Inter-relationship of body weight and egg weight in the domestic fowl.

by

JOHN MITCHELL MANSON, B.Sc., M.S. (Calif.)

A thesis presented to the University of Edinburgh for the degree
of Doctor of Philosophy.

July 1970.

TABLE OF CONTENTS

SUMMARY

Egg weight and body weight in the fowl are genetically positively correlated so that a change in one of the traits in a given direction is expected to be accompanied by a change in the same direction in the other. It is probably to the net economic advantage of the poultry breeder, however, to attempt to select these two traits in opposing directions, i.e. reduced body weight but increased egg weight, provided rate of lay is not impaired in the process.

This thesis is concerned with describing the results of a 5-year selection experiment which set out to test the feasibility of selecting for lower body weight or higher egg weight without incurring the expected associated change in the correlated trait.

Four sub-lines were established within each of 2 strains (S2 and S5) of White Leghorns, while a pedigreed, random-bred population also derived from the same base population was maintained as a control line within each strain. The selection lines comprised:-

1. Selection for increased egg weight (Egg Weight line).
2. Selection for decreased body weight (Body Weight line).
3. Selection on the value of the ratio of the individual hen's egg weight to body weight (Ratio line).
4. Selection on an index taking the form, I = Egg Weight - (b) Body Weight (Regression line), b in this instance being the calculated average genetic regression of egg weight on body weight in the base populations.

Both body weight and egg weight had estimated heritabilities of approximately 0.50 from variance analyses in the base populations and a genetic correlation between the 2 traits of the order of +0.3 to +0.4.

Selection for high egg weight or low body weight in lines 1 and 2 over 5 generations was apparently equally effective (realised heritabilities around 0.40). Body weight selection was accompanied by a marked correlated decline in egg weight, but in the case of egg weight selection the expected correlated increase in body weight was only observed in S2, pointing to some asymmetry in the correlated responses in S5.

Selection in lines 3 and 4 over only 4 generations has altered the relative egg weight to body weight relationship in both strains more effectively than single trait selection. The Regression lines had the highest mean egg weight, the increase amounting to as much as 12 per cent, while body weight has remained constant. On the other hand, the Ratio lines had substantially the greatest proportionate egg weight, body weight having been reduced by 16 per cent and 22 per cent in S2 and S5 respectively. Egg weight increased concurrently in S2 by 2 to 3 per cent, while a reduction of 11 per cent was noted in S5 (compared to a decline of 16 per cent in egg weight in the S5 Body Weight line).

The effect of these selection procedures on the overall economic and biological efficiency of the strains is discussed at length. It

would appear that a substantial decline in egg production, which cannot be accounted for by inbreeding, has occurred within the Regression lines, although egg numbers have possibly increased as a correlated response in the Ratio lines.

LIST OF TABLES

LIST OF TABLES

(continued)

LIST OF TABLES

(continued)

LIST OF TABLES

(continued)

LIST OF FIGURES

Time trends in Control Population, Strain 2:

Time trends in Control Population, Strain 5:

LIST OF FIGURES

(continued)

LIST OF SYMBOLS FREQUENTLY USED IN THIS THESIS

The following are the meanings of certain symbols and abbreviations used in the text. Most of the symbols used follow the notation used by Falconer (1960) pp. 346-348 An Introduction to Quantitative Genetics, Oliver and Boyd, Edinburgh.

b = Regression coefficient

C.R. = Correlated response to selection:

  $C.R._{1.2}$ = Correlated response in trait 1, following selection on trait 2

d.f. = Degrees of Freedom used in analysis of variance

$\triangle$ = Change of: e.g. $\triangle F$ = rate of inbreeding

F = Coefficient of inbreeding

h^2 = Heritability = $\frac{V_g}{V_p}$; $h = \frac{\sigma G}{\sigma P}$

$\bar{i}$ = Intensity of selection: i.e. selection differential in units of the phenotypic standard deviation

N = Population size: i.e. number of breeding individuals in a population or line

Ne = Effective population size

n = Number: e.g. number of progeny per line

R or $\triangle G$ = Response to selection

r = Correlations between 2 characters:

  $r_{1.2 \text{ or } xy}$ = Correlation of trait 1 with trait 2 or trait x and y

  r_g = additive genetic correlation (cf. r_A (Falconer))

  r_p = phenotypic correlation

LIST OF SYMBOLS

(continued)

S or $\triangle P$ = Selection differential

σ = Standard deviation:

- σ_p = Phenotypic standard deviation
- σ_g = Genetic standard deviation

t = Phenotypic correlation between members of families

V = Variance:

- V_p = Phenotypic variance
- V_g = Genetic variance. $V_{g\ S+D}$ = Genetic variance as computed from twice the joint sire and dam component of variance $(V_S + V_D)$

Cov = Covariance: Cov_g = Genetic covariance, etc.

$\overline{x}, \overline{r}$ = Mean of x, r

ACKNOWLEDGMENTS

I should like to record my thanks first to Professor Sir Stephen J. Watson who allowed me the use of the breeding flocks on the Edinburgh School of Agriculture Poultry Unit for this study and gave me every encouragement along the way.

I am indebted to Professor Alan Robertson for his guidance and advice on many matters regarding the planning, execution and analysis of the experiment.

Several people have, in a variety of ways, assisted me to conduct the experiment. Dr. Barnet Woolf and Dr. W. G. Hill of the Institute of Animal Genetics provided me with computer programmes to facilitate analysis of the data, while Dr. George Clayton, also from the Institute, has provided advice and rousing encouragement throughout. Mr. David McDonald, Manager of the School of Agriculture Poultry Unit, assisted me in the laborious task of arranging pedigreed matings and I am extremely grateful to him for his help and for his careful management of the experimental stock.

A number of personnel assisted in the recording of the performance of several thousand birds and the compilation of records, but greatest credit must go to Mrs. Margaret Roan who completed the recording of the data, always with painstaking accuracy.

My final word of thanks goes to Miss Anne Revolta who obligingly prepared the typewritten manuscript with great patience, skill and exactitude.

1. INTRODUCTION

Within the last two decades there has been an obvious trend on the part of commercial poultry breeders to develop a small light-weight hybrid for egg production, replacing the heavier, dual-purpose egg and meat producing bird, on account largely of the development of intensive systems of production in which density of stocking and efficiency of feed utilisation have assumed major importance and the value of the cull bird has declined.

Under such conditions of intensive husbandry the economically most successful strains will be those having the smallest body size (weight) consistent with reasonable egg production, egg size and viability. The question arises as to how much further body weight can be reduced by genetic selection before a decline in these other criteria of performance negates any advantage gained from a saving in food costs. Body weight influences the quantity of food the bird requires for its own body maintenance while the food consumption above that required for maintenance is widely assumed to be linearly related to the level of egg output (Brody, 1945; Wells and Clawson, 1933) although these general assumptions are unlikely to be strictly and universally valid (Hansen and Mighell, 1952; Heady <u>et al</u>., 1966). In broad terms, however, it can be considered that the food required for maintenance represents a fixed cost and is determined largely by the bird's body weight, the larger bird being more costly to maintain, unless it compensates by giving a higher output of egg. Since many commercial strains of egg-type poultry appear to have "plateaued" in any case as regards egg numbers, selection to reduce body weight still further would appear to offer the next best means of effecting an improvement in the overall economic efficiency of the commercial layer, provided egg output is not impaired in the process.

Egg weight itself, although probably of lesser importance within limits, is economically vital in so far as mean egg weight will determine the relative proportion of eggs falling into the heavier weight classifications which carry additional price benefits to the egg producer, generally out of proportion to the actual additional egg mass involved. It may be possible using appropriate breeding techniques to raise mean egg size without increasing body weight or reducing egg numbers.

One question common to either breeding objective is that of the degree of relationship between body weight and egg weight and the extent to which the relationship may change as the mean value for the traits changes, or the extent to which the normal association between the two traits may be modified using appropriate selection procedures.

This thesis is concerned with describing the results of a five year selection study which set out to test to what extent either body weight could be reduced or egg weight increased without the concurrent decrease in egg weight or increase in body weight respectively that would be predicted on the basis of the genetic correlation between these traits.

Acknowledgment: This study was made possible through the financial support of the Agricultural Research Council (Research Grant G15/21). This support for part of the period of the experiment is gratefully acknowledged.

2. REVIEW

Amongst non-domesticated species of birds there is an obvious phenotypic relationship, generally, between the mean egg weight and mature body weight of the species, egg weight increasing linearly with body weight (Heinroth, 1922; Huxley, 1927).

The egg of the Ostrich (Struthio camelus) weighs about 1.6 kg. and is the largest of any living bird, but is only about 1.75 per cent of the bird's body weight. Some of the smallest species of birds lay eggs which may weigh 8-10 per cent of their body weight; in some instances more. The Kiwi (Apteryx australis), for example, lays eggs which weigh more than 14 per cent of its own adult body weight. There is a decided tendency within any given family of birds, which itself will tend to have a characteristic egg to body weight relationship, for the smaller species to have proportionately heavier eggs than the larger species. This has been pointed out by Lack (1968), amongst others, who suggests that the explanation in an evolutionary context is probably that since the smaller chick from the smaller species has a proportionately larger surface area and will lose heat more rapidly, it is likely to require proportionately more food reserves and hence a proportionately larger egg.

Lack (1968) lists the proportionate egg weight of 50 species within the family Phasianidae of which the domestic fowl is a member and he quotes the wild Red Jungle Fowl (Gallus gallus murghii) as having an adult body weight of 800 grams and a proportionate egg weight of 3.5 per cent. The other species listed range in their proportionate egg weights from 2.6 per cent to

13.7 per cent. The typical domestic fowl is quoted, by comparison, as laying an egg which will be 3.9 per cent of the adult body weight quoted of 1,500 grams, i.e. an egg weighing between 58 and 59 grams. The difference in proportionate egg weight between it and its wild relative is taken to be evidence of the strong selection which has been directed to breeding for larger eggs solely for human consumption in commercial flocks of poultry. However, the average adult body weight and proportionate egg weight quoted above are difficult to accept as characteristic of modern strains of commercial fowl in practice. Morgan and Carlson (1968) suggested that the eggs from year old hens from commercial strains averaged 3.3 per cent of the bird's body weight, with a range between strains of from less than 3 per cent to 3.6 per cent.

It would thus appear that the average egg weight/body weight relationship may not have been all that radically altered in spite of the changes effected by breeders in the performance characteristics of modern strains of poultry. Lerner (1951) concluded that mean egg size in commercial strains of poultry, however, had reached a level at which reproductive fitness was impaired having passed beyond the optimum with respect to its biological fitness.

Studies of breeding populations of domestic fowl have indicated that egg weight and body weight are moderately strongly positively correlated with one another, both phenotypically and genetically. (Abplanalp, 1956; King, 1961; King _et_ _al_, 1963; Clayton and Robertson, 1966; Kinney _et_ _al_, 1968). The genetic correlations found by all of these researchers would tend to confirm the prediction that as the breeder selects for increased egg weight, body weight will tend to increase concurrently. Alternatively, if he attempts to reduce body weight he will run up against the problem of a correlated decrease in egg weight.

The existence of even a moderately strong genetic correlation ($r_g = + 0.3 - 0.4$) does not, however, imply that the overall broad relationship between mean body weight of the bird and its mean egg weight is absolute and that the degree of their association cannot be altered using appropriate selection procedures.

A genetic association, as indicated by a genetic correlation between any two traits, can arise from two possible causes. Firstly, the traits concerned could conceivably be partly controlled by individual genes or blocks of genes which are closely linked on the same chromosome. This form of association of characters might be expected if a population derives from a recent cross between markedly disparate breeds or strains. In this case, there will be a tendency for the association of similar characteristics present in the parent strains to persist in the cross-bred population until linkage equilibrium is re-established after several generations have elapsed, when the genetic correlation between the two characters ought to have disappeared completely. The degree to which the connection will persist, therefore, will depend upon the degree of linkage between the particular genetic loci involved (Robertson, 1961).

The more likely basis, however, of a genetic correlation in many instances is that individual genes have a direct physiological effect on more than one trait, i.e. a certain proportion of the genes which are segregating are pleiotropic in their action. Considering the specific case of the genetic association between body weight and egg weight in poultry, presumably many genes exist which affect either trait independently of the other, but as most populations of fowl have been subjected to several generations of selection for larger egg size, and perhaps also to a lesser degree small body size, many of these independently acting genes having major effects are now approaching frequencies of near zero or one. Once this has occurred, most of the remaining genetic covariance will arise from genes which affect the trait in a similar direction. However, if the genetic correlation between body weight and egg weight, for example, (which after all are only moderately positively correlated) arises from pleitropy of only a proportion of the genes concerned, then it should be possible to select for genes which affect either egg weight or body weight alone.

Reeve (1950) reported a genetic correlation of +0.7 between wing length and thorax length in Drosophila melanogaster. In spite of the apparent high degree of association between these morphological traits, Robertson (1962) succeeded in altering the wing length to thorax ratio over 10 generations by as much as 30 per cent through selecting solely for high and low values of the wing length/thorax ratio. There was no evidence that the response to selection had ceased by the time the experiment was terminated. Nearly all of the difference effected in the ratio was due to changes in wing length; thorax size having been virtually unaffected by the changes in relative wing size. There is no doubt in this instance that genetic variation in wing length independent of thorax size is both appreciable and highly heritable, in spite of the existence of a strong positive correlation between the two traits.

Cockrem (1959) reported an experiment in the mouse in which he demonstrated quite clearly that it was possible to make fairly rapid progress in selection for relationships between body weight and tail length different from those predictable from the expected correlated response based upon the genetic correlation between these two characters (r_g = + 0.6 – 0.7).

Clayton (1968) comparing the performance of a number of commercial strains of poultry in random sample tests in the United States of America drew attention to at least one example of a strain in which egg weight showed a marked divergence from the average. The strain in question had the lowest mature body weight and yet was one of the highest in mean egg weight. This fact, combined with a high rate of egg production, resulted in this particular strain proving the most profitable overall when judged on the basis of total income over food costs. On the other hand, the control strain cited in the same paper and in which, of course, all intentional selection had been relaxed, provided another example of a notable divergence in the average body weight/egg weight relationship. In the latter case it was one of the heaviest strains with by far the smallest egg size.

Festing and Nordskog (1967) reported some results from a selection experiment in the fowl in which two lines had been established in which selection was intentionally directed towards creating a divergent response in body weight and egg weight; one line having been selected for large body/small egg and the other for small body/large egg. Results up to the eighth generation of selection (Nordskog, unpublished) indicated that the two traits continued to diverge, but that the changes from selection for body weight appeared to swamp out much of the opposing selection for egg weight. Egg weight (55 weeks of age) in the large body/small egg line had declined to only 2 per cent of the body weight, while it was equivalent to 4.5 per cent of the body weight in the small body/large egg line.

The selection procedures which were adopted in the present study with the view to examining the extent to which the egg weight/body weight relationship could be altered in 2 egg-type strains, comprised, in the first instance, a selection for maximum values of the egg weight/body weight ratio. Since smaller birds tend to lay disproportionately larger eggs anyway, selection on a ratio value would tend to select smaller than average individuals, while maintaining a relatively satisfactory egg weight by comparison with selection purely for lower body weight.

The second experiment entailed selecting birds whose egg weight exceeded a predicted egg weight based upon the average regression of egg weight on body weight within the population. Such a procedure would again tend to select birds laying a disproportionately large egg, but without, in this case, altering body weight significantly.

Apart from the obvious "academic" interest in these selection procedures, they are also worth testing as a relatively simple selection technique for use, for example, within strains in which egg numbers have ceased to respond to further selection. Many commercial strains appear relatively intractable to continued selection for increased egg production. (Dempster *et al.*, 1952; Dickerson, 1955; 1963; Yamada *et al.*, 1958; Clayton, 1968). If it is possible to make notable gains in egg weight, or to achieve a marked reduction in body weight without adversely affecting egg numbers, this might prove a more fruitful short-term approach to improving the overall economic worth of strains apparently plateaued for egg numbers.

3. MATERIALS AND METHODS

3. 1 Description of Base Populations

Some details concerning the strains used in this study have already been given by Clayton and Robertson (1966). However, a further description of these strains will no doubt be pertinent here.

Two distinct strains had been maintained as completely closed flocks on the University farm for 5 years at the time this study was initiated. The two flocks were each derived from initial small samples of between 40-60 chicks hatched in 1956-57 from eggs obtained from two commercially successful White Leghorn strains. Flock matings were adopted during the subsequent two seasons to multiply up each strain to a flock size of around 1,000 pullets housed in the laying house.

These two strains have been designated Strain 2 and Strain 5, implying that probably at least another three were introduced at the same time, but only the two mentioned were retained. These two were more than likely continued on account of their worthwhile performance, particularly when crossed together, as confirmed by the relative success of a strain-cross entry in a subsequent commercial random sample egg production test in 1959 (see Table 1). The overall economic success of this particular cross, however, declined relative to competing entries from commercial breeders over the 4 year period up to 1963, ranking tenth out of a total of 20 entries in the last test entered, compared to its position in the 1959/60 test when it was placed second.

TABLE 1

Performance of strain-cross entry (Strain 2 x 5) in the B.O.C.M. 500 day random sample test, Stoke Mandeville

Year	Number of Entries		Final ranking in Test (Income over Food Costs)	Number of eggs per Pullet housed	
				Test Average	Strain Cross
1959-60	15	(29)	2	194	227
1960-61	18	(30)	4	186	207
1961-62*	20	(27)	6	152	158
1962-63	20	(45)	10	217	222

( ) = sample size; number of pullets housed at point of lay

* Terminated after 32 weeks' production due to outbreak of Fowl Pest at test location

There is no evidence that the egg production potential of the cross had declined as a result of relaxed selection over the period in question. The placing of the entry in these tests had declined, therefore, presumably largely on account of improvements effected in other breeders' stocks rather than because of a deterioration in the components of overall economic performance in the cross, unless mean egg size had deteriorated.

Clayton and Robertson (1966) have presented data on the mean performance of relatively large populations of the two strains over the three year period 1959-62 while the strains were random-mated (Table 2). It would appear from their data that egg size had reached an unsatisfactory level, particularly in Strain 5 in which the mean egg weight was some 4-5 grams below what is normally considered an acceptable level commercially. This drop in egg weight most probably occurred, however, as a result of genetic sampling during the multiplication period itself and there was no evidence of any further decline in egg weight as a result of relaxation of selection over the period 1959-62.

TABLE 2

Mean Performance, Strain 2 and Strain 5, 1959-1962
(Clayton and Robertson, 1966)

	Strain 2		Strain 5	
	Mean	σ_p	Mean	σ_p
Body Weight at 44 weeks (grams)	2,049	204	1,995	212
Egg Weight at 44 weeks (grams)	57.1	3.5	53.0	3.5
Egg Production of Survivors to 44 weeks	108.4	23.4	101.1	22.2
Percentage Production	76.7	-	75.8	-
Sex. Maturity (Age at 1st Egg) (weeks)	23.8	1.7	25.1	1.5
Laying House Mortality (per cent)	5.4	-	14.3	-

The deficit in egg size in the resultant strain-cross is clearly reflected in the average egg grading results for the strain-cross under test with other commercial entries (Table 3). These relatively unsatisfactory grading results gave a sound practical reason for the decision reached to initiate an experiment which partly aimed at selecting for improved egg size.

The information in Table 2 does not strictly allow a direct comparison in the performance of the two strains because they were not contemporaneous, nor housed together. Strain 2, however, would appear to have the slightly heavier body weight, higher mean egg weight and lower laying house mortality. The advantage in Strain 2 of almost two weeks' earlier average age at first egg is not an apparent intrinsic difference between the two strains, but was attributable to variation in the light pattern experienced by the winter/spring hatched strain (Strain 2) compared to the autumn hatched strain (Strain 5) when reared and housed in windowed quarters. Taking this environmental difference into account, there would not appear to be much between the strains as regards egg laying ability; mean percentage hen-day production being more or less identical for the two populations.

Of particular value in the selection experiment to be undertaken was the existence of reasonably precise estimates of the genetic parameters within the populations prior to the initiation of selection (Clayton and Robertson, 1966). These are reproduced in Tables 4 and 5 and were consulted in later computations involving the prediction of selection responses referred to later in this thesis. These estimates had particular merit in that they had been derived within 2 random-bred populations which had undergone no intentional selection for any specific trait over several generations.

TABLE 3

Average egg gradings of strain-cross entry

(National Poultry Tests Limited
1965-66 random sample egg production test)

	Percentage of eggs laid:			
	"Large"	"Standard"	"Medium"	"Small"
7th month	2.2 (2.2)	6.5 (17.9)	59.1 (61.3)	22.8 (13.7)
8th "	1.6 (2.9)	31.6 (52.6)	61.2 (41.6)	-
10th "	8.2 (17.2)	64.2 (64.5)	19.8 (10.9)	-
11th "	20.5 (34.0)	62.7 (53.8)	8.6 (4.4)	-

( ) = Average gradings for all commercial entries

TABLE 4

Genetic parameters of principal performance traits (Strain 2)*

	Body Weight			Egg Weight		Egg Nos. (Part Record)	Sexual Maturity
	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks	20-44 weeks	(Age 1st Egg)
h^2	Genetic Correlations (r_g)						
Body Weight:							
12 weeks	0.50	0.65	0.55	0.19	0.17	0.11	-0.38
28 weeks		0.46	0.91	0.31	0.25	0.03	-0.01
44 weeks			0.43	0.33	0.25	0.02	-0.07
Egg Weight:							
28 weeks				0.49	0.95	-0.24	0.11
44 weeks					0.53	-0.27	0.12
Egg Numbers: (Part Record)							
20-44 weeks						0.27	-0.60
Sexual Maturity: (Age 1st Egg)							0.27
σ_p	g. 94	g. 163	g. 204	g. 3.2	g. 3.5	eggs 10.0	wk. 1.7

*After Clayton and Robertson (1966)

All correlations and heritabilities based on joint sire and dam components of variance and covariance

TABLE 5

Genetic parameters of principal performance traits (Strain 5)*

	Body Weight			Egg Weight		Egg Nos. (Part Record)	Sexual Maturity
	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks	20-44 weeks	(Age 1st Egg)
h^2	Genetic Correlations (r_g)						
Body Weight:							
12 weeks	0.66	0.76	0.72	0.41	0.47	0.11	-0.13
28 weeks		0.65	0.94	0.42	0.47	-0.09	0.11
44 weeks			0.58	0.46	0.56	0.13	-0.04
Egg Weight:							
28 weeks				0.50	0.93	-0.08	-0.21
44 weeks					0.52	-0.16	-0.17
Egg Numbers: (Part Record)							
20-44 weeks						0.29	-0.56
Sexual Maturity: (Age 1st Egg)							0.32
σ_p	g.	g.	g.	g.	g.	eggs	wk.
	94	173	212	2.8	3.5	9.5	1.5

*After Clayton and Robertson (1966)

All correlations and heritabilities based on joint sire and dam components of variance and covariance

3.2 Control Populations

The flocks just described not only provided the base populations for the selection study, but were also continued as unselected control populations to assist in the interpretation of genetic change. Any precise check on the agreement between actual and expected response in a selection experiment extending over several years depends upon differentiating clearly between actual genetic and purely environmental trends. This necessitates having some type of unselected control population available with which the selected population(s) can be compared. Control populations have been used for some time in selection studies with laboratory animals, e.g. Drosophila (Robertson, 1955). The virtual absence of any control in selection studies with poultry until recent years may cast some doubt upon some of the conclusions of earlier selection experiments. (See, for example, Pearl and Surface, 1909; Dryden, 1921; Hall, 1934; Lamoreux *et al.*, 1943; Lerner, 1950; Dickerson, 1955). Use of some semblance of a control population, however, has been used in a few selection studies with poultry (Hutt and Cole, 1947; 1953; Skaller, 1956; Abplanalp, 1960; 1962) but in all of these experiments the control populations have been of limited size and usefulness.

The first function of a control population is to serve to assess the magnitude of short-term fluctuations in the environment and to furnish a means of correcting for them. The second and more difficult function to ensure, is the provision of a population which we can safely assume will remain genetically constant between generations. "Relaxed selection" control strains in which there is no deliberate selection have been proposed to provide genetically constant controls (Gowe and Johnson, 1956; Gowe et al., 1959_a) and a randomly mated flock of White Leghorns has been used to interpret results of genetic selection in poultry (Gowe et al., 1959_a; 1963).

On the other hand, King et al. (1959; 1963) have described the maintenance of a pedigreed control population in which an attempt was made to eliminate, as far as practicable, the possibility of natural selection, by reproducing the control strain with breeders carefully chosen to represent the entire breeding structure of the population. This particular population has subsequently been used in selection studies with poultry (Nordskog et al., 1962; 1967; Festing and Nordskog, 1967). Gowe et al., (1959_b) in a paper discussing the design and reliability of control strains for poultry, conclude that the pedigreed flock has sufficient advantage over the random-mated flock, in most circumstances, (by increasing the effective number of parents and minimising natural selection among families) to justify the extra labour involved in maintaining a pedigreed flock.

The control populations within the two strains used in this study were reproduced on a random-bred basis, and since 1965 have been maintained as pedigreed flocks based upon the use of approximately 30 sires and 90 dams annually. Mates were assigned, with the exception of the avoidance of any full-sib matings, at random; 3 females being allocated to each male. In choosing the breeding individuals each season, some effort was made to ensure that each sire in the previous set of parents contributed 1 male to the current list of breeders and, similarly, 1 female parent was chosen at random, as far as possible from the group of female progeny surviving from each dam in the previous generation. Sufficient progeny (3 males and 5-6 females) were hatched from each mating, the aim being that each female parent would have one daughter alive and laying eggs and each male parent would have one son alive and producing semen at the time breeding of the subsequent generation took place.

No conscious selection was made of highly reproductive females when arranging the matings each season, although occasional hens which had been selected at random and were found to be non-layers were replaced. Artificial insemination was used to effect the matings from the 1965 hatching season onwards to ensure, as far as possible, that each female was fertile and contributed progeny to the next generation. On average, less than 8 per cent of the female parents produced no surviving progeny, while only 3 sires in 5 years failed to contribute any progeny surviving to breeding age. If all the progeny of one family were missing due to low fertility, poor hatchability or heavy mortality, the number of males and females mated each generation was maintained at close to 30 males and 90 females by randomly choosing from amongst the flock, avoiding selecting more than 2 full-sibs from each half-sib family group in the case of females, and for males avoiding full-sibs completely and more than 2 half-sibs. Both the amount of genetic drift and the degree of inbreeding resulting in any closed population is normally determined by considering the effective number of parents (Ne) for the population (Crow, 1954;

Crow and Morton, 1955). In a random breeding population with M males and F females the effective number of parents is given by:-

$$\frac{1}{Ne} = \frac{1}{4M} + \frac{1}{4F} \qquad \text{(Wright, 1940)}$$

where M and F are the effective number of sires and dams, i.e. the number with progeny surviving to breeding age.

In the case of a pedigreed control flock, however, the effective number of parents can be calculated from the formula:-

$$\frac{1}{Ne} = \frac{3}{16(M)} + \frac{1}{16(F)} \qquad \text{(Gowe al 1959}_b\text{)}$$

Thus, for the flock structure described above:-

$$\frac{1}{Ne} = \frac{3}{16(30)} + \frac{1}{16(90)} = \frac{1}{144}$$

and the expected increase in the inbreeding coefficient (F) per generation is given by the formula:-

$$\triangle F = \frac{1}{2Ne}$$

$$= \frac{1}{2(144)} = 0.35 \text{ per cent per generation}$$

(or 1.75 per cent over 5 generations)

3.3 Selection Procedures

The selection procedures examined in this study have comprised the following:-

3.3 . 1 Deviation from Regression

Selection for maximum positive values in the deviations from the average genetic regression of egg weight on body weight using an index of the form:-

$$I = \text{Egg Weight } (E) - b. \text{ Body Weight } (W)$$

where 'b' is the calculated value for the slope of the linear genetic regression of egg weight on body weight.

The deviation from regression selection was directed towards exploiting the variation in egg weight which was independent of the covariation with body weight, by using the linear regression line as a base line for selection of individuals showing the greatest deviation above the line. A similar approach has been successfully employed by Cockrem (1959) in selecting for large body size but short tail length in mice, normally assumed to be incompatible. These two characteristics in the mouse are more strongly correlated genetically ($r_g = + 0.6$) than the two traits considered in this study.

An earlier study had estimated the genetic parameters within the flocks used in this experiment and found the genetic correlation between body weight and egg weight to be + 0.3 - 0.4 (Clayton and Robertson, 1966). This estimate would imply that only between 9-16 per cent of the genetic variance in egg weight is attributable to the genetic regression of egg weight on body weight. In view of the fact that around 50 per cent additive genetic variance remains in egg weight, sufficient usable independent genetic variance should exist to allow of a significant increase in egg weight, while avoiding a correlated increase in body weight through the action of positively acting pleiotropic genes.

The genetic regression constant (b) of 28 week egg weight (E) on 28 week body weight (W) was calculated using the appropriate genetic variance and covariance from twice the pooled joint sire and dam components of variance and covariance within the two strains for the three years that the strains were random-bred (Table 6).

$$\text{i.e.}\quad b = \frac{\mathrm{Cov}_g\ E.W}{V_g\ W} = 0.061 \qquad \underline{\hspace{4cm}}\ (1)$$

There was little difference between Strain 2 and Strain 5 in the actual value calculated for the regression constant and, in fact, a common factor of 0.061 was used throughout in calculating the index values.

TABLE 6

Combined estimates of the parameters for 28 week body weight and egg weight used in computations involving the index or ratio traits

	Strain 2		Strain 5	
	28 week Body Weight	28 week Egg Weight	28 week Body Weight	28 week Egg Weight
$\overline{X}$	180.49 Dg.	48.29 g.	186.52 Dg.	45.38 g.
V_g 2(S + D)	122.44	4.92	200.43	4.10
V_p (S + D + I)	267.30	10.13	303.05	8.31
h^2	0.49	0.50	0.65	0.50
Cov_g 2(S + D)	7.60		12.05	
Cov_p (S + D + I)	10.82		14.24	
r_p	0.2		0.3	
r_g	0.3		0.4	

The genetic covariance of the index (I) with the component body weight trait (W) will be zero and so body weight should remain unchanged by selecting on the index (Purser, 1960), although egg weight (E) will be increased by almost as much as selection for egg weight alone.

The genetic variance for the index itself can be calculated using the formula:-

$$V_gI = V_gE \left[1 - r^2_g \right] \qquad (2)$$

while the corresponding derivation for the phenotypic variance is:-

$$V_pI = V_pE \left[1 + r^2_g . \frac{h^2_E}{h^2_W} - 2r_g . r_p . \frac{h_E}{h_W} \right] \qquad (3)$$

Thus the heritability for the index itself can be readily calculated as:-

$$h^2_I = \frac{V_gI}{V_pI}$$

The relative efficiency of the index as a means of improving egg weight, compared with selection for egg weight alone, can be computed using the formula suggested by Searle, 1965:-

Relative Selection Efficiency (R.S.E.) $= \dfrac{1 - r_g^2}{\sqrt{1 - 2r_p . P + P^2}}$, where r_g = genetic correlation

r_p = phenotypic correlation

$P = r_g . \sqrt{\dfrac{h^2_E}{h^2_W}}$

The genetic covariance of the index with egg weight, knowing the genetic variance for egg weight and its covariance with body weight, is derived thus:-

$$\text{Cov}_g\ E.I = V_gE - b\ \text{Cov}_g\ W.E \qquad (4)$$

from which the genetic correlation of index values with egg weight can be estimated:-

$$r_g = \frac{\text{Cov}_g\ E.I}{\sqrt{V_gE.\ V_gI}}$$

TABLE 7

Heritability of index, $I = E - (b)\ W$, its genetic correlation (r_g) with 28 week egg weight and its relative selection efficiency (R.S.E.)

	h^2	r_g	R.S.E.
Strain 2	0.44	0.95	0.91
Strain 5	0.42	0.85	0.84

Calculations using the above formulae and based upon the information included in Table 6 produced the estimates given in Table 7. The heritability of the index in both strains is only slightly less than the heritability value for egg weight itself, while the efficiency of selection for the index was calculated to be 0.91 times as efficient for Strain 2 (0.84 times for Strain 5) compared with selection for egg weight alone; a small loss in efficiency, presumably, considering the potential advantage of maintaining body weight constant.

