# THE EFFECTS OF INBREEDING ON THE PRODUCTION CHARACTERISTICS OF POULTRY UNDERGOING SELECTION

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# SUMMARY

The magnitude of inbreeding occurring in the course of selection in 4 sublines of a White Leghorn population over 4-5 generations was computed using the co-ancestry method of analysis (Cruden, 1949).

Manson (1970) had previously reported the realised responses in each of these selected populations designated as follows:

1. Egg Weight (E.W.) (selected for increased egg weight)
2. Body Weight (B.W.) (selected for decreased body weight)
3. Regression (I) (selected for maximum values of an index, (I) = E.W. - b×B.W., in which b was the estimated linear genetic regression of egg weight on body weight)
4. Ratio (r) (selected on maximum values of a ratio of egg weight/body weight).

The computed inbreeding within all 4 selected lines was estimated to exceed the predicted level of inbreeding based upon the average population size. The cumulative additional inbreeding ($\Delta F$) that occurred during selection was calculated as 8.5, 9.0, 11.8 and 8.0 <u>per cent</u> respectively in each of the above lines.

Following adjustment for inbreeding, it was concluded that:

(a) Only about two thirds of the decline in egg numbers to 60 weeks observed by Manson (1970) as a correlated response in the Egg Weight and Regression lines was due to inbreeding depression.

(b) Latent gains in egg numbers, obscured by inbreeding depression were likely to have occurred as a correlated response in the case of Body Weight and Ratio selection.

The mean performance of the selected lines was observed following a single generation of relaxed selection but no significant and consistent effects of relaxation were observed in egg numbers, sexual maturity, egg weight and body weight.

Crosses were made between the two high egg weight lines (E.W. and I) and between the two low body weight lines (B.W. and r). Examination of the mean performance of the crosses indicated some heterosis in egg weight in the low body weight crosses. As regards reciprocal cross differences a significant sire line effect in body weight and egg weight was observed between the Egg Weight and Regression crosses. No significant dam line effects were however observed.

A number of test matings were arranged to test the hypothesis that a major sex-linked gene causing a reduction in body weight was present in the low body weight population. The segregation ratio observed among the progeny supported this hypothesis, the 'dwarf' female progeny weighing 15 per cent less, laying 10 per cent fewer and 3 per cent smaller eggs when compared with their contemporaneous non-dwarfed full-sibs. An examination of the phenotypic effects of this gene suggests that it may be a similar mutant to the 'B' allele (Jaap, 1971) at the Dw locus on the sex chromosome of the fowl (Hutt, 1959).

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# INTRODUCTION

There is very little controlled experimental evidence on the magnitude of the effect of inbreeding on the performance of poultry undergoing selection. On theoretical grounds, intense inbreeding tends to cause fixation of alleles at some loci (Falconer, 1964). Therefore, both the total response and the duration of response are expected to be reduced particularly if the selection is carried out in a small population with a fairly high rate of inbreeding.

This thesis re-examines some results of selection in poultry for body weight and egg weight within four White Leghorn lines of common origin. This study was concerned initially with reporting the yearly increases in inbreeding coefficients in the selected lines. The four lines for which inbreeding coefficients have been calculated, consisted of two lines in which selection over 4-5 generations had resulted in a substantial increase (15 per cent) in egg weight and two further lines in which selection had significantly decreased body weight (Manson, 1970). The performance of the selected lines following one generation of relaxed selection will also be reported and compared with the performance of crosses produced between the 2 high egg weight and between the 2 small body weight lines.

In addition a dwarf male was detected in the small body weight line and considered to be carrying a major dwarfing gene, possibly similar to the sex-linked recessive gene first reported by Hutt (1953). Progeny of this male provided the material for a study reported in the later part of this thesis concerned with confirming the presence of this major gene. The direct effects of the 'dwarfing' gene on body size and the correlated effects on traits such as egg weight and egg number were also investigated and presented with a view to providing a preliminary evaluation of the economic potential of this gene.

# PART I

# THE EFFECTS OF CONCURRENT INBREEDING AND SELECTION IN THE DOMESTIC FOWL

# 1. REVIEW OF LITERATURE

## Inbreeding effects on the production characteristics of the domestic fowl

There are a number of reports published in the literature of the adverse effects of inbreeding on production traits in the fowl. Jull (1933), Shoffner (1948), Duzgunes (1950) and Stephenson, Wyatt and Nordskog (1953), have reviewed the literature dealing with the consequences of deliberate close mating programmes. In these circumstances with the attendant high rate of increase in the levels of inbreeding, most fitness characters are impaired to such an extent that the very existence of the inbred population could be in danger (Falconer, 1964).

The primary effect of inbreeding is to produce homozygosis, i.e. an increase in the frequency of homozygous genotypes and a decrease in the frequency of the heterozygous genotypes. The observable consequence is a reduction of the mean phenotypic value in those traits which tend to be most closely or directly related to reproductive capacity or fitness (Falconer, 1964). The reaction of a character to inbreeding appears to be related to the proportion of non-additive genetic variance. Those with a greater proportion of non-additive variance (e.g. egg number in Drosophila - Robertson, 1957a) suffer greater inbreeding depression than those with a smaller proportion of non-additive variance (e.g. length of thorax and ovary size in Drosophila - Robertson, 1957a,b). It would be reasonable to expect that in the domestic fowl, egg number would tend to be more depressed than egg weight or body weight.

The production characteristics of poultry in which inbreeding effects have been reported in the literature are egg weight, body weight, sexual maturity and a major group of reproductive traits such as egg production, fertility, hatchability and viability. These effects will be reviewed in turn.

Egg Numbers: The extensive literature regarding the effect of inbreeding on egg numbers has been reviewed by Shoffner (1948) and Stephenson *et al*. (1953). These workers amongst many others, e.g. Hays (1924), Jull (1933), Wilson (1948a), Blow and Glazener (1953), Tebb (1958), and Casey and Nordskog (1971), have reported adverse effects of inbreeding on egg numbers.

There was general agreement (Hays, 1924; Stephenson *et al*. 1953; Tebb, 1958) that in the case of coefficients of inbreeding above 25%, there is a linear decline of egg numbers with increasing levels of inbreeding. With an intensity of inbreeding below 25%, however, (Stephenson *et al*. 1953; Tebb, 1958) evidence of a linear relationship was apparently inconclusive.

A summary of the average regression of annual egg production with increasing levels of inbreeding is given in Table 1.

Table 1.

Average Decline in Annual Egg Production for each 1 per cent increase in F.

| Reduction in egg numbers | Reference |
|---|---|
| -0·9 | Shoffner (1948) |
| -0·8 | Wilson (1948a) |
| -1·6 | Stephenson *et al*. (1953) |
| -1·0 | Tebb (1958) |
| -1·9 | Casey and Nordskog (1971). |

From Table 1 it will be noted that a 1·0 per cent increase in F, for example, produced an average depression in annual egg production of between 0·8 and 1·9 eggs (average of 1·2 eggs). In the case of Shoffner's (1948) study, the values have been biased by the inclusion of the effect of sexual maturity which is confounded with the egg production record to 500 days of age. The remainder of the investigators adopted the common practice of recording egg production over 12 months. Shoffner (1948), Wilson (1948a), Stephenson _et al_. (1953), based their estimates on survivor's production, which did not take into account the effect of viability, although estimates by Tebb (1958), Casey and Nordskog (1971) were based on the hen-housed record. From the above, one may conclude that the depression in egg production observed by Stephenson _et al_. (1953) and Casey and Nordskog (1971) was higher when compared to other workers. No valid explanation can be found to explain this difference as the method of study is on the whole similar to that reported by Wilson (1948a) or Tebb (1958). A probable reason is the genetic differences between the populations studied (Shoffner, 1948).

_Fertility, Hatchability and Viability of offspring:_ With regard to inbreeding effects on reproductive traits other than egg numbers, viz. fertility, hatchability and viability of offspring, the literature has been summarised by Blow and Glazener (1953), Duzgunes (1950), Landauer (1948) and Wilson (1948a,b).

_Fertility_: Wilson (1948a) concluded that the regression of fertility on inbreeding was practically zero. Duzgunes (1950) concluded that inbreeding of the dam had no effect on the fertility of her eggs.

Duzgunes (1950) reported that in general, inbreeding tended to reduce the number of offspring of a mating surviving to breeding age, but that this reduction is brought about largely through a decrease in hatchability.

Hatchability: Many workers such as Shoffner (1948), Bernier (1947), Duzgunes (1950), Blow and Glazener (1953) have concluded that it is the inbreeding of the embryo rather than that of the dam, which has a more deleterious effect on hatchability. Wilson (1948b) disagreed with this view. However, on balance, the literature favours the view that inbreeding of the embryo is a more important factor than the female parental level of inbreeding in the maintenance of inbred lines of poultry. Shoffner (1948) and Duzgunes (1950) reported a decline of 4·4 per cent in hatchability for every 10 per cent increase in the degree of inbreeding of the embryo itself. Blow and Glazener (1953) reported a decline of 3·7 per cent. A smaller decline of 2·6 per cent was recorded by Nordskog and Hassan (1971).

Viability: The level of inbreeding also affects the viability of offspring. Duzgunes (1950) concluded that the embryo's inbreeding appeared generally to have a greater effect on its own viability than the inbreeding of the dam. It may be noted here that Wilson (1948b) reported that the degree of inbreeding of the dam exercised a greater influence on the viability of her offspring than did the level of inbreeding amongst the progeny themselves. For a ten per cent increase in the degree of inbreeding Wilson (1948b) reported an increase of 1·4 per cent pullet offspring mortality and Casey and Nordskog (1971) recorded an increase of adult mortality of 2·1 per cent.

Sexual Maturity: Sexual maturity is another trait which has been recorded to be affected by inbreeding. Several workers have reported that sexual maturity tended to be delayed with inbreeding. It has been estimated that sexual maturity is delayed from 3 (Stephenson and Nordskog, 1950; Blow and Glazener, 1953) to 6 days (Shoffner, 1948) for every 10 per cent increase in inbreeding. In a later work, Casey and Nordskog (1971) reported a delay of 4·0 days.

Body weight and egg weight: As regards inbreeding effects on body weight and egg weight, Shoffner (1948) found practically no change in mature body weight (300 days) nor egg weight, which confirmed earlier observations by Goodale (1927), Waters and Lambert (1936), Waters (1941 and 1945a). Blow and Glazener (1953) also reported that the effects of inbreeding on body weight and egg weight were negligible or non existent.

Schultz (1953) studied the effects of concomitant inbreeding and selection in the chicken for 7 generations. The characters studied were egg number and egg weight. He found that close consanguinous mating caused a decline in November egg number ($7\frac{1}{2}$ months old) in the second and third generation of selection, with no further decline occurring in the following four generations, even though the degree of inbreeding greatly increased. Artificial selection was not therefore sufficient to prevent the severe decline. A correlated decline in November egg weight began coincident with the cessation of the degeneration in egg number and continued throughout the duration of the experiment. Responses to selection for egg weight were immediately apparent, but apparently ceased by the fourth generation.

Tebb (1958) examined the effects of inbreeding on egg production when the level of inbreeding was kept at a minimum consistent with the size of the flock and the selection pressure exercised. It is emphasized that these are the effects which are likely to be operative in most cases of selection within closed flocks, except where an intensive programme of inbreeding is adopted by the breeder to produce highly inbred lines or strains. It would, however, be unnecessary, considering the attendant risks and losses, to develop highly inbred strains (of over 40 per cent inbreeding) for crossing, as there is sufficient heterosis to be obtained from crossing strains not particularly highly inbred (Hutt and Cole, 1952).

As pointed out earlier (Table 1), the finding by Tebb (1958) of the average depression in annual egg production of 10 eggs for a 10 per cent rise in inbreeding, is similar to other workers working with flocks of higher rates of inbreeding.

Festing and Nordskog (1967), Nordskog, Festing and Verghese (1967) and Casey and Nordskog (1971), published studies on the direct and correlated responses following selection for egg weight, body weight and egg production, when inbreeding within the selected populations was minimal.

One feature of the long term responses obtained over 7 generations of selection in Festing and Nordskog's (1967) study was the correlated decline in egg number when selection was for either body weight or egg weight. In this context it was important to distinguish between the decline in fitness associated with the effects of inbreeding per se and the decline in fitness due to selection. The authors were of the opinion that the decline in egg production rate that occurred in the course of selection for egg weight was greater than could be explained solely by inbreeding depression.

In a study carried out by Nordskog et al. (1967) eight generations of selection in two breeds on the early part record per cent egg production showed no significant increase in egg production. The anticipated increase in egg numbers based on population parameter estimates adjusted for inbreeding depression however indicated that there ought to have been a significant increase in egg production. This further serves to stress the importance of conducting empirical selection experiments in order to determine the actual realised responses achieved in practice.

## 2. MATERIALS AND METHODS

The data used in this study pertain to a strain of White Leghorns (designated strain 2), first introduced on to the Edinburgh School of Agriculture poultry unit in 1956. Some details concerning this strain have already been recorded by Clayton and Robertson (1966), Manson (1970).

Strain 2 derived from an original importation of between 40-60 day-old chicks which were subsequently multiplied to form a population of around 1,000 pullets housed annually. For a 3 year period from 1959 to 1962, no selection was carried out within this population which was maintained on a random-bred basis in order to estimate the important genetic parameters for the major production traits in a large randomly mated population (Clayton and Robertson, 1966). Subsequently a genetic selection programme was initiated in 1962 to test a simplified form of index selection designed to include only two traits, namely egg weight and body weight. The primary objective of the experiment was to test a method of selection aimed at counteracting the positive genetic correlation between these two traits and consequently improve the strain's net economic worth by effecting either a marked increase in egg weight or alternatively decreasing mean body weight, without a concurrent change in the correlated trait.

### 2.1. Description of populations studied.

### 2.1.1. Selected lines

Four distinct sub-lines were established within the strain, consisting of:

(1) selection for increased egg weight at 28 weeks of age (Egg Weight line)

(2) selection for positive deviations from the average genetic regression of 28 week egg weight on body weight, referred to as the Regression line.

(3) selection for maximum values of the 28 week $\frac{\text{Egg Weight}}{\text{Body weight}}$ ratio or Ratio selection.

(4) selection for decreased body weight at 12 weeks of age, i.e. Body Weight selection.

The Egg Weight and Body Weight lines were started a season earlier than the Ratio and Regression lines and consequently have undergone an additional generation of mild selection.

The size of each selected sub-line has varied from between 200 to 250 pullets housed each generation comprising the progeny from approximately 12 - 15 selected sires and 40 - 60 dams.

At the commencement of the selection experiment, mating of selected birds was arranged using 40 sets of individual male breeding pens with 4 or 5 females. Because of the limited accommodation it was necessary to make up only two lines at one time, the breeders being replaced by the parents selected to reproduce the remaining two selection lines once collection of fertile eggs for two complete hatches had ceased.

Beginning with the 1965 hatches, however, all matings were effected by using artificial insemination, which allowed for hatching of all selection lines simultaneously. Four hatches were generally taken at fortnightly intervals over a 6 week period.

Pedigreed chicks were sexed and wing-banded at hatching. All chicks in any one hatch, irrespective of lines, were brooded together and reared intermingled in the same windowless intensive rearing house. Hatch groups were penned separately as a hatch in littered floor pens.

In 1967, selection was relaxed in the four lines, after 4 to 5 generations of selection. Reciprocal crosses between the lines in which egg weight had been markedly increased (Egg Weight and Regression) and between the 2 lines in which body weight had been reduced by selection (Body Weight and Ratio) were arranged. In most cases the same males as used to reproduce the selection lines themselves were used to produce line-cross progeny.

On housing at point-of-lay, the birds were placed at random in individual bird battery cages having a 9" frontage to the cage. The windowless laying house contained three blocks of double-sided, 3 tier battery cages which provide facilities for recording of individual bird performance. The flock was managed as in any normal commercial premises and fed a home-mixed layers ration.

The data analysed ~~is~~ are based on the record of survivors' egg production to 44 weeks of age. The week in which each bird laid its first egg was noted and egg production recorded on 3 days each week from 20 to 60 weeks of age. A high degree of correlation (r = 0·96) between 3 day per week recording and the full production record has been reported (Faber, 1960; Wheat, 1956). Any birds which died during this period were not included. All birds were weighed at 12, 28, 44 and latterly 60 weeks of age.

Eggs were weighed at 28, 44 and latterly 60 weeks of age, the birds egg weight record comprising the average of 3 - 4 eggs laid per hen within the week following that in which the bird reached the specific age.

## 2.1.2. Control population

This has been maintained as a pedigreed flock (except for 1963 and 1964) based upon the use of approximately 30 sires and 90 dams annually following a controlled random breeding procedure (Gowe, Alan Robertson and Latter, 1959). Thus an expected increase in the inbreeding coefficient ($\Delta F$) per generation of 0·35% can be calculated from the formula for a pedigreed control flock.

$$\Delta F = \frac{3}{32M} + \frac{1}{32F} \quad \text{(Gowe \underline{et al}., 1959)}$$

At the commencement of the experiment unlike the selected lines the control matings were kept together for all 4 hatches, although a rota of males was used in the control line breeding pens. Therefore, in the 1963 and 1964 generations, the control flock was only pedigreed to the dams but not the sires due to a shortage of accommodation. From 1965 onwards, when all matings were carried out by artificial insemination, a fully pedigreed control line was maintained.

## 2.2. Method of Computing Inbreeding Coefficients.

In this study, the actual inbreeding coefficients of the individuals were computed by a method first reported by Cruden (1949), Emick and Terrill (1949) and later designated the "coancestry" method by Falconer (1964). The coancestry technique calls for the computation of all possible combinations of matings between individuals of the base generation (Cruden, 1949). Falconer (1964) noted that this method did not differ in principle from Wright's (1922) coefficient of inbreeding method. Instead of considering the inbreeding of the progeny viz., inbreeding coefficient of Wright (1922), one could work out the degree of relationship by descent of its two parents, i.e. their 'coancestry' (Falconer, 1964). As the coefficient of inbreeding of an individual was dependent on the amount of common ancestry in its two parents, the coancestry value would be identical with that of the inbreeding coefficient.

A computer programme* (written in Atlas Autocode) was used to facilitate calculations of the inbreeding coefficients, using the coancestry matrix method (Cruden, 1949; Falconer, 1964) from the full pedigree information available on all the breeding individuals. The information required for preparation of the computer input was firstly the identity number** for the male and female breeders each generation along with their parental identity including the generation year.

