A STUDY OF INTERACTIONS IN BREEDING OF POULTRY FOR EGG PRODUCTION

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ABSTRACT

Data from a European poultry breeding company and the U.K. Random Sample Test Station were analysed for evidence of purebred-crossbred and genotype x environment interactions respectively in egg-laying poultry. All the 6 pure lines used in making the crosses, comprising 319 sires, 1,822 dams and 16,726 pullets were analysed for estimates of heritability and genetic correlations. The pooled heritabilities based on sire and full-sib variance components were respectively 0.40 and 0.38 for sexual maturity, 0.30 and 0.31 for hen-housed egg number, 0.10 and 0.16 for rate of lay, 0.50 and 0.46 for egg weight, 0.61 and 0.55 for housing body weight, 0.49 and 0.48 for adult body weight. Evidence of the distribution and linearity of offspring on parent regressions for the traits were also obtained on the pure lines.

124 sires which had 5,831 purebred and 5,018 crossbred progeny were involved in the purebred-crossbred studies. Weighted covariances, genetic regressions (cross on pure) and correlations were computed. The pooled correlations were 0.21 for sexual maturity, 0.32 for egg number, 0.28 for rate of lay, 0.54 (or 0.89 after excluding FXE crosses) for egg weight, 0.92 and 0.65 for housing and adult body weights respectively.

In the experiments analysed for stock x environment interactions, the variable environmental factors were dietary fibre and protein levels, lighting and feeding regimes, as well as a comparison of breeder's management conditions and those of the random sample tests. Stock x environment interactions were found to be unimportant for practically all the traits including profitability.

The main impression from the study is that some crossbred-based improvement programme may be beneficial to rate of lay, and that any gains made would not be blocked by genotype x environment interactions assuming sires would respond as these stocks, to similar environmental variables.

I. GENERAL INTRODUCTION

The species of livestock on which scientific principles of livestock improvement have long been applied is the domestic fowl (Gallus domesticus). Much success has been claimed in the genetic improvement of growth rate and efficiency of broiler-type poultry (Dickerson, 1968; Clayton, 1972 and Nordskog, 1977). However, the role of applied genetics in increasing the egg producing ability of the fowl is still a subject of much controversy. Clayton (1972) considers that domestication per se, enhanced by improved technology of feeding, disease control and general husbandry are responsible for the increased egg production of today's chicken. On the other hand, Dickerson (1968) and Dickerson and Mather (1976) attribute much of the improvement to applied genetics.

One source of information which should help resolve the controversy is the United States Department of Agriculture's Random Sample Test results. The tests compare annually the performance of all the leading commercial strains with some unselected control stocks under the same climatic, management and feeding conditions. However, due to the inconsistencies in the performance of the control stocks, the interpretation of genetic trends in the commercial stocks have been various. The decline in control performance has been interpreted to be genetic (Clayton, 1968) whilst Dickerson (1968) blames it on the sensitivity of the control stocks to worsening test environment.

An undisputed picture which emerges from the results is that the best six commercial strains have not exceeded 240 eggs per hen-housed per annum over several years.

Reports about the phenomenon, plateau to selection for egg production, are available in the literature (Dickerson, 1955; Yamada et al., 1958; Nordskog et al., 1967). Various reasons have been assigned and the

major ones may be summarised as follows:

(i) Exhaustion of genetic variation (Yamada et al., 1958).

(ii) Existence of a condition resembling overdominance or epistasis in which genetic variation existed yet no response to selection was observed (Dickerson, 1955; Dickerson, 1963; Nordskog et al., 1967).

(iii) Genotype x environment interaction which prevent gains made under a particular environment to be realized under other environmental conditions in which performance is desired (Dickerson, 1955; Nordskog et al., 1967).

(iv) Ineffective breeding plans resulting from erroneous data and faulty assumptions underlying the models used to analyse genetic data (Thompson, 1978; Clayton, 1975 and Shalev, 1977). Under this may be included, departures from normality such as skewed and kurtotic distributions of the egg production traits, and the asymmetry of genetic parameters. More information on the genetics of egg production is thus required in view of such reports.

The first three causes refer to non-additive genetic factors. The suggestion therefore has been made that some sort of crossbreeding would be beneficial. The fact that egg production traits exhibit highly exploitable heterosis lends an additional support for the suggestion.

The exact detail of it, however, would depend upon the importance of purebred-crossbred interaction between strains participating in such a crossbreeding programme. Operationally, such an interaction means that sires would rank differently when used in their own strains and

in another strain.

A further problem to consider in using crossbreeding would be the environment under which to carry out selection. Modern commercial strains of poultry are required to perform under various types of environment most of which differ from those under which they were bred. This has become necessary in view of the expense involved in the breeding itself, as well as the need to adopt several cheaper methods of production by commercial producers to increase their profit margins in a highly competitive market. The reports (cited earlier), that genotype x environment interaction are important would imply that some of the environmental modifications applied by producers would influence, in an unpredictable manner, the choice of strains.

In principle the two considerations, purebred-crossbred and genotype x environment interactions, are aspects of the same concept namely interactions in breeding for high egg output. Their effect, individually or combined, is to block genetic progress if neglected in a breeding programme.

The main objective of the thesis is therefore to examine relevant data from a commercial poultry breeder and the United Kingdom National Poultry Tests for evidence of the two types of interaction and suggest the necessary breeding policy to adopt in order to overcome or minimise their effect (Parts II and III).

Information relevant to the genetics of purebred egg production, such as distributions and linearity of genetic parameters of economic traits were also obtained and appear in Part I.

PLAN OF WORK

Two (2) sets of data are being used for the study. The first set consists of pure and cross data from a commercial Poultry Breeding Company.

The second, which is also used to study genotype-environment interactions, comes from the National Poultry Test Grounds at Milford, Surrey in the United Kingdom.

The thesis is subdivided into three parts to enable various aspects of the problem to be more fully investigated. Part I deals with the genetics of egg production and the main interests are:

(i) To analyse the pure lines involved in the crossing to establish the relative importance of additive and non-additive genes in these lines using heritabilities based on the sire and dam components of variance.

(ii) The importance of hatch effects as well as the homogeneity of variance among hatches, using Bartlett's Test.

(iii) The distribution of egg production traits is studied using skewness and kurtosis statistics.

(iv) The effect of the distribution of the traits on the symmetry or 'linearity' of genetic parameters, heritability and genetic correlation is ascertained under different intensities of selection.

In Part II, a comparative study of pure and cross performances is made with a view to determining the relative efficiencies of cross-bred-based and purebred-based selection schemes. By considering the pure and cross progeny performances of the same sire as different traits, the genetic correlation between them would indicate the extent

to which the two performances are under similar genetic control. A high correlation, for instance, would indicate that additive set of genes control both pure and cross performances. The genetic correlations, so obtained, are then used to obtain the respective weights for pure and cross information in a sire selection index.

Genotype x environment interaction is the main subject dealt with in Part III. Performance of relatives in different environments are being considered as different traits, and as under Part II, the genetic correlation is also used to quantify the significance of the interactions. Within strain information is not available, hence a strong assumption is being made that the strains and strain-crosses involved in the tests are a random sample from an infinite number of selected strains.

Four experiments in which the environments considered are all non-genetic factors likely to vary among farms within the same location are involved. This is because (i) interactions of such factors with genotypes are more important in a climatically homogenous country and (ii) in future, details of management and nutrition are most likely to vary among farms, as production costs and methods of bringing them down would tend to vary most among production units (or farms).

The main inferences in the various parts are integrated into a final 'Discussion and Conclusion' chapter, where impressions from the project on the relative efficiencies of crossbred-based and purebred-based breeding policies as well as the environment under which such policies should be carried out, appear.

2 GENETICS OF EGG PRODUCTION

2.1 INTRODUCTION

Justification for making any breeding plan for the improvement of an economic trait depends upon the nature of genetic variability in the population concerned. This is because the nature of gene action responsible for the genetic variability is likely to vary among different populations in response to forces changing gene frequencies such as inbreeding and selection pressure, to which the population has been exposed in the past (Falconer, 1960).

The main purpose of this chapter then is to analyse the pure lines used in making the crosses to obtain genetic parameters, the most important of which are the heritabilities of and genetic correlations between traits that must be improved simultaneously.

Shalev (1977) concluded from an extensive literature survey, that realized response to pure-line selection for egg production was far short of expectations, a view also shared by Nordskog (1977). Thus a re-appraisal of the genetics of pure line egg production in poultry is desirable, and that will also be done in this chapter.

King and Henderson (1954a, b) were among the earliest to lay down the statistical premises for the analysis of genetic data from selection experiments on poultry. Their model was based on the usual heirarchical structure of poultry populations in which pullets are pedigreed to and nested within dams, with sires on top of the hierarchy. Several estimates of heritabilities and genetic correlations of the important economic traits of poultry have since been published. Kinney (1969) has compiled these parameters, which show marked variations within traits measured in different populations.

In general, however, rate of lay, hen-housed and survivors egg

production (see 2.2 for definitions) are lowly heritable (h^2 = 0.1 - 0.25), sexual maturity is of moderate heritability (h^2 = 0.3 - 0.4) whereas egg and body weights are regarded as moderate to high in heritability (h^2 = 0.4 - 0.6).

The trait of most importance to breeders of egg-type poultry is egg number due to its effect on feed efficiency and hence profitability, followed by egg weight. The two are however known to be negatively correlated in most modern high-producing strains (Dickerson, 1957). The genetic correlations between pairs of the other traits may be found in Dickerson (1957) and Kinney (1969).

The assumptions that underlie the model used to analyse data to yield the genetic parameters include, large population size, additivity and independence of genetic and environmental components of the phenotypic variance. Until recently (Clayton, 1975), these assumptions were seldom verified.

The assumption of large populations is required to ensure that the various parameter estimates closely approximate their expected values. In poultry this would involve accumulating eggs over a long period and hatching the progeny to be tested in a single operation. However, long storage of eggs is detrimental to hatchability. The usual practice, therefore, is to reproduce the progeny to be tested over several hatches, with fixed time interval between adjacent hatches, and pool the results. If hatch effects are significant, then a correction needs to be applied. Thompson (1974) has shown that if hatch sub-population sizes are unequal, then converting records into deviants of the respective hatch means, as is done by some workers, would be inefficient. Whole removal of hatch effects using least-square analysis of variance would seem preferable.

Implicit in the methods of double and triple shifts of sires introduced by Hutt (1949) and the method of hatch correction outlined above as well as that suggested by Lerner and Taylor (1940), is the assumption that genotype and environment act independently. In the double and triple shifts, progeny of a particular sire may appear only in one of several hatches.

Reports on sire x hatch interactions are conflicting. Abplanalp (1956) and King (1961) delegated no importance to such interactions regarding all egg-production traits. The significant shifts in sire ranks across hatches reported by Osborne (1951, 1954) and Yamada (1958) in respect of sexual maturity and hen-housed egg number, could have been mediated by the long hatching period which covered several months. If sire x hatch effects are in fact important, then the sire variance component, as well as the intra-class correlation based upon it, would be biased upwards by an amount σ^2_{sh}/σ^2_s, where σ^2_{sh} and σ^2_s are the interaction and sire components respectively (Enfield and Comstock, 1969). Such a bias would cause erroneous and ineffective breeding plans to be drawn up.

The assumption of normality of egg production traits has been questioned recently. Survivor egg production (Clayton, 1975; Thompson, 1974), hen-housed egg number, hen-day percent (Shalev, 1977) all measures of egg laying ability, are skewed negatively and leptokurtic. The departure from normality was greatest in the early part-year production records, usually the object of improvement plans, and persisted even after culling from the population all individuals inferior to the overall mean by more than two standard deviations. Further, as the culling did not increase heritability, Clayton (1975) suggested that the negative skewness might have been caused by non-random environmental

factors. Thus it would not be helpful to regard the low (or zero) producers as 'accident-victims' or aberrants of Thompson (1974).

Shalev (1977) considers that the physiological limit of one egg a day, has contributed to the abnormal distribution of egg production; a view supported by the finding of Clayton (1975) that there was shortage of individuals whose egg production exceeded their strain's mean by two standard deviations in a highly prolific strain. For completeness, it is worth mentioning that sexual maturity is skewed positively due to the fact that egg recording for all pullets starts from a specific date, whereas egg and body weights fit a normal distribution (Shalev, 1977 and Thompson, 1974).

The consequences of the negative skewness of the egg production trait on the efficacy of pureline selection schemes designed to improve it are as follows. Selection intensities based upon the normal distribution will exceed what can actually be achieved. A more serious consequence concerns the question whether the regression of offspring on parent performance for the high ranking individuals differ from that of the low ranking group. Clayton (1975) and Shalev (1977) have provided evidence suggesting a lower regression in the left tail than among the high producers. If indeed offspring on parent regression is non-linear, the mean of control populations used to monitor genetic trends in selection experiments for egg production would be unstable. This is because offspring of the high ranking parents will look more like their parents than those of low-producing parents, thereby generating a selection differential and hence shifts in the population mean.

The combined effect of biased selection intensities, non-linear offspring on parent regression as well as unstable control performance

would cause expectations of response to selection for egg production, based on normality assumptions to be unrealizable. The experience of Nordskog (1977) and the findings of Shalev(1977) that predictions of selection response for egg production have almost always been over-estimates, would seem to support the above.

The genetic correlation between egg weight and number has also been reported to follow the same pattern as the offspring on parent regressions for egg number, i.e. its magnitude increases with performance (Shalev, 1977). However, this non-linearity may not have been caused solely by the abnormal distribution of egg production, since low egg production is not necessarily incompatible with large egg weight (Blyth and Sang, 1960).

More information is obviously required on the genetics of pure egg production and if all points unequivocally to invalidity of the usual assumptions presently in use, then new genetic models ought to be sought. In the present study the large number of strains as well as population sizes available, make it suitable to investigate some of the anomalies raised in the above review.

2.2 MATERIALS AND METHODS

Data for this part of the study were provided by a European Poultry Breeding Company which made available data on two kinds of crosses each year since 1975, involving brown and white egg-laying strains. In 1975 and 1976, the same pairs of strains were involved in the crossing programme, but in 1977 different pairs were used.

The Strains

Six pure strains and a single-cross (involved in a 3-way cross in 1977) were used in making the commercial crosses. Particulars of the pure strains regarding their population sizes, numbers of sires and dams, and the number of hatches accumulated to reproduce them are presented in Table 2.1. The designation of the strains follows a simple nomenclature. The letters distinguish among the different strains whereas the numbers refer to the years when the strains were hatched. For example code A5 refers to strain A hatched in 1975.

The full history of the strains has not been made available, but the following is known about them.

Strain A is a long established, white leghorn-type egg-laying strain of medium size.

Strain C is also a medium-sized white leghorn type, but of a more recent selection history.

Strain E lays brown eggs but is a white-feathered synthetic line originally based on Rhode Island Red x White Leghorn breed cross. The proportion of males and females of each breed used in forming this strain is not known.

Strain F was extracted from the New Hampshire breed and lays dark-brown eggs.

TABLE 2.1 Particulars of Populations (Pure) Used in Test Crosses

Strain	Code	Hatching Year	Number of: Sires	Dams	Pullets	Hatches
A	A5	1975	30	141	1350	4
	A6	1976	19	90	1020	4
C	C5	1975	20	91	1039	4
	C6	1976	20	94	931	3
D	D7	1977	30	145	1478	4
E	E5	1975	50	389	3524	5
	E6	1976	44	264	2705	5
	E7	1977	48	324	2177	4
F	F5	1975	19	98	1021	4
	F6	1976	19	91	633	4
G	G7	1977	20	95	848	3
TOTAL			319	1822	16726	44

Strain G is of pure white leghorn extraction, but has much larger body weight than the other Leghorns.

Strain D is a pure Rhode Island type.

All the above lines were closed and improved annually by conventional pure line selection procedures even though the objective has been to improve crossbred performance.

For each strain, hatching was done fortnightly until the required population sizes were obtained. Three to five hatches in all were used (Table 2.1). Chicks were banded at day-old and pedigreed to dams and sires. Each hatch was reared and housed separately but, within hatches, progeny of all the sires of a strain were intermingled. Floor rearing of all chicks until 18 weeks of age was followed by individual cage housing and recording. All pullets were trapped and recorded 5 days each week for the duration of the performance test. The duration of the tests depended upon the age of pullets in the last hatch and therefore could vary among strains and years. But, in general, the tests were continued until the youngest pullets were 36 weeks old, to ensure a generation interval of one year. Records of the older hatches were then corrected to the age of the youngest hatch, by merely rejecting the records beyond this age.

Definition of Traits

Sexual Maturity (SM) is the age at which an individual pure strain type pullet laid its first egg after housing.

Hen-Housed Production (HHP) of a pullet measures the total number of eggs laid on trap days (5 days/week) for the period of the tests (18 - 36 weeks).

Hen-Day Percent (HDP) refers to the rate of lay of a pullet and is calculated as the number of eggs actually laid on trap days relative to that possible if it had laid an egg on each trap day, from the first egg.

Egg Weight (EW) is defined as the average weight of a week's eggs laid at 30 weeks of age.

Housing Body Weight (BW1) is the weight of a pullet at 18 weeks of age.

Adult Body Weight (BW2) was measured at the end of the laying period.

Preparation of data for Analysis

Data on all traits available on each strain and year were screened for 'aberrant values', atypical because they were too low or too high. Some of these observations might have arisen from biological (e.g. illness) or experimental (e.g. recording or measurement error) sources, others may in fact, represent true values arising from the tails of the underlying distribution. The objective of the 'screening process' applied was to remove observations clearly outlying and replace those genuinely missing (e.g. Zero egg and body weights), thereby retaining only true values for the statistical and genetic analysis.

A uniform method of dealing with each trait was adopted for all the strains and years, except for the 1976 lines which had been previously screened by the breeding company. Briefly, the breeding company deleted all individuals the egg production (HHP) of which fell below 10 eggs, and replaced all zero egg and body weights by their respective hatch means. Despite their screening, some aberrant observations were occasionally encountered regarding SM, EW, BW1 and BW2, and were subjected to the same procedure as for data from other years to be described.

The procedure applied to HHP was exactly the same as that applied by the breeding company. However, for SM, EW, BW1 and BW2, all individuals having performance for any of these traits which was greater or smaller than three phenotypic standard deviations from the mean of the strain were deleted from the data. This was based mainly on practical considerations, in that for instance, a few individuals were encountered with SM less than 126 days (age at housing), whilst a few started laying eggs some nine (9) weeks after housing. All such individuals fell outside the retention threshold and were thus deleted. Zero egg and body weights of individuals which survived the initial screening on HHP were replaced by their respective sire x hatch subclass means. Zeros were assumed to occur at random in all sire families, so that the screening applied would not bias the between-sire variance component.

Statistical Analyses

The following analyses were done on each trait within strains and years.

Heterogeneity of Variances:

Variances among hatches within each strain and year were tested for heterogeneity in respect of each trait using Bartlett's chi-square test as outlined by Snedecor and Cochran (1972). Variances among years were similarly tested for strain E on which 3-years' data were available. However, the F-test (Snedecor and Cochran) was used regarding variances between years for strains A, C and F since only 2-years' records were involved.

Tests of Normality:

The assumption of normality of the distribution of the individual observations on each trait is the basis for using most statistical techniques including the analysis of variance. Two kinds of departure

from normality, namely skewness and kurtosis were tested for all the traits. The coefficient of skewness (G1) statistic is (Snedecor and Cochran, 1972):

$$G1 = m_3/(m_2\sqrt{m_2}) \quad \ldots\ 2.2$$

where $m_3 = \Sigma(X - \bar{X})^3/n$

$m_2 = \Sigma(X - \bar{X})^2/n$

A significant negative value indicates bunching of high values close to the mean and extension of low values far below the mean.

Kurtosis refers to the peakedness of the distribution and is quantified by the G2 statistic obtainable from equation 2.3 below (Snedecor and Cochran, 1972):

$$G2 = (m_4/m_2^2) - 3 \quad \ldots\ 2.3$$

where $m_4 = \Sigma(X - \bar{X})^4/n$

Significant negative values result from curves that have a flatter top than the normal.

Statistical Model

All genetic parameters were obtained by using the least squares analysis of variance programme of Harvey (1972). For each year and strain, traits were analysed on the basis of the usual hierarchical classification as set up in mixed model 2.4. In a preliminary analysis of some lines, sire x hatch interaction was found to be unimportant in all the traits, and was thus not fitted in the final analyses.

$$Yijkl = \mu + hi + Sj + Djk + \varepsilon ijkl \quad \ldots\ 2.4$$

where:

Yijkl = an observation on the l^{th} progeny of the k^{th} dam mated to the j^{th} sire in the i^{th} hatch.

μ = overall mean

hi = effect of the i^{th} hatch (assumed variance = σ^2_h)

Sj = effect of the j^{th} sire (assumed variance = σ^2_S)

Djk = effect of the k^{th} dam mated to the j^{th} sire (assumed variance = σ^2_d)

εijkl = random error (Variance = σ^2_w)

Hatch effects were classified as fixed since any adjacent hatches had a fixed time interval (2 weeks) between them, whilst sire and dam effects were assumed to be random. Further, variance components for hi, Sj, Djk and εijkl were assumed to be σ^2_h, σ^2_S, σ^2_d, σ^2_w. The Yijkl observations were assumed normally distributed.

The expectation of the mean squares for the model follows:

Source	MS	EMS
Sires	S	$\sigma^2_w + k_2\sigma^2_d + k_3\sigma^2_S$
Dams within sires	D	$\sigma^2_w + k_1\sigma^2_d$
Hatches	H	$\sigma^2_w + k\sigma^2_h$
Residual	R	σ^2_w

The various variance components were obtained by equating the mean squares to their respective expectations. Formulae for the two estimates of heritabilities reported on for each trait of a strain were as given by Falconer (1960).

$$\hat{h}^2_s = \frac{4\sigma^2_s}{\sigma^2_s + \sigma^2_d + \sigma^2_w} \qquad \ldots\ldots 2.5$$

$$\hat{h}^2_c = \frac{2(\sigma^2_s + \sigma^2_d)}{\sigma^2_s + \sigma^2_d + \sigma^2_p} \qquad \ldots\ldots 2.6$$

where:

$\hat{h}^2_s$ = estimates based on paternal half-sibs.

$\hat{h}^2_c$ = estimates based on full sibs.

The estimate based on full sibs ($\hat{h}^2_c$) is biassed upwards by dominance and maternal effects, if present. It is being reported on here to obtain an idea of the importance of non-additive genetic effects. Standard errors for both estimates came from Harvey (1972). The genetic correlations between any two traits, as well as their standard errors, were also output from Harvey's (1972) least squares programmes. Only the correlations based on paternal half-sibs are reported.

All analysis were made within strains and years, but the different years for each strain were pooled by summing sums of squares and cross products and recalculating the variance components and standard errors. Thompson (1974) observed that this manner of pooling genetic parameters resulted in an estimate (from a hypothetical population) which was markedly different from the unweighted mean of the within year estimates. His example, however, was based upon an unlikely combination of family structure and variability. The family structure between years in the strains used were satisfactory, and the method of pooling should not suffer much in efficiency. Similar methods were also used to pool estimates over all strains and years for each trait.