3.3.2 Ratio Selection

Turner (1959) has previously discussed the use of a ratio as a means of improving the efficiency of selection in breeding for fleece weight per unit of body size in sheep and has presented formulae to derive the heritability of the ratio itself or the correlation of the ratio to its component traits. Robertson (unpublished), however, has suggested a simpler method of deriving these estimates directly from the variance and covariance of the component traits forming the ratio.

Taking any two traits, A and B, then the variances (genetic or phenotypic) of the ratio (r) of $\frac{A}{B}$ are derived thus:-

In logs, $\log \frac{A}{B} = \log A - \log B$

Let $r = \frac{A}{B}$, then $\frac{\delta r}{\bar{r}} = \frac{\delta A}{\bar{A}} - \frac{\delta B}{\bar{B}}$

Squaring $\frac{Vr}{\bar{r}^2} = \frac{VA}{\bar{A}^2} + \frac{VB}{\bar{B}^2} - \frac{2.\text{Cov. } A.B}{\bar{A}.\bar{B}}$

$$\text{Therefore } V_r = \bar{r}^2 \left[\frac{VA}{\bar{A}^2} + \frac{VB}{\bar{B}^2} - \frac{2.\text{Cov. } A.B}{\bar{A}.\bar{B}} \right] \text{ ——— } (5)$$

Knowing the genetic and phenotypic variances, the heritability $(\frac{V_g}{V_p})$ can easily be obtained.

Similarly, the genetic correlation of the ratio with any other trait can be obtained by first deriving the appropriate covariance.

Since $\frac{\text{Cov. }(X.r)}{\bar{r}} = \frac{\text{Cov. }(X.A)}{\bar{A}} - \frac{\text{Cov. }(X.B)}{\bar{B}}$

$$\text{Therefore Cov. }(X.r) = \bar{r} \left[\frac{\text{Cov. }(X.A)}{\bar{A}} - \frac{\text{Cov. }(X.B)}{\bar{B}} \right] \text{ ——— } (6)$$

The genetic correlation (r_G) is then a straightforward estimate:-

$$r_G\ (X.r) = \frac{\mathrm{Cov}_g\ (X.r)}{\sqrt{V_g X.\ V_g r}}$$

The heritability of the ratio and its genetic correlation with the two traits comprising the ratio were calculated for each strain and are detailed in Table 8.

TABLE 8

Heritabilities and genetic correlations of
body weight (BW), egg weight (EW) and of
the ratio $\frac{EW}{BW}$ in Strain 2 (S2) and Strain 5 (S5)*

	BW (12 weeks)	BW (28 weeks)	EW (28 weeks)	$\frac{EW}{BW}$ (28 weeks)
	h^2	Genetic correlations r_g		
BW (12 weeks)	S2 0.50 S5 0.66	+0.65	+0.19	-0.50
BW (28 weeks)	+0.76	S2 0.46 S5 0.65	+0.31	-0.73
EW (28 weeks)	+0.41	+0.42	S2 0.49 S5 0.50	+0.41
$\frac{EW}{BW}$ (28 weeks)	-0.55	-0.81	+0.18	S2 0.41 S5 0.52

Genetic correlations r_g

*Estimates for Strain 2 lie above the diagonal,
those for Strain 5 below the diagonal

Heritability of the ratio is only 0.86 times the heritability of egg weight in the case of Strain 2 and 0.78 in the case of Strain 5. Selection on the basis of a ratio of EW/BW should increase egg weight, but the rate of progress will only be about 0.2 times for Strain 5 and 0.4 times for Strain 2 that obtained following direct selection for egg weight.

However, as can be noted from the magnitude of the negative genetic correlations between the ratio and body weight, selection on the basis of a ratio should result at the same time in a substantial decrease in body weight. The importance of such a substantial decrease in body weight must await a closer assessment first of all of the relationship of body weight to reproductive performance and to viability. However, a significant decrease in body weight ought to confer a useful advantage because of a reduction in the food required for body maintenance.

3.4 Experimental Procedure

The programme of selection started in earnest with the 1963 hatches with the establishment of four distinct sub-lines within both populations of Strain 2 and Strain 5. These comprised:-

1. Selection for increased egg weight at 28 weeks of age, which will be referred to hereafter as the Egg Weight line.
2. Selection for positive deviations from the average genetic regression of 28 week egg weight on body weight, as described earlier, and subsequently referred to as the Regression line.
3. Selection for maximum values of the $\frac{EW}{BW}$ ratio or Ratio selection.
4. Selection for decreased body weight at 12 weeks of age, i.e. Body Weight line

The purpose of including the Large Egg Weight and Small Body Weight selection lines was to observe the magnitude of the actual correlated responses following selection for increased egg weight and decreased body weight and to compare the response in the primary traits with the responses obtained in the Regression and Ratio lines.

The Egg Weight and Body Weight lines had, in fact, been initiated the previous season by mating the same 30-35 males used to propagate the random-bred population each to 2 additional females; one selected for maximum egg weight, the other for minimum body weight from within the base population. Thus, both these lines have undergone one additional generation of mild selection as compared with the Ratio and Regression lines.

Each selection line was reproduced annually from 10-15 selected males on average per generation, each mated to 4 selected females, making a total of between 40-60 female parents.

A maximum of 6-7 pullet chicks and 3 males from each mating were wing-banded at hatching as far as possible. Because of restricted accommodation in the laying house, a small proportion of the pullets pedigreed was discarded at random within each group on transferring the birds to individual bird cages just prior to point-of-lay.

Of the 3 male progeny in each full-sib family that were pedigreed at hatching, 2 were retained, as far as possible, up to the stage at which selection decisions were available. These numbers should have allowed a selection intensity of approximately 1 in 8 on the male side, compared with about 1 in 4 on the female side.

The actual basis of selection was standardised for all lines. Males were selected on their sister's family average (sib selection), i.e. the male's own body weight was disregarded in reaching a selection decision, since naturally no comparable information was available in selection involving the egg weight trait. Since each family group contained a variable number of individuals, both overall as well as within any one hatch group, the average performance of a group of female full sibs was expressed as their average deviation from the respective hatch mean within each line. The average deviation was then weighted according to the total number of individuals, the weighting factor used corresponding to the weighting used to calculate the heritability of family means, $\frac{0.5\ n}{1 + (n - 1)\ t}$, Falconer (1960), 'n' being the number of full sisters in the full-sib group and 't' the phenotypic correlation between full sisters. The appropriate value for the latter was calculated from the average of the variance components for the traits involved as determined by Clayton and Robertson (1966). (See Table 9).

In the special case of computation for the ratio selection, the full-sib average comprised the average deviation of the individual ratio values from the hatch mean ratio, i.e. a mean of the individual ratios as compared with the ratio of the means (Turner, 1959).

Computation of deviations from the regression and egg weight/body weight ratios was greatly facilitated using an appropriate computer programme.(1)

Female selections within all four selection lines were based solely on their individual value, expressed as a deviation from their respective hatch mean.

At the commencement of the experiment, matings of selected birds were arranged using 40 individual male breeding pens. Because of the limited accommodation it was necessary to mate up only two lines at one time, the

---

(1) The use of a computer programme written by Dr. W. G. Hill, Institute of Animal Genetics, Edinburgh, is gratefully acknowledged.

breeders being replaced by the parents selected to reproduce the remaining two selection lines once collection of fertile eggs for two complete hatches had ceased. The control matings, of course, were kept together for all 4 hatches, although a rota of males was used in the control line breeding pens.

TABLE 9

Phenotypic correlation (t) between full-sibs,
Strain 2 (S2) and Strain 5 (S5)

Trait			Variance Components			$t = \frac{V_S + V_D}{V_S + V_D + V_I}$
			V_S	V_D	V_I	
Body Weight	12 weeks	S2	9.7394	12.6327	66.2176	0.25
		S5	16.0954	13.4401	60.4141	0.33
	28 weeks	S2	19.6264	41.6004	206.0749	0.23
		S5	54.8090	45.4098	202.8358	0.33
Egg Weight	28 weeks	S2	1.1168	1.3477	7.6667	0.24
		S5	0.9439	1.1073	6.2574	0.25

Starting with the 1965 hatches, however, all matings were effected using A.I., which meant that all selection lines could be hatched at the same time, while it was also possible to maintain a fully pedigreed control line.

Four hatches were generally taken off over a 5-6 week period each breeding season. Pedigreed chicks were wing-banded at hatching. All chicks in any one hatch, irrespective of line, were brooded together and reared intermingled in the same windowless intensive rearing house. Hatch groups were penned separately as a batch in littered floor pens. Unfortunately, from the point of view of uniformity in sexual maturity between hatch groups, it was the practice until latterly to rear the birds under a reduced "daylength" pattern, followed by an increasing light regime from point-of-lay onwards in the laying house. Because of the difference in age between the various hatch groups, it proved impossible to provide a lighting pattern similar for all hatch groups. The last hatch taken off was around 6 weeks later than the first batch of chicks hatched and sexual maturity in the earlier hatches tended to be as much as 1-2 weeks later than for the later hatches which experienced a correspondingly more rapid increase in the light pattern they received in the laying quarters. Recent evidence, however, (Proudfoot and Gowe, 1967) has suggested that a constant light pattern of around 14 hours throughout the rearing and laying period is, contrary to previous conclusions, probably as effective a light pattern for maximum egg production. Thus, latterly this set light pattern has been adopted, since it means that all hatch groups, in spite of chronological differences, experience an identical light regime.

Each strain was housed during the laying period in a separate, windowless laying house containing 3 blocks of double-sided, 3 tier, 9 inch wide individual bird battery cages. These provided suitable accommodation for keeping records of individual bird performance. On housing at point-of-lay birds were placed entirely at random in the individual bird cages.

The stock was managed as for any normal commercial flock and fed a medium energy home-mixed layer's ration, latterly of the following composition:-

Composition of Layer's Mash

Ingredient		Cwt. per Ton Mix
Maize		8.75
Wheat		6.00
White Fish Meal		1.00
Meat and Bone Meal		1.00
Soya Bean Meal		0.75
Sunflower Meal		0.75
Dried Grass Meal		0.50
Limestone Grit.	128 lb.	
Salt	5 lb.	
Vitamin + Mineral Premix*	7 lb.	1.25

* Colborn Vitafeeds Limited No. 100

Approximate analyses:	Percentage Crude Protein	16.00 per cent
	Energy (M.E.)	1,287 Cals. per lb.
	Ca	2.95 per cent
	P	0.63 per cent

All pullets on experiment were weighed individually at 12, 28 and 44 weeks of age. The week in which each bird laid its first egg was noted and egg production recorded on 3 days each week from 20 to 60 weeks of age. Faber (1960) and Wheat (1956) have reported a high degree of correlation ($r = 0.96$) between 3 days per week recording and the full production record. For the purposes of analysis the egg record has been considered in two parts: an early egg record up to 44 weeks of age and a subsequent record from 44-60 weeks.

Eggs were weighed at two stages in the laying period, at 28 weeks and 44 weeks of age, and the actual individual egg weight record consisted of the average weight of 3-4 eggs per hen laid within the week following that in which the bird reached the appropriate age.

Since each generation was produced from up to 4 (and on occasion 5) weekly or fortnightly hatches, the data collected on the performance of the experimental population was liable to include variation due to the spread in ages of the birds. This source of variation was first removed as far as possible before carrying out any statistical analyses by expressing all individual records as deviations from their respective hatch average within each line. This method of hatch correction was preferred on account of the particular environmental conditions (stocking density in rearing pens, light pattern, etc.) experienced by particular hatch groups (Skaller, 1954). A number of investigators have published evidence of a genotype interaction between the date of hatch within a given year and performance, notably sexual maturity, at a single location, but it may be questioned whether they are of much significance (Osborne, 1952; 1954; Skaller and Sheldon, 1953). Abplanalp (1956) suggested that they could justifiably be disregarded without impairing efficiency in selection programmes within closed populations.

Individual hen records were excluded from subsequent analyses if the individual had died before completing the period up to 44 weeks of age, or was already ailing. In the case of occasional missing data for a single trait, principally one or other of the egg weight measurements due to a bird not being in lay when eggs were sampled, the overall mean value for the hatch of which the individual bird belonged was inserted instead. This was necessary because the computer programme used in the analysis was not equipped to deal with missing data. Considering the frequency of such missing data, this step would have a negligible effect on the variance for the trait and, of course, would not affect the mean.

Heritabilities and genetic correlations were estimated each generation from the data collected for up to 15 traits in each of the selection lines using a hierarchal analysis of variance and covariance within lines and years (King and Henderson, 1954). These analyses were facilitated by the provision of an appropriate computer programme developed by Dr. B. Woolf(2) and latterly modified by Dr. W. G. Hill for use on a more recent computer system. The estimates to be quoted later in this thesis are those derived by using twice the fraction of the sire and dam variance (Falconer, 1960). Although such estimates are inflated by unknown amounts of non-additive, sex-linked and maternal effects (Kempthorne, 1957) the sampling error is only half as large as that from heritability estimated separately from the sire or dam component.

---

(2) Grateful acknowledgment is made to Dr. Barnet Woolf for the use of his Computer Programme No. 604, B.W. PLA.

4. RESULTS AND DISCUSSION

4.1 Time Trends in Control Populations

The objective in maintaining a random-bred control population for each strain in this study was to provide a means of eliminating environmental, as distinct from genetic, change occurring over several generations of selection. Since the presumed genetic changes occurring within the selected lines are to be discussed subsequently as deviations from these control populations, it is necessary first of all to discuss the performance of the control populations themselves over the period covered by the experiment.

4.1.1 Breeding Structure of Control Populations

The basis for reproducing these control populations has already been discussed and Table 10 summarises the actual number of effective sires and dams, i.e. those parents contributing progeny each generation in maintaining the random-bred populations. With the exception of the 1963 series of matings in both strains and also of the 1964 matings in the case of Strain 2, the progeny were fully pedigreed to both sire and dam. Because of building operations during the 1963-64 seasons, however, it was necessary to reproduce the two populations using a limited number of breeding pens and in these circumstances several males were mated to the same set of females using a shift system. The males were changed weekly and, because hatching eggs were collected continuously from the breeding pens, it was only possible to pedigree to the dam. The total number of males placed in the breeding pens, however, is given in Table 10, but whether they actually contributed progeny to the subsequent generation is unfortunately impossible to say with certainty. The effective number of parents (Ne) each generation is also included in Table 10. In the case of the fully pedigreed generation this latter parameter was estimated using the formula given by Gowe, et al. (1959_b) and is governed by the least numerous sex, in this instance the number of males, in the parental population.

The aim with both control flocks at the outset was to assign 30 males at random to 90 females. Slightly more males were, in fact, used on occasion. Using the calculated figure for the effective number of parents it is possible to predict the anticipated increase in the average inbreeding coefficient within the control population. The anticipated inbreeding amounts to 0.48 per cent per generation, or between 2.3 and 2.4 per cent over the 5 generations that each flock has been reproduced.

It has been assumed in all of these calculations that all parents did contribute equally to the set of parents in the subsequent generation, which was not necessarily true. The effect of differential mortality is likely to have been small however. Over the 5-year period that these control populations were maintained, only 3 males in the case of Strain 5, and none in the case of Strain 2, failed to contribute any progeny to the subsequent parental population.

More female progeny were normally hatched from the control line

TABLE 10

Effective number of breeding individuals and effective number of parents (Ne) in control lines throughout 5 generations of selection experiment

Strain 2

Generation	Year	Number of Parents M	F	Ne	△ F**
0	1962-63	35	124	172	0.0029
1	1963-64	(80)	29	85*	0.0059
2	1964-65	(70)	42	105*	0.0048
3	1965-66	32	82	154	0.0032
4	1966-67	32	77	150	0.0033
5	1967-68	33	85	154	0.0033
				Total	0.023

Strain 5

Generation	Year	Number of Parents M	F	Ne	△ F**
0	1962-63	35	100	170	0.0029
1	1963-64	(80)	30	87*	0.0057
2	1964-65	20	54	95	0.0053
3	1965-66	34	92	161	0.0031
4	1966-67	29	67	135	0.0037
5	1967-68	30	82	144	0.0035
				Total	0.024

$\frac{1}{Ne} = \frac{3}{16M} + \frac{1}{16F}$ (Gowe <u>et</u> <u>al</u>. 1959_b)

* $\frac{1}{Ne} = \frac{1}{4M} + \frac{1}{4F}$ (Wright, 1940)

** $\triangle F = \frac{1}{2Ne}$

( ) = Total number of males placed in breeding pens, but not necessarily effective matings than were actually required to serve as a control group in the laying house. Table 11 lists the number of pullets hatched annually within both populations and the number subsequently housed along with the selected populations in the laying house. On housing a sample of birds from the control line no selection of birds was made, although some attempt was made to equalise, as far as possible, the number housed from the various family groups, in addition to attempting to provide a total of between 50 to 60 pullets as a control group within each hatch. Mortality in the laying house up to breeding age was moderate, with the exception of one season only in both strains when mortality was over 10 per cent. (Table 11).

In so far as the assumed genetic changes effected within the selection lines will be referred to later in terms of deviations from the control populations, the overall trends in performance of the random-bred populations over the 5-year period will be examined in some detail.

4.1.2 Changes in Mean Performance of Control Lines

Clayton and Robertson (1966) when reporting the earlier performance of these populations commented upon how these strains had reacted to the continued relaxation of any conscious selection pressure. Table 12 presents some data on the mean performance since 1960 for Strain 2 through the 5-year period up to 1968 covered by this particular study. Table 13 presents similar data for Strain 5. Casual examination of

TABLE 11

Numbers of Control line female progeny housed and recorded

Strain 2

Year	Pedigreed	Housed	Number with complete records	% Mortality to breeding age
1963-64	233	149	138	7.4
1964-65	259	229	205	10.5
1965-66	485	310	292	5.8
1966-67	318	271	261	3.7
1967-68	348	250	243	2.8
Overall Totals	1,643	1,209	1,139	

Strain 5

Year	Pedigreed	Housed	Number with complete records	% Mortality to breeding age
1963-64	286	268	215	12.9
1964-65	146	136	130	4.4
1965-66	347	311	298	4.2
1966-67	257	243	230	5.3
1967-68	296	274	254	6.9
Overall Totals	1,332	1,232	1,127	

TABLE 12

Performance of Strain 2 Control Population
1960-1968
(Means of pullets recorded)

Year	n	Body Weight	Egg Weight	Age 1st Egg	Egg Numbers*		
		44 wks.	44 wks.	wks.	20-44 wks.	44-60 wks.	20-60 wks.
1960-61	908	2,056	57.7	24.7	103.8	-	-
1961-62	915	1,949	56.1	23.3	109.9	-	-
1962-63	799	2,141	57.7	23.5	111.5	-	-
1963-64	138	1,997	56.2	23.2	117.6	-	-
1964-65	205	2,019	57.3	24.9	102.9	65.1	168.0
1965-66	292	2,048	57.9	24.7	104.0	60.4	164.4
1966-67	261	2,210	60.0	24.2	105.2	74.6	179.8
1967-68	243	2,101	58.4	23.9	110.4	64.9	175.3

* Estimated by multiplying the 3 days per week record by a fraction x $\frac{7}{3}$

TABLE 13

Performance of Strain 5 Control Population
1960–1968
(Means of pullets recorded)

Year	n	Body Weight	Egg Weight	Age 1st Egg		Egg Numbers*	
		44 wks.	44 wks.	wks.	20–44 wks.	44–60 wks.	20–60 wks.
1960–61	848	1,962	53.7	24.6	104.7	–	–
1961–62	785	2,005	52.9	25.2	101.2	–	–
1962–63	591	2,017	52.6	25.6	97.3	–	–
1963–64	215	1,820	55.3	25.6	95.9	58.5	154.4
1964–65	130	1,901	53.8	23.9	108.9	54.6	163.5
1965–66	298	1,954	55.4	25.7	105.2	67.2	172.4
1966–67	230	2,062	56.7	24.4	113.1	61.1	174.2
1967–68	254	2,060	57.4	23.9	107.3	65.8	173.1

* Estimated by multiplying the 3 days per week record by a fraction x $\frac{7}{3}$

these figures would suggest that there has been no depression in any of the principal traits over the 8-year period and that the strains have sustained the same potential for egg production. Mean body weight and egg weight have, if anything, increased, no doubt as a result of an improving environment in the laying house, rather than on account of any genetic change.

Figures 1 to 6 present the trends in the mean performance of both control populations in graphical form for each of two measures of body weight, egg weight and egg production for the specific 5-year period under review. The average regression over this period was calculated for each recorded trait and the values for the regression coefficients are summarised in Table 14.

(i) Strain 2

Body weight, whether measured at 12 or 28 weeks (Figure 1) has shown some fluctuation between years, but these fluctuations appear to follow the same pattern at both ages. There is an indication also of an overall upward trend in body weight which is not significant, however, when considering 12 week body weight, but is significant for body weight at 28 weeks and 44 weeks.

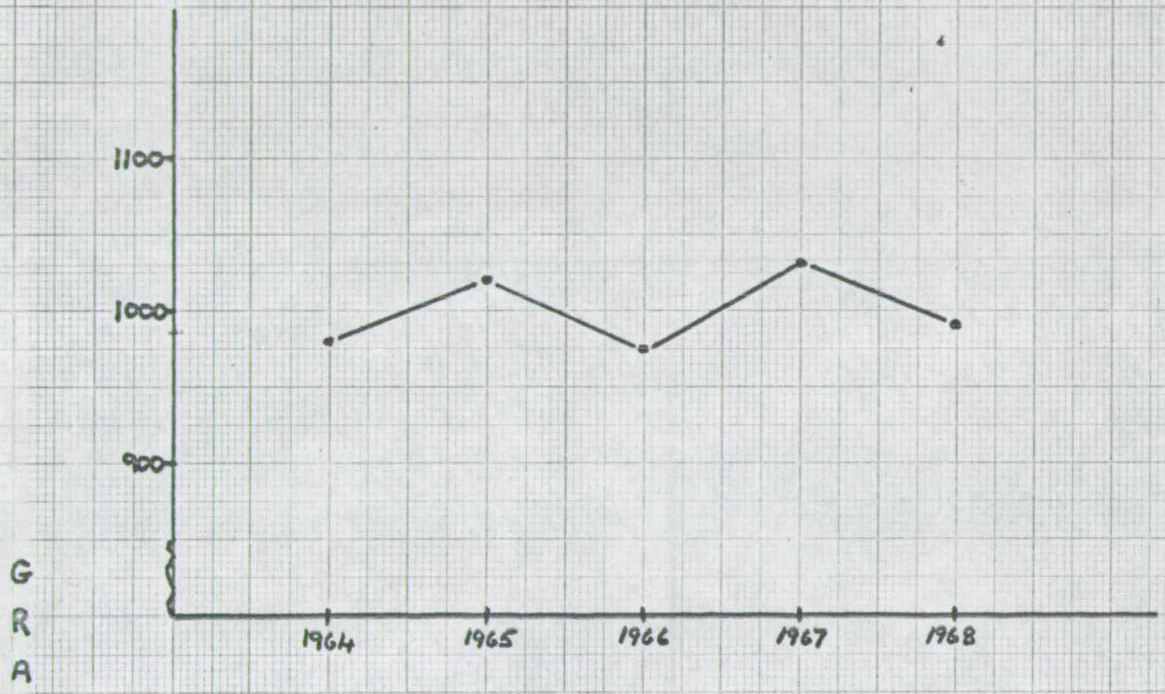
Egg weights (Figure 2) have also shown an upward trend over the 5-year period and the positive regression is significant, both for 28 week and 44 week egg weight. The egg weight measurement has, at the same time, shown less yearly fluctuation in contrast to body weight which has tended to fluctuate more, particularly the 12 week weight

Fig 1

TIME TRENDS IN CONTROL POPULATION, STRAIN 2
1963/64 - 1968

a) BODY WEIGHT

(i) <u>12 WEEKS.</u>



(ii) <u>28 WEEKS</u>

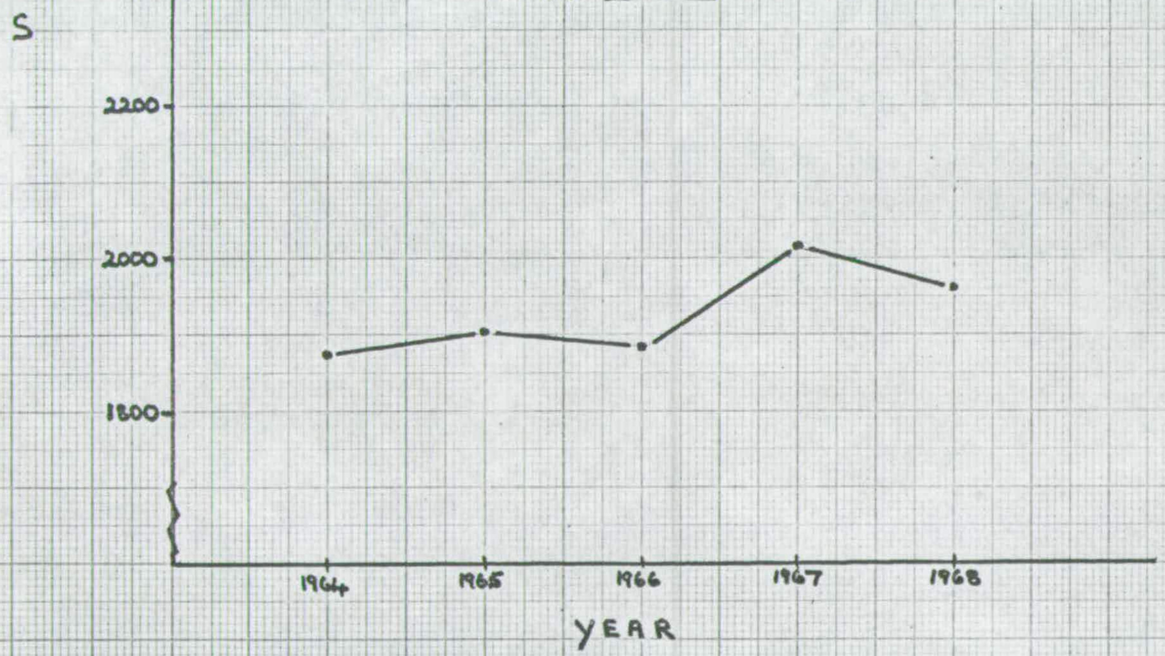
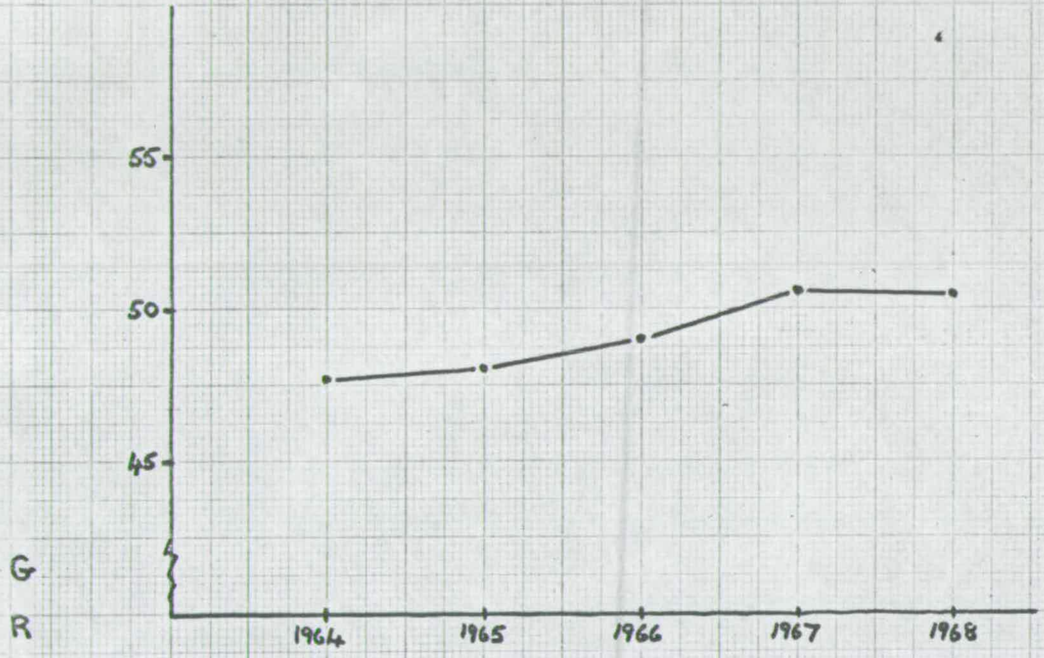


FIG 2

TIME TRENDS IN CONTROL POPULATION, STRAIN 2
1963/64 – 1968

b) EGG WEIGHT

(i) 28 WEEKS



(ii) 44 WEEKS

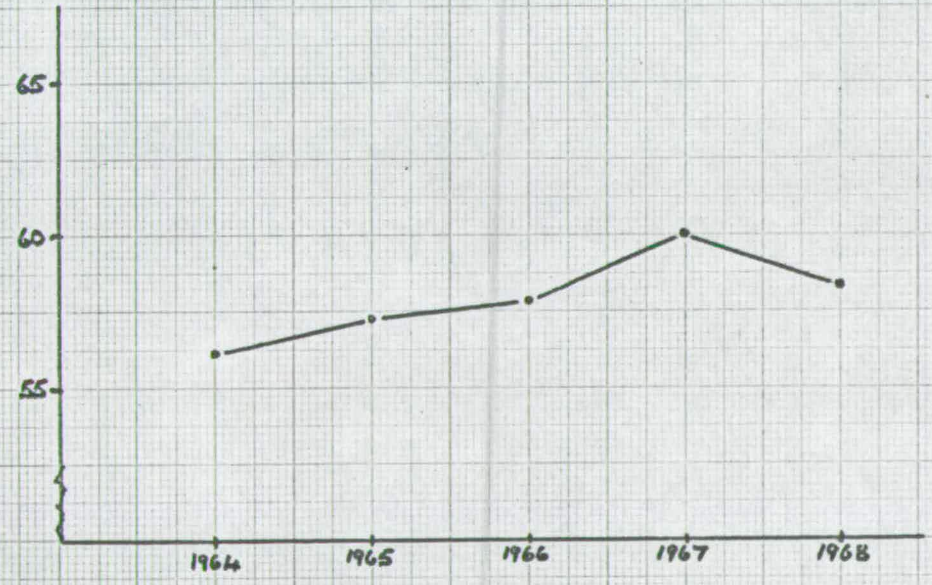


TABLE 14

Calculated average annual regression in performance
of Control Strains over five years, 1963-1968

		Strain 2			Strain 5		
		b	s.e. of b		b	s.e. of b	
Body Weight							
12 weeks	g.	+ 7.9	±13.12	N.S.	+ 9.3	±6.78	N.S.
28 weeks	g.	+30.7	±12.32	*	+46.4	±9.76	**
44 weeks	g.	+39.9	±18.02	*	+63.9	±7.76	***
Egg Weight							
28 weeks	g.	+0.81	± 0.13	***	+0.69	±0.11	***
44 weeks	g.	+0.71	± 0.27	*	+0.71	±0.26	*
Age 1st Egg	wk.	+0.07	± 0.21	N.S.	-0.53	±0.24	N.S.
Egg Numbers							
(Part Record)							
20-44 weeks	eggs	-0.52	± 0.78	N.S.	+1.19	±0.65	N.S.
44-60 weeks	eggs	+0.58	± 1.10	N.S.	+0.91	±0.55	N.S.

N.S. = Value for b is not significantly different from zero

* = b is significantly different from zero at 90% level; 3 d.f.

** = b is significantly different from zero at 95% level; "

*** = b is significantly different from zero at 99% level; "

which was possibly most affected by seasonal environmental conditions.

In contrast, egg numbers (Figure 3) show no consistent trend. The early part record for the period 20-44 weeks, for example, has shown a slight downward trend, but egg production over the later period has increased slightly, although neither trend is statistically significant. Sexual maturity (age at first egg), although not graphed, has also shown no indication of any significant overall trend.

(ii) Strain 5

Broadly, the same trends are reflected in the performance of the Strain 5 control population with an upward and significant trend in 28 and 44 week body weight, but not 12 week body weight (Figure 4) and a highly significant upward trend in 28 week and 44 week egg weight (Figure 5).

