

QUANTITATIVE EFFECTS ASSOCIATED WITH A
DWARFING GENE IN POULTRY

by

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SUMMARY

Comparisons of body weights and shank lengths of dwarf and normal birds were made in two ways. A Dwarf Group, produced by mating dwarf to dwarf, and a Normal Group, produced by mating normal to normal were used to compare unrelated dwarf and normal birds. Related dwarf and normal birds were compared within a Segregating Group, produced by mating heterozygous sires, which are phenotypically normal, to dwarf dams. Due to the sex-linked recessive inheritance of the dwarfing gene the Segregating Group produced dwarf and normal female, and dwarf and heterozygous male offspring.

Measurements made on birds used as parents in this study indicated that dwarfs lay eggs which are on average 10% smaller than those from normal birds. There was no apparent reproductive disadvantage associated with either dwarf dams or sires relative to normal birds.

Within the progeny produced there was no indication of any disturbance in the segregation of sex or in the segregation of the dwarfing gene. The day-old body weight of birds was shown to be closely related to the average egg weight of their dam, but by 6 weeks there was no apparent effect of average egg weight of dam on body weights for either dwarf or normal offspring. Dwarf birds showed greater retardation of body weights and shank length at 12 than at

6 weeks relative to normal birds despite having the same day-old body weight. Retardations of 17% and 27% for body weights and 11% and 19% for shank lengths at 6 and 12 weeks respectively were observed for dwarf compared with normal birds.

The variances of body weight and shank length measurements were shown to be the same for related dwarf and normal birds and the coefficients of variation the same in unrelated dwarf and normal birds. Variance associated with the sex-chromosomes (sex-linkage) was shown to be more important in dwarf than in normal birds in determining body weights and shank lengths.

Common environment or maternal effects were shown to be important in determining the day-old body weights of both dwarf and normal birds, but were not apparent for body weight or shank length measurements at 6 or at 12 weeks. No difference was detected between dwarf and normal birds for any of the heritability estimates of body weights or shank lengths. Correlation estimates showed a close genetic relationship between all combinations of body weight and shank length measurements at 6 and 12 weeks, with no apparent difference between dwarf and normal birds.

DECLARATION

I declare that this thesis contains no material which has been accepted for the award of any other degree in any University and to my knowledge contains no material previously published or written by another person except where due reference is made.

R.W. Polkinghorne

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INTRODUCTION

Although the existence of dwarfing in the domestic fowl due to genic action has been known for nearly 50 years precise studies of their action have been reported only in the last two decades.

Landauer (1929) described a thyrogenous dwarf condition which was shown to be controlled by an autosomal recessive gene *td* by Upp (1934). Maw (1935) reported the existence of a sex-linked gene dominant in its action in Golden Sebright bantams which reduced the length of the leg bones. The results of Godfrey (1953) suggested, however, that the controlling factor might in fact be recessive.

Hutt (1949) described the phenotypic effects of a sex-linked recessive dwarfing gene notated as *dw* which caused reduced body weights and shank lengths. Hutt (1959) used *Dw* to indicate the dominant normal allele of *dw* and this convention will be used in this dissertation.

Custodio and Jaap (1970), (1973) suggested that the factor causing reduced body size in Golden Sebright bantams was a sex-linked recessive gene dw^B which was possibly allelic to *dw*. Jaap (1971) indicated that in hemizygous females of a light (2 kg) strain the dw^B allele gave body weights about 90% of birds with the normal allele. The dwarf birds with dw^B were similar in body proportions to normal birds in contrast to the shortened shanks of dwarf birds carrying the *dw* allele where body weight was reduced to 65-70% of normal. An autosomal dwarfing gene *adw* was reported by Cole (1973) which reduces shank length in a similar manner to the *dw* gene.

The *dw* gene is presently being studied by a number of groups. In the U.S.A. Bernier and Arscott at Oregon State University and Quisenberry at Texas A and M University are studying the genetics and nutrition of dwarf layers. At Ohio State University Jaap is investigating the use of dwarf broiler breeders. At the University of Guelph in Canada a group is working under the direction of Summers, and reports have been published by Selvarajah in Malaysia and by Guillaume and Merat of the Institut National de la Recherche Agronomique (I.N.R.A.) in France. In France the I.N.R.A. has released a commercial line of dwarf broiler breeders (Vedette I.N.R.A. J.V. 15) and there has been at least one commercial release of dwarf layers in the U.S.A. (Colonial True Lines).

The use of dwarf broiler breeders assumes that the same scope for selection of desirable attributes exists within dwarf flocks as within flocks of normal birds, and also that the results of any selection within the dwarf flocks will be transferred to their normal phenotype offspring when mated to normal genotype males.

An examination of the heritabilities of various characters in dwarf and normal flocks would be the logical starting point for an examination of these assumptions. For example, should the heritability of body weight be the same or similar in dwarf and normal flocks it would seem reasonable to expect similar responses to selection at least in the short term. The assumption of similar responses may however, be complicated by scale effects because the gain in average weight of a given amount would represent a larger percentage

increase in dwarfs than in normal birds. A knowledge of such heritabilities will not give any answer to the question as to whether the results of selection will be transferred to the normal phenotype offspring of dwarf breeders to the same extent as occurs in normal genotype birds.

The major aims of this project were to estimate the heritability of body weight and shank length in dwarf and normal birds at various ages, to estimate correlations between the measurements made, and to see if there are any gross differences between the two genotypes. A sex-linked recessive dwarfing gene was reported in Australia by Dolling, Lowe and Polkinghorne (1971) and this is the gene which was used in this study. Polkinghorne (1974a) presented evidence that suggested that the Australian gene was probably *dw*, and this assumption will be used.

SPECIFIC PHENOTYPIC EFFECTS OF THE SEX-LINKED DWARFING GENE (*dw*)

(a) Physiological Effects

Most published reports agree that the *dw* gene is associated with hypothyroidic activity although not all writers agree that this activity is the cause of dwarfing e.g. van Tienhoven, Williamson, Tomlinson and MacInnes (1966) and Guillaume (1971), (1972).

A number of studies have been reported which involve the feeding of thyroactive substances (e.g. Protamone, which is iodinated protein with about 1% thyroxin activity) to test the hypothesis of hypothyroid activity. When van Tienhoven, Williamson, Tomlinson and MacInnes (1966) fed 0.04% Protamone

to dwarf birds they had a higher body weight at 4 and 6 weeks, but a lower body weight at 8 weeks, than dwarf controls. Rajaratnam, Selvarajah and Summers (1969) observed that feeding 0.033% Protamone increased 9 week body weight of dwarf pullets more than did the feeding of 0.066%. The higher level of Protamone decreased body weight of normal birds relative to the normal controls. The feeding of Protamone did not bring the body weights of dwarfs up to those of normal birds. Dorminey, Arscott and Bernier (1972b), (1973) reported that feeding 0.033% Protamone to dwarfs resulted in increased body weight from 4-16 weeks but that the difference from dwarf controls was not significant at 24 and 44 weeks. However, Rajaratnam, Summers, Wood and Moran (1971a) observed that dwarfs fed 0.033% Protamone were heavier than dwarf controls at 22 weeks.

The effect on the shank length of dwarf birds fed Protamone is similar to the effect on body weight in that Protamone increases the shank length of dwarfs but not up to the length of normal birds (van Tienhoven, Williamson, Tomlinson and MacInnes (1966), Rajaratnam, Summers, Wood and Moran (1971a)).

Dwarf birds have a lower body temperature than normal birds with most reports indicating reductions of about 0.5°C, (Rajaratnam, Selvarajah and Summers (1969), Summers, Rajaratnam and Moran (1970), Mather and Ahmad (1971), Rajaratnam, Summers, Wood and Moran (1971a) and Touchburn, Leclercq, Guillaume and Blum (1972)). The feeding of thyroxin increases the body temperature of dwarfs to that of normal

birds (Rajaratnam, Selvarajah and Summers (1969), Rajaratnam, Summers, Wood and Moran (1971a) (1971b)). However, Dorminey, Arscott and Bernier (1973) observed that although feeding Protamone increased body temperature of dwarfs to the level of normals at 8 weeks, at 16 weeks the body temperature was intermediate between untreated dwarfs and normals and at 24 weeks the body temperature of Protamone fed dwarfs was lower than that of the control dwarfs.

When comparing dwarf layers fed Protamone with control dwarfs no increase in laying performance was observed by Summers, Rajaratnam and Moran (1970), or by Rajaratnam, Summers, Wood and Moran (1971b). Lower egg production from dwarfs fed Protamone was reported by Dorminey, Arscott and Bernier (1973).

A feature of dwarf birds is the higher content of fat in the carcass. Higher fat levels in dwarfs compared with normal birds have been reported by Merat and Guillaume (1969), Summers, Rajaratnam and Moran (1970), Ricard (1970), Rajaratnam, Summers, Wood and Moran (1971a), Touchburn, Leclercq, Guillaume and Blum (1972), Guillaume (1969), Ouhayoun (1970) and Polkinghorne (1974b). Summers, Rajaratnam and Moran (1970) showed that feeding thyroxin reduced the fat level in dwarfs to that in normal birds as did Rajaratnam, Summers, Wood and Moran (1971a) who also noted an increased fat level in normal birds fed thyroxin. Thiouracil (a goitrogenic agent) was also fed to dwarf and normal birds by Rajaratnam, Summers, Wood and Moran (1971a) who observed that this resulted in decreased fat content of dwarfs and increased content in normal birds.

A lower oxygen consumption per unit body weight in dwarf compared with normal birds was shown by Guillaume (1969) and Touchburn (1971). Bayley, McDonald and Hunton (1971) concluded that dwarf and normal meat type birds have similar metabolic rates per unit of body weight, but that the dwarfs have a lower maintenance requirement per unit of body weight because when fasted their metabolic rate dropped to a level lower than that of normal birds. Similarly, Rajaratnam, Summers, Wood and Moran (1971a) showed lower oxygen consumption and basal metabolic rate per unit body weight in dwarfs when compared with normals. Feeding Protamone increased levels of these two characters to a similar extent in dwarf and normal birds.

Wood, Brown, Summers and Reinhart (1971) showed that the levels of serine were reduced and the levels of methionine greatly increased in the blood serum of dwarfs compared with normal birds. Guillaume (1971) also measured reduced levels of threonine, serine and glycine in the muscles of dwarf compared with normal pullets.

Brown, Wood, Reinhart and Longworth (1972) showed a higher amino acid activation rate in dwarf compared with normal birds, which they suggested was due to differences in amino acid activating enzymes. They also postulated that this effect was independent of the proposed hypothyroidism of dwarfs. The blood constituents of dwarfs and normals were compared by Wood, Reinhart, Rajaratnam and Summers (1971), who found lower haemoglobin concentrations in dwarfs and higher red blood cell counts in one dwarf strain but not

in another. Lower blood levels of sugar, total lipids and cholesterol were observed by Guillaume (1971).

The weight of the thyroid glands of dwarf and normal birds were shown to be similar by van Tienhoven, Williamson, Tomlinson and MacInnes (1966) when expressed as a proportion of body weight, yet Merat and Guillaume (1969) found that the thyroid glands of dwarfs were smaller as a percentage of body weight. Evidence for a hypothyroidic condition in dwarfs was given in the study of Grandhi, Brown, Summers and Walker (1973) who showed that dwarfs had a significantly lower ^{131}I uptake than normal birds although there was no difference in the pattern of ^{131}I release. However, Guillaume (1971) showed a significant difference between dwarf and normal pullets in the rate of ^{131}I release, and Merat and Guillaume (1969) a reduced secretion rate of thyroxin in dwarf birds.

Grandhi, Brown and Reinhart (1973) examined the effect of triiodothyronine and thyroxin injections on liver glycogen levels and concluded that there was a different physiological mechanism controlling glycogen metabolism in dwarf and normal birds.

Ricard and Cochez (1971) reported that dwarf broiler breeder hens showed higher fertility and hatchability than did normal hens when mated to normal sires, and although the differences were not significant 14% more chickens were obtained from the dwarf as compared with the normal dams. Despite a lower hatchability Sherwood (1971) showed that dwarf breeders gave 15% more chickens per hen housed than

did normal dams, when mated to normal sires.

Petitjean and de Reviers (1972) examined the sexual characteristics of dwarf and heterozygote cockerels and observed that on average dwarfs were 10 days older at the age of first ejaculation, that the volume of ejaculate was reduced by 19%, and that the sperm concentration was similar to the heterozygotes. Dwarf cockerels showed a superior sperm motility.

From the evidence in the literature it is apparent that dwarf birds are different from normal birds in at least some aspects of their physiology. It would appear that for at least part of their life that dwarfs are hypothyroidic as the feeding of thyroxin reduces the difference between dwarf and normal birds in terms of body weight, shank length, fat content and body temperature, but not egg production.

It would seem reasonable to assume that the observed hypothyroidism is not however the basic cause of the dwarf condition, but rather a related effect. If hypothyroid activity was the only cause of dwarfing then the administration of thyroxin would be expected to produce birds that were quite normal, and this is not what in fact occurs.

(b) Phenotypic Expression in High and Low Body Weight Strains

The expression of the *dw* gene appears to be quite different in heavy broiler type breeds than in the lighter type of bird associated with egg production. The *dw* gene reduces body weight by about 30% in the light breeds used for egg production while body weight reductions of about 20% are found when the *dw* gene is transferred into heavier broiler breeds.

Bernier and Arscott (1960) observed that dwarf birds from a laying strain laid fewer eggs and eggs with thinner shells than did normal layers and suggested that this may indicate a higher requirement for calcium in dwarf layers. Support for the suggestion of a higher calcium requirement for dwarfs was obtained in the results of Arscott, Rachapaetayakom, Bernier and Adams (1962) who recorded that increasing the dietary calcium from 2.25% to 3.00% for dwarf layers caused a "non-significant increase" in egg production and a significant increase in the specific gravity of eggs, which the authors used as an indirect measure of shell thickness.

Prod'homme and Merat (1969) however, when working with a high body weight strain found that increasing the calcium level fed to dwarfs from 2.50% to 3.54% did not effect laying performance or shell thickness, and suggested that the discrepancy in results between low and high body weight strains was due to the difference in size itself, rather than the presence of the *dw* gene.

Egg production in dwarf laying strains is reduced. Published reductions vary from 1% to 25% (Selvarajah 1970) when dwarf layers are compared with related normal birds. In contrast to the observed reduction in egg numbers in laying strains a number of reports, for example Prod'homme and Merat (1969), Ricard and Cochez (1971), Sherwood (1971), Yamada, Watanabe, Ebisawa and Futamura (1972) indicate that the laying ability of dwarf broiler breeders is not reduced, or not reduced to the same extent as in egg production type breeds.

Jaap (1969) suggested that the reason that egg production was not reduced in dwarf broiler breeders was associated with a lower rate of yolk accumulation in the ovaries of dwarf birds, as was shown by Jaap and Mohammadian (1969). Jaap and Clancy (1968) had shown that there were more ovarian follicles undergoing rapid development in the ovaries of broiler type pullets laying at 56% than White Leghorns laying at 84%. Jaap (1969) suggested that the reason for this may have been that selection for high growth rate in the broiler breeds had resulted in higher protein anabolism with an associated increase in yolk deposition rate in the ovarian follicles.

Jaap (1969) suggested that a lack of harmony between ovary and oviduct function in broiler pullets resulted in the commonly observed low egg production and high incidence of defective eggs. Because the *dw* gene reduced the rate of yolk accumulation Jaap (1969) suggested that the dwarf broiler pullet is better able to synchronise yolk production and oviduct function than its normal relatives, thus no decrease in egg production is observed when the *dw* gene is introduced to broiler breeds. When the *dw* gene is introduced to egg production type breeds, where presumably ovary and oviduct function are already synchronised the decrease in yolk production is reflected in a reduced number of eggs.

Jaap and Mohammadian (1969) indicated that the *dw* gene may also reduce the rate of intraperitoneal absorption of yolks in broiler pullets as a factor to their advantage. Consequently the rate of lay of defective eggs was 1.3% in

dwarf pullets as compared with 3.8% in related normal birds. Fewer abnormal eggs from dwarf as compared with normal broiler breeders were also observed by van Middelkoop (1972) and 7.6% of cracked eggs from dwarfs against 26.4% from normal birds were measured by Ricard and Cochez (1971).

