance of close matings, had opposite effects on the rate of approach to homozygosis, but it is evident that the former was more powerful than the latter.

EFFECT OF INBREEDING ON EGG PRODUCTION

The rate at which homozygosis can be increased without fixing undesirable genes depends on selection intensity, the number of genes involved, and gene

frequency. Since the last two factors are likely to remain unknown for productive characters, the matter can be decided only by experimentation and observation. There are indications (see JULY 1940 for numerous references) that intense inbreeding systems lead to significant deterioration in the productive characters of poultry. In the flock under study, production (figure 1) and inbreeding (table 5) were positively correlated due to a temporal trend. Apparently intense selection can override the deleterious effects of inbreeding when the latter proceeds at the observed rate of 2.1 percent per generation. Nevertheless, it must be kept in mind that the inbreeding is calculable in theoretical

TABLE 6
Inbreeding and relationship in the upper quartile of the flock.

YEAR OF HATCH	<i>Inter se</i> RELATIONSHIP	INBREEDING COEFFICIENT	EXPECTED INBREEDING COEFFICIENT
1935	9.2	2.0	5.1
1937	14.0	4.1	8.2
1939	12.7	3.8	7.3
1941	17.4	8.9	10.5

terms only, and that selection of heterozygotes may have retarded slightly the approach to homozygosis indicated by the inbreeding coefficient. Hence it is of interest to determine whether within a given year (where the effect of the time trend would be absent) a relation between production and inbreeding exists. This relation was investigated in three different ways.

Firstly, the inbreeding coefficients for the families in the upper and lower quartiles of the egg-production frequency distribution were computed for the years 1935, 1937, 1939 and 1941 (table 5). The average inbreeding coefficients were larger in the upper than in the lower quartile in two years and smaller in the other two. Secondly, the inbreeding coefficients were calculated for parents of families in these quartiles (table 7). Once more no definite differences were noted. Finally, regression coefficients of egg production on the coefficients of inbreeding were calculated. They were found to be -0.54 , -0.46 , -5.81 and 0.84 for 1935, 1937, 1939 and 1941, respectively. Since the average for the four years (-1.20) was not statistically significant it cannot be stated with certainty that inbreeding had a detrimental effect on egg production, but at least one of the negative regressions (-5.81) was significant. Hence, the question whether a relatively slow loss of heterozygosis is detrimental to egg production must be left open, but the effect in the concrete case under discussion could not have been large.

RÔLE OF CHANCE

The effect of chance during gene segregation and in the choice of parents is to change gene frequency in a random manner. With N diploid parents (the product of $2N$ gametes from the preceding generation), the sampling variance of gene frequency at a particular locus is

$$\frac{q(1-q)}{2N}$$

q being the frequency of the allele in the generation from which the gametes come. In populations where generations overlap, the rôle of chance is most con-

TABLE 7
Average inbreeding coefficients of the sires and dams of the upper and lower quartiles and of the entire flock by years.

YEAR OF HATCH OF FLOCK	PULLETS IN UPPER QUARTILE		PULLETS IN LOWER QUARTILE		ALL PULLETS	
	SIRES	DAMS	SIRES	DAMS	SIRES	DAMS
1935	0	1.0	0	0	0	0.3
1937	0.2	2.9	0.4	2.8	0.6	1.6
1939	5.9	1.6	8.1	1.7	6.3	2.7
1941	8.6	4.6	7.3	6.4	8.2	5.2

veniently measured by the inbreeding coefficient. Thus the standard error per generation in the present flock is $100\sqrt{.021 q(1-q)} = 15\sqrt{q(1-q)}$ percent. This is about 7.5 percent for genes with a frequency near 50 percent and 1.5 percent for genes with a frequency near one percent.

As an example of the importance of chance, we may consider the gene frequency array expected for 100 loci with an original frequency of 50 percent after one generation of segregation. The expected array is:

Frequency (percent)	Number of loci
Below 35	2.1
35 -42.5	13.6
42.5-50	34.2
50 -57.5	34.2
57.5-65	13.6
Above 65	2.1

When gene frequency is near 0 or 100 percent, chance operates with greater finality, although with less magnitude quantitatively than when frequency is in the intermediate range. Thus genes having a frequency of less than 5 percent would appear to be in danger of extinction each generation. Of 100 genes with low frequency, it is to be expected that a few would be lost entirely from the flock, most would be transmitted without great change in frequency, while a few (which happened to be present in some of the males chosen as sires) would appear in the succeeding generation in greatly increased frequency. Since sampling accidents occur in a random manner they may or may not be cumulative.

Hence, the genetic constitution of a flock no larger than this is likely to be altered considerably in a few generations by the effects of chance alone.

DISCUSSION

The actual improvement in egg production in the 12 years covered by this study was from an average of about 120 eggs to about 220 eggs per bird per year. This does not necessarily represent the maximum possible rate of progress, but is sufficient to attest to the power of the genetic forces brought to bear on the flock.

