

THE SPREAD OF GENES BY NATURAL AND ARTIFICIAL SELECTION IN CLOSED POULTRY FLOCK

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INTRODUCTION

Since Wright and McPhee (1925) developed a method of sampling pedigrees to estimate coefficients of inbreeding and relationship, several pedigree studies have been made, mostly on data taken from the herd books of different breeds of cattle. The form taken by these studies in the thirties is illustrated by the work of Yoder and Lush (1937), Willham (1937) and Lush and Anderson (1939). These analyses provided information on inbreeding, *inter se* relationships, tendencies to family formation, generation lengths; and relationship of the breed to certain prominent ancestors. The object was to discover the methods which had been used in building up the breed.

More recently, especially in Great Britain, pedigrees have been used [e.g., Robertson and Asker (1951), Wiener (1953)] to determine the structure of breeds in terms of stud groups. These investigations showed that any improvement in a breed must be made in a relatively small group of top studs. The dissemination of this improvement to commercial herds is then accomplished by patterns of migration through secondary and tertiary stud groups. This work has provided much information as the size of the top stud group, the number and size of lower layers of studs in the hierarchy and thus the lag in the rate of dissemination of improvement from the top studs, and the stability of stud structure.

This work was done with the breed as a basis, but Lerner and Hazel (1947) in studying the genetics of a poultry flock under artificial selection, made use of pedigrees. They analysed the relationship of inbreeding coefficients of groups of birds to the production of the groups, and also estimated the effects of individual ancestors and migration on the gene pool of the flock.

Ideally, information on a selection programme would give details of changes in frequency of all genes, which changes could be related to changes in the population mean. When, as usually happens, the characters under selection are inherited polygenically, this situation cannot be achieved. However, since selection changes gene frequency by eliminating poor genotypes and increasing reproductive efficiency of good genotypes, an approach can be made by the use of pedigrees. These enable us to trace the fate of genotypes as shown by the changes in the percentage of genes which each genotype has contributed to the flock. To the extent that variation in the characters under selection is additive, the changes in the proportion of genes in the flock derived from any genotype will be, with some limitations, regular from generation to generation. Irregular changes will arise from the effects of chance, non-additive genetic variation, and different aims of selection at different times.

Changes in relative importance of any genotype from one generation to the next will be the result of the total selective force applied to that genotype during that period. In a selection programme the total selective forces will include both natural and artificial selection. The spread of genes from a genotype can be partitioned into components attributable to the different forces acting, and these components can then be related to production characters.

Most selection programmes are carried out on populations for which full pedigrees and production records are kept. These are a potential source of valuable information, and this study has been made to realise some of that potential.

MATERIALS AND METHODS

The data for this study were provided by the records of the Queensland University's poultry flock, which consists entirely of Australorps. The flock was begun in 1953 with about 120 birds whose half sib relationships were known, obtained from a commercial breeder using the "Hagedoorn system". In 1954 the flock was increased to 240 birds and in 1955 to 480, when a control flock was begun. All mating has been done by artificial insemination, and pedigrees tracing back to foundation stock are available for all birds. No new birds have been introduced. The selection programme has been aimed at increasing egg production.

In 1953, thirteen males were mated to sixty females, and since then twelve males have been mated to ninety females each year (approximate figures). Full and half sib matings have been avoided, otherwise mating has been at random. The restriction on random mating was imposed to limit inbreeding. Hatching extends from August to early October.

At the end of May, pullets' production indices based on individual and family performance are calculated from production to that date corrected for date of hatch. Selection of females to be parents of the next generation is made on these indices; males are weighed at 12 weeks of age and the heaviest two in each full sib family are retained, except offspring from matings with poor fertility and hatchability. From the cockerels retained, selection is made on full sisters' performance.

From the pedigrees an estimate of the percentage of genes in the selected flock contributed by each ancestor was made. This was done by assuming that each parent contributed one half of the genes in a bird's genic complement, each grand parent one quarter, and so on. These proportions were then summed over all members of the flock at the stage in question to give an estimate of the percentage of genes in the flock derived from the ancestor under consideration. The percentage of genes inherited from each foundation flock member was estimated at different stages in the development of the flock. These stages were—

- (i) When matings were made (generation n) each mating was taken as a unit and the percentage of genes in these units estimated for each ancestor;
- (ii) The eggs set for incubation were taken as units and the percentage of genes calculated on the basis of 100% fertility;

(iii) Offspring (generation $n+1$) of each mating which survive to be available for selection were taken as units for the percentage of genes calculation.