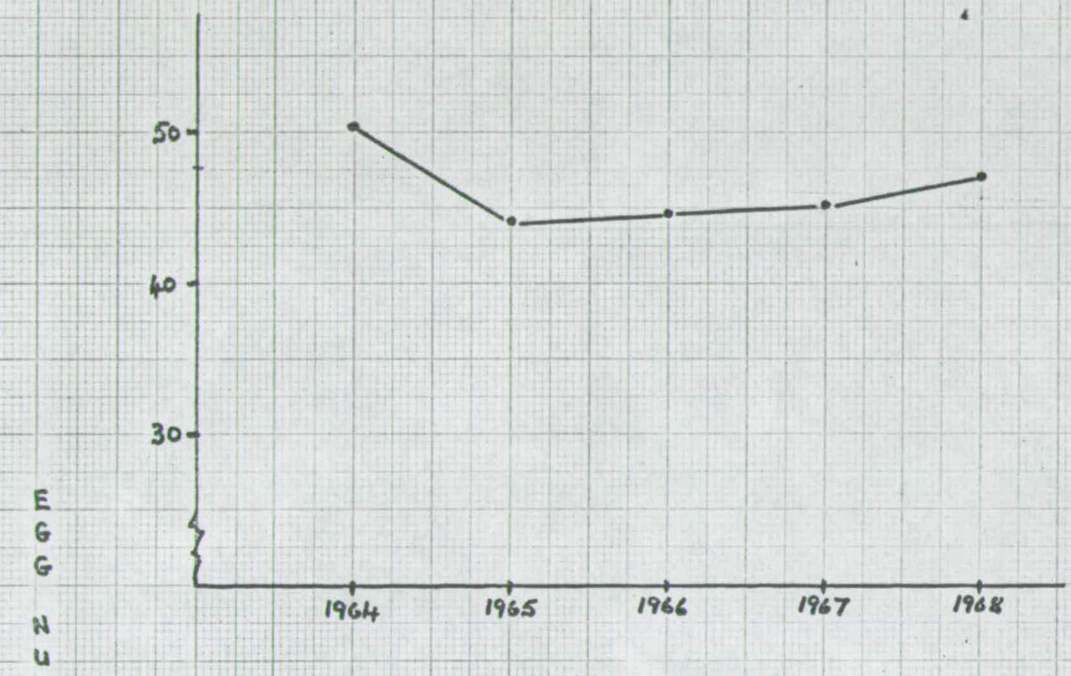
While a positive trend in both the early and late egg production record is indicated, in neither case are the regression coefficients significant. In contrast to Strain 2, the autumn reared control population in Strain 5 has shown a trend towards earlier sexual maturity (negative regression in age at first egg). This is explicable presumably on account of the housing of both strains latterly under windowless conditions enabling the use of a non-seasonal artificial light pattern, which meant that the latter strain could be subjected to an increasing light pattern at point of lay in common with Strain 2 reared in the spring. The overall trend towards earlier sexual maturity, while marked, just fails to reach significance at the 90 per cent level.

Fig 3

TIME TRENDS IN CONTROL POPULATION, STRAIN 2
1963/64 - 1968

c) EGG NUMBERS (PART RECORD)

(i) 20-44 WEEKS



(ii) 44-60 WEEKS

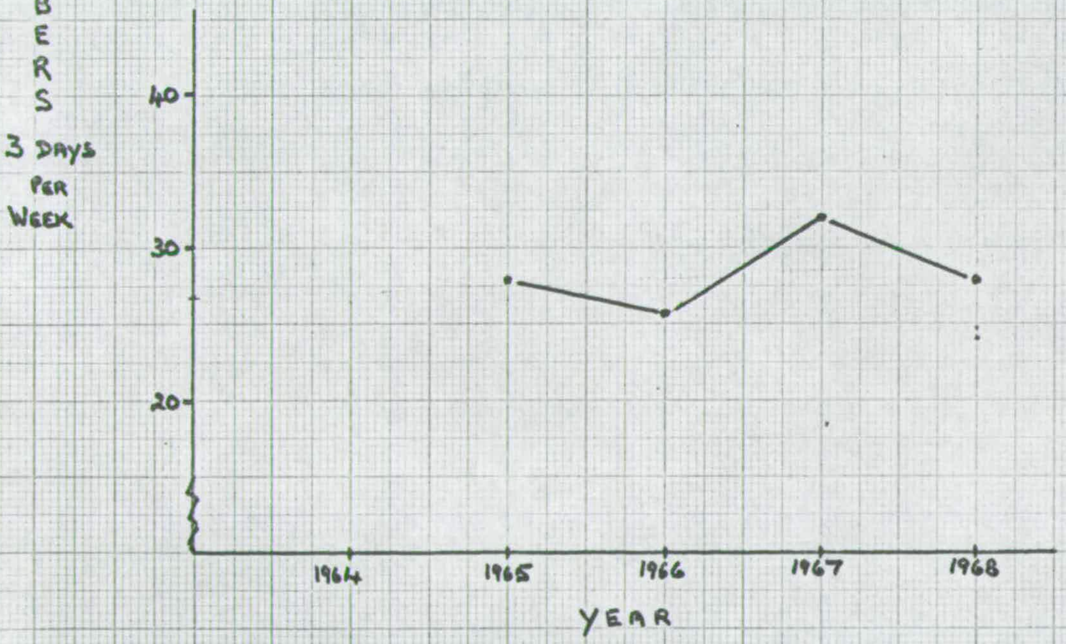
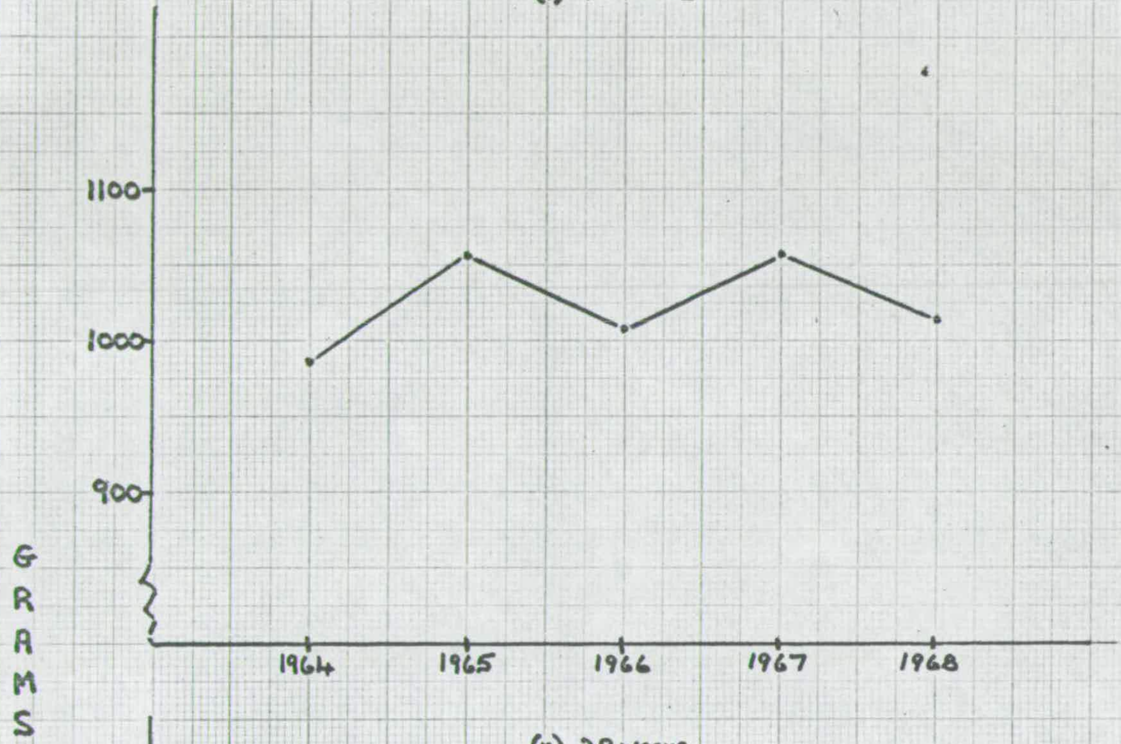


Fig 4

TIME TRENDS IN CONTROL POPULATION, STRAIN 5
1963/64 - 1968

a) BODY WEIGHT

(i) 12 WEEKS



(ii) 28 WEEKS

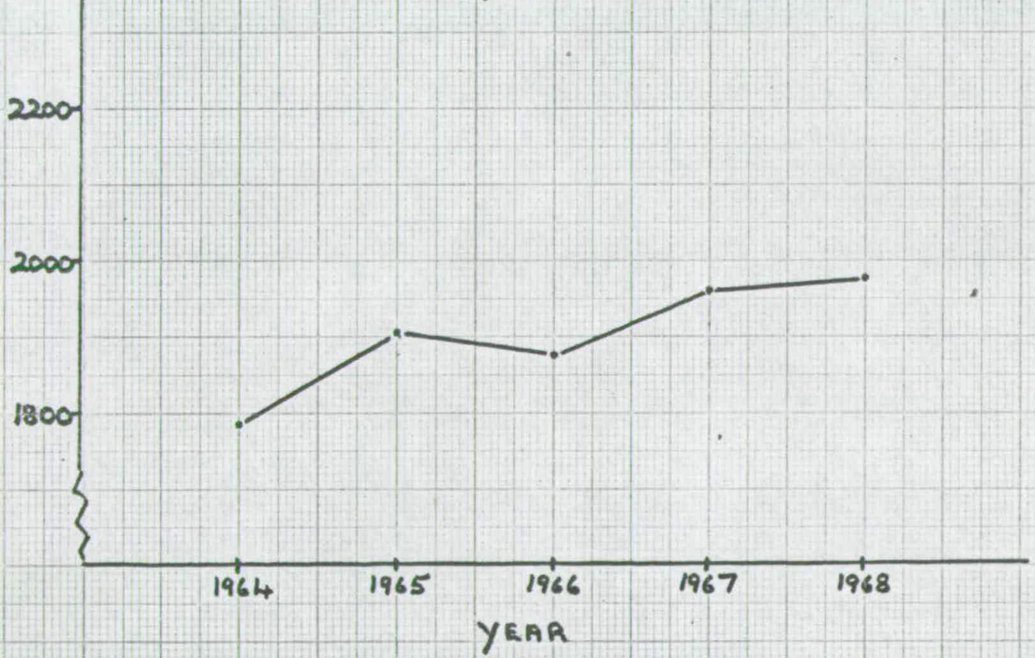
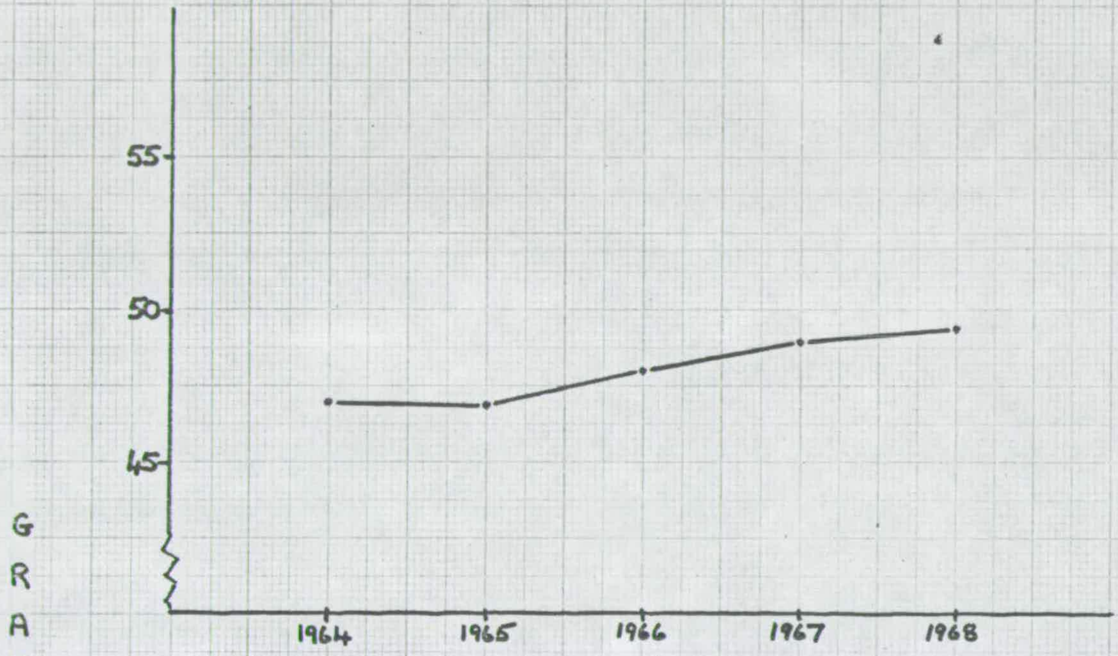


Fig 5

TIME TRENDS IN CONTROL POPULATION, STRAIN 5
1963/64 - 1968

b) EGG WEIGHT

(i) 28 WEEKS



(ii) 44 WEEKS

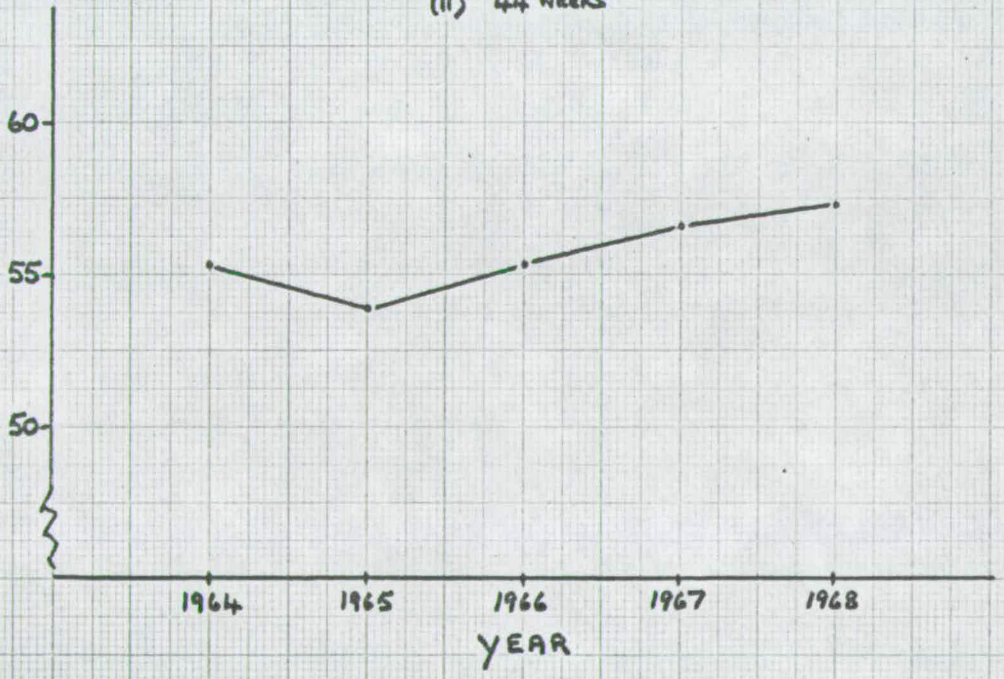
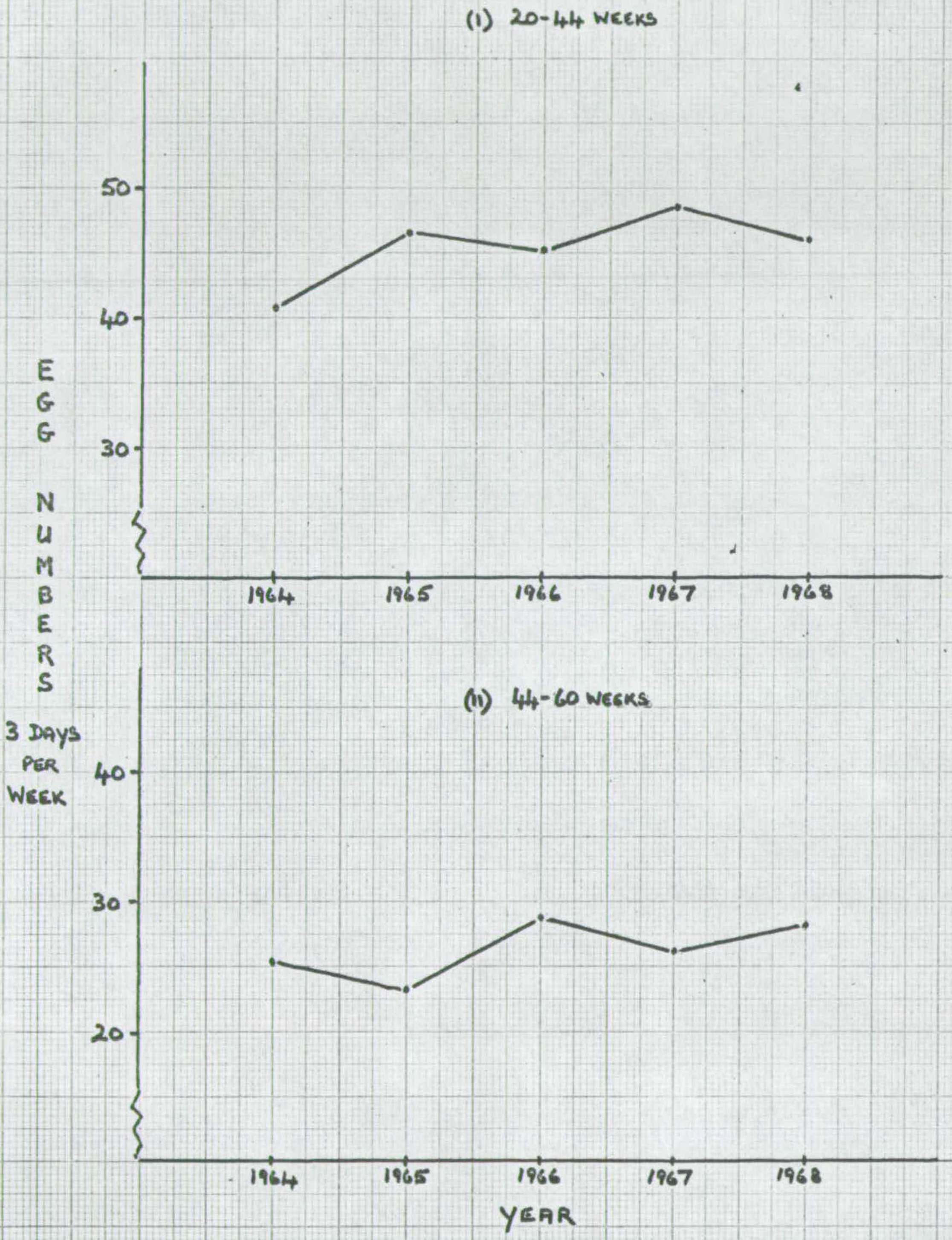


Fig 6

TIME TRENDS IN CONTROL POPULATION, STRAIN 5
1963/64 - 1968

c) EGG NUMBERS (PART RECORD)



4.1.3 Estimates of Genetic Parameters within Control Populations

Obvious changes in the estimates of the genetic parameters over a period of years might indicate whether any genetic changes have taken place in a control population due to natural selection, genetic drift or inbreeding.

Tables 15 and 16 summarise the estimates of the phenotypic standard deviations, heritabilities and genetic correlations within both control populations over the last 3 years that these populations have been maintained. The heritabilities and genetic correlations were computed from the joint sire and dam components of variance and covariance and, as would be expected, were subject to very large sampling errors on account of the relatively small population sizes.

It is difficult to distinguish any consistent or meaningful trends, however, in these parameters. The standard deviation for body weight appears to have increased latterly, compared with the variability noted in the base population for both strains. This also appears to be the case for egg weight in Strain 5. In spite of the increase in phenotypic variance in these traits, however, the heritability has not declined. In fact, the heritability of body weight and egg weight, with the exception of 12 week body weight in Strain 2, has remained very much at the same level as in the base population. The marked decline in the heritability of 12 week body weight and not the later measures of body weight in Strain 2 is difficult to explain, since a reduction in the amount of additive genetic variance at 12 weeks would be expected, on account of the high

TABLE 15

Summary of estimates of heritabilities, genetic correlations and phenotypic standard deviations within the control population, Strain 2, for the last 3 years of random mating

		Body Weight			Egg Weight			Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks	Age 1st Egg	20–44 weeks	44–60 weeks	20–60 weeks
		Genetic Correlations (r_g)								
Body Weight										
12 weeks	(3)	0.15	0.761	0.762	0.489	0.312	−0.611	0.322	0.025	0.184
	(4)	0.56	0.727	0.627	0.151	0.319	−0.617	0.407	−0.230	0.306
	(5)	0.17	0.777	0.362	0.462	−0.227	−0.443	0.596	−0.894	−0.092
28 weeks	(3)		0.52	0.984	0.352	0.469	−0.158	0.439	0.476	0.537
	(4)		0.51	1.000	0.159	0.114	−0.506	0.497	−0.030	0.376
	(5)		0.48	0.885	0.575	0.275	−0.436	0.644	−0.075	0.390
44 weeks	(3)			0.43	0.437	0.528	0.083	0.050	0.271	0.201
	(4)			0.47	0.190	0.037	−0.595	0.481	0.036	0.398
	(5)			0.62	0.616	0.392	−0.190	0.490	0.378	0.543
Egg Weight										
28 weeks	(3)				0.72	1.000	−0.051	−0.169	−0.394	−0.343
	(4)				0.65	1.000	0.014	−0.042	−0.337	−0.234
	(5)				0.40	1.000	−0.167	−0.261	−0.347	−0.357
44 weeks	(3)					0.57	−0.207	−0.121	−0.418	−0.333
	(4)					0.57	−0.409	0.137	−0.432	−0.153
	(5)					0.39	0.185	−0.325	−0.212	−0.350
Age 1st Egg	(3)						0.46	−0.461	0.189	−0.118
	(4)						0.25	−0.802	0.246	−0.474
	(5)						0.24	0.127	0.822	0.559
Egg Numbers (Part Record)										
20–44 weeks	(3)							0.32	0.460	0.819
	(4)							0.26	0.043	0.800
	(5)							0.26	0.325	0.841
44–60 weeks	(3)								0.26	0.886
	(4)								0.11	0.633
	(5)								0.15	0.789
20–60 weeks	(3)									0.29
	(4)									0.13
	(5)									0.18
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(3)	102.6	177.9	239.7	3.00	3.37	1.72	7.96	10.83	15.85
	(4)	90.4	191.9	218.6	2.98	3.51	1.97	6.95	8.37	12.62
	(5)	95.7	189.9	245.3	3.09	3.63	1.27	8.82	8.95	14.83

Degrees of Freedom

(3) Estimates for 1965/66 generation: Sires - 31; Dams - 50; Individuals - 206

(4) Estimates for 1966/67 generation: Sires - 31; Dams - 45; Individuals - 180

(5) Estimates for 1967/68 generation: Sires - 31; Dams - 54; Individuals - 154

TABLE 16

Summary of estimates of heritabilities, genetic correlations and phenotypic standard deviations within the control population, Strain 5, for the last 3 years of random mating

		Body Weight			Egg Weight			Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks	Age 1st Egg	20-44 weeks	44-60 weeks	20-60 weeks
		Genetic Correlations (r_g)								
Body Weight										
12 weeks	(3)	0.68	0.899	0.802	0.657	0.878	-0.170	0.093	-0.140	-0.019
	(4)	0.83	0.970	0.874	0.614	0.744	-0.484	0.209	0.110	0.186
	(5)	0.54	0.857	0.817	0.924	0.676	-0.341	0.029	-0.196	-0.080
28 weeks	(3)		0.65	0.929	0.651	0.745	0.042	-0.127	-0.247	-0.190
	(4)		0.86	0.988	0.682	0.752	-0.286	0.118	0.268	0.202
	(5)		0.54	0.955	1.000	0.739	-0.068	-0.242	-0.448	-0.340
44 weeks	(3)			0.61	0.515	0.487	-0.181	0.141	-0.158	-0.002
	(4)			0.88	0.559	0.672	-0.223	0.059	0.242	0.153
	(5)			0.51	0.739	0.506	-0.128	-0.053	-0.239	-0.123
Egg Weight										
28 weeks	(3)				0.62	0.783	-0.296	0.088	-0.077	0.009
	(4)				0.57	0.887	-0.242	-0.169	-0.219	-0.212
	(5)				0.08	1.000	-0.243	-0.278	-0.965	-0.611
44 weeks	(3)					0.71	-0.146	-0.167	-0.334	-0.255
	(4)					0.65	-0.459	-0.033	-0.115	-0.076
	(5)					0.41	-0.266	-0.183	-0.495	-0.325
Age 1st Egg	(3)						0.77	-0.576	-0.234	-0.425
	(4)						0.72	-0.769	-0.012	-0.499
	(5)						0.48	-0.724	-0.608	-0.679
Egg Numbers										
(Part Record)										
20-44 weeks	(3)							0.65	0.879	0.972
	(4)							0.64	0.610	0.927
	(5)							0.55	0.847	0.963
44-60 weeks	(3)								0.33	0.967
	(4)								0.19	0.863
	(5)								0.37	0.954
20-60 weeks	(3)									0.57
	(4)									0.41
	(5)									0.55
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(3)	119.5	185.7	212.1	2.85	3.90	1.45	7.84	10.13	15.59
	(4)	124.2	207.3	257.8	3.28	4.29	1.49	7.40	9.97	14.52
	(5)	98.7	216.5	241.6	4.08	3.79	2.00	9.66	9.81	17.04

Degrees of Freedom

(3) Estimates for 1965/66 generation: Sires - 33; Dams - 58; Individuals - 203
(4) Estimates for 1966/67 generation: Sires - 28; Dams - 38; Individuals - 160
(5) Estimates for 1967/68 generation: Sires - ; Dams - ; Individuals -

genetic correlations, to lower the heritability of body weight at a later age also.

So far as the general pattern which emerges from the tabled values for the genetic correlations is concerned, the following points may be made:-

(a) The genetic correlations between body weight and egg weight were generally much more strongly positive within the Strain 5 population than in Strain 2, a feature which was also apparent in the base population. The genetic correlation between 28 week body weight and 28 week egg weight, for example, averaged +0.77 for Strain 5, compared with a mean estimate of +0.36 for Strain 2.

(b) The pooled estimates suggest an apparent difference between strains in the direction of the genetic correlation between body weight and egg production. The correlations (see, for example, Table 17) are decidedly positive in Strain 2, but are marginally negative in the case of Strain 5.

This apparent strain difference was not evident between the estimates for the two base populations, but could be very important if these estimates are representative, in view of the relatively large standard errors attached to these estimates. Previous estimates reported for control strains suggested a positive relationship between egg numbers and body weight (Wilson _et al_., 1966; King _et al_., 1963). However, Merritt (1968) stressed the need for further studies to establish whether these relationships can vary as the mean body weight of the strain varies, and he drew attention to the study of a meat-type control strain by Jaap et al. (1962) in which, although they reported a positive correlation of body weight with egg numbers, the realised correlation derived from a selection experiment was negative. Merritt (1968) himself reported the existence of a strong negative genetic correlation between adult body weight and egg numbers in a random-bred control strain of meat-type fowl.

TABLE 17

Comparison between strains in average genetic correlation between body weight (28 weeks) and part record egg production ($r_g S+D$)

Strain	Genetic correlation of 28 week body weight with: Part Record 20-44 weeks	Part Record 44-60 weeks	Total 20-60 weeks
2	+0.53 ±.13*	+0.12 ±.20	+0.43 ±.15
5	-0.08 ±.12	-0.14 ±.14	-0.11 ±.12

* Standard errors computed using the formula given by Robertson (1959)

The estimates included in Tables 15 and 16 involving the post-44 week egg record are, of course, important because the study of the interrelationship of the production traits in the base populations did not include any information for this later period. Firstly, in the case of Strain 2 the average estimate of the heritability of the later egg record was lower (0.17) compared with 0.28 for the earlier record. The estimated heritability in Strain 5 was also lower for the 44 to 60 week period (0.29), compared with the comparable estimate for the 20 to 44 week period (0.61), although both values were notably higher than those for Strain 2.

Both egg weight measures appear to be strongly negatively correlated with later egg production in both strains to a higher degree than with the early record.

One aspect of obvious interest is the degree of correlation between the early egg record and subsequent laying ability. In the case of Strain 2 the correlation between the first period and the second was only +0.28, but in Strain 5 the correlation between the early and late part record was of the order of +0.7, with the result that egg production in either the early or late period was more highly correlated ($r_g > +0.9$) with the cumulative record to 60 weeks than in the case of Strain 2.

The conclusion which can be drawn from these estimates is that selection within Strain 5 solely on an early part record is likely to result in a correlated increase in the later part record to 60 weeks almost equivalent to the response which would be obtained were an equivalent selection pressure applied directly to the later part record, on account largely of the higher heritability for the earlier record. Selection on the early record alone in Strain 5 would be as efficient in increasing total egg production as selection for total egg production itself.

In the case of Strain 2, however, selection on the early record would only be 35 per cent as efficient in increasing egg production between 44 and 60 weeks, as compared with direct selection for egg production over that period. The predicted responses in subsequent egg production, following selection based upon the early part record, are summarised for both strains in Table 18 and feature the importance of precise estimates of the underlying genetic parameters to the practical breeder in formulating his breeding plans.

TABLE 18

Comparison of predicted gains in egg production (part record) in Strain 2 and Strain 5, given an equal selection intensity on the early part record of 2 units in the standardised selection differential

	Direct Responses in*	Indirect Responses in**	
Strain	20-44 week Record	44-60 week Record	Total Record to 60 weeks
2	+ 4.4 eggs	+1.1 eggs	+ 5.5 eggs
5	+10.1 eggs	+6.3 eggs	+16.3 eggs

$$* \; R_x = \bar{I}.h^2_x.\sigma_{Px}$$

$$** \; C.R._{y.x} = \bar{I}.h_x.h_y.r_A.\sigma_{Py}$$

4.1.4 Discussion

It is perhaps unfortunate that the two control populations were not hatched contemporaneously, nor housed together, since it is not possible to reach any final conclusion regarding the basis of the trends in mean performance noted above. Considering the population sizes involved however, the populations ought to have remained relatively stable with little likelihood of much genetic drift having taken place over the period of the selection experiment (Gowe et al., 1959_b). The overall increase in the average degree of inbreeding of around 2.5 per cent would be expected to have a minimal effect in terms of any inbreeding depression in performance of these populations (Blow et al., 1953; Stephenson et al., 1953; Tebb, 1958). The results do not suggest, however, any significant negative regression within these populations in any of the performance traits. Reports of other control populations have indicated a significant decline in some production characters over several generations of relaxed selection (Kinney and Lowe, 1968; Gowe et al., 1959_a) but these were ascribed to an environmental component depressing the phenotypic mean.

It is suggested that the positive trends noted in this study were also largely environmental in causation, although it is not possible to be dogmatic in the absence of a control for the control population itself. The significant increase in egg weight, and to a lesser degree body weight, in both strains may have been attributable to a change-over latterly to a ration containing maize as part of the cereal portion of the diet, in substitution for wheat or barley. Edwards and Morris (1959), for example, have reported that the inclusion of maize, or maize oil, in the ration may increase average individual egg weight by as much as 2-3 grams.

4.2 Changes in Mean Performance of Selected Populations

The numbers of pullets pedigreed, the numbers housed and those with completed records of laying house performance within each of the 4 selected lines annually are detailed in Table 19 (Strain 2) and Table 20 (Strain 5). A total of over 8,000 female progeny were recorded in the course of the selection experiment.

4.2.1 Egg Weight and Body Weight Lines

Figures 7 and 8 present some of the trends which have occurred in the mean performance of the Egg Weight and Body Weight lines in Strains 2 and 5 respectively. The absolute trends have been regressed over the 5 years (Table 21) and indicate that mean body weight has increased markedly in the Egg Weight line in Strain 2 and that this increase has been highly significant. There is an indication too of an increase in body weight in the Egg Weight line in Strain 5, but the trend in this instance is not significant.