The total number of breeders represented in each generation were then listed in their numerical sequence classified according to sex, along with their parentage (see Appendix 1).

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* Kindly loaned by Dr. W.G. Hill of the Institute of Animal Genetics, University of Edinburgh.

** A unique identification number is assigned to each member. This number once allocated cannot be changed from one generation to another.

The computation of coancestry began two years before the inception of the respective selection lines in order to obtain the inbreeding coefficients of the individuals of the generation before the so-called year of inception. In the case of the control line, computation of the coefficients of coancestry started in 1959, when random breeding for the whole strain was still in practice.

It should be noted that the original population in this study is a fairly large random-bred population from which the selected sub-lines and the control line were derived. This is assumed to be equivalent to the base population as defined by Falconer (1964) and by definition, it is assumed to possess an inbreeding coefficient of zero. Thus the designation of an individual as belonging to the original base population means that it will be assumed to have zero inbreeding coefficient.

# 3. RESULTS AND DISCUSSION

## 3.1.1. Calculated cumulative inbreeding levels in control population.

The effective number of breeding individuals (males (M) and females (F)) i.e. the number of parents in each generation with progeny surviving to breeding age, as well as the calculated effective number of parents (Ne), are given in Table 2.

Table 2

Effective number of breeding individuals, effective population size (Ne and changes in inbreeding (ΔF) in the randombred control population. (Strain 2, 1961-67).

| | Number of Parents | | | |
|---|---|---|---|---|
| Year | Males | Females | Ne† | ΔF** |
| 1961-62 | 34 | 162 | 169 | ·003 |
| 1962-63 | 35 | 124 | 172 | ·003 |
| 1963-64 | 80 | 29 | 85* | ·005 |
| 1964-65 | 70 | 42 | 105* | ·005 |
| 1965-66 | 32 | 82 | 154 | ·003 |
| 1966-67 | 32 | 77 | 150 | ·003 |
| 1967-68 | 33 | 85 | 154 | ·003 |
| | | | Total | ·025 |

† Ne (pedigreed randombred population)

*Ne = (Random mating) $\frac{4(M)(F)}{M + F}$ (Wright 1940)

** $\Delta F = \frac{3}{32M} + \frac{1}{32F}$ (Gowe *et al.*, 1959)

As mentioned earlier in the 1963 and 1964 generations, the control flock was only pedigreed to the dams but not the sires. The formula devised by Wright (1940) was used to calculate the effective population size for these two generations.

It is noted that the total cumulated F over the seven years of the control line, predicted from the calculated effective population size (Gowe et al., 1959) amounted to 2·5%, i.e. an average increase of 0·4% per year. This represents about one third of the average rate of increase in the inbreeding of the selection lines over 5 to 6 years. See Table 3, page 19.

### 3.1.2. Calculated cumulative inbreeding levels in selected populations.

The expected cumulative inbreeding coefficients within each of the 4 lines are given in Table 3. The computed estimates are also presented in the same table, making it possible to compare the rates of inbreeding as predicted from the effective population size (Wright, 1940) or from the actual pedigree information using the coancestry method (Cruden, 1949; Falconer, 1964). In the latter case the average annual increase in inbreeding over the 5 - 6 generations (1962-1967) are 1·4, 2·3, 1·5 and 1·6% in the Egg Weight, Regression, Body Weight and Ratio lines respectively, while the corresponding predicted levels were 1·0, 1·0, 1·0 and 1·1% respectively.

The actual rate of inbreeding as computed directly from the pedigree information is higher in all lines on account of the fact that the number of parents of both sexes represented each generation (see Appendices 2 and 3) were considerably more restricted than the effective number of breeders used to predict the rate of inbreeding. This situation can be caused through

## Table 3

## Effective Population size and changes in inbreeding (ΔF) annually in each of the selection lines

| Line | Year | Effective Population Size | | ΔF *Expected | ΔF **Actual |
|---|---|---|---|---|---|
| Egg Weight | 1961 | 112 | | ·004 | ·000 |
| | 1962 | 66 | → | ·008 | ·005 |
| | 1963 | 44 | | ·011 | ·000 |
| | 1964 | 48 | | ·010 | ·027 |
| | 1965 | 52 | | ·009 | ·007 |
| | 1966 | 39 | | ·013 | ·029 |
| | 1967 | 55 | | ·009 | ·017 |
| | | | Total | ·064 | ·085 |
| Regression | 1961 | - | | - | - |
| | 1962 | 112 | | ·004 | ·003 |
| | 1963 | 46 | → | ·011 | ·004 |
| | 1964 | 49 | | ·010 | ·041 |
| | 1965 | 44 | | ·011 | ·045 |
| | 1966 | 43 | | ·012 | ·020 |
| | 1967 | 66 | | ·008 | ·005 |
| | | | Total | ·056 | ·118 |
| Body Weight | 1961 | 112 | | ·004 | ·001 |
| | 1962 | 70 | → | ·007 | ·013 |
| | 1963 | 48 | | ·011 | ·000 |
| | 1964 | 48 | | ·011 | ·025 |
| | 1965 | 51 | | ·010 | ·034 |
| | 1966 | 41 | | ·012 | ·000 |
| | 1967 | 52 | | ·009 | ·017 |
| | | | Total | ·064 | ·090 |
| Ratio | 1961 | - | | - | - |
| | 1962 | 109 | | ·004 | ·000 |
| | 1963 | 45 | | ·011 | ·004 |
| | 1964 | 48 | → | ·010 | ·001 |
| | 1965 | 47 | | ·011 | ·038 |
| | 1966 | 38 | | ·013 | ·017 |
| | 1967 | 53 | | ·009 | ·020 |
| | | | Total | ·058 | ·080 |

* Predicted ΔF (approximately) = $\frac{1}{2}$Ne

where $Ne = \frac{4(NmNf)}{Nm + Nf}$ (Wright, 1940)

** Calculated F from actual pedigree was carried out by computer programme (coancestry matrix method) kindly loaned by Dr.W.G.Hill, Institute of Animal Genetics, University of Edinburgh.

→ Start of selection programme.

the lowered fertility of some parents or mortality resulting in the complete elimination of entire family groups.

The discrepancy between the expected and actual level of inbreeding is most noticeable in the Regression Line in which the computed total cumulative inbreeding coefficient is double the level estimated, i.e. 11·8% as compared to 5·6% (Table 3).

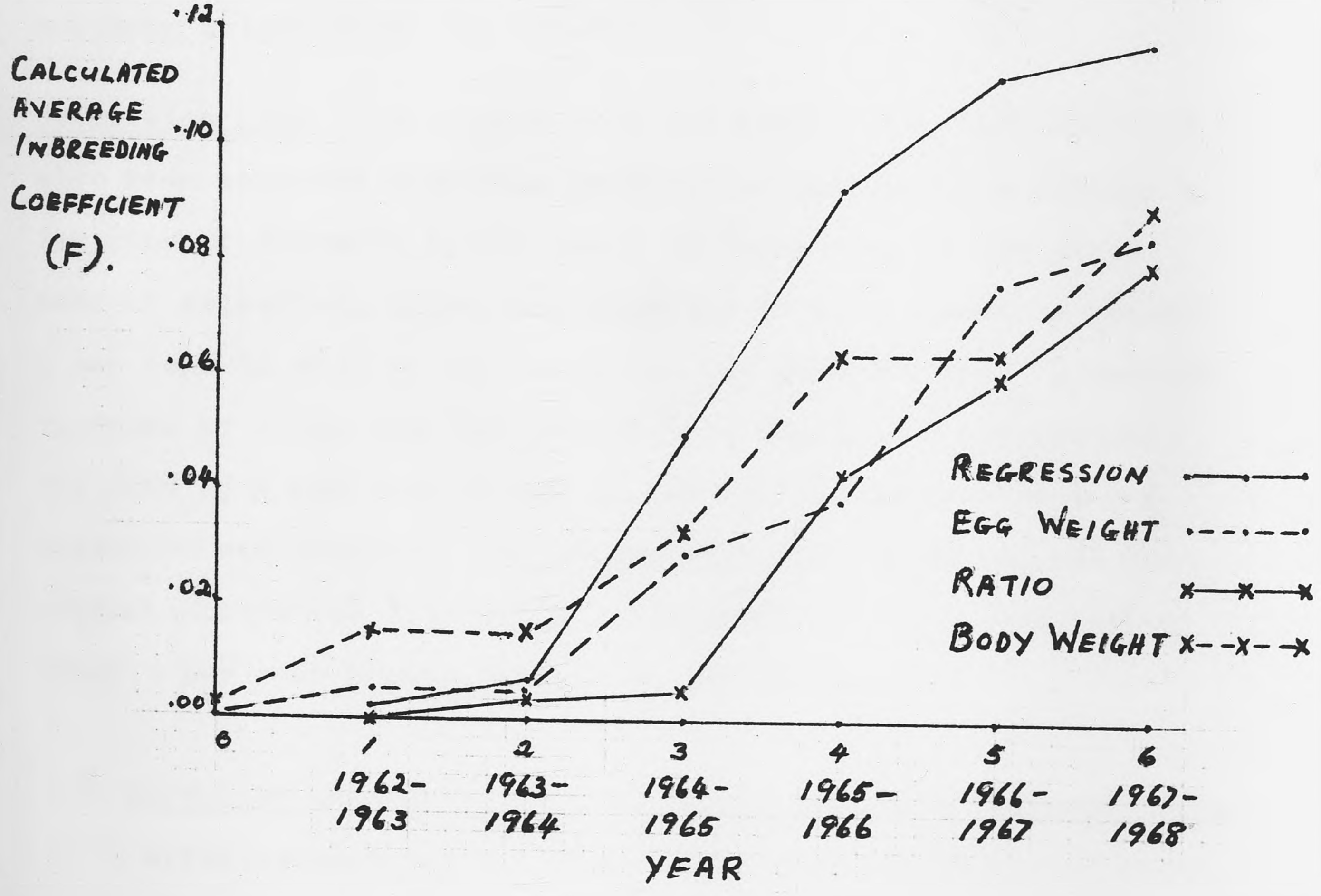
The calculated cumulative inbreeding coefficients within the four selected lines in Strain 2 are plotted graphically (Fig. 1). This is average unweighted inbreeding coefficient per generation.

Egg Weight and Body Weight Lines. As explained earlier, these selected sub-lines were initiated a year ahead of the other 2 lines. It is apparent that for the first generation of mild selection the amount of inbreeding within these 2 lines was minimal, similarly for the subsequent generation. However, commencing with the third generation of selection the rate of increase in the cumulative level of inbreeding rose markedly, with the exception of the fifth generation in the Body Weight line when no increase in the inbreeding coefficient resulted. Following five generations of selection the levels of inbreeding reached in the Egg Weight and Body Weight lines were 8 per cent and 7 per cent respectively. In the following generation of relaxed selection the level of inbreeding increased by a further 1 per cent approximately in the Egg Weight line and by almost 2 per cent in the Body Weight line.

Ratio Line. Although this line had been selected over four generations in comparison with the five generations in the Egg

FIGURE 1.

CHANGE IN THE UNWEIGHTED AVERAGE INBREEDING COEFFICIENTS WITHIN 4 SELECTED WHITE LEGHORN POPULATIONS.



Weight and Body Weight lines, the level of inbreeding approaches the level of inbreeding in the sixth generation of the Egg Weight and Body Weight lines. A low rate of increase in the level of inbreeding characterised the first two years of selection, increasing markedly to an increment of 4 per cent in the third generation and a more moderate increase of 2 per cent in the fourth generation. In 1967-68, when selection was relaxed, a similar rate of inbreeding to that evident in the Egg Weight and Body Weight lines was evident.

Regression Line. In common with the Ratio line, this line had also been selected over four generations and showed a similar low rate of increase in the level of inbreeding in the first year of selection, increasing markedly to an increase of around 4 per cent in each of the following two generations. A smaller increase of 2 per cent was recorded in the fourth generation, followed by ½ per cent change in the 1967-68 generation when selection was relaxed. The Regression line, however, had the highest cumulative inbreeding coefficient of all 5 lines being about 3 per cent higher than in any of the others.

### 3.2 Effect of inbreeding on performance traits in selected lines.

After determining the amount of inbreeding which had taken place in the course of selection over a period of 4 to 5 generations and 1 generation of relaxation, an attempt to estimate the likely effect of inbreeding on the overall performance in egg number and sexual maturity of the selection lines was carried out. Egg weight and body weight were not included because the effects of inbreeding on them were reported to be negligible or non-existent. (Blow and Glazener, 1953; Waters, 1941, 1945; Shoffner, 1948).

Table 4

Cumulative level of inbreeding and predicted depression in egg production traits within selected and control lines (Strain 2, 1967-68 generation)

| | | Predicted Depression in: | |
|---|---|---|---|
| Line: | Cum. ΔF (per cent) | Annual Egg Record (ΔF x 1·2) | Sexual Maturity (days) (ΔF x 0·4) |
| Egg Weight | 8·5 | 10·35 | 3·40 |
| Regression | 11·8 | 14·16 | 4·72 |
| Body Weight | 9·0 | 10·80 | 3·60 |
| Ratio | 8·0 | 9·60 | 3·20 |
| Control | 2·5 | 3·00 | 1·00 |

From the literature, the decline in annual egg production has been estimated to amount to 1·2 eggs (see text, page 6) for a 1 per cent increase in inbreeding. Thus the estimated decline in egg production to 60 weeks of age due to inbreeding in each of the selected lines should have amounted to 10·4, 14·2, 10·8 and 9·6 eggs in the Egg Weight, Regression, Body Weight and Ratio lines respectively (Table 4). The delay in sexual maturity, similarly, should, from prediction, have been of the order of 3·4, 4·7, 3·6 and 3·2 days respectively.

The predicted inbreeding depression in egg number and sexual maturity expressed as deviations from the control line were calculated from Table 4 above and listed in Table 5 beside the actual observed deviations.

Table 5

Predicted inbreeding depression in egg number and sexual maturity as compared to the observed deviations from the control.

| Line. | Full Egg Production Record (20-60 weeks) | | Sexual Maturity (days) | |
|---|---|---|---|---|
| | Observed Deviations | Predicted Depression Due to Inbreeding | Observed Deviations | Predicted Delay Due to Inbreeding |
| Egg Weight | -11·7** | -7·4 | -0·7 | +2·4 |
| Regression | -19·8*** | -11·2 | +3·5* | +3·7 |
| Body Weight | +6·0 | -7·8 | -1·4 | +2·6 |
| Ratio | +1·2 | -6·6 | +0·7 | +2·2 |

* Significant deviation from control line mean (P < 0·05)
** " " " " " " (P < 0·01)
*** " " " " " " (P < 0·001)

Thus the loss in egg number, after correction for the predicted effects of inbreeding (Table 5) in the Egg Weight and Regression lines were 4·3 and 8·6 eggs respectively (Table 6) and likewise the 'latent' gain in the 20-60 week egg number due to a downward selection of body weight in the Body Weight and Ratio lines were estimated to be 13·8 and 7·8 eggs respectively (Table 6).

Table 6

Assumed 'latent' genetic change in selected lines after correction for predicted inbreeding depression.

| Line | Full Egg Number Record (20-60 weeks) | Sexual Maturity (days) |
|---|---|---|
| Egg Weight | -4·3 | -3·1* |
| Regression | -8·6* | -0·2 |
| Body Weight | +13·8*** | -4·0** |
| Ratio | +7·8* | -1·5 |

*Significant deviation from control line mean (P < ·05)
** " " " " " " (P < ·01)
*** " " " " " " )P < ·001)

Egg number

It is noted that in the lines selected for high egg weight, the depression in egg number due to inbreeding accounted for about 2/3 of the observed deviation from the control (Table 5). Festing and Nordskog (1967) similarly found that, the decline in egg production rate, which occurred in the course of selection for egg weight in White Leghorn and Fayoumi poultry, was greater than could be accounted for solely by inbreeding depression.

The observed mean 20-60 week egg number in the Egg Weight and Regression lines was significantly lower ($P < \cdot 01$ and $\cdot 001$ respectively) than the control population (Table 5). This was expected as Manson (1970) reported a negative genetic correlation of 0·31 between 28 week egg weight and 20-60 week egg number in this particular poultry population.

After correction for predicted inbreeding depression, however, the 20-60 week egg number in the Egg Weight line was not significantly different, whereas in the Regression line egg number had remained significantly lower ($P < \cdot 05$) than the control (Table 6). It would thus appear that evidence of a realised negative genetic correlation between egg weight and egg number was not consistent in this experiment.

Casey and Nordskog (1967) had reported that egg number in their high egg weight selected line was lower than in the control line. Presumably the effect of inbreeding had been taken into account in their conclusion.

In the two lines selected for low body weight, the observed

20-60 week egg number mean in the Body Weight and the Ratio lines were 6·0 and 1·2 eggs respectively greater than the control mean but these differences were not significant. After correction for the effect of inbreeding, however, egg number in both the low body weight lines was significantly ($P < \cdot001$, $P < \cdot05$) higher than in the control line (Table 6) indicating the existence of a realised negative genetic correlation between body weight and egg number in this particular population of fowls. However, Manson (1970) had reported a positive genetic correlation of 0·43 between 28-week body weight and 20-60 week egg number part record for the same strain. Casey and Nordskog (1967) observed in their experiment a reduced egg number in their low body weight line, but a similar decline was also noted in the high body weight line.

### Sexual maturity

As regards age at first egg, the observed result in the Regression line was significantly higher ($P < \cdot05$) than that in the control population (Table 5). However, after adjustment for inbreeding effect, the age at first egg was not significantly different from the control (Table 6). On the other hand, in the Egg Weight line, age at first egg was not significantly different from that observed in the control but after adjustment it was found to be significantly earlier ($P < \cdot05$).

In the case of the 2 body weight sub-lines the observed results in both of them were not significantly different from that observed in the control. After adjustment for inbreeding effect, however, age at first egg in the Body Weight line was significantly

($P < \cdot05$) earlier than in the control population (Table 6).