For more detailed work further stages could be used, for example, here (iii) could be divided into (iii)*a*, fertile eggs, (iii)*b*, chicks hatched and (iii)*c*, surviving birds. However, the three stages used here were considered adequate for this study. The percentage of genes from each ancestor was calculated for these stages each year. Call these estimates (i) mating percentage of genes, (ii) egg percentage of genes and (iii) survivors' percentage of genes. Consider changes in the percentage of genes from stage to stage.

The number of eggs laid by females produces a change from mating percentage genes (i) to egg percentage genes (ii). Changes through the female may be regarded as due to natural selection, but since males are mated at random, any change through the male is due to chance. Call this the chance change C. Change from egg percentage to survivors' percentage is caused by differential elimination of offspring after the effects of fertility, which are forces of natural selection. Call this change the natural selection change N. Change from survivors' percentage to mating percentage is caused by the artificial selection practised. Call this change the artificial selection Change A.

The method used to measure the changes was the ratio of the percentage of genes after change to the percentages of genes before change. Ratios were used instead of actual percentages of genes because the magnitude of changes in the percentage of genes was positively related to the magnitude of the percentage of genes before the change. Thus, if the actual changes had been used, the measure of selection at any time would have been affected by the selection which had taken place previously. This would have involved confounding the effects of natural and artificial selection. The use of ratios enables a better separation to be made.

The changes in the percentage of genes from stage to stage in the development of the flock have then been separated into three components, although not with perfect accuracy. The percentage of genes of original birds only have been studied, as at the time of analysis there was insufficient information on the spread of genes from later birds.

It should be pointed out that the measure of selection is that of selection between and not within genotypes of original ancestors. For instance, if one half of the flock were selected, and two families were descendants of one individual with equal percentages of genes in each family, if one family was selected and the other culled, there would be no selective effect on the percentage of genes in the flock from that ancestor.

The changes in percentage of genes together with production records were analysed to discover the relations between them.

The form of progeny test used here is not delicate but is adequate for the purpose. When production indices are calculated, a family correction is made in the form $w(f-m)$, where w is the weighting for family size calculated according to the formula given by Lerner (1950), f is the mean full sib family production and m is the flock mean. The mean of family corrections of this offspring is then used as a progeny

test of the sire, while the deviation of her offsprings' family correction from the sire's value was taken as a progeny test of the dam. This test will be more accurate for males than for females (see Osborne, 1957).

The most frequently used statistical technique was that of regression. However, because of great differences in magnitudes of variables and because attention is here focussed on the extent to which the variables are related, the statistic used to present results is r , which measures the proportion of variance accounted for by the regression.

The assumption on which the estimation of the percentage of genes is based is not strictly correct, because random segregation and recombination will alter the percentages in individuals. However, when these estimates are summed over a number of individuals the errors generated by the random processes tend to cancel. Any error introduced by selection of birds with more or less than the average number of genes from an ancestor will be systematic but incalculable. Such errors should not, however, be very large and do not invalidate use of the estimates.

RESULTS

Since males are mated at random (with one small restriction) it may be assumed that the average quality of his mates is the same for each male. Then the spread of a male's genes is largely independent of the particular females to which he is mated. However, each female receives only one mate, so the fate of her genes is linked with that of one male. Consequently, the spread of genes from males and females must be considered separately.

Table I. *Regressions for Males*

Variables	<i>N.</i>	<i>b.</i>	r^2	<i>p.</i>
mean A on mean family score	14.	0.0260 ± 0.0050	0.6918	< .001
1st A on mean family score	14.	0.0383 ± 0.0076	0.6763	< .001
sum A_2, A_3 on mean family score	14.	0.0371 ± 0.0107	0.5014	< .01

Table I shows the regressions of A on the mean family score for the males of the original stock. Although neither of the variables is measured with complete accuracy, a high degree of correlation is found to exist between them. This relationship would be expected in the case of A (first change) merely on the grounds that selection is made partly on the figures which are used in estimating genotypic value. The elimination of A reduces the correlation which is still, however, large, and when all three changes are considered, no reduction occurs. This evidence of a large degree of additivity of genetic variance is of great importance with regard to the progress of selection, specially when it is remembered that by the time the last selection change is measured, the genes from any individual have been included in many different combinations.

