

## Genetic stability of the Cornell randombred control population of White Leghorns†

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### 1. INTRODUCTION

Control populations in poultry selection experiments have come into use relatively recently, but experimental evidence as to their effectiveness in maintaining a stable genotype has been limited. Unselected populations have been used for a much longer time in selection experiments which utilized laboratory organisms as the experimental animal. Lately more consideration has been given to theoretical or experimental evidence relative to the effectiveness of genetic and environmental control populations. Goodwin, Dickerson & Lamoreux (1955) proposed a repeat mating scheme as a means of estimating environmental and genetic changes. The small population size and relatively rapid increase in inbreeding reduced the effectiveness of Skaller's (1956) control population. Gowe and Johnson (1956) and Gowe *et al.* (1959) discussed the value of a randombred control strain of chickens in a selection study. King, Carson & Doolittle (1959) considered various means of providing adequate controls and described the development and maintenance procedures adopted for the Connecticut and Cornell randombred populations utilized in their research. Gowe, Robertson & Latter (1959) considered ways to minimize genetic drift in the design of poultry control strains. Bray, Bell & King (1962) studied the importance of genotype by environment interaction with reference to control populations, using *Tribolium castaneum* as the experimental animal. Weinland, Carson & King (1963) studied ten unifactorial characters in a randombred population of chickens and found no significant gene frequency changes over a period of four generations.

The purpose of this paper is to present a genetic analysis of the first six years of data obtained from the Cornell randombred control population of chickens, for

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which the original P<sub>1</sub> matings were made in 1955. Genetic parameters such as means, variances and correlations for several economic traits will be evaluated for possible indications of genetic change.

## 2. METHODS AND MATERIALS

### (i) *Biological*

A detailed description of the foundation flock history of the Cornell randombred control population may be found in King, Carson & Doolittle (1959). For purposes of this discussion it will suffice to say that this flock of White Leghorns has a broad genetic base and that 50 males and 250 females were mated at the beginning of each breeding season. A restricted random mating scheme was followed in that no full or half sib matings were permitted and, in so far as possible, each sire was limited to one son and each dam to one daughter in the succeeding breeding population.

In order to make it possible to estimate the importance of sire by dam interactions, a two-shift mating plan was followed each year with one hatch per shift. After hatching eggs from the first shift were collected for 14 days the females were re-assigned to the same set of sires under a new randomization with the restriction that no female be mated to the same sire in both shifts. Sires lost by death before the second shift were replaced; thus more than 50 sires appear in the analyses for some years. Matings were made by artificial insemination and at least 14 days elapsed between shifts before hatching eggs were saved again. Hatch dates for the two shifts were at least four weeks and generally five weeks apart.

Management of the progeny was as near alike as possible both between shifts and over years, but there were some unavoidable differences between years. The hatch dates were nearly constant from year to year and the same lighting programme was followed over the six-year period. An all mash feeding system was employed in the laying house. Trap-nesting was done 15 days each month and records terminated when the birds reached 500 days of age. Egg records were corrected to approximately 7-day-week trap-nest basis by doubling the actual record.

### (ii) *Statistical*

The analysis of the data was divided into two phases: (1) the estimation of components of variance under a model which was as complete as possible and (2) the estimation of genetic and phenotypic correlations among the ten traits from a simpler statistical model.

The complete model was

$$y_{jklm} = \mu + h_j + s_k + d_l + (sh)_{jk} + (i)_{jkl} + e_{jklm}$$

where  $y_{jklm}$  was the observation on the  $m$ th daughter of the  $k$ th sire and the  $l$ th dam from the  $j$ th hatch (shift).  $\mu$  was a population constant. The other elements of the model were considered random effects (model II of Eisenhart, 1947) with zero means and variances  $H$ ,  $S$ ,  $D$ ,  $(SH)$ ,  $(I)$ , and  $E$ , where  $H$  is attributed to hatch effects,  $S$  to

sire effects,  $D$  to dam effects,  $(SH)$  to sire by hatch interaction effects,  $(I)$  to other interaction effects (sire by dam, dam by hatch, and sire by dam by hatch) which are confounded together because of the mating design, and  $E$ , the residual or non-attributable variance.

The components of variance were estimated for each trait for each year of the experiment (except for 32-week egg-weight and 32-week body-weight for the 1960–61 season) according to method I of Henderson (1953) under which sums of squares for the elements of the model are equated to their expectations in terms of the model.

After inspection of these estimates it was decided to re-estimate the components of variance associated with the main effects of the model deleting those elements associated with the interaction effects. This was called the reduced model. The estimation procedure followed that for the complete model except that the appropriate rows and columns were deleted from the coefficient matrix,  $(SH)$  and  $(I)$  from the vector of unknowns and the sums of squares due to  $(sh)$  and  $(i)$  from the sums of squares vector.