(c) Growth Rate of Progeny

When comparing growth rates of progeny from dwarf and normal broiler strain sisters which had been mated to normal genotype sires Ricard (1971) showed that the day-old weights of chickens from dwarf dams were 1g lighter in both sexes. At 8 weeks the heterozygous males from dwarf dams were 96.7% of the weight of normal genotype males from the normal dams. Normal pullets from the dwarf dams were 0.7% heavier than normal pullets from the normal dams. Sherwood (1971) reported that progeny from dwarf dams were 94.7% of the body weight of those from normal dams without specifying age or sex differences.

By averaging the results of two experiments reported by Chambers, Smith, McMillan and Friars (1972), who also compared dwarf and normal pullets as broiler dams, male and female offspring from dwarfs were respectively 93.5% and 96.2% of the body weight of birds from normal dams at 8 weeks. In a similar experiment Yamada, Watanabe, Ebisawa and Futamura (1972) concluded that there was no significant difference in body weight of offspring at 10 weeks due to the dams' genotype.

Ricard (1971) reported that the body form of normal phenotype offspring from dwarf and normal dams was not different. Further, no differences due to dam genotype were found for any "dissection characteristics".

When Mohammadian and Jaap (1972) crossed a broiler sire to dwarf and normal White Leghorn sisters the 8 week body weight of the normal genotype female offspring was identical for the two dam types. The heterozygous males from the dwarf dams were 97.5% of the weight of the normal genotype males from the normal dams, the difference not being statistically significant. However, when the heterozygous males from this mating were crossed to normal broiler types females there was no difference between the body weights of the heterozygote and normal males which were classified by means of the sex-linked marker gene *K* (slow feathering).

Mohammadian and Jaap (1972) concluded that the depressed weight of heterozygous males in the White Leghorn crosses was not due to the *dw* gene being incompletely recessive but due to the maternal effect of smaller egg size in the dwarf dams. The normal genotype females do not seem to suffer from the smaller egg size of dwarf dams, as shown by the White Leghorn matings, and also other matings made between broiler type birds by Mohammadian and Jaap (1972). They therefore postulated that there was an interaction between the *dw* allele in heterozygous males and the reduced egg size of the dwarf dam that causes the depressed growth. When dwarf broiler males were mated to dwarf and normal broiler females the dwarf female offspring from the dwarf dams were smaller than those from the normal dams, presumably due to the reduced egg size of the dwarf dams. Mohammadian and Jaap (1972) therefore further suggested that there is an interaction between the maternal effect of the dwarf dam and the normal allele of *dw*

(i.e. *Dw*) in her normal daughters that permits normal female offspring from dwarf dams to overcome the effect of reduced egg size. A further mating indicated that the substitution of *Dw* for *dw* in heterozygous males (*Dwdw*) causes a proportionately similar body weight reduction as the same substitution in females.

After mating dwarf and normal broiler pullets to normal broiler sires Chambers, Smith, McMillan and Friars (1972) estimated the regression of 8 week body weight of the normal phenotype offspring on the weight of the egg from which the chicken hatched. Their results indicated that the body weight of female offspring was related to egg weight, but that in the male offspring the effect of dwarf dam was also contributing to body weight differences.

Normal and dwarf sires were mated to dwarf dams by Khan, Jaap and Harvey (1973) who calculated the regression of 8 week body weight on the weight of individual eggs from which chickens hatched as well as on average egg weight of the dam. For offspring of the normal sires both regressions were significant and linear for both sexes. For the offspring of dwarf sires the regression on individual egg weight was linear and significant for female offspring but was quadratic and significant for male offspring, with maximum body weights coming from eggs weighing 63g. The regression on average egg weight of dam was non-significant for both sexes for dwarf offspring.

There is very little published information on the effect of the *dw* gene on genetic parameters such as

heritabilities and correlations. Mohammadian (1970) reported a higher coefficient of variation for 8 week body weight in a flock of dwarf as compared with normal birds. Ricard and Cochez (1972) also reported higher variability and coefficients of variation for dwarf compared with normal birds for body weights and shank lengths measured at 4, 8 and 12 weeks. Increased heritabilities, especially at the sire component level were also recorded for dwarf birds by Ricard and Cochez (1972), although no figures were given. They concluded that "breeding possibilities for growth and size characteristics are higher in birds carrying the *dw* gene". A heritability estimate of 0.46 for 8 week body weight in dwarfs was obtained by Khan, Jaap and Harvey (1973) compared with a heritability of 0.54 obtained from the normal phenotype offspring from normal males mated to dwarf females.

COMMERCIAL APPLICATION OF SEX-LINKED DWARFING GENES

(a) Meat Production

Selection for rapid growth rate in lines of birds bred for meat production has resulted, presumably as a correlated response, in large increases in the adult size of birds retained for further breeding. Feed consumption of these large birds is increased relative to smaller birds and thus the cost of eggs produced by the large birds is increased. Introducing the *dw* gene into such high body weight lines results in decreases of 20-30% in body weight with a corresponding reduction in feed consumption. The cost of maintaining breeder birds and the cost of the eggs they

produce can therefore be reduced.

The advantage in using the *dw* gene rather than other dwarfing genes is due to the sex-linked recessive action of *dw*. When normal genotype males are mated to dwarf females the female offspring are genetically normal and the male offspring are heterozygous with respect to the *dw* gene and therefore phenotypically normal. By using dwarf females which are mated to normal genotype males to produce normal phenotype broiler offspring there is the possibility that savings can be made in the cost associated with the breeding of broiler chickens.

There are, of course, some assumptions made in advocating the use of dwarf broiler breeder females which would need to be investigated before the advantages could be proved:

- (1) That egg production of dwarf breeders is similar to that of normal breeders, so that cost savings associated with the reduced feed consumption of dwarfs are not eroded.
- (2) That the reduced egg size in dwarf breeders does not effect the body weight of resulting offspring at the time the offspring are of marketable age.
- (3) That the viability of dwarf breeders is similar to that of normal birds, as measured by such characters as mortality, fertility and hatchability

- (4) That there are no deleterious effects due to dwarf dams on the growth rate of offspring, apart from the possible egg size effects mentioned previously.

Should one or more of these assumptions prove to be invalid the postulated advantage of dwarf breeders is not necessarily negated. A careful economic analysis would be needed to determine the overall balance of advantages and disadvantages and would also need to include such factors as a possible increase in stocking density that would be obtainable with dwarfs.

Two separate breeding flocks would be necessary if dwarf breeders were to be used commercially. A dwarf flock would be required to produce the dwarf hens and a genetically normal flock would be needed to produce the sires to be mated to the dwarfs. This should not be necessarily taken as a disadvantage to the use of dwarfs however, as the crossing of two distinct lines, utilizing the resulting heterosis is the usual method for the production of broiler chickens.

(b) Egg Production

The type of bird used for egg production is quite different from that used in the production of meat, having been selected for high rate of lay rather than rapid growth rate.

The decrease in size resulting from the incorporation of a sex-linked dwarfing gene into a laying strain could result in a decrease in the amount of feed required per unit

weight of egg product, in the same way as was outlined for the broiler breeder bird. Any reduction in egg number and size in dwarf birds used for egg production would be more of a disadvantage in laying strains than in broiler breeder strains. The egg is the end product in layer strains and is sold according to size as distinct from the broiler breeder case where the resulting chicken is the end product, and therefore perhaps less sensitive to the effect of reduced egg size.

The possibility of advantages resulting from the commercial use of dwarf layers has attracted studies dealing with:-

(i) Comparison of Dwarf and Normal Hens

Studies on various aspects of the laying performance of dwarf compared with related normal hens were performed by Bernier and Arscott (1960), French and Nordskog (1969), Selvarajah, Jerome, Summers and Reinhart (1970), Selvarajah (1970), (1971), McLung, Jones and Patrick (1971), Merat (1971), Akinkuolie and Jaap (1973) and McLung and Jones (1973).

(ii) Nutrition of Dwarf Layers

Various studies have been made on the optimum protein and energy requirements of dwarf layers. Some studies also examined calcium, phosphorus and vitamin requirements.

Papers have been published by Arscott, Rachapaetaykom and Bernier (1961), Arscott, Rachapaetaykom, Bernier and Adams (1962), Bernier and Arscott (1966), Arscott and Bernier (1968), Magruder and Coune (1969), Quisenberry, Gonzales and Bradley (1969), Damron and Harms (1970), Selvarajah, Summers and

Jerome (1970), Summers (1971) and Quisenberry (1971).

(iii) Management of Dwarf Layers

The effect of different stocking density in cages and the presence or absence of perches have been studied by Dorminey, Arscott and Bernier (1971), (1972a), (1973) and Quisenberry and Bradley (1971).

Polkinghorne and Lowe (1973) when using a sex-linked dwarfing gene (assumed to be *dw*), in a layer type cross observed an 11.3% reduction in egg numbers from dwarf as compared with normal hens with a decrease of 10.2% in average egg weight. The dwarfs however, showed a 9.4% better conversion of feed to eggs than the normal birds. These results are typical of other studies that have used the *dw* gene. There is probably a combination of feed and egg prices that would result in economic superiority of dwarf layers but the analysis would be complex due to the different price paid for different weight grades of eggs. The case for the use of the *dw* gene in laying birds would seem to be less obvious than the case for the incorporation into broiler breeder birds.

MATERIALS AND METHODS

(a) Origin of Stock

Birds used in the original matings reported in this study were drawn from the Para-meat line. Polkinghorne (1973) detailed the breeding of this line which originated in 1959 at the Parafield Poultry Research Centre (South Australian

Department of Agriculture) from crosses between White Leghorn, Light Sussex and Rhode Island Red birds.

The Para-meat line is annually regenerated from about 15 sires each mated to 10-12 hens. The pedigree of individual birds is recorded through the sire only and birds are mass selected on the basis of body weight at 8 weeks.

Details of the breeding of the antecedents of the birds used in this study are shown in Table (1) which also shows the wingband numbers of birds used in the first generation of this study. In 1970 i.e. before the start of this study, dwarf males from the Para-1 White Leghorn strain had been crossed to normal genotype females from the Para-meat line to give heterozygous male and dwarf female progeny. In 1971 the male progeny were crossed to normal genotype Para-meat females, providing progeny segregating with approximately equal numbers of dwarf and normal females, of which only the dwarfs were retained. Normal genotype Para-meat males were crossed to the dwarf females resulting from the 1970 matings and the resulting heterozygous males retained.

The heterozygous males from the 1971 matings were mated in early 1972 to normal genotype Para-meat females and also separately to the dwarf females that resulted from the 1971 matings. The dwarf and normal female offspring that resulted were used as parents for the first generation involved in this study. To increase the number of dwarf females used in this study the survivors from the dwarf females mated in early 1972 were also retained.

Table (1) Origin of Birds used for First Pedigreed Generation

<u>1970 MATINGS</u>		
PARENTS:	DWARF WHITE LEGHORN MALES X	PARA-MEAT FEMALES
Progeny:	heterozygous males	dwarf females
<u>1971 MATINGS</u>		
PARENTS:	HETEROZYGOUS MALES X (from 1970 matings)	PARA-MEAT FEMALES
Progeny:	$\frac{1}{2}$ heterozygous males (discarded)	$\frac{1}{2}$ normal females (discarded)
	$\frac{1}{2}$ normal males (discarded)	$\frac{1}{2}$ dwarf females (retained)
PARENTS:	PARA-MEAT MALES X	DWARF FEMALES (from 1970 matings)
Progeny:	heterozygous males (retained)	normal females (discarded)
<u>EARLY 1972 MATINGS</u>		
PARENTS:	HETEROZYGOUS MALES X (from 1971 matings) (wingbands 001-009)	DWARF FEMALES (from 1971 matings) (wingbands 172-180)
Progeny:	$\frac{1}{2}$ heterozygous males (discarded)	$\frac{1}{2}$ normal females (wingbands 181-195)
	$\frac{1}{2}$ dwarf males (discarded)	$\frac{1}{2}$ dwarf females (wingbands 151-171)
PARENTS:	HETEROZYGOUS MALES X (from 1971 matings) (wingbands 001-009)	PARA-MEAT FEMALES
Progeny:	$\frac{1}{2}$ normal males (discarded)	$\frac{1}{2}$ normal females (wingbands 181-195)
	$\frac{1}{2}$ heterozygous males (discarded)	$\frac{1}{2}$ dwarf females (wingbands 151-171)

The heterozygous males used as sires for the first generation of this study were those which had resulted from the 1971 matings, and had been previously used in early 1972. The normal genotype sires used for the first generation were drawn from the Para-meat line.

The heterozygous males (wingbands 001-009) were the result of two crosses into the Para-meat line from the original White Leghorn. The normal genotype males (010-014) did not have this White Leghorn influence in their recent breeding. No selection for bodyweight had been performed in the transfer of the dwarf gene from the White Leghorns into the meat type background.

(b) Mating Programme

Two generations of pedigreed matings were involved in this study.

(i) 1972 Matings

Wingband numbers of birds which were mated in December, 1972, are summarised in Table (2). Mating Group (1) consisted of 9 heterozygous sires each mated to 3 dwarf females. Dwarf females numbered 162, 173 and 175 were not mated as they were not producing eggs. Sire 003 proved to be infertile despite the production of satisfactory semen volumes. Similarly sire 009 produced only 4 offspring, two of which died before the age of 12 weeks. Mating Group (2) consisted of 5 normal genotype sires each mated to 3 normal genotype hens.

Three hatches, each 2 weeks apart were taken for both groups on 28th November, 12th December and 22nd December, 1972, providing 149, 192 and 121 chickens respectively to give a total of 462 birds. Consecutively numbered wingbands were attached to each chick hatched.

Table (2) Details of Matings December 1972

Mating Group (1) Heterozygous Males x Dwarf Females					
Sire	Dam	Sire	Dam	Sire	Dam
001	151	004	160	007	170
	152		161		171
	153		163		172
002	154	005	164	008	174
	155		165		176
	156		166		177
003*	157	006	167	009**	178
	158		168		179
	159		169		180
Mating Group (2) Normal Males x Normal Females					
Sire	Dam	Sire	Dam	Sire	Dam
010	181	012	187	014	193
	182		188		194
	183		189		195
011	184	013	190		
	185		191		
	186		192		

* Infertile - no offspring

** Low fertility - few offspring

(ii) 1973 Matings

In March 1973 all 44 surviving dwarf females were retained. Twenty-four normal genotype females were randomly selected from the 113 birds available. Males retained for breeding were selected in pairs of full sibs. A number was selected from Random Number Tables and the bird with that wingband number retained if the number corresponded to a surviving male who also had a surviving full sib brother. Both birds were then kept. On this basis 9 pairs of dwarf, 10 pairs of heterozygous and 9 pairs of genetically normal birds were selected. By selecting birds in pairs a reserve cockerel could be substituted for any bird that failed to produce semen for artificial insemination, or who died during the mating period.

Details of wingband numbers of birds mated in November 1973 are summarised in Table (3). Six dwarf males were each mated to 3 dwarf hens to form Mating Group (3). Mortality between the selection of cockerels in March 1973 and the commencement of insemination in November 1973 had reduced the number of surviving full sib pairs from the selected 9 pairs down to 4. Two cockerels were therefore used without the provision of a full sib reserve.

Six normal genotype sires were each mated to 3 normal genotype hens to form Mating Group (4). As in Mating Group (3) only 4 intact pairs were

surviving in November from the original 9 pairs in March. Two further cockerels were therefore used without the provision of reserves. Mating Group (4) was between the same genotypes as Mating Group (2).

Table (3) Details of Matings November 1973

Mating Group (3) Dwarf Males x Dwarf Females

Sire	Dam	Sire	Dam	Sire	Dam
112**	375 348 195	094	279 133 400	257	388 239 203
204	108 180 099	219	386 064 236	244	110 367 155

Mating Group (4) Normal Males x Normal Females

Sire	Dam	Sire	Dam	Sire	Dam
299	339 274 384	009	333 430 146	316	034 005 319
318	298 336 202	310	253 441 331	433	455 148 183

Mating Group (5) Heterozygous Males x Dwarf Females

Sire	Dam	Sire	Dam
378	436 118 268	062	345 090 213
286**	374 185 079	057	364 211 412

** Low fertility - few offspring

Mating Group (5) consisted of 4 heterozygous sires each mated to 3 dwarf hens, i.e. the same genotypes as used in Mating Group (1). Mortality had been heavy in this group also and only 3 intact full sib pairs survived until November. A further cockerel was used without provision for a reserve.

The birds mated were between 46 and 52 weeks old, depending on hatch date, when the first eggs were set for incubation in December 1973. Four hatches, each two weeks apart were performed on 21st December, 1973, 4th January, 1974, 18th January, 1974 and 1st February, 1974, providing 55, 149, 145 and 148 chickens respectively for a total of 497 birds. All birds hatched were wingbanded.