From the situation in the spread of males' genes, a correlation is expected between the score of a male and the spread of genes of a female to which he has been mated, because this is also a measure of the spread of a proportion of his genes.

Table II. *Regressions for Females represented 2 years or more*

Variables	N.	b.	r ²	p.
mean A on year production	27.	-0.007 ± 0.0043	0.0010	0.85
mean A on production index	27.	-0.0067 ± 0.0102	0.0175	0.50
mean A on age 1st egg	27.	0.0031 ± 0.0111	0.0032	0.80
mean A on offspring family score	27.	0.0090 ± 0.0074	0.0587	0.25
mean A on mean family score of mate	27.	0.0185 ± 0.0065	0.2445	0.01
mean A on male and female components of family score	27.	b ♂ 0.0259	0.2500	0.04
	27.	b ♀ 0.0136		

Table II shows that this is in fact the case. A significant amount (24%) of the spread is accounted for by linear regression. The regression of spread of female's genes on family score of her offspring is much smaller (6%). Osborne (1957) has shown that this score is less accurate than that for the male, so that such a result is quite consistent with the much higher male regression. A multiple regression was calculated showing a higher effect of male score (about twice the effect of female score) but which failed to increase the degree of relationship shown, although making use of more information. Intrasire rank correlations of gene spread and family score, although based on only three or four observations, each showed an average value of nearly 0.75, indicating some relationship of these variables although it is not as direct as in the case of male family scores. There are no demonstrable relationships between gene spread and various production characteristics, presumably because of the low heritability of these characteristics.

Table III. *Regressions for Females still represented by offspring*

Variables	N.	b.	r ²	p.
mean A on year production	18.	-0.0032 ± 0.0045	0.0303	0.50
mean N on year production	18.	-0.0016 ± 0.0024	0.0229	0.60
mean A on mean N	18.	-0.2860 ± 0.4613	0.0270	0.50

It is generally considered that selection for high egg production is opposed by natural selection operating through fertility and hatchability. Lerner and Hazel (1947) found no evidence to support the view, but emphasised that their results in no way disproved the hypothesis. In this study (Table IV) a non-significant negative relation was found between the natural selection effect and the preceding artificial selection. Since the preceding natural selection is considered in artificial selection (males from poor fertility and hatchability families being culled) some reinforcement of the two forces might be expected on the basis of their independence. This is not found to be so. It would appear that the two forces are in opposition but that in this flock the culling of males from families naturally selected against is partially balancing these forces; but the evidence is inconclusive while being suggestive. The relatively higher fertility and hatchability of the control flock on this farm is a further suggestion that the two selective forces tend to act in opposition.

Table IV. *Regressions for Birds represented 2 years or more*

Variables	<i>N.</i>	<i>b.</i>	<i>r</i> ²	<i>p.</i>
A on N preceding	78.	0.2454 ± 0.1957	0.0200	0.30
N on A preceding	52.	-0.1519 ± 0.1035	0.0413	0.25

Despite the deliberate avoidance of full and half sib matings the coefficient of inbreeding of this flock has been increasing at the rate of 2% per generation, taking the foundation stock as base, the value of *F* now being 0.0656. The foundation stock, consisting of nine inbred groups and one outbred group, had a coefficient of inbreeding of approximately 25%, so that the flock is now considerably inbred.

Of the genes at present in the flock, it is estimated that 14% come from each of two full or half brothers, B67 and B77, and a further 10% come from a female G13, which was mated to B77. Thus one-fifth of the genes in the flock are descended from one mating B77 × G13, and another one-sixth from the mating, B76 × R56. Of the original thirteen males, sixty-two females selected, ten males and eighteen females are still represented by descendants in the flock. The percentages of genes in the flock derived from the nine males are shown in Table V.