Parameter Estimates by Regression using Collateral Relatives

The negative skewness in egg production trait reported by some workers (Thompson, 1974 and Clayton, 1975) has been found to result in asymmetrical regression of progeny on parent (Shalev, 1977). It is thus of interest to provide further evidence of the phenomenon, namely, whether the regression in the direction of desired improvement

of some of the traits being studied, is of the same magnitude as that in the opposite direction. In situations where only single generations, or where only selected parents of limited range of phenotype, are available, Abplanalp (1961) suggested thatuse of "linear heritability estimation" which essentially considers the regression on an individual's performance of the mean performance of his collateral relatives. The method is similar to a selection experiment except that "paper" selection based on an individual's own performance is practised and the mean computed for their corresponding families. In this study, half-sib families were considered. If the mean calculated for the sibs is for a trait different from the one on which the individual was selected, then the genetic regression of one trait on the other, may also be obtained.

Hill (1978, in press) clarified and generalised the formulations to include unbalanced data. The following formulae used in this thesis are thus after Hill (1978).

$$\hat{h}^2_{s_L} = 4\hat{t}_{L(HS)} = \frac{\Sigma\Sigma\Sigma(\bar{X}'_{i\cdot\cdot(j)} - \bar{X}'_{\cdot\cdot\cdot(i)})}{\Sigma\Sigma\Sigma(X_{ijk} - \bar{X}'_{\cdot\cdot\cdot(i)})} \times 4 \qquad \ldots\ 2.7$$

$$b_{X.Y_L} = \frac{\Sigma\Sigma\Sigma(\bar{X}'_{i\cdot\cdot(j)} - \bar{X}'_{\cdot\cdot\cdot(i)})Y_{ijk}}{\Sigma\Sigma\Sigma(Y_{ijk} - \bar{Y}'_{\cdot\cdot\cdot(i)})Y_{ijk}} \qquad \ldots\ 2.8$$

where:

$\hat{h}^2_{s_L}$ = "Linear" heritability estimate

$\hat{t}_{L(HS)}$ = regression of sibs on sibs based on paternal half-sibs.

$\bar{X}'_{i\cdot\cdot(j)}$ = mean of half-sibs with full-sib family j of the individual excluded.

$\bar{X}'..._{(i)}$ = mean of individuals unrelated to members of family i.

(In both $\bar{X}'_{i}..._{(j)}$ and $\bar{X}'..._{(i)}$, individual itself is excluded.

X_{ijk} = the individual selected to be in a particular segment of the distribution for trait X.

$\hat{b}_{X.Y_L}$ = linear estimator of regression of family effects for trait X on trait Y.

Y_{ijk} and $Y..._{(i)}$ follow similar definitions as X.

It is assumed here that symmetry in regression of X on Y would imply symmetry of the genetic correlation between them. The effects of the proportion selected on the $\hat{t}_{L(HS)}$ values for selected 'up' and 'down' segments of the distribution were also investigated, the proportions being 10% and 20%. All observations were converted to deviants of their respective hatch means, a method which would be slightly inefficient if hatch sub-population numbers were widely unequal. However, previous analyses using this method yielded similar heritability and genetic correlation estimates as a method based on whole removal of hatch effects.

Three years' data on strain E, involving 8,406 records were used in this part of the thesis; the formulae 2.7 and 2.8 were applied to 4 traits, namely SM, HHP, EW and BW1.

2.3 RESULTS

Annual Means of Traits

The least square means and their standard errors for the traits involved in the study appear in Table 2.2 for each strain and year. Of the three strains represented in the means of 1977, only E contributed to the means of the other years. The overall results for 1977 shown in this table are therefore likely to be biassed. This qualification should be borne in mind when considering trends in the various traits. For instance, the sudden appearance of the rather heavy strain D inflated markedly, the overall picture for BW1 and BW2. Despite the brevity of the period covered by this study, trends in all the traits are detectable.

The age at first egg (SM) has been brought forward in practically all the lines, averaging some 5 days per generation overall. A corresponding increase in the HHP of nearly 10 eggs since 1975 has also occured. The improvement in rate of lay (HDP) over the same period amounts to more than 10% except in strain C which gained only 5% in one generation. In this strain (C), gain in SM was also minimal, even though it also shared in the phenomenal increases in HHP. The coefficient of variation results are also set out in Table 2.2 for each trait and strain. These show consistent decline over the years for both the traits showing increased means as well as for those which have not changed appreciably over the years. It would appear therefore that precision of recording or management practices or both have improved over the years.

In contrast to SM, HHP and HDP, BW1 and BW2 appear to be stable overall, even though some strains are in fact becoming lighter (e.g.

TABLE 2.2 Performance of the Pure Strains

Strain Code	TRAITS																	
	SM (days)			HHP (No.)			HDP (%)			EW (g)			BW1 (kg)			BW2 (kg)		
	Mean	SE	CV*	Mean	SE	CV	Mean	SE	CV	Mean	SE	CV	Mean	SE ($\times 10^{-3}$)	CV	Mean	SE ($\times 10^{-2}$)	CV
A5	157	0.8	6	36	0.6	21	66	0.6	16	57	0.2	6	1.09	0.7	8	1.48	1.1	9
A6	154	0.7	5	50	0.6	15	79	0.5	11	57	0.3	5	1.08	0.8	7	1.51	1.3	9
C5	155	0.6	6	42	0.5	16	81	0.7	12	50	0.3	6	1.16	1.0	7	1.45	1.5	10
C6	154	0.7	5	53	o.5	15	86	0.4	12	53	0.3	5	1.05	0.7	7	1.46	1.3	8
D7	144	0.3	4	48	0.3	14	82	0.4	13	52	0.3	7	1.36	0.7	8	2.02	1.3	11
E5	162	0.6	6	38	0.5	19	73	0.4	15	49	0.2	7	1.31	1.0	9	1.86	1.5	11
E6	154	0.5	5	44	0.3	15	84	0.3	11	50	0.3	7	1.31	0.7	9	1.84	1.3	11
E7	149	0.4	6	47	0.3	16	84	0.3	15	50	0.2	7	1.33	0.6	8	1.83	0.6	7
F5	154	0.7	8	39	0.6	23	70	0.9	17	49	0.4	8	1.33	1.5	10	1.78	1.8	10
F6	146	0.8	5	48	0.5	15	83	0.5	12	51	0.3	6	1.38	1.4	8	1.85	1.6	10
G7	150	1.1	7	42	0.9	22	78	1.0	17	53	0.3	7	1.29	1.2	9	1.67	1.6	10
Mean 1975	157	0.7	7	39	0.5	20	73	0.6	15	51	0.3	7	1.22	1.0	9	1.64	1.5	10
Mean 1976	152	0.7	5	49	0.5	15	83	0.4	11	53	0.3	6	1.20	0.9	8	1.66	1.4	10
Mean 1977	148	0.6	6	46	0.5	17	81	0.6	15	52	0.3	7	1.33	0.8	8	1.84	1.2	9

* CV is in percent (%)

strain A and C for BW1 and strain E for BW2). EW has changed only little over the years and strains covered in the study.

Distribution of Traits

Results of tests of normality of the distribution of the various traits for the lines and years appear in Table 2.3. Overall, sexual maturity shows significant positive skewness (G1), whilst the negative skewness of HHP and HDP seem rather consistent and widespread despite the culling of all low producers. In contrast, there does not seem to be any consistent trend in the G1 statistic of EW; for though a few strains in some years give indication of departure from normality, the general impression overall is that the data would fit a normal distribution.

In seven out of eleven cases, the G1 statistic for BW1 and BW2 were significantly positive, though of a relatively smaller magnitude compared with those for the HHP and HDP, and would thus readily disappear by lowering the screening threshold to say 2.5 standard deviations from the mean instead of the three used in this study.

The leptokurtosis (G2) of the SM, HHP and HDP indicate a further departure from normality in these traits, though over all strains, SM would not be highly so. Except for a few strains during some years, the G2 statistic for EW, BW1 and BW2 present an overall normal picture.

Heterogeneity of Variance

Table 2.3 shows the χ^2-square statistic for the heterogeneity of hatches within strains and years for each trait. In nearly 50% of the results for SM, HHP, HDP and BW1, hatch variances are significantly heterogenous. This is in marked contrast with the extreme stability of variances over hatches for EW and BW2. The difference in the

TABLE 2.3 Showing Skewness, Kurtosis and χ^2-square Statistics

Strain Code	TRAIT																	
	SM			HHP			HDP(%)			EW			BW1			BW2		
	G1	G2	χ^2	G1	G2	χ^2	G1	G2	χ^2	G1	G2	χ^2	G1	G2	χ^2	G1	G2	χ^2
A5	0.3**	-0.8**	12**	-0.4**	-0.5	16**	-0.9**	-1.8**	6	-0.3**	0	2	0.2**	0.2	7	0.2*	-0.2	8*
A6	0.7**	1.3**	10*	-0.7**	1.6**	5	-1.6**	5.3**	10*	0	0	1	0.2**	0.8*	4	0.6**	1.0**	6
C5	0.5**	0.6**	7	-0.7**	1.6**	1.6	-1.2**	3.4**	1.9	0.3**	1.3**	5	0.4**	0.6**	19**	0.5**	0.4*	4
C6	0.4**	0.3	<1	-1.4**	4.2**	<1	-2.8**	11.9**	<1	0.1	0.1	2	0.3**	0.2*	4	0.1	0.8*	2
D7	1.0**	-4.2**	13**	-1.3**	-11.6**	8**	-2.9**	-46.8**	20**	0.1	-0.3	11**	0	-1.8*	30**	0	-2*	<1
E5	-0.1	-0.2*	17**	-0.1**	0.1	7	-0.8**	1.1**	18**	0	0	4	0.1**	-0.2*	4	0.2**	0	6
E6	0.3**	0.4**	5	-0.8**	1.7**	4	-2.0**	6.9**	7	0.2**	0.2*	13**	0.1	0	9	0.3**	0.6**	5
E7	0.4**	0.4**	7	-1.0**	2.3**	11*	-3.2**	15.7**	108**	0	0	8	0.3**	0.1	43**	0	-1.1*	2
F5	0.3**	-0.2	23**	-0.5**	0.1	27**	-0.9**	0.9**	21**	-0.6**	1.7**	4	0.3**	0.7**	16	0.2**	1.0**	<1
F6	1.0**	1.9**	6	-1.4**	3.9**	15**	-2.5**	10.5**	33**	0.1	0.2	6	0	0.2	1	0	0.1	1.1
G7	0.4	0	5	-1.0**	1.7**	47**	-1.9**	4.9**	11**	-0.1	0.3*	1	0.1	0.3*	17**	0.2*	0.1	5

* indicates P < 0.05; ** indicates P < 0.01

χ^2-square statistics shown by BW1 and BW2 could be due to both compensatory growth which might have occured since BW1 was measured as well as the strong influence of SM on BW1. As for SM, HHP and HDP, the rather strong departure from the normal distribution (G1 and G2) could have contributed to the apparent heterogeneity of variances among hatches.

Between years, Table 2.4 indicates a rather wide-spread heterogeneity of error variances, irrespective of traits. This could be due not only to variable management factors, but mainly to the heterogeneity within years already mentioned. Data were, however, pooled over hatches and years in order to calculate the genetic parameters, as the apparent heterogeneity of variances observed were believed to be mere statistical artefacts and not real.

Heritabilities

The heritabilities of the traits pooled over years for each strain are presented in Table 2.5. Within year analyses were pooled by adding-up the respective sum of squares and re-calculating the variance components. The pooled estimates over all lines obtained by a similar procedure, also appear in the same table. Standard errors for the individual and pooled estimates were calculated using the formula by Falconer (1963) and ranged from 0.02 to 0.17. The two measures of heritability, based on sire (h^2_s) and full-sib (h^2_c) components of variance differ within some traits over lines. In general, the heritability estimates indicate substantial levels of additive genetic variance for all the traits except for HDP. The heritability of HDP varied from 0 - 0.19 when based on the sire component, but .04 - 0.33 when based on the combined sire and dam components of variance.

TABLE 2.4 Test for Homogeneity of Variance among Years

Strain	TRAIT					
	DF	SM	HHP	HDP	EW	BW1	BW2
A	1206/927	1.51**	1.11*	1.68**	1.29**	1.04	1.23**
C	945/835	1.14*	1.32**	1.02	1.13*	1.50**	1.61**
E	2[+]	117.31**	9.30**	162.79**	39.41**	60.5**	521.61**
F	920/539	2.37**	1.26**	1.34**	1.69**	1.04	1.07

[+] Bartlett's χ^2-test was used for strain E, F-ratio for the other strains.

* $P < 0.05$; ** $P < 0.01$

χ^2(2d.f.) 0.05 = 5.99; 0.01 = 9.21

TABLE 2.5 Heritabilities and Standard Errors of Traits in Pure Strains

Strain		TRAITS SM	HHP	HDP	EW	BW1	BW2
A	h_s^{2+}	0.48±.15	0.38±.12	0.19±.08	0.47±.16	0.64±.17	0.51±.17
	h_c^{2*}	0.44±.08	0.41±.08	0.23±.06	0.50±.09	0.62±.09	0.52±.09
C	h_s^2	0.28±.12	0.21±.10	0.12±.07	0.52±.18	0.62±.19	0.62±.20
	h_c^2	0.33±.08	0.25±.06	0.14±.05	0.48±.09	0.64±.10	0.67±.11
D	h_s^2	0.17±.07	0.11±.05	0	0.74±.18	0.26±.09	0.19±.07
	h_c^2	0.24±.05	0.18±.04	0.04±.03	0.54±.08	0.43±.07	0.36±.06
E	h_s^2	0.43±.10	0.30±.07	0.07±.03	0.49±.10	0.61±.12	0.52±.09
	h_c^2	0.39±.05	0.32±.04	0.13±.03	0.41±.05	0.51±.05	0.46±.05
F	h_s^2	0.18±.12	0.14±.09	0.19±.09	0.43±.16	0.79±.24	0.51±.17
	h_c^2	0.33±.08	0.32±.07	0.24±.06	0.50±.09	0.73±.11	0.52±.10
G	h_s^2	0.47±.17	0.37±.14	0.13±.07	0.21±.10	0.40±.15	0.32±.13
	h_c^2	0.43±.09	0.51±.09	0.33±.08	0.40±.08	0.45±.09	0.39±.08
ALL STRAINS							
	h_s^2	0.40±.04	0.30±.03	0.10±.02	0.50±.05	0.61±.05	0.49±.05
	h_c^2	0.38±.02	0.31±.02	0.16±.01	0.46±.02	0.55±.03	0.48±.02

+ h_s^2 = heritability estimate from paternal half-sibs

* h_c^2 = combined heritability estimate from full-sibs.

Genetic Correlations

The genetic correlations for all pairs of traits within strains shown in Table 2.6 are based upon paternal half-sibs' component of variance and covariance. These correlations are based on data pooled over years by summing sum of cross products and recomputing covariance components, and are thus subject to the same restrictions mentioned under Section 2.2 regarding pooled heritabilities. Overall averages similarly obtained are also presented. Standard errorsof the individual estimates (not shown) range from 0.07 to 0.38, but those for the pooled estimates (formula of Pobertson, 1959) are reasonably low (0.02 - 0.10).

A general observation is that the correlation between any of the reproductive traits (SM, HHP and HDP) and the highly heritable traits (EW, BW1 and BW2) is low or negligible but consistent in trend. It is noteworthy that line F consistently behaves contrary to the general trends in the correlations mentioned between the lowly heritable traits and EW. For example, the consistent positive and small relationship between SM and EW is tempered by the rather highly negative value of line F. Similarly, the only positive value in the negative correlations between HHP and EW is for strain F.

Among the reproductive traits themselves, the consistently strong and negative relationships between SM and HHP are a necessary consequence of the methods of recording. The correlation between SM and rate of lay (HDP) however, dwindles to zero in some lines, though the overall estimate indicates a slightly negative relationship. HHP is positively correlated with HDP.

Among the highly heritable traits, the positive correlations between BW1 and BW2 are high whereas that between EW and any of them is rather low.

TABLE 2.6 Genetic Correlations and Standard Errors among Traits of the Pure Lines

Trait & Strain	TRAIT HHP	HDP	EW	BW1	BW2
SM					
A	-0.89	-0.44	0.37	-0.37	0.06
C	-0.88	-0.32	0.25	0.07	0.20
D	-0.96	0	0.34	-0.39	-0.43
E	-0.95	-0.37	0.25	-0.21	0.09
F	-0.55	-0.11	-0.46	-0.45	-0.11
G	-0.93	-0.50	0.08	-0.18	-0.15
Pooled	-.89 ± .02	-0.32 ± .09	0.20 ± .07	-0.24 ± .06	0.02 ± .07
HHP					
A		0.77	-0.57	0.39	0.02
C		0.69	-0.28	-0.03	-0.10
D		0	-0.63	-0.06	0.15
E		0.53	-0.31	0.16	-0.10
F		0.69	0.50	0.09	-0.20
G		0.80	-0.12	0.60	0.48
Pooled		0.57 ± .07	-0.28 ± .07	0.17 ± .04	-0.04 ± .07
HDP					
A			-0.52	0.28	0.06
C			-0.14	0.02	0.02
D			0	0	0
E			-0.09	-0.05	-0.07
F			0.14	-0.40	-0.57
G			-0.04	0.98	0.85
Pooled			-0.12 ± .10	0.03 ± .09	-0.04 ± .10
EW					
A				0.34	0.39
C				0.26	0.51
D				0.37	0.44
E				0.23	0.33
F				0.40	0.22
G				0.34	0.28
Pooled				0.28 ± .06	0.36 ± .06
BW1					
A					0.85
C					0.83
D					0.51
E					0.72
F					0.85
G					0.88
Pooled					0.75 ± .02

Regression of 'Sibs on Sibs'

The results of using formulae 2.7 and 2.8 are presented in Table 2.7. Diagonals are the heritabilities whereas the off diagonals represent the regressions. T1, T2, B2 and B1 refer to the top, 2nd top, 2nd bottom and bottom-most performance groups of the distribution. The middle ranking groups (T2 and B2) tend to give rather wild estimates, as deviations of individuals from the mean tend to be smaller, and are thus not shown for the regressions.

A comparison of T1 and B1 indicates that the estimates for SM and EW are in good agreement, whilst HHP and BW1 do not appear so. The top ranking individuals in HHP have higher heritabilities than the low, whilst the reverse is true for BW1; however, the significance of the differences cannot be confirmed as no formulae are yet available for computing standard errors. The results agree with the skewness statistics presented in Table 2.3 for HHP and BW1 of the 3 years' data for line E. Probably the further elimination of aberrants in BW1 by lowering the screening threshold would correct the anomally in this trait, but the same cannot be expected of HHP since departures from normality are rather more serious.

The overall picture for the regressions of sibs on sibs for different traits, has been married somewhat by the low genetic correlations between the reproductive traits (SM and HHP) and the highly heritable ones (EW and BW1) presented earlier elsewhere. However, it seems clear that both linear and non-linear regressions occur.

The two intensities of selection studied show agreement for the 'top' and 'bottom' groups regarding the two parameters.

TABLE 2.7. 'Linear' Heritability and Regression at 2 Selection Intensities for Line E.

TRAIT & RANK OF GROUPS	TRAIT AND PROPORTION SELECTED							
	HHP		SM		EW		BW1	
	10%	20%	10%	20%	10%	20%	10%	20%
HHP								
T1*	0.37	0.39	-0.12	-0.13	-0.18	-0.15	0.06	0.06
T2	0.41	0.26						
B2	0.37	0.51						
B1	0.23	0.28	-0.07	-0.09	-0.15	-0.19	0.01	0.01
SM								
T1	-0.07	-0.07	0.43	0.47	0.20	0.19	0.01	-0.02
T2			0.54	0.43				
B2			0.55	0.40				
B1	-0.07	-0.07	0.45	0.45	0.09	0.11	-0.05	-0.04
EW								
T1	0.02	0.02	-0.01	-0.01	0.48	0.51	0.01	0.01
T2					0.57	0.45		
B2					0.38	0.56		
B1	0.01	0.01	0	0	0.48	0.45	0.02	0.01
BW1								
T1	0	-0.01	0	0.01	0.09	0.07	0.49	0.52
T2							0.57	0.68
B2							0.74	0.49
B1	-0.03	-0.03	0.02	0.02	0.11	0.11	0.62	0.66

*T1 = Highest scoring 10% or 20% individuals of the distribution
T2 = 2nd highest scoring 10% or 20% individuals of the distribution
B2 = 2nd lowest scoring 10% or 20% individuals of the distribution
B1 = Least scoring 10% or 20% individuals of the distribution.

2.4 DISCUSSION

The brevity of the periods involved in this study as well as lack of control populations make any inferences from the trends in SM, HHP and HDP rather restrictive. In particular, the relative contribution of the breeding programme applied and improvements in nutrition and husbandry practices cannot be assessed.

The additive genetic variation in hen-housed egg number (pooled h^2_s) is high compared with estimates in the literature, but this reflects its close relationship with sexual maturity which is itself moderately heritable in these strains. There are suggestions in the literature that response to selection for HHP (part-year record) is usually at the expense of SM (Morris, 1963) with no real effect on the rate of lay (HDP) needed if persistency, and hence annual egg production is to be sustained. The impression from this study seems to be that efforts to improve annual egg number should be directed at SM and HDP, which are its components, simultaneously. Pressure put on egg number itself would result in improving SM, the more highly heritable of the components, whilst rate of lay remains unaltered or probably deteriorates. Yet the rather low levels of additive variation (h^2_s) in rate of lay suggests that it cannot withstand intense selection pressures for a long time.

There are, however, indications from the consistently high full sib heritability estimates (h^2_c), assuming negligible maternal effects, that non-additive genes may be important in rate of lay. Silva *et al.* (1976) arrived at a similar conclusion but their estimates were also biassed upwards by possible maternal effects, as is the case with hierarchical population structures. However, many other workers, including Jerome *et al.*, 1956 and Sato and Nordskog, 1977, who cross-

classified sires with dams, also found high levels of non-additive genetic variation in the rate of egg production. Hen-housed egg production (HHP) follows rate of lay as another trait with respectable levels of non-additive genetic variation (assuming again no maternal effects) in some lines albeit negligible overall. The two traits should benefit from a similar breeding scheme. Non-additive gene action seems to be of negligible importance in EW, BW1 and BW2 as revealed by the relative magnitudes of the h^2_s and h^2_c for these traits.

The strange relationships between the reproductive traits and EW of line F may be explained at least partly by the facts that (i) EW is rather low (mean of 49.7g over 2 years and standard deviation of less than 4g), (ii) EW was measured at 26 weeks of age in 1976 instead of the 30 weeks for the other strains hence the sample of pullets which provided eggs would not be representative, since it would exclude many late maturers which lay large eggs. Blyth and Sang (1960) reported negative genetic correlations between EW and HHP among the high egg producers, but a positive correlation among hens which laid few eggs. Most of the other published work found negative relationships (Dickerson, 1957), but were usually obtained from highly productive strains.