### 3.3. Mean performance of selected lines following a generation of relaxed selection.

Previous workers have shown a regression when selection in a population is suspended for any length of time following several generations of intense selection, in Drosophila abdominal bristles by Mather and Harrison (1949), Robertson and Reeve (1952), Clayton, Morris and Robertson (1957); in the case of selection for shank length in poultry by Lerner (1958) and for adult viability by Moultrie, Cottier and King (1956). However, Shoffner and Grant (1960) did not find any significant regression for egg production, viability, hatchability, or 8-week-body weight after three generations of relaxed selection in a White Leghorn strain selected mainly for egg number over 25 generations. Bohren and McKean (1964) found no evidence of a decline due to relaxation in a White Leghorn population previously selected for high egg numbers.

Nordskog and Giesbrecht (1964) observed a significant regression for egg number but not for adult viability, fertility or hatchability in three commercial strains of chicken when selection was relaxed for 7 generations. The populations were assumed to have plateaued for egg production and the amount of inbreeding was estimated to be 1·7 per cent per generation. The authors reckoned that about one quarter of the egg production decline from relaxed selection in their experiment can be accounted for by inbreeding.

In order to observe the effects of one generation of relaxed selection on the mean performance of the selected lines, the annual trend in performance of the selected lines relative to the control line are presented graphically in Figures 2, 3 and 4.

Egg Weight line:

It will be noted in Figure 2 that body weight in the Egg Weight line, after 5 generations of selection was significantly greater than in the control (P < ·001) as a result of the correlated response to selection for 28-week egg weight (See Appendix 4). After the second or third generation, however, the upward trends were checked and in 1966 the body weight traits showed a downward trend. This agreed with the findings of Festing and Nordskog (1967), Schultz (1953).

After one generation of relaxed selection in egg weight, the secondary body weight traits were still maintained significantly above (P < ·001) the control population. The 28-week body weight had begun to rise again, while the 44-week body weight carried on the downward trend. Nordskog and Giesbrecht (1964) found no regression in adult body weight after relaxation of selection.

The primary selected trait, i.e. egg weight at 28 weeks, continued to respond to selection up to the 5th generation (Fig. 3).

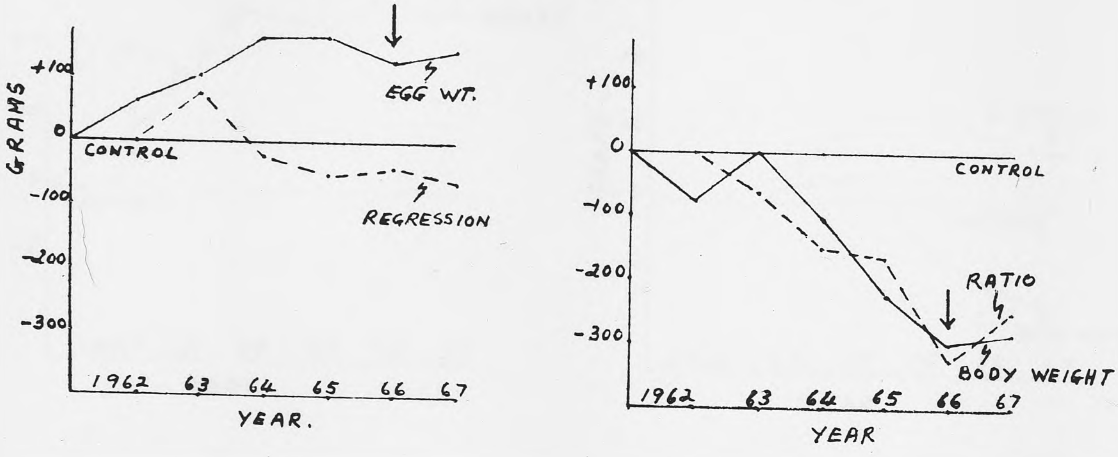
Following one generation of relaxed selection, egg weight still remained significantly (P < ·001) above the control population mean. In fact, 28 week egg weight increased still further on relaxation. Nordskog and Giesbrecht reported some regression in egg weight after relaxation of selection.

Because egg numbers have a low heritability and closely

FIG. 2

CONTINUATION OF TRENDS IN BODY WEIGHT IN SELECTED LINES, STRAIN 2, 1962-67 (DEVIATIONS FROM CONTROL).

28 WEEKS



44 WEEKS

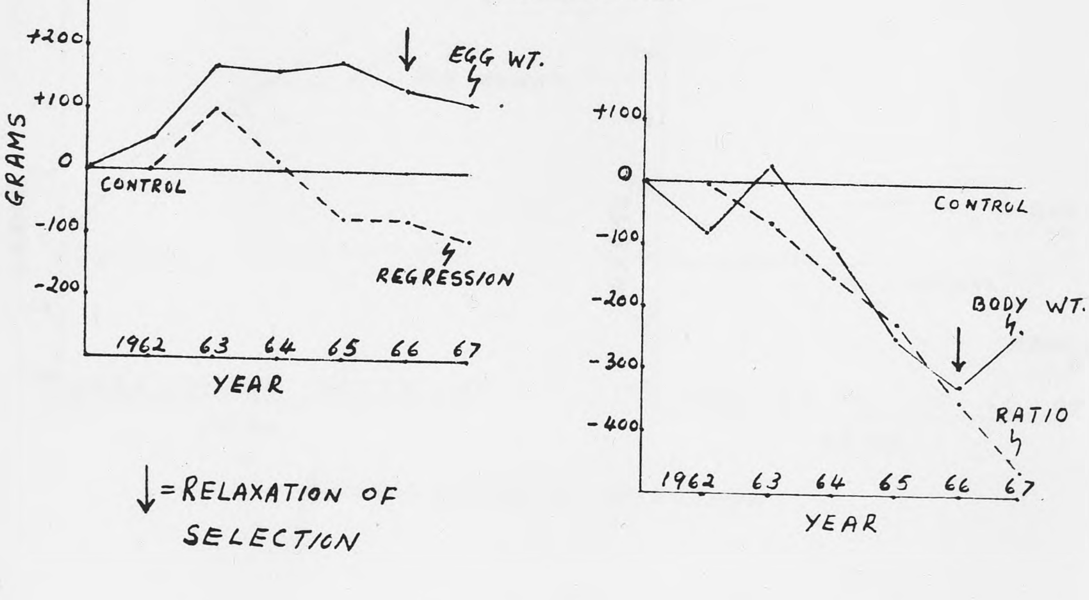
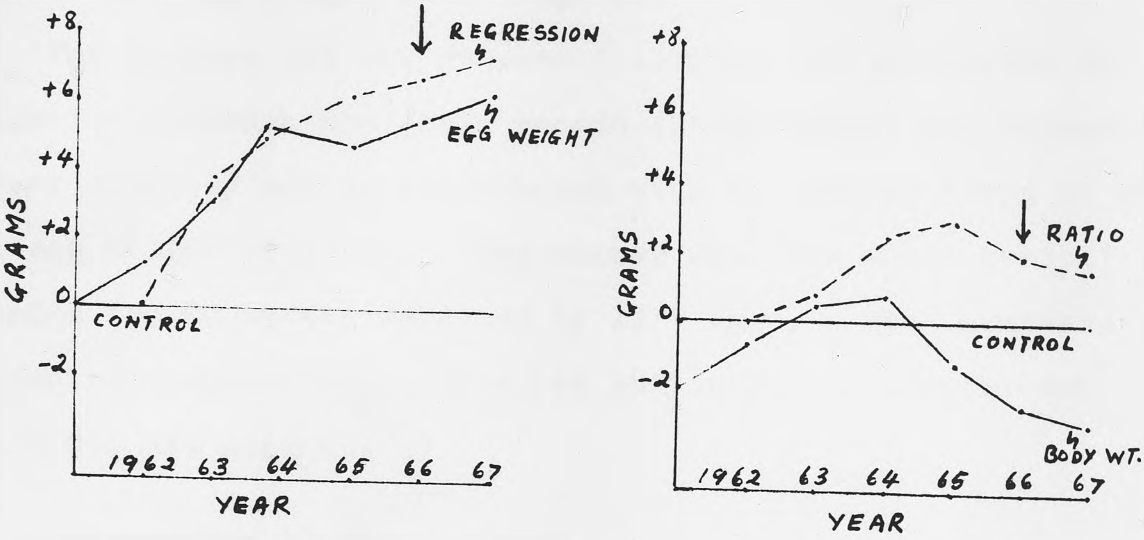


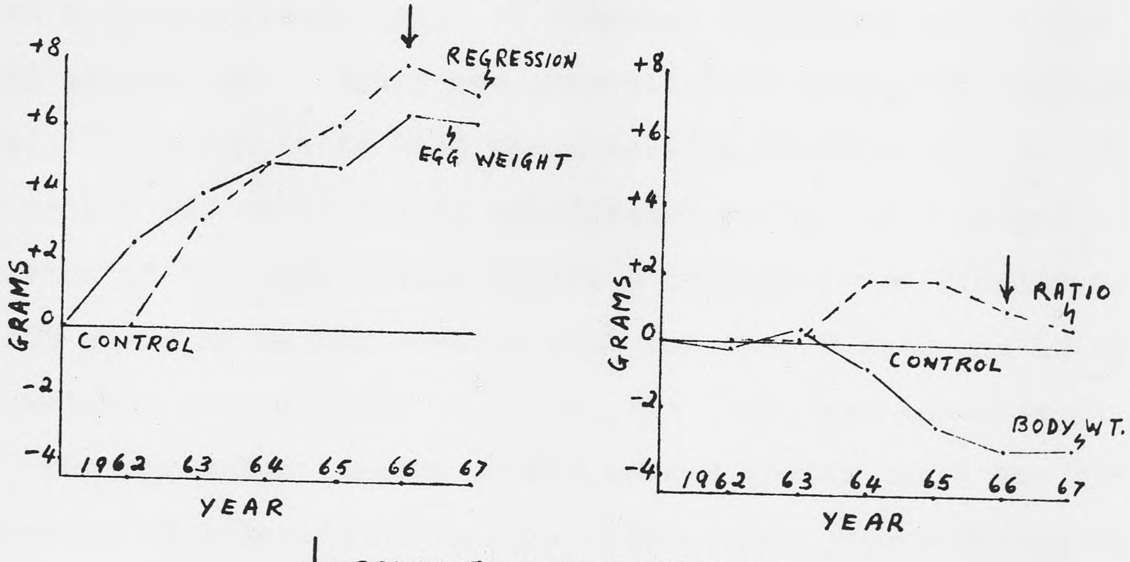
FIG. 3

CONTINUATION OF TRENDS IN EGG WEIGHT IN SELECTED LINES, STRAIN 2, 1962-67, (DEVIATIONS FROM CONTROL).

28 WEEKS



44 WEEKS



↓=RELAXATION OF SELECTION

related to natural fitness, this trait tends to be most affected by inbreeding depression. This combined with the fact that egg numbers are negatively correlated genetically with egg weight, egg numbers would be expected to decline below the control line means in the Egg Weight line (Fig. 4).

Egg numbers did not recover following one generation of relaxation although the early record (20-44 weeks) did appear to recover slightly and in association with an upwards trend in 28-week egg weight (Fig. 3). Egg number over the whole period recorded (20-60 weeks) declined by 11·7 eggs, when compared to the control population. This was statistically significant (P < 0·01, see Appendix 4).

### Regression line:

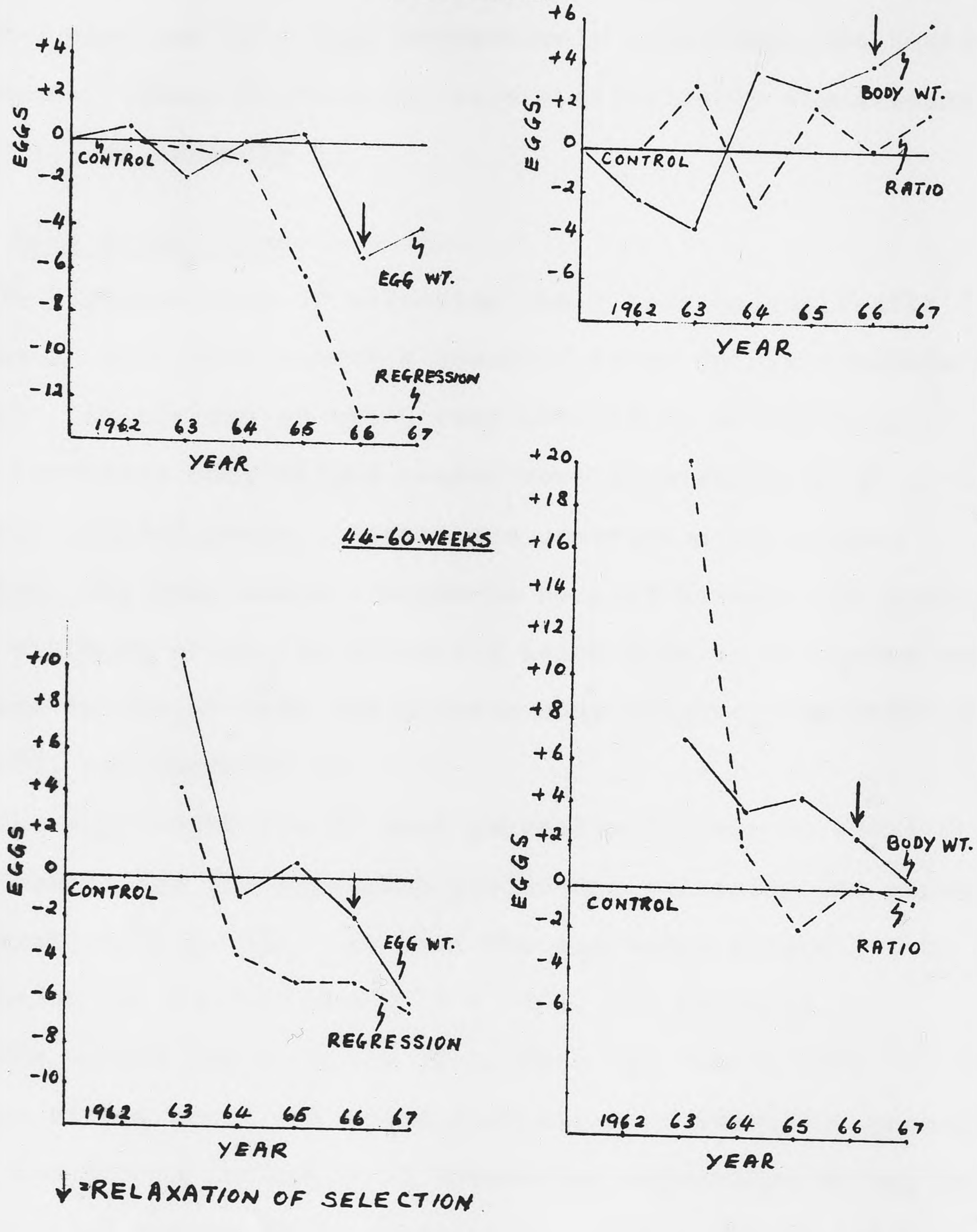
After 4 generations of selection, the body weight traits showed downward trends (Fig. 2) somewhat levelling off at the fourth generation. After one generation of supposedly relaxation (it will be shown later that the selection differential in 28-week body weight was still fairly significant being -27·8 grams) reduction of the body weight traits continued, to be finally 60 grams, and 109 grams below the control line for the 28 week and 44 week body weights respectively (P < ·01, P < ·001; see Appendix 4).

The egg weight traits showed upward trends until the final generation of selection (Fig. 3). The early 28-week egg weight continued to increase even after a generation of relaxed selection but the later 44-week egg weight had levelled off. The egg weights were then about 6 grams heavier than the control line (P < ·001; see Appendix 4).

FIG. 4.

CONTINUATION OF TRENDS IN EGG NUMBER (FULL RECORD) IN SELECTED LINES, STRAIN 2, 1962 – 67 (DEVIATIONS FROM CONTROL).

20-44 WEEKS



↓ = RELAXATION OF SELECTION

After 5 generations of selection, the egg number traits had fallen below the control line means. After a generation of relaxed selection the egg number traits had levelled out. The egg numbers (full record) of the 20-44 week and 20-60 week periods were 12·7 eggs and 15·2 eggs respectively lower than the control line means. These differences were statistically significant (P < ·001, see Appendix 4).

Body Weight line.

In 5 generations of selection the 2 body weight traits recorded in this line showed a downward trend fairly consistently (Fig. 2) At the end of the 5 year selection period these highly heritable body weight traits were significantly (P < ·001) below the control means. After one generation of relaxed selection, the body weights began to recover towards the control means, although still significantly below them by 280 grams and 244 grams in the 28-week and 44-week body weights respectively (P< ·001, see Appendix 4).

The egg weight trends were generally similar to those of body weight trends for the selection period and following one generation of relaxation (Fig. 3). By then the egg weights were 2·5 to 3·3 grams below the control means (P < ·001, see Appendix 4).

The upward trend of the 20-44 week egg number (Fig. 4) did not take effect until the third generation of selection probably due to the strong influence of inbreeding depression on egg number counteracting the negative correlated response due to low body weight selection. The 44-60 week egg number record was started only in the second year of selection. The egg number in the 44-60 week period followed a slightly downward trend; this trend was carried on after one year of relaxed selection in low body weight. The early egg number (20-44 week) carried on an upward trend after relaxation of selection to be significantly ($P < \cdot05$) above the control mean by 6 eggs.

### Ratio line.

The body weight traits showed downward trend until the final year of selection (Fig. 2). After one generation of relaxation, the 28-week body weight reversed direction to an upward trend, but the 44 week body weight continued the downward trend. Both traits were still significantly below the control means ($P < \cdot001$).

The egg weight traits showed an upward trend (Fig. 3) early on in the selection and levelled off by the third generation. After one year of relaxed selection the 28-week egg weight was significantly ($P < \cdot001$) above the control mean whereas the 44-week egg weight was no different from the control mean (see Appendix 4).

The egg number traits were greater than the control means after the first year of selection but fell to the level of the control population and remained so after one generation of relaxation.

### Incidental selection differentials applied in selection lines following relaxation of selection.

A summary of the calculated realised selection differentials presented in Table 7 indicated that the primary traits i.e. up selection for egg weight and down selection for body weight have been relaxed in all lines in the last generation. One exception is the down selection of body weight in the Regression line, the selection differential in 28-week body weight was in the region of -28 grams (-1½ per cent of the mean 28-week body weight of the previous generation of the Regression line).