The interaction components fluctuated widely from year to year without apparent pattern. For this reason, and also because of the costly and time-consuming process of estimating covariance components for the full model, genetic and phenotypic correlations were estimated from a simpler analysis which assumed no interaction. The simpler model for each trait was  $y_{jkl} = \mu^* + s_j^* + d_{jk}^* + e_{jkl}^*$ , where  $y_{jkl}$  is the observation from the  $l$ th daughter of the  $j$ th sire mated to the  $k$ th dam. Variances and covariances for each hatch were estimated from all available information, for example, if 10 observations were available for egg yield, 8 for 32-week body-weight, and 6 of these birds had both measurements, then components of variance for the egg-yield trait would be estimated from 10 observations, the variance components for body-weight from 8 observations, and the covariance components from the 6 common observations.

To obtain a comparison between the results from the simpler model and the cross classification models (complete and reduced) the  $S^*$ ,  $D^*$ , and  $E^*$  components of variance for the two-yearly hatches were pooled by simply averaging them.

Pooled components of variance and covariance for the 12 hatches also were obtained by averaging since the number of observations for each hatch was roughly equivalent.

Genetic correlations were then estimated by the usual procedure from the pooled sire and dam components of variance and covariance, i.e.

$$g_s = \frac{Spq}{(Spp \cdot Sqq)^{1/2}}$$

$$g_d = \frac{Dpq}{(Dpp \cdot Dqq)^{1/2}}$$

and

$$g_{s,d} = \frac{Spq + Dpq}{[(Spp + Dpp) \cdot (Sqq + Dqq)]^{1/2}}$$

Phenotypic correlations were estimated from the pooled total variances or covariances, where

$$T = S + D + E \quad \text{and} \quad P = \frac{T_{pq}}{(T_{pp} \cdot T_{qq})^{1/2}}$$

If no observations were taken for a trait for some year then the number of yearly components averaged may be different for the three elements of the correlation. For example,  $T_{pq}$  will be the average of five covariance components,  $T_{pp}$  of six variance components, and  $T_{qq}$  of five when  $p =$  egg production and  $q =$  32-week egg-weight or 32-week body-weight.

### 3. RESULTS AND DISCUSSION

#### (i) Genetic stability

Until one is certain that he has a genetically stable control population, the paramount problem is to determine how to evaluate one's success in developing such a population. Since only a limited amount of data was available to serve as a control to detect genetic and environmental changes during the development and maintenance of the Cornell control population, it became necessary to resort to other means of evaluating its stability. Every effort was made to keep constant from one shift to the next and from year to year those environmental factors that could be controlled through the application of uniform management. Such things as season of hatch, feeding régimes, lighting programme, floor space, etc., remained constant and other factors such as disease exposure, climatic conditions and housing assignments are assumed to have been random, so that time trends caused by environmental changes should be relatively unimportant. Given these circumstances, an analysis of means, variances and correlations for several economic traits over the six-year period should shed some light on the degree of stability maintained by the control population in question.

The number of parents having progeny tested, together with the number of their progeny trap-nested in each shift, is shown in Table 1. Since the numbers in each shift and in each year are relatively uniform, simple averages were used in presenting the yearly means of each trait in Table 2. There is enough variation from year to

Table 1. *Population sizes at housing time by years*

Year	Parents		Progeny		
	Sires	Dams	Shift I	Shift II	Total
1955-56	50	226	567	490	1057
1956-57	53	199	411	404	815
1957-58	56	178	428	396	824
1958-59	52	216	478	429	907
1959-60	52	213	393	486	879
1960-61	49	180	490	455	945
Totals	312	1212	2767	2660	5427

year so that time trends are not immediately apparent. In order to explore the possibility of less easily recognized trends the data for each trait were plotted separately by shifts, and regression equations were computed and plotted for both the means and their average standard deviations. These are presented in Figs. 1 and 2 for eight important economic traits.

Table 2. *Average performance by trait and year*

Trait	Year					
	1955-56	1956-57	1957-58	1958-59	1959-60	1960-61
Fertility (%)	94.1	85.9	85.0	74.3	82.7	81.7
Hatchability (%)	88.6	87.1	81.6	89.5	92.3	90.3
8-week body-weight (gr.)	658	698	628	686	697	701
32-week body-weight (lb.)	4.43	4.24	4.39	4.32	4.33	—
55-week body-weight (lb.)	4.72	4.56	4.45	4.50	4.52	4.70
Age at maturity (days)	178.3	177.2	184.5	175.3	180.4	181.1
Hen-housed 500-day egg production (number)	170.6	176.9	183.1	197.1	187.1	201.2
32-week egg-weight (gr.)	53.0	52.6	54.7	54.1	52.6	—
55-week egg-weight (gr.)	61.8	61.3	62.2	61.0	61.5	61.0
Albumen (USDA score)	4.19	3.82	3.62	3.78	3.72	3.84
Blood spot (score)	1.094	1.076	1.107	1.090	1.073	1.073
Specific gravity (score)	2.60	2.87	2.76	2.98	3.13	2.91
Laying house mortality (%)	17.30	15.85	12.58	12.43	15.20	6.36