Table V. *Percentage genes in flock (1956) from foundation males*

B76	B77	Y5	Y6	W59	B21	R74	R79	R80	R85
13.681	14.167	1.736	8.264	0.069	4.236	1.806	0.278	2.639	6.111

The absolute magnitudes of the changes in percentage of genes are of interest in estimating the relative intensities at which the two selective forces are working. In Table VI are shown the total and net changes of the percentage of genes attributed to natural and artificial selection. For both, about two-thirds of the selective effect

Table VI. *Quantitative effects of natural and artificial selection on the percentage of genes of 9 male ancestors*

Bird	Artificial		Natural	
	Total	Nett	Total	Nett
W.59	1.551	+1.551	1.558	1.496
W.60	3.766	+3.418	0.728	0.674
R.74	4.139	1.921	1.641	0.401
R.77	3.539	3.539	0.505	0.505
R.79	4.037	4.037	0.943	0.399
R.80	3.004	2.276	0.906	0.906
R.85	4.307	4.037	1.924	1.652
B.16	1.958	1.958	0.642	0.642
B.21	3.783	1.053	1.458	1.458
B.76	8.967	7.367	3.342	3.342
B.77	9.949	9.949	1.978	1.466
Y.5	3.497	1.103	2.055	1.201
Y.6	10.489	2.419	4.947	1.987
	62.786	44.624	22.627	15.929

is in the same direction from generation to generation, while in both absolute magnitude and net effect, artificial selection seems to be about three times as strong as natural

selection. When the strength of artificial selection is considered, natural selection appears quite powerful.

DISCUSSION

It has been seen that in this flock a considerable proportion at least of the genetic variance acts additively, so selection should be capable of producing improvement, except insofar as opposing natural selection may overcome its effects.

Two estimates of genotypic merit have been made and correlated—one based on phenotype and the other on spread of genes. The first is subject to errors arising from environmental effects, the second to errors arising through random segregation and errors of technique in the selection programme. When males are considered, the two measures agree well, but when females are considered, the agreement is not nearly so good. It is obvious that for females both measures are of less accuracy than for males. An improvement in the phenotypic estimate can be made by including Osborne's sire family weighting. An increase in the accuracy of the second can be made only by revision of the methods of the selection programme.

Such a revision in fact involves a change in the mating system used. In this flock, the restriction on random mating has at any time produced only slight deviations from randomness, so a relaxation of the restriction would not produce the desired change. The alternative is some form of assortative mating, on either a genotypic or phenotypic level. Since strong inbreeding has been found, for example, by Shoffner *et al.* (1953), to be undesirable in chickens, genotypic assortative mating cannot be favourably looked upon. Phenotypic assortative mating then remains to be considered.

The most suitable scheme of assortative mating appears to be the division of the selected birds into groups on phenotypic resemblance, and to mate at random within these groups. If this caused too high a degree of inbreeding, the avoidance of full-sib matings could be practised.

If such a scheme is to be practised it must show advantages over the more usual system of mating at random. The main purpose of random mating is to conserve genetic variability from which to make further selection. The results of this study suggest that it also reduces the efficacy of spreading genes from good female genotypes through a flock.

On the other hand, although assortative mating should speed the progress of selection by spreading favourable genes faster and increase the differences between families, thus increasing efficiency of selection, it has disadvantages. First, it will increase the rate of inbreeding, although this may be of not too great consequence if matings are carefully made. Second, it tends to reduce the supply of genetic variability available for selection. The practical importance of this is difficult to assess, as by the time this may be necessary for further progress the pattern of selection seems to be broken up, as Clayton and Robertson (1957) found to be the case in *Drosophila*. Third, assortative mating calls for a change in selective techniques, as those used at present are based on the assumption of random mating. In view of the uncertainty of the fate of selection programmes after the initial period of success, it is difficult to assess the exact value of assortative mating in a selection programme, but it seems at least

worthy of serious consideration. The possibility of speeding selection is well worth testing especially when it may have no great effect in reducing the reach.

SUMMARY

The pedigrees of birds in a poultry flock under artificial selection were analysed to trace the spread of genes from original flock members.

The changes in gene percentage from generation to generation were separated into parts attributed to chance, natural and artificial selection.

The changes due to artificial selection were related to various production characters. The spread of the male's genes was 70% determined by a progeny test which also 25% determined the spread of genes of birds mated to him. The progeny test of the female did not contribute equally to determination of the gene spread. This was attributed to lesser accuracy of the female progeny test and less complete determination of spread of genes by value of genotype.

Despite avoidance of sib matings, inbreeding has increased 2% per generation.

Evidence that natural selection was opposing artificial selection was suggestive but inconclusive.

It was suggested that assortative mating would increase the determination of gene spread by genotypic value. This was considered worth testing.

ACKNOWLEDGEMENT

Acknowledgement is due to the Commonwealth Bank Rural Credits Development Fund which provided facilities for poultry breeding research at this University and also a Fellowship which enabled one of us (J.W.J.) to carry out this work.

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