In the analyses subsequently performed results were pooled over the two years of this study and the 5 Mating Groups classified into 3 distinct classes. The classification made, and the terminology to be used in the following text has been summarised in Table (4).

Comparisons between dwarf and normal birds were made in two ways. Measurements were made within the Dwarf Group and the Normal Group and comparisons made between them, and in addition comparisons were made within the Segregating Group. The Segregating Group was generated by mating heterozygous males to dwarf females and thus the normal males in the Segregating Group were heterozygous for the *dw* gene.

Table (4) Classification of Mating Groups, and
Terminology used in Text

Classification	Genotype of Parents	Terminology used in Text to Describe Progeny
Mating Group (3) - 1973 (Dwarf Matings)	dwarf males x dwarf females	Dwarf Group
Mating Group (2) - 1972, and Mating Group (4) - 1973 (Normal Matings)	normal males x normal females	Normal Group
Mating Group (1) - 1972, and Mating Group (5) - 1973 (Heterozygote Matings)	heterozygous males x dwarf females	Segregating Group

The experimental design required to undertake heritability and correlation estimates also allowed other comparisons to be made between dwarf and normal birds, for example average egg weight, reproductive performance and the relationship between body weight of progeny and average egg weight of dam, and these comparisons were made when possible.

(c) Facilities and Management

In both years birds were reared from hatching until 4 weeks in electrically heated multi-tiered battery brooders. Each floor of the brooder measured 4 feet (ft) x 3 ft, and contained approximately 90 chickens. Feed was supplied *ad libitum* during the brooding period consisting of a mash containing about 18% crude protein and 2,500 Kcalories

of metabolizable energy per kilogram of feed.

In the first year birds were placed in battery weaner cages from 4 to 6 weeks of age. Each floor of a weaner cage measures 6 ft x 3 ft, on which was placed approximately 40 chickens.

When birds were 6 weeks in the first year, and 4 weeks old in the second year they were transferred to deep litter pens 18 ft x 20 ft. Each deep litter pen contained all birds from a given hatch. A grower mash containing about 16% crude protein and 2,500 Kcalories of metabolizable energy per kilogram was fed *ad libitum* from 4 to 20 weeks.

The only vaccination performed was against Fowl Pox when birds were between 10 and 12 weeks old, in both years. All birds, in both years, were debeaked at about 6 weeks to prevent feather picking and cannibalism.

Adult cockerels were housed in small floor pens (1½ ft x 5 ft) at two birds per pen. In the first year cockerels from whom semen was to be collected were kept one per pen in the floor pen described above. This was not entirely satisfactory as the cockerels could become disturbed when being caught, which sometimes made semen collection difficult. In the second year cockerels from whom semen was required were placed in laying cages similar to those in which the hens were housed. This was more suitable for the dwarf than for the larger heterozygote and normal cockerels. Catching the cockerels was however much quicker and less traumatic on the birds and the semen collection much quicker and more effective.

From 20 weeks until required for artificial insemination adult females were kept at 10-15 birds in deep litter pens with floor space 6 ft x 8 ft. These pens were equipped with nests and perches. Hens required for artificial insemination were placed individually in laying cages measuring 9 inches (ins) x 18 ins. These cages were constructed such that eggs from any one bird could not be confused with those from others.

(d) Breeding Techniques

(i) Insemination

Semen was collected in small glass vials to which was attached a small plastic funnel with a shortened stem. Semen was washed from the funnel into the vial with diluent from a Pasteur pipette. A graduated 1ml syringe was attached to a glass eye dropper and used to draw up the diluted semen from the vial and to deliver the semen into the hen's oviduct.

Two operators were required to milk semen from the cockerels, one to hold the cockerel, the other to hold the funnel and vial and to manipulate the cockerel. Training was required before the cockerels would readily protrude the penis to allow easy collection of sufficient semen. In the first year the diluent used was a sterile solution of 0.9% saline. In the second year a commercially available diluent was used. (Trade name Tyrode, supplied by the Commonwealth Serum Laboratories). When the semen was washed into the

vial the funnel was removed and the vial capped. The vial was then placed in a rack which was numbered with the pen or cage in which the cockerel was housed. Semen was always used fresh, the time between milking of the cockerels and insemination of the hens being not more than about 45 minutes.

Hens to be inseminated with the same semen were housed in adjacent cages. Record sheets showed the cage numbers of hens against the pen or cage numbers of the required cockerels. Hens were removed from the laying cages and their oviducts everted by exerting pressure on the abdomen. Approximately 0.15 ml of diluted semen was then injected directly into the oviduct. Three operators were used. One to handle the hens, one to inject the semen, and a third to handle the vials and ensure that no mistakes were made. Insemination of hens was performed on two days of each week, in the afternoon. Hens which had not laid at least one egg in the previous week, or had an egg in the uterus were not inseminated.

(ii) Collection of Eggs

Eggs were collected daily in the afternoon. The laying cages were constructed such that eggs from a given bird could not be confused with those from any other bird. Each egg was marked with the date and the cage number of the bird which had laid that egg. Eggs with cracks or soft shells were discarded. All usable eggs were weighed to the

nearest 0.1g and stored in a cool room (13°C) until required for setting in the incubator.

(iii) Incubation of Fertile Eggs

Eggs were set at 2 week intervals. All eggs were sorted according to cage number of the dam, and set out in the incubator trays such that the eggs from each hen formed one row. After 6 days incubation at 37.8°C the incubator trays were removed and all eggs candled with a strong light. Infertile eggs and eggs containing dead embryos were removed. After further incubation the eggs were candled again on the 18th day and eggs containing dead embryos removed. The cage number and date identification of all eggs removed was recorded.

After candling on the 18th day the eggs were transferred to hatching trays. These consisted of trays subdivided such that eggs from one dam could be placed in a compartment so that chickens hatching from those eggs would not be confused with other chickens. Chickens were removed from the hatching trays after 21 days of incubation and each compartment, which corresponded with eggs from a given dam, was scored for the number of healthy chickens.

To allow subsequent identification of individual chickens consecutively numbered wingbands were attached to the right wing of all chickens hatched. The identification of each chicken's dam was recorded against the individual wingband numbers. The parents

of each chicken were therefore known from the record of its dam and the record of the cockerel used to inseminate that dam.

(e) Scoring of Birds

At hatching the day-old body weight (DOBW) of each chicken was recorded to the nearest gram. Body weights to the nearest 5g were recorded at 6 weeks (6WKBW) and 12 weeks (12WKBW).

The shank length of the right leg of all birds was recorded at 6 weeks (6WKSL) and 12 weeks (12WKSL). Shank length was estimated with vernier calipers by placing one arm of the calipers on the furthest part of the hock joint when the metatarsus bone was held at about right angles to the tibia. The third metatarsal bone (the middle toe) was bent downwards at right angles to the metatarsus and the end of the calipers adjusted until it rested against the the metatarsal. The calipers were read to the nearest 0.05cm.

A random sample of 5 birds from each of the 5 possible genotypes (i.e. dwarf, heterozygous and normal males; dwarf and normal females) was slaughtered in March 1973 to determine the relationship between the shank length as measured above and the length of the dissected metatarsus bone. The birds used were between 11 and 15 weeks old. The results are summarised in Appendix (1) and show an extremely close regression of shank length measured on the live bird on dissected metatarsus length ($b = 1.0300 \pm 0.0453$).

The sex of birds was recorded at 6 weeks on the basis of comb and wattle development. This was checked at

12 weeks by which time the sexual difference in hackle feathers becomes apparent.

Birds were scored as dwarf or normal at 12 weeks. The visual classification of normal males included heterozygous as well as genotypically normal birds. The heterozygote birds could be separated only by reference to the genotype of the sire and dam. The difference between dwarf and normal birds was not visually apparent at 6 weeks, and classification with any degree of confidence was not possible before about 10 weeks of age.

In the first year the sex of birds that died before six weeks was not recorded. In the second year dead birds were internally examined and the sex recorded on the basis of presence of testes or ovary. The scoring of the genotype of dead birds was not possible where the segregation of dwarf and normal occurred.

RESULTS AND DISCUSSION

(a) Parents

(i) Average Egg Weight

The average weight of eggs laid by all birds used in this study, calculated from eggs that were set for hatching are presented in Table (5), together with the results of an analysis of variance. Dams were grouped by mating type in each of the two years for the analysis of variance. The Least Significant Difference calculated from the analysis indicated

Table (5) Average Egg Weight (AEW) of Dams (g)

Dwarf Dams						Normal Dams			
Dwarf Matings		Heterozygote Matings				Normal Matings			
1973		1972		1973		1972		1973	
Dam	AEW	Dam	AEW	Dam	AEW	Dam	AEW	Dam	AEW
348	51.2	151	58.2	118	47.5	181	46.1	339	54.6
195	48.4	152	52.1	374	48.4	182	51.8	274	55.5
108	47.5	153	56.9	345	52.3	183	60.5	298	58.0
180	49.4	154	55.5	090	61.5	184	55.1	202	56.2
099	55.5	155	54.3	213	54.3	185	60.1	333	59.8
279	54.4	156	46.5	364	53.7	186	58.9	430	57.4
400	52.7	160	47.4	211	52.6	187	60.8	146	60.4
064	43.7	161	51.5	412	47.5	188	58.9	253	54.7
236	47.3	163	48.0			189	51.9	441	61.4
388	48.8	164	48.4			190	68.3	034	59.0
239	51.0	165	48.8			191	55.1	005	59.5
110	57.1	166	48.8			192	54.6	319	56.3
367	51.5	167	55.6			193	55.3	455	57.0
155	47.5	168	54.8			194	53.0	148	59.8
		169	48.8			195	64.2	183	55.8
		170	55.2						
		171	52.8						
		172	57.1						
		174	53.2						
		176	53.8						
		177	58.1						
		178	54.3						
		179	55.6						
		180	55.6						
Average		50.4	53.0	52.2		57.0		57.7	
Weighted average for all dwarf dams				52.1					
Weighted average for all normal dams								57.3	
Analysis of Variance									
Source of variation				df	MS	F			
Between groups				4	141.20	8.97**			
Within groups				71	15.75				
Total				75					
Least Significant Difference = 3.07g									
** significant at 1% confidence level									

that at a 5% confidence level there were no significant differences between any of the groupings of dwarf dams, either between the Dwarf and Heterozygote Matings, or between years. There was also no difference in average egg weight between normal dams used in the two years. The average egg weight of dwarf dams was however significantly less at a 5% confidence level than the average egg weight of normal dams.

Eggs from the dwarf hens were, on average, 90.9% of the weight of eggs from normal hens. This reduction of about 10% is very similar to the 9% reduction observed by Prod'homme and Merat (1969) when examining dwarf and normal birds from a heavy breed. Smaller reductions in egg weight from dwarf birds in heavy breeds were observed by Ricard and Cochez (1971), where a difference of only 1g was measured, and by Yamada, Watanabe, Ebisawa and Futamura (1972) who measured a 5% reduction.

Reductions of about 10% in average egg weight of dwarfs are usual in lighter egg strains (Polkinghorne 1974a). Using the same gene as was used in this study in a layer strain Polkinghorne and Lowe (1973) observed egg weights from dwarfs that were 10.2% less than those from normal birds.

(ii) Incubation

Data on the reproductive performance of sires in the Dwarf, Normal and Heterozygote Matings are shown in Tables (6), (7) and (8) respectively.

Table (6) Incubation Data, Sire Totals for Dwarf Matings

Sire	Number eggs set	Number eggs fertile	Number chickens hatched
112	49	11	9
204	72	61	53
094	41	19	13
219	63	41	37
257	73	30	23
244	85	60	51
Totals	383	222	186
Fertility		58.0%	
Hatchability			83.8%

Homogeneity test	Size of table	df	χ^2	
Fertility and Hatchability	6 x 3	10	30.756	P<0.001
Hatchability	6 x 2	5	0.568	P>0.99
Fertility	6 x 2	5	18.420	0.001<P<0.01
Fertility (excluding 112)	5 x 2	4	8.568	0.10 <P<0.20
Fertility and Hatchability (excluding 112)	5 x 3	8	15.346	0.05 <P<0.10

Data on the performance of the dams mated to the respective sires is shown in Tables (b), (c) and (d) of Appendix (2). Incubation data were tested for homogeneity for the number of eggs set, the number of eggs fertile and the number of chickens hatched by means of homogeneity chi-square tests on the sire totals. As shown in Table (6) the combined fertility

and hatchability totals for the Dwarf Matings were markedly heterogeneous. Hatchability totals (number of chickens hatched to number of eggs fertile) when tested separately were however homogeneous, and the fertility totals (number of eggs fertile to number of eggs set) heterogeneous. Low fertility sires which were arbitrarily defined as those having less than 40% of eggs set being fertile were excluded (i.e. sire 112) and the fertility data re-analysed, and shown then to be homogeneous. Accordingly the sire totals for the combined fertility and hatchability totals excluding sire 112 were re-analysed and shown to be homogeneous.

Data from the Normal Matings were similar as shown in Table (7). When all sire totals were analysed the combined fertility and hatchability data were heterogeneous, the hatchability totals homogeneous, and the fertility totals heterogeneous. When sire 316 was excluded from the analysis as being of low fertility the fertility totals became homogeneous. Also when sire 316 was excluded sire totals for the combined fertility and hatchability data became homogeneous.

Again, as shown in Table (8) sire totals from the Heterozygote Matings were heterogeneous for the combined fertility and hatchability data, hatchability totals were homogeneous and fertility totals heterogeneous. When the low fertility sires

Table (7) Incubation Data, Sire Totals for Normal Matings

Sire	Number eggs set	Number eggs fertile	Number chickens hatched
010	55	44	32
011	51	44	32
012	51	43	27
013	73	32	22
014	62	42	31
299	54	32	26
318	69	45	33
009	105	54	32
310	46	25	24
316	95	19	16
433	111	74	68
Totals	772	454	343
Fertility		58.8%	
Hatchability			75.6%

Homogeneity test	Size of table	df	χ^2	
Fertility and Hatchability	11 x 3	20	53.052	P<0.001
Hatchability	11 x 2	10	4.201	0.90<P<0.95
Fertility	11 x 2	10	33.356	P<0.001
Fertility (excluding 316)	10 x 2	9	10.774	0.30<P<0.50
Fertility and Hatchability (excluding 316)	10 x 3	18	20.564	0.30<P<0.50

Table (8) Incubation Data, Sire Totals for Heterozygote Matings

Sire	Number eggs set	Number eggs fertile	Number chickens hatched		
001	81	30	26		
002	86	79	66		
004	86	39	36		
005	82	64	59		
006	92	68	53		
007	79	59	44		
008	57	42	30		
009	52	10	4		
378	55	32	9		
286	115	2	2		
062	85	45	35		
057	98	77	66		
Totals	968	547	430		
Fertility		56.5%			
Hatchability			78.6%		
Homogeneity test		Size of table	df	χ^2	
Fertility and Hatchability		12 x 3	22	183.104	P<0.001
Hatchability		12 x 2	11	11.546	0.30<P<0.50
Fertility		12 x 2	11	101.750	P<0.001
Fertility (excluding 001, 009 and 286)		9 x 2	8	12.518	0.10<P<0.20
Fertility and Hatchability (excluding 001, 009 and 286)		9 x 3	16	31.248	0.01<P<0.02
(excluding 001, 009, 286 and 378)		8 x 3	14	17.716	0.20<P<0.30

(001, 009, 286) were excluded the fertility totals became homogeneous. However, when the low fertility sires were excluded and the combined fertility and hatchability data re-analysed, the sire totals remained heterogeneous. Sire 378 had an inferior hatching record compared to the other sires due to dam 268, to which he was mated, failing to hatch any chickens from 22 fertile eggs. This low hatchability did not cause any significant heterogeneity in the hatchability chi-square test on the sire totals. When data on dam 268 was excluded from sire 378's record he then came into the classification of a low fertility sire. When all the data on sire 378 was excluded, along with the other low fertility sires the analysis of the combined fertility and hatchability data proved to be homogeneous.

The performance of the 3 mating types were compared by means of a homogeneity chi-square test on the totals for each mating type, which are shown in Table (9). When the low fertility sires were excluded the data showed good homogeneity ($\chi^2_4 = 4.980$; $0.2 < P < 0.3$). A similar test on the totals including the low fertility sires, which are also shown in Table (9) still shows good homogeneity of the mating type totals ($\chi^2_4 = 1.145$; $0.7 < P < 0.8$). The internal heterogeneity of the fertility data was not sufficient to disturb the homogeneity of the Mating Type totals. There is very little difference in the overall fertility or hatchability of the three mating types.