At first glance the slopes of the regressions for egg production stand out. The regression of the shift I means is not significant, but the shift II regression is significant at the 5% level. Also significant at the 5% level is the regression of the average standard deviation for egg production. Closer observation reveals that the atypical egg production of shift II in 1955-56 is probably the cause of this significant trend and when considered in the light of the shift I results the reality of this trend may be discounted. Unfortunately the number of points on which to base these regressions is limited, but the opposite slopes between shifts for some traits and the very slight slopes of others, with only the regressions for both egg production and specific gravity score in shift II being significant, lend support to the conclusion that no important changes in means or standard deviations have occurred.

Presented in Table 3 are the estimates of the percent of the total variation exhibited by *H*, *S*, *D*, and *E* obtained under the reduced model. The reasons for using the estimates under this model as points of discussion will become apparent later. It may be noted that the *H* or hatch-shift effect accounted for 20% of the variance in 8-week body-weights, only 4% in egg production (most of this from the first year) and was of minor importance in all other traits. On the average the *S* percentage of the total variance is smaller than the *D* component for each of the traits analysed. The degree of uniformity of the estimates over years is rather good, usually with only a single year being out of line where major differences occur. The year to year changes are such that clear-cut time trends are not evident.

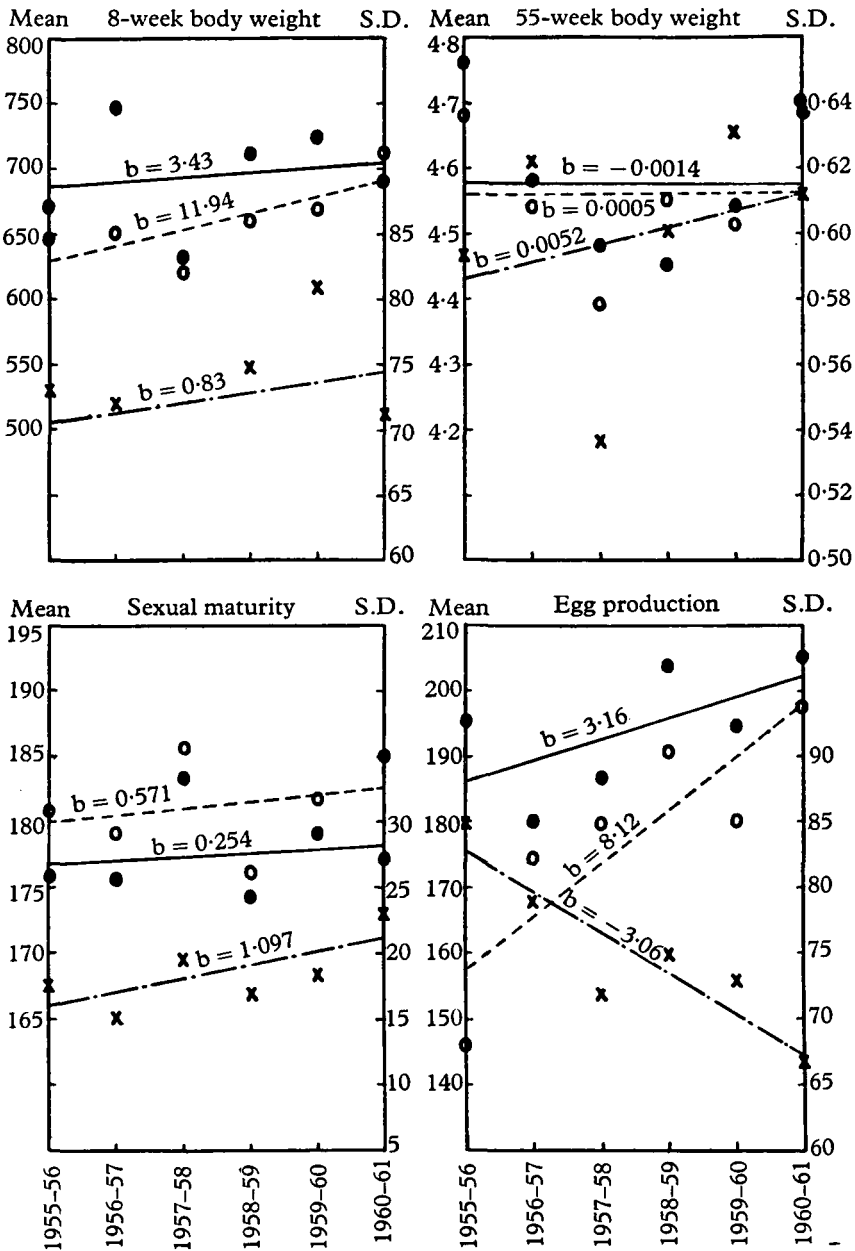


Fig. 1. Regressions of means and standard deviations for 8-week weight, 55-week weight, sexual maturity and egg production over six years.