Table 7

Selection differentials applied incidentally through relaxation of selection within selected lines, Strain 2, 1967-68.

| Line | Body Weight (grams) 12 weeks | Body Weight (grams) 28 weeks | Egg Weight (grams) 28 week |
|---|---|---|---|
| Egg Weight | -1·1 | -17·2 | +0·2 |
| Regression | -16·5 | -27·8 | +0·1 |
| Body Weight | -4·0 | -11·3 | +0·7 |
| Ratio | +7·7 | +16·3 | 0 |

## 3.4 Comparative performance of crosses between selected populations

The mean performance of the selected lines following one generation of relaxed selection and of the specific crosses between them are compared alongside the performance of the control population in Tables 8 and 9.

### Egg Weight and Regression lines and their reciprocal crosses

Mean body weight in the Egg Weight line (Table 8) was substantially greater, while it was significantly ($P < \cdot 001$) lower in the case of the Regression line compared with the Control. Both reciprocal crosses were higher in mean body weight when compared to the control population, but the observed differences were only

# TABLE 8

Weighted mean deviations of selected lines (Egg Weight, Regression) and inter-line crosses from randombred control (1967-68)

|  | TRAIT |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| LINE | Body Weight (grams) |  | Egg Weight (grams) |  |  | Age at first egg (weeks) | Egg Number (Part record) |  |  | Number of pullets recorded |
|  | 28 (weeks) | 44 | 28 | 44 (weeks) | 60 |  | 20-44 | 44-60 (weeks) | 20-60 |  |
| CONTROL MEAN: | 1966 | 2101 | 50·5 | 58·4 | 62·3 | 23·9 | 47·3 | 27·8 | 75·2 | 243 |
| DEVIATIONS FROM CONTROL MEAN: |  |  |  |  |  |  |  |  |  |  |
| EGG WEIGHT | $+140^{***}$ | $+85^{***}$ | $+6·2^{***}$ | $+6·1^{***}$ | $+5·6^{***}$ | -0·1 | -1·7 | $-3·5^{**}$ | $-5·1^{**}$ | 104 |
| REGRESSION | $-60^{**}$ | $-109^{***}$ | $+7·1^{***}$ | $+7·3^{***}$ | $+6·8^{***}$ | $+0·5^{*}$ | $-5·5^{***}$ | $-3·1^{*}$ | $-8·6^{***}$ | 124 |
| EGG WEIGHT x REGRESSION | $+85^{***}$ | +34 | $+6·5^{***}$ | $+6·2^{***}$ | $+5·6^{***}$ | -0·1 | $-4·2^{**}$ | $-3·5^{**}$ | $-7·8^{***}$ | 123 |
| REGRESSION x EGG WEIGHT | $+38^{*}$ | +15 | $+7·3^{***}$ | $+7·0^{***}$ | $+6·9^{***}$ | +0·1 | $-3·4^{**}$ | $-3·8^{***}$ | $-7·2^{***}$ | 117 |
| STD. ERROR OF DIFFERENCE BETWEEN CONTROL LINE & SELECTED POPULATION: | ±19 | ±24 | ±0·4 | ±0·4 | ±0·6 | ±0·2 | ±1·3 | ±1·1 | ±1·7 | - |

* Significant difference (P < ·05)

** " " (P < ·01)

*** " " (P < ·001)

significant at 28 weeks of age. It was also noted that the body weight of the crosses was significantly different ($P < 0{\cdot}05$ - Table 9) from the mid-parental value in the Egg Weight x Regression cross. The Egg Weight x Regression cross was heavier than the reciprocal cross at 28 and 44 weeks of age but only significantly ($P < {\cdot}05$) so at 28 weeks (Table 10).

Egg weight measured at 28, 44 and 60 weeks as expected, was significantly ($P < {\cdot}001$) above the Control line mean in both pure lines and the reciprocal crosses (Table 8). The egg weight of the Regression x Egg Weight cross was above the midparental value, but not significantly so (Table 9). At 28 weeks old, the Regression x Egg Weight cross laid eggs which were significantly ($P < {\cdot}05$) heavier than those of the reciprocal cross by 0·8 grams (Table 10).

Age at first egg in the Regression line was significantly retarded ($P < {\cdot}05$) compared with the control population, while that of the Egg Weight line and both the reciprocal crosses remained approximately the same as the control (Table 8).

Egg numbers in both the Egg Weight and Regression lines had declined appreciably during the course of selection (Manson, 1970), and were still significantly ($P < {\cdot}001$) below the control line mean in the 20-60 week period. However in the case of the Egg Weight line, the early (20-44 week) egg number record was not significantly declined (Table 8). Both reciprocal crosses also produced significantly ($P < {\cdot}001$) fewer eggs when compared to the control population (Table 8) but their mean egg production level did not

## TABLE 9

Midparent performance of selection lines (Egg Weight and Regression) and the mean performance of their reciprocal crosses. Strain 2. 1967-68.

| | TRAIT | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Body Weight (grams) | | Egg Weight (grams) | | Age at first egg (weeks) | Egg Number (Part record) (weeks) | | | Number of pullets recorded |
| | 28 (weeks) | 44 | 28 (weeks) | 44 | | 20-44 | 44-60 | 20-60 | |
| Midparent performance between Egg Weight and Regression lines | 2006 | 2089 | 57·2 | 65·1 | 24·1 | 43·7 | 25·5 | 69·2 | 228 |
| Egg Weight x Regression inter-line cross | 2051 | 2135 | 57·0 | 64·6 | 23·8 | 43·1 | 24·3 | 67·4 | 123 |
| Differences between Midparent Performance and Egg Weight x Regression | +45* | +54* | -0·2 | -0·5 | -0·3 | -0·6 | -1·2 | -1·8 | - |
| Regression x Egg Weight inter-line cross | 2004 | 2116 | 57·8 | 65·4 | 24·0 | 43·9 | 24·0 | 68·0 | 117 |
| Difference between Midparent Performance and Regression x Egg Weight | 2 | +27 | +0·6 | +0·3 | -0·1 | +0·2 | -1·5 | -1·2 | - |
| Standard Error of Difference between Midparent and the Crossbred Population | ± 18·4 | ± 23·0 | ±0·4 | ±0·4 | ±0·2 | ±1·2 | ±1·1 | ±1·7 | - |

* Significant difference (P < ·05)
** " " (P < ·01)
*** " " (P < ·001)

## TABLE 10

Differences in Mean Performance Between the Selection Line Reciprocal Crosses

| | TRAIT | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Body Weight (grams) | | Egg Weight (grams) | | Age at first egg (weeks) | Egg Number (Part record) | | | No. of Pullets recorded |
| | 28 (weeks) | 44 | 28 (weeks) | 44 | | 20-44 (weeks) | 44-60 | 20-60 | |
| Difference between the reciprocal crosses:- | | | | | | | | | |
| (a) (Egg Weight x Regression) - (Regression x Egg Weight) | +47* | +19 | -0·8* | -0·8 | -0·2 | -0·8 | +0·3 | -0·6 | 120 |
| (b) (Body Weight x Ratio) - (Ratio x Body Weight) | +20 | -157*** | -0·1 | +0·1 | -0·2 | +1·7 | +0·6 | +2·5 | 130 |
| Standard Error of difference between reciprocal crosses: | ±21·1 | ±26·4 | ±0·4 | ±0·5 | ±0·2 | ±1·4 | ±1·2 | ±1·9 | - |

* Significant difference (P < ·05)
** " " (P < ·01)
*** " " (P < ·001)

deviate from the midparental value (Table 9).

Body Weight and Ratio lines and their reciprocal crosses

In these two low body weight selected lines and their reciprocal crosses, body weight at all recorded ages has been significantly ($P < \cdot 001$) reduced from the control population (Table 11). Only the mean 44-week body weight of the reciprocal crosses was significantly ($P < \cdot 05$; $P < \cdot 001$) above the midparental value (Table 12). Although this is so, the 44-week body weight of the interline crosses, as noted above, was still significantly ($P < \cdot 001$) below the control line mean (Table 11).

The Ratio x Body Weight cross showed a high 44-week body weight and the reciprocal difference (+ 157 grams) was significant ($P < \cdot 001$) when compared to the Body Weight x Ratio crossbred line (Table 10).

In the Body Weight line, egg weight was significantly ( $P < \cdot 001$) below the control (Table 11). In the Ratio line, on the other hand, egg weight exceeded that in the control but only the difference for 28-week egg weight was significant ($P < \cdot 001$).

In the Body Weight x Ratio cross, the 44-week and 60-week egg weights were significantly ($P < \cdot 05$) below the control means (Table 11). In the reciprocal, Ratio x Body Weight cross, the 28-week egg weight was significantly ($P < \cdot 01$) greater than the control mean, although the 44 and 60-week egg weights were significantly ($P < \cdot 05$) below the control means similar to those noted in the other cross.

## TABLE 11

Weighted mean deviations of selection lines (Body Weight, Ratio) and interline crosses from randombred control (1967-68)

TRAIT

| LINE | Body Weight (grams) | | Egg Weight (grams) | | | Age at first egg (weeks) | Egg Number (Part record) | | | Number of pullets recorded |
|---|---|---|---|---|---|---|---|---|---|---|
| | 28 (weeks) | 44 | 28 | 44 (weeks) | 60 | | 20-44 | 44-60 (weeks) | 20-60 | |
| CONTROL MEAN | 1966 | 2101 | 50·5 | 58·4 | 62·3 | 23·9 | 47·3 | 27·8 | 75·2 | 243 |
| BODY WEIGHT | -280*** | -244*** | -2·5*** | -2·9*** | -3·3*** | -0·2 | +2·6* | +0·1 | +2·6 | 116 |
| RATIO | -246*** | -456*** | +1·7*** | +0·3 | +0·5 | +0·1 | +0·8 | -0·2 | +0·5 | 132 |
| BODY WEIGHT x RATIO | -269*** | -305*** | +0·2 | -0·9* | -1·2* | -0·1 | +2·7* | +1·5 | +4·3* | 128 |
| RATIO x BODY WEIGHT | -289*** | -148*** | +1·2** | -1·0* | +1·6** | +0·1 | +1·0 | +0·9 | +1·8 | 132 |
| STD. ERROR OF DIFFERENCE BETWEEN CONTROL LINE & SELECTED POPULATION: | ±19 | ±24 | ±0·4 | ±0·4 | ±0·6 | ±0·2 | ±1·3 | ±1·1 | ±1·7 | - |

* Significant difference (P < ·05)
** " " (P < ·01)
*** " " (P < ·001)

## TABLE 12

Midparent performance of selection lines (Body Weight and Ratio) and the mean performance of their reciprocal crosses. Strain 2. 1967-68.

| | TRAIT | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Body Weight (grams) | | Egg Weight (grams) | | Age at first egg (weeks) | Egg Number (Part record) | | | Number of pullets recorded |
| | 28 (weeks) | 44 | 28 (weeks) | 44 | | 20-44 (weeks) | 44-60 | 20-60 | |
| Midparent performance between Body Weight and Ratio lines | 1703 | 1751 | 50·1 | 57·1 | 23·8 | 49·0 | 27·7 | 76·7 | 248 |
| Body Weight x Ratio interline cross | 1697 | 1796 | 50·7 | 57·5 | 23·8 | 50·0 | 29·3 | 79·4 | 128 |
| Difference between Midparent Performance and Body Weight x Ratio | -6 | +45* | +0·6* | +0·4 | 0·0 | +1·0 | +1·6 | +2·7 | - |
| Ratio x Body Weight interline cross | 1677 | 1953 | 51·7 | 57·4 | 24·0 | 48·3 | 28·6 | 77·0 | 132 |
| Difference between Midparent Performance and Ratio x Body Weight | -26 | +202*** | +1·6*** | +0·3 | +0·2 | -0·7 | +0·9 | +0·3 | - |
| Standard Error of Difference between Midparent and the Crossbred population | ±17·9 | ±22·4 | ±0·3 | ±0·4 | ±0·2 | ±1·2 | ±1·0 | ±1·6 | - |

* Significant difference (P < ·05)
** " " (P < ·01)
*** " " (P < ·001)

No reciprocal differences were found in the egg weight traits (Table 10).

Age at first egg was not significantly different from the control mean in the pure lines and in the reciprocal crosses (Table 11).

Egg numbers in the Ratio line were approximately the same as the Control line, while those in the Body Weight line had increased, but the difference was only significant ($P < \cdot 05$) in the 20-44 week period (Table 11). The Body Weight x Ratio cross gave a significantly ($P < \cdot 05$) higher egg production than the control in the 20-44 week period, but the Ratio x Body Weight cross did not show a similar gain. No heterosis above the midparental value in respect of egg number was detected.

There were no significant reciprocal differences detected in the egg number traits in the low body weight selected lines.

In summarising the performance of the selected lines and their reciprocal crosses it is relevant to determine if there was any evidence of:

(a) A permanent loss of egg production genes in any of the selection lines

(b) Apparent heterosis as regards the performance of inter-line crosses

(c) Significant reciprocal cross differences amongst the above crosses which might indicate sex-linked or maternal effects.

### (a) Correlated decline in egg numbers following egg weight selection

There is evidence of a permanent decline in egg numbers in the high egg weight selected lines since the mean egg production of the reciprocal crosses was significantly ($P < .001$) below the control (Table 8). The decline in egg numbers when expressed as a full egg number record (2.33 x part record) to 60 weeks of age, was -18.2 and -16.8 eggs in the case of the Egg Weight x Regression and Regression x Egg Weight crosses respectively. This decline must presumably be attributed to the process of selection *per se* and/or random drift.

Casey and Nordskog (1967) examined the performance of crosses between lines selected for body weight and egg weight in opposite directions, but found no evidence of any permanent loss in egg production following 5 to 9 generations of selection.

### (b) Heterotic effects in performance of line crosses

As regards evidence of heterosis in the performance of the inter-line crosses mean body weight measured both at 28 and 44 weeks of age was significantly ($P < .05$) higher than the mid-parental value in the Egg Weight x Regression progeny (Table 9).

Both reciprocal crosses between the Body Weight and Ratio lines were significantly heavier at 44 weeks and also produced significantly heavier eggs at 28 weeks compared with the midparent value for each of these traits (Table 12). No heterosis was evident in sexual maturity in any of the crosses.

Hutt and Cole (1952) reported that White Leghorn interstrain crosses, when compared to their purebred half-sisters, began laying 5 days earlier, laid more, and heavier eggs and were heavier in body weight at maturity. The estimated inbreeding coefficients in the White Leghorn strains in the above study ranged from 0.08 to 0.12. On the other hand, Warren (1942) working with crosses between strains of Leghorns with unstated degrees of inbreeding, found the strain-crosses to excel the parental strains in egg production only and no heterotic effects on the other economic characters were detected.

In this experiment, the evidence for heterosis in the principal performance traits was not consistent. This is not unexpected considering that the 4 sub-lines were:-

(i) from a common base population (strain 2)

(ii) selected for improvements and maintained as distinct lines for only 4 to 5 generations

(iii) The crosses were between high egg weight lines or low body weight lines selected in the same direction.

(c) Reciprocal cross differences

The reciprocal differences observed in this study indicated that sex-linked inheritance may be of importance with respect to body weight and egg weight in the domestic fowl; e.g. the Egg Weight x Regression cross was significantly ($P < .05$) heavier by 47 grams at 28 weeks when compared with the reciprocal cross (Table 10). Since the Egg Weight line (sire line) was heavier than the Regression line at 28 weeks (Manson, 1970), it may be assumed that a sex-linked inheritance in 28-week body weight had caused the significant increase in the female 28-week body weight of the Egg Weight x Regression cross.

Furthermore, 28-week egg weight was observed to be significantly ($P < .05$) greater by 0.8 grams in the Regression x Egg Weight cross, compared with the reciprocal cross (Table 10). As the sire line, in this case the Regression line, has been shown to lay heavier eggs at 28 weeks of age than the Egg Weight line (Manson, 1970), a sex-linked effect on egg weight inheritance is suggested. Osborne (1953) found evidence of sex linkage in the inheritance of spring egg weight in the domestic fowl.

There was no evidence in this experiment from the reciprocal crosses studied of any maternal effects on any of the performance traits measured. It was not surprising that no maternal effects were observed at least for mature body weight, as a number of investigators (Wiley, 1950; Callenback, 1953; Pope and Schaible, 1958; Goodwin, 1961; and Oluyemi, 1965) have reported that a maternal effect operating through the egg weight of the dam on growth rate of the domestic fowl is transient, and while significant at least up to broiler age, is no longer apparent at maturity.

## [illegible]

The degree of inbreeding computed directly from the recorded pedigrees ([illegible], [illegible]) and estimated indirectly from the population size ([illegible], [illegible]) were presented for comparison. Computed from the pedigrees, the average rates of inbreeding over the 5/6 generations were [illegible], [illegible], 1·5, and 1·6 per cent in the Egg Weight, Regression, Body Weight and Ratio lines respectively. Computed from the population size, the average rates of inbreeding over the same periods were estimated to be 1·0, 1·0, 1·0 and 1·1 per cent in the respective lines. It was apparent that the rates of inbreeding computed from the pedigrees were on the whole higher. The average rate of inbreeding of the control population estimated indirectly from the population size was around 0·4 per cent per generation.

An estimate of the likely effect of the cumulative inbreeding over a period of 4/5 generations in each of the selected lines on the egg number record, enabled the reporting of the adjusted values in the 20-60 week egg number record. These corrected values indicated a significant ([illegible]) loss of 8·6 eggs in the Regression line (Table [illegible]). [illegible] (1970) had reported a substantial decline in egg production occurring within the Regression line when investigating data of a previous generation and which cannot be accounted for entirely by inbreeding. In this study concerning the 1967 generation, [illegible] of the decline has been shown to be due to inbreeding (Table [illegible]).

There was only some evidence of a realised negative genetic correlation (rg) between [illegible]-week egg weight and 20-60 week egg

## 4. CONCLUSIONS

The degree of inbreeding computed directly from the recorded pedigrees (Cruden, 1949) and estimated indirectly from the population size (Wright, 1940) were presented for comparison. Computed from the pedigree, the average rates of inbreeding over the 5/6 generations were 1·4, 2·3, 1·5, and 1·6 per cent in the Egg Weight, Regression, Body Weight and Ratio lines respectively. Computed from the population size, the average rates of inbreeding over the same periods were estimated to be 1·0, 1·0, 1·0 and 1·1 per cent in the respective lines. It was apparent that the rates of inbreeding computed from the pedigrees were on the whole higher. The average rate of inbreeding of the control population estimated indirectly from the population size was around 0·4 per cent per generation.