Mean egg weight has increased appreciably in both lines selected for egg weight, but average egg weight has not declined in the Body Weight lines as one might have predicted. Another surprising feature in the Body Weight lines is the absence of a significant downward trend in mean 12 week body weight in view of the selection applied to reduce

TABLE 19

Number of pullets pedigreed and recorded in selected lines, Strain 2

	Egg Weight Line			Body Weight Line		
Year	Pedigreed	Housed	Completed Records	Pedigreed	Housed	Completed Records
1962/63	251	118	115	295	116	111
1963/64	237	237	219	241	241	215
1964/65	277	258	239	305	259	235
1965/66	296	239	222	291	239	218
1966/67	296	261	250	299	269	259
Totals:	1,357	1,113	1,045	1,431	1,124	1,038

	Regression Line			Ratio Line		
Year	Pedigreed	Housed	Completed Records	Pedigreed	Housed	Completed Records
1963/64	175	175	164	228	228	214
1964/65	336	288	269	304	289	271
1965/66	263	223	195	347	236	223
1966/67	312	288	274	280	257	243
Totals:	1,086	974	902	1,159	1,010	951

TABLE 20

Number of pullets pedigreed and recorded in selected lines, Strain 5

	Egg Weight Line			Body Weight Line		
Year	Pedigreed	Housed	Completed Records	Pedigreed	Housed	Completed Records
1962/63	234	172	149	284	176	158
1963/64	280	261	178	281	268	236
1964/65	151	144	133	155	138	136
1965/66	309	280	257	274	243	239
1966/67	226	212	198	273	245	237
Totals:	1,200	1,069	915	1,267	1,070	1,006

	Regression Line			Ratio Line		
Year	Pedigreed	Housed	Completed Records	Pedigreed	Housed	Completed Records
1963/64	319	306	277	223	203	189
1965/66	218	202	189	204	186	173
1966/67	228	215	205	290	268	261
1967/68	203	185	167	171	152	140
Totals:	968	908	838	888	809	763

Fig 7

Absolute Trends in Mean Performance of Selected Lines

Strain 2

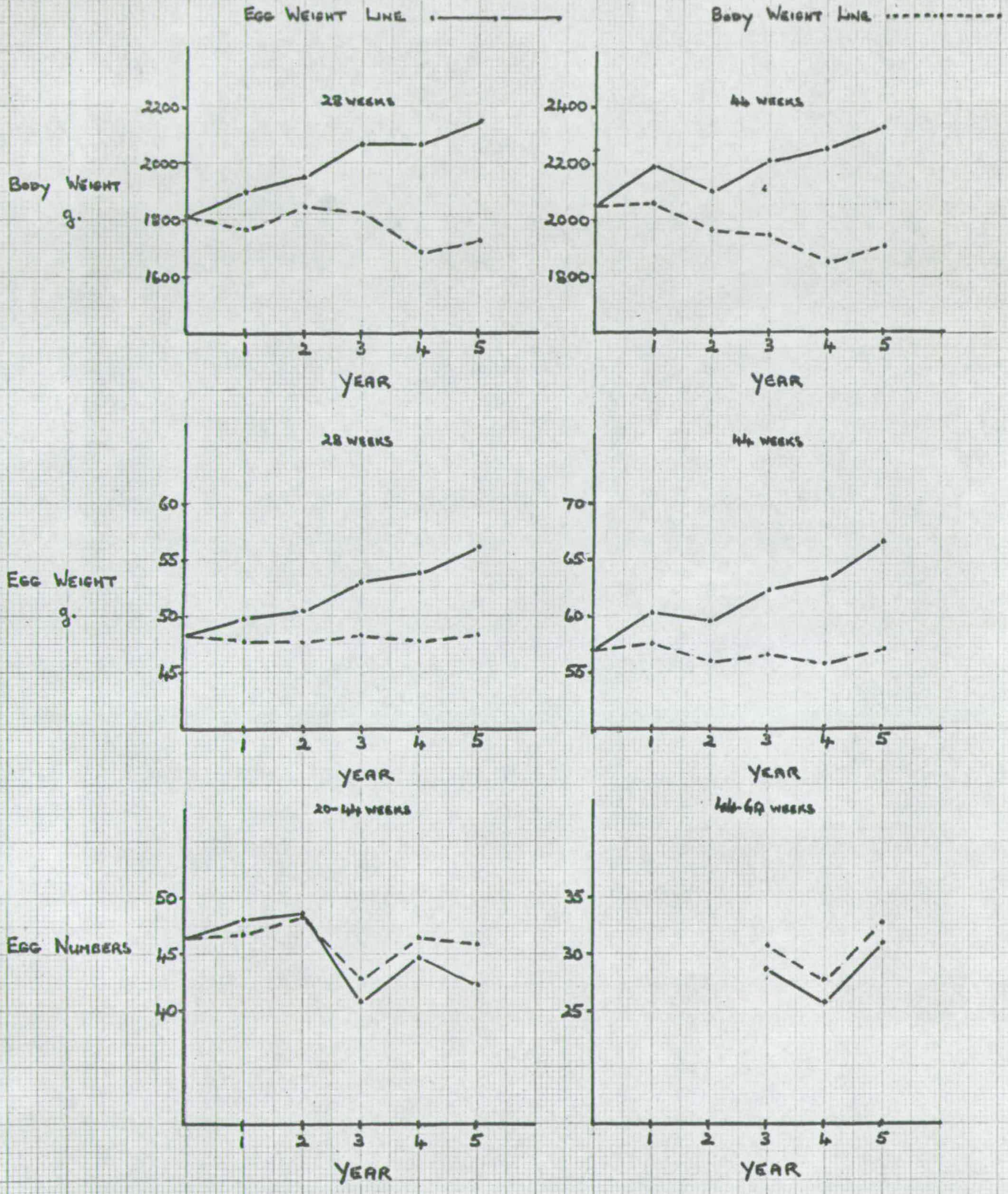


Fig 8

ABSOLUTE TRENDS IN MEAN PERFORMANCE OF SELECTED LINES
STRAIN 5

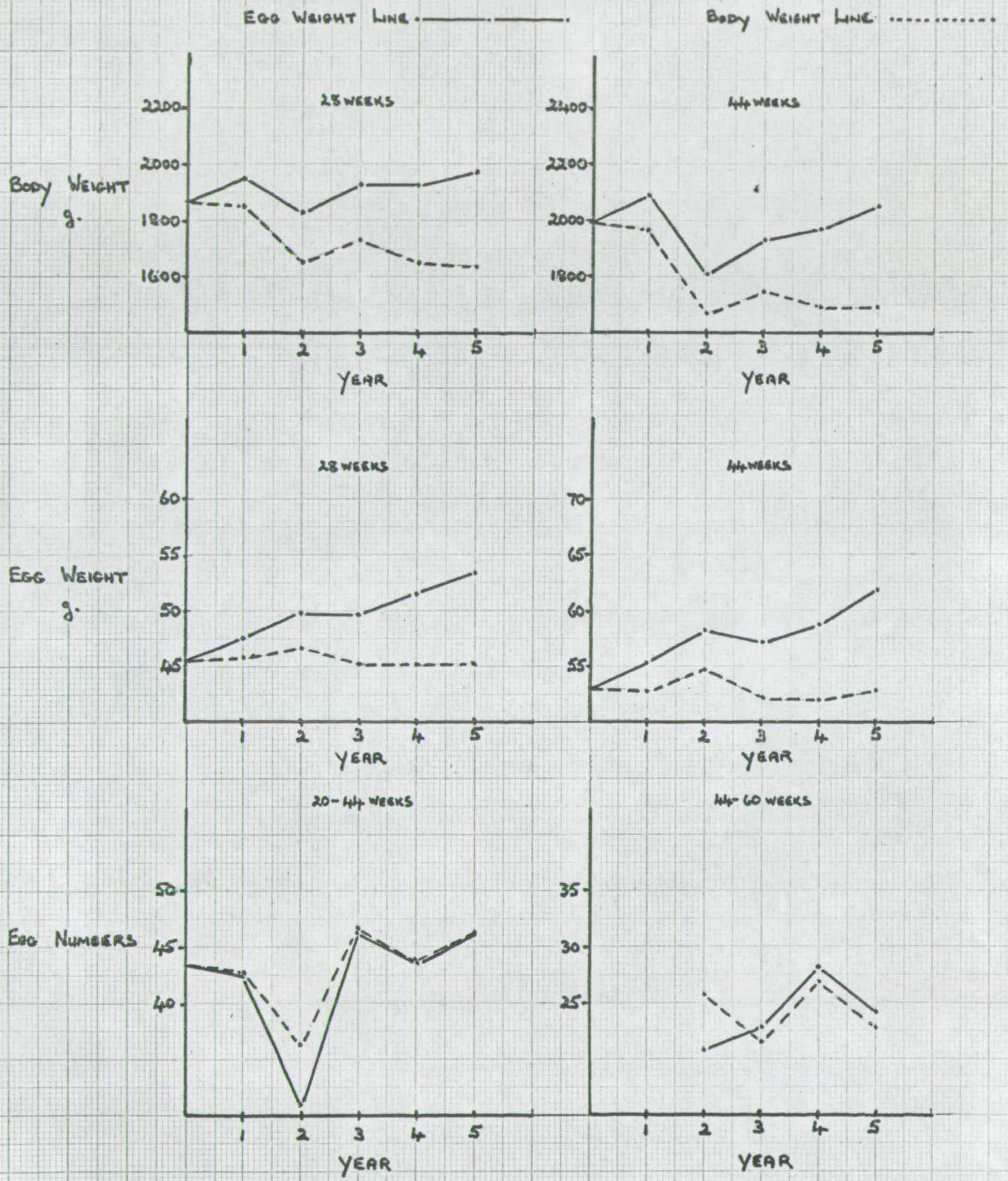


TABLE 21

Regression (b) in phenotypic means of Egg Weight and Body Weight selected lines over 5 generations of selection, 1963/68

		Egg Weight Lines						Body Weight Lines					
		Strain 2			Strain 5			Strain 2			Strain 5		
Trait		b	s.e. of b		b	s.e. of b		b	s.e. of b		b	s.e. of b	
Body Weight:													
12 weeks	g.	+42.0	± 7.6	***	+22.9	± 7.9	**	- 4.9	±11.3	N.S.	-12.7	± 6.6	N.S.
28 weeks	g.	+66.7	± 6.3	***	+15.4	±12.0	N.S.	-17.3	±11.5	N.S.	-47.4	±12.2	**
44 weeks	g.	+48.7	±11.1	**	+ 1.4	±23.6	N.S.	-37.9	± 8.0	***	-65.5	±20.0	**
Egg Weight:													
28 weeks	g.	+1.56	± .10	***	+1.46	± .13	***	+0.04	± .08	N.S.	-0.12	± .12	N.S.
44 weeks	g.	+1.66	± .22	***	+1.52	± .24	***	-0.15	± .13	N.S.	-0.16	± .20	N.S.
Age 1st Egg:	wk.	+0.26	± .22	N.S.	-0.20	± .26	N.S.	+0.28	± .19	N.S.	-0.10	± .27	N.S.
Egg Numbers:													
(Part Record)													
20-44 weeks		-1.11	± .58	N.S.	+0.92	±1.3	N.S.	-0.26	± .40	N.S.	+0.82	± .83	N.S.
44-60 weeks		+1.15	±1.65	N.S.	+1.53	±1.1	N.S.	+1.10	±1.71	N.S.	-0.32	±1.12	N.S.

N.S. = Value for b is not significantly different from zero

** = b is significantly different from zero at 95% level; 4 d.f.

*** = b is significantly different from zero at 99% level; 4 d.f.

12 week body weight.

Egg numbers have tended to fluctuate quite erratically between years and in neither strain has there been any significant trend in either the early or late egg record. Sexual maturity does not appear to have been significantly affected in either line in both strains.

4.2.2 Regression and Ratio Lines

The absolute trends in the mean level for 6 of the 8 recorded traits within the Regression and Ratio lines are plotted graphically (Figures 9 and 10) and the average regression for each trait over 4 years is summarised in Table 22. The latter estimates point to a significant reduction in body weight in the Ratio line in both strains. In the Regression lines the body weight trends are not consistent. In the first instance there is an absence of any significant trend in Strain 2, while in Strain 5 the earlier body weight measurements show a significant upward trend which does not apply at 44 weeks of age.

Egg weight at 28 weeks shows a significant upward trend in both the Ratio and Regression lines within both strains. Although a positive trend is also apparent in egg weight at 44 weeks of age in both strains, the trend is only significant in Strain 2.

A significant and marked decline in the early egg record is apparent in the Regression line in Strain 2, but on the other hand a positive and significant trend is evident in the Strain 5 Regression line. No significant trends are noted for the later egg record, but a significant

Fig 9

Absolute Trends in Mean Performance of Selected Lines

Strain 2

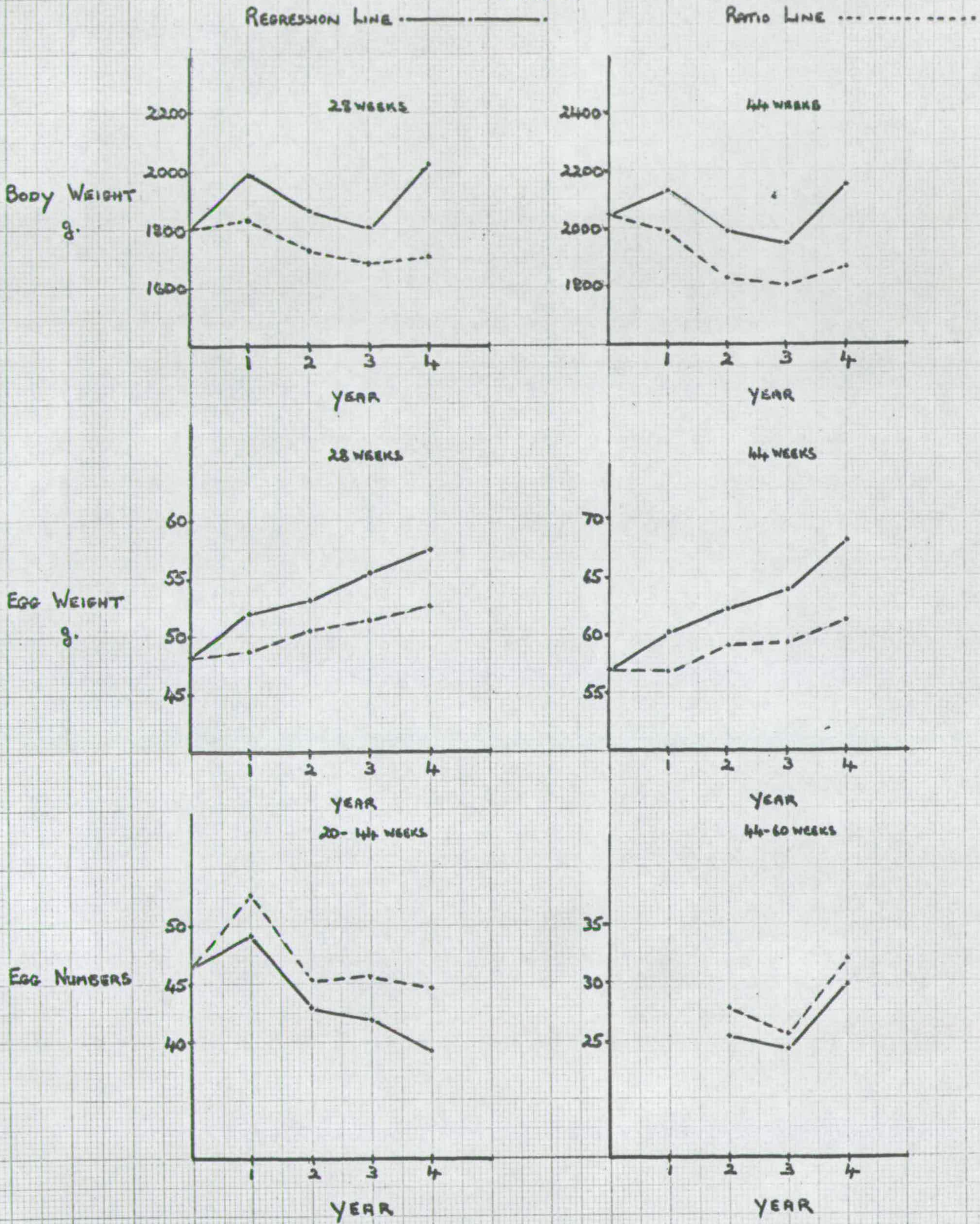


Fig 10

ABSOLUTE TRENDS IN MEAN PERFORMANCE OF SELECTED LINES
STRAIN 5

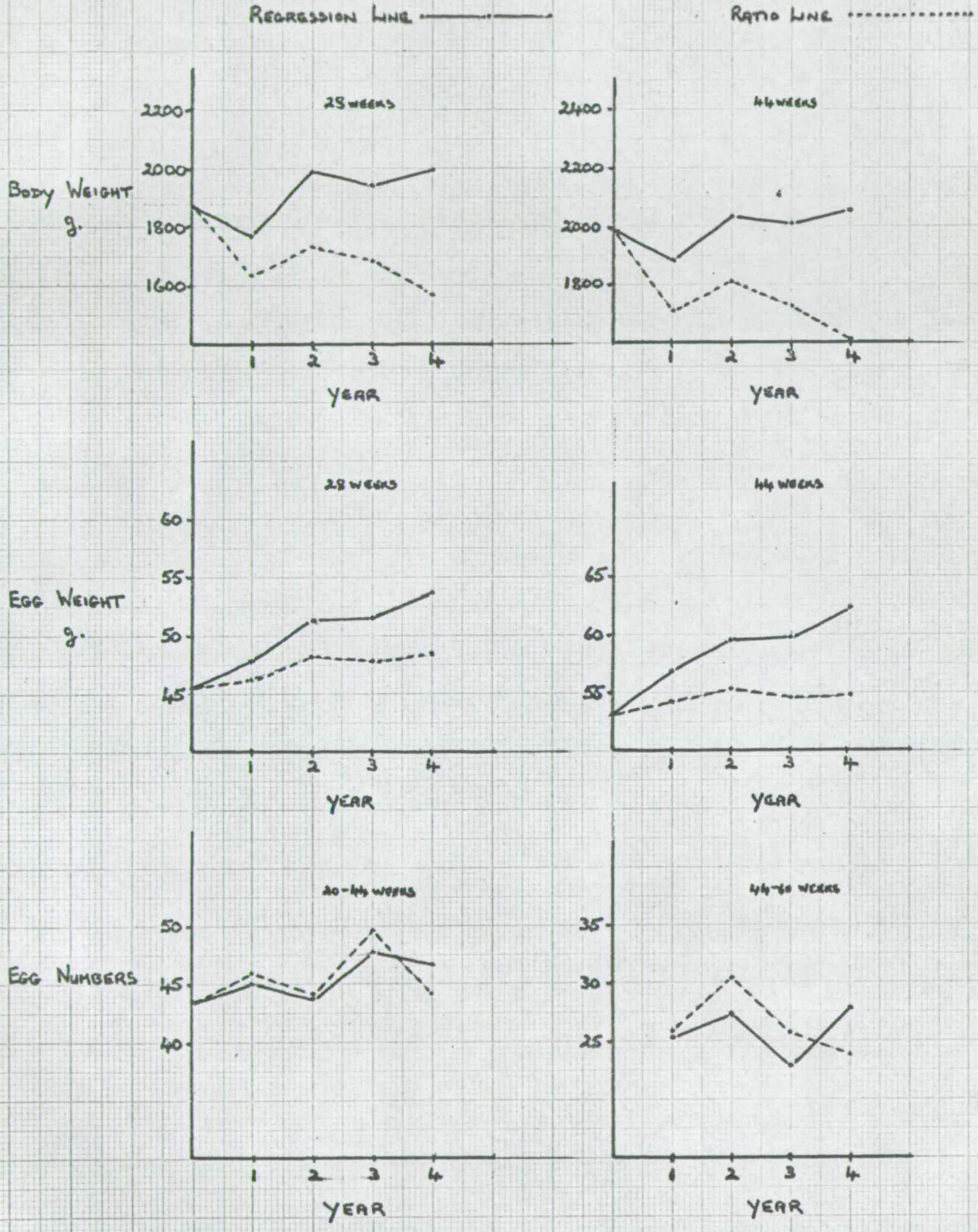


TABLE 22

Regression (b) in phenotypic means of Regression and Ratio selected lines over 4 generations of selection, 1964/68

		Regression Lines						Ratio Lines					
		Strain 2			Strain 5			Strain 2			Strain 5		
Trait		b	s.e. of b		b	s.e. of b		b	s.e. of b		b	s.e. of b	
Body Weight:													
12 weeks	g.	+30.4	± 9.9	**	+34.3	±12.9	*	+ 6.0	± 8.6	N.S.	-14.3	±12.8	N.S.
28 weeks	g.	+26.1	±30.2	N.S.	+43.3	±19.8	*	-36.1	±10.8	**	-53.0	±21.9	**
44 weeks	g.	+ 2.7	±28.3	N.S.	+25.3	±17.3	N.S.	-54.1	±18.4	**	-74.2	±24.9	**
Egg Weight:													
28 weeks	g.	+2.15	± .17	***	+2.02	± .24	***	+1.09	± .06	**	+0.76	± .16	**
44 weeks	g.	+2.52	± .20	***	+2.14	± .30	***	+1.03	± .19	***	+0.38	± .18	N.S.
Age 1st Egg:	wk.	+0.35	± .11	**	-0.29	± .23	N.S.	+0.23	± .13	N.S.	-0.27	± .27	N.S.
Egg Numbers: (Part Record)													
20-44 weeks		-2.20	± .58	**	+0.94	± .35	*	-1.06	± .86	N.S.	+0.52	± .75	N.S.
44-60 weeks		+2.25	± 1.4	N.S.	+0.35	± 1.0	N.S.	+2.10	±1.9	N.S.	-1.04	±1.06	N.S.

N.S. = Value for b is not significantly different from zero

* = b is significantly different from zero at 90% level; 3 d.f.

** = b is significantly different from zero at 95% level; 3 d.f.

*** = b is significantly different from zero at 99% level; 3 d.f.

delay in sexual maturity is apparent in the Strain 2 Regression line and possibly explains, in part at least, the reduction in the early egg record noted above.

4.2.3 Elimination of Environmental Time Trends

Gowe *et al*. (1959) have clearly demonstrated the value of a control strain by comparing absolute trends within two selected strains with the trends as estimated from the mean annual deviations from a control population.

The fact that a significant upward trend has already been noted in some of the body weight measurements, and in the 2 egg weight measurements in both control populations, suggests that correction for a positive environmental trend must be made within the selected populations before attempting to estimate genetic change.

For these reasons, it is preferable to examine the changes that have occurred within the selected lines by dealing with the annual deviation in mean performance of the selected line from its contemporaneous control population. These deviations were computed first of all within hatches and weighted according to the value for $\frac{n_1 + n_2}{n_1 \cdot n_2}$, where n_1 and n_2 were the number of individuals in the selected and control group within the particular hatch.

The mean deviations for each of the five generations in the Egg Weight and Body Weight lines and for each of the four generations in the Ratio and Regression lines are tabulated in Tables 1 and 2 (Appendix B) and many of these deviations assume a high degree of significance. The standard error for each mean deviation was calculated as:-

$$\text{S.E. of difference} = \sqrt{\frac{1}{n_1} + \frac{1}{n_2}} \cdot \sigma$$

n_1 and n_2 being the total number of individuals recorded in the selected and control populations respectively. The results to be discussed in the following sections, concerned with the genetic changes in the selected populations, are based, therefore, on the mean deviations of the lines from their respective controls, rather than on the means themselves.

4.3 Selection Response in Body Weight and Egg Weight in Single Trait Selected Lines

Tables 23 and 24 include the average regression in the weighted mean deviations from the control populations (see Tables 1 and 2, Appendix B) for body weight and egg weight in the Egg Weight and Body Weight selected lines over the 5 generations of selection. The calculated regression constant (b) for a linear regression of the form, $y = bx$, was taken to indicate the average assumed genetic response per generation. The observed deviations for the selected line from the control population for each trait in the last selected generation are also given in Tables 23 and 24, along with the standard errors of these observed differences.

TABLE 23

Regression (b) in mean deviations in body weight and egg weight in the Egg Weight lines over 5 generations of selection

		Strain 2					Strain 5				
Trait		b	s.e. of b		O[†]		b	s.e. of b		O[†]	
Body Weight:											
12 weeks	g.	+14.8	± 5.4	*	+ 57	± 8	+4.4	± 8.4	N.S.	- 5	± 9
28 weeks	g.	+36.5	±13.2	*	+127	±14	+6.6	±13.0	N.S.	-10	±17
44 weeks	g.	+38.5	±19.6	N.S.	+114	±18	+3.9	±14.3	N.S.	-17	±21
Egg Weight:											
28 weeks	g.	+1.27	±0.26	**	+5.5	±0.28	+0.93	±0.15	***	+4.7	±0.27
44 weeks	g.	+1.39	±0.33	**	+6.4	±0.31	+1.06	±0.31	**	+5.2	±0.33

[†] O = Observed mean deviation from control in final generation ± s.e. of difference $= \sqrt{\left(\frac{1}{n_1} + \frac{1}{n_2}\right)} \cdot \sigma$

N.S. = Value of b is not significantly different from zero

* = Value of b is significantly different from zero at 90% level

** = Value of b is significantly different from zero at 95% level

*** = Value of b is significantly different from zero at 99% level

TABLE 24

Regression (b) in mean deviations in body weight and egg weight in the Body Weight lines over 5 generations of selection

		Strain 2					Strain 5				
Trait		b	s.e. of b		O†		b	s.e. of b		O†	
Body Weight:											
12 weeks	g.	-34.0	± 7.2	**	-185	± 8	-35.5	± 5.0	***	-190	± 9
28 weeks	g.	-49.6	±20.0	*	-300	±14	-61.3	± 8.8	***	-340	±16
44 weeks	g.	-52.0	±25.5	N.S.	-329	±18	-65.5	±14.8	**	-379	±20
Egg Weight:											
28 weeks	g.	-0.27	±0.31	N.S.	-2.5	±0.28	-0.63	±0.15	**	-3.5	±0.25
44 weeks	g.	-0.49	±0.28	N.S.	-3.1	±0.31	-0.62	±0.20	**	-3.7	±0.32

†O = Observed mean deviation from control in final generation ± s.e. of difference $= \sqrt{(\frac{1}{n_1} + \frac{1}{n_2})}.\ \sigma$

N.S. = Value of b is not significantly different from zero

* = Value of b is significantly different from zero at 90% level

** = Value of b is significantly different from zero at 95% level

*** = Value of b is significantly different from zero at 99% level

4.3.1 Direct Responses in Egg Weight

Following 5 generations of selection for increased egg weight, the overall response in 28 week egg weight was 5.50 grams in Strain 2 and 4.69 grams in Strain 5; the average regression in egg weight per generation being +1.2 grams and +0.9 grams respectively (Table 23). The change in egg weight amounted to a shift of around 1.6 phenotypic standard deviations in each of the two Egg Weight lines.

The selection response obtained in controlled selection experiments is frequently compared with a measure of the selection applied to provide an estimate of the realised heritability (Falconer, 1955; 1960_a). The basic formula for the heritability of a quantitative trait can be simply expressed as $h^2 = \frac{\Delta G}{\Delta P}$, where ΔG is the response realised and ΔP is the selection applied. The amount of selection applied is normally measured in terms of the cumulative selection differential which, when divided by the phenotypic standard deviation, gives a standardised measure of the degree of selection applied, or the selection intensity ($\bar{i}$).

The selection differentials which were computed for 28 week egg weight in the Egg Weight selection lines are summarised in Table 25. These were computed for the selected male and female parents separately. In the case of females, the superiority of each selected female parent over its respective hatch mean was calculated in deriving the overall mean superiority of the initially selected female parents. Each average deviation was, however, weighted according to the number of progeny recorded in the subsequent generation to estimate the realised differential. The selection

TABLE 25

Calculated weighted and unweighted selection differentials (grams) in 28 week egg weight in Egg Weight lines

Strain 2

	Males		Females	
	A*	R*	A*	R*
Year 1	-	-	3.55	3.61
" 2	0.99	0.97	0.63	0.64
" 3	2.12	2.10	1.79	1.99
" 4	1.21	1.25	1.82	1.86
" 5	1.41	1.34	1.53	1.58
Cumulative:	5.73	5.66	9.32	9.68

$\frac{R}{A} = 0.99$ $\frac{R}{A} = 1.04$

Total realised ($\triangle P$) = 15.34 g. (4.94σ)

Strain 5

	Males		Females	
	A*	R*	A*	R*
Year 1	-	-	1.98	2.04
" 2	0.94	0.90	1.14	1.15
" 3	1.22	1.02	1.28	1.20
" 4	1.20	1.13	1.41	1.32
" 5	1.66	1.72	1.89	1.85
Cumulative:	5.02	4.77	7.70	7.56

$\frac{R}{A} = 0.95$ $\frac{R}{A} = 0.98$

Total realised ($\triangle P$) = 12.33 g. (4.41σ)

*A = Attempted selection differential
*R = Realised selection differential

differential on the male side was calculated from the mean within hatch deviation of the egg weight record of the male's full sisters. The full sib mean was weighted using the factor appropriate to the heritability of family means, viz. $\frac{0.5n}{1 + (n - 1)t}$, 'n' representing the number of full sisters and 't' the phenotypic correlation between full sibs. Later, in calculating the realised male differential, each sib group family mean deviation was weighted according to the number of progeny contributed by each selected sire to the subsequent set of recorded pullets.

The realised selection differentials in the majority of cases are very close in magnitude to the attempted differentials. The ratio of the realised to the attempted differential is close to unity in all cases, suggesting that there has been little or no natural selection operating either for or against the selection criterion adopted within these populations.

The experiment had been planned initially to allow a selection intensity of approximately 1 in 4 on the female side and about 1 in 8 on the male side, giving a mean selection intensity of around 1.4 phenotypic standard deviation units per generation, or a cumulative selection differential of 7σ after 5 generations of selection. The realised selection intensities, in practice, have fallen far short of this level, reaching a total of only 4.94σ for the cumulative selection differential for 28 week egg weight in Strain 2 and 4.41σ in Strain 5, due in large part to the relatively low selection pressure applied on the male side.

This was attributable to quite heavy losses occurring amongst the young cockerels held in temporary accommodation outdoors up to the stage at which selection decisions were made.

The linear regression of the response on the cumulative selection differential provides a useful estimate of the realised heritability and is plotted in Figure 11. The overall value for the realised heritability of 0.41 ± 0.09 in Strain 2 is in reasonably close agreement with the estimate of 0.49 ± 0.09 for the heritability of 28 week egg weight reported within the base population (Clayton and Robertson, 1966). The corresponding estimate for the realised heritability in Strain 5 of 0.40 ± 0.07 compares with an estimate of 0.50 ± 0.10 given for the unselected population.

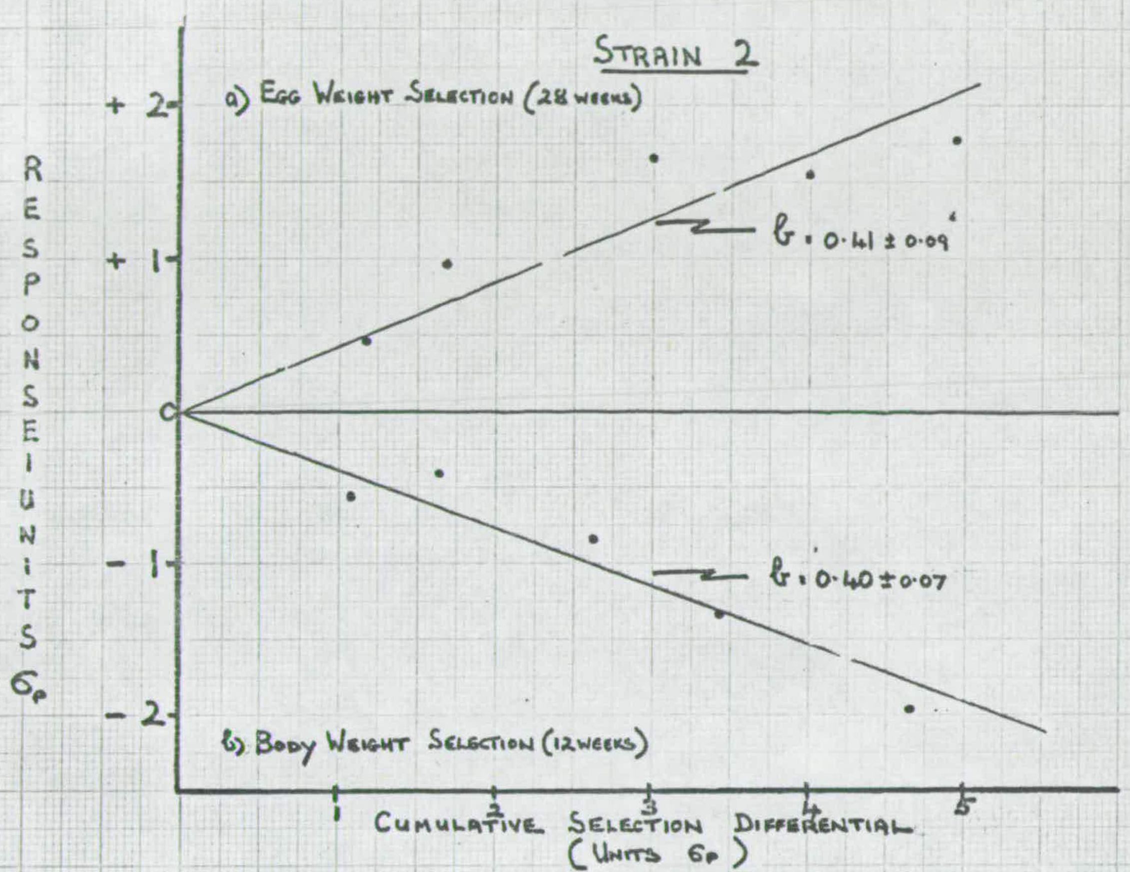
4.3.2 Direct responses in Body Weight

Five generations of selection for reduced body weight resulted in an observed decrease in 12 week body weight in the final generation of 185 grams in the Strain 2 Body Weight line and of 190 grams in the replicate line in Strain 5 (Table 24). These overall changes amount to an average decline of 34 and 35 grams respectively per generation and an overall reduction of just on $2\sigma_p$ in the mean 12 week body weight.