—●— Shift 1 mean  
 - - - ○ - - - Shift 2 mean  
 - . - . - x - . - . Average Standard deviation

x

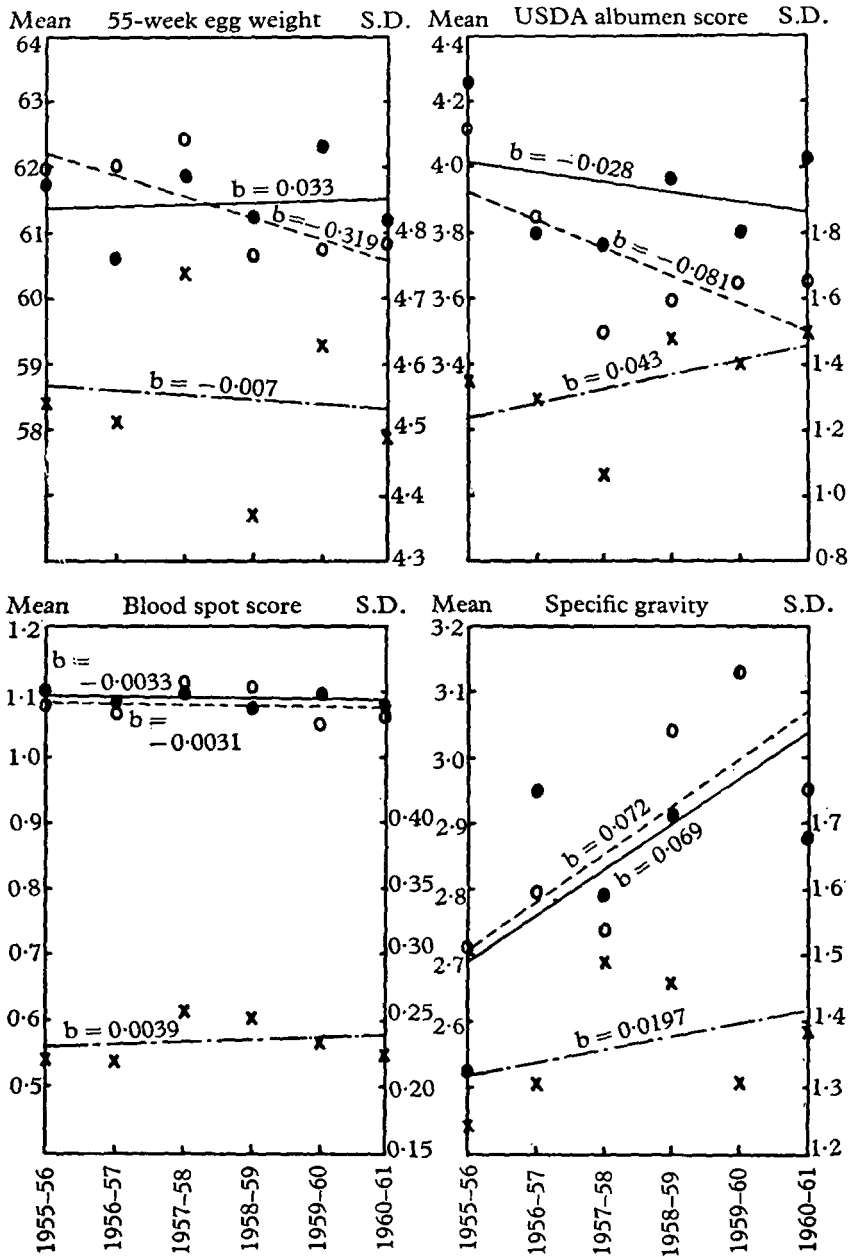


Fig. 2. Regression of means and standard deviations for 55 week egg-weight, albumen score, blood spots and specific gravity over six years.

— ● Shift 1 mean  
 - - - ○ Shift 2 mean  
 - . - . × Average standard deviation

Table 3. *Per cent of total variation exhibited by elements of the reduced model by traits and years*