Clayton and Robertson (1966) obtained some low genetic correlations between housing and mature body weights. In the present work, genetic correlation between these two body weights were consistently high indicating very limited possibility of changing the growth curve of the hens during the laying year.

A general observation on the heritability estimates is their variability among strains for the same trait. Such variations represent mainly differences in gene frequencies of the various lines as well as sampling or population size. Variations observed among different

workers, however, is often a reflection of varying definitions of traits and methods of analysis. For example, King and Henderson (1954b) reported that ignoring hatch effects depressed heritability estimates, and in fact, affected ranking of sires based on unweighted pooled means in an unbalanced situation.

Hale and Clayton (1965) expressed reservations regarding the value of their pooled estimates of heritability and genetic correlation because of the significant heterogeneity of variance among the years in practically all of the traits studied. In a subsequent report, however, Clayton (1975) provided evidence for the negatively skewed distribution of egg production traits (e.g. HHP) much in consonance with the findings of Thompson (1974) and Shalev (1977). In dealing with skewed populations, Thompson (1974) observed that truncating all individuals with body weights greater or less than 2.5 standard deviations from the mean removed the skewness. But, he did not follow this up with Bartlett's test of heterogeneity of variance. Clayton (1975), however, did. He found that HHP needed intense screening involving all those beyond one phenotypic standard deviation from the mean before the skewness and the heterogeneity disappeared. According to Box (1953, quoted by Snedecor and Cochran), Bartlett's test of heterogeneity of variance is sensitive to non-normality in the data. It would appear therefore, that the heterogeneity of variances among hatches within years and between years for some of the traits could have been caused by the widespread departure from normality. The phenomenon, apparent heterogeneity, would thus not invalidate the pooling of the parameters, as it was not real.

The strong skewness statistic for egg production (HHP and HDP) observed in this study would reinforce the findings of Thompson (1974)

and Clayton (1975) that these traits are inherently skewed, particularly as few breeders would like to work with a population in which the residual variation (after screening) spans only two standard deviations, at which the skewness disappears (Clayton, 1975).

PART II. PUREBRED-CROSSBRED RELATIONSHIPS

3 PUREBRED - CROSSBRED RELATIONSHIPS

3.1 INTRODUCTION AND LITERATURE REVIEW

Genetic parameters obtained from pure lines are useful in pointing to characters likely to benefit from crossbreeding. In egg-type poultry, crossbreeding has been utilised mainly to exploit heterosis, though crosses have often been used to form new populations with desirable characters from each of the parental strains or breeds, and perhaps increased variability to enhance progress in later selection. Heterosis may be caused by allelic or non-allelic interaction of genes (Bowman, 1959), hence the predictability of cross performance from parental phenotypes may present difficulties even under some standard environment. Elaborate testing may then be necessary in order to obtain the most efficient purebred combination for present performance, and also to improve such a cross. Most poultry breeders, however, are faced with the latter problem of how to improve their best available crosses.

Reports in the literature on the importance of purebred-crossbred interactions have not been unequivocal and more information is needed. In this part of the thesis, results of investigations into the relationships between related pure and cross populations will be reported. The term 'crossbred' would refer to progeny of matings between two closed populations even though they were from the same breed.

Detection and quantification of heterotic interactions

In diallel crosses, applied to livestock originally by Schmidt (1922) inbreds are crossed in all possible combinations, and the best single cross chosen to reproduce commercial progeny. The introduction

of the concepts of general (GCA) and specific combining abilities (SCA) (Sprague and Tatum, 1942) enabled the technique to be used not only to detect, but also to quantify gene actions. Additive genes control GCA whilst non-additive genes cause SCA. A general discussion of the theory and analysis of diallel crosses, as well as variants of the basic design may be found in Hayman (1954,1960). In segregating populations, sires and dams replace lines and the sire x dam interaction component estimates SCA (King, 1961; Hale and Clayton, 1965; Sato and Nordskog, 1977).

The regression of cross on pure progeny performance was suggested by Bowman (1960) as a means of detecting gene action. A negative regression would indicate that overdominant genes were predominant on the basis of a single locus gene action. Bowman (1960), however, conceded that the interpretation of a zero or small positive regression would be inconclusive. Operationally, regressions may have a predictive value in connection with progress in cross performance expected from selection within pure lines.

Falconer (1952) was the first to extend the idea of genetic correlations to a situation in which measurements are made in different environments. Its use in similar situations has become widespread because it enables alternative breeding plans to be compared. In the context of purebred-crossbred relationships, measurements are made in different genetic environments. The covariance,(Cov($\bar{X}$pi., $\bar{X}$ci.)) of a sire's pure ($\bar{X}$pi.) and crossbred ($\bar{X}$ci.) progeny performances, and the between-sire variance components within the purebreds (σ^2_s) and the crossbreds ($\sigma^2_{s'}$) are all that is needed to calculate the genetic correlation (rg_pg_c):

$$r_{g_p g_c} = \frac{Cov(\bar{X}pi., \bar{X}ci.)}{\sqrt{\sigma^2_s . \sigma^2_{s'}}} \quad \ldots\ 3.1$$

Where progeny group size varies markedly, a weighting factor, due to Robertson (1962) is introduced into the covariance (expression 3.1 above). The weight for the i^{th} sire W_i, may be obtained as:

$$W_i = \frac{1}{(\sigma^2_s + \frac{\sigma^2_e}{n_{pi}})(\sigma^2_{s'} + \frac{\sigma^2_{\bar{e}}}{n_{ci}})}$$

where σ^2_e, $\sigma^2_{\bar{e}}$ = within-sire variance components for the purebred and crossbred populations respectively.

n_{pi}, n_{ci} = i^{th} sire's pure and cross progeny group sizes respectively.

The weighted covariance may then be computed as:

$$Cov(\bar{X}pi., \bar{X}ci.) = \frac{\Sigma W_i \bar{X}pi.\bar{X}ci. - \frac{((\Sigma W_i \bar{X}pi.)(\Sigma W_i \bar{X}ci.))}{\Sigma W_i}}{\Sigma W_i - \Sigma W_i^2 / \Sigma W_i} \quad \ldots\ 3.2$$

For a completely additive model, the expectation of the expression 3.1 becomes:

$$E(r_{g_p g_c}) = \frac{rCov_A}{\sqrt{rV_A . rV_{A'}}} \quad \ldots\ 3.3$$

where r = coefficient of relationships among progeny groups

Cov_A = genetic covariance

VA, VA' = additive genetic variance within the pure strain and crossbreds respectively.

As $Cov_A = V_A = V_{A'}$, equation 3.3 attains its maximum value of unity. However, if purebred-crossbred interactions are present, the covariance will decline. Thus Cov_A primarily detects departures from additivity, though the sire component from which V_A, comes, may be

inflated by gene effects showing dominance in the crosses (Pirchner, 1969).

This sensitivity of the genetic correlation, r_{gpgc} to various genetic situations (e.g. additive or overdominant) underlies its usefulness in detecting purebred-crossbred interactions, and thereby point to the relevant breeding policy to be adopted.

Improvement of heterotic traits

The evolution of breeding plans to exploit heterosis has followed closely changing ideas about gene action responsible for heterosis. Implicit in the method of inbreeding and hybridization (IH) in which selection is mainly among specific F_1 crosses of inbred lines, is that heterozygote superiority causes heterosis (Shull, 1909). The method led to tremendous improvements in maize yields in the United States (Russell, 1974). Success in livestock however, has not been that spectacular due to the infertility problems (Donald, 1955) associated with high levels of inbreeding at which non-additive genetic variance contributes substantially to total variance.

Hull (1945) pointed out that continued application of IH resulted in less profitable improvement than the first cycle. He therefore outlined a plan, recurrent selection to a homozygous tester strain (RST), in which favourable genes were accumulated in successive cycles, in the segregating strain. The plan was based on the reasoning that if allelic interaction of genes caused heterosis, then only test-crosses could reveal superior genotypes for cross performance.

Comstock et al. (1949), however, concluded that even though there were overdominance at some loci, partial dominance could be the rule at

others. The breeding plan which they devised, reciprocal recurrent selection (RRS), is similar to RST except that 2 segregating populations preferably known to 'nick' well are required and selection is made in both. Falconer (1960) has argued that under any condition of dominance other than heterozygote superiority, conventional pure line selection methods (PLS) would be effective in making all individuals homozygous for the favourable allele.

Bowman (1959) expressed a pessimistic view regarding the effectiveness of RST and RRS, and favoured PLS methods. Theoretical comparisons of the relative efficiencies of RST, RRS and PLS under assumptions of infinite population size (Comstock et al., 1949 and Dickerson, 1952) or finite population size (Hill, 1970) reached similar conclusions namely that the relative efficiency depended mainly on the nature of gene action. Hill (1970) further observed that it will be possible to attain higher product of population size and selection intensities with PLS than with either RRS or RST by using individual selection with reduced generation interval. So that if overdominant loci are not predominant, PLS will exceed the other alternatives both in rate of improvement in the cross and the final advance. However, all the theoretical studies disregarded epistasis, multiple allelism and linkage disequilibrium which are considered pertinent in explaining heterosis (Bowman, 1959). Further, none of them considered economic aspects. In that case, PLS would benefit from additional income likely from the gains made in the pure lines themselves.

In view of the limitations of the theoretical studies, evidence need be sought from experimental and practical situations.

I. Laboratory Animals

Drosophila and Tribolium species have been the most used. In studies involving a heterotic trait, egg number in D. melanogaster, RRS (or modified RRS) has been found to rank superior to RST or PLS (Bell et al., 1955; Rasmuson, 1956; Brown and Bell, 1960). Bell et al., (1955) however, observed that IH was superior to RRS, but since the RRS line had not plateaued, it might have surpassed the best single cross through continued selection. The same workers reported PLS to rank highest for the more highly heritable egg size in which GCA was found to be more important than SCA. However, in an RST programme in which a plateaued population was used as the "tester" strain, Bowman (1960) obtained response comparable to that expected from PLS. The trait was low bristle number in which evidence for overdominance was lacking.

Bell and Moore (1958) found PLS to be superior to RRS or IH in improving body weight (heritability = 0.60 - 0.80) in Tribolium castaneum. Intensity of selection was higher in PLS than for RRS. Wong and Boylan (1970) observed that the correlated response in crossbred performance as purebred's improved through PLS, was consistent with a completely additive model. However, the genetic correlation between purebred and crossbred pupa weight was low (0.40 ± 0.17). Yamada (1974) reviewing results obtained in T. castaneum at Purdue found (1) RRS and PLS to exploit different gene effects and (2) RRS to be superior to PLS regarding the lowly heritable traits (e.g. egg number) and also at latter generations regarding the highly heritable traits.

There is paucity of literature regarding similar comparative experiments in mice. Bowman (1962) undertook to increase litter size

through BST. In 4 generations he obtained response which was in accord with an additive model. However, neither heterosis nor over-dominance was found in the initial populations. Hansson and Lindkvist (1962, quoted by Pirchner, 1969) reported that PLS proved more successful than a crossbred-based scheme in improving growth rate, but also found the methods to exploit different components of the genetic variance.

II. Farm Livestock

Works reported on in farm animals have come mainly from swine and poultry due to the shorter generation interval and higher reproductive rates attainable with these species.

Dickerson et al. (1954) confirmed the need for crossbreeding due to the ineffectiveness of mass selection (PLS) to improve most economic traits in swine. Henderson (1949) and Donald (1955) reported non-additive gene effects to be more important than additive in the pre-weaning traits, whilst the reverse seems to be true for the postweaning traits (Hetzer et al., 1959). Dickerson (1952) considered that failure of selection to prevent inbreeding decline was indicative of heterozygote superiority in the preweaning traits. Other workers have obtained negative or non-significant genetic covariances and correlations between purebred and crossbred performances for the traits (Enfield and Rempel, 1962; Wilson et al., 1962; Robinson et al., 1964). Standal (1968), however, reported high genetic correlations for all 10 traits studied, but no preweaning traits were involved.

Even though 3-way crosses have been somewhat successful in swine (Pirchner, 1964) the cost of producing and maintaining the inbred lines

seems prohibitive (Craft, 1953; Donald, 1955). The real alternative is RRS. Krehbiel et al. (1971) found RRS to be more effective than PLS in a comparative selection experiment to improve litter size. Rempel (1974) presented genetic trends which indicated that purebred selection was superior or equal to crossbred selection in the improvement of crossbred performance in all traits except litter size and weaning weight.

In poultry, both inbreeding depression (Shoffner, 1948) and heterosis (King and Bruckner,1952; Nordskog and Ghostley, 1954) have been reported to affect egg number, rate of lay, viability and other lowly heritable reproductive traits, but not egg and body weights. Through genetic analyses, Briles et al. (1957) suggested that overdominant loci could be important sources of variation. However, Abplanalp (1973) concluded that despite the role of overdominant genes in inbreeding depression, the ultimate breeding of highly inbred lines with good production was possible.

Several diallel studies have found SCA to be more important than GCA (Yao, 1961; Wearden, Tindell and Craig, 1965; Sato and Nordskog, 1977) in egg number and rate of lay, though Hill and Nordskog (1958) using lines with little selection history, obtained contrary results.

According to Blyth and Sang (1960) crossbred performance was predictable from parental line performance. However, only one of their lines had been previously selected for egg production. Krause, Yamada and Bell (1965) on the other hand, obtained non-significant purebred-crossbred genetic correlations for sexual maturity and survivor's egg production. The results of comparative selection experiments have been contradictory. After 5 generations of RRS, Hale and Clayton (1965)

concluded that it was not advantageous for egg production, though scatter diagram, purebred-crossbred genetic correlation as well as results of the last generation for one line indicated otherwise. In the long-term experiments of Saadeh et al. (1968), RRS overtook PLS in the 5th generation. In several papers, Pirchner and his co-workers (Pirchner and Von Krosigk, 1973; Pirchner and Mergl, 1977) presented information that favoured use of RRS in improving fertility traits (rate of lay) in poultry. In a long-term selection programme, Cole and Hutt (1973) strongly favoured PLS in improving egg production. However, intensity of selection for egg production was low as the main objective was to improve resistance to leucosis complex. Further, generation interval was high as more than 3 year old cocks were often used, thus substantial levels of additive genetic variation must be present in their populations.

Inferences from the Literature Review

Even though conflicting reports regarding the relative efficiencies of RRS and PLS in improving crossbred performance has been presented, the majority view would support expectations. In that for highly heritable traits such as growth rate, carcass and other weight traits, PLS proved definitely preferable. However, for reproductive traits, especially in populations which had had substantial history of artificial selection, and in which non-additive gene effects caused the heterosis, RRS would be favoured.

Departures from such expectations would be resolved in some cases by aspects of design such as small population sizes, and small intensities of selection in the RRS. Further, in cases an index in which

the reproductive traits have small weights (due to their heritabilities, or deliberately imposed) have been the criteria of selection, and would thus have the same effect as lowered selection intensity for the heterotic traits. A real problem so far, is the lack of an effective tool to detect the components of the non-additive source of variation. So that RRS, which is capable of utilizing all the components would be preferable to RST which singles out only overdominance.

Inbreeding and hybridization, even though once claimed to have been successful with livestock, is losing ground to strain-crosses because (1) it is still a haphazard and expensive programme in the sense that neither the direction of change nor the loss of lines can be predictably controlled. (2) The inbred lines would be difficult to maintain profitably. (3) Additive traits (e.g. egg weight) also affect profitability of poultry. (4) It confers less flexibility to cope either with the deterioration of hybrid-performance, and/or with changing market demands.

3.2 MATERIALS AND METHODS

All the pure strains involved in the crossing programme were covered under Section 2.2. The only 2-way cross (coded $F_1$7) used as the female line in the 3-way cross with line G, was made from 2 large-bodied white leghorn strains. However, information on the performance of the 2-way cross was not made available. The particulars of the crosses made, regarding the number of sires as well as the corresponding number of pure and cross progeny utilised in the study, appear in Table 3.1.

TABLE 3.1 Particulars of contemporary purebreds and crossbreds

Code of			Number of			
Strains crossed	Contemporary pure strains	Cross-breds	Sires	Pure progeny	Cross progeny	Pens or hatches
C x A	C5, A5	CA5	20	1039	895	2
	C6, A6	CA6	20	931	903	2
F x E	F5, E5	FE5	18	981	740	2
	F6, E6	FE6	18	632	790	2
D x E	D7, E7	DE7	29	1448	1012	2
G x F_1	G7, $F_1$7	G$F_1$7	19	800	678	2
	Total		124	5831	5018	12
	Average per sire		1	47	41	2

Codes used above have already been explained in Section 2.2. The numbers of sires and pure progeny given here may not necessarily agree with those given in Table 2.1 because in some strains, some of the sires did not have any cross progeny and were thus not included in the pure-bred-crossbred studies.

Management

Semen were collected from each sire and used to inseminate the pullets of its own (pure) and the other strain of the cross. However, unlike the pure types which were pedigreed to dams and sires, the crossbred chicks were pedigreed only to the sires. The progeny group of each sire from each hatch was housed in a single pen and records were kept on pen basis. This meant that only 2 records were available on each sire in the crossbred population, since there were only 2 hatches (Table 3.1).

Definition of Traits

As a result of the different housing and recording systems adopted for the cross progeny, the definitions for some of the traits do not correspond exactly to those of the pure strains. The disparities and their likely effects on subsequent genetic correlation estimates follows.

Sexual maturity (SM) in the crossbreds refers to the age of a 'pen' on the first of 2 consecutive days when the pen reached 50% egg production.

Part-year egg production (HHP). The number of eggs accredited to each pullet in the cross, was obtained by dividing the total number of eggs laid by the entire pen, by the total number of pullets housed at the beginning of the laying season. The laying season for the crossbreds was often longer than that for the pure strains by some 2 to 4 weeks.

Part-year henday percent (HDP) refers to rate of lay of a pen and was calculated as the total number of eggs laid over the testing period (same as HHP) as a percentage of the total hendays, each henday being defined as the number of days on which a bird was on test after reaching SM.

On crossbreds DE7 and $GF_1$7, recording was continued until 59 weeks of age and hence some additional traits, HHP1, HHP2 and HDP1, were measured on them.

Annual egg number (HHP1) refers to the average number of eggs per hen-housed in a pen during the periods from 18 to 59 weeks of age.

Residual egg number (HHP2) is the difference between HHP1 and HHP of the cross population.

Annual henday percent (HDP1) refers to the rate of lay of a pen from housing till 59 weeks of age.

It is clear that HHP1, HHP2 and HDP1 have no corresponding measures in the pure strains. However, since the objective of all pure line selection programmes is to improve annual performance, it is of interest to note how the early measures in the pure lines relate to and predict them.

A comparison of the above definitions and those of section 2.2 indicates that SM and HHP in the crossbreds are composite traits. Both will be influenced by non-layers whereas the purebreds would consist solely of layers, after the screening process. Further, non-surviving layers would affect HHP of the crossbreds. Thus under certain conditions (e.g. high proportion of non-layers, high levels of mortality) crossbred SM and HHP cannot be considered as similar to those of the pure strains even if the gene action were entirely additive.

The definitions of the more highly heritable traits which follow, may, however, not be necessarily influenced by factors outlined for the reproductive traits above.

Egg Weight (EW) refers to the average weight of all the eggs laid by birds alive in a pen over one week at an age corresponding to that for the pure strains (Section 2.2).

Housing body weight (BW1) is defined as the average weight of all birds housed in a pen at 18 weeks of age.

Adult body weight (BW2) follows similar definitionas BW1 except that weighing was done at the end of the laying period (period as for pure strains).

Statistical Analyses

Pen means were hatch-corrected, using respective constant estimates for each hatch, and weighted by the relevant sire x hatch subclass numbers to obtain an overall mean for each sire. The genetic parameters, $\sigma^2_{s'}$ and σ^2_e needed to calculate the purebred-crossbred genetic correlations were computed for each trait within each crossbred population using model 3.2 below.

$$Yij = \mu + hi + Sj + \varepsilon ij \qquad \ldots.3.2$$

$$i = 1,2; \quad j = 1, \ldots.N$$

where

Yij = a pen mean of the j^{th} sire from the i^{th} hatch

μ = overall mean

hi = fixed effect of the i^{th} hatch

Sj = random effect of the j^{th} sire

εij = random error associated with each pen mean

Variances for the hi, Sj and εij effects were assumed to be σ^2_h, $\sigma^2_{s'}$ and σ^2_e respectively.

The expectations of the mean squares of model 3.2 are

Source	MS	E(MS)
Hatches	H	$\sigma^2_e + k\sigma^2_h$ (not interesting)
Sires	S	$\sigma^2_e + 2\sigma^2_{s'}$
Between pens	E	σ^2_e

As usual, $\sigma^2_{s'} = \frac{S - E}{2}$

The overall parameters for each trait were obtained by pooling the sum of squares and degrees of freedom from model 3.2.

Purebred-crossbred genetic covariances, regressions and correlations

For each sire, purebred and crossbred means were available on each trait. These were used to calculate the weighted genetic covariances according to formula 3.2 presented earlier. The presence of full-sibs within the sire families meant that the between group variance component in the crossbreds was inflated by a quantity equal to $\frac{\sigma_d^2}{6}$, where σ_d^2 is the between dam variance component and 6, the number of dams mated to each sire. This quantity has therefore to be subtracted (σ_d^2 used was that obtained for the female line of each cross) from the component σ_s^2, before calculating the genetic regressions and correlations. The genetic regression of crossbred on purebred performance ($bg_{c.p}$) was obtained by dividing the genetic covariance by the corrected σ_s^2. The genetic correlation was calculated according to formula 3.1 using the weighted genetic covariance. All computations were done for each trait and strain-cross, but were later pooled to give a single estimate for each trait. Pooling was done by adding the sum of crossproducts and sum of squares for the male lines and is thus subject to limitations under Section 2.2.

Only a crude estimate of the probable standard errors of the purebred-crossbred genetic correlation coefficients was obtained using the usual formula; $\frac{1-r_o^2}{\sqrt{df}}$, where r_o is the observed correlation between the 2 performances, and df the degrees of freddom. The standard error of the genetic correlation was then obtained by multiplying that for the observed correlation by the factor by which the genetic correlation differs from the observed correlation. Robertson (1979, pers.commun.) suggested this approach. The formula by Robertson (1959) could not be used since heritabilities and progeny groups in the 2 genetic environments differed. This approach is however, not very efficient in dealing with high observed correlations.

3.3. RESULTS

Annual means of Traits

The least square means for the traits in the crossbreds are given in Table 3.2. Only traits which have equivalent definitions in the purebreds are presented. However, a direct comparison with the performance of the pure lines for purposes of estimating heterosis is probably invalid since some of the traits were measured at different periods in the two genetic environments for some years. This complication was referred to elsewhere (Section 2.2) as being due to management requirements. Unlike the pure lines where the requirement for many hatches to reproduce a strain occasionally necessitated termination of the tests before the target 40 weeks, the 2 hatches of the crossbreds nearly always completed the tests. An exception is 1976 where available records on the crosses cover 36 weeks.