Table (9) Incubation Data, Mating Type Totals

(a) Totals Excluding Low Fertility Sires

	Number eggs set	Number eggs fertile	Number chickens hatched	Total
Dwarf Matings	334	211	177	722
Normal Matings	677	435	327	1439
Heterozygote Matings	665	473	389	1527
Total	1676	1119	893	3688

(b) Totals Including Low Fertility Sires

	Number eggs set	Number eggs fertile	Number chickens hatched	Total
Dwarf Matings	383	222	186	791
Normal Matings	772	454	343	1569
Heterozygote Matings	968	547	430	1945
Total	2123	1223	959	4305

(See Tables (6), (7) and (8)). The fertility percentages are low, although this is probably due to the generally poor reproductive performance of the Para-meat Line (Polkinghorne 1973) from which the birds used in this study were originally drawn. A comparison of the Dwarf Matings with the Heterozygote Matings compares dwarf and heterozygous sires since dwarf dams were used for both groups. The comparison of dwarf and normal sires is confounded by the different dam genotypes used in the Dwarf and

Normal Matings. Despite this limitation the similarity of the overall percentages would suggest that there is no major reproductive disadvantage associated with dwarf sires or dams. This result is in general agreement with other published results from heavy strains e.g. Ricard and Cochez (1971).

(b) Progeny

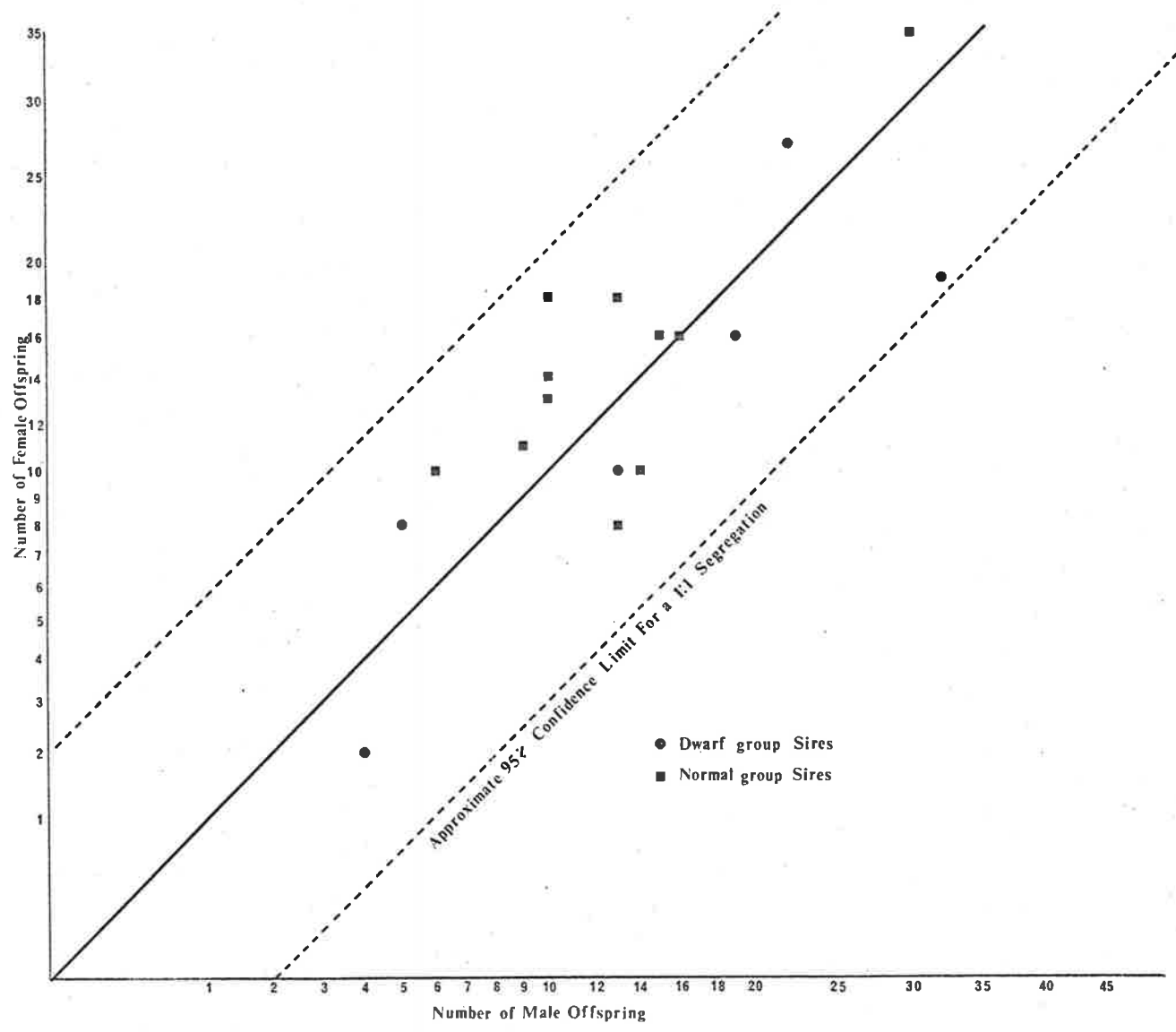
(i) Segregation for Sex and Genotype

The number of male and female offspring for each sire and each dam are shown in Tables (e), (f) and (g) of Appendix (3) for the Dwarf, Normal and Segregating Groups respectively. Only birds who survived to 12 weeks have been included, because the sex of dead birds was not recorded in 1972.

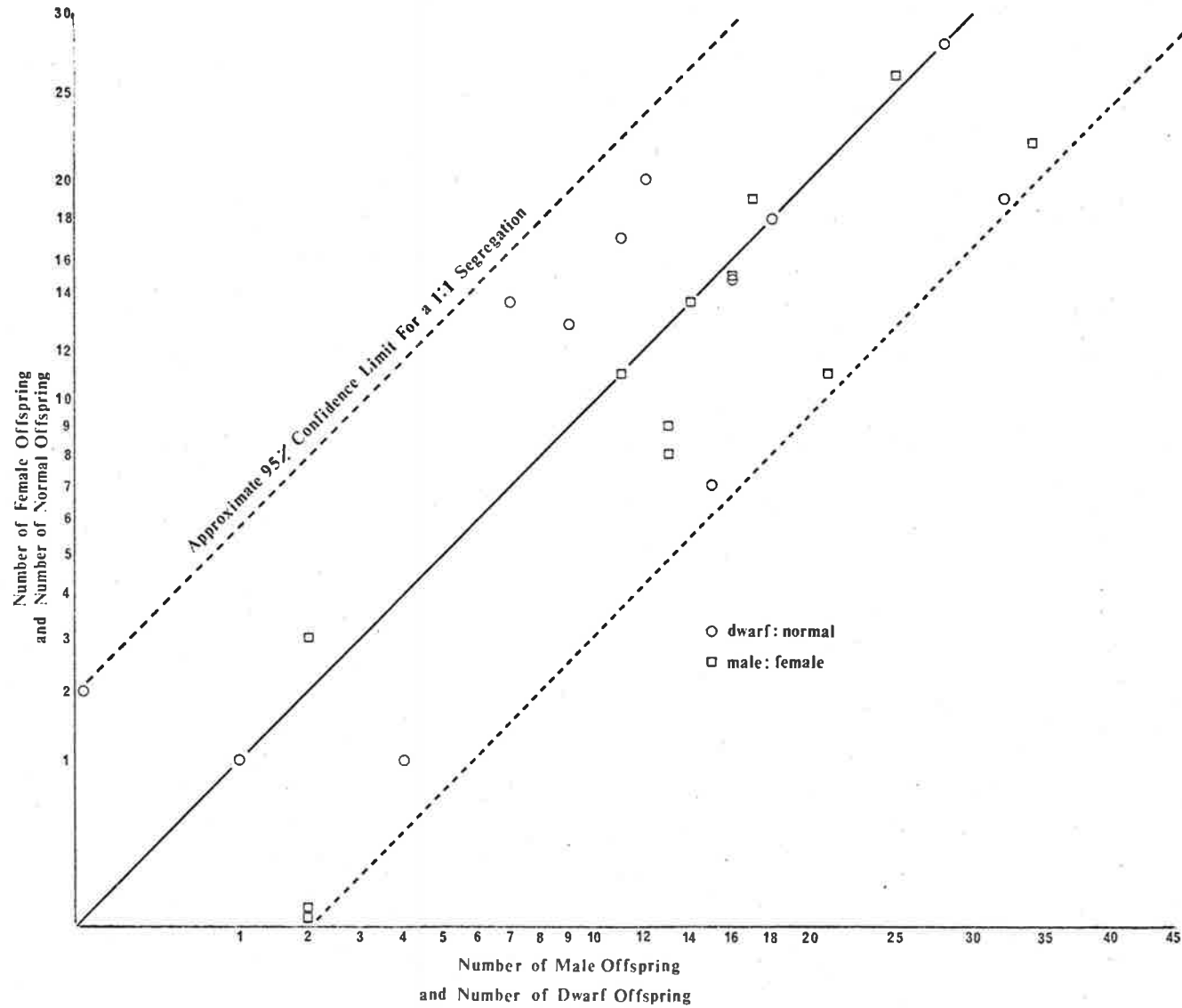
The number of male against female offspring for each sire in the Dwarf and the Normal Groups has been plotted in Figure (1). A square-root scale has been used and the approximate 95% confidence limits for an expected 1 male : 1 female segregation indicated. The square-root scale makes the confidence interval a constant perpendicular distance from the line representing a 1:1 segregation regardless of the number of individuals scored. Figure (1) indicates that for the Dwarf and Normal Group no sire totals gave sex segregations more abnormal than would be expected by chance alone, and also that sex segregations were homogeneous.

The sex segregations for each sire in the

Figure(1) Segregation of Sex, Dwarf and Normal Groups



Figure(2) Segregation of Sex and of Genotype,
Segregating Group Sires



Segregating Group have been plotted in a similar manner in Figure (2). Also plotted, for each sire is the segregation of offspring into dwarf and normal. Female offspring segregated between dwarf and normal and male offspring between dwarf and heterozygote. Figure (2) shows that for the Segregating Group sire totals did not show significant deviations from an expected 1:1 segregation for either the segregation of sex, or the segregation of dwarf to normal, when considered separately. A chi-square test was used to test the goodness of fit of the sire totals to the expected segregation of 1 dwarf male : 1 heterozygote male : 1 dwarf female : 1 normal female. Sire totals and chi-square values relevant to these segregations are given in Table (10), and the totals for dams within sires are given in Table (h) of Appendix (4). Sires 009, 378 and 286 were excluded from the analysis because of the low number of offspring they contributed. None of the sire totals shown in Table (10) indicated deviations greater than would be expected by chance alone, and the chi-square calculated on the totals also showed a good fit to the expected segregation. As is also shown in Table (10) the homogeneity of the sire totals was tested by subtracting the χ^2_3 calculated for the grand totals from the χ^2_{27} calculated from the sum of the chi-squares for each sire, giving a χ^2_{24} which indicated a good

Table (10) Sire Totals by Sex and Genotype for Segregating Group

Sire	Numbers of offspring			
	dwarf males	heterozygote males	dwarf females	normal females
001	3	8	6	5
002	18	16	10	12
004	8	8	8	7
005	7	14	5	6
006	9	4	6	3
007	10	7	8	11
008	7	6	0	8
009	0	2	0	0
378	1	1	3	0
286	1	1	0	0
062	3	11	8	6
057	14	11	18	8
Total (excluding 009, 378 and 062).	79	85	69	66
Overall Total	81	89	72	66

Test of homogeneity of sire totals

	χ^2	df	
Deviation of grand totals from 1:1:1:1	3.114	3	0.30 < P < 0.50
Heterogeneity of sire totals	29.915	24	0.30 < P < 0.50
<hr/> Total	33.029	27	

degree of homogeneity of the sire totals. The data does not therefore show any evidence of a disturbed segregation of the *dw* gene or any large degree of misclassification of dwarf and normal (or heterozygote) birds. There are no published reports that suggest that there are any disturbances associated with segregations involving the *dw* gene.

(ii) Analyses of Variance

An analysis of variance was performed for each sex, for the 5 characters measured within each of the progeny groups. The same program package was used for this analysis as was used for the estimation of genetic parameters and will be described in more detail in a later section. A nested analysis was performed, the levels being hatches, sires within hatches, dams within sires and sibs within dams. In combining data from the two years the first, second and third hatches from each year have been combined, with a fourth hatch occurring only in the second year. Despite this limitation no significant variation due to hatch was detected in any of the analyses.

Relevant degrees of freedom, Mean Squares and significance of F ratios are given in Tables (i), (j), (k) and (l) of Appendix (5) for the Dwarf Group, Normal Group, dwarfs from the Segregating Group and normal birds from the Segregating Group respectively.

A summary of significant F ratios, for 5% and

1% confidence levels are presented in Table (11). There is a consistent and significant effect of dam on DOBW. This is to be expected as DOBW is a function of the weight of the egg from which the chicken hatches and thus related to the average egg weight of the dam. There is an overall effect of sire on 6WKBW of male but not female progeny for dwarf and normal birds, and there is the suggestion of a dam effect on female but not male progeny. The effect of sire on male progeny seems more marked in normal than in dwarf progeny as it remains significant at a 1% confidence level in the Normal Group and in the normal offspring of the Segregating Group. The sire effect on dwarf and normal male progeny is also apparent for 12WKBW (except the dwarf offspring of the Segregating Group).

Any effect of significant variation associated with the sex chromosomes (sex-linkage) on the characters measured would be indicated, either separately or jointly, by significant variation due to sire on female offspring, and by significant variation due to dam on male offspring. Evidence for sex-linked effects on the body weights and shank lengths of dwarfs (excepting DOBW) is contained in Table (11). Within the Dwarf Group there is significant variation in female offspring due to sire for 12WKBW, 6WKSL and 12WKSL. There is also significant variation due to dam for male offspring

Table (11) Summary of Significant Factors in Analyses of Variance

(a) 5% Confidence Level

	DOBW		6WKBW		12WKBW		6WKSL		12WKSL	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Dwarf Group	S,D	D	S		S	S	D	S		S
Normal Group	D	D	S	D	S	D	S	D	S,D	
Segregating Group										
dwarf offspring	D	D	S	D	D			S	S	
normal offspring	S,D	D	S	S	S		S			

S = Significant variation (5%) due to Sires within Hatches.
 D = Significant variation (5%) due to Dams within Sires.

(b) 1% Confidence Level

	DOBW		6WKBW		12WKBW		6WKSL		12WKSL	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Dwarf Group	D	D				S				
Normal Group	D	D	S	D		D	S		S,D	
Segregating Group										
dwarf offspring	D	D			D					
normal offspring	D	D	S							

S = Significant variation (1%) due to Sires within Hatches.
 D = Significant variation (1%) due to Dams within Sires.

with respect to 6WKSL. Also, within the dwarf offspring of the Segregating Group there is significant variation due to sire on female offspring for 6WKSL and significant variation due to dam on male offspring for 12WKBW.

The only indication of sex-linked effects within the Normal Group is the significant effect due to dam on 12WKBW of males. Apart from this and excluding DOBW, there is a consistent effect due to sire on male offspring and due to dam on female offspring. In the normal offspring of the Segregating Group the significant effect of sire on male offspring is further confirmed, except for 12WKSL. The only indication of sex-linkage in the normal offspring of the Segregating Group is the sire effect on female offspring with respect to 6WKBW. It would appear that sex-linked effects are much more important in determining the body weights and shank lengths of dwarf as compared with normal birds.

The variances of dwarf and normal offspring from the Segregating Group were compared using F tests. The results for male and female offspring are presented in Table (12). The comparison of dwarf and normal birds within the Segregating Group is more appropriate than comparing the Dwarf and the Normal Group because the same dams and sires are used to produce the different genotypes. The F tests indicated that within the Segregating Group for both males and females similar variances were observed in dwarf and normal offspring for each of the five characters measured.