Component of variance	Per cent of total variance						
	1955-56	1956-57	1957-58	1958-59	1959-60	1960-61	Average
	8-week body-weight						
<i>H</i>	4.9	47.1	0.8	17.7	20.0	3.5	20.0
<i>S</i>	6.2	0.4	6.9	10.5	14.4	6.4	7.3
<i>D</i>	20.7	13.2	30.7	15.0	12.5	21.8	17.3
<i>E</i>	68.2	39.3	61.7	56.7	53.1	68.3	55.3
	32-week body-weight						
<i>H</i>	-0.2	1.8	-0.3	2.8	-0.2	—	0.8
<i>S</i>	6.4	10.6	13.9	12.2	17.2	—	12.1
<i>D</i>	25.4	18.1	27.8	19.2	20.7	—	22.2
<i>E</i>	68.3	69.4	58.6	65.8	62.3	—	64.9
	55-week body-weight						
<i>H</i>	0.8	0.0	0.8	1.2	-0.1	-0.1	0.4
<i>S</i>	7.1	10.5	13.2	12.6	15.1	7.6	11.0
<i>D</i>	19.7	16.0	23.0	16.8	16.7	22.4	18.9
<i>E</i>	72.5	73.5	63.1	69.5	68.4	70.1	69.7
	Age at maturity						
<i>H</i>	3.8	2.3	0.4	0.3	0.8	5.0	2.5
<i>S</i>	7.0	1.1	1.7	1.0	5.2	-0.3	2.3
<i>D</i>	7.2	11.6	29.6	10.3	0.2	8.5	11.3
<i>E</i>	82.0	85.0	68.2	88.4	93.8	86.8	83.9
	Hen-housed egg production—500 days						
<i>H</i>	14.1	0.0	0.3	1.4	1.9	0.4	4.0
<i>S</i>	3.2	1.6	0.4	1.7	3.4	-0.2	1.9
<i>D</i>	12.3	20.7	22.7	16.0	9.1	7.5	14.8
<i>E</i>	70.4	77.7	76.6	80.9	85.6	92.3	79.4
	32-week egg-weight						
<i>H</i>	0.6	5.9	-0.3	0.6	0.6	—	1.5
<i>S</i>	11.9	19.4	15.0	6.8	10.8	—	12.8
<i>D</i>	16.3	12.6	19.1	16.4	16.4	—	16.1
<i>E</i>	71.3	62.2	66.2	76.3	72.3	—	69.6
	55-week egg-weight						
<i>H</i>	-0.2	4.4	0.3	0.6	5.3	0.0	1.8
<i>S</i>	12.2	14.4	21.2	9.8	16.3	4.4	13.3
<i>D</i>	23.4	4.7	14.8	11.9	18.2	13.8	14.5
<i>E</i>	64.6	76.5	63.7	77.7	60.2	81.2	70.5
	Albumen score						
<i>H</i>	0.2	-0.3	2.8	2.7	0.2	3.0	1.5
<i>S</i>	7.5	10.8	-2.2	15.7	6.7	2.1	7.3
<i>D</i>	13.0	5.4	15.2	12.1	11.3	4.9	10.0
<i>E</i>	79.4	84.2	84.2	69.4	81.7	90.0	81.2



Table 3—continued

Component of variance	Per cent of total variance						
	1955-56	1956-57	1957-58	1958-59	1959-60	1960-61	Average
	Blood spot score						
<i>H</i>	0.2	-0.3	-0.3	0.2	0.9	-0.2	0.1
<i>S</i>	1.3	-1.0	6.1	5.4	3.0	1.4	3.3
<i>D</i>	3.8	-1.1	22.2	12.0	-9.6	5.9	7.1
<i>E</i>	94.7	102.5	72.0	82.5	105.8	93.0	89.6
	Specific gravity						
<i>H</i>	0.7	0.3	-0.3	0.1	-0.4	-0.1	0.0
<i>S</i>	10.1	5.5	8.9	12.2	11.6	2.4	8.5
<i>D</i>	8.8	0.3	7.2	10.4	15.2	8.0	8.3
<i>E</i>	80.4	93.9	84.2	77.3	73.5	89.7	83.2

## (ii) Genetic parameters

Estimates of heritability and maternal effects are presented in Table 4. Since these estimates involve six years of data collected from 5427 progeny from 2761 dams and 312 sires, they may be considered quite reliable as genetic parameters for

Table 4. Estimates of heritability and maternal effects based on the reduced model

	$h_s^2$ (%)	$h_d^2$ (%)	$\sigma_m^2$ (%)
8-week body-weight	29	69	10
32-week body-weight	48	89	10
55-week body-weight	44	76	8
Age at maturity	9	45	9
Hen-housed egg production	7	59	13
32-week egg-weight	51	64	3
55-week egg-weight	53	58	1
Albumen score	29	40	3
Blood spot score	13	28	4
Specific gravity score	34	33	0

this population under similar conditions. Of particular interest are the estimates for maternal effects. The estimate for hen-housed egg production to 500 days of age is 13%, which is nearly double the heritability estimated from sire components of variance, and is of the same order of magnitude as reported by King (1961). Also of interest is the fact that the maternal effect of 10% for 8-week body-weight still held at 10% for the 32-week weight and 8% for the 55-week weight. Sexual maturity exhibited a similar large maternal effect, while the more highly heritable egg traits had smaller variation from this source. If sex-linked effects influence egg-weight, as is commonly believed, then the real maternal effect may be larger than our data indicates because it is estimated by the difference between the sire and dam components.