The generally higher egg numbers (HHP) in the crosses is mainly a consequence of the longer laying period mentioned above. Laying continued for 40 weeks in 1975, 36 weeks in 1976 and 37 weeks in 1977 in the crosses. HDP in the crosses thus covered periods beyond the peak production, hence the generally lower values observed compared with the pure strains. Egg and body weights (BW1) in 1975 are much higher for the crosses than the corresponding mean of the pure parental strains. No information was made available regarding the age at which these traits (EW and BW1) were measured in the 2 genetic environments for 1975. However, in 1976, EW was measured at 26 and 30 weeks in the pure and crossbreds respectively. Adult body weights (BW2) are available only for 1976 and 1977. No evidence of heterosis is indicated in these traits. There seems, however, to be evidence of heterosis in sexual maturity for 1975, crosses maturing earlier than their mid-parental

TABLE 3.2 Performance of the Crossbreds

Crossbred Code	SM (Days)		HHP		HDP %		EW g		BW1 kg		BW2 kg	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
CA5	144.3	2.0	73.1	1.6	47.7	1.0	58.2	0.4	1.19	0.01	+	-
CA6	184.8	1.4	59.6	1.1	56.2	1.0	56.1	0.3	1.04	0.01	1.49	0.01
FE5	135.3	1.3	86.2	2.1	57.6	1.2	57.3	0.4	1.55	0.01	+	-
FE6	179.7	1.9	65.8	1.5	61.0	1.1	55.0	0.3	1.31	0.01	1.80	0.02
DE7	162.9	0.9	85.8	1.0	72.5	0.8	52.9	0.3	1.44	0.01	2.04	0.02
$GF_1 7$	163.9	1.6	80.8	1.8	69.7	1.4	55.9	0.3	1.35	0.01	1.82	0.02
Mean 1975	139.8	1.7	79.7	1.9	52.7	1.1	57.8	0.4	1.37	0.01	-	-
Mean 1976	182.3	1.7	62.7	1.3	58.6	1.1	55.6	0.3	1.18	0.01	1.65	0.02
Mean 1977	163.4	1.3	83.3	1.4	71.1	1.1	54.4	0.3	1.40	0.01	1.93	0.02

+ Data not provided

means as well as the better of the parents by 18 and 15 days respectively. A reversal of this trend, however, is observable in 1976 as the crosses are markedly delayed in contrast with the pure strains.

Variances and Covariances

The relative magnitudes of variance components between and within sires in the purebred and crossbred 'genetic' environments as well as the weighted purebred-crossbred genetic covariances are given in Appendix C. In case of the crossbreds, the variance component within sires is actually between pens and not individuals. The purebred parameters are for the strain providing males for the particular cross. The first letter of each cross code refers to this male line. The zero between sire component for D7 is replaced by that for the female line of the DE7 cross. The result of applying a correction to the variance components between sires of the crossbred population due to dams within sires, appear in parenthesis by the sides of the respective variances which were corrected. In the case of $GF_1$7, data on the female line $F_1$7 was not available, hence σ^2_s for G7 was assumed similar to the dam component and used to correct the corresponding σ^2_s,.

The value of overall estimates for the parameters, given in Table 3.3 and obtained by pooling sum of squares and crossproducts of all the lines and crosses, is arguable as the lines come from different base populations and breeds. They are provided here, however, to serve mainly as guides.

The consist picture for SM, HHP and HDP is that the between-sire components for the crossbreds are much larger than for the purebreds. The correction applied to the crossbred components did little to change this trend in these traits. However, after similar correction regarding

TABLE 3.3 Pooled Purebred-Crossbred Genetic Variances and Covariances

Trait	Purebred		Crossbred		
	σ^2_s	σ^2_e	$\sigma^2_{s'}$	σ^2_e	Cov_s
SM	5.16	61.56	17.53 (16.36)	55.5	1.95
HHP	3.03	45.25	30.11 (29.41)	33.80	2.98
HDP	4.05	103.02	13.63 (12.59)	19.78	2.00
EW	1.33	8.42	1.91 (1.72)	1.01	0.82(1.35)*
BW1	14.77	81.77	15.15 (12.85)	15.68	12.63
BW2	22.03	232.93	37.20 (31.27)	37.52	17.18

* Covariance, with FE crosses excluded is inserted in parenthesis.

EW, BW1 and BW2, the between sire components appear fairly similar and occasionally, the pure components are even larger than those for the crossbreds (e.g. EW for CA6, the overall BW1 and BW2 for CA6). The weighted covariances are helpful in revealing the gene action predominant in the crosses as: $\sigma^2_s = \sigma^2_{s'} = Cov_s$ in an entirely additive situation. Any trends in the various traits are somewhat confused by the peculiar behaviour of covariances of the F x E crosses. Apart from these, the results indicate overall, lower covariances for SM, HDP and to a limited extent for BW2 than for, say, the corresponding pure line variances. There is, however, a fair agreement between the covariances and the corresponding purebred and crossbred components for EW (after excluding FE crosses) and BW1. When compared with the crossbred components however, covariances for SM, HHP and HDP are markedly lower, whilst those for EW, BW1 and even BW2 are in relatively fair agreement.

The pecularities in F x E crosses involve mainly EW and to some

extent SM and HHP. Covariances for EW are low, being negative in 1975 and insignificant in 1976. Negative purebred-crossbred covariances during the same periods (1975 and 1976) are also indicated for SM. The rather high covariance in 1975 for HHP becomes negative in 1976.

Purebred-Crossbred Genetic Regressions and Correlations

The genetic regression of crossbred on purebred performances and the genetic correlation between them are presented in Tables 3.4 and 3.5 respectively.

TABLE 3.4 Regression of Crossbred on Purebred Performance

	T R A I T					
Pure-Cross	SM	HHP	HDP	EW	BW1	BW2
C_5-CA5	-0.35	0.63	0.75	1.33	0.83	-
C6-CA6	0.65	0.50	-0.65	1.05	1.30	0.90
F5-FE5	-1.04	4.04	0.36	-0.47	0.23	-
F6-FE6	-1.36	-0.74	1.66	0.14	0.50	0.75
D7-DE7	1.95	3.02	1.02	1.19	1.59	0.76
G7-$GF_1$7	0.81	1.63	0.67	1.68	0.59	0.57
Pooled	0.38	0.98	0.49	0.62(1.02)*	0.86	0.78

* Figure in parenthesis excludes cross F x E.

Marked variation in the regressions exist in all but BW1 and BW2. The consistency in the traits is again marred by peculiarities of F x E crosses. Overall, HHP, BW1, BW2 and EW (after excluding F x E crosses) have very high regressions.

TABLE 3.5 Purebred-Crossbred Genetic Correlations

Pure-Cross	TRAIT					
	SM	HHP	HDP	EW	BW1	BW2
C5 CA5	-0.35±.23	0.17±.39	0.46±.35	0.95±.14	0.75±.18	-
C6 CA6	0.33±.28	0.28±.34	-0.18±.24	1.12±.19	1.17±.37	0.90±.15
F5 FE5	-1.04±.25	0.95±.47	0.25±.38	-0.40±.22	0.34±.23	-
F6 FE6	-0.53±.26	-0.24±.26	1.36±.82	0.12±.33	1.38±.64	0.61±.32
D7 DE7	0.83±.39	0.78±.30	0.50±.27	1.11±.06	0.88±.11	0.61±.31
G7 $GF_1$7	0.46±.26	0.64±.26	0.31±.44	1.21±.33	0.65±.30	0.41±.32
Pooled	0.21	0.32	0.28	0.54(.89)*	0.92	0.65
s.e.	± 0.18	± 0.10	± 0.13	± 0.08	± 0.13	± 0.15

* Figure in parenthesis excludes cross F x E.

The genetic correlations between purebred and crossbred performances for SM, HHP and HDP are generally very low, whilst those for BW1, BW2 are appreciable. The consistently high correlations for EW are tempered by the behaviour of those for the F x E crosses. Scatter diagrams relating the performance of the sire's purebred and crossbred progenies for FE5 and FE6 appear in Figures 3.1A and B respectively. Figures 3.2A and B show consistency in performance of the crossbred progeny of the sires in 1975 and 1976 over the 2 hatches for EW.

'Part-whole' Relationships

The relationship between early part-year egg production of purebreds and full-year performance of crossbreds appear in Table 3.6 for the 1977 crosses only. Relationships between early part egg number for purebreds and late part-year production for the crossbreds have also been included.

TRAIT : EGG WEIGHT

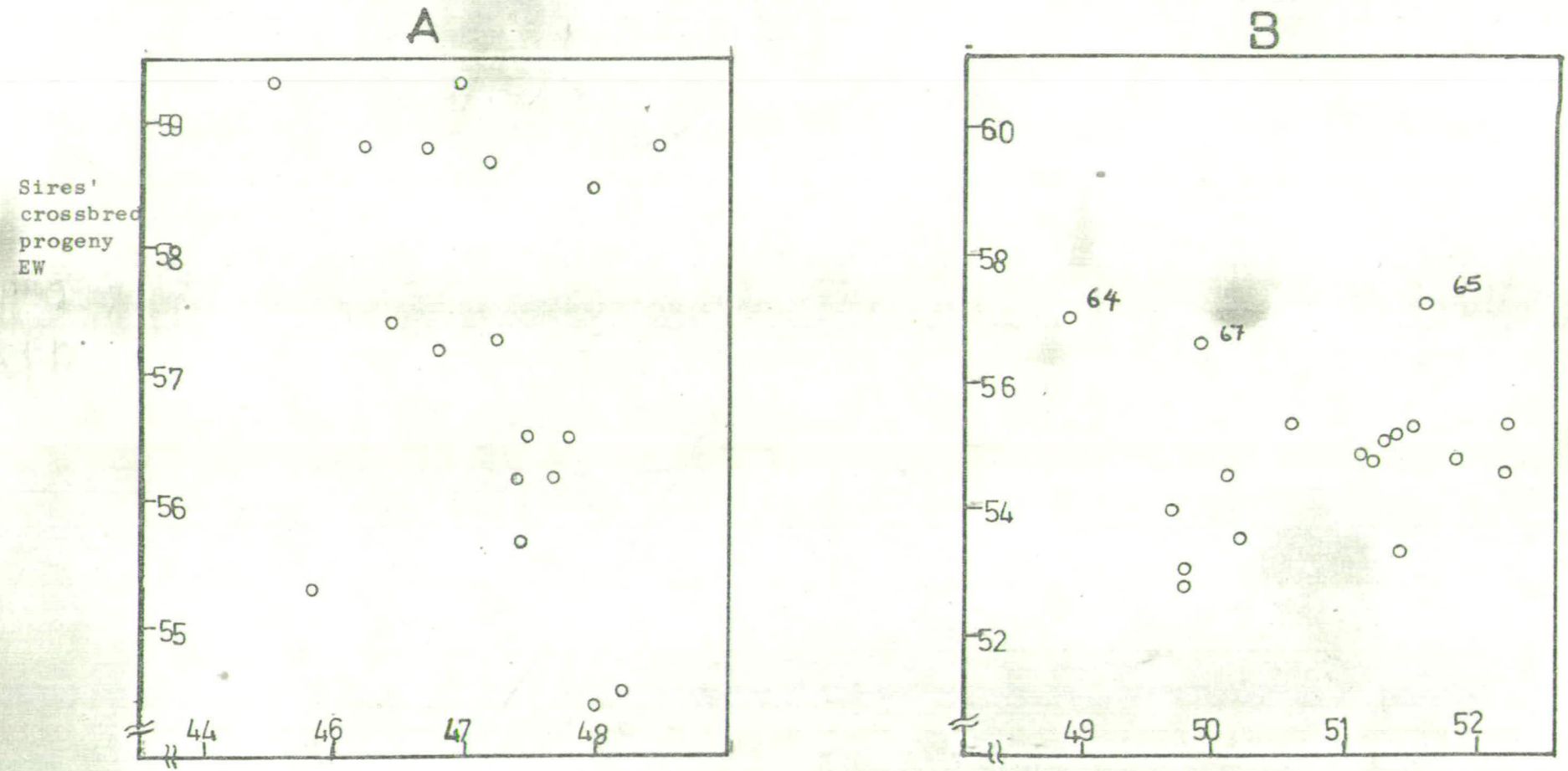

Figure 3.1. Purebred (FS)-crossbred (FE5) relationship for EW in 1975 (A) and 1976 (B).

TRAIT : EGG WEIGHT

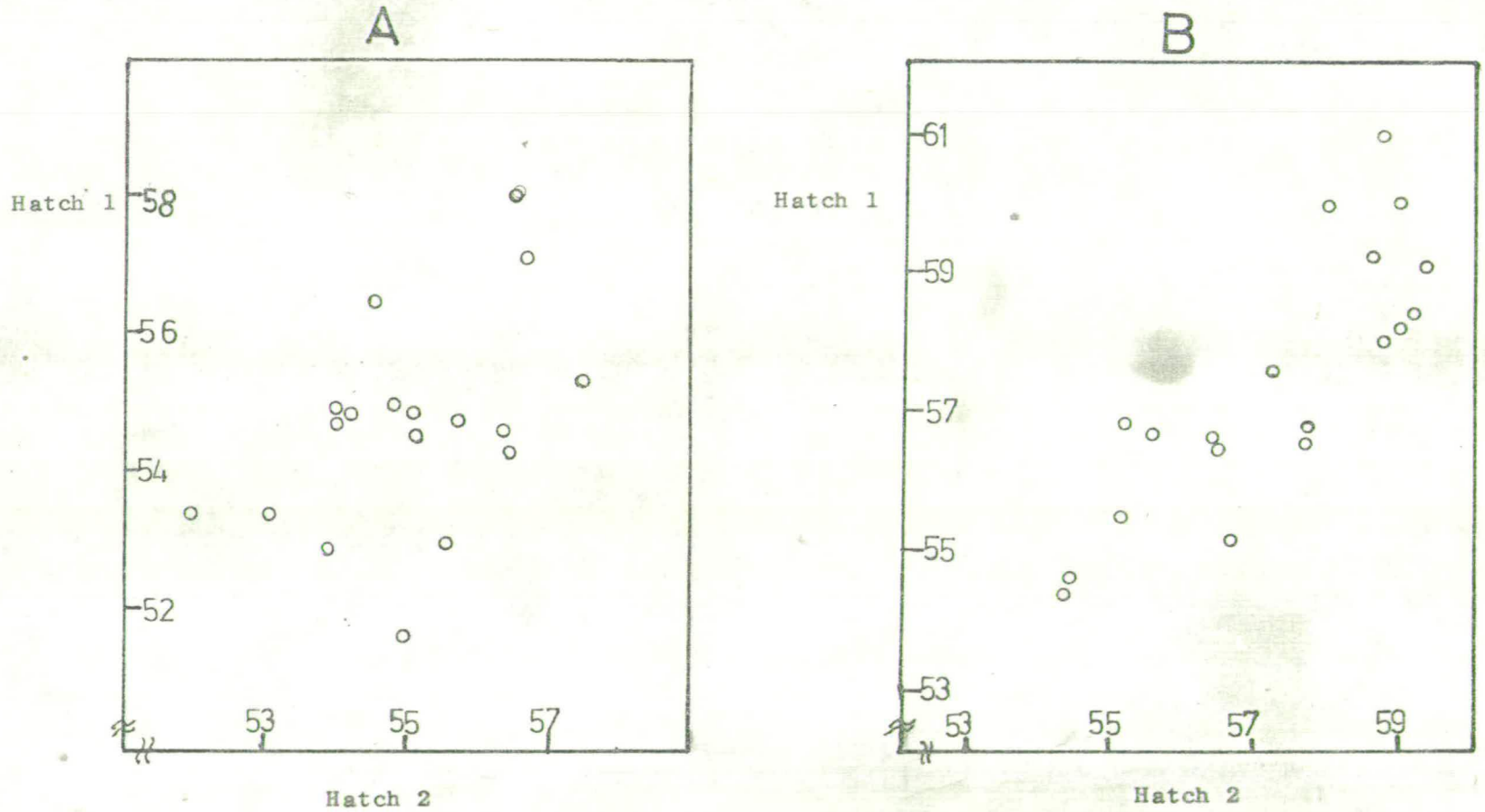

Figure 3.2. Consistency of sires' crossbred progeny performances over 2 hatches for EW of F x E crosses in 1976 (A) and 1975 (B).

TABLE 3.6 Purebred-Crossbred 'Part-Whole' Relationships

Pure	Cross	Trait in Pure	Trait in Cross	Genetic Parameter $bg_{c.p}$	Genetic Parameter $rg_p g_c$
D7	DE7	HHP	HHP1	2.50	0.45 ±.36
		HHP	HHP2	-0.27	-0.12 ±.19
		HDP	HDP1	0.65	0.48 ±.15
G7	$GF_1$7	HHP	HHP1	3.77	0.88 ±.27
		HHP	HHP2	2.15	1.05 ±.32
		HDP	HDP1	0.76	0.62 ±.57

Regressions and correlations are high for the 3-way cross ($GF_1$7). Scatter diagrams relating the sire's purebred and crossbred performances for egg number are presented in Figures 3.3A and B and for rate of lay in Figures 3.4A and B; both illustrate the relationships in the D x E cross. In this cross, the regression of HHP1 on HHP is high, but the correlation between them is low. Both the regression and correlation regarding HHP and HHP2 are negative whilst those for rate of lay (HDP and HDP1) are moderate.

TRAIT : EGG NUMBER

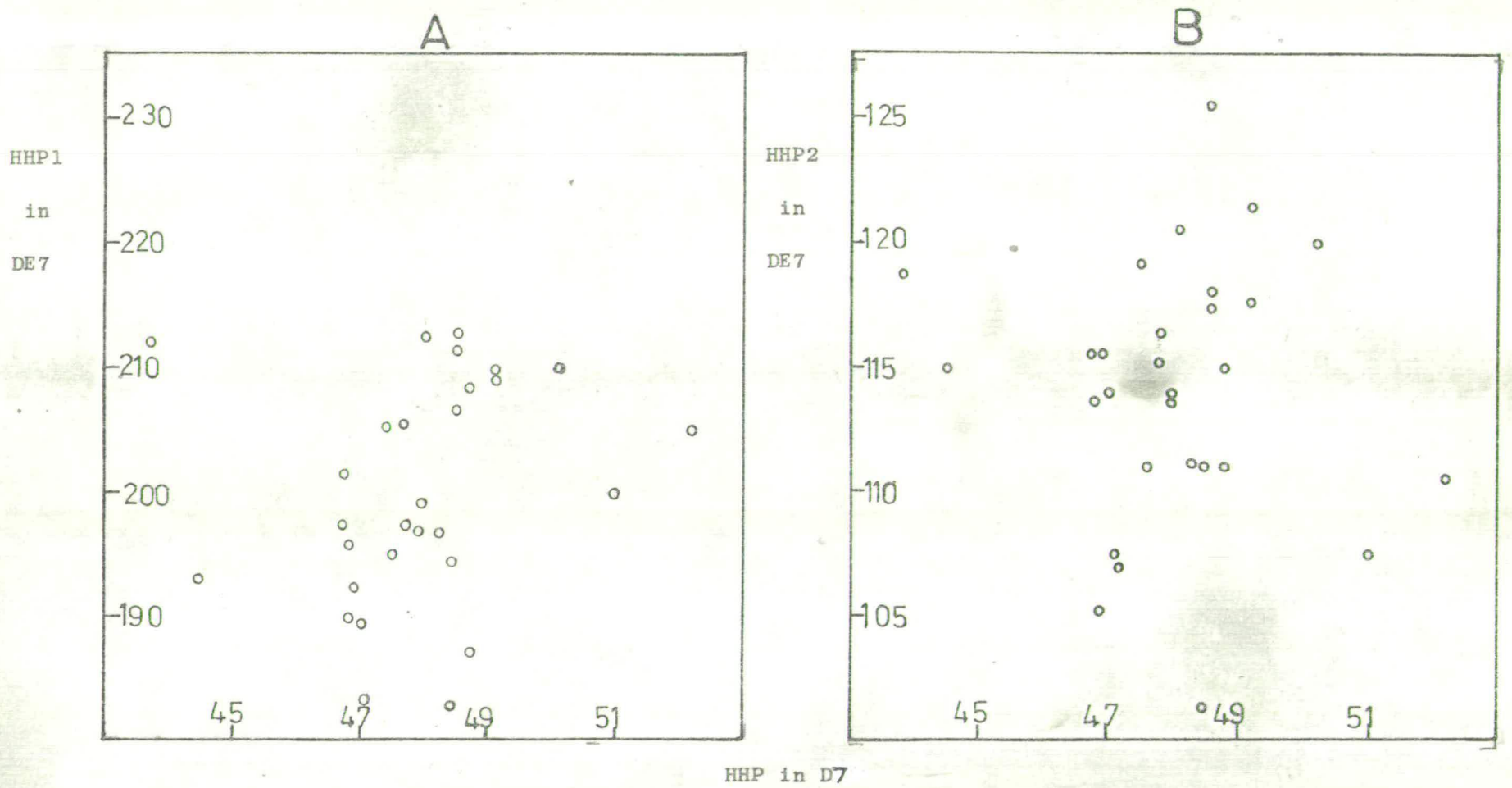

Figure 3.3. Relationship between sires' purebred-crossbred progeny egg number for D7 - DE7.