An estimate of the likely effect of the cumulative inbreeding over a period of 4/5 generations in each of the selected lines on the egg number record, enabled the reporting of the adjusted values in the 20-60 week egg number record. These corrected values indicated a significant ($P < \cdot 05$) loss of 8·6 eggs in the Regression line (Table 6). Manson (1970) had reported a substantial decline in egg production occurring within the Regression line when investigating data of a previous generation and which cannot be accounted for entirely by inbreeding. In this study concerning the 1967 generation, 2/3 of the decline has been shown to be due to inbreeding (Table 5).

There was only some evidence of a realised negative genetic correlation ($r_g$) between 28-week egg weight and 20-60 week egg number in this study to support the finding of a rg of -0·31 between the 2 traits in this particular White Leghorn population by Manson (1970), as the egg number recorded to 60 weeks of age in the Regression line has been shown to be significantly ($P < \cdot05$) lower than in the control (Table 6) but it was not so for the Egg Weight line.

Egg number records up to 60 weeks of age, adjusted for inbreeding effect, were estimated to be significantly ($P < \cdot001$; $P < \cdot05$) higher by 13·8 and 7·8 eggs respectively, in the Body Weight and Ratio lines, when compared to the control line (Table 6). These results, however, are contradictory to expectations as a positive genetic correlation (rg = +0·43) between 28-week body weight and 20 - 60-week egg number in this particular poultry population has been reported by Manson (1970).

Age at first egg, after correction for the effect of inbreeding was estimated to have significantly declined by 3·1 ($P < \cdot05$) and 4·0 ($P < \cdot01$) days respectively in the Egg Weight and Body Weight lines, when compared to the control population.

The significant ($P < \cdot05$) egg number increase found in the Ratio line was perhaps the result of an increase in the rate of egg production since the age at first egg in this line was concluded to be not significantly earlier.

The effect of one generation of relaxed selection on mean performance following termination of the selection experiment was observed. Body weight in the selection lines showed significant recovery towards the control means after relaxation of selection, for 44-week body weight in the Regression, Body Weight and Ratio lines and also for the 28-week body weight in the Ratio line, when compared with the selection line means.of the previous generation (Appendix 6). As regards egg weight there was recovery towards the control means for the 28-week egg weight in the Egg Weight line and for the 44-week egg weight in the Ratio line. Recovery in sexual maturity was noted only in the Regression line, whereas no evidence of significant recovery towards the control mean was observed for egg number in any of the selection lines.

As regards heterosis for the performance of the inter-line crosses, significant ($P < \cdot 05$) increases of about 50 grams were observed for 28-week body weight in the Egg Weight x Regression (Table 9) and the Body Weight x Ratio inter-line crosses (Table 12) and also for 44-week body weight in the latter cross (Table 12). The highest significant ($P < \cdot 001$) heterotic effect, observed in body weights, was an increase of 202 grams above the midparent in the Ratio x Body Weight inter-line cross measured at 44 weeks of age (Table 12).

As regards egg weight measured at 28 and 44 weeks of age, significant heterosis above the midparent was not observed in the inter-line crosses of the selected populations except in the case of egg weight measured at 28 weeks (which amounted to 1·6 grams above the midparent performance) in the Ratio x Body Weight cross (Table 12).

A significant heterotic effect was not detected in any of the inter-line crosses in age at first egg and in the egg number records.

A conclusion of economic consequence was the confirmation of an apparent permanent decline in egg numbers in both the Egg Weight and Regression lines as egg numbers in both reciprocal crosses were significantly ($P < .001$) reduced relative to the control line. The full egg number record to 60 weeks of age the Egg Weight x Regression cross and its reciprocal cross was respectively 18 and 17 eggs below the control line mean (Table 8).

The Egg Weight x Regression cross was slightly but sitnificantly ($P < .05$) heavier than the reciprocal cross (Table 10) at 28 weeks of age, suggestive of a sex-linked effect as the sire line, in this case the Egg Weight line, was reported to be heavier at 28 weeks (Manson, 1970). Likewise an apparent sex-linked effect in the inheritance of egg weight was detected in this experiment to support the finding of sex-linkage inheritance in spring egg weight by Osborne (1953). Egg weight (28 weeks) in the Regression x Egg Weight cross was observed to be significantly ($P < .05$) greater by 0.8 gram than in the reciprocal cross, the sire line in this case (Regression) possessing the higher mean egg weight compared with the dam line (Egg Weight).

No maternal effects were detected for the performance traits measured as regards the reciprocal cross comparison.

# PART II

## STUDY OF A SUSPECTED DWARF CONDITION IN A POPULATION UNDERGOING BODY WEIGHT SELECTION

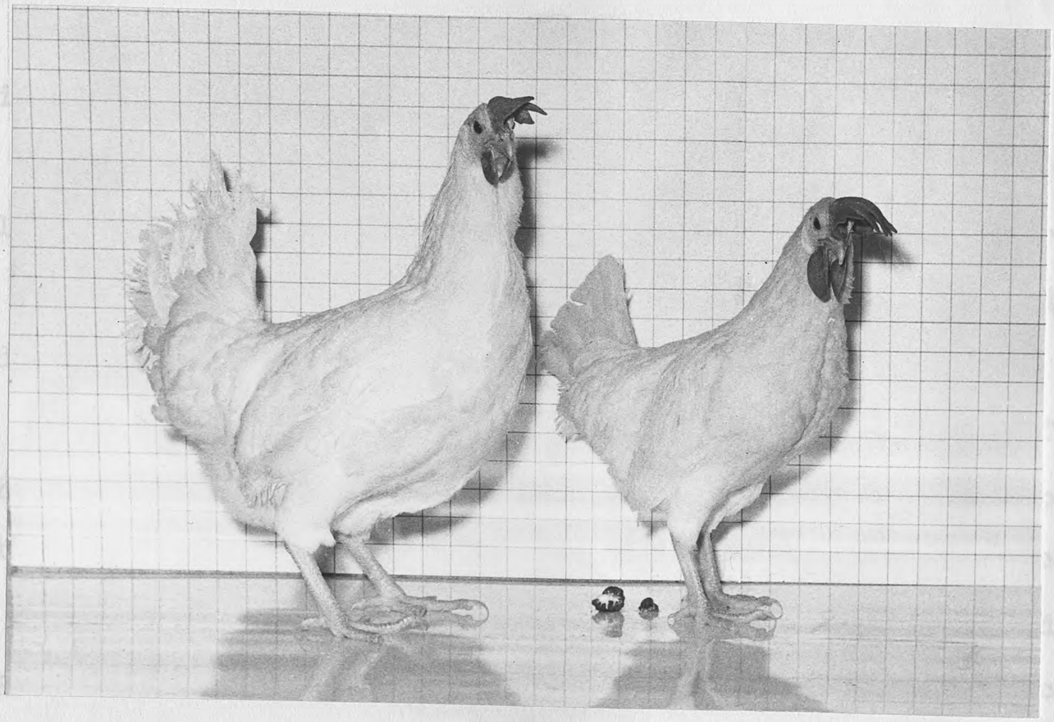


FIGURE 5

Assumed homozygous 'dwarf' female (920 gms) compared with normal Strain 2 female (1890 gms).

# 1. INTRODUCTION

## Genetic dwarfism in a selection line

The existence of a positive genetic correlation between body weight and egg weight has presented breeders with a problem when selecting for an overall economic improvement for layer-type poultry. Since selection for egg weight to increase saleable value would cause a correlated concurrent increase in body weight (egg weight is strongly positively correlated with body weight as reported by Wyatt, 1954; Jaffe, 1966; and Kinney, Lowe, Bohren and Wilson, 1968), and therefore reduces the overall economic gain desired.

Recent reports of the form of sex-linked genetic dwarfism in poultry (Hutt, 1959) has naturally created increased interest in the possibility of developing a small dwarf layer provided that it produces sufficiently large eggs of saleable size.

Some workers have already reported feed efficiency of the dwarfs in terms of feed per dozen eggs as being highly superior to that of the non-dwarfs (Bernier and Arscott, 1960; Arscott and Bernier, 1968). On the other hand, others have found only slight superiority in the dwarfs' efficiency in egg production (Magruder and Coune, 1969; Quisenberry, Gonzalez and Bradley, 1969) and in one report, even less efficient egg laying in the dwarfs has been recorded (Selvarajah, 1970). Nevertheless, on balance, it may be generally accepted that the dwarfs are more efficient than the non-dwarfs as egg layers.

The following study set out to substantiate the suspicion that a cockeral (W.B. 520) first detected in the 1966/67 generation of the Body Weight selection line was homozygous for the recessive sex-linked dwarfing gene designated 'dw' by Hutt (1959). The effects of this dwarfing gene on body size and correlated production traits such as egg weight and egg number were investigated and presented, with a view also to evaluating the economic potential of the dwarfing gene if incorporated into an egg producing strain.

## 2. REVIEW OF LITERATURE

### Dwarf forms of the domestic fowl

Various dwarf conditions have been reported in many species of animals in addition to poultry and many of these appear to have a comparable genetic basis. There are for example dwarf races or strains resulting from the cumulative action of many genes (Goodale, 1938; Fowler, 1958) or in some instances a single major gene affecting size or growth. In the latter category there are the general group of achondroplastic defectives caused by mutations that induce disproportionate retardation of growth. For example, the Creeper (cp) fowl (Landauer, 1934), which was reported to be due to a general growth retardation at specific periods of development. The Dexter cattle (Brandt, 1941; Mead, Gregory and Regan, 1946), and abnormal dwarfing in man (Hutt, 1964) and in rodents (De Beer and Gruneberg, 1940) are other examples. However, the sex-linked dwarf fowl first reported by Hutt (1953) does not appear to be achondroplastic.

More recently, Fowler and Edwards (1961) described the 'midget', a dwarfed condition in the house mouse caused by a single autosomal recessive gene which is dependent on a genetic background of small body size for its expression. This also appears to be the case with the sex-linked dw dwarfing gene in the fowl (Jaap, 1971a).

The study of the inheritance of these genetic conditions affecting the adult size of several species of animals has helped towards a better understanding of gene action, particularly the genic control of development and form (Sinnot, Dunn & Dobzhansky, 1958). Genetic disorders of the endocrine glands cause fowls (Landauer, 1929) mice, rabbits and guinea pigs (Boettiger and Osborn, 1938) to be stunted and barren. However, the physiological basis of the sex-linked dwarfed condition has not yet been established.

Hutt (1959) listed five different types of genetic dwarfing occurring in the domestic fowl which have been identified and studied.

(a) Normal sex-dimorphism in size:

Adult females are 19 to 23 per cent less heavy than their full grown male sibs. The combined length of the three long bones (femur, tibio-tarsus and tarso-metatarsus) is shorter in females than in males by 12 to 17 per cent (Hutt, 1929; Maw, 1935). Hutt (1929) also concluded that the reduced body size of the female is not a secondary sex character since poulardes and capons do not differ from normal fowls in skeletal size. Normal sex-dimorphism reduces the lengths of all 3 long bones more uniformly than any of the 3 dwarf mutants listed below.

(b) Dominant sex-linked genes (Maw, 1935):

Whether this dwarfing condition is caused by any single mutant gene is uncertain. It is more likely the expression of sex-linked quantitative genes depressing size some of which may be alleles of the sex-linked genes responsible for normal sex-dimorphism in size in larger breeds.

(c) Creeper, Cp.:

Described by Landauer (1934, 1937) as an autosomal dominant, which results in the heterozygous condition in a reduction of the 3 long bones by about 27 per cent in males and 21 per cent in females. The eyes, head and caudal end of the vertebral column are also affected. Such effects are the results of retardation of growth detectable in the early embryo (36 hours after incubation). The gene acts as a lethal in the homozygous condition.

(d) Thyrogenous dwarfism, td.:

Described by Landauer (1929) and shown by Upp (1934) to be a simple autosomal recessive mutation, lethal in most cases. The few survivors never become sexually mature. It causes brachycephaly, distortion of the sacrum, and reduction of the 3 long bones of the leg by about 39 per cent in females. Landauer (1929) first designated it Myxoedema infantalis. Histological studies revealed enlarged thyroids but with little active tissue present.

(e) Sex-linked dwarfism, dw:

First reported by Hutt (1949b, 1953, 1959) as caused by a completely sex-linked gene. The expressivity of this gene is remarkably complete. The 3 long bones femur, tibiotarsus and tarso-metatarsus are reduced in homozygous males by about 32 per cent, whilst the reduction in long bones in dwarf females was estimated to be unlikely to exceed 24 per cent. The body size of homozygous adult males was found to be reduced by 43 per cent below normal and those of hemizygous adult females by 29 per cent. These dwarfs were proportionate in shape and bred normally. Viability, fertility and hatchability of eggs were apparently not impaired in any way. Average egg size was reduced by about 10 per cent.

So far this gene has been detected in New Hampshires and White Leghorns. Hutt (1959) suggests that this mutation is not uncommon and could be found presumably in most bantam breeds.

Hutt (1959) clearly showed that this type of dwarfism was caused by a sex-linked gene which was recessive in heterozygous males. Growth curves from over 2,300 classified offspring showed a significant retardation in dwarfs by six weeks old, but individual birds sometimes could not be classified with certainty until 10 to 15 weeks of age or even later. This difficulty in classification at earlier ages is due to 2 factors,

(i) no detectable disproportionate development of any part of the body, head or limbs

(ii) the ranges of size in dwarfs and full-sized birds overlap for more than 3 months after hatching.

Sex-linked dwarfism, rg or B:

Godfrey (1953) has reported one other sex-linked gene in the Rose Comb Black Bantam breed (which he designated rg) that reduced growth rate and adult body size of normal Barred Plymouth Rock poultry. He was of the opinion that the rg allele is "recessive" to normal size. Jaap (1969) has also detected a similar gene (which he designated B) but in the Sebright Bantam breed. Jaap (1971a) reported that the B gene was "dominant" to the dw-allele in heterozygous males. The B allele may be the same mutant as the rg gene of Godfrey (1953).

Effect of dwarfing genes (dw and B) on embryonic development and subsequent growth

Comparison of chick weights on hatching indicated that the "dw" gene does not retard growth of the chick embryo during incubation

(Hutt, 1959).

Growth curves for "dw" dwarfs and their normal siblings indicated that the growth of dwarfed progeny of both sexes, was only retarded from 6 weeks onwards but continued throughout the normal period of growth. This was unlike the action of the gene causing pituitary dwarfism in the mouse (Boettiger and Osborn, 1938), which induced almost complete cessation of growth at 17 to 35 days of age. In actual fact, the 2 week body weight of offspring from dams with an average egg size of 60 grams indicated that the dwarfs were already significantly smaller than their sisters (by 11 per cent) which later attained full normal size. Therefore, Hutt (1959) concluded that this dwarfing gene began to retard growth sometime in the first 2 weeks after hatching.

Godfrey (1953) reported that the rg dwarfs exhibited similar percentage growth rates to the normals after 9 weeks of age and thus concluded that the rg dwarfing gene retarded growth prior to 9 weeks of age.

<u>Maternal influence</u>

It is known that the initial size of the chick is related to the size of the egg from which the chick hatches (Upp, 1928; Galpin, 1938; Hutt, 1949a; Wiley, 1950). A number of investigations have indicated that the maternal effect operating through the size of the hatching egg on the rate of growth of the domestic fowl is transient. Other workers suggested that up to broiler age and possibly subsequently, the effect of egg size on rate of growth of the chick is of practical significance (Tindell and Morris, 1963; Goodwin, 1961; Goodwin, Lamereux and Dickerson, 1960; Ragab and Kotby, 1959; Skoglund, Seager and Ringrose, 1952; Skoglund and Tomhove, 1949).

Wiley (1950), Hutt (1959), Oluyemi (1965) have reported hatching egg size effects to extend beyond 9 weeks up to 20 weeks of age or even further (Hutt, 1959). Wiley,(1950) also reported superior conformation, liveability and efficient food conversion in chicks from large sized eggs. However, Pope and Schaible (1957), Latimer (1924), Haibersleben and Mussehl (1921), found that by 5 weeks the effects were of no significance.

Oluyemi (1965a) summarised the correlation estimates (rp) between the weight of the hatching egg and the chick body weight at different stages of growth. The effect of egg weight on the body weight of the chick diminishes markedly from day old (rp = 0·85) to 2 or 3 weeks (rp = 0·3) and then gradually up to 8-12 weeks of age (rp = 0·2). By maturity, the effects have become insignificant (Callenbach, 1933).

Hutt (1959) showed that this relationship was also evident in dwarf progeny. Chicks of comparable genotype with respect to the dwarfing allele 'dw', when hatched from different sized eggs, differing in body weight up to at least 18 weeks of age.

Jaap (1971b) has reported some data on the magnitude of this maternal influence in dwarf matings. Heterozygous male broilers (+ dw) from dwarf dams were shown to be lighter at 8 weeks of age compared with males from ordinary broiler dams. On the other hand, heterozygous dwarf males from normal sized broiler dams grew as rapidly as the normal homozygotes. This maternal influence, however, did not reduce eight week body weight of normal daughters from dwarf dams, even when the dwarf mother laid eggs 4 grams less than those of her normal sisters.

Adult size

(a) Males

The gene 'dw' reduced the size of adult homozygous males as compared with heterozygotes, by about 43 per cent (Hutt, 1959). Hutt (1959) suggested that the gene was completely recessive. Among male progeny from matings of known heterozygous males with normal sized females which ought to have given a 1:1 ratio of normal to heterozygous carrier males he found no indication of a bimodal distribution with respect to body size. However, Jaap (1968) reported on data from an $F_1$ and first back-cross onto a broiler strain and demonstrated that 'dw' was not completely recessive in its effect on growth. Body weight of the heterozygous males was reduced by 2½ to 5 per cent at 8 weeks of age, compared with normal homozygotes.

Jaap (1971a) in a later article reported that the 'B' allele was more "dominant" than 'dw'. Jaap (1971b) also reported that the 8-week body weight of heterozygous (+ dw) males from dwarf dams was less than homozygous (++) males from normal sized (dams) but concluded that this reduction in 8-week body weight was due to a maternal influence.