In general, breeding programs may be designed to emphasize the rôles of selection, of migration, or of chance, individually, so that only one force is responsible for changes in the genetic composition of the population (except that mutation cannot be controlled). Deductive studies (summarized by WRIGHT 1942) indicate that most favorable conditions for genetic advance are attained when the evolutionary forces are balanced against each other rather than when any one completely dominates the situation. The breeding program used in this flock seems to be well balanced from this standpoint, although undoubtedly some refinements might make it more effective. Its chief criticism may be that selection has been so intense that rare beneficial genes have been eliminated by chance or that certain beneficial combinations of genes have been prevented from occurring. All of the selection has been in one direction and for one kind of genetic system, whereas, if control by selection had been somewhat less rigid, a greater number of gene combinations and genetic systems would have been formed and tested. The specific effects of chance, migration and selection, together with interrelations between them, may be next considered in that order.

The rôle of chance in determining changes in gene frequency from one generation to another has been quite important in this flock. This was in part a consequence of the kind of selection practiced. LUSH (1946) pointed out that intense selection was accompanied by restriction of ancestry in small populations of domestic animals. Although close mating was avoided where possible in this flock, inbreeding rose more rapidly than would have been expected in a flock of equal size where the parents were chosen at random. The intense family selection was responsible for the additional inbreeding and for the corresponding increase in the importance of random changes in gene frequency.

It seems probable that selection has been sufficiently intense to avoid the random fixation of genes which had undesirable effects unless their initial frequency was very high. The evidence concerning the detrimental effect of inbreeding was inconclusive but the effect was not pronounced if it existed at all. LUSH (1945, p. 284) stated "It is unlikely that inbreeding rates as high as three or four percent (per generation) can go on forever without harm, but certainly they can be continued for many generations." Nothing can be added to this statement from the present study except that an appreciable rate of improvement was maintained for several generations while the rate of inbreeding was more than two percent per generation.

Migration, or the introduction of breeding stock, was not an important fac-

tor quantitatively, since only seven sires have been introduced among approximately 100 used. Family selection, when combined with migration, provides an effective means of testing new gene combinations and accepting or rejecting them more quickly than is likely to occur in nature. In this case, the intense family selection practiced quickly eliminated genes from three of these sires and carried the frequency of genes from two others to relatively high levels.

Selection was the only directive force utilized in the breeding program. Considerable significance is attached to the general agreement between the actual rate of improvement and that calculated on the basis of the selection which has been practiced. Since this seems to be the first experimental test of the selection principles deduced in theoretical studies, the agreement between actual improvement and expected improvement was sufficiently close to be gratifying. To some extent then, those principles can be employed in applied breeding programs with greater confidence in their validity.

The three factors that determine the effectiveness of selection are selection intensity, selection accuracy or heritability, and the average age of parents. Although they can be manipulated by the breeder, they are not independent of each other. Thus accuracy of selection and the average age of parents exercise a pull in opposite directions. Similarly, as shown in table 1, the selection bases with lower heritabilities permit higher selection differentials than those with higher heritabilities. Hence, there undoubtedly must exist an optimum combination of these forces to provide the maximum rate of improvement. Whether or not the optimum combination was attained in the present flock is not an important question in this discussion. The significant point is that the rate of progress predictable from the factors discussed was realized, thereby substantiating the statistical and genetic principles upon which they were based.

SUMMARY

The rôles of selection, chance and migration were analyzed with respect to the improvement in egg production in the UNIVERSITY OF CALIFORNIA poultry flock over a period of 12 years. The important features of the mating system used were: annual flock size from 400-700 pullets, semi-closed system of breeding, emphasis on family and progeny performance, selection and breeding from females two years of age or older, and deliberate avoidance of close mating.

The analysis indicated that the theoretical gains expected on the basis of known selection intensity, heritability and average interval between generations were in close agreement with the actual gains realized (5.28 vs. 5.6 eggs per year). This is interpreted as a verification of the principles of population genetics derived deductively by earlier workers.

Progeny-testing was found to have made a significant contribution to the improvement obtained in spite of the increase in the average age of parents incident to its use.

The rate of approach to homozygosis was found to be of the order of two percent per generation, or one percent per year, in spite of the mating system used. This situation arose as a result of family selection which leads to a reduction

from 11-17 actual sires per generation to a calculated number of six effective sires. No significant detrimental effects of this rate of inbreeding on egg production could be established.

The rôle played by chance in changing gene frequencies was found to be rather large, the standard error of chance segregation being between 7.5 percent for genes with a frequency of 50 percent and 1.5 percent for genes with frequencies near one percent.

Migration was not an important factor quantitatively in this population, since the number of introduced sires was relatively low. It was shown that artificial selection provides potent means for rapid incorporation or elimination of introduced genes.

As a general conclusion, it may be stated that the currently accepted principles of population genetics (excluding the rôle of mutation) are empirically verifiable and lead to predictable rates of improvement in populations subjected to artificial selection.

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