Table (12) F Ratios* Comparing Variances of Dwarf and Normal Offspring in the Segregating Group (dwarf/normal)

	DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Males (F_{38}^{29})	1.49	1.34	0.57	1.29	0.87
Females (F_{24}^{25})	1.51	0.52	0.62	0.63	1.30

Critical Regions for 5% Confidence Interval

Males $F < 0.57$ $F > 1.74$

Females $F < 0.51$ $F > 1.98$

*Calculated as ratio of full-sibs within dam Mean Squares

Variances of dwarf and normal birds from the Dwarf Group and the Normal Group were also compared by the use of F tests, the results for male and female offspring being presented in Table (13). Within the male offspring, except for DOBW where there was no difference, dwarf birds showed significantly smaller variances than normal birds for the body weight and shank length measurements. For the female offspring dwarf birds showed a significantly higher variance for DOBW, significantly lower variances for 6WKBW, 12WKBW and 6WKSL and no difference for 12WKSL.

The confounding effect of different sires and dams in the Dwarf and Normal Groups, which does not occur for the comparisons within the Segregating Group

Table (13) F Ratios Comparing Variances in the Dwarf and Normal Groups (dwarf/normal)

	DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Males (F_{73}^{52})	0.95	0.45*	0.37*	0.58*	0.59*
Females (F_{91}^{35})	1.56*	0.48*	0.42*	0.63*	0.97

Critical Regions for 5% Confidence Interval

Males	$F < 0.65$	$F > 1.53$
Females	$F < 0.64$	$F > 1.55$

*Significant at 5% confidence level

may help to account for the differences between the two results. In Table (14) the coefficients of variation for male and female offspring in the Dwarf and Normal Groups have been presented, and show similar percentages for dwarf and normal offspring. The coefficients of variation allow for any scale effects that may have been confounding the comparisons between the Dwarf and Normal Groups. The evidence presented here suggests that overall there are no differences due to the presence of the dwarf gene in the variances of the body weight and shank length measurements made.

Average values of the body weight and shank length measurements for male and female offspring of each sire for the Dwarf Group, the Normal Group and the dwarf and normal offspring in the Segregating

Table (14) Coefficients of Variation* Dwarf and Normal Groups

(a) Males					
	DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Dwarf Group	4.4	17.1	15.3	6.5	6.2
Normal Group	3.8	18.2	15.1	7.1	6.0
(b) Females					
	DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Dwarf Group	4.7	18.9	17.2	6.8	7.5
Normal Group	3.4	18.5	14.9	7.1	5.6

*Calculated from $\sqrt{2}$ (full-sibs within dam mean squares)/average

Group are presented in Appendix (6), in Tables (m), (n), (o) and (p) respectively. The overall average values for each progeny group are shown in Table (15). Normal offspring from the Segregating Group have significantly lower body weights and shank lengths than birds of the same sex in the Normal Group. Standard Normal Deviate tests all have associated probabilities of less than 1%. There are a number of factors which could be associated with these differences. The genotypes of the parents of the two groups were distinctly different, the progeny in the Segregating Group having come from matings between heterozygous sires and dwarf dams, while the normal group was generated by mating normal genotype sires and dams. Dwarf hens have been previously shown to have had significantly lower average egg

Table (15) Body Weights (g) and Shank Lengths (cm), Average Values for Progeny Groups

	DOBW		6WKBW		12WKBW		6WKSL		12WKSL	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Dwarf Group	34.2	35.2	305	253	842	627	5.69	5.30	8.12	7.14
Normal Group	40.1	39.4	427	376	1411	1108	6.81	6.40	10.95	9.79
dwarf/normal (%)	85.3	89.3	71.4	67.3	59.7	56.6	83.6	82.8	74.2	72.9
Segregating Group										
dwarf offspring	35.8	36.4	275	268	812	718	5.50	5.39	8.11	7.50
normal offspring	36.0	35.9	350	308	1151	951	6.29	5.93	10.08	9.22
dwarf/normal (%)	99.4	101.4	78.6	87.0	70.5	75.5	87.4	90.9	80.5	81.3

weights than normal hens so that birds in the Segregating Group hatched from smaller eggs than birds from the Normal Group, which may also have contributed to the observed differences. This factor would almost certainly be the reason for the observed differences in DOBW, because, as will be shown in a later section, there is a significant regression of DOBW on the average egg weight of the dam. The differing amounts of White Leghorn ancestry in the birds used in the initial matings, which has been detailed in a previous section, also may have been contributing to the observed differences.

Standard Normal Deviate tests show that dwarf females from the Dwarf Group are lighter and have shorter shanks at 6 and 12 weeks than dwarf females from the Segregating Group. For 6WKBW, 12WKBW and 12WKSL the calculated probabilities are very low (less than 1%) and the difference in 6WKSL gives a probability of about 10%. For males however, the ranking is reversed. For 6WKBW and 6WKSL males from the Dwarf Group are heavier and have longer shanks (probabilities less than 1%), for 12WKBW the probability associated with the difference is 16% and for 12WKSL the difference is not significant ($P = 91\%$). The observation that females from the Dwarf Group are lighter, and males heavier than corresponding dwarf birds from the Segregating Group is partially explained by reference to Table (16) which presents the ratio

Table (16) Ratio of measurements, female/male (%)

	DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Dwarf Group	102.9	83.0	74.5	93.1	87.9
Normal Group	98.3	88.1	78.5	94.0	89.4
Segregating Group					
dwarf offspring	101.7	97.5	88.4	98.0	92.5
normal offspring	99.7	88.0	82.6	94.3	91.5

of measurements made in females and males for each progeny group. The sexual difference is much less marked in dwarfs from the Segregating Group than for any other group, which all give similar ratios. There is no immediately obvious explanation of why this should be so.

For each sex, the ratio of measurements made in dwarf birds, to measurements made in normal birds is presented with the average values in Table (15). The Dwarf Group is compared with the Normal Group for each of the measurements made and the dwarf and normal progeny within the Segregating Group are similarly compared. Due to differences in the sires and dams used, and to the different parental genotypes, similar difficulties to those that occurred in the comparison of the Normal Group with the normal offspring of the Segregating Group occur when the Dwarf and Normal Groups are compared. For example when looking at the ratio of DOBW in the Dwarf Group to that in the Normal

Group there is the confounding effect of the smaller average egg weight in the dwarf dams generating the Dwarf Group than in the normal dams generating the Normal Group. This explains why the observed ratio is smaller in the Dwarf Group to Normal Group comparison than in the comparison within the Segregating Group, where no dwarf to normal difference is observed. Because the same sires and dams were used to generate the dwarf and normal progeny in the Segregating Group more confidence can be put in the comparisons within the Segregating Group than the Dwarf Group to Normal Group comparisons. Despite these limitations the two comparisons show similar trends, although differing in the degree of difference between dwarf and normal birds. The difference between dwarf and normal birds is much more evident at 12 weeks than at 6 and the proportional difference in body weight is more marked than for shank length at both ages for both comparisons. For the comparisons within the Segregating Group, if results for males and females are averaged, body weight reductions in dwarf compared with normal birds of 17.2% and 27.0% are observed at 6 and 12 weeks respectively, and shank length reductions of 10.9% and 19.1% respectively at the same ages. A summary of relevant reports in the literature that quote body weights and shank lengths is given in Table (17). The observation in this study that in dwarfs there is a greater

Table (17) Reported Reductions of Body Weights and Shank Lengths in Heavy Strains of Birds

	Body Weight or Shank Length	Age (Weeks)	Dwarf/ Normal (%)
Merat (1969)	BW	52	65.3
	SL	52	76.3
Ricard (1970)	BW	4	80.7
	BW	8	73.1
	BW	11	71.2
Ricard and Cochez (1971)	BW	20	64
	BW	36	70
Zlochevskaya and Penionzhkevich (1972)	SL	Adult	77.2
Yamada, Watanabe, Ebisawa and Futamura (1972)	BW	Adult	77
	SL	Adult	70
Mohammadian and Jaap (1972)	BW	8	80.8
	BW	26	80.2
	SL	Adult	80.0
Khan, Jaap and Harvey (1973)	BW	8	60.2 (males)
			61.9 (females)

depression in body weight than in shank length relative to normal birds supports the report of Merat (1969) although not that of Yamada, Watanabe, Ebisawa and Futamura (1972). Both these reports were, however, for measurements made in adult birds. The greater retardations at 12 compared with 6 weeks observed in this study supports the data of Ricard (1970) who measured body weights of dwarf and normal birds at 4, 8 and 11 weeks and showed progressively greater retardation in dwarfs with increasing age.

However, Ricard and Cochez (1971) working with birds older than those measured in this study showed a greater retardation at 20 than at 36 weeks. Mohammadian and Jaap (1972) measured retardations that were similar at 8 and 26 weeks. For birds that were similar in age to those used in this study retardations in body weight as high as 39.8% (Khan, Jaap and Harvey 1973) and as low as 19.2% (Mohammadian and Jaap 1972) have been reported for heavy strain birds at 8 weeks.

(iii) Regressions of Body Weight on Average Egg Weight of Dam

The effect of egg size of dam on growth rates of progeny was examined by regressing average body weight of offspring on the average egg weight of their dam. Results for the Dwarf Group and the Normal Group are shown in Table (18). The average of both sexes weighted for the number of birds in each sex was used as the body weight variable in these analyses. The regressions of DOBW on average egg weight were highly significant for both progeny groups, but not significant for 6WKBW or 12WKBW. For dwarf birds DOBW was 60.1% and for normal birds 83.6% of the average egg weight of the dam. The difference between the two regression coefficients, as tested by a t test was however, not significant at a 5% confidence level.

Table (18) Regressions of Body Weight on Average Egg Weight of Dam, Dwarf and Normal Groups

	Dwarf Group		Normal Group	
	Regression Coefficient	F ₁₁ [†]	Regression Coefficient	F ₂₇ [†]
DOBW	0.857	60.59**	0.671	83.58**
6WKBW	1.053	0.07NS	3.242	1.06NS
12WKBW	-4.504	0.02NS	9.444	1.22NS

[†]Tests significance of regression.

**Significant at 1% confidence level.

NS Not significant at 5% confidence level.

A similar regression analysis was performed within the Segregating Group for dwarf and normal offspring of each sex. The regressions of DOBW on average egg weight were highly significant in all cases, as shown in Table (19). In only one other case, the regression of 6WKBW for dwarf females, was the regression coefficient significantly different from zero. It would appear that by the time that birds were 6 weeks old any effect due to the average egg weight of their dam had been overcome, for both dwarf and normal birds.

The result that any effect of average egg weight of dam has no effect on body weights by the

Table (19) Regressions of Body Weight on Average Egg Weight of Dam, Segregating Group

	dwarf males		heterozygous males		dwarf females		normal females	
	Regression Coefficient	F ₁ [†] 24	Regression Coefficient	F ₁ [†] 22	Regression Coefficient	F ₁ [†] 21	Regression Coefficient	F ₁ [†] 22
DOBW	0.807	134.73**	0.769	140.13**	0.690	32.81**	0.763	101.97**
6WKBW	-2.626	1.41NS	1.422	0.42NS	5.357	7.31*	-4.095	0.46NS
12WKBW	-6.085	1.52NS	5.746	1.00NS	5.492	1.77NS	1.791	0.44NS

†Tests significance of regression.

*Significant at 5% confidence level.

**Significant at 1% confidence level.

NS Not significant at 5% confidence level.

time birds are 6 weeks old, with the possible exception of the body weight of dwarf females is not entirely consistent with the results of similar regressions performed by Khan, Jaap and Harvey (1973). They used dwarf dams mated to dwarf and normal sires to generate the same offspring genotypes that were generated in this study in the Segregating Group. The regression of body weight at 8 weeks on average egg weight of dam calculated by Khan, Jaap and Harvey (1973) was significant and linear in heterozygous male and in normal female offspring. This does not agree with the result in this study that there is no apparent effect of average egg weight of dam on normal phenotype offspring by the time they reach 6 weeks. The regressions on average egg weight of dam for dwarf male and female offspring were not significant in the results of Khan, Jaap and Harvey (1973), which agrees with the results for the dwarf males in this study, although it should be kept in mind that there is a 2 week difference in the ages at which the measurements were made in the two studies.

In the results of this study the comparison of regressions in the Dwarf and Normal Groups and the comparison of regressions within the Segregating Group suggest that there is in general no difference between dwarf and normal birds in the effect of average egg weight of dam on body weight by the time that offspring are 6 weeks old, and that this result

is consistent for both dwarf and normal dams.

The only result that was not consistent with this pattern was the significance of the regression for 6WKBW in dwarf female offspring of the Segregating Group.

(c) Heritability Estimates

The birds used as parents in 1972 were made available for this project as adult birds, and so there was no record of their 6 or 12 week body weights or shank lengths. For this reason it was not possible to undertake heritability estimates using the method of offspring on parent regressions. It is unfortunate that this method could not be used as it may have resulted in more precise estimates of genetic parameters than the analysis of variance technique that was used as an alternative.

Throughout this project the number of birds recorded and measured was strictly limited by the facilities available. In order to maximise the numbers of birds contributing to each analysis, and thus to minimise the standard errors of estimates, measurements from offspring that were produced from matings between the same genotypes, but in different years were combined by bringing together data from respective hatches in the two years, as was previously described for the analyses of variance for the sexes separately, and measurements from the two sexes were combined. The combination of measurements in this way did not result in any significant variation due to hatch in the analyses of the sexes separately, or in the combined sex analyses used for the heritability

estimates. Large standard errors for the heritability estimates were still obtained however, despite the pooling of the data in the manner described, and because of the large standard errors the heritability estimates obtained frequently fail to show significant differences from zero. Notwithstanding these limitations there are, however, sufficient trends in the heritability values to warrant further investigation.

Heritability and correlation estimates were computed using the Program Package - NESREG (Hammond, Jackson and Miller 1972) and the University of Adelaide CDC 6400 computer. The NESREG program analyses data in the form of offspring on parent regressions or by nested analysis of variance and covariance. Only the analysis of variance (sib analysis) option of the NESREG program was used, because of the absence of body weight and shank length measurements for birds used as parents in 1972. The levels of nesting used for the analysis of variance (for the heritability estimates) and the analysis of covariance (for the correlation estimates) were full sibs within dams, dams within sires, sires within hatches, and hatches. The NESREG program package uses the techniques described by Becker (1964) for the calculation of heritabilities, correlations and the appropriate standard errors. The composition of the Expected Mean Squares from the analysis of variance and the formulas used for the calculation of the sire component, dam component, and combined sire and dam heritability estimates has been summarised in Table (20).

Table (20) Estimation of Heritability, Analysis of Variance
of Full-sibs, with Unequal Sub-class Numbers

Source of variation	Degrees of freedom	Mean Square	Expected Mean Square
Between sires	$s - 1$	MS_s	$\sigma_e^2 + k_1 \sigma_d^2 + k_2 \sigma_s^2$
Between dams within sires	$\sum_i (n_i - 1)$	MS_d	$\sigma_e^2 + k_3 \sigma_d^2$
Offspring within dams and sires	$N - \sum_i n_i$	MS_o	σ_e^2

Where s = total number of sires

n_i = the number of dams mated to the i th sire

n_{ij} = the number of offspring produced by the ij th dam

$N_i = \sum_j n_{ij}$ = the number of offspring produced by the i th sire

$N = \sum_{ij} n_{ij}$ = the total number of offspring

$$k_1 = \frac{\sum_i (\sum_j n_{ij}^2 / N_i) - \sum_{ij} n_{ij}^2 / N}{s - 1}$$

$$k_2 = \frac{N - \sum_i N_i^2 / N}{s - 1}$$

$$k_3 = \frac{N - \sum_i (\sum_j n_{ij} / N_i)}{\sum_i (n_i - 1)}$$

sire component heritability estimate

$$h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}$$

dam component heritability estimate

$$h^2 = \frac{4\sigma_d^2}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}$$

combined sire and dam estimate

$$h^2 = \frac{2(\sigma_s^2 + \sigma_d^2)}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}$$

(i) Heritability Estimates of DOBW

Heritability estimates of DOBW, from the sire and dam components are presented in Table (21) for the three progeny groups. Despite the large standard errors of the estimates Standard Normal Deviate tests show that for the Normal Group and the dwarf offspring of the Segregating Group the dam component estimate is significantly larger than the sire component estimate at a 5% confidence level. This result indicates significant variation due to common environment, at least in these two instances. For the Dwarf Group and the normal offspring of the Segregating Group the dam component estimates are larger than the sire component estimates although not to the extent of being statistically significant. The existence of a common environment effect on DOBW is not unexpected because, as has been previously shown, there is a significant regression of DOBW on the average egg weight of dam, which would contribute to a maternal, or common environment effect.