The estimates of heritability from both the sire and dam components were larger

for 32-week body-weight than for the 8-week weight. Evidently the more mature birds have greater resistance to environmental stresses.

Errors of estimating genetic correlations are large, but the pooling of six years of data from large numbers of progeny, dams and sires gives one some measure of confidence in the results shown in Tables 5 and 6. Genetic correlations were estimated from sire and dam components of variance and covariance separately and combined. In view of the large maternal effects comparisons between estimates from sire components and dam components are interesting. For example, the genetic correlation between egg production and 32-week egg-weight is  $-0.28$  from sire components and  $0.01$  for dam components. The situation is almost identical for egg production and 55-week egg-weight. There are other instances where estimates from sire as compared to dam components do not differ greatly, i.e. the correlation between 32-week body-weight and 32- or 55-week egg-weights.

The most important economic trait, egg production, presents no correlations that are seriously antagonistic to the desired direction of genetic improvement when considered from the point of view of the combined estimates in Table 6. However, the opposite signs exhibited by the sire and dam components estimates for the correlation between egg production and 32- or 55-week egg-weights suggest that maternal effects need to be reckoned with in designing a selection programme for this population.

It is interesting to note that, with the exception of the correlations involving 32-week body-weight and the other non-body-weight traits, the phenotypic correlations are generally of lesser magnitude than corresponding genetic correlations regardless of sign. This indicates that one could tend to be lulled into a false sense of security and give less weight to possible correlated responses, if he considered only phenotypic correlations in a selection programme.

The correlations between 32-week body-weight and egg-weight and between sexual maturity and egg-weight agree very well with King (1961). For other pairs of traits agreement is only partial or fails entirely when the signs do not agree for either one or both of the sire or dam components estimates.

### (iii) *Comparison of models*

In estimating the relative importance of different effects that may influence variation in economic traits, one desires to include in his assumed model all those effects for which it is logical to assume there is a real effect. However, there is always a risk of including elements that are unimportant and these extra unknowns in the matrix may contribute to a decrease in reliability of the estimates of the components that are real.

An inspection of the estimates of the per cent of the total variance exhibited by the elements of the complete model revealed that for each trait negative estimates often turned up in the yearly analyses and sometimes even when averaged over years. Most of the negative estimates were found for the interaction components (*SH*, genetic by environment) or (*I*, sire by dam), but occasionally a main effect

Table 5. *Estimates of genetic correlations between important economic traits based on sire or dam variances and covariances†*

Trait	8-wk. B.W.	32-wk. B.W.	Age, 1st egg	Egg prod.	32-wk. E.W.	55-wk. E.W.	Alb. sc.	Blood spots	Spec. gr.
8-week body-weight	—	0.87	0.00	-0.28	0.36	0.22	0.15	0.04	0.07
32-week body-weight	0.62	—	0.02	0.24	0.36	0.38	0.26	-0.01	0.17
Age at maturity	-0.23	0.26	—	-0.15	0.32	0.32	-0.41	-0.48	-0.09
Egg production	0.32	-0.26	-0.47	—	-0.28	-0.25	0.07	-0.05	-0.27
32-week egg-weight	0.30	0.45	0.12	0.01	—	1.03	0.04	0.11	0.25
55-week egg-weight	0.43	0.45	0.10	0.03	0.93	—	0.06	-0.07	0.41
Albumen score	-0.08	-0.11	0.05	0.04	-0.27	-0.24	—	0.08	0.03
Blood spot score	-0.18	-0.19	0.10	0.04	-0.06	0.05	-0.01	—	-0.03
Specific gravity score	-0.06	-0.25	0.14	-0.02	-0.10	-0.28	0.26	-0.48	—

† Estimates from sire components of variance and covariance above the diagonal and from dam components below the diagonal.

Table 6. *Estimates of genetic and phenotypic correlations between important economic traits†*

Trait	8-wk. B.W.	32-wk. B.W.	Age, 1st egg	Egg prod.	32-wk. E.W.	55-wk. E.W.	Alb. sc.	Blood spots	Spec. gr.
8-week body-weight	—	0.71	-0.17	0.20	0.32	0.34	-0.01	-0.09	-0.01
32-week body-weight	0.54	—	0.00	0.04	0.32	0.30	0.01	-0.13	-0.09
Age at maturity	-0.04	0.08	—	-0.44	0.18	0.16	-0.07	-0.09	0.06
Egg production	0.04	0.15	-0.20	—	-0.04	-0.01	0.04	0.01	-0.07
32-week egg-weight	0.21	0.41	0.04	0.00	—	0.98	-0.14	0.01	0.06
55-week egg-weight	0.24	0.40	0.03	-0.03	0.68	—	-0.11	-0.01	0.04
Albumen score	-0.02	-0.02	-0.03	0.04	-0.06	-0.05	—	0.02	0.05
Blood spot score	0.01	0.00	-0.01	0.00	0.01	0.00	0.00	—	-0.27
Specific gravity score	0.01	-0.01	0.03	-0.04	0.02	0.00	-0.08	0.00	—

† Estimates of genetic correlations above the diagonal (based on combined sire and dam components) and phenotypic correlations below the diagonal.