TRAIT : RATE OF LAY

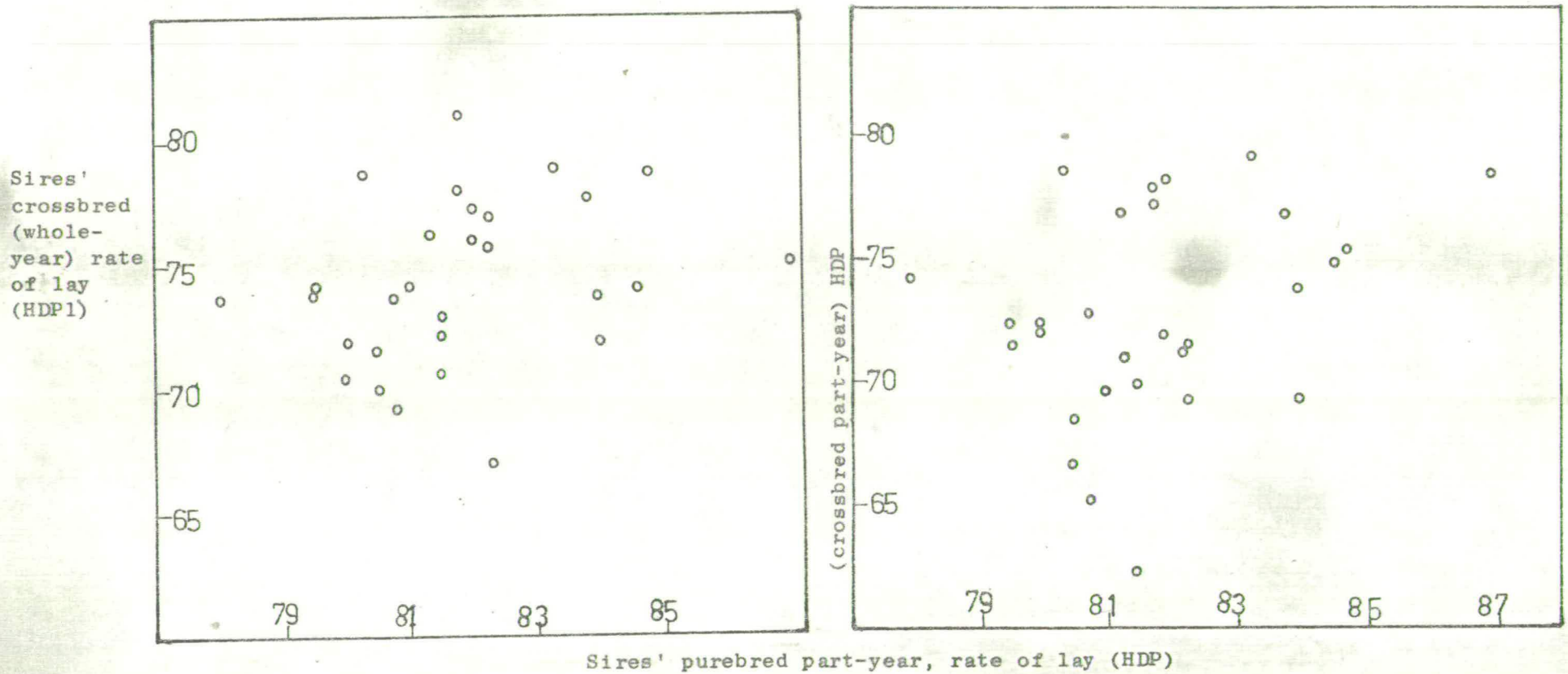

Figure 3.4. Relationship between sires' purebred-crossbred rate of lay for D7 - DE7.

3.4 DISCUSSION

Considering the extreme importance of heterosis in decisions regarding the profitability of certain crosses, it is somewhat regrettable that the data available did not allow any proper estimates of heterosis to be made. Interest has been shown by many workers in the trends of improvements in the crossbreds of a thriving crossbreeding programme. Saadeh *et al*. (1968) found that the crossbreds improved with advancing generations as did the heterosis. On the other hand, Cole and Hutt (1973) reported a constant measure of heterosis over several years of breeding. Both workers reported on egg number, but only Saadeh et.al.(1968) considered it as the primary objective of the programme. The present work however, does not offer any realistic contributions to this apparent dilemma due to the many restrictions outlined in the results.

Reports on the relative magnitudes of the purebred and crossbred components of variance between sires are however equivocal in respect of the reproductive traits. Hale and Clayton (1965), Krause, Yamada and Bell (1965) and Pirchner and Von Krosigk (1973) all found crossbred between-sire variances for SM, HHP and rate of lay to be higher than, and in cases, nearly twice as high as, purebred components.

In the present work, there are several reasons to expect a higher crossbreds' sire variance, even after correcting for dam effects. These include common environment, differences in definition of the traits between the 2 genetic environments, and non-additive genetic effects in the crossbreds.

The housing of each sire's crossbred progeny of a hatch in a single pen would tend to make them more alike than would be expected from their genetic relationships. This would also tend to exaggerate differences

among sires. Krause, Yamada and Bell (1965) used a similar housing design as that for the crossbreds of the present report. The between sire components obtained by them for the crossbreds regarding SM and survivor's rate of lay were similarly very large. Evidence on the importance of common environmental effects in poultry however, suggest that uncontrollable variations between pens treated alike are unimportant (Dudley and Read, 1949; Hale, 1952).

It was pointed out under Section 3.2 that SM and HHP as defined for the crossbreds could be influenced by non-layers. In the present report however, the proportion of non-layers in the unscreened purebred data was no more than 5%. This could have contributed to the higher variation between sire families in the crossbreds. The problem of non-layers will be dealt with in detail later in connection with purebred-crossbred interactions. A further source of difference in definition for some of the traits regards the age of pullets at which the measurement was taken in the 2 genetic environments. For instance, the laying periods in the crossbreds usually exceeded those in the purebreds by some 2 - 4 weeks.

Pirchner (1969) has suggested that genes with dominance effects would be expressed in the crossbreds and thereby increase crossbred components of variance between sires. This would, however, occur if gene frequencies are different in the 2 genetic environments, since that is the necessary requirement for dominant genes to contribute to the additive genetic variation represented by the between sire component. In the present work, it has not been possible to extricate maternal from dominant effects. However, assuming negligible maternal effects, there is a suggestion of appreciable dominance effects in rate of lay (see Section 2).

Purebred-Crossbred Interactions

The generally wide variation in the magnitudes of the genetic correlations between traits is in agreement with many reports including Pirchner and Von Krosigk (1973) and indicate, with only one exception regarding EW, that genetic interactions are probably unimportant in EW, BW1 and BW2. The only exception was EW in F x E crosses and will be dealt with more fully later in the Discussion. The negative correlations in SM and HHP, would be due at least in part to the presence of non-layers in these traits when measured in the crossbreds. Shalev (1977) has indicated that the difference in the performance among sire families disappeared when non-layers and low producers were removed. Non-laying as a trait, was found to be heritable by the same worker, and could also be induced by unfavourable environmental conditions. In the present report, 2 of the 3 negative values in SM were recorded in 1975 when mortality levels were running at 40% in some pens. However, low mortality figures do not preclude the possibility of high levels of non-layers as the phenomenon may be present as prolapse and other congenital or abnormal cases without necessarily causing death. This super-imposition of genetic variation for non-laying (including low production) on that for SM and HHP in the crossbreds, would make any genetic interpretation of the low correlations with the purebreds (where all non-layers were screened) somewhat confusing.

Krause, Yamada and Bell (1965) obtained even lower purebred-crossbred genetic correlations for SM, than some of those obtained in this study, and suggested the possibility of different sets of genes for purebred and crossbred performance. Their data came mainly from a farm in which pen records, instead of individual, were available on the sires' crossbred

progeny. Thus the possibility of non-layers reducing the correlations for sexual maturity in a manner similar to the present report cannot be ruled out.

On the other hand, both Hale and Clayton (1965) and Pirchner and Von Krosigk (1973) who used individual records in both the purebreds and crossbreds, obtained no evidence of interactions in SM.

Rate of lay (HDP) would, however, suffer only minimally if any, from effect of zero producers and purebred-crossbred correlations would mainly be influenced by gene action. Krause et.al. (1965) as well as Pirchner and Von Krosigk (1973) obtained purebred-crossbred correlations for this trait which were lower than 0.5, much in agreement with the overall estimate found in the present study. It would appear therefore that gene effects responsible for purebred rate of lay are different from those required for crossbred performance.

The low (and negative in 1975) purebred-crossbred correlations regarding EW in crosses involving strains F and E is rather strange as there is no such reports in the literature. According to the respective scatter diagrams, the complete lack of correlation between the sire's pure and cross progeny's EW in 1975 (Fig. 3.1A) improved in 1976 (Fig. 3.1B) but for the marked deviations from this trend by sires 64, 65 and 67. As the genetic correlation between HHP and EW was positive in strain F (see Table 2.6), it is possible that those sires the progeny of which had unusual EW were culled on the basis of HHP. Of those left therefore, only 64, 65 and 67 behaved unusually. Their removal from the data in 1976 caused the purebred-crossbred correlation to appreciate to levels close to unity. However, since their records were based on effective progeny gropp sizes $(\frac{n_c n_p}{n_c+n_p})$ higher than

average, their removal is not justified.

Before any genetic explanation is sought for the phenomenon, some management conditions that could cause such low correlations were investigated.

(1) If progeny groups were assigned to sires other than their own in crossbreds, negative correlations could result. Such errors in the pedigree could have occured possibly at hatching or housing. This explanation however, seems unlikely as the low correlations occured in both 1975 and 1976.

(2) Consistency of Performance.

Table 3.7 below shows the performance of the sires which behaved unusually in 1976, over hatches in their own pure lines and in crosses with the strain E.

TABLE 3.7 Consistency of Performance over Hatches for EW (in gms)

Sire Number	Pure Offspring				Cross Offspring	
	Hatch Code				Hatch Code	
	4	6	8	10	1	2
64	49.0	49.3	49.0	49.8	57.2	56.7
65	53.2	50.5	51.7	-	58.2	56.6
67	50.8	49.7	49.2	50.8	55.4	57.5

It is clear that the performance of these sires were consistent over hatches within the pure or cross populations. Figure 3.2A comprising all the sires, gives support to the above Table 3.7 regarding the crossbreds and would relegate no importance to any non-random effects of environment on EW of these sires.

(3) Unusual distribution of EW within sires in the crossbred.

The effect of high mortality is to reduce the number of pullets providing eggs for the measurement of EW in the crossbreds, that is if the deaths occured before the recording date. EW of the few survivors would not be representative of the pullets housed initially in the pen. Since this might not affect all sires equally, the ranking of the sires in the crossbreds could change.

In the present work, mortality in some pens in 1975 of the FE cross reached more than 40%. The possibility of the unusual distribution of EW affecting some of the sires in the crossbreds cannot therefore be ruled out.

(4) Genotype x type of housing interactions

The extent to which the cage housing of purebreds and the floor housing of the crossbreds might have affected the correlations between these genotypes cannot be assessed as genotypes were confounded with types of housing. The general impression from the literature (see for example, review and results of Hale,1961) is that EW is not affected by genotype by environment interaction involving housing, especially if feed and geographical locations are the same. However, if present, this type of interaction will cause a decline in the genetic covariance between the purebreds and crossbreds.

(5) Segregation of major genes.

A genetic model is required such that the purebred progeny of certain sires do not provide any guide as to the EW of their crossbred sibs. In this regard, a major gene, autosomal and recessive, segregating in Strain F may be considered. If the frequency of the gene is high, some of the sires could be recessive homozygotes in respect of it, and a number of

hens could be carriers at least. A mating of this sire with hens of its own line could result in a high proportion of homozygote pullets. When this sire is mated to females of another strain in which the gene is at low frequency, its expression would be suppressed and the EW of the cross progeny would differ markedly from that of the pure progeny.

Major genes, however, would become exposed mainly at very high inbreeding levels. An examination of the pedigree of Strain F revealed that the average genetic relationship among sires producing progeny in 1975 and 1976 were 0.20 and 0.12 respectively. In fact, the population went through some form of a bottleneck in 1974, when two males sired 75% of the entire population. Clearly, an hypothesis of major gene segregating in Strain F, would not be too wild a speculation especially considering the fact that sires 64, 65, which behaved unpredictably in 1976(of FE6) have the same grandsire.

Practically, this hypothesis may be investigated by setting up repeat matings involving sires 64, 65 and 67 with the same dams of the pure strains F and E, or their families if they themselves are not available. Some sires of Strain F known to have high repeatabilities of EW in the pure and crossbreds, should be involved to act as controls. Backcrosses should also be set up after the repetition of the 1976 matings.

The low correlations between the early egg production in Strain D and the whole or late part production of DE7 is probably a reflection of the relationships between these measures in the pure Strain D itself. The magnitude of the correlation (HDP - HDP1) is similar to that for early in the pure and early in the cross observed for this cross (Table 3.5). Morris (1963) has discussed this problem of declining genetic

correlations between early and late part production within the context of pure lines.

Utility of Purebred-Crossbred Genetic Correlations

Falconer (1952) used the genetic correlation between the performance of progeny of a sire in different environments in the context of correlated characters, to predict responses to various selection schemes. He noted that, under the assumption of equal selection intensities, indirect selection will be more efficient than direct if $h_I\, r_A > h_d$, where h_I, h_d are the heritabilities in environments I and d of the trait to be improved and r_A is the genetic correlation between performance in the two environments; d being the direct environment under which performance is eventually required.

By definition, h_I and h_d refer to the correlation between the criteria of selection, which was the individual's performance (X), and breeding value (A) and this may be generally represented as r_{AX}. By analogy, in the present work, selection in the purebreds would be recommended if $r_{A\bar{X}pi..}\, rg_pg_c > r_{A\bar{X}ci..}$; where the symbols here follow earlier definitions. It is clear, therefore, that if genetic correlation is significantly lower than unity, some use need be made of crossbred information, assuming as Falconer (1952), that selection intensities are the same in both genetic environments. This latter point is probably arguable as Comstock (1961), for example, has indicated that the ratio irrs/ipls is often between 0.4 and 0.8 depending upon the size of the programme, where irrs and ipls are the intensities attainable in the crossbreds and purebreds respectively. However, in traits with low heritability and low rg_pg_c, individual performance in the pure lines is of little importance anyway. Thus family selection in both genetic

environments will most probably be practised, in which case irrs/ipls = 1.0.

A realistic approach to combining information on purebreds and crossbreds is to use an index (Hazel, 1943). Then in the sire selection programme, the score, I, of any sire (i), may be given as:

$$I = b_1\bar{X}_{pi}.. + b_2\bar{X}_{ci}.. \qquad .... 3.$$

where b_1 and b_2 are the weights for the respective sources of information. The aggregate genotype (G) that is to be improved through selection based on the criteria I, is given by

$$G = a_1A_p + a_2A_c \qquad .... 3.$$

where A_p, A_c are the sire's genes for pure and cross performance and a_1, a_2 are their economic weights respectively. The variance-covariance matrices may then be set up as follows:

$$\begin{matrix} V(\bar{X}_{pi}..), & Cov(\bar{X}_{pi}.., \bar{X}_{ci}..) & b_1 & Cov(\bar{X}_{pi}..,A_p), & Cov(\bar{X}_{pi}..,Ad) & a_1 \\ & & = & & & \\ Cov(\bar{X}_{ci}..,\bar{X}_{pi}..), & V(\bar{X}_{ci}..) & b_2 & Cov(\bar{X}_{ci}..,A_p), & Cov(\bar{X}_{ci}..,Ac) & a_2 \end{matrix}$$

where V, Cov represent variances and covariances.

The following should also be noted:

$$V(\bar{X}_{pi}..) = (\tfrac{1}{2}h_p^2 + \frac{1}{4d}h_p^2 + (1 - \tfrac{1}{2}h_p^2)\frac{1}{nd})\ V_p$$

$$V(\bar{X}_{ci}..) = (\tfrac{1}{2}h_c^2 + \frac{1}{4d}h_c^2 + (1 - \tfrac{1}{2}h_c^2)\frac{1}{nd})V_p$$

$$Cov(\bar{X}_{pi}.., \bar{X}_{ci}..) = \tfrac{1}{2}rg_pg_c\sqrt{V_{Ap}V_{Ac}}$$

$$Cov(\bar{X}_{pi}.., A_p) = \tfrac{1}{2}V_{Ap}$$

$$Cov(\bar{X}_{pi}.., Ac) = \tfrac{1}{2}rg_pg_c\sqrt{V_{Ap}V_{Ac}}$$

$$\text{Cov}(\bar{X}_{ci}.., Ap) = \tfrac{1}{2} r g_p g_c \sqrt{V_{Ap} V_{Ac}}$$

$$\text{Cov}(\bar{X}_{ci}.., Ac) = \tfrac{1}{2} V_{Ac}$$

where

n = number of offspring per dam

d = number of dams mated to each sire

h_p^2, h_c^2 = heritabilities in the pure and cross environments

Vp = phenotypic variance

V_{Ap}, V_{Ac} = additive genetic variance of the purebreds and crossbreds respectively.

Based upon the above matrix, the ratio of b_2/b_1 was determined for several values of rg_pg_c and 3 relative values of economic weights under the following assumptions:- $h_p^2 = h_c^2 = 0.20$; $Vp = 1$, $n = 6$ for both pure and crossbreds, $nd = 42$ for both pure and crosses. The relationship between the ratio b_2/b_1 and varying rg_pg_c were studied when $a_1 = 0$ and $a_2 = 1$, or $a_1 = 0.1$ and $a_2 = 0.9$ or $a_1 = 0.2$ and $a_2 = 0.8$. These 3 relative economic weights were chosen in order to observe the effects on the relationship of b_2/b_1 as rg_pg_c varied, of improved performance of the purebreds themselves. The results of the simulation appears in Figure 3, where only a single trait has been considered.

It has already been indicated earlier that indirect selection may be as good, if not better under some circumstances (e.g. where facilities are not elaborately existent already for cross-based selection programmes) as selection in the crossbred (direct) genetic environment if $rg_pg_c = 1.0$. Figure 3.5 indicates that the same conclusion may in fact be true of rg_pg_c values greater than 0.65 as the curves do diverge rather more beyond that point. As expected, there would be no need to consider purebred performance at all when $rg_pg_c = 0$ and no economic weight is given to purebred performance. It may also be seen that as soon as the slightest economic

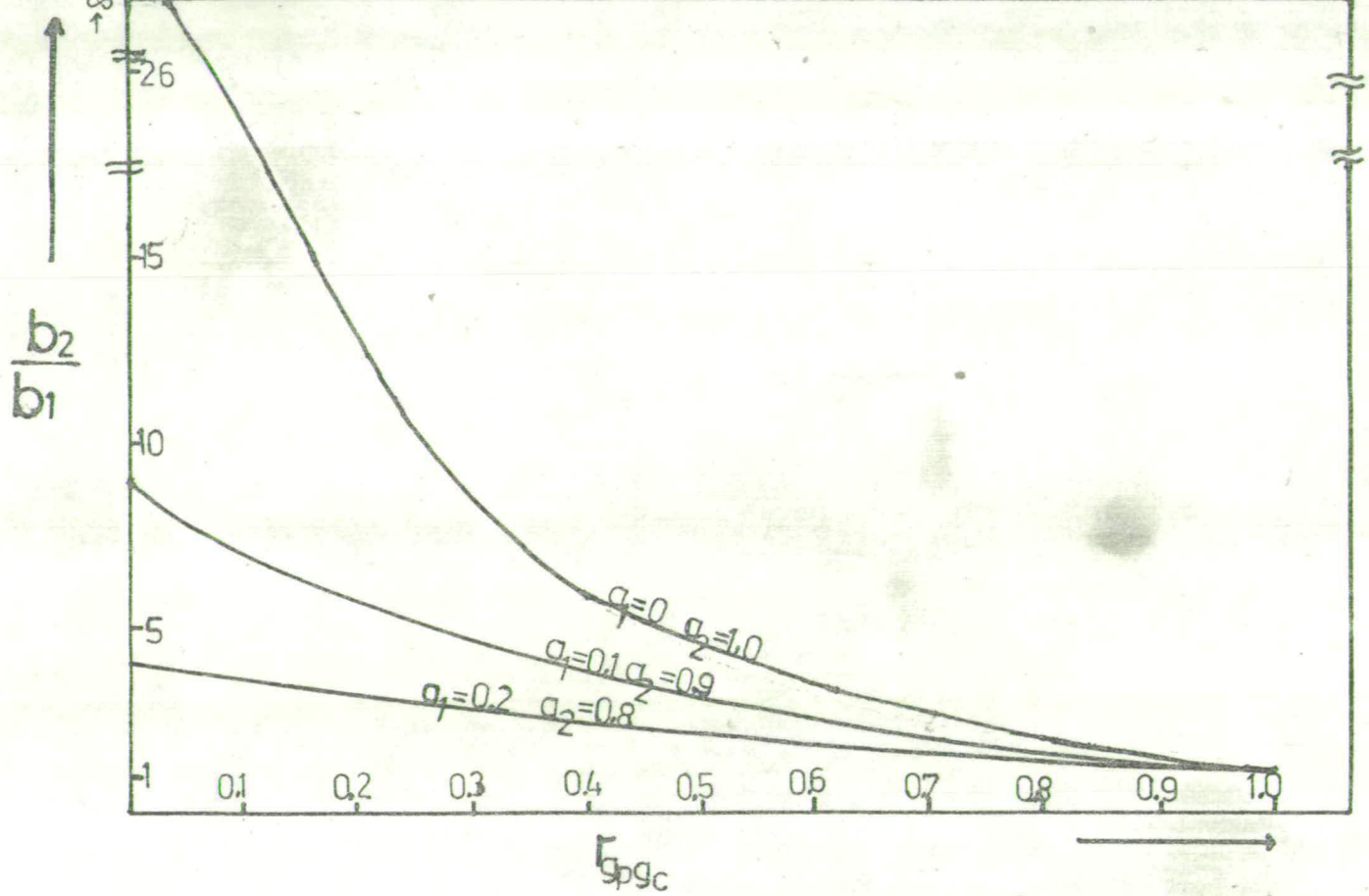

Figure 3.5 Relationship between relative weights of sires purebred and crossbred means, and the genetic correlation between them.

value is placed on purebred performance, the slope of the curve declines rather sharply and the advantage swings in favour of pure line-based selection schemes.

Argument is still on the efficacy of reciprocal recurrent selection which is a crossbred-based selection procedure proposed by Comstock et al. (1949). The major criticism of the programme has been the inevitable long generation interval and hence lower genetic progress expected with it. However, by selecting males on the basis of the performance of their half-sib crossbred sisters, the generation interval could become similar to that attainable with purebred selection schemes. Here, the assumption is that the sire which has been tested in the crosses, would give its crossing ability to its son. Thus this sib selection breaks down if cross performance is due to epistasis in which case the cross performance of each male need to be tested. Hence the need for breeders to know as much as possible about the exact gene action responsible for the heterosis in their population which they wish to exploit.

PART III. GENOTYPE x ENVIRONMENT INTERACTIONS IN EGG-LAYING POULTRY.

4.1 INTRODUCTION

Even though an effective breeding programme was obtained based on relevant genetic parameters, the environment under which to carry it out would need to be decided upon carefully. This is because if genotype x environment interactions exist, then improvements made in the breeding station may not be "carried over" to the commercial farms to which the improved stocks are transferred. Most of the earlier work involved genotype x climatic location interaction effects which Dickerson (1968) has found to be important. Presently however, breeders are concerned to know whether under small differences of environments, such as may exist among farms within a locality, interactions with genotypes do occur.

In this part of the thesis, data from the United Kingdom Central Random Sample Test (RSET) station were examined for evidence of stock x nutrition or management factor interactions. The primary objective of these tests held annually, is to compare the performance of egg-laying strains and crosses being distributed in the United Kingdom. Results of the tests are meant to aid farmers in choosing strains or crosses. Recently,however, several nutritional and management factors have been imposed on the RSET, in order to find out whether ranking of the genotypes would vary as the nutritional or management environment changes.

Detection of Genotype x Environment Interactions

Several methods have been employed in detecting genotype x environment interactions including, classification into types, use of first order statistics, percentages and repeatabilities using variance components (Pani and Larsely, 1972). These methods however, do not permit comparisons of the exact consequences of alternative breeding policies.