(b) Females

Over 200 full sib comparisons (Hutt, 1959) of dwarfed daughters with their normal sized sisters gave an unweighted average reduction of 29·5 per cent in adult body weight (the percentage reduction ranging from 25·7 to as much as 32·1 per cent). The distribution of the adult weights of 68 dwarf females and their 80 normal sized sisters and half sisters from one sire indicated that there was very little overlapping of the two categories.

Bernier and Arscott (1960), Arthur,(1968) and Selvarajoh (1970) reported average reductions of 37, 33 and 34 per cent respectively in adult body weight of 'dw' dwarfed pullets when compared to their normal full sibs.

Jaap (1971a) reported a difference in the reduction in adult body weight of the 'dw' female dwarfs derived from an egg type strain averaging 2 kilograms compared with their normal sibs and of those derived from a broiler type strain averaging 4 kilograms. The dwarfs were lighter by approximately 33·3 and 20 per cent respectively in the egg-type and broiler-type populations. It would therefore appear that the 'dw' gene requires an optimum body size genetic background for its expression to be complete. It has been suggested (Selvarajoh, 1970) that non-allelic growth genes in the larger broiler type strain were partially epistatic to the 'dw' allele, and thus inhibited the effect of 'dw' to some extent in the dwarf progeny of the broiler strain, assuming that such growth genes did not exist in the egg-type population.

Jaap (1971a) reported that the adult body weight of 'B' female dwarfs were reduced by only 10 per cent, compared with their normal counterparts in an egg-type strain.

## Sexual maturity

Age at first egg is normally taken as a measure of sexual maturity. The 'dw' dwarfs have been reported to reach sexual maturity later than their non-dwarf sibs on the average, although both genotypic groups commenced laying during the 19th week (Bernier and Arscott, 1960,1966; Selvarajah, 1970). Bernier and Arscott (1966) also noted that the dwarfs reached 25 per cent egg production at 25 weeks whereas the non-dwarfs reached it earlier at 23 weeks. McClung, Jones and Patrick (1971) reported similar observations when laying house performance was studied in cages and on slatted floors. In cages, fifty per cent production was reached at 22½ weeks and 28 weeks for non-dwarfs and dwarfed White Leghorns respectively. Whereas on slatted floors, the difference in age (5½ weeks) at reaching 50 per cent production was even greater.

Egg Production

Because of the variable environmental influences affecting sexual maturity, Hutt (1959) restricted his comparisons of egg production to survivors that laid throughout a 3 month period in the spring when the birds were between 47-60 weeks of age. Comparisons were made on a within sire family basis and egg production of the 'dw' dwarf females averaged 15 per cent less than their normal sized sisters, averaging 61·6 per cent production as compared with 68 to 78 percent for their normal-sized sibs.

Bernier and Arscott (1960), reported that the 'dw' dwarf laid 18 per cent fewer eggs than their non-dwarf sibs. Silvarajah (1970) in two separate experiments involving White Leghorn dwarfs found that the dwarfs laid as many eggs as their non-dwarf half-sisters but significantly fewer eggs (by 25 per cent) in the case of the full sisters. However, he considered environmental influences as a possible cause of the inconsistent behaviour of the half-sibs and full-sibs.

Jaap (1971a) commented that 'dw' reduced rate of lay much more than did its allele 'B' but was of the opinion that the greater reduction in egg production noted for the 'dw' gene was attributable to the effect of smaller body size *per se* (i.e. due to autosomal genes present in small body size females affecting egg production).

Jaap and Mansour Mohammadian (1969), Prod'homme and Merat (1969) reported that the 'dw' gene not only did not reduce the rate of lay in broiler-type dams but also appeared to reduce the percentage of defective eggs laid, thus increasing the number of 'settable' eggs.

Three investigations (Arscott and Bernier, 1968; Magruder and Coune, 1969; Jaap and Mohammadian, 1969) involving comparisons between unrelated egg-type poultry populations indicated that the 'dw' dwarfs laid 13, 25 and 37 per cent less eggs than non-dwarf commercial layers.

### Egg weight

The average reduction of egg size (at about 50 weeks) caused by the 'dw' dwarfing gene was reported (Hutt, 1959) to be about 10 per cent when compared with their normal sisters whose mean egg size was 58 grams. The dwarfs, however, laid larger eggs in relation to their body size as the proportionate weight of eggs ($\frac{\text{egg weight}}{\text{body weight}} \times 100$) was consistently greater in the dwarfs (2·9 per cent) when compared to their normal sized sisters (2·3 per cent) Hutt (1959).

When the relationship between average body size and egg size was studied more closely by computing the regression of egg weight on body weight in both the dwarfs and their normal sisters, Hutt (1959) found that the regression lines had more or less similar slopes, (Figure 6) and concluded that all small fowl tend to lay eggs that are larger in relation to their body weight, irrespective of whether they carry the dwarfing gene or not.

Bernier and Arscott (1960) reported that their 'dw' dwarfs laid eggs which weighed 10 per cent less, when the dwarfs themselves weighed 37 per cent less than their normal sized female sibs. Selvarajah (1970) found a 12 per cent reduction in egg weight, when the dwarfs were themselves 31 per cent lighter than their non-dwarf sibs, while Jaap (1971a) stated that the 'dw'-allele reduced egg weight of the broiler dam slightly less than in egg-type females, resulting in a reduction in mean egg weight in the former case by only 4 grams.

## Total output of egg material

It is expected that the total output of egg material in the dwarfs would be lowered significantly. Hutt (1959) reported a reduction of 21-28 per cent in egg mass over a 110 day period in the dwarfs when compared to their non-dwarfed sibs. Other investigators (Arscott and Bernier, 1960; Selvarajah, 1970) have also reported reductions in egg mass of similar magnitude.

## Reproduction and viability

In contrast to the thryrogenous or endocrine dwarfism, which die early and never survive till sexual maturity (Upp, 1934) the

## Figure 6

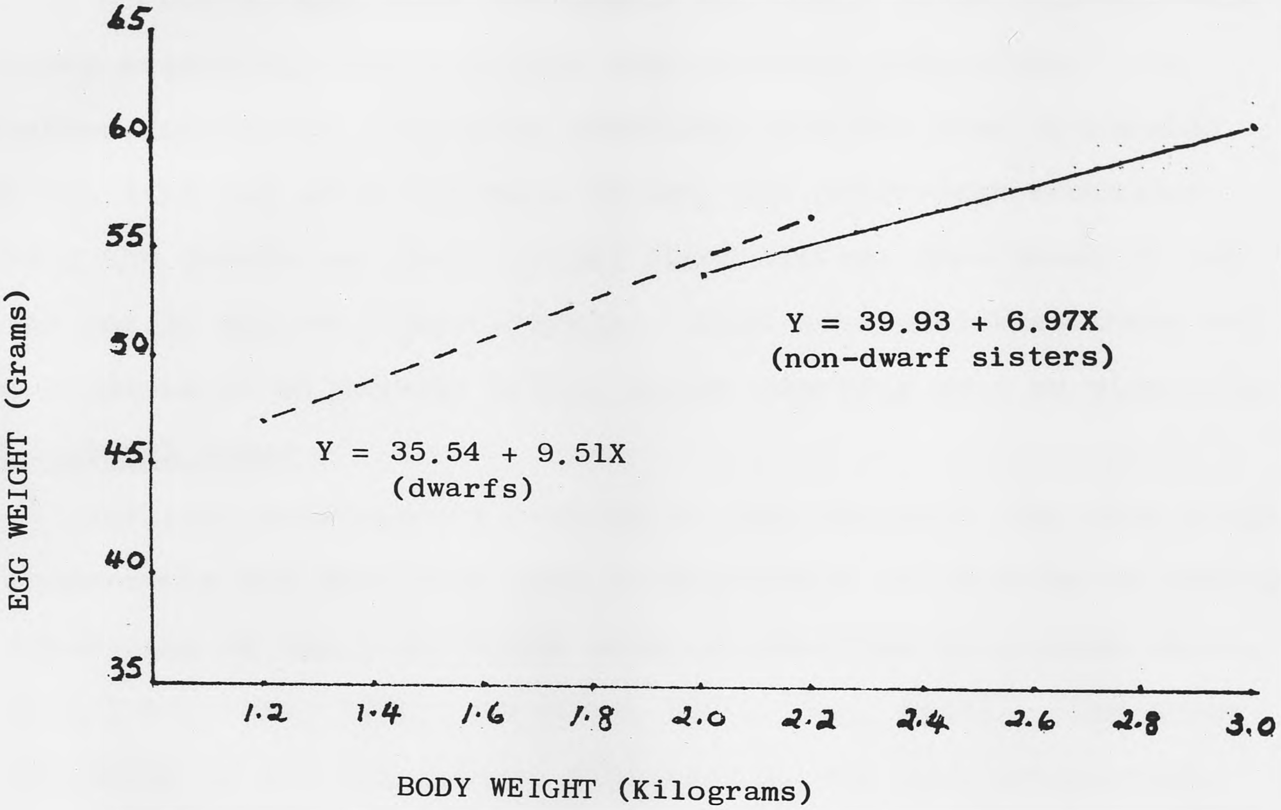


Figure Egg weight in relation to body weight (after Hutt 1959). Distributions of egg weight and body weight for dwarfs and their non-dwarf sisters, all from one sire.

sex-linked 'dw' dwarfs possess quite normal reproduction and viability in both sexes (Hutt, 1959). However, if reproductive fitness is measured as the number of potential offspring per dam, the sex-linked dwarfs will show a reduced rate in accordance with their reduced rate of egg production (i.e. 15 to 18 per cent reduction, Hutt, 1959; Bernier and Arscott, 1960).

Hutt (1959) observed no reduced viability in dwarfs through to 12 months of age, when the dwarfs and their normal sisters were housed separately from the time they could be identified. In another experiment, comparing viability from the time of housing at 150 days old until 420 days of age, the percentage mortality among the dwarfs and their normal sized sisters were about 11 per cent and 15 per cent respectively. Hutt concluded that there was no evidence of an adverse effect of the dwarfing gene on viability.

Individual bones

Skeletal measurements tend to be less variable than body weight measurements and have been used in preference on occasion in making comparisons of the 5 different kinds of dwarfism in poultry (Hutt, 1929, 1959; Maw, 1935; Landauer, 1929, 1934, 1937). The three long bones of the leg (femur, tibiotarsus, and tarsometatarsus), were the obvious choice of many investigators. In the live bird the tarsometatarsus or "shank" is the most accessible and was reported to be the most variable bone in normal sized fowls than any other bone in the appendicular skeleton (Hutt, 1959). In the sex-linked dwarf, the tarsometatarsus was reported to be shortened most, with the tibiotarsus being less affected and the femur the least affected (Hutt, 1959).

The tarsometatarsus was reduced by 24·4 per cent in Creeper females (Landauer, 1934). The combined length of the 3 bones was reduced more in the sex-linked dwarf females (24 per cent according to Hutt, 1959) than the Creeper females (21 per cent reduction as reported by Landauer, 1934). Moreover, as the tarsometatarsus showed the greatest proportionate reduction in all 3 kinds of dwarfism, its reduction in the sex-linked dwarfed females was likely to exceed 24·4 per cent.

Hutt (1959) in comparing 7 normal sized heterozygote males (average 112 mm) with 12 'dw' dwarf males (average 70 mm) reported a reduction in shank length of dwarfed males of 37·7 per cent. Thus, the reduction in shank lengths of the dwarfs was very similar in magnitude to the reduction in body weight.

Bernier and Arscott (1966) reported reductions of shank length measured at 8 and 17 weeks of age in 'dw' female dwarfs by 14 and 20 per cent respectively, when compared to their normal sibs. Jaap (1969) noted that the 'dw' female dwarfs were distinguishable by their shortness of legs; but not in the case of the 'B' dwarfs.

## 3. MATERIALS AND METHODS

The sire and dam of the suspected dwarfed cockerel (wing band 520) produced a total of 9 female progeny 4 of which completed full production records.

On the assumption that sire 520 was in fact homozygous for the dwarfing gene 'dw', this would imply that its sire must have been either a normal sized heterozygote or itself a homozygous dwarf, while the dam of 520 would require to have been a dwarfed hemizygous female (Fig. 7).

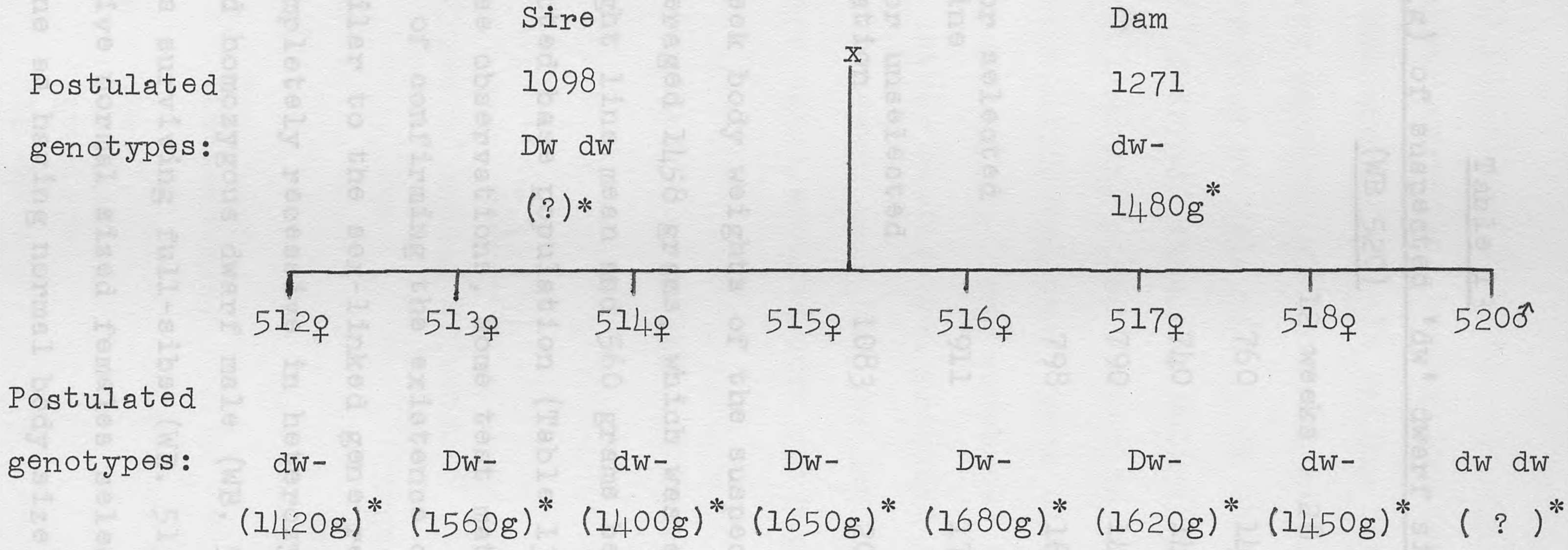
The fact that the sire of 520 had not been noted earlier as greatly reduced in size suggests that the former hypothesis is more likely. On the other hand the dam of 520 (WB. 1271) was, in fact, much reduced in body size weighing only 1480 grams at 28 weeks of age, which was around 400 grams below the mean of the unselected base population, and almost 200 grams below the mean body weight for the low body weight line. A tentative pedigree of Male 520 and its progeny is given in Fig. 7.

A total of 7 female full sibs of the suspected dwarf male survived to housing and 3 out of the 7 were on average 200 grams lighter than the remaining 4 females classified as normal. This would suggest segregation of the dwarfing gene giving an approximate 1:1 ratio of normal sized and dwarf females which would be expected if the sire of 520 was in fact, a heterozygous carrier.

The body weights of the 'dw' dwarfed female sibs of male 520 are summarised and compared with the mean body weight of their contemporaries in Table 13.

Figure 7

Pedigree of Male 520 and its Sibs



4 Normals: 3 Dwarfs (Female progeny)

* Body weight at 28 weeks of age.

Table 13

Mean body weights (g) of suspected 'dw' dwarf sisters of male (WB 520)

| Identity | 12 weeks | 28 weeks | 44 weeks |
|---|---|---|---|
| WB. 512 | 760 | 1420 | 1490 |
| 514 | 740 | 1400 | 1560 |
| 518 | 790 | 1450 | 1420 |
| 'Normal sisters' | 798 | 1628 | 1778 |
| Mean body weight for selected Body Weight line | 911 | 1734 | 1908 |
| Mean body weight for unselected Control population | 1083 | 2020 | 2211 |

The mean 28 week body weights of the suspected dwarf sisters of male WB. 520 averaged 1458 grams, which was about 280 grams below the Body Weight line mean and 560 grams below the original mean of the unselected base population (Table 13).

Following these observations, some test matings were arranged with the objective of confirming the existence of a major dwarfing gene, possibly similar to the sex-linked gene reported by Hutt (1959) as being completely recessive in heterozygous males.

1. The suspected homozygous dwarf male (WB. 520) was mated to four of its surviving full-sibs (WB. 513, 514, 515, 517) and also to five normal sized females selected from the Regression line as having normal body size but above average egg size. At a later date, Male 520 was again mated to some of its 'dw' daughters from the above full sib matings and also

to normal sized pullets.

2. Matings of another suspected homozygous dwarf male (WB. 2744) produced from the above full-sib mating between Male 520 and Female 514, were arranged with normal sized and suspected 'dw' dwarf female progeny of Male 520. In the case of matings involving 'dw' 'dwarfed' females, full-sib matings were avoided.
3. Test matings of 7 normal sized suspected heterozygous males (Dwdw), bred from different dams, were also carried out by mating to both normal (Dw-) and suspected dwarfed (dw-) females; the latter having been produced from the original set of matings of dwarf male 520, as detailed above. Full-sib matings were again avoided when matings involved dwarf females.

Progeny were thus obtained from matings of four different kinds (Table 14).