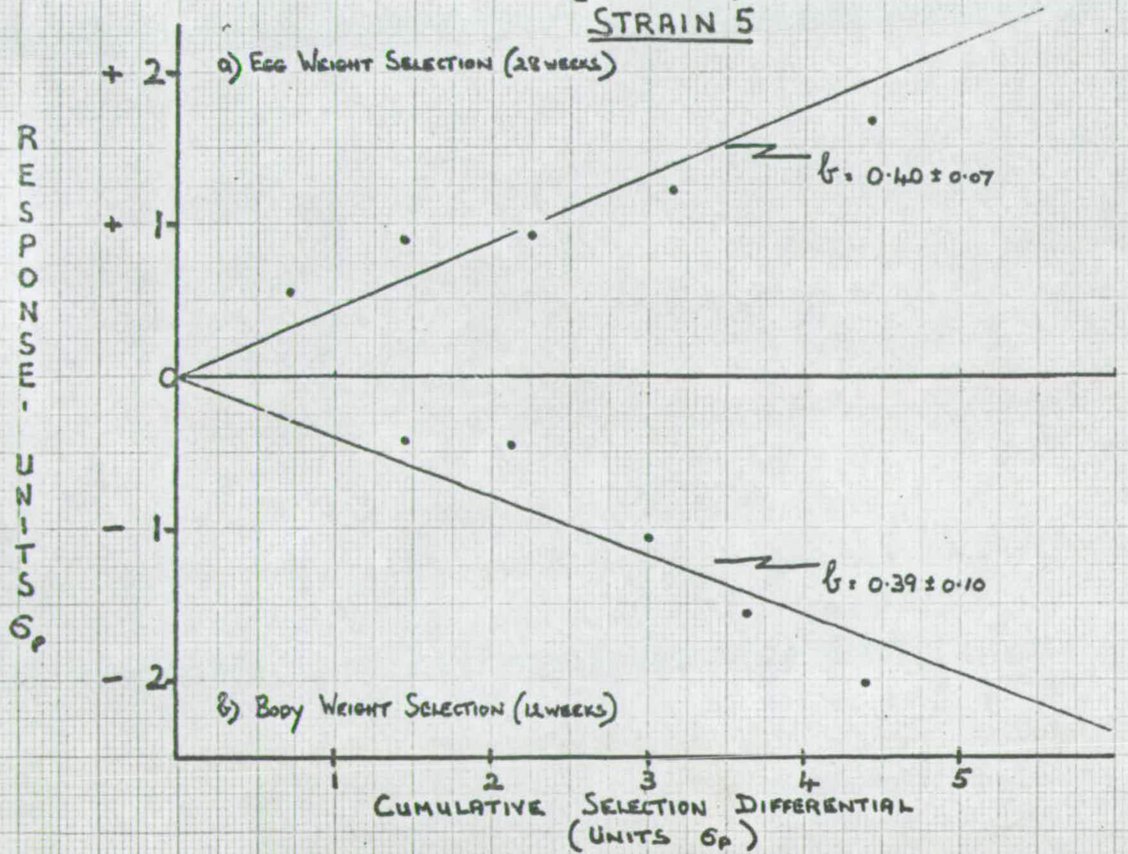
Table 26 lists the attempted and realised selection differentials applied to the primary trait being selected in the Body Weight lines. The differentials were computed in an identical manner to those for egg weight in the Egg Weight lines. As in the case of the egg weight

Fig 11

Regression of Response in Egg Weight and Body Weight on the Selection Differentials (Realised Heritabilities)



STRAIN 2



STRAIN 5

TABLE 26

Calculated weighted and unweighted selection differentials (grams) in 12 week body weight in Body Weight lines

Strain 2

	Males		Females	
	A*	R*	A*	R*
Year 1	-	-	-101	-102
" 2	- 33	- 35	- 19	- 16
" 3	- 52	- 52	- 43	- 44
" 4	- 33	- 30	- 44	- 43
" 5	- 60	- 59	- 61	- 57
Cumulative:	-178	-176	-268	-262

$\frac{R}{A} = 0.99$ $\frac{R}{A} = 0.98$

Total realised ($\triangle P$) = -438 g. (-4.66σ)

Strain 5

	Males		Females	
	A*	R*	A*	R*
Year 1	-	-	-132	-135
" 2	- 26	- 25	- 38	- 40
" 3	- 42	- 41	- 47	- 44
" 4	- 24	- 24	- 37	- 34
" 5	- 21	- 21	- 49	- 50
Cumulative:	-113	-111	-303	-303

$\frac{R}{A} = 0.98$ $\frac{R}{A} = 1.0$

Total realised ($\triangle P$) = -414 g. (-4.41σ)

A* = Attempted selection differential
R* = Realised selection differential

selection, the realised selection differentials are in close agreement with the attempted differentials. Also, the final cumulative realised selection differentials for low body weight were approximately of the same order of magnitude as achieved in selecting for high egg weight.

The linear regression of the body weight responses on the cumulative selection differentials are also plotted (Figure 11) and provide an estimate of the realised heritability for 12 week body weight. In this instance, the calculated values of 0.40 ± 0.07 (Strain 2) and 0.39 ± 0.10 (Strain 5) are appreciably less than the heritability estimates reported for the unselected population (0.50 ± 0.09 and 0.66 ± 0.11 respectively). One explanation for this may lie in the fact that selection in these lines was in a downward direction and that some asymmetry of response in that direction may have resulted in an overall lower rate of response than might apply were selection carried out in an upward direction. Previously reported selection experiments have shown the response for a given absolute selection differential to be greater in one direction than in the other. Thus for growth rate in mice Falconer (1960_b) found that the selection response in the direction of small body size was greater than in the direction for large size. Festing and Nordskog (1967) obtained a higher realised heritability for body weight when selection was carried out in a downward direction (52 per cent) compared with upward selection (34 per cent). That marked differences probably exist between strains, however, in this respect is suggested by the long-term selection experiment by Maloney et al. (1967) who observed a much slower response in their low body weight line compared with the line selected for high body weight, the estimates of the realised heritabilities for body weight from the low line selection being some 20-30 per cent lower than the corresponding estimates from the high line selection.

4.3.3 Indirect Responses in Body Weight and Egg Weight

In addition to comparing the direct responses effected in the above lines, it is of interest in terms of the validity of the use of the measure of genetic correlation in predicting selection response, to examine the magnitude of the indirect responses that have taken place within these lines.

It was considered desirable, however, before attempting to compare the actual with predicted correlated responses to compute the likely total genetic response that had occurred over the period that selection was carried out from the average response per generation, multiplied by the total number of generations, rather than using the absolute deviation in the final generation only as a measure of total response. The estimated total responses for the body and egg weight traits are detailed in Table 27. In some cases the estimated total response exceeds the observed deviation of the selected line in the final generation (Tables 23 and 24) while in others it is less. However, on account of the likelihood of chance yearly fluctuations, either in the control population or the selected line, affecting the magnitude of a deviation in one year only, it was considered that an estimate of overall response was preferable and would provide a more reliable indication of any consistent correlated trends.

TABLE 27

Estimated overall response (△G) from the average yearly change (b) in body weight and egg weight over 5 years in the Egg Weight and Body Weight lines

		Strain 2		Strain 5	
Line:		Egg Weight	Body Weight	Egg Weight	Body Weight
		△G	△G	△G	△G
Body Weight:					
12 weeks	g.	+ 74 ***	-170 ***	+ 22 *	-177 ***
28 weeks	g.	+182 ***	-248 ***	+ 33 N.S.	-306 ***
44 weeks	g.	+192 ***	-260 ***	+ 20 N.S.	-327 ***
Egg Weight:					
28 weeks	g.	+6.3 ***	-1.3 ***	+4.6 ***	-3.2 ***
44 weeks	g.	+6.9 ***	-2.4 ***	+5.3 ***	-3.1 ***

N.S. = Not significant

* = Significant at 95% level

*** = Significant at 99.9% level

It is possible, knowing the magnitude of the correlated response in trait 'y', given the direct response obtained in the same experiment in trait 'x' to estimate the realised genetic correlation between 'x' and 'y', since

$$C.R_y = i.h_x.h_y.\,r_{gxy}.\sigma y \quad \text{(Falconer, 1960}_a\text{)}$$

$$\text{Therefore, } r_{gxy} = \frac{C.R_y}{i.h_x.h_y.\sigma_y}$$

The realised genetic correlations, for example, between 28 and 44 week egg weight calculated from the estimated genetic responses were 0.92 for both strains. This value compares with the estimates calculated within the unselected population of 0.96 and 0.95 respectively.

Body weight was also recorded in the selected populations at three different ages and the response in the later body weight measurements showed a high degree of correlation with the direct response obtained at 12 weeks in the Body Weight lines, the realised genetic correlations between 12 and 28 week body weight being +0.90 (Strain 2) and +0.95 (Strain 5), which are higher than the estimates of 0.66 and 0.72 in the base population.

Less predictable, perhaps, is the consistency of the egg weight/body weight correlation and the magnitude of the correlated responses applying in practice when selection is made on egg weight or body weight alone. In the Egg Weight line in Strain 2 the change in egg weight was accompanied by a significant correlated trend in body weight, resulting in an estimated total response in 28 week body weight of 182 grams. In this case the realised genetic correlation between body weight and egg weight at 28 weeks was +0.55, compared with the population estimate of +0.32. Body weight in the Strain 2 line was consistently positively correlated with egg weight, the realised genetic correlation between the 12 week weight, for example, and 28 week egg weight being +0.37 and that between the 44 week body weight and 28 week egg weight +0.47.

Rather surprisingly, in view of the stronger positive genetic correlation noted earlier between body weight and egg weight in the other strain, there is a notable absence of a significant correlated increase in body weight in the Strain 5 Egg Weight line.

The correlated trends in egg weight, however, which occurred within the body weight selected lines present a different view of the relative importance of the body weight/egg weight correlation within the two strains. A significant reduction in egg weight has occurred in both Body Weight lines within the last two generations of selection, but it is only in the Strain 5 line that the overall negative trend is significant. In the latter case the overall decline in 28 week egg weight is estimated as 3.2 grams, which would suggest a realised genetic correlation between egg weight and body weight of as high as +0.73. The realised genetic correlation of egg weight on body weight, on the other hand, within Strain 2 following downward selection for body weight in the Body Weight line is calculated as +0.25, which is considerably lower than the estimated realised correlation for body weight on egg weight following upward selection for egg weight in the Egg Weight line.

These results, in Strain 5 at least, possibly point to some asymmetry of the egg weight/body weight genetic correlation. According to the conventional statistical formulation of correlated response, the genetic correlation between characters is assumed to be symmetrical, i.e. independent of the fact which of the two traits is subjected to selection. Festing and Nordskog (1967) reported a long-term selection experiment in the fowl in which they had lines selcted for egg weight in both an upward and a downward direction and similar selection for body weight in both directions. They noted that the agreement was good between the realised correlations in the downward selected lines with the estimates obtained from variance component analyses, but there was divergence between the two types of estimate in the upward selected lines. In particular, a weak correlated response in body weight was observed in the line selected for large egg size. This observation is similar to what has been noted in the case of the Strain 5 Egg Weight line.

4.4 Selection Responses in Body Weight and Egg Weight in Regression and Ratio Lines

The responses obtained under single trait selection in the Body Weight and Egg Weight lines have provided confirmatory empirical evidence of the existence of a moderately strong genetic correlation ($r_g > +0.4$) between body weight and egg weight within both strains used in this study, when selection was applied in practice to reducing body weight. The same magnitude of correlation was observed in Strain 2 between body weight and egg weight when selection was applied to egg weight in an upward direction. Observation of the selection responses, however, within the Strain 5 Egg Weight line has failed to indicate any significant realised correlation of body weight with egg weight. In addition, the magnitude of the direct responses obtained within these lines provides a useful yardstick with which to compare the selection efficiency of the two selection techniques used in an attempt to modify the normal egg weight to body weight relationship in the laying hen.

4.4.1 Regression Selection

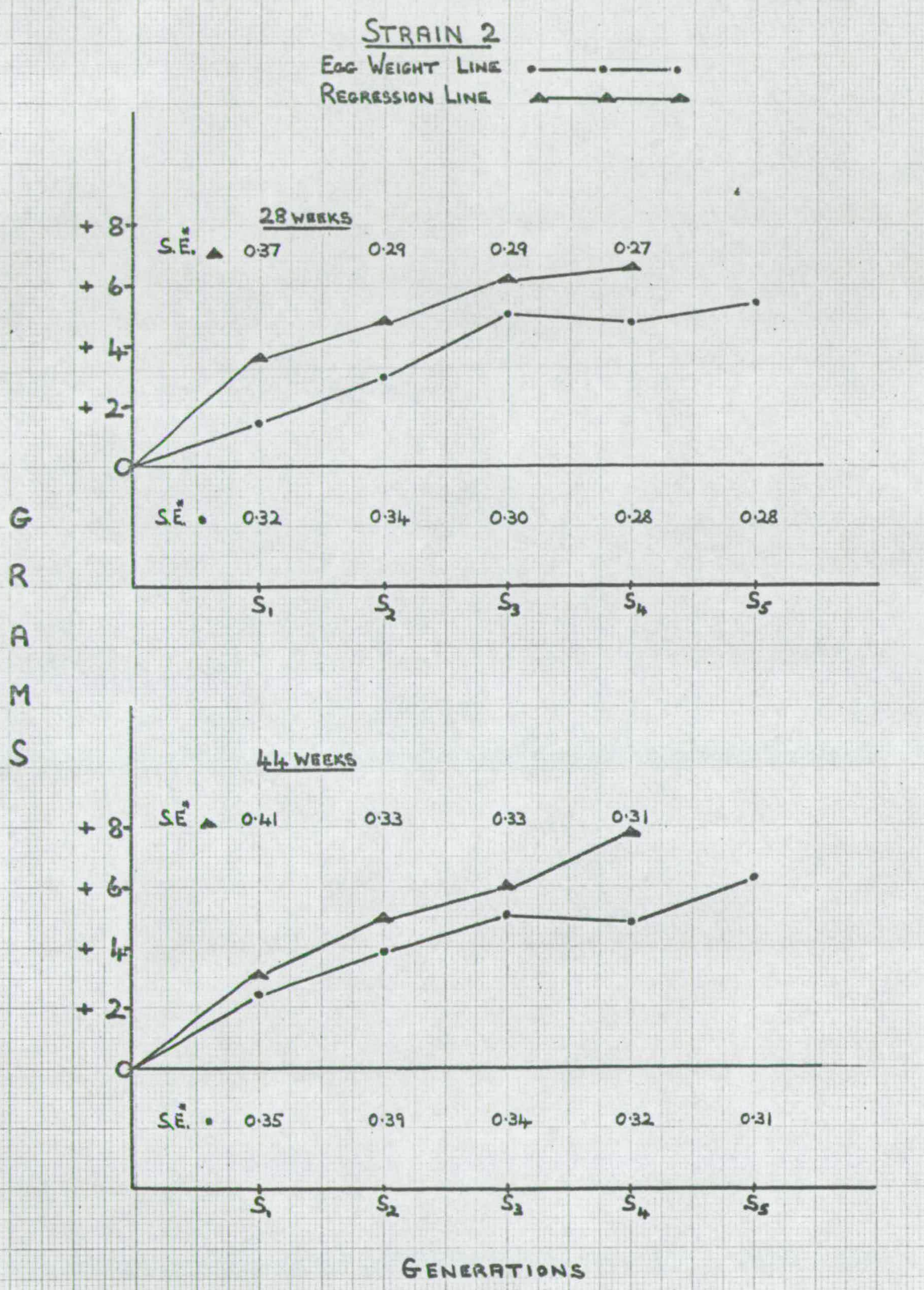
The postulated objective in the 2 Regression lines was to achieve the maximum gain in egg weight while maintaining constant body weight by using a simplified restricted index (Kempthorne and Nordskog, 1959; Abplanalp et al., 1963) in which body weight was negatively weighted by the average estimated genetic regression of body weight on egg weight within these particular breeding populations (cf. Purser, 1960).

(a) Genetic Changes in Egg Weight

Figures 12 and 13 present in graphical form the responses obtained in egg weight as observed at both 28 and 44 weeks of age in the Strain 2 and Strain 5 Regression lines respectively. These response curves are plotted alongside the observed change in egg weight in the Egg Weight lines. The average regression in the mean annual deviations from the control was also calculated and indicates, as would be expected, a highly significant upward trend in egg weight (Table 28). In the case of the

Fig 12

Genetic changes effected in Egg Weight (Deviations from Control)

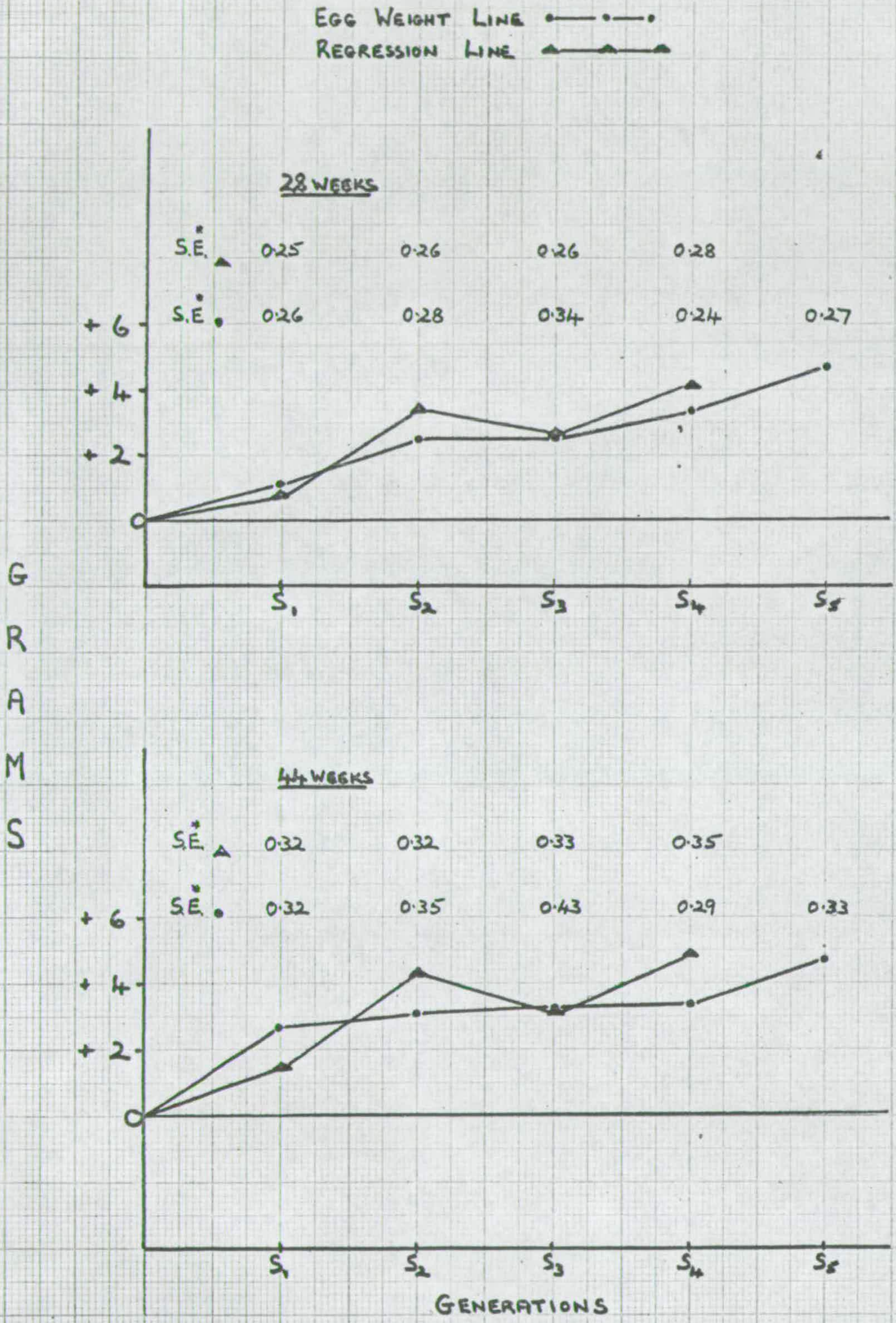


*S.E. of difference $= \sqrt{\frac{1}{n_1} + \frac{1}{n_2}} \cdot \sigma$

Fig 13

GENETIC CHANGES EFFECTED IN EGG WEIGHT (DEVIATIONS FROM CONTROL)

STRAIN 5



*S.E. of difference = $\sqrt{\frac{1}{n_1}+\frac{1}{n_2}}\cdot\sigma$

TABLE 28

Regression in mean deviations in body weight and egg weight in the Regression lines over 4 generations of selection

Strain 2

		b	s.e. of b		O†	
Body Weight:						
12 weeks	g.	- 1.3	± 3.2	N.S.	-14	± 8
28 weeks	g.	- 9.1	±24.8	N.S.	-41	±14
44 weeks	g.	-11.9	±32.0	N.S.	-67	±18
Egg Weight:						
28 weeks	g.	+1.98	±0.61	**	+6.8	±0.27
44 weeks	g.	+2.10	±0.37	**	+7.9	±0.31

Strain 5

		b	s.e. of b		O†	
Body Weight:						
12 weeks	g.	+15.4	±16.2	N.S.	+79	± 9
28 weeks	g.	+ 3.9	±27.7	N.S.	+14	±17
44 weeks	g.	- 0.4	±25.2	N.S.	0	±21
Egg Weight:						
28 weeks	g.	+1.07	±0.35	**	+4.1	±0.28
44 weeks	g.	+1.28	±0.48	*	+4.9	±0.35

†O = Observed mean deviation from control in final generation ± s.e. of difference = $\sqrt{(\frac{1}{n_1} + \frac{1}{n_2})} \cdot \sigma$

N.S. = Value of b is not significantly different from zero

* = Value of b is significantly different from zero at 90% level

** = Value of b is significantly different from zero at 95% level

Strain 2 Regression line the average response per generation of 1.57 grams has been notably higher than the average rate of response in the Egg Weight line. In Strain 5 the relative rate of response as between the regression and egg weight selection has been of approximately the same order of magnitude.

The total change effected in 28 week egg weight through selection on deviations from the egg weight/body weight regression over 4 generations is equivalent to a change of $2.2\sigma_p$ in Strain 2 and of $1.5\sigma_p$ in Strain 5, compared with $1.6\sigma_p$ after 5 generations of egg weight selection in both strains.

The response curves in 44 week egg weight closely follow the trends observed for egg weight at 28 weeks, although the magnitude of the absolute value for the deviation tends to be greater, corresponding to the increase in mean egg weight with age (Cowen et al., 1964).

On terminating the selection experiment, mean 28 week egg weight in the Regression lines had reached a level about 13 per cent in the case of Strain 2, and about 8 per cent in Strain 5, above the mean level in the control population.

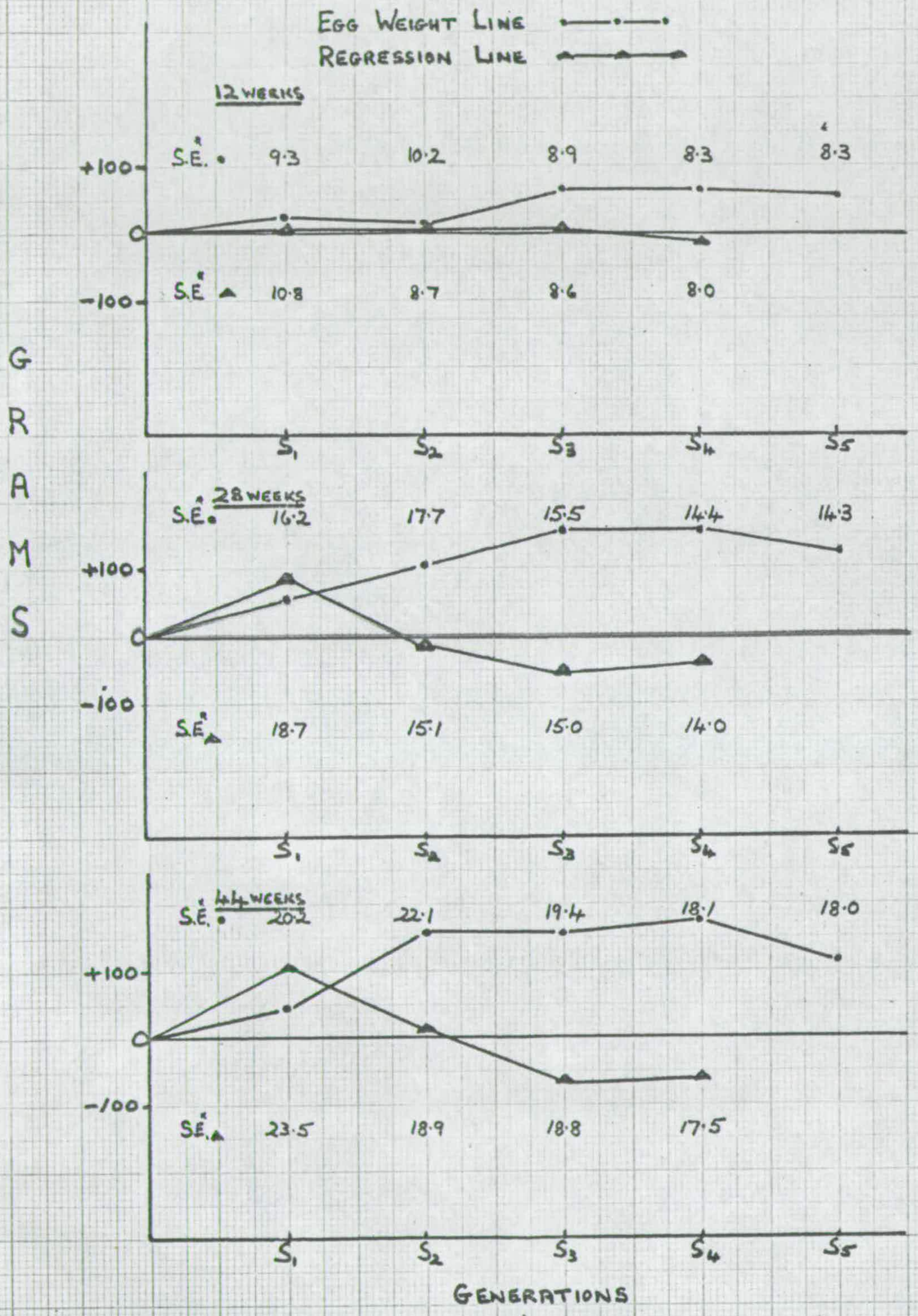
(b) Genetic Changes in Body Weight

The changes that have taken place in the Egg Weight and Regression lines relative to the control are plotted for 3 different ages in Figures 14 and 15. As anticipated, no significant overall changes were observed in body weight in the Regression lines. Thus, the regression selection technique has successfully prevented a correlated increase in body weight

Fig 14

GENETIC CHANGES EFFECTED IN BODY WEIGHT (DEVIATIONS FROM CONTROL)

STRAIN 2

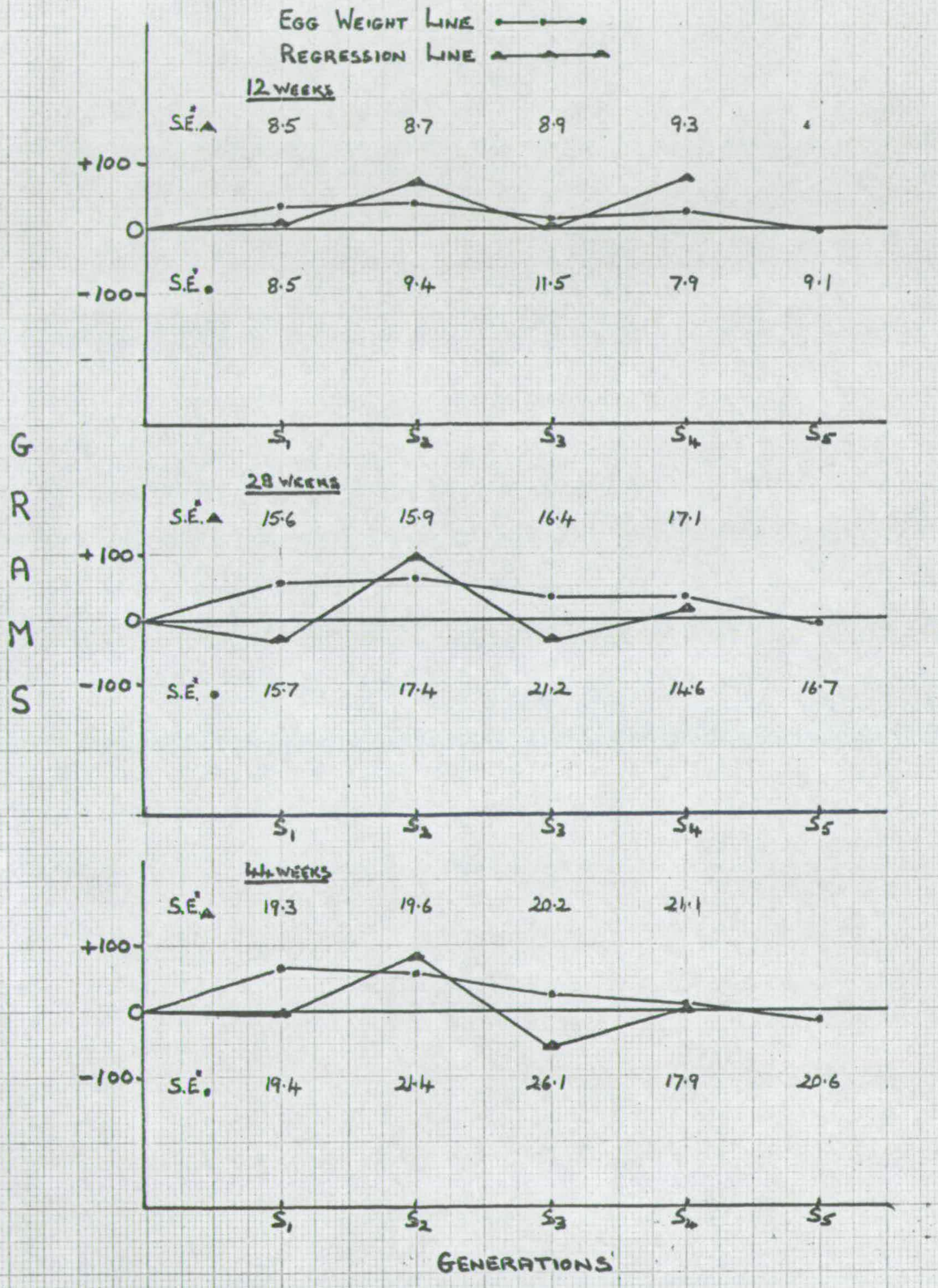


*S.E. of difference = $\sqrt{\frac{1}{n_1}+\frac{1}{n_2}} \cdot \sigma$

Fig 15

GENETIC CHANGES EFFECTED IN BODY WEIGHT (DEVIATIONS FROM CONTROL)

STRAIN 5



* S.E. of difference $= \sqrt{\frac{1}{n_1} + \frac{1}{n_2}} \cdot \sigma$

associated with the increase in mean egg weight in Strain 2, at least, in the short term. Mean body weight was latterly 10 per cent lower in the Strain 2 Regression line compared with the mean body weight for the Egg Weight line, although egg weight was 3 per cent higher in the Regression line.