Table (21) Estimates of Heritability of DOBW, with Standard Errors

	Dwarf Group	Normal Group	Segregating Group	
			dwarf offspring	normal offspring
Sire Component	1.64±0.93	0.53±0.59	0.22±0.60	1.52±0.76
Dam Component	1.74±0.57	2.83±0.67	3.15±0.78	2.11±0.54

Where common environment effects are present the best estimate of heritability is provided by the sire component. All the sire component estimates of DOBW have large standard errors, however the estimate from the Dwarf Group and the normal offspring from the Segregating Group give values which are significantly greater than zero at a 5% level of probability.

(ii) Heritability Estimates of Body Weights and Shank Lengths at 6 and at 12 Weeks

A summary of heritability estimates of 6 and 12 week body weights and shank lengths is made in Tables (22), (23) and (24) for the Dwarf, Normal and Segregating Groups respectively. The heritability of each of the characters measured is presented as an estimate from the sire component (covariance of half-sibs), an estimate from the dam component (covariance of full-sibs) and as a combined estimate. The standard error for each estimate is also presented.

Table (22) Heritability Estimates (\pm Standard Error) of 6 and 12 Week Body Weights and Shank Lengths, Dwarf Group

	6WKBW	6WKSL	12WKBW	12WKSL
Sire Component	1.40 \pm 0.67*	1.29 \pm 0.63*	1.06 \pm 0.53*	0.77 \pm 0.44
Dam Component	0.46 \pm 0.31	0.43 \pm 0.32	0.17 \pm 0.28	0.07 \pm 0.29
Combined Estimate	0.93 \pm 0.34*	0.86 \pm 0.32*	0.62 \pm 0.27*	0.42 \pm 0.23

*Indicates significantly greater than zero at a 5% probability level.

(1) Sire Component Heritability Estimates

As indicated in Tables (22) - (24) there is a general trend for the sire component estimates to be significantly greater than zero at a 5% level of probability. For both the Dwarf and Normal Groups three of the four estimates show significant deviations from zero, while within the Segregating Group two estimates for the dwarf offspring and three for the normal offspring are significantly greater than zero.

(2) Dam Component Heritability Estimates

The only dam component estimate that is significantly greater than zero at a 5% probability level is the estimate for 6WKBW in the Normal Group (Table 23). As shown in Table (24) negative heritability values are obtained for the dwarf and normal offspring of the Segregating Group, however none of these estimates are significantly different from zero.

Table (23) Heritability Estimates (\pm Standard Error) of 6 and 12 Week Body Weights and Shank Lengths, Normal Group

	6WKBW	6WKSL	12WKBW	12WKSL
Sire Component	1.03 \pm 0.46*	1.03 \pm 0.40*	0.49 \pm 0.30	0.53 \pm 0.26*
Dam Component	0.98 \pm 0.35*	0.46 \pm 0.27	0.50 \pm 0.32	0.08 \pm 0.25
Combined Estimate	1.00 \pm 0.22*	0.75 \pm 0.20*	0.49 \pm 0.15*	0.31 \pm 0.13*

*Indicates significantly greater than zero at a 5% probability level.

Table (24) Heritability Estimates (\pm Standard Error) of 6 and 12 Week Body Weights and Shank Lengths, Segregating Group

(a) Dwarf Offspring

	6WKBW	6WKSL	12WKBW	12WKSL
Sire Component	0.91 \pm 0.41*	0.98 \pm 0.42*	0.57 \pm 0.35	0.10 \pm 0.27
Dam Component	-0.35 \pm 0.41	-0.38 \pm 0.40	-0.26 \pm 0.45	-0.25 \pm 0.52
Combined Estimate	0.28 \pm 0.25	0.30 \pm 0.25	0.16 \pm 0.23	-0.08 \pm 0.21

(b) Normal Offspring

	6WKBW	6WKSL	12WKBW	12WKSL
Sire Component	1.40 \pm 0.49*	0.93 \pm 0.42*	0.56 \pm 0.34	0.87 \pm 0.42*
Dam Component	-0.50 \pm 0.30	-0.22 \pm 0.38	-0.28 \pm 0.42	-0.08 \pm 0.40
Combined Estimate	0.45 \pm 0.27	0.36 \pm 0.24	0.14 \pm 0.21	0.39 \pm 0.24

*Indicates significantly greater than zero at a 5% probability level.

(3) Comparisons of Sire and Dam Component Estimates

When comparing the heritability estimates from the sire and dam components for each of the progeny groups the only case in which the dam estimate is greater than the sire is for 12WKBW in the Normal Group, and even in this instance the difference is trivial. In all other cases the value computed from the dam component is numerically smaller than that computed from the sire component.

Within the Dwarf and the Normal Groups the difference between the sire component and the dam component heritability estimates is in no case

significant at a 5% confidence level, as tested by Standard Normal Deviate tests. Some of the differences within the Segregating Group, where negative dam component heritability estimates were obtained, were however statistically significant. For the dwarf offspring of the Segregating Group the sire component heritability estimate was significantly larger than the dam component estimate for 6WKBW and 6WKSL, and for the normal offspring the sire component estimate was significantly larger for 6WKBW, 6WKSL and 12WKSL. The statistically significant differences observed within the Segregating Group are perhaps the result of the small numbers of birds contributing to the analyses, rather than an indication of real differences. The comparisons in the Dwarf and Normal Groups where no difference was observed between the sire and dam component estimates despite sometimes quite large differences in their values are probably more reliable than those made within the Segregating Group where negative dam component estimates are confounding the comparisons.

The interpretation of heritability estimates made from the dam component differs from the interpretation of sire component estimates in that the dam component estimates contain a portion of the non-additive genetic variance and the variance due to common environment. Because in no cases

were the dam component estimates significantly larger than the sire component estimates the presence of large variation due to either of these two factors is not indicated for any of the progeny groups in the data presented here.

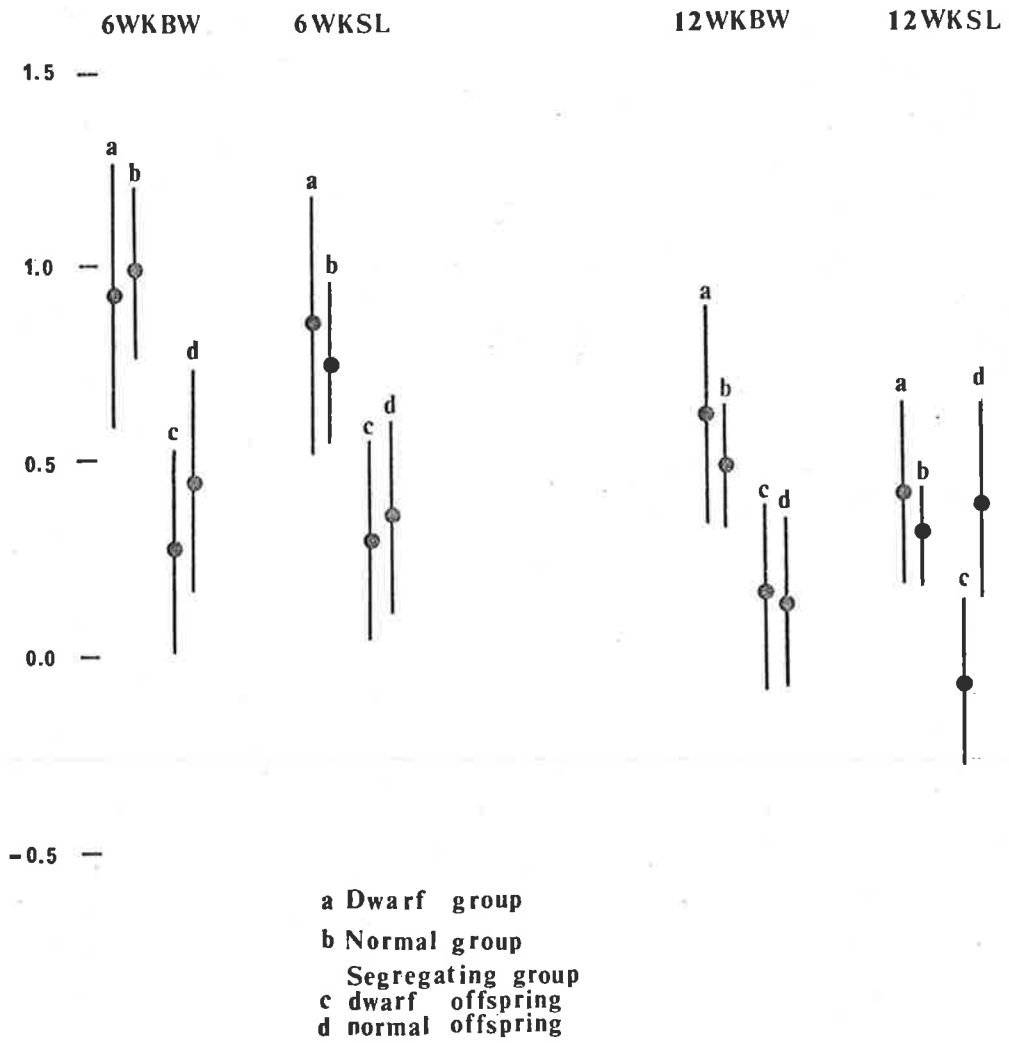
(4) Combined Sire and Dam Heritability Estimates

In Figure (3) the combined heritability estimates for the 6 and 12 week body weight and shank length measurements have been plotted for each of the progeny groups, together with the appropriate standard errors. By reference to Figure (3) it is seen that the estimated heritabilities within the Dwarf Group are similar in value to the estimates obtained from the Normal Group.

The standard errors of the estimates appear to be smaller for the Normal Group than for the Dwarf Group which would seem reasonable considering the numbers of birds contributing to the estimates were 296 and 151 respectively. For the Dwarf and Normal Groups, at both 6 and 12 weeks the heritability values for shank length appear to be less than the values for body weight, and similarly there is the suggestion that measurements taken at 12 weeks have lower heritabilities than those at 6 weeks of age. The large standard errors observed preclude any precise testing of these suggestions.

The comparison of estimates for dwarf and normal birds within the Segregating Group shows that

Figure(3) Combined Heritability Estimates
 (\pm Standard Error)



with the possible exception of 12WKSL similar heritability values are obtained for dwarf and normal offspring. The standard errors of the two sets of estimates within the Segregating Group are similar in value which is not surprising considering the similarity in the number of birds in the two groups. There were 146 dwarf and 150 normal offspring contributing to the estimates within the Segregating Group. The heritability values obtained for the Segregating Group appear to be lower than those obtained for the Dwarf and for the Normal Groups. Again, however the large values obtained for the standard errors means that this apparent difference is not statistically significant.

(d) Correlation Estimates

As was apparent for the heritability estimates the correlation estimates were marked by high standard errors due to the relatively small number of birds contributing to the analyses. This means that the interpretation of results of tests of significance between correlation coefficients must be treated with caution. However the pattern that is formed when only those coefficients that are significantly greater than zero at a 5% probability level are considered does show some interesting trends that warrant closer examination.

Any correlation coefficient is calculated as the covariance of two sets of measurements divided by the geometric mean of the variances of the two data sets. Unfortunately in the data obtained in this project some of the derived variance

estimates were negative and therefore the geometric means and thus the correlation coefficients could not be calculated.

For all the progeny groups the environmental variance of DOBW was negative and thus none of the environmental correlations involving DOBW could be calculated. Also, for the Normal Group the environmental variance of 6WKBW was negative as was the genetic variance of 12WKSL in the dwarf offspring of the Segregating Group so that none of the correlations involving these variances could be calculated. The gaps in tables of correlation coefficients that follow correspond to the estimates that could not be calculated for the above reason.

Discussion of the correlation estimates will be done by examining firstly those correlations that involve DOBW, then those between characters measured at the same age, and finally between characters measured at different ages subdivided into correlations within metrics (i.e. body weight or shank length) and between metrics. Environmental correlations can be dealt with briefly as they arise from a developmental environment that is shared by the two characters and do not affect the genetic association in subsequent generations.

(i) DOBW Correlations

Estimates of correlation coefficients that involve DOBW are presented in Table (25). All the genetic and phenotypic correlation estimates made within the Normal Group between DOBW and the other body weight and shank length measurements are significant at a 5% probability level, yet none of

Table (25) Estimates (\pm Standard Error) of Genetic and Phenotypic Correlations Between DOBW and Body Weight and Shank Length Measurements at 6 and 12 Weeks

(a) Genetic Correlations				
	6WKBW	6WKSL	12WKBW	12WKSL
Dwarf Group	0.11 \pm 0.22	0.24 \pm 0.22	-0.12 \pm 0.24	-0.01 \pm 0.27
Normal Group	0.50 \pm 0.11*	0.50 \pm 0.12*	0.55 \pm 0.13*	0.51 \pm 0.17*
Segregating Group				
dwarf offspring	0.45 \pm 0.28	0.54 \pm 0.27*	-0.20 \pm 0.37	
normal offspring	0.69 \pm 0.19*	0.76 \pm 0.23*	0.33 \pm 0.41	0.11 \pm 0.24
(b) Phenotypic Correlations				
	6WKBW	6WKSL	12WKBW	12WKSL
Dwarf Group	0.09 \pm 0.14	0.15 \pm 0.13	-0.07 \pm 0.13	-0.03 \pm 0.12
Normal Group	0.32 \pm 0.08*	0.28 \pm 0.08*	0.27 \pm 0.07*	0.21 \pm 0.07*
Segregating Group				
dwarf offspring	0.18 \pm 0.09*	0.26 \pm 0.09*	0.02 \pm 0.09	0.04 \pm 0.08
normal offspring	0.32 \pm 0.10*	0.30 \pm 0.09*	0.08 \pm 0.09	0.02 \pm 0.10

*Indicates significantly greater than zero at a 5% probability level.

the estimates within the Dwarf Group give a value that is significantly different from zero. Within the Normal Group homogeneity tests showed that the four phenotypic correlations showed good homogeneity ($\chi^2_3 = 2.1087$) with a weighted average correlation coefficient of 0.27. Similarly the four genetic correlations were homogeneous ($\chi^2_3 = 0.9836$) with a

weighted average coefficient of 0.52. Standard Normal Deviate tests showed that the weighted average genetic correlation coefficient was significantly larger at a 5% confidence level than the corresponding phenotypic correlation.

Within the Segregating Group none of the correlations between DOBW and measurements made at 12 weeks were significant at a 5% probability level. The phenotypic correlations between DOBW and 6WKBW were not significantly different from the correlations with 6WKSL for either the dwarf or the normal offspring. There was also no significant difference between the estimates in the dwarf and normal offspring for either 6WKBW or 6WKSL. For the dwarf offspring of the Segregating Group the only genetic correlation involving DOBW that was significant was that with 6WKSL, which was also significantly smaller than the corresponding estimate in the normal offspring. The genetic correlations involving 6WKBW and 6WKSL were significantly greater than zero for the normal offspring at a 5% level of probability.

The difference in the results obtained in the Dwarf and the Normal Groups suggest that there is a difference in dwarf and normal birds in the genetic relationship between DOBW and body weight and shank length measurements made later in life. It should be remembered, however, that offspring in the Dwarf Group come from dwarf dams which, as has been

previously shown, lay smaller eggs and thus produce smaller chickens than the normal dams which were used to produce the Normal Group. In the Segregating Group both dwarf and normal offspring were produced from dwarf dams and this group does not show nearly the same divergence in results between dwarf and normal as the comparison of the Dwarf and Normal Groups. The observed difference in results for the Dwarf and Normal Groups is therefore perhaps the result of differences in egg size of dam, and thus DOBW, rather than due to an effect associated with the dwarf gene.

(ii) Correlations Between Body Weights and Shank Lengths Measured at the Same Age

In Table (26) estimates of correlations between 6WKBW and 6WKSL and also between 12WKBW and 12WKSL are shown. All the phenotypic and genetic correlations are significantly greater than zero at a 5% probability level, and have very high values, indicating a very close genetic relationship between body weight and shank length. All the environmental correlations, except that between 6WKBW and 6WKSL in the Dwarf Group are positive and significantly greater than zero, and also show markedly high values.