Table 7. *Per cent of total variance in hen-housed egg production to 500 days exhibited by elements of the complete, reduced and simplest models*

Variance component	1955-56	1956-57	1957-58	1958-59	1959-60	1960-61	Average
Complete model							
<i>H</i>	14.1	0.2	-0.7	1.5	2.0	0.5	3.9
<i>S</i>	3.3	7.0	-48.6	2.7	3.9	2.6	-3.7
<i>D</i>	11.1	17.8	23.3	17.8	7.5	2.9	13.5
( <i>SH</i> )	-0.3	-10.0	55.5	-1.4	-1.4	-5.5	5.1
( <i>I</i> )	3.0	10.9	-8.0	-3.5	4.2	12.6	3.1
<i>E</i>	68.9	74.1	78.5	83.0	83.8	86.9	78.0
Reduced model							
<i>H</i>	14.1	0.0	0.3	1.4	1.9	0.4	4.0
<i>S</i>	3.2	1.6	0.4	1.7	3.4	-0.2	1.9
<i>D</i>	12.3	20.7	22.7	16.0	9.1	7.5	14.8
<i>E</i>	70.4	77.7	76.6	80.9	85.6	92.3	79.3
Simplest model							
<i>S*</i>	3.9	-2.8	6.4	1.2	1.9	-2.6	1.3
<i>D*</i>	16.0	28.9	14.6	14.5	12.8	15.5	17.3
<i>E*</i>	80.1	73.9	79.0	84.3	85.3	87.1	81.4

Table 8. *Per cent of the total variance exhibited by elements of the complete, reduced and simplest models averaged over years for each economic trait*

Variance component	8-wk. B.W.	32-wk. B.W.	55-wk. B.W.	Age, 1st egg	Egg prod.	32-wk. E.W.	55-wk. E.W.	Alb. sc.	Blood spots	Spec. gr.
Complete model										
<i>H</i>	19.8	0.7	0.5	2.3	3.9	1.5	1.7	1.4	-0.1	0.1
<i>S</i>	-0.4	9.0	17.4	-2.6	-3.7	13.6	11.7	6.2	-1.8	9.6
<i>D</i>	13.2	19.2	16.8	7.0	13.5	16.3	13.1	7.6	6.2	9.1
( <i>SH</i> )	11.1	3.2	-6.2	6.3	5.1	-0.6	1.7	1.0	7.4	-1.6
( <i>I</i> )	5.6	6.1	4.5	7.9	3.1	-0.7	3.0	5.3	-0.7	-1.1
<i>E</i>	50.8	61.7	67.0	79.1	78.0	69.9	68.8	78.5	88.9	84.0
Reduced model										
<i>H</i>	20.0	0.8	0.4	2.5	4.0	1.5	1.8	1.5	0.1	0.0
<i>S</i>	7.3	12.1	11.0	2.3	1.9	12.8	13.3	7.3	3.3	8.5
<i>D</i>	17.3	22.2	18.9	11.3	14.8	16.1	14.5	10.0	7.1	8.3
<i>E</i>	55.3	64.9	69.7	83.9	79.3	69.6	70.5	81.2	89.6	83.2
Simplest model										
<i>S*</i>	13.2	12.4	†	3.8	1.3	13.2	13.1	7.1	5.6	7.7
<i>D*</i>	23.7	25.4	†	15.6	17.3	15.8	15.3	13.7	5.8	8.0
<i>E*</i>	63.1	62.2	†	80.6	81.4	71.0	71.6	79.2	88.6	84.3

† 55-week body-weight was not analysed according to the simplest model.

was found to have a negative estimate, either for a single year or averaged over years. In most instances one finds that there is an offsetting interaction component that is way out of line on the positive side. Inspection of the estimates for 1957–58 in Table 7, which utilizes egg production as the trait, illustrates this point. Note that the (*SH*) component is negative in every year except 1957–58, when a very large positive component was found while the sire (*S*) component was highly negative.

These results suggested to us that the interaction components (*SH*) and (*I*) may fall in the category of unimportant elements. Therefore, these two elements were deleted from the model. Table 7 shows that under the reduced model negative components were substantially eliminated without changing the average main effects materially, while at the same time reducing their yearly variation. Resorting to the simplest model, Table 7, changed the average estimates for main effects very little, but increased the yearly variation for these estimates. We concluded that the reduced model yielded the most reasonable and reliable estimates.

A comparison of complete, reduced and simplest models is given in Table 8, which presents the per cent of the total variance exhibited for each element of the model by traits averaged over six years. On the average, the simplest model provided substantially the same estimates of the *S* and *D* elements of the model as the more complex models, except for 8-week body-weight.