Any advantage in using the regression selection in order to maintain constant body weight while increasing egg weight is not apparent on comparing the relative changes in mean body weight that have occurred in the Strain 5 Regression and Egg Weight lines, on account of the noted absence of any significant increase in any case in body weight following straightforward selection for increased egg weight. There has been no significant change in body weight in the Strain 5 Regression line, but then neither has there been any in the line selected for increased egg weight alone.

4.4.2 Ratio Selection

The anticipated result of selection on the egg weight to body weight ratio was a rapid decrease in body weight, accompanied by a slight increase in egg weight. This expectation was based upon the known variances and covariance of the component traits forming the ratio (Turner, 1959) and was fully discussed in Section 3.3.2.

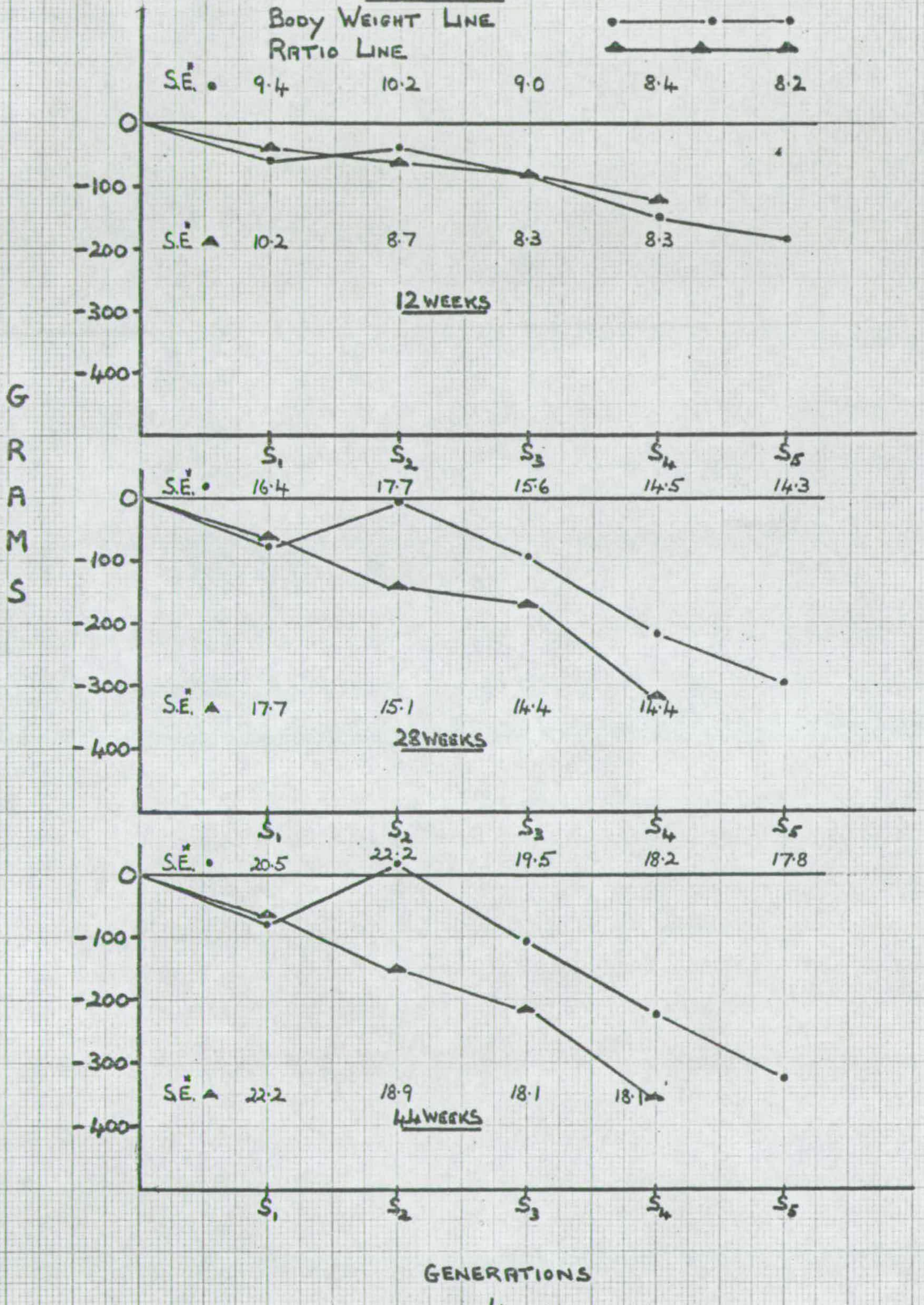
(a) Genetic Changes in Body Weight

The actual decline in body weight that has occurred over 4 generations of Ratio selection is plotted graphically in Figure 16 (Strain 2) and

Fig 16

GENETIC CHANGES EFFECTED IN BODY WEIGHT (DEVIATIONS FROM CONTROL)

STRAIN 2



*S.E of difference $= \sqrt{\frac{1}{n_1} + \frac{1}{n_2}} \cdot \sigma$

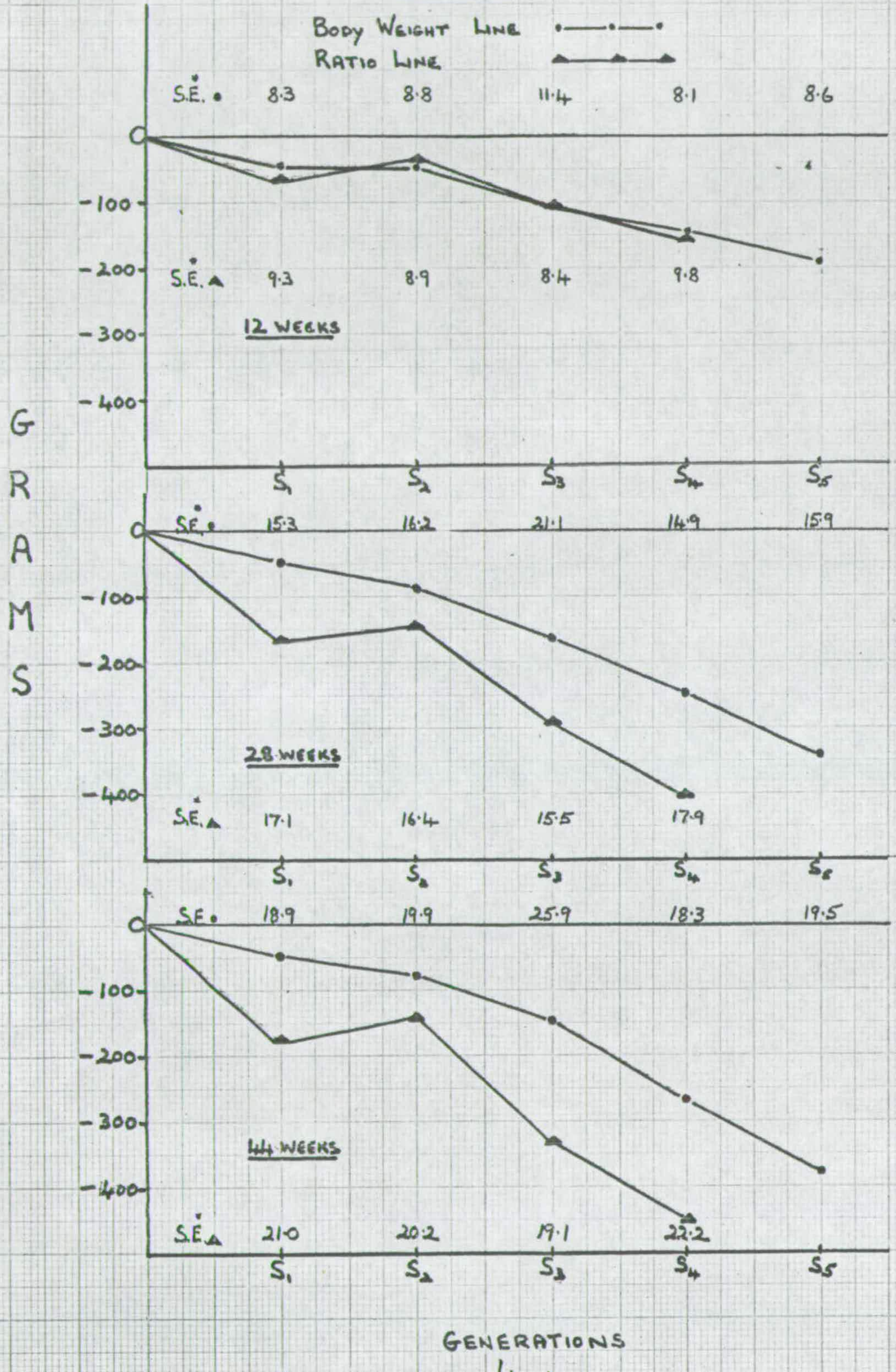
and Figure 17 (Strain 5). In both strains the total reduction effected in body weight is highly significant at all ages and at the later ages is more than comparable with the reduction in body weight brought about over 5 generations through selection on body weight at 12 weeks. For example, the estimated average rate of decline in 28 week body weight per generation, estimated by regressing the mean deviation in body weight on the generation number (Table 29) has been -70 grams and -98 grams in Strain 2 and Strain 5 respectively, which is considerably greater than the average decline noted in the Body Weight lines. However, it should be noted that the average rate of decline has been reduced in the Strain 2 Body Weight line in large part due to an upward trend contrary to the direction of selection which occurred in the second generation, in spite of a negative realised selection differential among the selected parents. This would imply that the realised heritability for that one generation had a negative value which, of course, is nonsense. The reason for the anomalous response in this particular instance remains unexplained, but it has reduced the overall rate of response considerably.

The more rapid decline in body weight noted at 28 and 44 weeks of age, however, in the Ratio lines compared with the Body Weight lines is not apparent at 12 weeks of age where the two sets of responses are more or less equal. This might suggest that selection at a later age (28 weeks) is less effective in changing body weight at a younger age than selection at an early age is in bringing about a change in body weight at an older age (cf. Abplanalp, 1963; Merritt, 1966; 1968) and that this

Fig 17

GENETIC CHANGES EFFECTED IN BODY WEIGHT (DEVIATIONS FROM CONTROL)

STRAIN 5



*S.E. of difference $= \sqrt{\frac{1}{n_1}+\frac{1}{n_2}} \cdot \sigma$

TABLE 29

Regression in mean deviations in body weight and egg weight in the Ratio lines over 4 generations of selection

Strain 2

		b	s.e. of b		O†	
Body Weight:						
12 weeks	g.	-28.7	± 5.1	**	-118	± 8
28 weeks	g.	-70.7	±15.5	**	-318	±14
44 weeks	g.	-80.6	±12.2	***	-354	±18
Egg Weight:						
28 weeks	g.	+0.70	±0.41	N.S.	+1.8	±.28
44 weeks	g.	+0.44	±0.32	N.S.	+1.1	±.32

Strain 5

		b	s.e. of b		O†	
Body Weight:						
12 weeks	g.	-36.2	±13.5	*	-159	±10
28 weeks	g.	-98.4	±22.1	**	-405	±18
44 weeks	g.	-109.4	±27.1	**	-453	±22
Egg Weight:						
28 weeks	g.	-0.31	±0.24	N.S.	-1.6	±0.29
44 weeks	g.	-0.59	±0.32	N.S.	-2.5	±0.36

†O = Observed mean deviation from control in final generation ± s.e. of difference = $\sqrt{\left(\frac{1}{n_1}+\frac{1}{n_2}\right)}\cdot\sigma$

N.S. = Value of b is not significantly different from zero

* = Value of b is significantly different from zero at 90% level

** = Value of b is significantly different from zero at 95% level

*** = Value of b is significantly different from zero at 99% level

would be reflected in some asymmetry in the realised genetic correlations. However, on account of the different selection procedures adopted in this study one cannot compare the correlated response in 12 week body weight directly with the response in 28 week body weight obtained by selecting on values for the ratio, since the response which has resulted in 28 week body weight is not a direct response. It was noted earlier, however, that the estimated realised genetic correlation between 28 week and 12 week body weight following selection for 12 week weight was notably higher ($r_g > +0.9$) than the estimates of around +0.7 obtained by variance analyses in the population. Would measurement of the correlated response in 12 week body weight, given single trait selection on 28 week weight, have yielded a lower estimate for the realised genetic correlation, say +0.5?

The overall reduction in 28 week body weight following 4 generations of Ratio selection amounted to $1.3\sigma_p$ and $2.3\sigma_p$ in Strain 2 and Strain 5 respectively.

(b) Genetic Changes in Egg Weight

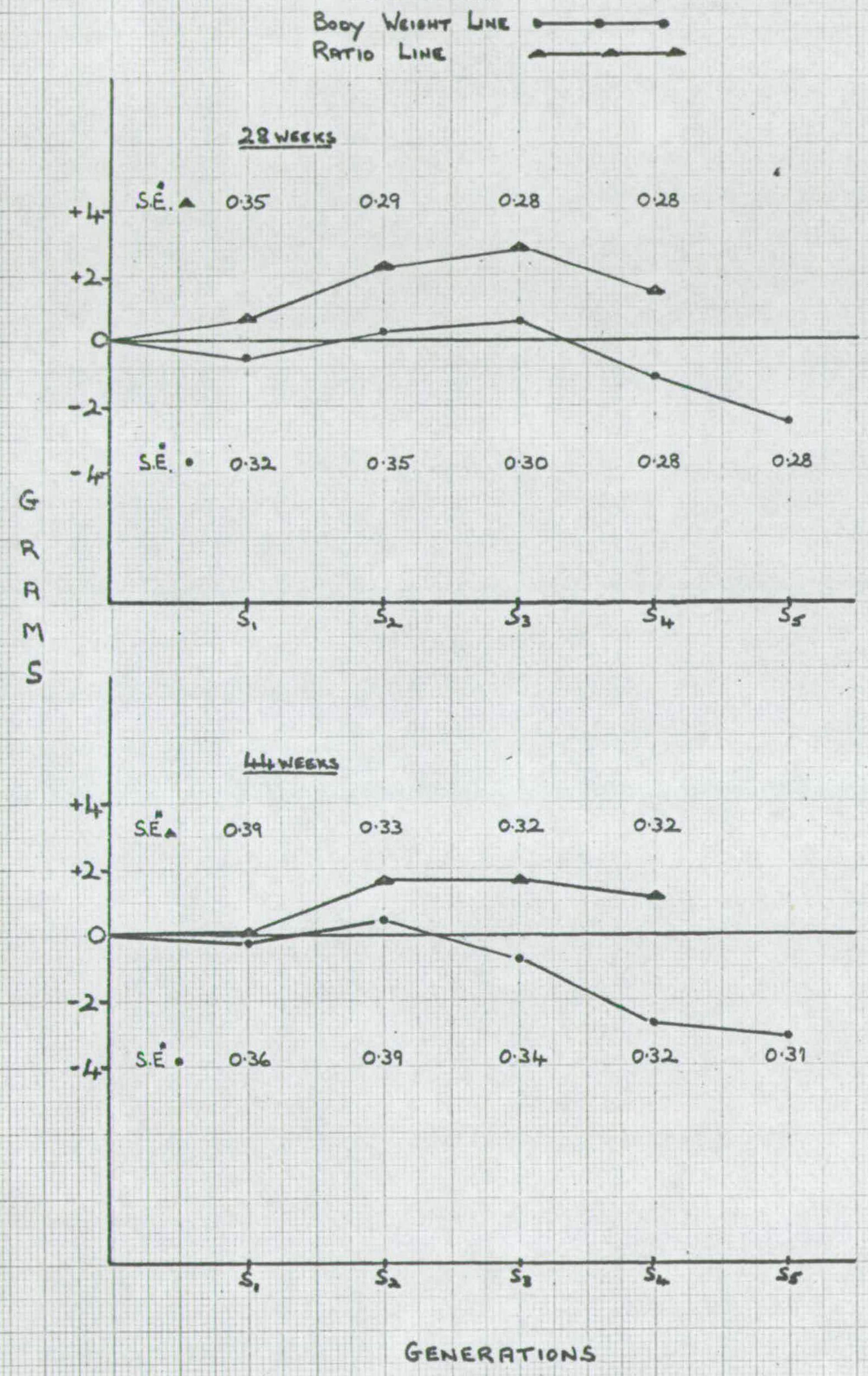
Figures 18 and 19 illustrate the changes that have occurred in mean egg weight in the Ratio lines in comparison with the consistently downward trends in egg weight that have occurred in both Body Weight lines following selection for lower body weight.

The Ratio selection in Strain 2 has been notably successful in maintaining egg weight (if not significantly increasing it) coincident with a reduction in mean 28 week body weight of over 15 per cent in this line. It should perhaps be noted here that regression of the phenotypic

Fig 18

GENETIC CHANGES EFFECTED IN EGG WEIGHT (DEVIATIONS FROM CONTROL)

STRAIN 2

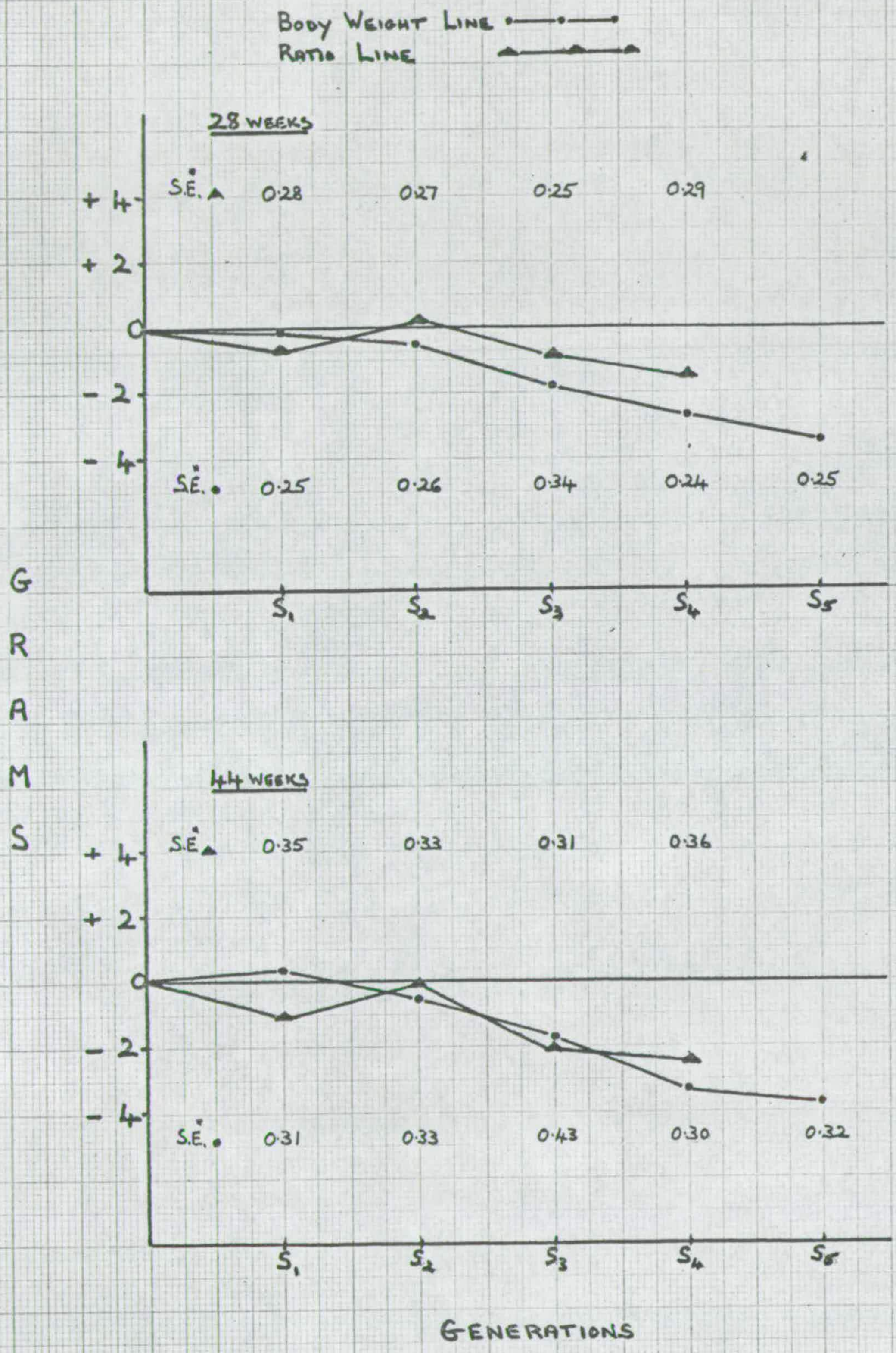


S.E. of difference = $\sqrt{\frac{1}{n_1}+\frac{1}{n_2}} \cdot \sigma$

Fig 19

GENETIC CHANGES EFFECTED IN EGG WEIGHT (DEVIATIONS FROM CONTROL)

STRAIN 5



*S.E. of difference $= \sqrt{\frac{1}{n_1}+\frac{1}{n_2}} \cdot \sigma$

means had indicated a significant upward trend in egg weight within the Ratio lines. Examination of the mean deviations from the control, however, suggests that these trends are no longer statistically significant, although a positive trend in the Strain 2 Ratio line is still clearly apparent. A reassessment of the overall trend in egg weight in the Strain 5 Ratio line on the basis of mean deviations suggests a negative rather than a positive overall trend, although the trend is not yet statistically significant. However, these two examples serve to illustrate how misleading changes in the mean performance alone can be.

Although mean egg weight has apparently declined in the Strain 5 Ratio line by between 1-2 grams, the mean level is nevertheless about 3 per cent higher in the Ratio compared with the Body Weight line, in spite of the fact that mean body weight is appreciably lower in the Ratio line.

4.4.3 Comparison of Ratio and Regression Selection Procedures

Table 30 summarises both the initial and final realised cumulative mean differentials for body weight and egg weight among the parents selected in the Ratio and Regression lines over 4 generations. These cannot be used directly, however, to estimate the efficacy of the selection response since selection on the ratio or deviation from regression involves selecting upon both body weight and egg weight simultaneously and these traits are not genetically independent. Thus, it is necessary to compute the realised selection differentials in this instance in terms of units of the index itself. These were calculated from the differentials

TABLE 30

Cumulative differentials (△) in body weight and egg weight among the selected parents in the Regression and Ratio lines

Strain 2

Line:	△ Body Weight 28 weeks g.		△ Egg Weight 28 weeks g.	
	I*	W*	I*	W*
Regression	-100	-100	+15.12	+14.97
Ratio	-604	-592	+ 5.96	+ 5.60

Strain 5

Line:	△ Body Weight 28 weeks g.		△ Egg Weight 28 weeks g.	
	I*	W*	I*	W*
Regression	-202	-179	+ 9.85	+ 9.70
Ratio	-653	-655	+ 0.99	+ 0.99

*I = Initial differential summed over all selected parents

*W = Weighted realised differential according to the number of progeny for body weight and egg weight observed among the selected parents. The resulting estimates are tabulated (Table 31), both as absolute values and in terms of standardised units of the phenotypic standard deviation of the selection criterion.

The primary response in the compound trait was also calculated indirectly from the observed change effected by the selection on body weight and egg weight separately.

The intensity of selection in the Strain 2 Regression line, amounting to 4.97 standardised units of the index, was as high as the intensity achieved for straightforward selection for body weight or egg weight in the single trait selected lines. However, the cumulative selection differentials in the other lines all fell below 4 standardised phenotypic units and were lower than the intensity achieved in the Body Weight and Egg Weight lines.

The realised heritabilities using the two selection procedures were estimated as a ratio of the observed response in relation to the total selection differential applied. The values obtained in Strain 2 were in close agreement with the earlier values predicted for the heritability of the ratio (0.46 predicted and 0.45 realised) and for the index for deviation from regression (0.44 predicted and 0.48 realised). In Strain 5 the realised heritability for ratio selection (0.49) was close to the estimated value of 0.51 (Table 8), while the realised value of 0.37 for the index selection was only marginally less than the heritability estimate derived earlier (0.42). (See Table 7, page 24).

TABLE 31

Actual selection differentials (ΔP), intensity of selection ($\bar{i}$) achieved and realised heritabilities in Regression and Ratio lines

Selection Criterion:	ΔP	$\bar{i}$	Response (ΔG) (Estimated)	$h^2 = \frac{\Delta G}{\Delta P}$
1. Regression[†] (I)				
Strain 2	+15.58	(+4.97)	+7.00	0.45
Strain 5	+10.79	(+3.85)	+4.02	0.37
2. Ratio (r)[*]				
Strain 2	+.0102	(+3.77)	+.00491	0.48
Strain 5	+.00808	(+3.73)	+.00436	0.49

[†] $\Delta I = \Delta EW - b \Delta BW$

[*] $\Delta r = \bar{r} \left[\frac{\Delta EW}{\overline{EW}} - \frac{\Delta BW}{\overline{BW}} \right]$

Given the standardised selection differentials applied within all 8 selected lines and using the formulae described in Section 3.3 to compute the essential parameters for the Ratio and Regression traits, it is possible to predict the expected direct and correlated responses in the index traits as well as in both component traits for each of the 4 selection criteria using the normal response equations (Falconer, 1960_a). Of particular interest, for example, is a comparison of the magnitude of the correlated responses in the index traits on selecting for body weight or egg weight solely.

Table 32 gives the calculated expected responses for all 4 selection lines in Strain 2 alongside the actual observed responses. Table 33 presents similar data for Strain 5. The observed responses given in the above tables are the weighted mean deviations of the selected line from the control population in the last selected generation. The standard errors of these observed differences are also included.

Egg weight selection in Strain 2 resulted in an increase in egg weight of $1.78\sigma_p$ as a direct response and a correlated response of $+0.77\sigma_p$ in body weight, with the result that while the mean deviation of the line from the average regression of egg weight on body weight has increased, the mean ratio has changed little. In Strain 5 the predicted correlated response of 182 grams in 28 week body weight did not materialise, with the result that the mean egg weight to body weight ratio has improved slightly in this line on account of an increase of $1.67\sigma_p$ in egg weight.

TABLE 32

Comparison of predicted with actual observed
responses within all 4 selected populations, Strain 2

Selection Criterion	Response measured in:							
	Egg Weight (28 weeks) g.		Body Weight (28 weeks) g.		Ratio $\frac{EW}{BW}$		Index (I = EW - b.BW)	
	E.*	O.*	E.*	O.*	E.*	O.*	E.*	O.*
1. Egg Weight	+ 7.2	+5.53† ±0.28	+117	+127 ±14.3	+0.025	+0.011	+6.92	+4.76
2. Body Weight	- 1.36	-2.47 ±0.28	-217	-185 ± 8.2	+0.029	+0.025	0	-0.65
3. Ratio	+ 2.18	+1.77 ±0.28	(12 weeks) -209	-318 ±14.4	+0.042	+0.049	+3.45**	+3.70
4. Regression	+ 6.89	+6.75 ±0.27	0	- 41 ±14.0	+0.034**	+0.028	+6.51	+7.00

Legend to Tables 32 and 33

*E. = Expected response calculated either as a direct response in x,

$R_x = \bar{i}.h^2.\sigma_{p_x}$; or as a correlated response in y following selection for x,

$CR_{y.x} = \bar{i}\ h_x.h_y.r_{g_{y.x}}.\sigma_{p_y}$ (Falconer, 1960$_a$).

*O. = Observed mean deviation for the selected line in egg weight and body weight from the mean for the control population in the last generation of selection; or in the case of the Ratio and Regression 'Traits' as calculated from the observed deviations in the component traits.

† Observed primary responses are underlined thus: +5.53 ±0.28.

** Correlated response in ratio or index following selection on the index or ratio respectively and calculated indirectly from the expected correlated responses in the component traits.

TABLE 33

Comparison of predicted with actual observed
responses within all 4 selected populations, Strain 5

Response measured in:

Selection Criterion	Egg Weight (28 weeks) g. E.*	O.*		Body Weight (28 weeks) g. E.*	O.*		Ratio $\frac{EW}{BW}$ E.*	O.*	Index (I = EW - b.BW) E.*	O.*
1. Egg Weight	+5.90	+4.69	±0.27	+182	- 10	±17	+0.009	+0.025	+5.1	+4.75
2. Body Weight	-2.91	-3.49	±0.25	-271 (12 weeks)	-190	±15.9	+0.033	+0.025	0	-1.42
3. Ratio	+0.96	-1.59	±0.29	-301	-405	±17.9	+0.046	+0.044	+1.76	+0.87
4. Regression	+4.49	+4.10	±0.28	0	+ 14	±17.1	+0.023	+0.019	+5.5	+4.02

See Footnote to Table 32 for Legend relating to the above Table

In the case of the Body Weight selection, the correlated responses are generally in the direction predicted, although the observed decline in egg weight as a correlated response to downward selection for body weight has, in fact, been substantially greater than predicted. The decline in egg weight amounted to $0.8\sigma_p$ in Strain 2 and $1.2\sigma_p$ in Strain 5, while body weight was reduced by approximately $2\sigma_p$ in both lines. The observed change in the mean egg weight/body weight ratio in the Strain 2 Body Weight line is in close agreement with the correlated change predicted. In the Strain 5 Body Weight line, however, in which the primary response in body weight was not as large as expected and the correlated decline in egg weight was more than predicted, the increase in the mean ratio value has not been as significant.

The Ratio selection has obviously altered the mean egg weight/body weight ratio most of all the selection procedures essayed. The observed response in the mean ratio in both Ratio lines was equivalent to a shift of 1.8 phenotypic standard deviations in the ratio. The correlated responses in the component traits which form the ratio matched predictions as far as the direction of the responses obtained in Strain 2, although the magnitude of the actual increase in egg weight has been less than predicted, while the observed decrease in body weight was considerably greater than predicted. In the Strain 5 Ratio line, egg weight has declined by $0.5\sigma_p$, although the predictions would have led one to expect a modest increase in egg weight. Body weight, however, has decreased by over 100 grams more than predicted. The Ratio selection in Strain 2 has increased the mean deviation from regression by just over $1\sigma p$, but in the replicate line in Strain 5 in which selection has reduced both body weight and egg weight, very little change has occurred in the mean deviation from regression.

The Regression selection within Strain 2 has brought about a substantial increase, amounting to $2.23\sigma p$, in the mean deviation from regression, achieved through an increase of $2.1\sigma p$ in egg weight in the absence of a correlated increase in body weight. Coincidentally the mean ratio increased in this line by approximately $1\sigma p$ (or about half the direct response observed in the Ratio line itself). In general, the response to Regression selection in Strain 5 has been less marked, although the correlated responses were all in reasonably close agreement with those predicted, the most noticeable discrepancy being in the direct response itself which was considerably lower than expected.