(iii) Correlations Between Body Weights and Between Shank Lengths Measured at Different Ages

Estimates of correlations between 6WKBW and 12WKBW are presented in Table (27). The phenotypic

Table (26) Estimates (\pm Standard Error) of Genetic, Environmental and Phenotypic Correlations Between Body Weight and Shank Length Measurements made at the Same Age

Correlation	Genetic	Environmental	Phenotypic
(a) Between 6WKBW and 6WKSL			
Dwarf Group	0.98 \pm 0.02*	0.55 \pm 0.76	0.93 \pm 0.02
Normal Group	0.94 \pm 0.03*		0.90 \pm 0.01
Segregating Group			
dwarf offspring	1.08 \pm 0.11*	0.79 \pm 0.07*	0.87 \pm 0.02
normal offspring	0.95 \pm 0.06*	0.88 \pm 0.05*	0.90 \pm 0.02
(b) Between 12WKBW and 12WKSL			
Dwarf Group	0.90 \pm 0.07*	0.95 \pm 0.05*	0.91 \pm 0.02
Normal Group	0.93 \pm 0.04*	0.93 \pm 0.02*	0.91 \pm 0.01
Segregating Group			
dwarf offspring		0.88 \pm 0.05*	0.77 \pm 0.03
normal offspring	0.94 \pm 0.22*	0.88 \pm 0.05*	0.85 \pm 0.02

*Indicates significantly greater than zero at a 5% probability level.

Table (27) Estimates (\pm Standard Error) of Genetic, Environmental and Phenotypic Correlations Between Body Weights and Between Shank Lengths Measured at Different Ages

Correlation	Genetic	Environmental	Phenotypic
(a) Between 6WKBW and 12WKBW			
Dwarf Group	0.99 \pm 0.03*	0.52 \pm 0.35	0.84 \pm 0.03*
Normal Group	0.87 \pm 0.06*		0.76 \pm 0.03*
Segregating Group			
dwarf offspring	0.60 \pm 0.48	0.69 \pm 0.11*	0.66 \pm 0.05*
normal offspring	0.57 \pm 0.41	0.73 \pm 0.11*	0.64 \pm 0.05*
(b) Between 6WKSL and 12WKSL			
Dwarf Group	0.89 \pm 0.09*	0.87 \pm 0.23*	0.78 \pm 0.04*
Normal Group	0.92 \pm 0.07*	0.82 \pm 0.08*	0.78 \pm 0.02*
Segregating Group			
dwarf offspring		0.86 \pm 0.09*	0.60 \pm 0.05*
normal offspring	0.57 \pm 0.27*	0.90 \pm 0.07*	0.77 \pm 0.04*

*Indicates significantly greater than zero
at a 5% probability level.

correlations are positive and significantly greater than zero for all of the progeny groups with the Dwarf Group estimate being significantly larger than the Normal Group estimate at a 5% confidence level. The estimates for dwarf and normal offspring within the Segregating Group are not however significantly different. The genetic correlations are significantly greater than zero in the Dwarf and Normal Groups, and the Dwarf Group estimate is significantly larger at a 5% confidence level than the Normal Group estimate. Within the Segregating Group neither of the genetic correlations are significantly different from zero.

Estimates of correlations between 6WKSL and 12WKSL are also shown in Table (27). The pattern of significance in the genetic and phenotypic correlations is very similar to the relationship between body weight measured at 6 and 12 weeks, which is of course not surprising considering the close relationship that has been previously shown between body weights and shank lengths measured at the same age. The only suggestion of a different relationship in shank length than in body weight is the significance of the correlation between 6WKSL and 12WKSL in the normal offspring of the Segregating Group which is not significant for the corresponding correlation in the body weight measurements. It should be noted however, that the two correlations

have identical values and that it is the difference in the standard errors that makes the shank length correlation and not the body weight correlation significantly greater than zero.

(iv) Correlations Between Body Weights and Shank Lengths Measured at Different Ages

Correlation estimates between 6WKBW and 12WKSL and also between 6WKSL and 12WKBW are presented in Table (28). Again, because of the very close relationship between body weight and shank length measurements made at the same age, the pattern of the results of correlations between body weight and shank length measurements made at 6 and 12 weeks is very similar to the results obtained for correlations between body weights and between shank lengths at the two ages. The phenotypic correlations are all significantly greater than zero at a 5% probability level with the genetic correlations being significant in the Dwarf and Normal Groups but not in the Segregating Group.

A reasonably clear pattern has emerged from the various combinations of correlation estimates between body weight and shank length measurements made at 6 and at 12 weeks. The relationship between body weights at 6 and 12 weeks has been shown to be analogous to the relationship between shank lengths at the respective ages. Because of a very close genetic relationship between body weight and shank length at both 6 and 12 weeks similar results were obtained for body weight

Table (28) Estimates (\pm Standard Error) of Genetic, Environmental and Phenotypic Correlations Between Body Weight and Shank Length Measurements made at Different Ages

Correlation	Genetic	Environmental	Phenotypic
(a) Between 6WKBW and 12WKSL			
Dwarf Group	0.88 \pm 0.10*	0.96 \pm 0.75	0.75 \pm 0.04*
Normal Group	0.77 \pm 0.12*		0.66 \pm 0.04*
Segregating Group			
dwarf offspring		0.59 \pm 0.13*	0.48 \pm 0.06*
normal offspring	0.48 \pm 0.29	0.80 \pm 0.12*	0.66 \pm 0.05*
(b) Between 6WKSL and 12WKBW			
Dwarf Group	0.92 \pm 0.06*	0.58 \pm 0.28*	0.80 \pm 0.04*
Normal Group	0.87 \pm 0.06*	0.65 \pm 0.12*	0.76 \pm 0.03*
Segregating Group			
dwarf offspring	0.05 \pm 0.88	0.85 \pm 0.09*	0.67 \pm 0.05*
normal offspring	0.45 \pm 0.50	0.78 \pm 0.09*	0.68 \pm 0.05*

*Indicates significantly greater than zero at a 5% probability level.

to body weight, shank length to shank length and body weight to shank length correlations.

Within the Dwarf and the Normal Groups phenotypic and genetic correlation coefficients were consistently positive and large in value, and consistently greater than zero at a 5% significance level. There was no indication of major differences between the Dwarf and Normal Groups in the magnitude of the correlation coefficients. Within the Segregating Group all the phenotypic correlation coefficients were positive and significantly greater than zero but were in general smaller than the phenotypic correlations in the Dwarf and Normal Groups. The genetic correlations within the Segregating Group were in general not significantly different from zero, for either the dwarf or normal offspring. There has been no indication of a different genetic relationship in terms of body weight or shank length in dwarf as compared with normal birds for either of the two methods of comparison, i.e. the Dwarf compared with the Normal Group and the comparison of dwarf and normal offspring within the Segregating Group.

CONCLUSIONS

Dwarf hens used as parents in this study showed a reduction in average egg weight of about 10% relative to normal hens, which is in good agreement with the report of Prod'homme and Merat (1969), but larger than the reductions measured by Ricard and Cochez (1971) and Yamada, Watanabe, Ebisawa and Futamura (1972) who also measured egg weight reductions in heavy strains of birds. Measurements made on

parents also indicated that there is no apparent reproductive disadvantage associated with either dwarf dams or sires relative to normal birds, which agrees with other published results e.g. Ricard and Cochez (1971). There was also no indication of disturbed segregations associated with the dwarf gene, in either the segregation of sex, or in the segregation of the dwarf gene itself.

Comparisons of related dwarf and normal birds showed that dwarf birds, although having the same body weight at hatching as normal relatives incurred a body weight depression of some 17% at 6 weeks increasing to a relative depression of 27% at 12 weeks of age. The reduction in shank length in dwarf as compared with normal birds was not as large as the reduction in body weight, being about 11% at 6 weeks increasing to about 19% at 12 weeks. The observation of increasing retardations of both body weight and shank length with increasing age agrees with most other published reports (see Table 17) and the extent of the observed reductions is within the range of reported reductions for birds of similar ages.

The variances of the body weight and shank length measurements made were shown to be the same in related dwarf and normal birds. In unrelated dwarf and normal birds coefficients of variation were calculated to allow for size differences between the two groups and were shown to be very similar. This contrasts with the results of Mohammadian (1970) and Ricard and Cochez (1972) who reported higher coefficients of variation in dwarf compared with normal flocks. Although

not mentioned in any other reports evidence has been presented in the results of this study that sex-linked effects are more important in dwarf than in normal birds in determining body weights and shank lengths at 6 and at 12 weeks of age.

Regression studies on the birds in this project showed that in both dwarf and normal birds body weight at hatching was closely related to the average egg weight of the dam. By the time birds were 6 weeks old however, for both dwarf and normals no relationship between body weight and average egg weight was apparent. This contrasts with the results of Khan, Jaap and Harvey (1973) where a significant relationship in normal but not in dwarf birds was present at 8 weeks. The difference in the results is probably due to a difference between the stock used.

The precision of estimates of genetic parameters in this study was severely limited by the number of birds contributing to the analyses. Notwithstanding the limitations imposed by the large standard errors there is no indication of major differences between dwarf and normal birds for any of the heritability estimates made. Khan, Jaap and Harvey (1973) also found no difference between dwarf and normal birds in the heritability of body weight at 8 weeks. There was the suggestion in the results of this study that the heritability of shank length was less than the heritability of body weight at both 6 and 12 weeks, and also that the heritabilities at 12 weeks were less than those at 6 weeks. The large standard errors observed precluded any precise testing of these suggestions.

There are no reports in the literature on the effect of the dwarf gene on the relationship between body weight and shank length measurements. Estimates of genetic and phenotypic correlations in this study were subject to large standard errors but there were marked trends in the estimates when only those correlations that were significantly greater than zero at a 5% significance level were considered. There was a very close genetic relationship between body weight and shank length when measured at the same age and also strong positive genetic and phenotypic relationships between these characteristics at 6 and at 12 weeks. As with the heritability estimates no differences were detected between correlation estimates made in dwarf and in normal birds.

Because no disadvantage has been shown to be associated with dwarf breeders, at least in terms of the heritabilities of body weight and shank length, and also because there appears to be no difference in the basic genetic relationship between body weights at 6 and 12 weeks, a logical extension of the work described here would involve a selection experiment in which a flock of dwarf breeder birds was selected on the basis of, for example high growth rate. If dwarf meat breeders were to be successful commercially it would be necessary to know if gains made as a result of selection in dwarf breeders would result in corresponding increases in the production performance of their normal phenotype offspring, which would be the commercial end point of such a breeding scheme.

Results presented in this dissertation would indicate that due to the similarity of the body weight heritabilities, initially at least, similar selection responses would be obtained in dwarf as in normal flocks. Predictions cannot be made from these results however as to the likely effect of such selection on the normal phenotype offspring of the dwarf dams.

Appendix (1) Regression of Live Shank Length on Length of
Metatarsus Bone

Materials and Methods

Five birds from each of the 5 possible genotypes were randomly selected from the offspring of the birds mated in 1972 when they were between 11 and 15 weeks old. The age difference is due to birds being selected from each of the 3 hatches.

The 5 genotypes are:-

- (i) Normal Males
- (ii) Heterozygote Males
- (iii) Dwarf Males
- (iv) Normal Females
- (v) Dwarf Females

The shank length of birds was measured in the manner described in the text. The birds were slaughtered and the right leg severed just above the hock joint. The identification (wingband number) of the birds was attached to the severed leg. The legs were then boiled, allowed to cool, and the flesh removed from around the metatarsus bone (shank bone). The bones were then dried and the length measured with the same calipers used for the live measurements.

Analysis

The regression of shank length on metatarsus bone was calculated for each of the genotypes, and an analysis of variance performed on the 5 regressions (Williams 1959).

Results and Discussion

A plot of shank length against metatarsus length is shown in Figure (a). The regression coefficients (b) varied from 0.9602 for the dwarf females to 1.3499 for the dwarf males. The combined regression coefficient was 1.0300 ± 0.0453 . Results of the analyses are shown in Table (a). The analysis of variance indicated that the combined regression was highly significant ($P < 0.005$) and that there was no significant differences between the regressions for the 5 genotypes.

The combined regression is described by:

$$\text{Shank Length} = 1.6265 + 1.0300 (\text{Length of Metatarsus})$$

The intercept value of 1.6265 would correspond to the "end error" associated with the live measurement comprised of the width of adjacent bones, cartilage layers and skin. The use of the technique used to measure shank length in the live bird is most satisfactory as an estimate of the length of the shank bone as shown by the high significance of the regression and the small difference of the regression coefficient from unity.

Figure (a) Shank Length versus Metatarsus Length

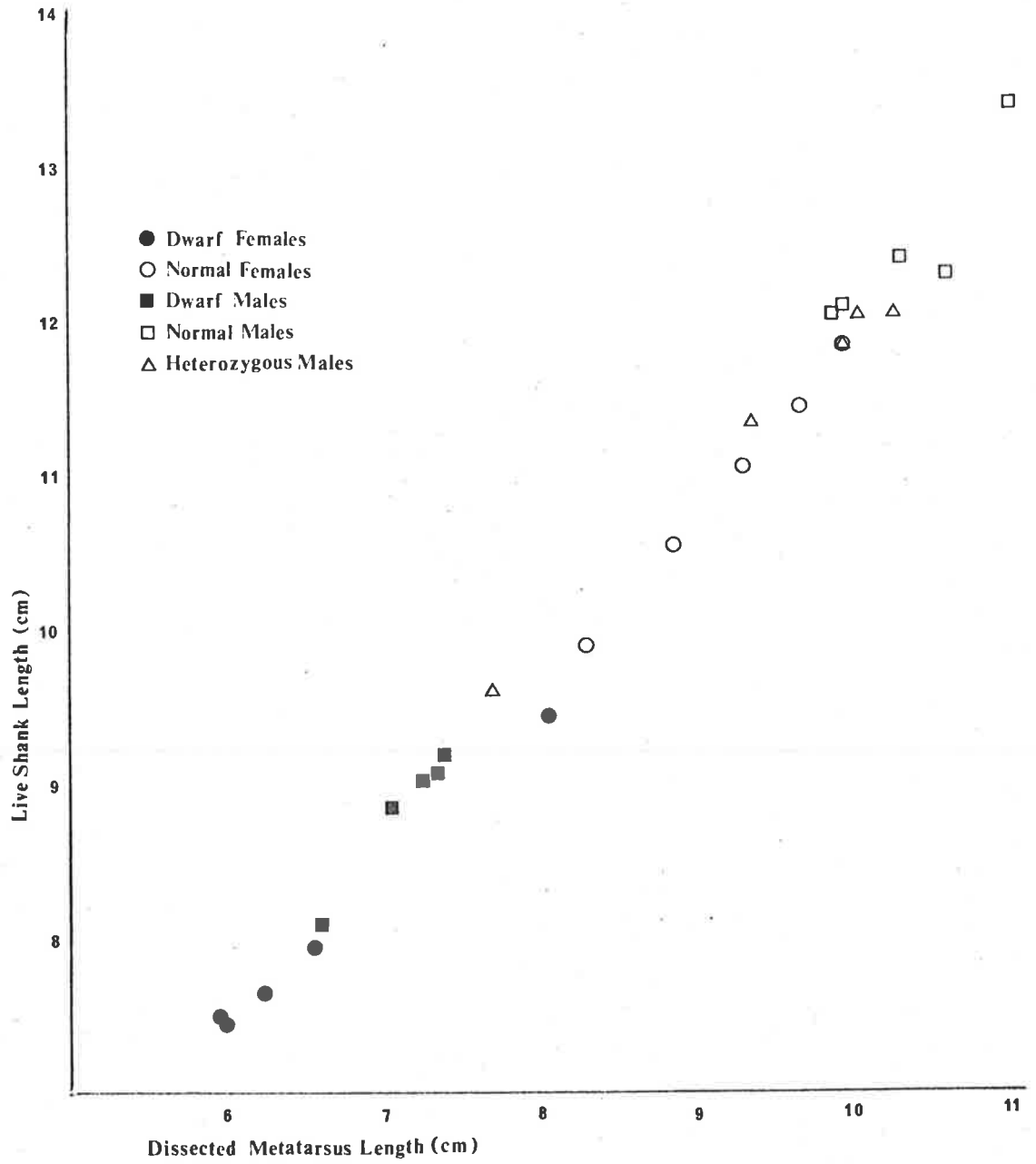


Table (a) Regression of Shank Length on Metatarsus Length

(a) Regressions

	Average Live Shank Length (cm)	Average Length of Metatarsus (cm)	Regression Coefficient
Normal Males	10.34	12.45	1.0284
Heterozygous Males	9.46	11.38	0.9928
Dwarf Males	7.13	8.86	1.3499
Normal Females	9.21	10.96	1.1684
Dwarf Females	6.56	8.00	0.9062

(b) Analysis of Variance

Source of variation	df	SS	MS	F
Combined Regression	1	10.9814	10.9814	515.5587***
Difference in Regressions	4	0.0965	0.0241	1.1315 NS
Combined Residual	15	0.3191	0.0213	
Total	20	11.3970		