Table 14

Types of Mating Effected

| Sire | Dam | Expected Ratios among Progeny | |
|---|---|---|---|
| | | Male<br>dwdw:Dwdw or DwDw | Female<br>dw-:Dw- |
| 1. Dwarf homozygote (assumed dwdw genotype) | Non dwarf (Dw-genotype) | 0:1 | 1:0 |
| 2. Dwarf homozygote (assumed dwdw genotype) | Dwarf (assumed dw- genotype) | 1:0 | 1:0 |
| 3. Normal sized heterozygote (assumed Dwdw genotype) | Non dwarf (Dw- genotype) | 0:2 | 1:1 |
| 4. Normal sized heterozygote (assumed Dwdw genotype) | Dwarf (assumed dw- genotype) | 1:1 | 1:1 |

All matings were effected using artificial insemination. Three hatches of about 75 chicks per hatch were involved for all the test-matings. It was unfortunate that due to an electrical fault in the brooder, about half the number of chicks in the second hatch were lost when they were under 1 week old. Although a third hatch was set in order to try and make up for this loss, the ultimate number of chicks surviving was still unfortunately limited, particularly for test mating analyses; 190 chicks of both sexes surviving to 28 weeks of age.

## Classification of offspring of test matings

Hutt (1959) noted that the sex-linked dwarfs, unlike other dwarfs in the domestic fowl, such as the Creeper fowl (Landauer, 1934, 1937) were not achondroplastic and therefore show no conspicuous disproportionate development of the body, cranium or limbs, facilitating ready identification. The range in body weight of dwarfs and normal sized birds overlap for more than 12 weeks after hatching. Thus, although significant and detectable retardation of growth is observed as early as six weeks of age, classification of individuals requires to be delayed until at least 10-15 weeks of age (Hutt, 1959). By 5 months of age the difference between dwarfs and normal sibs is obvious in all males and in about 98 per cent of the females (Hutt, 1949b). In this study, classification on a body weight basis was carried out at 28 weeks of age.

The mid-parental weights required for classification of the female progeny were obtained by reducing the sire's approximate

28 week weight* by 22 per cent to take account of normal sex dimorphism in size (Hutt, 1959).

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* Extrapolated from known 36 week body weight.

# 4. RESULTS AND DISCUSSION

## 4.1 Matings of suspected homozygous dw dwarf males

A series of daughter-dam comparisons of the 28-week body weight of the female progeny from matings involving a suspected homozygous dwarf male (WB 520) are summarised in Table 15.

Table 15

Matings of suspected homozygous 'dw' dwarf male (WB 520). Daughter-dam comparison of 28-week body weight

| Mating | Dam Body Weight (grams) | Female Offspring | | Range (grams) |
|---|---|---|---|---|
| | | n. | Average body weight (grams) | |
| 1 | 1400 | 3 | 1330 | 1190-1500 |
| 2 | 1540 | 5 | 1485 | 1290-1610 |
| 3 | 1560 | 3 | 1360 | 1310-1410 |
| 4 | 1620 | 3 | 1280 | 1020-1520 |
| 5 | 1620 | 2 | 1560 | 1510-1610 |
| 6 | 1650 | 4 | 1348 | 1250-1440 |
| 7 | 1790 | 1 | 1460 | - |
| 8 | 1840 | 8 | 1634 | 1540-1810 |
| 9 | 1850 | 2 | 1685 | 1620-1750 |
| 10 | 1880 | 2 | 1465 | 1390-1540 |
| 11 | 1920 | 10 | 1644 | 1500-1750 |
| 12 | 2090 | 2 | 1700 | 1660-1740 |
| 13 | 2170 | 3 | 1550 | 1500-1600 |
| | Mean 1774* | Total Progeny 48 | Mean 1500 | |

* Weighted according to number (n) of female progeny recorded.

It was noted from Table 15 that the female progeny of 'dwarf' male (WB 520) were consistently lighter in body weight than their dams. Out of 48 progeny, only 2 were heavier than the dam. The mean 28-week body weight of the daughters was reduced overall by an average of 15·4 per cent. These findings added greater confidence to the assumption that Male 520 was homozygous for a major gene affecting body weight.

The results of the matings of another suspected homozygous dwarf male (WB 2744) are given in Table 16, in which are summarised the 28-week body weights of its daughters compared to those of their dams.

Table 16

Matings of suspected 'dw' dwarf male (WB 2744).
Daughter-dam comparison of 28-week body weight.

| Mating | Dam's Body Weight (grams) | Female Offspring | | |
|---|---|---|---|---|
| | | n. | Average Body Weight (grams) | Range (grams) |
| 1 | 1440 | 5 | 1362 | 1290-1440 |
| 2 | 1460 | 5 | 1362 | 1120-1660 |
| 3 | 1760 | 2 | 1595 | 1580 & 1610 |
| 4 | 1960 | 6 | 1810 | 1650-1910 |
| Mean: | 1654* | Total progeny 18 | Mean: 1532 | |

Average mean body weight reduction = 7·4 per cent.

* Weighted according to number of female progeny recorded per dam.

Out of 18 female progeny only 1 was heavier than the dam at 28 weeks of age. It was likely therefore that Male 2744 was also a homozygote dwarf. However, its daughters' 28-week body weight, when compared to that of their dams, was reduced by 7·4 per cent, which is slightly less than half the reduction noted in the daughters of Male 520.

## 4.2 Body weight, egg weight and egg number of female dwarf progeny from homozygous dwarf males.

Having tested the postulated genotypes of suspected dwarf males (WB 520 and WB 2744), the performance of their dwarfed female progeny were investigated relative to their dam's performance. The results are presented in Table 17.

Table 17

Relative performance of dwarf female progeny from dwarfed sires (WB 520 and WB 2744)

| | n | 28-week Body weight (grams) | 44-week Egg weight (grams) | Per cent production to 60 weeks (from first egg) |
|---|---|---|---|---|
| Sire 520 | | | | |
| Progeny | 48 | 1500 | 56·1 | 60·0** |
| Dams | 13 | 1774* | 60·8* | 71·0* |
| Sire 2744 | | | | |
| Progeny | 18 | 1532 | 56·4 | - |
| Dams | 4 | 1654* | 58·4* | - |
| Overall average | | | | |
| Progeny | 66 | 1516 | 56·3 | - |
| Dams | 17 | 1741* | 60·1* | - |
| Per cent reduction | | 12·9 | 6·3 | 15·5 |

*Weighted according to number of female progeny recorded per dam.

**Data obtained from only 23 progeny surviving to 60 weeks.

The weighted overall average percentage reduction of 28-week body weight, 44-week egg weight and egg production to 60 weeks of age in the daughters were 12·9, 6·3 and 15·5 per cent respectively.

### 4.3 Test matings of suspected heterozygous 'dw' dwarf males

Results of test matings of the suspected heterozygous males for the 'dw' dwarfing gene, in which 7 sires yielded 85 classified progeny, are presented in Table 18.

Table 18
Test matings of 7 suspected heterozygous males (Dwdw).

| Dams | Progeny classification (28-week body weight) | | | | |
|---|---|---|---|---|---|
| | Males | | Females | | |
| | Dwarf | Non-dwarf | Dwarf | Non-dwarf | $X^2$* |
| Non-dwarf (Dw-) | 2 | 24 | 18 | 10 | 1·55 |
| 'Dwarf' (dw-) | 13 | 7 | 9 | 12 | 2·22 |
| | 15 | 31 | 17 | 22 | 2·30 |

*($X^2_{3df;\ P=0{\cdot}50} = 2{\cdot}37$)

The observed segregation obtained among the progeny was in fairly good agreement with the expected Mendelian ratio based on the assumption that the dwarfing condition could be accounted for by a recessive sex-linked gene, since the combined $X^2$ value did not exceed the tabular value of 2·37 (P = 0·50).

## 4.4 Comparative body weight, egg number, egg weight, proportionate egg weight and total output of egg material of dwarfed pullets and their non-dwarfed female sibs.

From recorded data of the classified progeny of the test matings of the same 7 heterozygous males, it was possible to make comparisons of body weight, egg number and egg weight, between dwarfed pullets and their non-dwarfed full-sibs. A comparison of body weights at 28 weeks of age of 17 dwarfed pullets with their 22 non-dwarfed full sibs showed that the dwarfs were lighter by amounts ranging from 10 per cent to as much as 25·4 per cent (Table 19). The overall weighted average reduction was 15·3 per cent.

'dw' dwarfs have been reported to be reduced in adult body weight by 30 (Hutt, 1959) to 37 (Bernier and Arscott, 1968) per cent. It appears that the dwarfs in this study have not been reduced in body weight quite so much. Their body weights were reduced by only 15 per cent. As the other major sex-linked dwarfing gene 'B' has been reported to reduce adult body weight by only 10 per cent (Jaap, 1971a) it is likely that the dwarfing gene in the population studied may be the 'B' gene.

### Egg number

Egg number (part record) was measured between 28 and 36 weeks of age (Table 20). The resulting data show~~s~~ that the average number of eggs laid by the "dwarfed" progeny were from 0·7 more

### Table 19

### Average 28-week body weight of dwarf females and their non-dwarfed full sibs

| Sires' | | Dams' | Midparent | Female Progeny | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Non-dwarf | | Dwarf | | |
| Identity (wing band) | *Body Weight 28 wks. (grams) | Body Weight 28 wks. (grams) | Body Weight 28 wks. (grams) | No. | Av.Wt. (grams) | No. | Av.Wt. (grams) | Reduction per cent |
| 2797 | 2009 | d.1520 | 1544 | 3 | 1710 | 4 | 1408 | 17·66 |
| " | " | N.2220 | 1894 | 1 | 2000 | 2 | 1730 | 13·50 |
| 2801 | 1929 | N.2160 | 1832 | 3 | 2025 | 1 | 1820 | 10·12 |
| 2843 | 2089 | d.1660 | 1645 | 1 | 1930 | 1 | 1600 | 17·09 |
| " | " | N.1800 | 1715 | 2 | 1835 | 3 | 1623 | 11·55 |
| 2848 | 1859 | d.1500 | 1475 | 2 | 1675 | 1 | 1480 | 11·64 |
| 2791 | 1909 | d.1520 | 1505 | 3 | 1587 | 2 | 1365 | 13·99 |
| " | " | N.1980 | 1735 | 1 | 1900 | 1 | 1580 | 16·84 |
| " | " | N.1950 | 1720 | 0 | - | 1 | 1490 | - |
| 2788 | 1734 | d.1550 | 1458 | 2 | 1810 | 1 | 1350 | 25·41 |
| " | " | N.2050 | 1708 | 2 | 1990 | 0 | - | - |
| 2798 | 2059 | d.1500 | 1550 | 1 | 1720 | 0 | - | - |
| " | " | N.1800 | 1700 | 1 | 1960 | 0 | - - | - |
| | | | | 22 | | 17 | Mean: | 15·31 |

* The sires' extrapolated 28-week body weight

d = dwarf.

N = non-dwarf.

to 5·8 less, for the 8 week period, than the corresponding figures for their non-dwarfed full sibs. The weighted average deficit in egg production (part record) of the "dwarfed" birds was 1·9, which was equivalent to a 9·8 per cent reduction.

Table 20

28 to 36 weeks egg number (part record) of dwarfs and their non-dwarfed full sibs

| | Progeny | | | | |
|---|---|---|---|---|---|
| Parents identity | Non-dwarfs Hens, No. | Eggs, Av. No. | Dwarfs Hens, No. | Eggs* No. | Per cent reduction |
| 2797 x dwarf female | 3 | 16·8 | 4 | -5·5 | -32·7 |
| " x normal " | 1 | 17·0 | 2 | -1·0 | -5·9 |
| 2801 x " " | 3 | 16·3 | 1 | +0·7 | +4·3 |
| 2843 x dwarf " | 1 | 15·0 | 1 | +1·0 | +6·7 |
| " x normal " | 2 | 20·5 | 3 | -5·8 | -28·3 |
| 2791 x dwarf " | 3 | 20·3 | 2 | -0·7 | -3·4 |
| " x normal " | 1 | 22·0 | 1 | -3·0 | -13·6 |
| 2788 x dwarf " | 1 | 18·0 | 1 | -1·0 | -5·6 |
| Total Progeny: | 15 | | 15 | | |
| Weighted Average: | | 18·2 | | -1·9 | -9·8 |

* Expressed as the difference of their average number from that for their non-dwarfed full sibs.

In the literature, Hutt (1959), Bernier and Arscott (1960), Selvarajah (1970) have all reported greater reductions in egg number (viz., 15, 18 and 25 per cent respectively) in the 'dw' dwarfs than the reduction detected in this study. Jaap (1971a) noted that 'dw' reduced rate of lay more than its allele 'B' but concluded that this was due to autosomal genes present in small body size pullets adversely affecting egg production. The average body weight at 28 weeks of age of the dwarfs in this study was 1540 grams (Table 19) which is greater than that of the 'dw' dwarfs reported (viz., 1030 grams at 44 weeks of age - Selvarajah, 1970). The heavier adult body weight of the dwarfs in this study and the smaller reduction in their egg production may imply that the 'B' gene is present in this dwarf poultry population instead of its allele 'dw'. Therefore supporting the findings of the egg weight results discussed earlier.

As egg weight is also a factor that affects the profitability of an egg producer, the effect of the dwarfing gene on average egg weight was examined. The 28-week egg weight of the dwarfs and their non-dwarfed full sibs are shown in Table 21.

Egg Weight

The 28-week egg weight of the dwarfs showed differences ranging from +3 to -5 grams when compared to their non-dwarfed full sisters (Table 22). Expressed otherwise, the average per cent reduction in the dwarfs was -2·85 per cent.

Previous investigators such as Hutt (1959), Bernier and Arscott (1960), Selvarajah (1970) have reported reductions in egg weight of

### Table 21

### 28-week Egg weight of dwarfs and non-dwarfed full sibs

| Parents' Identity | Progeny<br>Non-dwarfs<br>No. | <br><br>Av.Egg weight (grams) | <br>Dwarfs<br>No. | <br><br>Av.Egg weight* (grams) | <br><br>Per cent reduction |
|---|---|---|---|---|---|
| 2797 x dwarf female | 3 | 49·6 | 3 | -3·2 | -6·45 |
| " x normal " | 1 | 55·0 | 2 | -2·5 | -4·54 |
| 2801 x " " | 3 | 59·0 | 1 | +3·0 | +5·08 |
| 2843 x dwarf " | 1 | 57·0 | 1 | -2·0 | -3·50 |
| " x normal " | 2 | 54·5 | 2 | 0·0 | 0·0 |
| 2791 x dwarf " | 3 | 50·0 | 2 | -3·0 | -6·0 |
| " x normal " | 1 | 54·0 | 1 | +1·0 | +1·85 |
| 2788 x dwarf " | 1 | 54·0 | 1 | -5·0 | -9·25 |
| Total Progeny: | 15 | | 13 | | |
| Weighted average: | | 54·1 | | -1·5 | -2·85 |

* Expressed as the difference of their average weight from that for their non-dwarfed full sibs.

the dwarfs by 10 to 12 per cent, when compared to corresponding egg weight of their non-dwarfed full sibs. Reductions in egg weight, previously reported, were very much higher than that of this study. However, it is relevant to note from the economic standpoint, that the adult body weight of the dwarf of this study, as reported earlier in the thesis, was reduced in magnitude by 15 per cent (Table 19) which is approximately only ½ that found in

Table 22

Comparisons of dwarfs and non-dwarfed full-sibs in proportionate egg weights at 28 weeks of age.

| Parents' Identity | Progeny | | | |
|---|---|---|---|---|
| | Non-dwarfed | | Dwarfs | |
| | No. | $\frac{\text{Egg wt.}}{\text{Body wt.}} \times 100$ | No. | $\frac{\text{Egg wt.}}{\text{Body wt.}} \times 100$ |
| 2795 x dwarf female | 3 | 2·90 | 3 | 3·19 |
| " x normal " | 1 | 2·75 | 2 | 3·03 |
| 2801 x normal " | 3 | 2·93 | 1 | 3·30 |
| 2843 x dwarf " | 1 | 2·95 | 1 | 3·44 |
| " x normal " | 2 | 2·97 | 2 | 3·39 |
| 2791 x dwarf " | 3 | 3·15 | 2 | 3·44 |
| " x normal " | 1 | 2·84 | 1 | 3·48 |
| 2788 x dwarf " | 1 | 3·54 | 1 | 3·63 |
| Total Progeny: | 15 | | 13 | |
| Weighted average: | | 3·00 | | 3·36 |

the dwarf populations reported by Bernier and Arscott (1960) and Selvarajah (1970).

Proportionate egg weights ($\frac{\text{egg weight}}{\text{body weight}} \times 100$)

At 28 weeks of age the dwarfs in this study were laying rather heavier eggs in relation to their body weight, as the average egg weight in relation to their body weight was consistently higher for the dwarfs (Table 22). The average weights of eggs at 28 weeks of age for the dwarfs and their non-dwarfed full sibs were 3·4 and 3·0 per cent of the body weight respectively.

Hutt (1959), also reported similar findings of proportionate egg weight being greater consistently in the dwarfs (2·9 per cent) when compared to their non-dwarfed sibs (2·3 per cent).

### Total output of egg-material of "dwarf" pullets and their non-dwarf sisters.

Dwarf hens laying relatively large eggs can be of economic potential as a layer provided egg number is not overly reduced, and its feed efficiency is relatively good. Thus consideration of the egg mass output was carried out.

As the dwarfs lay less eggs (Table 20) than their non-dwarfed full sibs and also lighter ones (Table 21), their total output of egg material is expected to be significantly lower. The results computed from mean egg production per bird over an eight week period and mean 28 week egg weight per bird are presented in Table 23.

Table 23

Comparisons of dwarfs and their non-dwarfed full-sibs in average total output of egg material per bird (in grams) during 28 to 36 weeks of age.

| Parents' Identity | Progeny | | | | | |
|---|---|---|---|---|---|---|
| | Non dwarf | | "Dwarf" | | Difference | |
| | No. | Av.Egg Mass (grams) | No. | Av.Egg Mass (grams) | Grams | Per cent |
| 2797 x dearf female | 3 | 843·2 | 3 | 696·0 | -147·2 | -17·5 |
| " x normal " | 1 | 935·0 | 2 | 840·0 | -95·0 | -10·2 |
| 2801 x " " | 3 | 944·0 | 1 | 1054·0 | +110·0 | +11·7 |
| 2843 x dwarf " | 1 | 855·0 | 1 | 880·0 | +25·0 | +2·9 |
| " x normal " | 2 | 1144·5 | 2 | 817·5 | -327·0 | -28·6 |
| 2791 x dwarf " | 3 | 1000·0 | 2 | 893·0 | -107·0 | -10·7 |
| " x normal " | 1 | 1188·0 | 1 | 1045·0 | -143·0 | -12·0 |
| 2788 x dwarf " | 1 | 972·0 | 1 | 833·0 | -139·0 | -14·3 |
| Total Progeny: | 15 | | 13 | | | |
| Weighted Average: | | 985·2 | | 882·3 | -102·9 | -9·8 |

These comparisons show that the "output" of the "dwarfs" over a period of eight weeks averaged (weighted) 10 per cent below that of their non-dwarf full sibs.