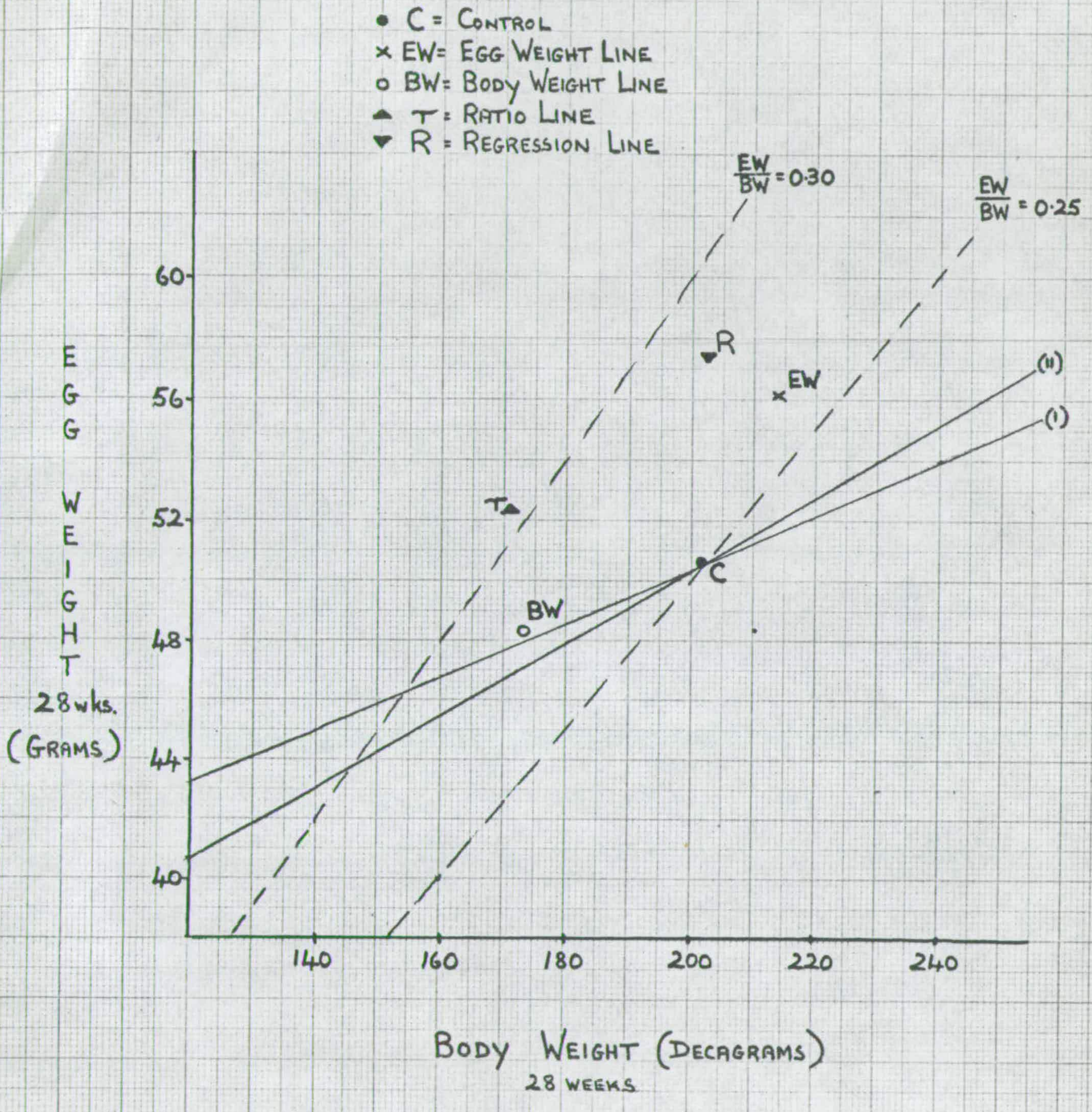
4.4.4 Conclusions

The relative mean 28 week body weight and egg weight of all 4 selected lines in the final recorded generation are compared with the control population in a graphical presentation in Figure 20 for Strain 2 and Figure 21 for Strain 5. These possibly depict the relative changes that have been effected within the Ratio and Regression lines much more clearly than any description.

Selection on deviations from the linear regression has obviously produced the greatest deviation from the average Regression line as

RELATIVE CHANGES IN EGG WEIGHT/BODY WEIGHT RELATIONSHIP BETWEEN SELECTED LINES - FINAL GENERATION, STRAIN 2

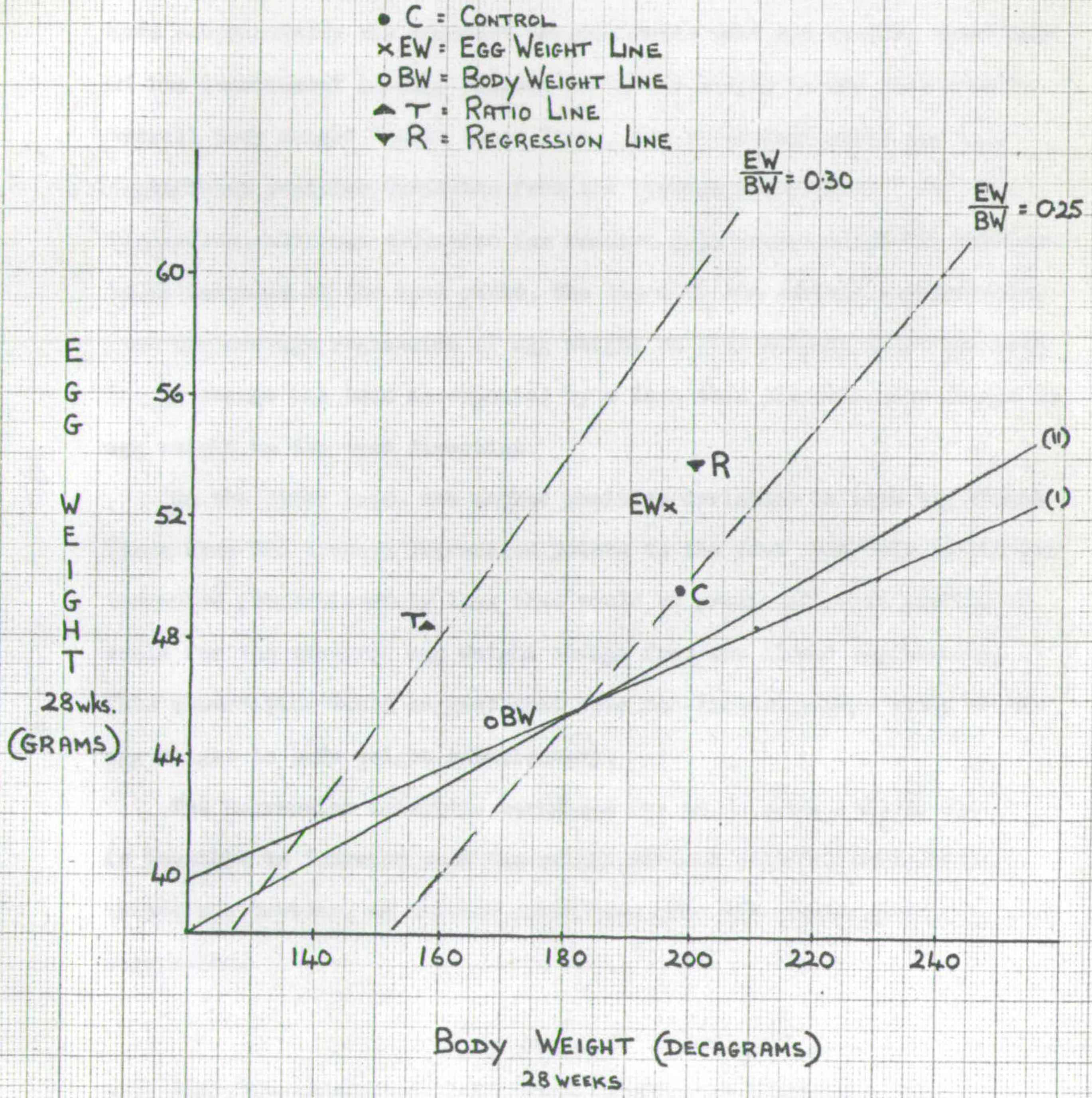
PLOTTED MEAN EGG WEIGHT AND BODY WEIGHT



(I) PHENOTYPIC REGRESSION $Y_e = 43.2 + 0.0469(BW)$
(II) GENETIC REGRESSION $Y_e = 40.7 + 0.0608(BW)$

RELATIVE CHANGES IN EGG WEIGHT/BODY WEIGHT RELATIONSHIP BETWEEN SELECTED LINES - FINAL GENERATION, STRAIN 5

PLOTTED MEAN EGG WEIGHT AND BODY WEIGHT



(I) PHENOTYPIC REGRESSION = 39·8 + 0·0469 (BW)
(II) GENETIC REGRESSION = 38·1 + 0·0608 (BW)

calculated within the base population. The Ratio lines, however, now have substantially the greatest proportionate mean egg weight, about half of the improvement in this respect being due simply to the reduction in overall body weight within these lines, the other half being due to a significant positive deviation from the average regression. In comparison, although selection for reduced body weight alone has resulted in an increase in the mean ratio, the lines do not deviate substantially from the average regression of egg weight on body weight, since the body weight change has been accompanied by a less than proportionate change in egg weight in the same direction.

On the other hand, the marked positive deviation in both Egg Weight lines from the average regression points to the fact that body weight has increased proportionately less than would be predicted on an arithmetic scale for the observed egg weight change from the linear regressions. This observation would suggest that some non-linearity must exist in the egg weight to body weight relationship.

The Regression selection technique has shown quite clearly that it is possible to increase mean egg weight without altering body weight by selecting, however, on maximum deviations from the assumed linear genetic regression.

4.5 Observed Changes in other Traits within the Selected Lines

The Ratio and Regression selection techniques have effectively altered the relative egg to body weight relationship within the two strains.

It is seldom, however, that the practical poultry breeder can restrict his attention, for reasons of overall balanced performance, solely to two traits. Thus the question must be asked: How have these selection procedures affected some of the other production characteristics of these lines?

4.5.1 Egg Production Traits

Figures 22 and 23 present the trends in survivors' egg production of the 4 selected lines as mean deviations from the control population over the 4-5 year period that selection was carried out.

In view of the quite marked yearly fluctuations, it is difficult to differentiate any consistent overall trends. The mean deviations were regressed on years and the only consistent overall trend that reached statistical significance (90 per cent level) was a decline of 1.25 eggs per generation in the early part record from 20 to 44 weeks of age in the Strain 2 Regression line. It is apparent, however, that a downward trend is also emerging within both the Body Weight and Ratio lines in Strain 5. The only suggestion of any upward trend in egg production was within the Strain 2 Body Weight line.

In order to compare the actual trends in the egg production traits, including sexual maturity (age at first egg), with the anticipated responses following selection for body weight or egg weight, the probable overall correlated change was estimated by using the calculated average yearly change and multiplying this by the number of generations. In view

FIG 22

CORRELATED CHANGES IN EGG NUMBERS (DEVIATIONS FROM CONTROL)

STRAIN 2

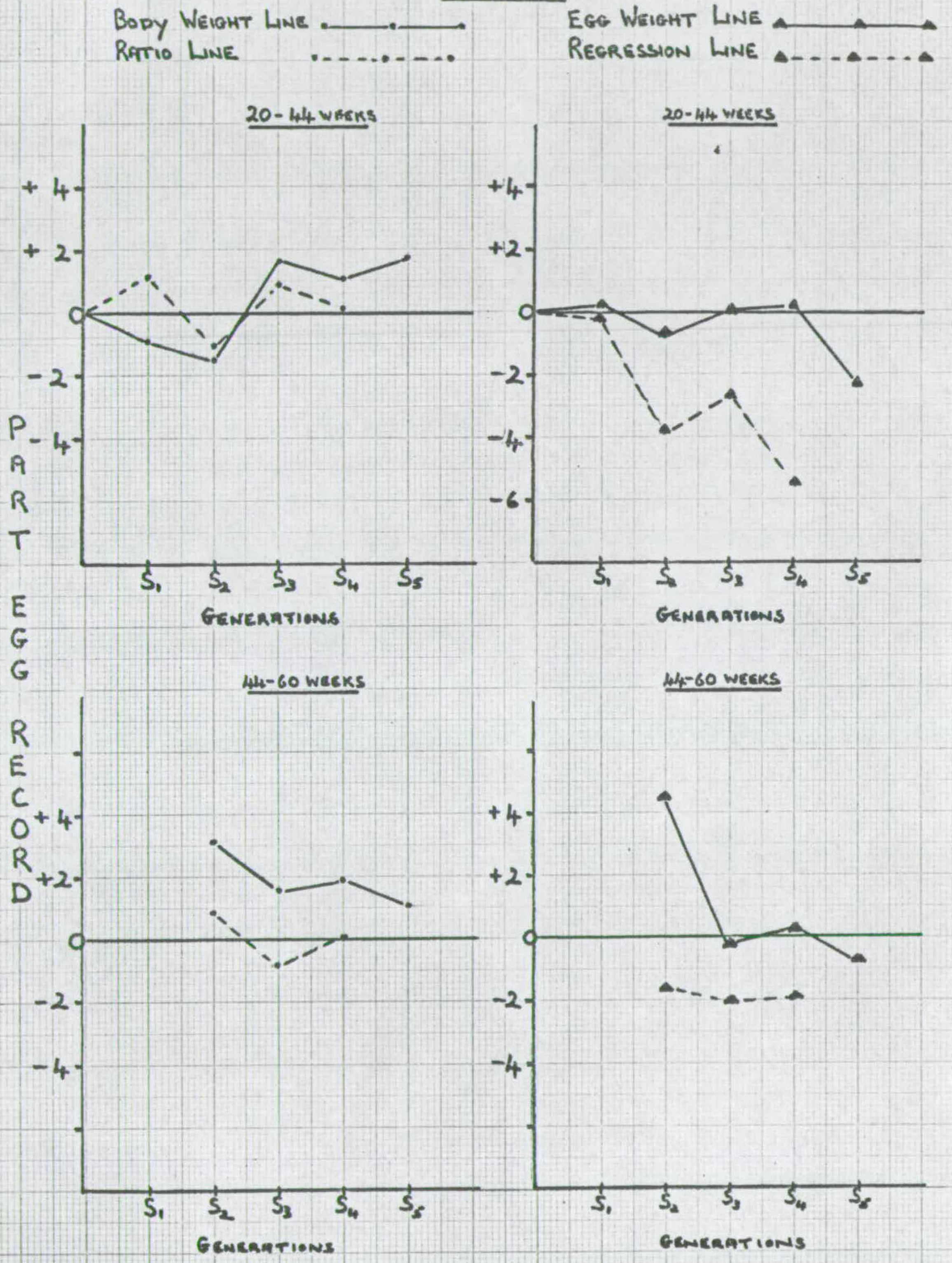
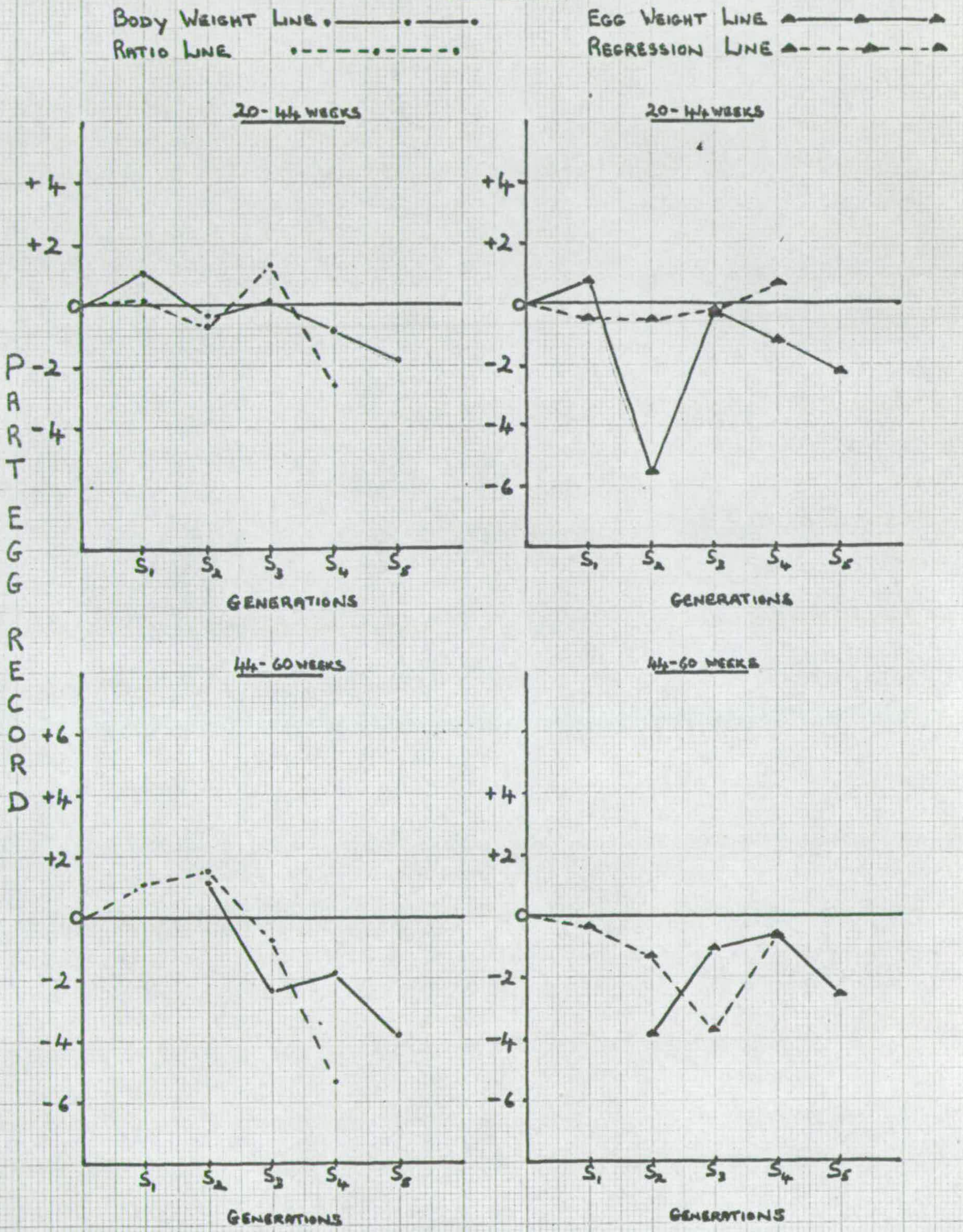


FIG 23

CORRELATED CHANGES IN EGG NUMBERS (DEVIATIONS FROM CONTROL)

STRAIN 5



of the yearly fluctuations it was thought this would give a more reliable estimate of the overall response than the simple deviation noted in the final generation. The changes thus noted in the Body Weight and Egg Weight lines are given in Table 34, along with the changes predicted as an indirect response to selection for reduced body weight or increased egg weight.

In the case of the former, selection for reduced 12 week body weight was anticipated to increase total egg production in Strain 2, although it would lower egg production in the early period through a delay of about 1 week in sexual maturity. In Strain 5 the selection on body weight ought to have had little effect on total egg production. In fact, egg numbers over the full period fell by almost 12 eggs per bird. In the Strain 2 Body Weight line, however, egg numbers increased by somewhat more than predicted.

In the case of the egg weight selections both sets of predictions suggested that the increase in egg weight achieved within these lines should have been accompanied by a quite marked decline in total egg production. However, the predicted decline in total egg production of almost 20 eggs in the Strain 2 Egg Weight line did not materialise in practice, egg numbers showing little significant change overall. Egg production has declined substantially, however, in the Strain 5 Egg Weight line in keeping with predictions.

Table 35 gives the overall changes noted in the egg production traits for the Regression and Ratio lines. The regression selection in

TABLE 34

Comparison of expected (E) and observed (O) change in egg production traits following single trait selection for body weight or egg weight

	Age 1st Egg		Egg Production					
			P_1*		P_2**		Total***	
	E	O	E	O	E	O	E	O
Strain 2:								
Body Weight	+1.1	+0.1	-1.5	+1.2	+4.8	+2.7	+ 7.7	+ 9.1
Egg Weight	+0.3	+0.1	-3.4	-1.1	-5.1	+0.3	-19.8	- 1.8
Strain 5:								
Body Weight	+0.4	+0.5	-1.8	-1.1	+1.5	-4.0	- 0.7	-11.9
Egg Weight	-0.6	-0.2	-1.1	-2.5	-7.0	-2.9	-15.6	-12.6

*P_1 = Part Record for the period 20-44 weeks

**P_2 = Part Record for the period 44-60 weeks

*** = Total egg production to 60 weeks estimated by summing 3 days per week part record and multiplying by a factor of 2.33.

TABLE 35

Changes in Egg Production Traits in Regression and Ratio lines

Regression Lines

	Strain 2		Strain 5	
Age 1st Egg	+ 0.5	wk.	-0.5	wk.
Egg Production				
P_1	- 5.0	eggs	0	eggs
P_2	- 2.1	eggs	-2.1	eggs
Total	-14.2	eggs	-4.9	eggs

Ratio Lines

	Strain 2		Strain 5	
Age 1st Egg	0	wk.	-0.3	wk.
Egg Production				
P_1	+0.2	eggs	-0.9	eggs
P_2	+1.1	eggs	-2.6	eggs
Total	+3.0	eggs	-8.1	eggs

Strain 2 has adversely affected egg numbers and, in fact, has resulted in the most marked decline amongst all 8 selected lines. The overall decline of 14 eggs in total egg production, amounting to a change of approximately $-0.4\sigma_p$, should be contrasted with the insignificant decline of 1.8 eggs in total egg production in the Strain 2 Egg Weight line, which might suggest that selecting for changes in egg weight independent of body weight has a more deleterious effect on egg numbers than straightforward egg weight selection. In the Strain 5 Regression line, however, egg numbers have declined by less than half the decline noted in the Egg Weight line.

The correlated responses in egg production in the Ratio populations appear to parallel those observed in the Body Weight lines, egg numbers tending to increase in Strain 2, but to decline in Strain 5. The magnitude of these changes is, however, less than in the case of the Body Weight lines.

In conclusion, it may be said that in view of the earlier erratic fluctuations in egg production among the various lines it is probably too early to confirm any overall trends in egg production accompanying these selection procedures after only 4 or 5 generations and, in the case of the later egg record, only 3 years' data. However, a significant and substantial decline of about 8 per cent in total egg production has taken place in the Strain 2 Regression line, while egg numbers are probably declining also in both the Egg Weight and Body Weight lines in Strain 5 and possibly in the Ratio line. Egg numbers have, however, increased if anything in the Strain 2 Body Weight and Ratio lines.

4.5.2 Laying House Mortality

The data kept on the respective viability of the lines has been limited to the mortality recorded in the laying house from point-of-lay to the stage at which breeders were selected. The average overall percentage mortality for each line over the 4-5 generations that each line has been maintained is given in Table 36. These figures do not suggest any noticeable difference between lines as regards their viability over this one particular period. With the exception of the Strain 5 Egg Weight line in the 1963-64 season, mortality has not exceeded 2 per cent per month. The exceptionally high mortality which occurred in the Strain 5 second generation of the Egg Weight line coincided with the occurence of a significant number of birds with a penguin-like posture, characterised by excessive weight and large swollen abdomens, although many remained in lay. A similar condition has been reported in White Leghorns (Williamson, 1964) and it can be attributed to the right, normally non-functional oviduct, becoming cystic. McBride (1962) postulated that a single gene was involved, but this has since been refuted by Williamson (1965). The condition was not investigated further in this particular flock. In selecting the subsequent set of female breeders obviously affected birds were excluded and the condition has not recurred to any noticeable extent. However, the reason for its occurrence and non-recurrence must remain for the present purely speculative.

TABLE 36

Percentage laying house mortality to 44 weeks of age

Strain 2

Year	Egg Weight	Regression	Ratio	Body Weight
1962-63	2.6	*	*	4.3
1963-64	7.6	6.3	6.2	10.8
1964-65	7.4	6.6	6.2	9.3
1965-66	7.1	12.6	5.5	8.8
1966-67	4.2	4.9	5.5	3.7

Strain 5

Year	Egg Weight	Regression	Ratio	Body Weight
1962-63	12.8	*	*	10.2
1963-64	29.9	8.9	6.9	10.6
1964-65	8.9	*	*	2.9
1965-66	8.2	6.9	7.0	1.6
1966-67	7.1	4.7	2.6	3.3
1967-68	*	9.8	7.9	*

* Line not recorded

4.5.3 Fertility and Hatchability

No comparative data will be presented for these traits because it was considered that the information available was affected by too many uncontrolled environmental variables. Eggs for setting in the first instance were collected over a 2-week period and the length of storage of hatching eggs was not standardised between hens on account of the difference in rate of lay between individuals. Hatchability was generally poor within all lines, including the control populations (Buvanendran, 1967).

Prolonged storage, combined with large egg size differences between lines would be expected to result in differences in hatching rates (MacLaury et al., 1968) and it is doubtful if one standard set of incubation conditions was equally best suited to the eggs from all lines when set together in the same incubator. It has been observed that the eggs from the large Egg Weight lines took significantly longer to hatch and it has been the practice latterly to set these eggs several hours earlier than the eggs from the other lines in an attempt to synchronise hatching time (Bohren et al., 1961; Crittenden and Bohren, 1961; 1962).

In view of the absence of detailed information on relative fertility and hatchability, the point should be made that the selection differential calculations presented earlier did not provide any evidence of a major fitness problem having arisen within any of the lines to date. In all cases the realised selection differentials were very close to the attempted selection differential.

5. CONCLUDING DISCUSSION

In presenting the foregoing results, the assumption has been made that where consistent and significant trends existed in the mean deviations of the selected line from the control population, these represented a genetic trend arising as a direct or correlated response to the selection applied. However, other factors could conceivably have affected mean performance.

Effect of inbreeding. One such possible confounding factor is the amount of additional inbreeding that occurred in the selected lines in the course of selection. The numbers of effective sires and dams used to reproduce each of the lines are tabulated in Appendix D. From these one can predict the anticipated increase in the average degree of inbreeding using Wright's 1940 formula. These calculations suggest that the cumulative change in the inbreeding coefficient did not exceed more than 6 per cent in any of the lines over the 4-5 generations of selection. However, Wright's formula does not strictly apply in the circumstances, for it assumes that mating for one thing is at random. Chong (1970) has calculated the average inbreeding within the Strain 2 lines from the known pedigrees using the co-ancestry method (Cruden, 1949; Emik and Terrill, 1949) and his calculated values, in all cases, are higher than those predicted. The most striking difference was in the Regression line in which the calculated increase of 11 per cent in the average inbreeding coefficient was more than double that predicted from the number of effective parents (4.4 per cent).

Craig *et al.* (1969) estimated the effects of mild inbreeding of between 5 and 7 per cent on a number of performance traits in several lines undergoing selection, but they concluded that adjustments for inbreeding were not warranted due to the inconsistencies, the lack of significance of the average regression of the traits and the relatively low levels of inbreeding attained. However, at the apparent level of inbreeding attained, in the Strain 2 Regression line at least, some decline in the egg production traits is likely to have occurred as a result of inbreeding depression (Stephenson *et al.*, 1953; Tebb, 1958), which might explain part, but not all, of the marked decline in egg production in the Strain 2 Regression line. On the other hand, it is conceivable that the modest increase in the average level of inbreeding has depressed egg production in some of the other lines, thereby masking the actual gains in potential egg production that may have arisen as a correlated response to selection.

As far as the selection responses in body weight and egg weight are concerned, Shoffner (1948) has reported little effect of inbreeding on these two traits. This was confirmed by Blow and Glazener (1953) and would suggest that the mean deviations in body weight and egg weight need not be corrected for inbreeding effects.

Constancy of control populations. One other important issue in relation to the results discussed is the question as to whether the control populations have, in fact, remained genetically stable, or whether they have responded to changing environmental conditions to the same extent as the selected lines. The mating scheme that was used ought to have minimised any possible change from inbreeding, drift and natural selection and further study of these populations might be useful. Computation of the mean realised selection differentials among the parents used annually to reproduce the control populations might confirm whether or not any selection has been applied incidentally, for example, to body weight and egg weight, in view of the significant upward trends noted in these traits. However, the fact that these trends were observed in both control populations would suggest that the trend was indeed environmental and not genetic.

The value of replication was also apparent in the analysis of the selection responses, particularly in revealing the lack of a correlated response in body weight in Strain 5 following selection for increased egg weight, and also as regards the lack of consistency in the associated trends in egg production between the several selected lines. On the other hand, the reasonably close agreement between the responses obtained using the Regression and Ratio procedures between the replicated lines provides more convincing evidence of their usefulness.

The fact that the breeding populations used in this study had been maintained under relaxed selection for at least 5 years, during the latter 3 of which they had been maintained as large random mated flocks (Clayton and Robertson, 1966) before establishing the control populations is pertinent in a discussion of the constancy of the controls. The period of relaxed selection meant that the populations had most probably reached some degree of genetic equilibrium before the experiment was initiated. This may have been particularly important with respect to egg weight in the context of this experiment, since it has been considered (Lerner, 1950) that populations of commercial chickens have been subjected to fairly intense pressure for egg weight with the result that egg weight is above the point of optimum biological efficiency. The period of relaxed selection preceding the commencement of the experiment meant that any loss of temporary epistatic superiority due to linkage disequilibrium under previous selection as commercial strains ought to have occurred beforehand. Egg weight in the two strains on commencing the experiment was about 2.5 per cent of body weight, suggesting that egg weight had previously regressed, not only as regards its absolute mean value, but also proportionate to body weight.

The principal concern of the study reported in this thesis was an empirical test of the usefulness of the Ratio and Regression selection procedures. Experimentation with these procedures ought to be of interest in two respects. The first is with regard to the genetic interrelationship of egg weight and body weight in the fowl, the nature of the genetic correlation that exists between them and the extent to which their biological association can be modified. The second area of interest concerns their usefulness as practical selection techniques to improve the overall economic performance of commercial egg producing strains of poultry.

(1) Genetic implications of changes effected by selection. It was pointed out earlier that in view of the moderate genetic correlation between egg weight and body weight and considering the amount of additive genetic variance for each of the two traits, it ought to be feasible to exploit the independent genetic variance in each of the traits. The Ratio selection would be expected to favour those genes which acted positively upon egg weight, but negatively upon body weight, or tended to reduce body weight with little or no effect on egg weight. The Ratio selection would be eventually expected, by acting upon those independent loci affecting body weight or those loci contributing to the negative covariance, to result in an increase in the positive correlation between egg weight and body weight. Since selection would ultimately be expected to bring about fixation at all loci other than those contributing to the positive covariance, the genetic correlation ought sooner or later to approach unity, i.e. all the variation remaining in either trait alone would be the result of pleiotropic or closely linked genes affecting both characters in the same direction.

The Regression selection, on the other hand, aimed to exploit the genetic variance in egg weight independent of the covariation between body weight and egg weight through selecting for genes having a positive effect on egg weight, but no effect on body weight.

Table 37 summarises the estimates of the body weight/egg weight correlation within the selected populations as computed within the last 2 generations (see Appendix C). These estimates would certainly point towards the suggestion of an increase in the magnitude of the positive correlation within both Ratio lines. However, one cannot place too great an emphasis on the absolute value for these estimates as they are subject to quite large sampling errors and, in some instances, show a marked fluctuation in their magnitude between years.

TABLE 37

Mean estimates of 28 week Body Weight/
Egg Weight genetic correlation in
final 2 generations within selected lines

	Strain 2	Strain 5
	$r_{g\,S+D}$	$r_{g\,S+D}$
Base Population	+0.31	+0.42
Line:		
Egg Weight	+0.83	+0.57
Regression	+0.48	+0.43
Body Weight	+0.36	+0.63
Ratio	+0.99	+0.82

Approximate standard errors of correlation estimates = ±0.10

In view of the high degree of correlation indicated in the Ratio line it was considered worthwhile recalculating the values as given in Table 8 (page 26) for the heritability of the Ratio and its correlation with the traits forming the Ratio. The earlier predictions had indicated a slight but positive correlation between the Ratio and egg weight, yet the later responses in egg weight in both Ratio lines have shown a downward response in egg weight, suggesting that the relationship of the Ratio to egg weight has altered as a result of a change in the underlying parameters. The recalculated heritabilities and genetic correlations for the Ratio are included in Table 38. These were calculated using the variances and covariances for egg weight and body weight estimated in the last 2 generations in the Strain 2 Ratio line and over the last 3 generations in Strain 5.

TABLE 38

Re-estimated values for the heritabilities
and genetic correlations of body weight,
egg weight and of the ratio $\frac{(EW)}{(BW)}$ in Ratio lines
Strain 2 (S2) and Strain 5 (S5)

h^{2*}	Body Weight 28 weeks	Egg Weight 28 weeks	Egg Weight / Body Weight
		Genetic correlations, r_g	
28 wk. Body Weight	S2 0.54 S5 0.73	+0.99	-0.82
28 wk. Egg Weight	+0.82	S2 0.45 S5 0.62	-0.30
Egg Weight / Body Weight	-0.79	-0.20	S2 0.23 S5 0.36
	Genetic correlations, r_g		

* Estimates for Strain 2 lie above, and
those for Strain 5 below the diagonal

These estimates reveal a remarkable change in the relationship between the Ratio trait and egg weight; the genetic correlations now being as strongly negative as formerly they were positive. The heritability of the Ratio trait has declined considerably, although the heritability of body weight and egg weight has not diminished. Continued selection on the basis of the Ratio would thus be expected to give a lessened response per generation and a correlated decline in mean egg weight although the Ratio value itself would increase.