Falconer (1952) thus made an important theoretical contribution by suggesting the use of the genetic correlation to quantify interactions; an idea already utilised under section 3 to quantify purebred-crossbred interactions. By regarding performance in different environments as different characters with genetic correlation between them, a comparison can be made between direct and indirect selection. The relevant ratio of the expected responses was given by Falconer (1952) as:

$$\frac{CR_Y}{R_Y} = r_g \frac{i_x h_x}{i_y h_y} \qquad \ldots\ldots 4.1$$

where R_Y, CR_Y are the responses to direct selection in environment Y, and the correlated response in Y obtained by selecting in environment X; i_y, i_x, h_y and h_x are the intensities of selection and roots of heritabilities in the respective direct (Y) and indirect (X) environments. r_g is the genetic correlation. Robertson (1959) extended the idea to a large number of different environments and also gave an expression for the relative contribution of changes in ranks and between-group variance to the interaction component. Dickerson (1962) suggested that where important variation between environments in the scale of genetic effects exist, an adjustment need be made in the following manner to the interaction component:

$$\gamma_g = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 - V(\sigma_{Gi})} \qquad \ldots\ldots 4.2$$

where σ_G^2, σ_{GE}^2, $V(\sigma_{Gi})$ are the between-group variation among environments, interaction component and variance of the genetic standard deviations within the environments respectively; γ_g is the genetic correlation.

Experiments used to determine the genetic correlation in livestock may be classified into two. In the dynamic approach pioneered by

Falconer and Latyszewski (1952), selection for the trait is carried out in each of the two environments, thus measuring direct responses. By "swapping" such adapted strains over environments, correlated responses may also be obtained. The genetic correlation is then obtained simply from the relation 4.1 above. The second approach is a static one involving a factorial design in which relatives are tested under several environments. Variance components obtained from the analysis of such experiments are used to compute γ_g based on expression 4.2 above.

Probably apart from Abplanalp's (1962) selection experiment, using feed shock treatments, not many reports are available on the dynamic approach in poultry. The static approach has, however, received considerable attention because it is cheaper and yields quicker results.

Basis of Genotype x Environment Interaction in Poultry

Several reviews on the subject are available including a recent one by Pani and Larsley (1972). These indicate that experimental results obtained mainly by the static methods are contradictory in respect of nearly all the interactions involving nutritional or management factors. Probably this outcome is not unexpected considering the fact that specific or fixed environmental factors are chosen which tend to differ among experiments thereby invalidating any generalisability of the results. There are several other reasons, all based upon genotypic variations, why repeatability among experiments may be low.

The first concerns the levels of the environmental factor applied to the genotypes. Often these are outside the range practically encountered in commercial farms, and results obtained would therefore be of little importance to breeders. Such results however may not be repeated by other workers who use narrow range of environments that enables

each genotype to meet its normal requirements. For instance it is common knowledge that heavier hens require more energy for maintenance than lighter ones. On a very low energy diet therefore, the lighter types are likely to be superior, whereas the reverse could be true on high energy diets. A similar trend would be noticed on a diet deficient or extremely low in certain essential amino acids as genetic variation exists in these (Harms et al., 1967; Nesheim and Hutt, 1962; Nesheim, 1968).

The second concerns confounding of environmental effects. This was implied in the review by Hughes (1975) regarding genotype x housing studies. He pointed out that even though cage-housing were being compared with floor housing, other factors which are known to affect production such as area and volume of space available per bird, have often confounded the true effects of housing.

Orozco (1976) has proposed a genetic model that could explain genotype x environment interactions involving stress conditions. He considers that genes required for expression of a trait in a normal environment would be additive, whereas overdominant genes would be responsible in a stress environment. He demonstrated this through a comparison of pureline (PLS) and reciprocal recurrent selection (RRS) schemes in Tribolium, under optimum and stress temperature environments. RRS was superior only in the stress environment. It is, however, not necessary to assume overdominant gene action in order to explain these results. In this context, it seems realistic to consider all traits as having a component that confers resistance to disease, inhibition of expression and death. This component would then be expressed only in the stress environment. If this component is negatively correlated with the trait

itself, an apparent overdominance could result. Further, if its heritability is low, then some progeny testing (of RRS) would be more efficient than mass selection (PLS) in revealing breeding values.

In the present, the experiments to be presented were properly planned and were somewhat generally free from some of the limitations mentioned. They should thus be of interest to breeders as the levels of factors chosen are being employed or likely to be used in commercial farms.

4.2 GENERAL MATERIALS AND METHODS

All the trials on which data were made available were run at the Milford Test Ground using the same facilities. Hence only details about housing and other methods that apply equally to all the trials will be mentioned here. Specific methods, however, will be detailed in the respective sections where they were employed.

Procurement of Stocks

In general, only day old chicks from the breeders were used for the trials. However, they could be obtained in two ways, depending upon the capacity of the breeder's operations. Firstly, if a single hatch could supply 8,000 pullet chicks, then day old chicks were sampled from the breeder's flock. Otherwise eggs were sampled from two of the breeding farms, provided these had 5,000 laying hens between them. They were then stamped and hatched on the same farms. Sufficient samples of each strain or strain-cross were taken in order to meet the requirements for the Random Sampling Tests, the main pre-occupation of the station, as well as the management trials imposed from time to time on the laying tests.

Further, in order to ensure that samples taken were representative of the strain or cross, another sample of each strain/cross was taken from customers who bought day old chicks from the same source. This latter sample was treated as a separate replicate throughout the tests.

As regards the strains/crosses themselves, breeders were under no obligation to declare the breeding of their genotypes, thus pure strains and crosses were tested together. However, these had to be available commercially to qualify to be tested. In this thesis, all entrants to the test will be referred to as "stock" even though they were pure strains or strain-crosses.

Housing Management

Each stock was reared separately on a floor compartment of a large brooding house from day old till 18 weeks of age. Each pen could accommodate 150 pullet chicks and had 14.4m^2 of floor area. Stocks were therefore not intermingled. However, except in cases where the rearing itself was being investigated, all participating stocks were treated alike regarding feeding and other management.

At 18 weeks of age, 6 experimental units or replicates were randomly selected from each stock and transferred to a laying house. An experimental unit comprised 48 point of lay pullets, housed 4 birds to a cage 46cm by 41cm (464.5cm^2 per bird) in 3-tier cage batteries. The replicates were completely randomized within the battery house.

Ventilation in the laying house was provided by extraction fans in the roof ridge and air inlets at the sides of the house.

Nutrition and Other Management

Standard diets were fed all replicates on the RSET from rearing till the end of the laying period. The calculated composition of the diets fed at various periods appear in Table 4.1. Feed and water were offered ad libitum throughout the test period to the controls.

TABLE 4.1 Calculated Composition* of diets fed RSET Controls.

Nutrient	Age of bird (in weeks) 0 - 8	8 - 18	18 - 76
Protein %	18.70	15.0	15.7
Oil %	2.80	2.30	2.70
Fibre %	4.30	4.40	3.50
M.E. (Kcals/Kg)	2762.5	2707.3	2727.1
Lysine %	0.98	0.72	0.79
Methionine %	0.37	0.29	0.33
Cystine %	0.33	0.29	-
Calcium %	1.17	1.00	3.50
Phosphorus %	0.80	0.78	0.74
Available Phosphorus %	0.50	0.46	0.40
Salt %	0.45	0.44	0.46

* Using values provided by Vitameals Advisory Service, Beecham Agricultural Products.

The birds were vaccinated according to the following schedule:

Vaccine	Age of Birds
Mareks	Day-old
Hitchner B1	21 days
La Sota	9 - 16 weeks
IBH 120	5 weeks
IBH 52	11 weeks
Epidemix Tremors	14 weeks

Definitions of Traits

Hen-housed egg production (HHP) is the number of eggs laid by a replicate during the period 20 - 76 weeks of age relative to the number of birds in the replicate at 20 weeks of age. Henday percent (HDP) measures the rate of lay of the birds after attaining 50% level of production and was calculated as the total number of eggs laid by a replicate

as a percentage of the total number of hendays, each henday being defined as the number of recording days on which a hen was alive.

Food per bird (FPB). This measure of food consumption is defined as the quantity of feed consumed by a replicate during the period 20 - 76 weeks of age divided by the number of pullets housed at 20 weeks.

Food bird-day (FBD) refers to the total feed consumed by a replicate divided by the total number of hendays.

Egg Weight (EW). Each month the production of all replicates over a one week period was weighed. The overall average for the laying period was obtained by weighting the monthly averages by the respective number of eggs weighed each month.

Livability Percent (LIVABL) of a replicate is defined as the proportion of the birds initially housed in a replicate that survived the whole period of the test.

Egg Value (EGGVAL). The average egg prices for the whole laying period were used to calculate income per bird from the total number of eggs laid in each grade by the end of the period. The egg prices used were the mean packer to producer prices published weekly by the Eggs Authority.

Feed cost in lay (Feed Val). The average price of feed per unit weight over the whole laying period and the total weight of feed consumed per replicate were used to calculate the feed cost per hen housed.

Egg Income Over Food Cost (IOFC). This essentially is a measure of the laying period profit margin and was simply the difference between Egg Val and Feed Val.

Units of Measurement of Traits.

The traits were measured in the following units respectively:

Trait	Unit
HHP	Number
HDP	%
FPB	kg/hen-housed
FBD	g/day
EW	g
EGGVAL	pence (p)/bird
FEEDVAL	pence (p)/bird
LIVABL	%
IOFC	pence (p)/bird

Statistical Analysis

Specific statistical models were used for the analysis of each experiment and will thus be presented under the appropriate sections. However, it is worth pointing out here that where practicable, all stocks were classified into two body weight groups, much in accordance with the test management's. The classification was somewhat arbitrary as it was based on the shell colour of the eggs laid by the stocks. All brown egg-laying stocks were classified as heavy and the rest (white and tinted) formed the low body weight class.

Stocks were classified as random and were assumed to have come from a large population of highly selected stocks. Regarding strains and crosses among them (stocks)as random is probably arguable, as stocks being marketed in the United Kingdom may be of finite number. A general discussion of the problem may be found in a paper by Taylor (1976) who considered that strains of each breed could be sampled at random. In the present study, the difference between any specific stocks is not of primary interest. Also in order to obtain variance components leading to the estimation of genetic correlation of performance of relatives

across environments, an assumption of random stock effects was deemed necessary. Formula for the computation of the genetic correlation (r_g) came from Robertson (1959) as:

$$r_g = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_{GE}} \qquad \ldots\ 4.1$$

where σ^2_G is the genetic variance between stocks across environments and σ^2_{GE}, the stock x environment interaction component.

It was not necessary to calculate standard errors for any of the estimates as the stock x environment interaction were generally not important.

Testing for Significance of Effects

The F-test was used to test the significance of effects. After testing, using the correct error line according to expectations of the mean squares, pooling was done from the residual line (or remainder) upwards involving all non-significant effects. However, in order to calculate the variance components, use was made of the original model (i.e. before the pooling).

4.3 BREEDER'S OPTION Vrs. RANDOM SAMPLE TEST CONDITIONS

This trial was originally designed to answer some of the criticisms of certain breeders, that the standard RSET conditions sometimes prevented certain stocks from demonstrating their true potential. From breeding point of view, a comparison of performance under breeder's selected conditions and under those considered optimal, would reveal whether any adaptation to specific management conditions has occurred. In the trial to be reported here, the options offered to breeders ranged from housing to feeding, starting from day old until the end of the laying period.

4.3.1 MATERIALS AND METHODS

Options offered to breeders were as follows:

(1) Debeaking

(i) No debeaking
(ii) At day old
(iii) At 7 days *
(iv) At 18 weeks

(2) Light Pattern in Rearing

(i) Constant 9 hour day to 18 weeks *
(ii) Step down to 9 hours at 11 weeks

(3) Rearing Feeding System

(i) Ad libitum *
(ii) Restrictions to a percentage of ad libitum
(iii) Planned quantitative feeding
(iv) Target body weight

(4) Laying Diets

	Protein	Period	Price per Tonne+
a.	16.5%	Throughout lay	£79.43
b.	16.5%	To 40 weeks)	£78.14
	15.5%	To end of lay)	
c.	15.5%	Throughout lay	£77.22 *

(4) Laying Diets (continued)

	Protein	Period	Price per Tonne+
d.	17.5%	To 40 weeks)	£81.85
	16.5%	To end of lay)	

* Random Sample Test control conditions

\+ Average prices over the test period.

Stocks

Seventeen stocks, comprising 9 brown and 8 white egg laying types, were involved in the trial. Three replicates of each stock at point of lay, were placed under each treatment(RSET or breeder's option) at 18 weeks of age in battery laying houses.

Statistical Model

The following mixed model was used to analyse data for all the traits measured:

$$Yijkl = \mu + Bi + Sij + Tk + (BT)ik + (ST)ijk + \varepsilon ijkl \quad ....4.3.1$$

where:

$Yijkl$ = the mean of the l^{th} replicate under the k^{th} treatment of the j^{th} stock within the i^{th} body weight class.

μ = overall mean

Bi = fixed effect of the i^{th} body weight class, $i = 1,2$

Sij = effect (random) of the j^{th} stock within the i^{th} body weight class, $j(i = 1) = 1, \ldots 9$ $j(i = 2) = 1, \ldots 8$.

Tk = effect of the k^{th} treatment (breeder's set of conditions and RSET conditions), $k = 1,2$

$(BT)ik$ = interaction of the i^{th} body weight class with the k^{th} treatment.

$(ST)ijk$ = interaction of the k^{th} treatment with the j^{th} strain of the i^{th} body weight class

$\varepsilon ijkl$ = random error associated with individual replicates, $l = 1,2,3$

Variances were defined as: $Var(Bi) = \sigma^2_B$, $Var(Sij) = \sigma^2_{S:B}$, $Var(Tk) = \sigma^2_t$

$Var(BT) = \sigma^2_{BT}$, $Var(ST)ijk = \sigma^2_{ST:B}$, $Var(\varepsilon ijkl) = \sigma^2_e$

The expectations of the mean squares are as follows:

Source	E(MS)
Body Weights (B)	$\sigma^2_e + 6\sigma^2_{S:B} + k_3\sigma^2_B$
Stocks Within Body Weight (S/B)	$\sigma^2_e + 6\sigma^2_{S:B}$
Treatments (Trt.)	$\sigma^2_e + 5\sigma^2_t + 3\sigma^2_{ST:B}$
Body Weight x Treatment (B x Trt.)	$\sigma^2_e + k_1\sigma^2_{BT} + 3\sigma^2_{ST:B}$
Stocks x Treatment Within Body Weights (ST/B)	$\sigma^2_e + 3\sigma^2_{ST:B}$
Remainder	σ^2_e

The necessary components of variance ($\sigma^2_{S:B}$, $\sigma^2_{ST:B}$) were obtained by equating the mean squares calculated from the analysis of variance to their respective expectations. F-test was used to test for significance of effects using the appropriate error line according to the above expectations.

4.3.2. RESULTS

The effect of stock on the traits and the means for the traits classified according to treatment and body weight classes appear in Table 4.3.1 and 4.3.2 respectively. The least-squares analysis of variance for model 4.3.1 may be found in Table 4.3.3. A more detailed

TABLE 4.3.1 Showing Stock Effects on the Traits

Stock	TRAIT								
	HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
1	274.0	72.3	58.9	493.6	44.3	117.2	343.9	93.4	149.7
2	243.9	67.9	61.8	479.2	46.2	128.6	359.0	85.4	120.2
3	281.5	72.9	59.6	525.6	46.3	119.9	360.6	94.8	165.0
4	275.7	71.5	61.5	537.9	47.6	123.4	370.2	96.9	167.7
5	262.5	68.6	62.2	519.1	44.4	116.0	348.6	95.5	170.5
6	267.7	71.0	61.6	526.6	46.0	122.1	357.8	92.4	168.8
7	277.9	72.4	61.9	541.1	47.9	124.9	373.5	95.5	167.6
8	257.4	67.4	62.3	513.3	44.6	116.5	347.6	95.1	165.7
9	288.6	74.6	62.3	571.3	49.8	128.7	383.9	96.2	187.4
10	283.0	75.3	58.0	475.4	42.1	111.6	328.7	90.3	146.7
11	291.5	76.2	61.2	516.0	44.6	116.2	346.2	95.1	169.8
12	268.2	72.4	57.5	447.9	42.4	114.3	332.4	89.9	115.5
13	293.0	77.0	59.2	501.4	44.4	117.0	346.2	92.7	155.2
14	253.6	67.7	59.3	446.5	40.7	109.2	320.7	91.0	125.8
15	285.6	75.8	59.5	495.1	44.2	117.2	344.0	92.4	151.1
16	271.5	72.1	60.0	475.7	42.3	112.2	332.5	90.3	143.2
17	295.6	77.3	59.9	523.8	44.5	116.5	346.5	95.8	177.3

TABLE 4.3.2. Means of Traits by Body Weight and Treatment

Trait	Body Weight Class	TREATMENT Breeder's	RSET
HHP	Light	283.1	277.3
	Heavy	269.3	270.5
HDP	Light	75.1	73.4
	Heavy	71.3	70.6
FPB	Light	43.4	42.8
	Heavy	46.2	46.5
FBD	Light	115.1	113.4
	Heavy	122.5	121.3
EGGVAL	Light	486.0	484.5
	Heavy	518.2	528.0
FUDVAL	Light	336.7	337.6
	Heavy	357.3	363.9
EGGWT	Light	59.1	59.7
	Heavy	61.2	61.5
LIVABL	Light	92.6	91.7
	Heavy	93.3	94.5
IOFC	Light	149.3	146.9
	Heavy	160.9	164.1

TABLE 4.3.3 Combined Least Squares Analysis of Variance for all Traits

Source	D.F.	MEAN SQUARES								
		HHP	HDP	FPB	FBD	EGGVAL	FUDVAL	EW	LIVABL	IOFC
Body wt.	1	2720.7	267.6*	261.1**	1492.7**	36436.8*	13961.8**	100.5**	74.8*	5288.8
S/BWt	15	1191.9**	49.4**	16.9**	104.1**	4667.9**	836.4**	8.63**	52.6**	2285.9**
Trt	1	131.3	34.3**	0.97	52.2**	435.8	354.7*	5.80*	0.74	4.17
Body wt x Trt	1	317.7	6.03	4.43	2.73	809.9	204.7	0.36	28.5	200.3
S x T/Bwt	15	80.8	3.94	0.92	5.29	187.1	56.1	0.98**	9.18	149.9
Remainder	68	86.8	2.85	1.85	3.63	317.0	116.6	0.34	20.2	179.2

* $P < 0.05$

** $P < 0.01$

table, showing the means for the traits by stock and treatment within body weight classes are given in Appendix A. The only consistent trend is the highly significant ($P < 0.01$) differences among stocks in all the traits (Table 4.3.1). Body weight had no effect on egg number, mortality and the most important trait, IOFC; and had only a slight effect on rate of lay (HDP) and EGGVAL, the lighter white egg stocks having higher rate but lower EGGVAL than the heavier brown egg layers. However, the heavier stocks ate significantly more food (FPB, FBD, FUDVAL) and laid heavier eggs than the white egg stocks.

The effect of the treatment on the various traits was variable. Stocks receiving 'breeder's option' laid at a higher rate, but also ate food at a higher rate (FBD) than those on the RSET regimes. However, replicates on the RSET treatment laid heavier eggs and were also slightly ($P < 0.05$) more expensive to feed (FUDVAL). Treatment imposed had no effect on the rest of the traits including profitability (IOFC).

The only significant body weight x treatment interaction was in respect of FPB, but disappeared when the non-significant ST/BW1 interactions were pooled into the residual to increase the power of the test. Similar to the above, stocks x treatment interactions are unimportant for all the traits except egg weight (EW).

The genetic correlations between the performance of the replicates of the stocks on the 2 treatments are given in Table 4.3.4 below for all the traits. They are all high and it is worth noting that even r_g for EW in which significant interaction was found, is rather high.

TABLE 4.3.4 Genetic correlations between performances on the treatments for the traits

Trait	HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
r_g	1.01	0.96	0.85	1.06	1.14	0.97	1.20	>1.0	1.02

4.3.3 DISCUSSION

No evidence appears in the literature of a similar experiment in which management practices of breeders have been tested against some optimal conditions. However, the lack of any significant treatment effect on economic performance (IOFC) observed in the trial would suggest that the RSET conditions have been as effective as those suggested by the breeders. The generally high genetic correlations for all the traits would indicate that any gains being made by the breeders are being wholly realised under conditions considered optimum by farmers. The claim of some breeders that the test conditions do not bring out the best from all stocks has not been supported by the results of this trial based on the most important trait, IOFC.

The validity of any comparisons among stocks is probably arguable as stocks were confounded by management practices selected by the breeders. In practice, however, if these were the conditions likely to be recommended alongside purchases of the stocks, then comparisons among stocks would be valid. In that case, the highly significant differences among stocks for all the traits coupled with the general lack of interactions suggest that farmers can enhance their profits by prudent choice of stock. The choice of management condition to employ should be accorded secondary importance, as it appears clear that the profitability of a given poor stock may not be necessarily enhanced even if a farmer were to follow strictly all the details of management suggested by the breeder.

4.4 STOCK x FIBRE LEVEL INTERACTIONS

It would be beneficial, both from the point of view of human nutrition and cost of production of poultry products, to cut down on whole grain sources of energy in poultry diets. The possible substitutes are likely to be more fibrous than would normally be considered suitable for laying hens. However, as established in the previous section (4.3), slight departures from the usual management conditions of a particular stock are unlikely to be detrimental to profitability.

The performance of six commercial laying stocks fed a highly fibrous diet was compared with that of control groups fed the usual RSET diet.

4.4.1 MATERIALS AND METHODS

The formulation and the calculated analysis of the trial diet appear in Table 4.4.1 and may be compared with the RSET diet (Table 4.1) especially regarding fibre and energy levels. Crude fibre level was twice as high in the trial diet as in the RSET diet, being 7% and 3.5% respectively. Energy and protein levels varied between the two diets.

TABLE 4.4.1 Experimental (High Fibre) Diet Formulation

Ingredient	% Inclusion		
Wheat bran	19.9	Calculated Analyses	
Distillers grains	14.9		
Barley	10.0	Crude Protein %	16.5
Oats	10.0	Fibre %	6.8
Grass meal	10.0	Oil %	9.7
Grain screenings	7.5	Lysine %	0.76
Colfat 60 (Prepared Tallow)	7.5	Methionine %	0.26
		Phosphorus %	0.56
Biscuit meal	5.0	Available Phosphorus%	0.32
White fishmeal	5.0	Calcium	3.44
Limestone	6.7	M.E. (Kcab/kg)	2097.0
Feather/Offal/Blood	2.5		
Mineral/Vitamin mix	0.5		
Salt	0.2		
Granite grit	0.3		

Laying Stocks

Three brown egg laying stocks, two white and a tinted egg laying stock classified as light bodied, were involved in the trial. Initially, three replicates of each of these stocks at point of lay, were placed on each treatment. However, during the 8th month of lay, it became necessary to eliminate one replicate of each white stock x treatment group from the trial due to water shortage.