#### (iv) *General considerations*

The Cornell randombred control population was established by crossing a strain cross line of males to several strain cross lines of females (King, Carson & Doolittle, 1959). The results of this study do not indicate any depression in performance in the years succeeding 1955–56, when the original strain cross progeny were tested. Perhaps one should not expect a rapid decline in the first year or two following the original cross, since neither the strain crosses used nor the parents themselves had been selected for their combining ability. However, the lack of any indication of a slow decline in performance supports the view that relaxed or no selection is not harmful. Since the regressions shown in Fig. 1 are determined from only six points, one can argue that the likelihood of finding significant regressions is not very great. A single aberrant value can swing such a regression line considerably off course. The trend indicated by egg production is considered to be non-genetic, since it is difficult to conceive how selection of any kind could have had any opportunity to cause improvement. There was opportunity for unknown environmental effects to cause such a trend.

When taken all together, the data on means, standard deviations, regressions, variances and covariances lead us to conclude that no important genetic changes have taken place in the Cornell randombred control population. Of course, this does not rule out the possibility of genetic drift at particular loci, the effects of which may be averaged out because of the many loci for traits of economic importance.

## 4. SUMMARY

Six years of data collected from two shifts of Cornell randombred control matings each year are analysed. Approximately 900 progeny were tested per year from 50 sires mated to 250 dams.

Means for the important economic traits are presented by years and regressions for nine such traits, together with their standard deviations, are shown. The only significant regressions are those for both egg production and specific gravity score in shift II. An abnormally low egg production the first year for this shift is considered responsible for this result and the reality of the regression is discounted.

Genetic variances are presented by trait and year. Year to year variability is evident, but no trends are indicated.

Estimates of heritability and genetic correlations between traits are presented. These estimates are considered to be quite reliable and will be useful as estimates of genetic parameters when this population is used in selection experiments. Estimates of heritability from the sire components of variance were as follows: 8-week body-weight, 0.29; 32-week body-weight, 0.48; 55-week body-weight, 0.44; age at maturity, 0.09; egg production to 500 days, 0.07; 32-week egg-weight, 0.51; 55-week egg-weight, 0.53; USDA albumen score, 0.29; blood spot score, 0.13; and specific gravity score, 0.34.

Important maternal effects were found for 8, 32 and 55-week body-weight, sexual maturity and egg production. Selection programmes should take into consideration the fact that maternal effects accounted for 13% of the total variation in egg production. Genetic correlations utilizing combined sire and dam components revealed no serious antagonisms between egg production and other economic traits. However, this conclusion must be considered in the light of what influence maternal effects may have, since correlations computed from sire and dam components separately may have opposite signs and be important.

The many negative estimates of interaction components (*SH*, genetic by environment) and (*I*, sire by dam) indicate that these elements of the model contributed little to the variation of the traits studied.

## REFERENCES

- BRAY, D. F., BELL, A. E. & KING, S. C. (1962). The importance of genotype by environment interaction with reference to control populations. *Genet. Res.* **3**, 282-302.
- EISENHART, C. (1947). The assumptions underlying the analysis of variance. *Biometrics*, **3**, 1-21.
- GOODWIN, K., DICKERSON, G. E. & LAMOREUX, W. F. (1955). A technique for measuring genetic progress in poultry breeding experiments. *Poult. Sci.* **34**, 1197.
- GOWE, R. S. & JOHNSON, A. S. (1956). The performance of a control strain of S.C. White Leghorn stock over four generations on test at several locations. *Poult. Sci.* **35**, 1146.
- GOWE, R. S., JOHNSON, A. S., DOWNS, J. H., GIBSON, R., MOUNTAIN, W. F., STRAIN, J. H. & TINNEY, B. F. (1959). Environment and poultry breeding problems. 4. The value of a random-bred control strain in a selection study. *Poult. Sci.* **38**, 443-462.
- GOWE, R. S., ROBERTSON, A. & LATTER, B. D. H. (1959). Environment and poultry breeding problems. 5. Design of poultry control strains. *Poult. Sci.* **38**, 462-471.

- HENDERSON, C. R. (1953). Estimation of variance and covariance components. *Biometrics*, **9**, 226–252.
- KING, S. C. (1961). Inheritance of economic traits in the Regional Cornell Control population. *Poult. Sci.* **40**, 975–986.
- KING, S. C., CARSON, J. R. & DOOLITTLE, D. P. (1959). The Connecticut and Cornell random-bred populations of chickens. *World's Poult. Sci. J.* **15**, 139–159.
- SKALLER, F. (1956). The Hagedoorn 'nucleus-system' of breeding—a critical evaluation based on an experiment with poultry. *Proc. Australian Soc. Animal Prod.* **1**, 165–176.
- WEINLAND, B. T., CARSON, J. R. & KING, S. C. (1963). Stability of gene frequencies in a randombred control population of chickens. *Poult. Sci.* **42** (submitted).