*** $P < 0.005$

NS Not Significant

Appendix (2) Incubation Data, Dam Totals within Sires

Table (b) Incubation Data, Dam Totals within Sires for Dwarf Matings

Sire	Dam	Number eggs set	Number eggs fertile	Number chickens hatched
112	375	0	0	0
	348	20	3	2
	195	29	8	7
204	108	27	24	21
	180	11	9	7
	099	34	28	25
094	279	23	7	6
	133	0	0	0
	400	18	12	7
219	386	0	0	0
	064	31	23	22
	236	32	18	15
257	388	36	17	14
	239	37	13	9
	203	0	0	0
244	110	24	20	19
	367	33	25	25
	155	28	15	7
Totals		383	222	186

Table (c) Incubation Data, Dam Totals within Sires for
Normal Matings

Sire	Dam	Number eggs set	Number eggs fertile	Number chickens hatched
010	181	29	27	22
	182	18	9	8
	183	8	8	2
011	184	16	13	8
	185	22	19	14
	186	13	12	10
012	187	13	9	3
	188	11	10	9
	189	27	24	15
013	190	21	15	9
	191	25	12	9
	192	27	5	4
014	193	18	10	7
	194	23	16	12
	195	21	16	12
299	339	11	2	2
	274	41	30	24
	384	2	0	0
318	298	37	21	19
	336	0	0	0
	202	32	24	14
009	333	35	16	15
	430	38	20	7
	146	32	18	10
310	253	15	7	7
	441	24	18	17
	331	7	0	0
316	034	24	16	13
	005	47	1	1
	319	24	2	2
433	455	37	18	16
	148	35	32	29
	183	39	24	23
Totals		772	454	343

Table (d) Incubation Data, Dam Totals within Sires
for Heterozygote Matings

Sire	Dam	Number eggs set	Number eggs fertile	Number chickens hatched
001	151	26	9	7
	152	27	11	11
	153	28	10	8
002	154	29	25	22
	155	28	28	21
	156	29	26	23
004	160	28	19	17
	161	30	5	5
	163	28	15	14
005	164	28	25	25
	165	27	26	24
	166	27	13	10
006	167	29	19	14
	168	35	22	18
	169	28	27	21
007	170	28	18	7
	171	30	23	22
	172	21	18	15
008	174	22	13	10
	176	18	14	11
	177	17	15	9
009	178	20	2	1
	179	14	3	0
	180	18	5	3
378	436	0	0	0
	118	28	10	9
	268	27	22	0
286	374	35	2	2
	185	42	0	0
	079	38	0	0
062	345	22	3	1
	090	42	36	31
	213	21	6	3
057	364	33	26	22
	211	28	25	20
	412	37	26	24
Totals		968	547	430

Appendix (3) Segregation of Sex, Sire and Dam Totals

Table (e) Dwarf Group, Segregation of Sex

Sire	Number Male Offspring	Number Female Offspring	Dam	Number Male Offspring	Number Female Offspring
112	4	2	195	4	2
204	32	19	108	10	9
			180	6	1
			099	16	9
094	5	8	279	2	4
			400	3	4
219	19	16	064	14	7
			236	5	9
257	13	10	388	9	5
			239	4	5
244	22	27	110	11	8
			367	8	15
			155	3	4
Total	95	82		95	82

Table (f) Normal Group, Segregation of Sex

Sire	Number Male Offspring	Number Female Offspring	Dam	Number Male Offspring	Number Female Offspring
010	10	13	181	8	7
			182	2	5
			183	0	1
011	10	18	184	2	6
			185	6	6
			186	2	6
012	9	11	188	3	5
			189	6	6
013	13	8	190	5	3
			191	5	4
			192	3	1
014	13	18	193	3	4
			194	5	7
			195	5	7
299	10	14	339	0	2
			274	10	12
318	15	16	298	11	7
			202	4	9
009	16	16	333	6	9
			430	3	4
			146	7	3
310	14	10	253	2	5
			441	12	5
316	6	10	034	6	7
			005	0	1
			319	0	2
433	30	35	455	10	6
			148	12	15
			183	8	14
Total	146	169		146	169

Table (g) Segregating Group, Segregation of Sex

Sire	Number Male Offspring	Number Female Offspring	Dam	Number Male Offspring	Number Female Offspring
001	11	11	151	3	4
			152	5	5
			153	3	2
002	34	22	154	11	8
			155	10	8
			156	13	6
004	16	15	160	7	8
			161	3	2
			163	6	5
005	21	11	164	12	6
			165	9	3
			166	0	2
006	13	9	167	2	2
			168	4	4
			169	7	3
007	17	19	170	3	1
			171	10	9
			172	4	9
008	13	8	174	3	4
			176	6	2
			177	4	2
009	2	0	180	2	0
378	2	3	118	2	3
286	2	0	374	2	0
062	14	14	345	0	1
			090	12	12
			213	2	1
057	25	26	364	7	8
			211	9	8
			412	9	10
Total	170	138		170	138

Appendix (4) Segregation of Sex and Genotype, Segregating Group

Table (h) Dam Totals by Sex and Genotype for Segregating Group

Sire	Dam	Numbers of offspring			
		Dwarf Males	Heterozygote Males	Dwarf Females	Normal Females
001	151	2	1	3	1
	152	1	4	2	3
	153	0	3	1	1
002	154	6	5	3	5
	155	3	7	4	4
	156	9	4	3	3
004	160	5	2	4	4
	161	2	1	1	1
	163	1	5	3	2
005	164	5	7	2	4
	165	2	7	2	1
	166	0	0	1	1
006	167	1	1	2	0
	168	3	1	2	2
	169	5	2	2	1
007	170	3	0	1	0
	171	3	7	4	5
	172	4	0	3	6
008	174	3	0	0	4
	176	3	3	0	2
	177	1	3	0	2
009	180	0	2	0	0
378	118	1	1	3	0
286	374	1	1	0	0
062	345	0	0	1	0
	090	2	10	7	5
	213	1	1	0	1
057	364	4	3	7	1
	211	5	4	6	2
	412	5	4	5	5
Total		81	89	72	66

Appendix (5) Analyses of Variance for Body Weight and
Shank Length Measurements

Table (i) Analyses of Variance, Dwarf Group

(a) Male Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	9.83	7735	16656	0.143	0.312
Sires within Hatches	15	63.51*	13192*	49723*	0.671	0.635
Dams within Sires	16	24.97**	4800	16122	0.287*	0.314
Full-sibs within Dams	52	2.24	2713	16692	0.136	0.251
Total	86					

(b) Female Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	43.35	17266	42647	0.409	0.356
Sires within Hatches	12	25.65	6674	40887**	0.457*	0.578*
Dams within Sires	13	14.90**	2741	8376	0.154	0.219
Full-sibs within Dams	35	2.77	2298	11567	0.130	0.290
Total	63					

* Significant at 5% confidence level

** Significant at 1% confidence level

Table (j) Analyses of Variance, Normal Group

(a) Male Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	27.60	19340	94640	0.281	1.269
Sires within Hatches	32	31.11	31618**	107528*	0.862**	0.806**
Dams within Sires	28	18.72**	8447	51918	0.237	0.316**
Full-sibs within Dams	73	2.36	6047	45684	0.234	0.429
Total	136					

(b) Female Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	76.49	5764	98813	0.304	1.413
Sires within Hatches	34	32.65	14932	43122	0.554	0.488
Dams within Sires	30	26.67**	11565**	52196**	0.375*	0.466
Full-sibs within Dams	91	1.77	4835	27252	0.208	0.300
Total	158					

* Significant at 5% confidence level

** Significant at 1% confidence level

Table (k) Analyses of Variance, Dwarf birds from the
Segregating Group

(a) Male Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	46.36	10407	38981	0.336	0.738
Sires within Hatches	21	16.49	3365*	37680	0.211	0.549*
Dams within Sires	23	24.24**	1459	18932**	0.128	0.226
Full-sibs within Dams	29	1.67	4502	20545	0.227	0.341
Total	76					

(b) Female Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	57.36	2379	2717	0.043	0.155
Sires within Hatches	21	26.48	5135	17132	0.314*	0.178
Dams within Sires	19	19.27**	2679*	16009	0.122	0.288
Full-sibs within Dams	25	3.32	1078	10278	0.077	0.189
Total	68					

* Significant at 5% confidence level

** Significant at 1% confidence level

Table (1) Analyses of Variance, Normal birds from the
Segregating Group

(a) Male Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	23.02	2435	7699	0.105	0.055
Sires within Hatches	22	42.05*	8044**	55339*	0.297*	0.413
Dams within Sires	20	18.96**	1830	20748	0.124	0.333
Full-sibs within Dams	38	1.12	3370	35990	0.176	0.394
Total	83					

(b) Female Offspring

Source of Variation	df	Mean Squares				
		DOBW	6WKBW	12WKBW	6WKSL	12WKSL
Hatches	3	16.07	7964	7876	0.367	0.293
Sires within Hatches	21	31.19	5097*	21422	0.214	0.399
Dams within Sires	17	14.45**	1906	15894	0.112	0.186
Full-sibs within Dams	24	2.20	2067	16592	0.122	0.145
Total	65					

* Significant at 5% confidence level

** Significant at 1% confidence level

Appendix (6) Average Body Weights and Shank Lengths

Table (m) Body Weights and Shank Lengths, Sire Averages by Sex, Dwarf Group

Sire	DOBW		6WKBW		12WKBW		6WKSL		12WKSL	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
112	28.0	31.0	385	390	1025	1105	5.68	6.05	7.85	8.50
204	35.6	36.1	356	298	926	707	6.00	5.68	8.41	7.40
094	37.5	37.9	283	251	805	601	5.96	5.23	7.88	7.01
219	28.7	30.5	291	204	832	519	5.49	4.92	7.94	6.65
257	31.8	32.7	255	228	783	612	5.45	5.17	8.32	7.25
244	37.1	36.6	265	242	749	602	5.45	5.20	7.77	7.08

Table (n) Body Weights and Shank Lengths Sire Averages by Sex, Normal Group

Sire	DOBW		6WKBW		12WKBW		6WKSL		12WKSL	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
010	32.8	32.3	342	325	1228	1008	6.47	6.12	10.69	9.57
011	39.9	39.3	389	353	1417	1134	6.80	6.43	11.06	10.00
012	36.3	36.7	288	328	1228	1151	6.10	6.23	10.60	9.96
013	38.8	38.9	327	354	1378	1140	6.44	6.41	11.02	10.08
014	40.8	39.3	384	340	1393	1134	6.70	6.24	10.96	9.84
299	40.4	39.0	356	307	1155	921	6.14	5.83	10.06	9.05
318	41.2	40.9	544	431	1621	1157	7.20	6.41	11.24	9.42
009	41.6	41.0	474	457	1473	1204	7.18	6.92	11.18	10.11
310	43.6	41.4	551	401	1583	1115	7.44	6.59	11.50	9.82
316	42.0	41.3	438	396	1408	1116	7.04	6.76	11.18	10.03
433	40.7	41.0	463	405	1420	1099	6.87	6.49	10.76	9.74

Table (o) Body Weights and Shank Lengths, Sire Averages by Sex, Dwarf birds from the Segregating Group

Sire	DOBW		6WKBW		12WKBW		6WKSL		12WKSL	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
001	39.0	35.3	273	274	878	773	5.65	5.31	8.25	7.56
002	34.3	36.3	273	268	793	681	5.41	5.31	7.84	7.29
004	33.4	32.8	292	267	931	780	5.69	5.33	8.49	7.68
005	32.3	31.8	252	199	851	614	5.36	5.02	8.03	7.24
006	35.6	36.0	228	208	742	632	5.29	4.92	7.97	7.08
007	37.0	37.9	268	302	693	736	5.49	5.62	8.02	7.64
008	37.9	-	253	-	759	-	5.26	-	7.91	-
062	42.7	43.4	282	313	837	775	5.55	5.74	8.77	7.51
057	37.1	36.3	321	270	874	716	5.80	5.51	8.34	7.67

Table (p) Body Weights and Shank Lengths, Sire Averages by Sex, Normal Birds from the Segregating Group

Sire	DOBW		6WKBW		12WKBW		6WKSL		12WKSL	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
001	35.8	34.4	361	258	1112	924	6.30	5.71	10.11	9.09
002	36.0	35.6	354	316	1152	981	6.30	5.91	10.04	9.28
004	33.3	32.4	361	325	1172	1027	6.35	5.99	10.29	9.59
005	31.6	32.2	283	295	1092	1053	5.88	5.92	9.94	9.56
006	33.8	36.0	278	218	995	847	5.83	5.28	9.49	8.28
007	36.4	37.5	350	332	1201	915	6.49	6.13	10.24	9.27
008	39.3	38.3	338	272	1107	840	6.14	5.81	9.79	8.79
062	42.6	42.5	418	388	1273	1009	6.74	6.26	10.41	9.32
057	35.5	33.1	379	299	1165	940	6.39	5.91	10.10	9.24

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QUANTITATIVE EFFECTS ASSOCIATED WITH A

DWARFING GENE IN POULTRY

ADDENDUM

Further comment is appropriate relative to the pooling procedure that was used in the analyses of variance (see page 44, paragraph 2 and page 60, paragraph 3). The fact that the pooling procedure did not result in any significant variation due to hatch (page 44, paragraph 2, last sentence) does not preclude the possibility that hatch effects in the two years somehow cancelled each other out. This would be unlikely however, especially when it is remembered that the analysis for the Dwarf Group used data that was collected within one year only (i.e. there was no pooling) and no significant hatch effects were observed. The test of significance for hatch effects has been made against the variation due to sires within hatches which is appropriate when hatches are considered as fixed effects (which they are in this experiment). All other effects, i.e. sires, dams and full-sibs can be considered as random effects. Variation observed due to hatches does not in any way contribute to the heritability or correlation estimates which use variance components estimated from sires within hatches, dams within sires and full-sibs within dams. The technique used may not have been appropriate if one had been interested in estimating the magnitude of hatch effects.

The pooling of the two sexes for the heritability and correlation estimates (page 60, paragraph 3) can strictly

only be justified if the variance of the two sexes were the same. In Table (29) appropriate F values have been shown for tests of equality in males and females of the variance of the five characters measured. Thirteen of the twenty F values are not significant at a 5% confidence level and in only one case is the value greatly in excess of that required for significance at a 5% level. The justification for pooling in this manner, despite the significance of some of the F tests, is the more serious problem of the effect of the relatively small numbers on the standard error of the heritabilities and the correlations. Even with the increased numbers after pooling the standard errors are very large, making interpretation difficult. Without the pooling of the two sexes there would be twice the number of estimates with even larger standard errors. Without the pooling of the two sexes interpretations would have less meaning because of the greater confounding of chance effects with the even smaller numbers.

Some of the heterozygous birds (numbers 001-009) were used twice [Table (1)] so that some of the progeny in the Segregating Group may have been inbred due to the possibility of some sire on daughter matings. For uniformly inbred populations Dickerson (1942) presented appropriate corrections for the coefficients of the variance components, k_1 , k_2 , and k_3 [see Table (20)]. However a general solution that allows for different amounts of inbreeding among the offspring has not yet been published. In light of the difficulties in interpretation mentioned above due to the

limited numbers the amount of inbreeding in this experiment would be unlikely to cause any differences to the conclusions made when it is ignored. A further confounding effect, which I also suggest would not alter the conclusions of this experiment is the observation that there was some difference in the background genotypes of the Mating Groups, with the Dwarf and Segregating Groups having some White Leghorn ancestry that the Normal Group did not. This is made clear in Table (1) and was referred to in the text (page 21, paragraph 2).

REFERENCE

DICKERSON, G.E. (1942) -

Experimental design for testing inbred lines
of swine.

Journal of Animal Science 1: 326

Table (29) F tests for homogeneity of residual variances
 (full-sibs within dams) of male and female
 offspring - larger/smaller mean square[#]

	DOBW	6WKSL	12WKBW	6WKSL	12WKSL
Dwarf Group					
male/female (F ₃₅ ⁵²)	-	1.181	1.433	1.046	-
female/male (F ₃₂ ³⁵)	1.237	-	-	-	1.155
Normal Group					
male/female (F ₉₁ ⁷³)	1.333	1.251	1.676*	1.125	1.430
Segregating Group					
Dwarf Offspring					
male/female (F ₂₅ ²⁹)	-	4.176*	1.999*	29.481***	1.804
female/male (F ₂₉ ²⁵)	1.988*	-	-	-	-
Normal Offspring					
male/female (F ₂₄ ³⁸)	-	1.630	2.169*	1.443	2.717*
female/male (F ₃₈ ²⁴)	1.964	-	-	-	-

[#]Calculated from Tables (i), (j), (k) and (l) of
 Appendix (5).