A 10 per cent reduction in "output" of the dwarfs in this study is very much less than that reported by others (Hutt, 1959; Arscott and Bernier, 1960; Selvarajah, 1970), who recorded reductions averaging 24 per cent.

# 5. CONCLUDING DISCUSSION

## 5.1. Existence of a recessive sex-linked dwarfing gene ('B' or 'dw' allele).

The statistical evidence obtained has shown that the dwarf population in this study is likely to be due to a recessive sex-linked gene. It cannot be concluded from this investigation however which sex-linked dwarfing allele (i.e. 'dw' or 'B') is implicated. Although the heavier adult body weight of dwarfs in this study (1540 grams vs. 1030 grams of dwarfs in the report by Selvarajah, 1970) relative to other 'dw' dwarfs and the smaller reductions in body weight, egg number and egg weight, when compared to their non-dwarf female full sibs, all indicated that it may be the 'B' mutant, since the 'B' allele has been reported to reduce these traits to a lesser extent compared to the 'dw' allele. Jaap (1971a) reported a 10 per cent reduction in adult body weight by the 'B' allele, whereas adult body weight was reported to be reduced by an average of 33 per cent (Hutt, 1959; Bernier and Arscott, 1960; Selvarajah, 1970) by the 'dw' allele. In the case of egg number, Hutt (1959), Bernier and Arscott (1960), Selvarajah (1970) have consistently reported higher reductions (ranging from 15 - 25 per cent) in 'dw' dwarf layers, than the 10 per cent reduction reported in this study. Jaap (1971a) reported that the 'B' dwarfs rate of lay was reduced less than the 'dw' dwarfs probably because of the existence of autosomal genes in the 'dw' dwarfs which adversely affected egg production. As regards egg weight of the dwarfs, a reduction of -10 to -12 per cent relative to egg weight of the non dwarfed full sibs were recorded by Hutt (1959), Bernier and Arscott (1960), and Selvarajah (1970). These differences were very much greater than those recorded in this study, which averaged only -3 per cent.

## 5.2 The economic values of the 'dw'-dwarfing gene.

A reduction in output of egg material of 10 per cent or even 24 per cent may not affect the future of dwarf layers adversely from the economic standpoint provided their food consumption is reduced sufficiently to compensate for the reduction in output. Contrary to the general view that smaller animals use up proportionately greater amounts of feed for maintenance than larger ones, Bernier and Arscott (1960) had reported better feed efficiency of the 'dw' dwarf both in relation to egg number and egg mass output. Selvarajah (1970), however, found the dwarfs to be more efficient in terms of output of egg number but not of egg mass. In the dwarf population reported in this study, where the output of egg material was reduced by only 10 per cent, the prospect of the dwarf pullets producing egg mass efficiently appear to be good. However a specific trial would require to be carried out in order to determine their relative economic and biological efficiency.

As regards other dwarf populations, Selvarajah (1970) computing the differential economics in egg production of dwarfs and non-dwarfs based on assumptions made from information contained in the literature, concluded that in West Malaysia, the dwarf egg producer showed an improved overall profit margin per bird amounting to Malaysian $0·62 (equivalent to £0·09*) compared to the non-dwarf layer. Stocking density per 10 inch cage (3 dwarfs vs. 2 non-dwarfs), chick cost, feed cost both during the rearing and laying periods, and carcase salvage value were included in his costing. Other costs of production were assumed to be the same for both types of bird. Thus it appears that the economic prospects of the dwarf layer may be assured at least in tropical countries, where the higher feed costs and the climatic conditions may favour the smaller body size of the dwarf bird. However, the future of dwarf layers in the highly competitive European poultry industry is still uncertain and must await further information regarding the egg production of the dwarf layer relative to such factors as density of stocking, feed requirements and final value of the cull hens.

Although egg number and egg size of the dwarfs in their present state of overall genetic development are inferior to those of the normal sized commercial layer-type poultry, genetic selection may be able to improve the dwarf egg producer to be more efficient in these areas.

For example, it is known that egg size is highly heritable, although there would be an anatomical limitation for the large egg genotype in the dwarfs. The potential overall number of large eggs

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* M. $1 = £0·14.

that the dwarfs lay may not be equivalent to that in non dwarfed egg producers because of their small body size at point of lay and are therefore unlikely to produce equivalent large eggs until a later age (Magruder and Coune, 1969). However both persistent selection for increased egg size and improvements in the nutrient intake of the dwarf layer (Quisenberry, 1971) may be expected to significantly improve egg size in the dwarf layer.

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## APPENDIX 1

Computer data input for calculating inbreeding coefficient.

| | BREEDERS | | PARENTS | | | |
|---|---|---|---|---|---|---|
| Sex | Year | Wing Band | Male | | Female | |
| | | | Year | Wing Band | Year | Wing Band |
| *1 | 60 | 746 | 59 | 39 | 59 | 111 |
| 1 | 60 | 747 | 59 | 24 | 59 | 73 |
| 1 | 60 | 748 | 59 | 21 | 59 | 61 |
| 1 | 60 | 749 | 59 | 42 | 59 | 125 |
| 1 | 60 | 750 | 59 | 19 | 59 | 53 |
| 1 | 60 | 751 | 59 | 6 | 59 | 22 |
| 1 | 60 | 752 | 59 | 15 | 59 | 39 |
| 1 | 60 | 753 | 59 | 8 | 59 | 33 |
| 1 | 60 | 754 | 59 | 27 | 59 | 82 |
| 1 | 60 | 755 | 59 | 20 | 59 | 56 |
| 1 | 60 | 756 | 59 | 4 | 59 | 15 |
| 1 | 60 | 757 | 59 | 5 | 59 | 17 |
| 1 | 60 | 758 | 59 | 15 | 59 | 36 |
| 1 | 60 | 759 | 59 | 8 | 59 | 34 |
| 1 | 60 | 760 | 59 | 18 | 59 | 46 |
| 1 | 60 | 761 | 59 | 4 | 59 | 13 |
| 1 | 60 | 762 | 59 | 38 | 59 | 108 |
| 1 | 60 | 763 | 59 | 7 | 59 | 26 |
| 1 | 60 | 765 | 59 | 25 | 59 | 66 |
| 1 | 60 | 766 | 59 | 5 | 59 | 20 |
| 1 | 60 | 767 | 59 | 21 | 59 | 63 |
| 1 | 60 | 768 | 59 | 19 | 59 | 55 |
| 1 | 60 | 769 | 59 | 33 | 59 | 91 |
| 1 | 60 | 770 | 59 | 41 | 59 | 116 |
| 1 | 60 | 771 | 59 | 6 | 59 | 23 |
| 1 | 60 | 772 | 59 | 16 | 59 | 43 |
| 1 | 60 | 773 | 59 | 20 | 59 | 59 |
| 1 | 60 | 774 | 59 | 18 | 59 | 50 |
| 1 | 60 | 775 | 59 | 38 | 59 | 110 |
| 1 | 60 | 776 | 59 | 30 | 59 | 102 |
| 1 | 60 | 777 | 59 | 30 | 59 | 105 |
| 1 | 60 | 778 | 59 | 1 | 59 | 1 |
| 1 | 60 | 779 | 59 | 1 | 59 | 5 |
| 1 | 60 | 780 | 59 | 26 | 59 | 78 |
| *2 | 60 | 1 | 59 | 26 | 59 | 78 |
| 2 | 60 | 2 | 59 | 41 | 59 | 120 |
| 2 | 60 | 3 | 59 | 4 | 59 | 11 |
| 2 | 60 | 4 | 59 | 27 | 59 | 82 |
| 2 | 60 | 5 | 59 | 21 | 59 | 65 |
| 2 | 60 | 6 | 59 | 15 | 59 | 40 |
| 2 | 60 | 7 | 59 | 4 | 59 | 15 |
| 2 | 60 | 8 | 59 | 41 | 59 | 118 |
| 2 | 60 | 9 | 59 | 15 | 59 | 36 |
| 2 | 60 | 10 | 59 | 19 | 59 | 53 |
| 2 | 60 | 11 | 59 | 15 | 59 | 40 |
| 2 | 60 | 12 | 59 | 30 | 59 | 101 |

* 1 = Male
2 = Female

# APPENDIX 2

## The Effective Number of Breeding Individuals used Annually in Each of Selection Lines

| LINE | EGG WEIGHT | | REGRESSION | |
|---|---|---|---|---|
| Year | Sires | Dams | Sires | Dams |
| 1961 | 34 | 162 | - | - |
| 1962 | 33 | 33 | 35 | 140 |
| 1963 | 15 | 54 | 15 | 48 |
| 1964 | 15 | 60 | 15 | 64 |
| 1965 | 16 | 66 | 14 | 52 |
| 1966 | 12 | 52 | 14 | 47 |
| 1967 | 22 | 37 | 25 | 49 |

| LINE | BODY WEIGHT | | RATIO | |
|---|---|---|---|---|
| Year | Sires | Dams | Sires | Dams |
| 1961 | 34 | 162 | - | - |
| 1962 | 35 | 35 | 35 | 124 |
| 1963 | 15 | 48 | 15 | 47 |
| 1964 | 15 | 59 | 15 | 61 |
| 1965 | 16 | 62 | 15 | 55 |
| 1966 | 13 | 49 | 12 | 43 |
| 1967 | 20 | 38 | 20 | 40 |

## APPENDIX 3

Numbers of represented* males and females of selection lines.

| Line | Egg Weight | | Regression | | Body Weight | | Ratio | |
|---|---|---|---|---|---|---|---|---|
| | Sires | Dams | Sires | Dams | Sires | Dams | Sires | Dams |
| Year | | | | | | | | |
| 1961 | 33 | 58 | - | - | 33 | 58 | - | - |
| 1962 | 21 | 22 | 23 | 38 | 22 | 22 | 26 | 46 |
| 1963 | 15 | 37 | 15 | 35 | 14 | 33 | 14 | 35 |
| 1964 | 14 | 37 | 14 | 32 | 14 | 38 | 14 | 32 |
| 1965 | 16 | 36 | 12 | 30 | 15 | 33 | 14 | 33 |
| 1966 | 12 | 43 | 13 | 40 | 12 | 33 | 12 | 33 |
| 1967** | 22 | 37 | 25 | 49 | 17 | 30 | 19 | 37 |

* i.e. the number of males and females whose progeny which are represented amongst the breeders of the following generation.

** It is obvious that the numbers quoted for the last generation are given with the assumption that all the breeders for that generation will be represented in the next generation.

# APPENDIX 4

## Mean deviations of selection lines and inter-line crosses from randombred control (1967-68)

| LINE. | TRAIT<br>Body wt. (grams) 28 (weeks) | <br>Body wt. (grams) 44 (weeks) | <br>Egg Weight (grams) 28 (weeks) | <br>Egg Weight (grams) 44 (weeks) | <br>Egg Weight (grams) 60 (weeks) | <br>Age at first egg (weeks) | <br>Egg number (part record) 20-44 (weeks) | <br>Egg number (part record) 44-60 (weeks) | <br>Egg number (part record) 20-60 (weeks) | <br>No. of Pullets recorded |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1966 | 2101 | 50·5 | 58·4 | 62·3 | 23·9 | 47·3 | 27·8 | 75·2 | 243 |
| EGG WEIGHT | +140*** | +85*** | +6·2*** | +6·1*** | +5·6*** | -0·1 | -1·7 | -3·5** | -5·1** | 104 |
| REGRESSION | -60** | -109*** | +7·1*** | +7·3*** | +6·8*** | +0·5* | -5·5*** | -3·1* | -8·6*** | 124 |
| EGG WT. X REGRESSION | +85*** | +34 | +6·5*** | +6·2*** | +5·6*** | -0·1 | -4·2** | -3·5** | -7·8*** | 123 |
| REGRESSION X EGG WT. | +38* | +15 | +7·3*** | +7·0*** | +6·9*** | +0·1 | -3·4** | -3·8*** | -7·2*** | 117 |
| BODY WEIGHT | -280*** | -244*** | -2·5*** | -2·9*** | -3·3*** | -0·2 | +2·6* | +0·1 | +2·6 | 116 |
| RATIO | -246*** | -456*** | +1·7*** | +0·3 | +0·5 | +0·1 | +0·8 | -0·2 | +0·5 | 132 |
| BODY WT. X RATIO | -269*** | -305*** | +0·2 | -0·9* | -1·2* | -0·1 | +2·7* | +1·3** | +4·3* | 128 |
| RATIO X BODY WT. | -289*** | -148*** | +1·2** | -1·0* | -1·6** | +0·1 | +1·0 | +0·9* | +1·8 | 132 |
| STD. ERROR OF DIFFERENCE BETWEEN CONTROL LINE AND SELECTED POPULATIONS | ±19 | ±24 | ±0·4 | ±0·4 | ±0·6 | ±0·2 | ±1·3 | ±1·1 | ±1·7 | |

* Significant difference (P < ·05)

** " " (P < ·01)

*** " " (P < ·001)

## Appendix 5

## Mean deviation of selection lines from randombred control (1966-67)[x]

| | Body Weight (grams) | | Egg Weight (grams) | | Age at First Egg (weeks) | Egg Number (Part record) | | | Number of Pullets Recorded |
|---|---|---|---|---|---|---|---|---|---|
| | 28 (weeks) | 44 | 28 (weeks) | 44 | | 20-44 | 44-60 (weeks) | 20-60 | |
| Control Line, σp | 163 | 204 | 3·1 | 3·5 | 1·7 | 11·0 | 9·6 | (14·7) | 243 |
| Overall Mean | 1805 | 2049 | 48·3 | 57·1 | 23·8 | 46·4 | 28·7 | 75·1 | |
| Egg Weight line | +127*** | +115*** | +5·5*** | +6·4*** | +0·1 | -2·3* | -0·8 | -3·1* | 250 |
| Regression line | -41*** | -67*** | +6·8*** | +7·9*** | +1·0*** | -5·6*** | -2·1* | -7·7*** | 247 |
| Body Weight line | -301*** | -329*** | -2·5*** | -3·1*** | 0 | +1·7 | +1·1 | +2·8* | 259 |
| Ratio line | -319*** | -354*** | +1·8*** | +1·1*** | +0·2 | 0 | +0·1 | +0·1 | 243 |
| Standard error of difference between selection lines and control population | ±14 | ±18 | ±0·3 | ±0·3 | ±0·2 | ±1·0 | ±0·9 | ±1·3 | - |

* Significant difference (P < ·05)

** " " (P < ·01)

*** " " (P < ·001)

[x] **After Manson** (1970)

## Appendix 6

Differences in mean deviations from the control in performances of the respective selection lines in 1966-67 and 1967-68 generations.

| | TRAIT | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Body Weight (grams) | | Egg Weight (grams) | | Age at first egg (weeks) | Egg number (part record) | | |
| | 28 (weeks) | 44 | 28 (weeks) | 44 | | 20-44 | 44-60 (weeks) | 20-60 |
| Egg Weight line (1967 deviation - 1966 deviation) | +13 | -30 | 0·7* | -0·2 | -0·2 | +0·5 | -1·7 | +2·0 |
| Regression line (1967 deviation - 1966 deviation) | -20 | -42* | 0·3 | -0·6 | -0·5* | +0·1 | -1·0 | -0·9 |
| Body Weight line (1967 deviation - 1966 deviation) | +21 | +85*** | 0 | +0·2 | -0·2 | +0·9 | -1·1 | -0·2 |
| Ratio line (1967 deviation - 1966 deviation) | +73*** | -102*** | -0·1 | -0·8* | -0·1 | +0·8 | -0·3 | +0·4 |
| Standard error of difference between mean deviation of 1967 and 1966 generations | ±16·5 | ±20·7 | ±0·3 | ±0·4 | ±0·2 | ±1·1 | ±1·0 | ±1·5 |

* Significant difference (P < ·05)
** " " (P < ·01)
*** " " (P < ·001)

## Appendix 7

28-week body weight of progeny from 7 heterozygous males (Dwdw)

| Sires | | Dams | Progeny | |
|---|---|---|---|---|
| Identity (wing band) | Body weight 36 wks (grams) | Genotype | Sex | Body Weight (28 wks) (grams) |
| 2797 | 2110 | dw | M | 2140, 1890, 1850, 1920, 2020. |
| | | | F | 1510, 1260, 1520, 1890, 1610, 1340, 1630. |
| " | " | Dw | M | 2960, 2430, 2030, 2040, 2440. |
| | | | F | 1640, 2000, 1820. |
| 2801 | 2030 | Dw | M | 2030, 2100, 2050. |
| | | | F | 1970, 1820, 1950, 2130. |
| 2843 | 2190 | dw | M | 1920, 2030, 1920. |
| | | | F | 1600, 1930. |
| " | " | Dw | M | 2440, 2320 2340, 2070, 2480, 2170, 2060. |
| | | | F | 1540, 1650, 1870, 1800, 1680. |
| 2848 | 1955 | dw | M | 2120, 2200, 1970, 1830. |
| | | | F | 1530, 1820, 1480. |
| 2791 | 2010 | dw | M | 1710, 1730. |
| | | | F | 1350, 1380, 1600, 1610, 1550. |
| " | " | Dw | M | 2030. |
| | | | F | 1900, 1580. |
| " | " | Dw | M | 2000. |
| | | | F | 1490. |
| 2788 | 1835 | dw | M | 1880, 1610, 1840, 1780. |
| | | | F | 1800, 1350, 1820. |

(Contd.

## Appendix 7 (Contd.)

| Sires |  | Dams | Progeny |  |
|---|---|---|---|---|
| Identity (wing band) | Body weight 36 wks (grams) | Genotype | Sex | Body Weight (28 wks) (grams) |
| 2788 | 1835 | Dw | M | 2290, 1940. |
|  |  |  | F | 1850, 2130. |
| 2798 | 2160 | dw | M | 1940, 2010. |
|  |  |  | F | 1720. |
| " | " | Dw | M | 2230, 2460, 2080, 1960. |
|  |  |  | F | 1960. |

M = male

F = female.