Statistical model

The mixed model underlying the least square analysis of the data using Harvey's (1970) programme follows:

$$Yijkl = \mu + Bi + Sij + Tk + (BT)ik + (ST)ijk + \varepsilon ijkl$$

$i = 1, \ldots.2$ $\quad$ $k = 1, \ldots.2$

$j(i=1) = 1, \ldots.3$ $\quad$ $j(i=2) = 1, \ldots.3$

Definitions of terms in the model as well as variances of effects are exactly the same as for Section 4.3.1. The expectations of the mean squares also do not change.

4.4.2 RESULTS

Table 4.4.2 shows the importance of the various sources of variation affecting each trait. The means for the body weight classes are given in Table 4.4.3. Significant differences in the body weight classes appear only in the food consumption characters (FPB, FBD), the heavier brown layers consuming more and hence being the more expensive to feed (FUDVAL). The egg output (HHP x EW) of the browns, however, more than compensates for the higher feed intake and are therefore as profitable (IOFC) as the lighter stocks. Means showing the effects of dietary fibre on the various traits are also given in Table 4.4.3. The diets

offered have had no effect on egg production characters (HHP, HDP, EW) including EGGVAL. However, replicates receiving the low energy high fibre diet ate significantly more (FBD, FPB) than those on control diet and this has resulted in the rather higher cost of feeding them (FUDVAL). Effect of fibre level in the diet is also highly significant ($P < 0.01$) in IOFC, the RSET replicates returning higher profits than those on the high fibre diet.

The means for the traits by stocks and diets appear in Table 4.4.4. With the exception of livability, differences among stocks are highly significant ($P < 0.01$) for the rest of the traits. The effect of fibre level in the diet appears to be similar on all the stocks, as indicated by the general lack of significant stock x dietary fibre level interaction, even despite the strong differences in some traits among stocks and between treatments.

According to Table 4.4.5 the genetic correlation between replicate performances of the stocks in the two diets for all the traits, are rather high.

TABLE 4.4.5 Genetic Correlation between Performance of Replicates on Different Diets for all Traits

Trait	HHP	HDP	FPB	FBD	EGGVAL	FUDVAL	EW	LIVABL	IOFC
rg	1.07	0.86	1.47	1.17	1.01	1.34	1.00	0.81	0.83

TABLE 4.4.2 Analysis of Variance for all Traits

Source	df	MEAN SQUARES								
		HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
Body weight (BWT)	1	35.6	6.93	0.21	8881.1	177.6**	770.1*	20819.4**	149.4	2505.0
Stocks within body weight (S:B)	4	522.8**	20.0**	8.58**	3814.4**	5.32**	36.6**	628.2**	20.5	2511.1
Fibre levels (Trt)	1	61.8	10.1	0.23	31.1	198.0**	1226.0**	21284.2**	53.1	22942.7
Bwt x Trt	1	130.2	9.4	1.33	570.5	3.31	19.2*	687.4*	22.9	5.44
Stocks x Trt within Bwt	4	42.0	3.9	0.39	332.5	0.48	2.13	60.2	14.0	369.8
Remainder	18	57.6	2.5	0.40	349.9	1.15	4.47	124.3	13.2	131.0

TABLE 4.4.3 Means of Traits by Body Weight and Fibre Level

Trait	Body Weight	FIBRE LEVEL Low (RSET)	High	Body Weight Mean
HHP	Light	284.5	277.3	280.9
	Heavy	282.5	283.8	283.2
Fibre level means:		283.5	280.6	
HDP	Light	75.8	73.5	74.7
	Heavy	73.7	73.7	73.7
Fibre level means:		74.8	73.6	
FPB	Light	43.3	47.8	45.6
	Heavy	47.6	53.5	50.6
Fibre level means:		45.5	50.7	
FBD	Light	115.4	126.8	121.1
	Heavy	124.1	138.8	131.5
Fibre level means:		119.8	132.8	
FUDVAL	Light	459.6	504.2	481.9
	Heavy	503.6	567.8	535.7
Fibre level means:		481.6	536.0	
EW	Light	60.4	60.7	60.6
	Heavy	61.0	60.4	60.7
Fibre level means:		60.7	60.6	
EGGVAL	Light	646.8	635.8	641.3
	Heavy	673.0	679.8	676.4
Fibre level means:		659.9	657.8	
LIVABL	Light	88.6	93.1	90.9
	Heavy	94.9	95.8	95.4
Fibre level means:		91.8	94.5	
IOFC	Light	187.1	131.5	159.3
	Heavy	169.3	112.0	140.7
Fibre level means:		178.2	121.8	

TABLE 4.4.4 Means for the Traits by Fibre Level and Stocks Within Body Weight Classes.

Body Weight	Stock	Fibre Level	TRAIT								
			HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
Light	1	RSET	279.5	76.4	60.1	634.7	43.6	119.1	462.3	82.3	172.4
		High	269.7	71.7	61.4	623.6	49.0	130.2	516.8	92.7	106.8
	Stock Mean:		274.6	74.1	60.8	629.2	46.3	124.7	489.6	87.5	139.6
	2	RSET	276.4	73.8	60.4	625.5	41.8	111.5	444.8	90.6	180.7
		High	274.5	72.9	60.2	622.8	45.7	121.5	481.0	92.7	141.8
	Stock Mean:		275.5	73.4	60.3	624.2	43.8	116.5	462.9	91.7	161.3
	3	RSET	297.7	77.2	60.2	680.1	44.3	115.1	471.6	92.7	208.5
		High	287.7	75.8	60.5	660.9	48.9	128.8	514.9	93.7	146.0
	Stock Mean:		292.8	76.5	60.4	670.5	46.6	122.0	493.3	93.2	177.3
Heavy	4	RSET	289.2	75.4	58.8	673.6	47.6	124.2	503.8	94.4	169.8
		High	283.7	73.6	58.8	661.4	53.6	139.0	569.3	95.1	92.1
	Stock Mean:		286.5	74.5	58.8	667.5	50.6	131.6	536.6	94.8	131.0
	5	RSET	268.0	70.8	61.6	639.1	46.9	123.9	496.1	93.7	143.0
		High	275.3	71.6	61.2	666.7	53.5	139.0	564.5	95.8	102.2
	Stock Mean:		271.7	71.2	61.4	652.9	50.2	131.5	530.3	94.8	122.6
	6	RSET	290.2	74.9	62.5	706.1	48.1	124.3	511.0	96.5	195.1
		High	292.4	75.8	61.2	711.4	53.4	138.5	569.6	96.5	141.8
	Stock Mean:		291.3	75.4	61.9	708.9	50.8	131.4	540.3	96.5	168.5

4.4.3 DISCUSSION

An interesting aspect of the results concern the fact that the low energy, high fibre diet supported a similar level of egg production as did the RSETcontrol diet. This was true of all the stocks. Due to the low energetic content of the more fibrous diet, the stocks had to eat more in order to achieve similar levels of production. Rather against expectation, the low energy diet was as expensive as the control, since the by-products used were not cheaply available in the United Kingdom. Thus the egg income over feed cost favoured the control diet. The result on IOFC, would thus be variable depending mainly upon the country as the grain by-products are likely to be cheaper than the whole grains in some countries.

Properly conducted experiments aimed at investigating the effect of fibre on different genotypes in poultry are lacking especially in the developed world. This could be due to the fact that cellulose, which represents much of the fibre in feeds is considered unessential in the nutrition of the chicken (Scott, Nesheim and Young, 1969). The inference from the present report does not wholly subscribe to this idea, and countries in which fibrous diets are abundantly and cheaply available may expect to maintain egg output, by using fibre sparingly.

4.5 STOCK x PROTEIN LEVEL INTERACTION

Another dietary constituent being manipulated to decrease cost of production is the protein. It is necessary thus to determine whether all the improvements being made by breeders using fixed dietary proteins, are being realized by producers who feed different levels to the stocks. In the experiment to be described, three commercial stocks fed two different levels of protein were involved.

4.5.1 MATERIALS AND METHODS

The diets fed were isocaloric and differed mainly in their protein contents, being 18% in the experimental diet and the usual 15.7% of the RSET diet. The average cost of the diets over the laying period were £112.39 and £105.64 for the 18% and RSET diets respectively.

Stock

Only 3 brown egg laying, commercial stocks were involved in this trial. As usual three replicates of each, consisting of pullets, at point of lay were placed on each treatment.

Statistical Model

$$Yijk = \mu + Si + Tj + (ST)ij + \varepsilon ijk$$

where $i = 1, \ldots 3$; $j = 1, \ldots 2$; $k = 1, \ldots 3$

Definitions of the various effects are similar to the previous sections, the exception being the Si effects which are not nested within body weight (Bi) groups since all stock (Si) are of similar body weights. Variance of the Si and (ST)ij effects are thus σ^2_S and σ^2_{ST} respectively, whilst that of $\varepsilon ijk = \sigma^2_e$ as usual. Expectations of the mean squares from which the variance components are obtained are:

Source	E(MS)
Stock (S)	$\sigma_e^2 + 6\sigma_S^2$
Protein level (Trt)	$\sigma_e^2 + 18\sigma_T^2 + 3\sigma_{ST}^2$
Protein level x Stock (SxT)	$\sigma_e^2 + 3\sigma_{ST}^2$
Remainder (R)	σ_e^2

4.5.2. RESULTS

Table 4.5.1 shows the means for all the traits regarding the effects of stocks, dietary protein levels and stocks x protein level interactions. The results of the least squares analysis of variance appear in Table 4.5.2 for all the traits. Except for livability, the effect of stocks on all the traits is significant, even though not highly so in IOFC where only one stock was markedly superior to the rest.

Replicates receiving the higher protein diet show significantly higher rate of lay and EGGVAL, are more expensive to feed (FUDVAL) and on the whole, returned lower profits (IOFC). Dietary protein level shows no significant influence on feed consumption, egg weight, livability and egg numbers. Stock x protein level interactions never reaches statistical significance in any of the traits. Genetic correlations between performance of replicates of the same stock on the two protein diets appear in Table 4.5.3 below.

TABLE 4.5.3 Genetic Correlations between replicates for all the Traits

Trait	HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
rg	1.08	1.14	0.52	1.02	1.10	1.16	1.08	>1.0	1.23

The genetic correlations are all very high for all but EW. The estimate for this trait barely increased from 0.53 to 0.58 when the correction for differences in variance among stocks in the two protein diets was applied (Dickerson, 1962).

TABLE 4.5.1 Showing Effects of Stock and Dietary Protein Level on the Traits Studied.

Stock	Protein level	TRAIT HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
1	RSET	287.4	73.9	62.1	680.8	47.5	122.3	506.3	95.8	174.3
	High	289.5	75.3	61.9	685.5	47.0	122.2	541.2	95.8	144.3
Stock means:		288.4	74.6	62.0	683.2	47.1	122.3	523.7	95.8	159.3
2	RSET	280.0	72.4	60.8	661.4	45.0	116.4	477.0	95.8	184.4
	High	287.5	74.0	61.1	686.8	44.9	115.6	514.9	97.2	171.9
Stock means:		283.8	73.2	61.0	674.1	45.0	116.0	495.9	96.5	178.2
3	RSET	264.9	68.7	61.5	623.7	44.4	115.1	466.7	93.1	157.0
	High	271.2	70.7	63.0	650.9	43.9	114.5	506.5	92.4	144.4
Stock means:		268.1	69.7	62.3	637.3	44.2	114.8	486.6	92.8	150.7
Fibre Level Means:										
	RSET	277.4	71.7	61.5	655.3	45.6	117.9	483.3	94.9	171.9
	High	282.7	73.3	62.0	674.4	45.3	117.4	520.9	95.1	153.5

TABLE 4.5.2 Analysis of Variance for all Traits

Source	df	MEAN SQUARES								
		HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
Stock	2	685.8**	37.4**	2.94**	3535.0**	15.8**	95.7**	2239.3**	24.8	1178.1*
Protein levels	1	126.4	12.1**	1.23	1645.6**	0.61	1.22	6339.1**	0.22	1525.1*
Stock x Protein Levels	2	11.9	0.17	1.14	235.7	0.07	0.16	9.16	1.62	157.2
Remainder	12	36.0	2.34	0.32	269.6	0.75	6.21	88.2	9.30	244.7

* P < 0.05; ** P < 0.01

4.5.3 DISCUSSION

Harms and Waldroup (1962) observed significant strain x protein level interaction in the rate of lay, body and egg weights in a study involving two strains. In a latter study involving six stocks, stocks x protein level interaction regarding egg production and body weight were reported to be significant but not egg weight (Harms, Damron and Waldroup, 1966). In both studies the protein levels ranged from 11% to 17%, and both White Leghorn and heavy-bodied New Hampshire stocks were involved. Interactions are therefore not unexpected as the lower protein levels could not furnish adequate amounts of the essential amino acids the requirements of which are reported to vary among genotypes (Nesheim and Hutt, 1962; Harms *et al.*, 1967; and Nesheim, 1968). Marks *et al.* (1969), on the other hand, found that stock x protein level interaction was not significant for any of the traits studied. They, however, reported higher egg production and weight on the higher protein diets.

In the present study, differences in the protein levels and hence essential amino acids were not large enough to result in interactions. The low genetic correlation for EW could have resulted from the larger eggs laid by replicates of stock 3 on the higher protein diet. Under the conditions of this trial, the cost of the higher protein diet makes it unprofitable to feed to layers despite the higher rate of lay and egg income (EGGVAL) attainable on such diets. The lack of significant interactions and the generally high estimates of genetic correlations indicate that breeders may expect to "carry over" any gains being made on the lower, cheaper protein diet.

4.6 EFFECT OF REARING LIGHTING AND FEEDING REGIME ON LAYING PERFORMANCE OF DIFFERENT EGG LAYING STOCKS

The main purpose in rearing replacement pullets is to produce hens with a potential for the highest possible rate of sustained egg production. The lighting as well as feeding programmes not only influence the rate of attainment of sexual maturity, but also egg size and number as these are correlated with sexual maturity. Since these correlations differ among populations, treatments that affect sexual maturity would have variable influence on egg production of different populations.

The effect of two different lighting and feeding programmes during rearing on 8 different commercial egg-laying stocks are reported on in this chapter.

4.6.1 MATERIALS AND METHODS

The Treatments

The 2 lighting programmes employed were:

(i) 3 days at 23½ hours-light, then constant 9 hour daylength to 18 weeks of age (i.e. constant light regime).

(ii) 3 days at 23½ hours light, 4 days at 21 hours light, then daylength was reduced by 2 hours a week for each of the next 2 weeks. Daylength was then decreased by an hour each week to give minimum of 9 hours at 11 weeks of age (i.e. step down light pattern).

The brooder house was divided into 2 halves in order that the lighting for each could be independently controlled.

The usual Random Sample Test diets were fed to all stocks from day old till the end of the laying period at 72 weeks of age. However, during the rearing period (3 days - 18 weeks of age), 2 feeding programmes

were employed within each half of the brooder house to 2 replicates of each stock. The programmes were:

(i) Ad libitum feeding throughout rearing.

(ii) Restricted feeding to give an 18 week body weight which was 15% below the ad libitum fed birds for brown stocks and 20% below for white stocks. A predetermined feeding plan was followed for each stock in order to achieve these targets and fortnightly adjustments based upon check weighings were often made. The restricted regime was started in week 7.

Stocks

8 commercial egg laying stocks comprising equal numbers of light and heavy-bodied types were involved in the study. There were 150 day-old chicks per each treatment-combination for each stock at the brooder house. During the laying period, 3 replicates of each stock were placed from each treatment-combination. Thus there were 12 replicates of each stock altogether all of which received the same diet throughout the 52-weeks laying period.

Statistical Model

$$Yijklm = \mu + Bi + Sij + Lk + Fl + (BL)ik + (BF)il + (SL)ijk + (SF)ijl + \varepsilon ijklm \quad \ldots\ 4.6.1$$

$i = 1, \ldots 2;\ j(i=1) = 1, \ldots 4;\ j(i=2) = 1, \ldots 4;\ k = 1, \ldots 2;$

$l = 1, \ldots 2;\ m = 1, \ldots 3.$

where:

$Yijklm$ = mean of the m^{th} replicate on the l^{th} feeding regime under the k^{th} light pattern of the j^{th} stock nested within the i^{th} body weight class.

μ = overall mean

Bi = fixed effect of the i^{th} body weight class

Sij = random effect of the j^{th} stock within the i^{th} body weight class

Lk = fixed effect of the k^{th} light pattern

Fl = fixed effect of the l^{th} feeding regime

(BL)ik = interaction effect of the i^{th} body weight class with the k^{th} light pattern

(BF)il = interaction effect of the i^{th} body weight class with the l^{th} feeding regime

(SL)ijk = interaction effect of the k^{th} light pattern with the j^{th} stock nested within the i^{th} body weight class

(SF)ijl = interaction effect of the l^{th} feeding regime with the j^{th} stock nested within the i^{th} body weight class

εijklm = random error associated with the mean of each replicate

Variance for effects are as follows:

$$Bi = \sigma^2_B, \quad Sij = \sigma^2_{S:B}, \quad Lk = \sigma^2_k, \quad Fl = \sigma^2_L, \quad (BL)ik = \sigma^2_{BL},$$

$$(BF)il = \sigma^2_{BF}, \quad (SL)ijk = \sigma^2_{SL:B}, \quad (SF)ijl = \sigma^2_{SF:B}, \quad \varepsilon ijklm = \sigma^2_e$$

The expectations of the mean squares are given below.

Source	MS	E(MS)
Body weight	MSB	$\sigma^2_e + 12\sigma^2_{S:B} + 48\sigma^2_B$
Stock within body weight	MSS	$\sigma^2_e + 12\sigma^2_{S:B}$
Light pattern	MSL	$\sigma^2_e + 6\sigma^2_{SL:B} + 48\sigma^2_L$
Feeding Regime	MSF	$\sigma^2_e + 6\sigma^2_{SF:B} + 48\sigma^2_F$
Bodyweight x Feeding Regime	MSBF	$\sigma^2_e + 6\sigma^2_{SF:B} + 48\sigma^2_{BF}$

Source	MS	E(MS)
Bodyweight x Light Pattern	MSBL	$\sigma^2_e + 6\sigma^2_{SL:B} + 48\sigma^2_{BL}$
Stock x Feeding Regime	MSSF	$\sigma^2_e + 6\sigma^2_{SF:B}$
Stock x Light Pattern	MSSL	$\sigma^2_e + 6\sigma^2_{SL:B}$
Between Replicates	MSE	σ^2_e
(Remainder)		

The variance components were obtained by equating the mean squares to their respective expectation.

The model being considered, 4.6.1, did not fall into either of the six types of mixed models for which Harvey's (1970) programme was especially written to complete. It was therefore broken up into the following models and the results of their analyses were synthesized to give model 4.6.1. Using the same notations as above, the models follow as:

$$Yijklm = \mu + Bi + Sij + Lk + (BL)ik + (SL)ijk + Fl + \varepsilon ijklm \quad \ldots 4.6.2$$

$$Yijklm = \mu + Bi + Sij + Fl + (BF)il + (SF)ijl + Lk + \varepsilon ijklm \quad \ldots 4.6.3$$

The difference between the 2 models is that the two interaction effects differ. By subtracting one from the other, all the results needed to complete analysis of model 4.6.1 are obtained.

The main interest in the study was to detect interactions involving stocks. Even so, a second order interaction (stock x light x feeding regimes) was ignored in the initial analysis and would have been fitted if the two-factor interactions involving stocks were found significant.

4.6.2 RESULTS

A summary of the results of this section of the thesis appear in Appendix B, from which extracts have been prepared for purposes of discussing the various effects. Bodyweight had no effect on any of the traits according to Table 4.6.2 and the results of the least squares analysis of variance presented in Table 4.6.3. However, small-bodied stocks laid slightly heavier eggs when fed ad libitum than when placed on the restricted feeding regime, whereas the reverse was true of two of the heavy-bodied stocks (Table 4.6.4). Also, the daily food consumption of the stocks when exposed to any of the light patterns depended upon their bodyweights (Table 4.6.5).

Differences among stocks were consistently highly significant regarding all the traits (Table 4.6.2).

TABLE 4.6.2 Effect of body weight and stock on economic traits of poultry

Body Weight	Stock	TRAIT HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
Low	1	253.7	73.9	58.4	456.8	39.3	114.6	332.4	86.5	124.4
	2	279.7	78.7	59.0	516.2	41.3	116.2	350.6	95.3	165.7
	3	265.2	75.2	59.3	491.4	41.2	116.8	349.4	93.6	142.0
	4	271.4	76.6	60.8	514.6	41.2	116.0	347.0	95.3	167.6
Mean (Low):		267.5	76.1	59.4	494.8	40.8	115.9	344.9	92.7	149.9
High	5	254.2	71.7	59.8	505.6	41.0	115.6	347.1	93.6	158.5
	6	257.6	72.4	60.3	518.6	42.0	118.0	355.0	93.9	163.6
	7	251.3	71.1	60.8	513.3	41.2	116.7	348.9	94.6	164.4
	8	273.9	76.1	59.9	552.2	43.6	120.9	368.6	96.7	183.6
Mean (High):		259.3	72.8	60.2	522.4	42.0	117.8	354.9	94.7	167.5

Noteworthy is the fact that a heavy-bodied stock (Stock 8) returned the highest profit (IOFC), whilst a low-bodied stock was the least profitable (Stock 1).

TABLE 4.6.3 Analysis of variance for all the economic traits studied

		MEAN SQUARES FOR TRAITS								
Source	df	HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
Body weight (Bwt)	1	1622.8	255.9	15.8	18376.2	34.7	87.0	2441.8	100.9	7420.8
Stocks/Bwt (S:B)	6	1335.6**	54.7**	7.5**	7146.9**	13.2**	37.7**	993.1**	118.4**	3276.2**
Light Pattern (L)	1	1982.9**	107.1**	30.2**	139.9	0.79	1.3	81.8	20.4	7.8
Feeding Regime (F)	1	18.8	14.2	1.9	25.0	9.6*	23.8*	749.6	10.0	501.0
Bwt x F	1	122.2	9.4	3.6*	5.6	1.1	11.1	56.1	1.2	26.2
Bwt x L	1	46.9	9.1	0.01	750.0	2.9	42.3*	217.5	1.1	159.8
S x F/Bwt	6	138.0	6.3	0.33	444.4	1.3	3.2	130.7	10.0	197.1
S x L/Bwt	6	21.0	0.58	0.63	123.9	1.3	5.6	108.1	9.9	123.8
Remainder	72	79.5	3.6	0.58	296.6	0.9	2.8	57.4	16.6	172.3

TABLE 4.6.4. Effects of rearing feeding regime and stock x feeding regime interaction on economic traits of poultry.

Stock	Feed* Regime	TRAIT HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
1	F	248.3	72.9	58.6	448.6	39.2	115.2	331.9	85.8	116.8
	R	259.1	74.9	58.2	464.9	39.4	113.9	332.9	87.2	132.1
2	F	279.5	78.0	59.2	517.4	42.0	117.2	357.7	95.8	159.7
	R	280.0	79.4	58.8	515.1	40.7	115.2	343.5	94.8	171.6
3	F	260.2	73.8	59.8	489.1	41.4	117.3	349.3	93.1	139.8
	R	270.2	76.7	58.8	493.7	41.0	116.3	349.5	94.1	144.2
4	F	275.6	76.9	61.2	526.9	42.1	117.2	354.7	96.9	172.2
	R	267.0	76.2	60.4	502.3	40.3	114.9	339.3	93.8	163.1
5	F	253.7	71.5	59.9	505.1	41.3	116.1	349.7	93.8	155.4
	R	254.8	72.0	59.7	506.2	40.8	115.0	344.6	93.4	159.6
6	F	257.6	72.2	60.3	518.4	42.3	118.6	357.9	93.8	160.5
	R	257.6	72.6	60.2	518.8	41.7	117.4	352.1	94.1	166.7
7	F	252.0	70.4	60.6	514.1	41.5	115.8	351.6	96.2	162.6
	R	250.6	71.9	61.0	512.5	41.0	117.5	346.2	93.1	166.3
8	F	276.6	77.0	59.7	553.2	43.6	121.3	368.6	96.9	184.7
	R	271.3	75.2	60.1	551.1	43.5	120.6	368.6	96.5	182.6
Mean	F	262.9	74.1	59.9	509.1	41.7	117.3	352.6	94.0	156.4
	R	263.8	74.8	59.6	508.1	41.0	116.3	347.1	93.4	161.0

* F = ad libitum feeding regime
R = restricted feeding regime

TABLE 4.6.5 Showing importance of rearing light and stock x light pattern interactions on traits studied

Stock	Light* Pattern	TRAIT HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
1	C	257.3	74.2	57.9	454.0	39.5	113.8	334.0	87.8	120.0
	S	250.1	73.6	58.8	459.5	39.1	115.3	330.7	85.1	128.8
2	C	284.4	79.5	58.7	518.6	41.6	116.2	353.1	96.2	165.5
	S	275.1	77.8	59.3	513.8	41.1	116.2	348.0	94.4	165.8
3	C	269.2	76.1	58.4	486.6	41.1	116.2	348.4	93.4	138.2
	S	261.1	74.3	60.1	496.2	41.2	117.4	350.3	93.7	145.9
4	C	274.4	77.5	60.1	513.4	40.4	114.2	341.5	95.5	172.0
	S	268.3	75.6	61.5	515.7	41.9	117.8	352.5	95.1	163.2
5	C	261.1	72.9	59.5	513.5	41.6	116.0	352.5	95.1	161.0
	S	247.4	70.5	60.0	497.7	40.4	115.2	341.8	92.0	155.9
6	C	263.5	73.9	59.6	522.8	42.3	118.5	357.8	93.7	165.0
	S	251.6	70.8	60.8	514.3	41.7	117.5	352.2	94.1	162.1
7	C	254.1	72.5	60.1	513.0	41.3	118.0	349.8	93.7	163.2
	S	248.5	69.7	61.5	513.6	41.1	115.3	348.0	95.5	165.6
8	C	279.3	77.3	59.3	556.3	43.6	120.9	369.2	97.6	187.1
	S	268.5	74.9	60.5	547.9	43.4	121.0	367.9	95.8	180.0
Mean	C	267.9	75.5	59.2	509.8	41.4	116.7	350.8	94.1	159.0
	S	258.8	73.4	60.3	507.4	41.2	117.0	348.9	93.2	158.4

* C = constant lighting during rearing
S = step down lighting during rearing

Rearing light pattern significantly influenced HHP, HDP and EW. Replicates on constant light pattern laid more eggs at a higher rate, but those on the step down pattern laid heavier eggs (Table 4.6.5). No other traits were, however, significantly affected by the rearing light patterns.

Apart from FPB and FBD, rearing feeding regime had no significant effect on any of the traits studied. Replicates on the ad libitum regime tended to eat more than those on the restricted regime.

Of course, none of the interactions involving stocks (i.e. stock x feed regime, stock x light pattern) was significant. The genetic correlations between performance of replicates on different light or feed regimes were all high (Table 4.6.6).

TABLE 4.6.6 Genetic Correlations between performances on different light and feeding regimes

Trait	HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
rg^{1}_{S-L}	1.10	1.14	0.99	1.05	0.93	0.86	0.90	1.15	1.03
rg^{2}_{S-F}	0.91	0.91	1.08	0.96	0.93	0.98	0.86	1.15	0.98

$^{1}rg_{S-L}$ = stock x light pattern interaction

$^{2}rg_{S-F}$ - stock x feeding regime interaction

4.6.3 DISCUSSION

Reports of earlier work regarding main effects of rearing light pattern on egg production, reviewed by Proudfoot and Gowe (1967) were contradictory, probably due to the differences in the experimental design and the fact that single strains were involved in most of them. In the present study, the significant effect of rearing light pattern on egg number, rate of lay and egg weight could have been mediated through age at sexual maturity as decreasing daylength is considered to delay onset of egg production (Card and Nesheim, 1972; Proudfoot and Gowe, 1967). Strain x light pattern interactions have not been studied extensively. One of the few experiments on the subject was conducted by Proudfoot and Gowe (1967). They reported highly significant strain x light pattern interactions for egg production and monetary returns in 2 of the 4 experiments. Thus their results contradict those of the present report. However, an important difference in the designs need be pointed out. Proudfoot and Gowe (1967) employed 4 different light patterns during the rearing period, but confounded their effects with another set of 4 differing patterns during the laying period. A pooling of their results over the 4 experiments would probably have been beneficial as the individual experiments were small. Bowman, Jones and Knight (1964), however, exposed all the differently reared replicates to 2 different laying lighting patterns, but also concluded that light patterns will have to be decided by experimentation for different strains. Their experiment involved stocks of varying body weights. In the present report, body weight x light pattern interaction was found to be significant for food consumption. Thus the interaction reported by Bowman *et al.* (1964) could have, in fact, been due mainly to confounding effect of variable

body weights. McClary (1960), in agreement with the present work, found no stock x lighting pattern interactions. He used 2 growing period light patterns very similar to the present report - constant versus step down patterns - and 16 stocks. The treatments also influenced age at sexual maturity and egg size significantly.

Several reports indicate that rearing feed restrictions delay sexual maturity and increase egg size, rate of lay and monetary returns (Hollands and Gowe, 1965; Strain et al., 1965). Proudfoot and Gowe (1967) did not confirm these results. Most of the workers however, used similar restrictions on all stocks, hence stocks with extreme appetites would be handicapped. In the present, the restriction was related to the appetites of the different stocks which probably explains the lack of significant main effects of feed restriction on the other traits than food consumption. Strain x feeding pattern interactions were of no importance in the trial reported here, though Proudfoot and Gowe (1967) found significant interactions for egg size, sexual maturity and body weight, but not monetary returns nor egg production. Again, this may be explained as being due to the effects of applying the same restrictions to all stocks irrespective of their body weights and appetites.

4.7 DISCUSSION ON THE STOCK x ENVIRONMENT INTERACTION EXPERIMENTS

Like other studies, difficulty has been encountered particularly in the choice of diets that differ only in the nutrient being investigated, the only exception here being the stock x dietary protein experiment where protein level was the main variable. For example in the stock x fibre interaction experiment, fibre, energy and protein levels varied between the 2 diets, so that it is difficult to attribute the results to

the effects of fibre level alone.

The stocks used in these experiments were supposed to be high egg layers. Yet highly consistent differences existed among them for all the traits studied. The extent to which this variation reflects differences in the breeding programmes being employed by the various breeding companies is unclear. What seems clear, however, is the fact that none of the stocks demonstrated any real adaptation to certain specific environmental variables. This view comes from the general lack of stock x nutrition or management interaction in practically all the traits especially profitability. The only apparent unexpected behaviour was by egg weight in 2 of the experiments (Sections 4.3 and 4.6), however these had no economic consequences (i.e. IOFC unaffected) and should therefore not influence breeding programmes. Interactions are more likely if stock and treatment main effects are large (Hull and Gowe, 1962). In the present trials, despite the large main effects due to stocks, the effects of the environmental factors imposed were small, hence the general absence of significant interactions.

5 GENERAL DISCUSSION AND CONCLUSIONS

Due mainly to economic reasons, most poultry breeders carry out their selection programmes under conditions considered to be biologically and economically optimum, and expect gains being made to be transferred to any other environments. In theory, several environmental variables may be identified under nutrition and management. In practice, however, only those which have the most influence on profitability, such as those considered in this study, are likely to be of interest to breeders. Improvement programmes are directed at several traits (the most important of which is saleable egg number) which affect profitability of egg production in poultry. Evidence from this study would indicate that all the traits are not likely to benefit from the same breeding policy. Egg and body weights are highly heritable and may be improved by pureline selection methods. As regards the fertility traits, the overall impression seems to be that whereas egg number may be altered by selection pressures on the moderately heritable sexual maturity, rate of lay may not. Persistency would thus suffer. Even though it has not been possible to determine any maternal effects that may be present in the combined heritability for rate of lay, it appears that non-additive gene action may be present in this trait. Support for this view comes from the rather low purebred-crossbred genetic correlations obtained for this trait in Part II. Rate of lay may thus benefit from some crossbred-based breeding scheme.

The question arises then, as to what testing facilities should be devoted to the pure lines and crossbreds in say, an RRS scheme. It appears, however, that these should be proportional to the weights given each type of information in the selection index combining both. The

relative magnitudes of the weights have been shown in this study (Part II) to depend upon the purebred-crossbred genetic correlations. As these correlations have been found in other studies (e.g. Pirchner and Von Krosigk, 1973) to decline with time, it may be necessary to re-allocate facilities based upon the current values of the purebred-crossbred genetic correlation. In this case, facilities will be adapted gradually towards an eventual RRS scheme in which no purebred information is considered. This approach seems reasonable as it avoids the high cost involved in changing facilities overnight from a complete purebred to a complete RRS scheme.

In the genotype x environment experiments, no stock has demonstrated adaptation to specific environmental conditions. The environment in which improvement programmes are carried out therefore may be varied from time to time, within limits of the levels employed in the present study, depending upon other factors as cost and availability. The main assumption implicit in this recommendation however, is that sires of closed flocks would respond similarly to the treatments considered in this study, as the stocks. Large consistent variations were observed among strains for virtually all the traits and elimination of the low-performing stocks would certainly raise the average levels of performance of egg-laying stocks in the United Kingdom. If the variation is a reflection of differences in the breeding methods among breeders, then the recommendation seems to be that the breeders of the lowly performing stocks need reconsider their methods.

Notwithstanding the results of this study, the existence of genotype x environment interactions could cause problems in evaluating the effectiveness of purebred-crossbred improvement programmes especially

if genotypes are confounded with environments. This could be the case where commercial crossbreds are maintained in different environments from that of the parental purebred strains in a PLS programme. The diagram below (Fig. 5.1) illustrates how genotype x environment interactions could influence the magnitude of the purebred-crossbred genetic correlation.

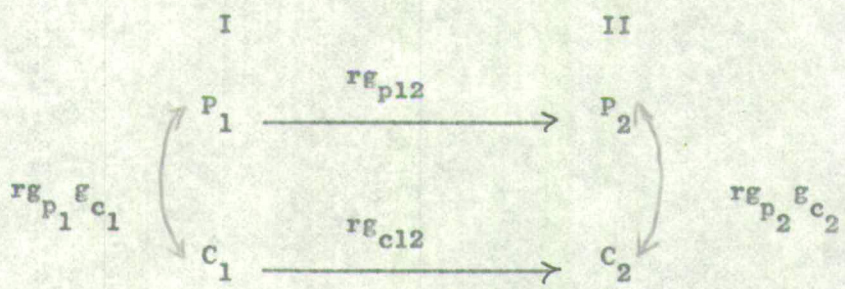

Figure 5.1. Effects of genotype x environment interaction on purebred-crossbred relationships.

In Figure 5.1, P_1 and C_1 are purebred and crossbred genotypes in environment I, whilst P_2 and C_2 are the performances of the same genotypes under environment II. If crossbred performance is desired in environment I, then the relevant purebred-crossbred genetic correlation is $rg_{p_1 g_{c_1}}$. If crossbred performance is required in environment II, then the magnitude of the purebred-crossbred genetic correlation, $rg_{p_2 g_{c_2}}$ would be much lower than $rg_{p_1 g_{c_1}}$. It would then be as follows

$$rg_{p_2 g_{c_2}} = rg_{p_1 g_{c_1}} . rg_{c_{12}} . rg_{p_{12}} . \quad \ldots\ldots 5.1$$

Genotype x environment interaction would act through $rg_{c_{12}}$ and $rg_{p_{12}}$. It is clear from expression 5.1 that if genotype x environment interaction exists it can give a misleading impression of the existence of purebred-

crossbred interactions, and PLS would appear ineffective. If the objective is to find out about the gene action underlying heterosis or about the efficacy of PLS, it may be necessary to evaluate both genotypes within the same environment. On the other hand, if both types of interactions exist, then the breeding programme would be far from simple as it may then be beneficial to test cross progeny under several environments.

APPENDIX A. Showing Means of Traits by Treatment and Stock Within Body Weight Classes

Body Weight	Stock	Trt*	HHP	HDP	T R A I T S EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
HEAVY	1	RSET	271.7	72.8	58.8	492.2	44.0	118.0	339.7	93.7	152.5
		B.O.	276.2	71.8	59.0	495.0	44.5	116.4	348.0	93.1	147.0
	2	RSET	242.7	68.4	62.2	477.9	45.9	129.2	355.3	84.7	122.6
		B.O.	245.2	67.5	61.3	480.5	46.5	127.9	362.7	86.1	117.8
	3	RSET	281.6	73.6	59.1	516.0	46.2	120.8	357.1	92.4	158.9
		B.O.	281.3	72.1	60.1	535.3	46.4	119.0	364.2	98.2	171.1
	4	RSET	279.9	73.0	61.3	543.1	47.5	124.0	367.9	95.1	175.2
		B.O.	271.5	69.9	61.7	532.6	47.7	122.8	372.5	98.6	160.1
	5	RSET	263.6	69.5	61.1	509.0	43.9	115.7	339.2	93.7	169.8
		B.O.	261.5	67.7	63.3	529.2	44.9	116.2	358.0	97.2	171.2
	6	RSET	259.0	69.5	62.1	514.7	45.7	122.7	353.0	92.4	161.7
		B.O.	276.4	72.4	61.2	538.6	46.4	121.5	362.5	92.4	176.1
	7	RSET	278.2	72.7	61.5	531.3	47.9	125.1	370.4	95.1	160.9
		B.O.	277.7	72.1	62.2	551.1	47.9	124.6	376.6	95.8	174.5
	8	RSET	259.2	67.7	62.3	514.3	45.2	118.0	349.0	95.8	165.3
		B.O.	255.5	67.2	62.3	512.3	44.0	114.9	346.3	94.4	166.0
	9	RSET	287.5	74.2	62.1	565.5	49.9	128.6	383.9	96.5	181.6
		B.O.	289.7	75.1	62.6	577.1	49.6	128.7	383.9	95.8	193.2
LIGHT	10	RSET	286.6	76.1	57.6	475.7	42.4	112.2	326.9	92.4	148.8
		B.O.	279.4	74.5	58.5	475.1	41.8	111.0	330.4	88.2	144.7
	11	RSET	292.2	76.9	61.0	516.8	44.9	118.2	348.4	94.4	168.4
		B.O.	290.8	75.5	61.3	515.1	44.2	114.1	344.0	95.8	171.1
	12	RSET	278.5	74.2	57.2	460.3	43.2	115.2	333.9	91.0	126.4
		B.O.	257.9	70.5	57.9	435.4	41.5	113.4	330.9	88.9	104.5
	13	RSET	298.9	78.9	58.4	501.3	44.1	116.4	341.6	92.4	159.7
		B.O.	287.1	75.2	60.0	501.5	44.6	117.5	350.8	93.1	150.7
	14	RSET	253.7	69.0	58.9	443.1	40.8	111.7	318.0	88.9	125.1
		B.O.	253.6	66.6	59.7	449.9	40.6	106.6	323.3	93.1	126.6
	15	RSET	285.9	75.5	59.5	494.2	44.2	116.8	342.6	93.1	151.6
		B.O.	285.2	76.1	59.4	496.1	44.1	117.6	345.3	91.7	150.8
	16	RSET	270.3	71.9	60.1	476.3	43.3	115.1	337.4	91.3	138.9
		B.O.	272.6	72.3	59.9	475.0	41.2	109.3	327.5	88.9	147.5
	17	RSET	299.1	78.0	59.3	520.0	44.5	116.1	344.5	97.2	175.5
		B.O.	292.0	76.6	60.3	527.6	44.5	116.9	348.4	94.4	179.2

* Trt = Treatment

RSET = Random Sample Test Conditions

B.O. = Breeder's Option

APPENDIX B. Effect of body weight, stock, rearing feed and light patterns on traits of poultry

Body Weight	Stock	Trt	T R A I T S HHP	HDP	EW	EGGVAL	FPB	FBD	FUDVAL	LIVABL	IOFC
LIGHT	1	CF	253.5	73.1	58.4	448.3	39.9	115.2	338.4	87.5	109.9
		CR	261.1	75.3	57.5	459.6	39.0	112.5	329.5	88.2	130.1
		SF	243.1	72.7	58.8	448.9	38.5	115.2	325.3	84.0	123.6
		SR	257.0	74.4	58.8	470.2	39.8	115.3	336.2	86.1	134.0
	2	CF	283.2	78.3	59.0	520.3	42.2	116.7	359.2	97.9	161.1
		CR	285.6	80.7	58.4	516.9	41.0	115.7	347.1	94.4	169.8
		SF	275.7	77.6	59.4	514.5	41.8	117.7	356.2	93.7	158.3
		SR	274.4	78.0	59.2	513.2	40.3	114.7	339.8	95.1	173.4
	3	CF	266.7	75.5	59.1	488.5	41.0	116.2	345.1	92.4	143.4
		CR	271.7	76.7	57.8	484.6	41.1	116.1	351.7	94.4	132.9
		SF	253.6	72.0	60.5	489.7	41.7	118.4	353.5	93.7	136.2
		SR	268.6	76.7	59.8	502.7	40.8	116.4	347.2	93.7	155.5
	4	CF	280.4	78.1	60.6	528.2	41.3	114.9	348.9	97.9	179.3
		CR	268.5	76.9	59.5	498.6	39.6	113.5	333.9	93.1	164.7
		SF	271.1	75.7	61.7	525.5	42.8	119.4	360.5	95.8	165.0
		SR	265.5	75.5	61.2	506.0	40.9	116.3	344.6	94.4	161.4
HEAVY	5	CF	264.4	73.4	59.9	520.9	42.1	116.7	357.7	97.2	163.2
		CR	257.7	72.5	59.1	506.2	41.0	115.2	347.3	93.1	158.9
		SF	243.0	69.5	59.9	489.2	40.4	115.5	341.6	90.3	147.6
		SR	251.8	71.5	60.2	506.2	40.5	114.8	341.9	93.7	164.3
	6	CF	265.6	74.3	59.9	527.9	42.8	119.7	362.2	93.1	165.7
		CR	261.5	73.5	59.5	517.7	41.7	117.3	353.4	94.4	164.3
		SF	249.5	70.1	60.7	508.8	41.8	117.4	353.6	94.4	155.2
		SR	253.7	71.6	60.9	519.9	41.6	117.5	350.8	93.7	169.1
	7	CF	253.5	71.2	60.3	512.3	41.8	117.4	354.2	95.8	158.1
		CR	254.7	73.9	59.9	513.6	40.9	118.6	345.3	91.7	168.3
		SF	250.4	69.6	60.9	515.9	41.1	114.2	348.9	96.5	167.0
		SR	246.5	69.8	62.1	511.4	41.1	116.4	347.1	94.4	164.3
	8	CF	278.7	77.6	59.2	553.5	43.9	122.1	370.6	97.2	182.9
		CR	279.9	77.1	59.3	559.2	43.4	119.6	367.7	97.9	191.5
		SF	274.4	76.4	60.1	552.9	43.3	120.5	366.5	96.5	186.4
		SR	262.7	73.3	60.8	543.0	43.6	121.5	369.4	95.1	173.6

APPENDIX C. Purebred-Crossbred Variance and Covariance Components

Trait	Line-Cross	PURE		CROSS		
		σ^2_s	σ^2_e	$\sigma^2_{s'}$	σ^2_e	Covs
SM	CA5	3.45	72.8	3.45	157.6	-1.22
	CA6	6.98	63.2	28.4 (26.9)	19.5	4.55
	FE5	3.99	134.4	3.99+	63.5	-4.16
	FE6	6.46	56.0	43.4 (42.7)	59.9	-8.76
	DE7	1.51	33.5	9.3 (8.26)	28.9	2.94
	$GF_1$7	12.25	92.3	39.6 (37.6)	14.5	9.87
HHP	CA5	2.31	44.2	34.0 (33.2)	34.1	1.45
	CA6	3.26	57.8	11.3 (9.97)	24.5	1.62
	FE5	2.61	76.4	48.0 (47.1)	70.3	10.55
	FE6	2.48	51.8	23.8 (23.3)	43.2	-1.83
	DE7	1.24	42.3	19.1 (18.3)	22.2	3.74
	$GF_1$7	7.87	77.8	51.8 (50.5)	15.1	12.83
HDP	CA5	4.82	89.1	14.0 (12.9)	11.8	3.63
	CA6	0.78	92.2	10.1 (10.0)	18.6	-0.51
	FE5	8.33	135.2	17.7 (16.6)	20.6	3.00
	FE6	1.90	89.5	3.4 (2.84)	39.7	3.16
	DE7	2.60	115.3	11.0 (10.7)	13.1	2.65
	$GF_1$7	5.92	177.5	28.0 (27.0)	18.0	3.95
EW	CA5	1.24	8.2	2.62 (2.43)	0.95	1.65
	CA6	0.98	6.6	1.10 (0.87)	1.12	1.03
	FE5	1.72	12.8	2.56 (2.37)	0.48	-0.81
	FE6	0.63	7.4	1.07 (0.91)	1.43	0.09
	DE7	2.07	9.1	2.52 (2.38)	1.17	2.47
	$GF_1$7	0.62	11.5	1.29 (1.19)	0.80	1.04
BW1	CA5	11.90	58.2	16.2 (14.4)	28.3	9.84
	CA6	6.17	40.4	9.2 (7.66)	13.8	8.05
	FE5	34.7	120.4	18.8 (16.5)	13.9	8.13
	FE6	20.30	116.1	6.1 (2.62)	25.1	10.06
	DE7	7.18	102.6	24.7 (23.6)	9.2	11.41
	$GF_1$7	13.43	121.2	11.4 (11.1)	6.2	7.94
BW2	CA6	23.40	114.4	27.4 (23.2)	11.2	21.04
	FE6	19.30	264.0	37.9 (28.8)	26.8	14.48
	DE7	21.74	446.5	36.2 (34.3)	72.4	16.55
	$GF_1$7	23.13	266.7	48.3 (44.5)	22.4	13.09

+Negative components replaced.

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