The Regression selection lines have responded very much as predicted. Egg weight has continued to increase up to the last generation of selection, although the realised heritability in Strain 5 has been somewhat lower than the estimated heritability for deviations from Regression. Body weight has been effectively maintained constant. The current level of heritability of the Regression index in the selected lines was calculated within the last 2 generations and this is included in Table 39. The estimate for Strain 2 has declined, suggesting that the rate of response to selection for deviations from Regression will begin to diminish. For the present, however, the heritability of the index in the Strain 5 Regression line appears as yet undiminished.

In summary, the overall fit of observed with predicted changes in the principal traits examined in this study has been reasonably good. A notable discrepancy, however, was the absence of a significant correlated increase in body weight in Strain 5 following egg weight selection in an

TABLE 39

Comparison of current estimates of egg weight, body weight and deviations from Regression in final 2 generations of Regression lines with the estimates in the unselected population

	h^2 28 wk. BW	h^2 28 wk. EW	$r_{p_{EW/BW}}$	$r_{g_{EW/BW}}$	h^{2*}_{I}
Strain 2					
Base Population	0.46	0.48	+0.17	+0.31	0.44
Current Population	0.68	0.44	+0.26	+0.48	0.37
Strain 5					
Base Population	0.66	0.49	+0.23	+0.42	0.42
Current Population	0.60	0.44	+0.34	+0.43	0.57

* Heritability of the index (I) = E - b.W.

upward direction, although the realised genetic correlation between egg weight and body weight when selection was applied to body weight in a downward direction was considerably higher than the estimated genetic correlation between the two traits. This points to a marked asymmetry in the genetic correlation as has previously been noted in a number of two-way selection experiments; in chickens by Nordskog and Festing, 1962 and Siegel, 1962; in mice by Falconer, 1960_b and in Drosophila melanogaster by Clayton et al., 1957. Bohren et al. (1967) have discussed the conditions likely to result in asymmetrical correlated responses to selection. They concluded that the most likely cause of asymmetry is loci contributing negatively to the covariance between the two traits concerned and having gene frequencies other than 0.5. They suggested too that asymmetry of correlated response is likely to be found fairly frequently.

Another area in which there has been some inconsistency has been in the changes in the egg production traits associated with selection for increased egg weight or decreased body weight. Further information regarding the correlation, particularly of body weight with egg production, is of considerable importance to the practical breeder, in view of the dominant effect that egg-laying ability has on the profitability of commercial stocks (Nordskog, 1959; Foster, 1967).

The genetic correlation between body weight and total egg production has been reported as positive, Krueger et al., 1952 (+0.07); Wyatt, 1954 (+0.56), but negative, for example, by Hogsett and Nordskog, 1958 (-0.24) and Johansson and Rendel, 1968 (-0.10). The control populations which have been maintained throughout this experiment have provided an opportunity to obtain further estimates of the genetic correlations between body weight and egg production for both the early and later part of the laying year. These estimates are summarised in Table 40 and are the average of the yearly estimates within the Strain 2 and Strain 5 control populations as presented in Tables 15 and 16 (pages 53 and 54). The magnitude, and in some cases the sign, of the correlation between body weight and egg production depends partly on the age at which body weight is measured. In both strains, for example, 12 week body weight is negatively correlated with age at first egg, positively correlated with egg production over the first 6 months in lay, but negatively correlated with egg production over the following 4 months. These estimates also highlight the difference in magnitude of the correlation of body weight with egg production between the two strains. In the case of Strain 2 body weight is positively and strongly correlated with egg production throughout, the only exception being the negative correlation between 12 week body weight and egg production in the later period. However, in the case of Strain 5, the correlation of 12 week and 44 week body weight with total egg production is almost zero, while the correlation between 28 week body weight and egg production is significantly negative.

Finally, in this context, it is of interest to note what effect, if any, selection for the body weight and egg weight traits has had upon the magnitude of the genetic correlation between body weight and egg production.

TABLE 40

Average estimates of the genetic correlations between body weight and egg production traits over 3 years in the control populations

		Age at 1st Egg	Egg Numbers (Part Record)		
			P_1	P_2	Total
Body Weight:	*				
12 weeks	S2	-0.56	+0.44	-0.37	+0.13
	S5	-0.33	+0.11	-0.08	+0.03
28 weeks	S2	-0.37	+0.53	+0.12	+0.43
	S5	-0.10	-0.08	-0.14	-0.11
44 weeks	S2	-0.23	+0.34	+0.23	+0.38
	S5	-0.18	+0.05	-0.05	+0.01

* Estimates for Strain 2 (S2) on the first line, Strain 5 (S5) underneath

P_1 = Period from 20-40 weeks; P_2 = Period from 40-60 weeks

Total = Total record 20-60 weeks

The average of the estimates for the genetic correlations between body weight at 28 and 44 weeks and total egg production in the last two generations for each of the selected lines are given in Table 41. These estimates are, of course, subject to quite large sampling errors and, in some cases, the individual estimates for the correlations (see Appendix C) show quite marked fluctuations between years, with the result that one would not place too great a reliance on individual estimates. However, Table 41 does appear to indicate that there has been a tendency for a negative correlation between body weight and egg production to develop in those lines selected for large eggs, while in the lines selected for smaller body weight the correlation has remained or turned increasingly positive.

The changes in the magnitude, and in some instances the sign, of the transient genetic correlations that have occurred in the course of 4-5 generations of selection in this particular study are worth noting in view of the use of estimates of genetic correlations in formulating multiple-trait selection indices. Bohren _et_ _al_. (1967) have suggested that the static description of a population in terms of additive genetic variances and covariances will be valid in prediction over a much shorter period for correlated responses than it will be for direct responses, and that predictions really require to be based upon the genetic parameters estimated in each generation.

TABLE 41

Average estimates of the genetic correlations between body weight and total egg production within the selected populations

Strain 2

	r_g 28 wk. BW/Egg Production	r_g 44 wk. BW/Egg Production
Base Population	+0.43	+0.38
Line:		
Egg Weight	+0.11	-0.07
Regression	-0.28	-0.26
Body Weight	+0.39	+0.27
Ratio	+0.39	+0.27

Strain 5

	r_g 28 wk. BW/Egg Production	r_g 44 wk. BW/Egg Production
Base Population	-0.11	+0.01
Line:		
Egg Weight	-0.08	-0.21
Regression	+0.03	-0.05
Body Weight	+0.18	+0.29
Ratio	+0.20	+0.21

(2) Economic implications of changes effected by selection. The Ratio and Regression selection procedures have undoubtedly been effective in the short term as a means of selecting body weight and egg weight in contrary directions. Egg weight in the Regression lines has been raised to a commercially satisfactory level (indeed, in the Strain 2 Regression line mean egg weight is now well above the normal level attained by commercial strains) the improvement having been achieved without any increase in mean body weight. The Ratio selection technique, on the other hand, has reduced body weight substantially, with a less than proportionate associated decrease in egg weight. In terms of their usefulness in practice, a great deal depends upon the relative economic value placed upon a unit change in either egg weight or body weight, and also upon the correlated changes in egg production. The suggestion was made earlier that if these procedures proved to be effective in achieving a significant improvement in the relative egg weight to body weight relationship within a given strain, without incurring any permanent loss of egg production genes, they might be used to effect a substantial reduction in body weight or an increase in egg weight within a given strain to be used subsequently in a complementary fashion in a strain-crossing programme.

In order to obtain an assessment of the outcome of these selection procedures upon the overall commercial performance of the strains used in this study, an entry consisting of two separate samples of crosses between the two Ratio lines and between the two Regression lines was submitted for independent testing, together with an entry comprising a cross between the two control populations in a Random Sample Test of commercial breeders' stock. In all instances, the experimental entries, submitted as day-old chicks, were produced by crossing a representative sample of Strain 5 males crossed onto Strain 2 females. A summary of the comparative performance of these 3 entries on test is given in Table 42. The comparison provides useful information, not only on the overall performance of these lines, but also features the effect that the relative changes in the biological components of performance have had upon the overall economic return.

The Ratio cross entry had a significantly lower average body weight, not only compared with the Control entry, but also in relation to the average body weight of commercial hybrids on test. As a result of the reduced body weight it also had a significantly lower food consumption (saving of 5-6 lb. per bird in total food consumption during lay). The Ratio entry also had a substantially higher rate of lay and hen-housed average than either the Control or Regression entry, the hen-housed average exceeding the average for the test. Although percent 'large' eggs was lower compared with the Control, the Ratio entry had a higher percentage of 'standard' eggs. Mean egg weight has not changed perceptibly therefore. The overall margin per bird for the Ratio entry was about equal to the average for the test and was of the order of three shillings per bird more than for the Control. The Regression entry showed a notable improvement in egg gradings, the percentage large and standard amounting to 74 per cent compared with 57 per cent for the Control, while body weight is no heavier

TABLE 42

Relative performance of strain cross entries
from the Ratio, Regression and Control lines
in the National Poultry Tests Limited,
Random Sample Egg Production Test, 1968-69[†]

	(Entry No. 21)	(Entry No. 4)			
		4A	4B	Test Average	L.S.D.*
	Control	Ratio	Regression		
Performance Trait:					
Margin (shillings)**	12.56	15.58	13.00	16.68	2.44
Hen-housed average	245	260	228	252	12.2
Hen-day % Prod.*	64.0	66.6	60.7	66.0	2.4
% Mortality					
(127-532 days)	13.5	9.9	15.1	13.3	5.7
Food Consumption:					
lb. 127-532 days	103.3	97.7	106.4	106.2	3.2
oz. per bird per day	4.10	3.85	4.20	4.21	0.13
Body Weight: (lb.)					
126 days	3.20	2.94	3.14	3.30	-
Survivors	4.57	3.92	4.63	4.49	0.19
Age to 50% Prod.* (days)	158	154	156	159	-
Egg Gradings:					
% Large	14.0 } 57.5	11.8 } 59.4	37.3 } 74.5	29.5 } 71.5	5.1
% Standard	43.5 }	47.6 }	37.2 }	42.0 }	-
% Medium	24.8	23.4	12.7	15.5	-
% Small	4.2	3.6	1.5	2.0	-
% Ex. Small	2.6	2.1	0.8	1.1	-
% Seconds	9.0	8.6	8.5	8.5	2.7
% Rejects	1.9	3.0	2.0	1.4	-

* L.S.D. = Least significant difference estimate between entries in test (95% level).

** = Income from eggs and carcass minus food cost from 0 to 532 days of age on a per bird housed basis.

[†] The co-operation of National Poultry Tests Limited, Milford Test Ground, Enton, Godalming, Surrey in providing this additional information is gratefully acknowledged.

Ref. Third National Random Sample Egg Production Test, 1968-69 Final Report.

than for the Control. Egg production (both rate of lay and hen-housed average) is significantly and substantially lower (-17 eggs in the hen-housed average) compared to the Control, while food consumption, in spite of the lower number of eggs produced, has increased on account of the increase in average egg weight. The overall margin per bird was only slightly better than for the Control.

The information provided by this test indicates that the decline in egg production noted in the Regression selected lines has not been recouped on crossing the two lines together, confirming that there has been a real loss of egg production genes in the Regression lines as a result of selecting solely for increased egg weight independent of body weight. This would appear to confirm that selection for an extreme phenotype in a metric trait inevitably results eventually in a correlated response in some other component, in this instance egg numbers, in order to maintain a physiological balance of total egg yield (numbers x weight) to body weight (Williams, 1959). Thus, although a notable improvement has been achieved in the commercial egg gradings within the Regression lines, the increase in total egg mass has not been very marked (Table 43) and is less than even the modest increase in total yield obtained in the Ratio lines where selection has been applied to egg weight and body weight in opposing directions.

Somewhat unexpectedly the reduction in body weight resulting from selecting on the ratio has been accompanied by a correlated increase in the egg number trait. Thus, selection on the ratio trait, in this instance,

TABLE 43

Comparative Biological Efficiency of Selected Populations

	Body Weight g.	Egg Numbers	Average Egg Weight g.	Total Egg Mass Kg.	Egg Mass / Body Weight	Food Consumed Kg.	Food / Egg Product
Control	2,088	245	58	14.21	6.8	46.89	3.3
Ratio	1,770	260	58	15.08	8.5	44.35	2.9
Regression	2,088	228	65	14.82	7.0	48.30	3.2
Regr. x Ratio?	1,929	245	61	14.95	7.7	46.30	3.0

appears to have served as an excellent way of indirectly increasing rate of lay and hen-housed egg production. This is surprising in view of the positive correlation noted earlier between body weight and total egg production. However, Jaap _et al_. (1962) reported a negative realised genetic correlation between body weight and egg numbers in a selection experiment in a meat-type strain, although they had earlier predicted a positive correlation. Several experiments which have examined selection for increased egg production have observed a decline in body weight as a correlated response to selection for increased egg production (e.g. Gowe and Strain, 1963; Morris, 1963; Nordskog _et al_., 1967 and Saadeh _et al_., 1968).

In common with most selection studies with animals, the experiments reported in this thesis raise more questions than they have answered. For the present, however, this study has shown empirically that the Ratio selection procedure has not only successfully increased the egg weight to body weight ratio within the selected lines, but has also resulted in a marked improvement in both the biological and economic efficiency of the lines in which this relatively simple selection criterion was adopted. One question, at least, remains: How much farther can the Ratio selection take us? Nordskog (unpublished) has reported reaching a definite ceiling when selection is for large egg size and small body size. How close have we come to the physiological limit within the Ratio lines? Continued selection for the ratio has been shown from the calculated genetic parameters to be likely to result from now on in a negative response in egg weight. How much farther, for example, can the downward response in body weight continue before egg numbers are likely to regress also?

The Regression selection has been shown to be remarkably effective in increasing egg weight independent of body weight, but a possible physiological limit would appear to have been reached already within these lines; further selection is likely to produce a lowered rate of response in egg weight and a continued decline in egg numbers.

It would, however, be interesting to experiment farther with these techniques in the same populations. The deviation from Regression selection might, for example, be worth testing within a sub-line derived from the Ratio line to ascertain the extent to which egg weight might be increased in this population while maintaining body weight at the existing level. On the other hand, it would possibly be worthwhile comparing the efficiency of a simple index of the same form, the object of which was to select for reduced body weight independent of egg weight. The Ratio selection produced a positive increase in egg weight concurrent with a decrease in body weight during the earlier stages of this experiment, but the resultant increase in egg weight is likely to be more than eroded if selection on the ratio continues.

BIBLIOGRAPHY

Abplanalp, H. (1956). Selection procedures for poultry flocks with many hatches. Poult. Sci. 35, 1285.

Abplanalp, H. (1957). Genetic and environmental correlations among production traits of poultry. Poult. Sci. 36, 226.

Abplanalp, H. (1961). Linear heritability estimates. Genet. Res. 2, 439.

Abplanalp, H. (1962). Modification of selection limits for egg number. Genet. Res. 3, 210.

Abplanalp, H., Azmundson, V. S. and Lerner, I. M. (1960). Experimental test of a selection index. Poult. Sci. 39, 151.

Abplanalp, H., Ogasawara, F. X. and Azmundson, V. S. (1963). Influence of selection for body weight at different ages on growth of turkeys. Br. Poult. Sci. 4, 71.

Arthur, J. A. (1966). Drawbacks to the use of a random-bred control for hybrid populations. Poult. Sci. 45, 1066 (Abstr. only).

Beilharz, R. G. (1962). A review of the importance of sex-linkage in inheritance. XII Wld's. Poult. Congr., Sect. Papers, 63.

Bichard, M. and Mound, B. A. (1963). The prediction of egg weight and value from samples. Br. Poult. Sci. 4, 209.

Blow, W. L. and Glazener, E. W. (1953). The effect of inbreeding on some production characters in poultry. Poult. Sci. 32, 696.

Blyth, J. S. S. (1952). The correlation between egg number and egg weight in the fowl: an investigation of its inconsistency. Poult. Sci. 31, 254.

Bohren, B. B. Crittenden, L. B. and King, R. T. (1961). Hatching time and hatchability in the fowl. Poult. Sci. 40, 620.

Bohren, B. B., Hill, W. G. and Robertson, A. (1966). Some observations on asymmetrical correlated responses to selection. Genet. Res. 1, 44.

Bohren, B. B. and McKean, H. E. (1964). Relaxed selection in a closed flock of White Leghorns. Genetics 49, 279.

Bray, D. F., Bell, A. E. and King, S. C. (1962). The importance of genotype by environment interaction, with reference to control populations. Genet. Res. 3, 282.

Briggs, D. M. and Nordskog, A. W. (1967). Antagonistic selection for body weight and egg weight. Poult. Sci. 46, 1237 (Abstr. only).

Brody, S. (1945). Bioenergetics and Growth. Reinhold Publ. Co., New York.

Buvanendran, V. (1967). A search for an association between maternal egg white protein polymorphisms and embryonic mortality in the domestic fowl. Br. Poult. Sci. 8, 1.

Carte, I. F. and Siegel, P. B. (1968). Correlated heritabilities of unselected traits: a check on procedure. Poult. Sci. 47, 1821.

Chong, S. N. (1970). Unpublished data, University of Edinburgh.

Clayton, G. A. (1968). Some implications of selection results in poultry. Wld's. Poult. Sci. J. 24, 37.

Clayton, G. A., Morris, J. A. and Robertson, A. (1957). An experimental check on quantitative genetic theory. 1. Short-term responses to selection. J. Genet. 55, 131.

Clayton, G. A. and Robertson, A. (1966). Genetics of changes in economic traits during the laying year. Br. Poult. Sci. 7, 143.

Cochran, W. G. (1951). Improvement by means of selection. Proc. 2nd Berkeley Symp. on Math. Stat. and Prob., Univ. Calif. Press, 449.

Cock, A. G. (1963_a). Genetical studies on growth and form in the fowl. 1. Phenotypic variation in the relative growth patterns of shank length and body weight. Genet. Res. 4, 167.

Cock, A. G. (1963). Quantitative developmental genetics of body shape and size in domestic fowl. Proc. XI Int. Congr. Genetics, The Hague. Section Papers, 261.

Cock, A. G. (1969). Genetical studies on growth and form in the fowl. 2. The complexity of changes in skeletal proportions produced by selection. Genet. Res. 14, 237.

Cockrem, F. (1959). Selection for relationships opposite to those predicted by the genetic correlation between two traits in the house mouse. (Mus Musculus). Nature, Lond. 183, 342.

Cowen, N. S., Bohren, B. B. and McKean, H. E. (1964). Increase in pullet egg size with age. Poult. Sci. 43, 482.

Craig, J. V., Biswas, D. K. and Saadeh, H. K. (1969). Genetic variation and correlated responses in chickens selected for part-year rate of egg production. Poult. Sci. 48, 1288.

Crittenden, L. B. and Bohren, B. B. (1961). The genetic and environmental effects of hatching time, egg weight and holding time on hatchability. Poult. Sci. 40, 1736.

Crittenden, L. B. and Bohren, B. B. (1962). The effects of current egg production, time in production, age of pullet and inbreeding on hatchability and hatching time. Poult. Sci. 41, 426.

Crow, J. F. (1954). Breeding structure of populations. 2. Effective population number in Statistics and Mathematics in Biology, 543. Ed. Kempthorne, O., Bancroft, T. A., Gowen, J. W. and Lush, J. L. Iowa State College Press.

Crow, J. F. and Morton, N. E. (1955). Measurement of gene frequency drift in small populations. Evolution 9, 202.

Cruden, D. (1949). The computation of inbreeding coefficients in closed populations. J. Hered. 40, 248.

Dev, D. S., Jaap, R. G. and Harvey, W. R. (1969). Results of selection for eight-week body weight in three broiler populations of chickens. Poult. Sci. 48, 1336.

Dickerson, G. E. (1955). Genetic slippage in response to selection for multiple objectives. Cold. Spr. Harb. Symp. quant. Biol. 20, 213.

Dickerson, G. E. (1957). Genetic variation in some economic characters of Leghorn-type chickens. Poult. Sci. 36, 1113.

Dickerson, G. E. (1962). Experimental evaluation of selection theory in poultry. Proc. XII Wld's. Poult. Congr. (Sydney) Symposia, 17.

Dickerson, G. E. (1963). Experimental evaluation of selection theory in poultry. Proc. XI Int. Congr. Genet. 3, 747.

Dickerson, G. E. (1968). Lessons to be learned from poultry breeding. Proc. Symp. Animal Breeding in the age of A.l. Univ. Wisconsin, Madison, 69.

Dickerson, G. E. (1970). Efficiency of animal production: Molding the biological components. J. Anim. Sci. 30, 849.

Dryden, J. (1921). Egg laying characteristics of the hen. Oregon Agr. Expt. St. Bull. 180.

Edwards, D. G. and Morris, T. R. (1967). The effect of maize and maize oil on egg weight. Br. Poult. Sci. 8, 163.

Emik, L. O. and Terrill, C. E. (1949). Systematic procedures for calculating inbreeding coefficients. J. Hered. 40, 51.

Faber, H. von (1960). Methoden zur Verkürzung der Fallnestkontrolle unter Berücksichtigung der Familienauslese. Arch. Geflugelk., 24, 35.

Falconer, D. S. (1954). Validity of the theory of genetic correlation. J. Hered. 45, 42.

Falconer, D. S. (1955). Patterns of response in selection experiments with mice. Cold. Spr. Harb. Symp. quant. Biol. 20, 178.

Falconer, D. S. (1960_a). Introduction to Quantitative Genetics. Oliver and Boyd, Edinburgh.

Falconer, D. S. (1960_b). Selection of mice for growth on high and low planes of nutrition. Genet. Res. 1, 91.

Festing, M. F. and Nordskog, A. W. (1967). Response to selection for body weight and egg weight in chickens. Genetics 55, 219.

Foster, W. H. (1967). The relative importance of traits reported in the first three Gosford random sample tests. Br. Poult. Sci. 8, 201.

Friars, G. W., Bohren, B. B. and McKean, H. E. (1962). Time trends in estimates of genetic parameters in a population of chickens subjected to multiple objective selection. Poult. Sci. 41, 1773.

Goodwin, K., Dickerson, G. E. and Lamoreux, W. F. (1960). An experimental design for separating genetic and environmental changes in animal populations under selection in Biometrical Genetics, Ed. Kempthorne, O., 117. Pergamon Press.

Goodwin, K., Dickerson, G. E. and Lamoreux, W. F. (1955). A technique for measuring genetic progress in poultry breeding experiments. Poult. Sci. 34, 1197.

Gowe, R. S. and Johnson, A. S. (1956). The performance of a control strain of S. C. White Leghorn stock over four generations on test at several locations. Poult. Sci. 35, 1146.

Gowe, R. S., Johnson, A. S., Downs, J. H., Gibson, R., Mountain, W. F., Strain, J. H. and Tinney, B. F. (1959_a). Environment and poultry breeding problems. 4. The value of a random-bred control strain in a selection study. Poult. Sci. 38, 443.

Gowe, R. S., Robertson, A. and Latter, B. D. H. (1959_b). Environment and poultry breeding problems. 5. The design of poultry control strains. Poult. Sci. 38, 462.

Gowe, R. S. and Strain, J. H. (1963). Effect of selection for increased egg production based on part-year records in two strains of White Leghorns. Canad. J. Genet. and Cyt. 5, 99.

Hall, G. O. (1934). Breeding a low producing strain of single comb White Leghorns. Poult. Sci. 13, 123.

Hansen, P. L. and Mighell, R. L. (1952). Economics of input/output relationships in feeding for egg production. Agric. Econ. Res. 4, 1.

Hazel, L. N. (1943). The genetic basis for constructing selection indexes. Genetics 28, 476.

Heady, E. O., Balloun, S. and Townsley, R. J. (1966). Co-operative research on input/output relationships in poultry production. O.E.C.D. Documentation in Agric. and Fd. 1966 Series No. 81.

Heinroth, O. (1922). Die Beziehungen zwischen Vogelwicht, Eigewicht, Gelegegewicht und Brutdauer. J. Orn. 70, 172.

Hogsett, M. L. and Nordskog, A. W. (1958). Genetic-economic value in selecting for egg production rate, body weight and egg weight. Poult. Sci. 37, 1406.

Hutt, F. B. and Cole, R. K. (1947). Genetic control of lymphomatosis in the fowl. Science, 106, 379.

Hutt, F. B. and Cole, R. K. (1953). The interaction of genetic and environmental influences affecting the incidence of avian leucosis. Science 117, 695.

Huxley, J. S. (1927). On the relation between egg weight and body weight in birds. J. Linean Soc., Lond. 36, 457.

Ideta, G. and Siegel, P. B. (1966). Selection for body weight at eight weeks of age. 3. Realised heritabilities of unselected traits. Poult. Sci. 45, 923.

Jaffe, W. P. (1966). Egg production, body weight and egg quality characters; their heritability and the correlations between them. Br. Poult. Sci. 7, 91.

Jaap, R. G., Smith, J. H. and Goodman, B. L. (1962). A genetic analysis of growth and egg production in meat-type chickens. Poult. Sci. 41, 1439.

Jerome, F. N., Henderson, C. R. and King, S. C. (1956). Heritabilities gene-interactions and correlations associated with certain traits in the domestic fowl. Poult. Sci. 35, 995.

Johansson, I. and Rendel, J. (1968). Genetics and Animal Breeding. Oliver and Boyd, Edinburgh and London.

Kempthorne, O. (1957). An Introduction to Genetic Statistics. John Wiley and Sons, New York.

Kempthorne, O. and Nordskog, A. W. (1959). Restricted selection indexes. Biometrics 15, 10.

King, S. C. and Henderson, C. R. (1954). Variance components analysis in heritability studies. Poult. Sci. 33, 147.

King, S. C. and Henderson, C. R. (1954). Heritability studies on egg production in the domestic fowl. Poult. Sci. 33, 155.

King, S. C., Carson, J. P. and Doolittle, D. P. (1959). The Connecticut and Cornell random-bred populations of chickens. Wld's. Poult. Sci. J. 15, 139.

King, S. C. (1961). Inheritance of economic traits in the regional Cornell control population. Poult. Sci. 40, 975.

King, S. C., Van Vleck, L. D. and Doolittle, D. P. (1963). Genetic stability of the Cornell random-bred control population of White Leghorns. Genet. Res. 4, 290.

Kinney, T. B. Jnr. and Lowe, P. C. (1968). Genetic and phenotypic variation in the Regional Red Controls over nine years. Poult. Sci. 47, 1105.

Kinney, T. B. Jnr., Lowe, P. C., Bohren, B. B. and Wilson, S. P. (1968). Genetic and phenotypic variation in random-bred White Leghorn controls over several generations. Poult. Sci. 47, 113.

Koch, R. M., Swiger, L. A., Chambers, D. and Gregory, K. E. (1963). Efficiency of feed use in beef cattle. J. Anim. Sci. 22, 486.

Krueger, W. F., Dickerson, G. E., Kinder, Q. B. and Kempster, H. L. (1952). The genetic and environmental relationship of total egg production to its components and to body weight in the domestic fowl. Poult. Sci. 31, 922.

Lack, D. (1968). Ecological Adaptations for Breeding in Birds. Methuen, London.

Lamoureux, W. F., Hutt, F. B. and Hall, G. O. (1943). Breeding for low fecundity in the fowl with the aid of a progeny test. Poult. Sci. 22, 161.

Latter, B. D. H. (1959). Genetic sampling in a random mating control population of constant size and sex ratio. Aust. J. biol. Sci.

Lerner, I. M. (1950). Population Genetics and Animal Improvement. Camb. Univ. Press.

Lerner, I. M. (1951). Natural selection and egg size in poultry. Amer. Nat. 85, 365.

Lerner, I. M. (1958). The Genetics Basis of Selection. John Wiley and Sons, New York.

Lerner, I. M. and Dempster, E. R. (1951). Attenuation of genetic progress under continued selection in poultry. Hered. 5, 75.

Lerner, I. M. and Donald, H. P. (1966). Modern developments in animal breeding. Academic Press, London and New York.

Lerner, I. M. and Gunns, C. A. (1952). Egg size and reproductive fitness. Poult. Sci. 31, 537.

Lerner, I. M. and Taylor, L. W. (1943). The inheritance of egg production in the domestic fowl. Amer. Nat. 77, 119.

Le Roy, H. L. (1963). Correlation between characters: its causes. Z. Tierz. Zücḧt, Biol. 79, 86.

Lowry, D. C. and Abplanalp, H. (1970). Genetic adaptation of White Leghorn hens to life in single cages. Br. Poult. Sci. 11, 117.

MacLaury, D. W. and Insko, W. M. Junr. (1968). Relation of pre-incubation factors and post-hatching performance to length of incubation period. 1. Effects of egg weight and storage time on length of incubation period. Poult. Sci. 47, 305.

McBride, G. (1962). The inheritance of right oviduct development in the domestic hen. XII Wld's. Poult. Congr., Sydney, Australia, 77.

Maloney, M. A., Gilbreath, J. C. and Morrison, R. D. (1963). Two-way selection for body weight in chickens. 1. The effectiveness of selection for twelve-week body weight. Poult. Sci. 42, 326.

Maloney, M. A., Gilbreath, J. C. and Morrison, R. D. (1963). Two-way selection for body weight in chickens. 2. The effect of selection for body weight on other traits. Poult. Sci. 42, 334.

Maloney, M. A., Gilbreath, J. C., Tierce, J. F. and Morrison, R. D. (1967). Divergent selection for twelve-week body weight in the domestic fowl. Poult. Sci. 46, 1116.

Merritt, E. S. (1964). Pre-incubation storage effects on subsequent performance of chickens. Br. Poult. Sci. 5, 67.

Merritt, E. S. (1968). Genetic parameter estimates for growth and reproductive traits in a random-bred control strain of meat type fowl. Poult. Sci. 47, 190.

Merritt, E. Z., Zawalsky, M. and Slen, S. B. (1966). Direct and correlated responses to selection for 63-day body weight in chickens. XIII Wld's. Poult. Congr., Kiev, 86.

Morgan, W. and Carlson, C. W. (1968). Proposed measure of performance efficiency in laying hens. Poult. Sci. 47, 22.

Morris, J. A. (1956). Genetic parameters associated with characters affecting egg production in the domestic fowl. 2. Heritability of egg production for two part-annual periods of measurement and the genetic correlation between them. Aust. J. agr. Res. 7, 630.

Morris, J. A. (1962). The effect of mild inbreeding in two lines of White Leghorn. Aust. J. agr. Res. 13, 362.

Morris, J. A. (1963). Continuous selection for egg production using short-term records. Aust. J. biol. Sci. 14, 909.

Nordskog, A. W. (1960). Importance of egg size and other factors in determining net income in random sample tests. Poult. Sci. 39, 327.

Nordskog, A. W. and Festing, M. (1962). Selection and correlated responses in the fowl. Proc. XII Wld's Poult. Congr., Sydney, Section Papers, 25.

Nordskog, A. W., Festing, M. and Verghese Mergrith W. (1967). Selection for egg production and correlated responses in the fowl. Genetics 55, 179.

Nordskog, A. W., French, H. and Balloun, S. L. (1969). Direct versus indirect estimation of feed efficiency as a measure of performance. Poult. Sci. 48, 1303.

Nordskog, A. W. and Giesbrecht, F. O. (1964). Regression in egg production in the domestic fowl when selection is relaxed. Genetics 50, 407.

Osborne, R. (1952). Sexual maturity in Brown Leghorns. The interactions of genotype and environment. Proc. roy. Soc., Edinb. (B) 64, 445.

Osborne, R. (1957_a). Correction for regression on a secondary trait as a method of increasing the efficiency of selective breeding. Aust. J. biol. Sci. 10, 365.

Osborne, R. (1957_b). The use of sire and dam family averages in increasing the efficiency of selective breeding under a hierarchical breeding system. Heredity 11, 96.

Osborne, R. and Patterson, W. S. B. (1953). On the sampling variance of heritability estimates derived from variance analyses. Proc. roy. Soc. Edinb. (B) 65, 456.

Pearl, R. and Surface, F. M. (1909). A biometrical study of egg production in the domestic fowl. 1. Variation in annual egg production. U.S.D.A. Bur. Animal Ind. Bul. 110.

Proudfoot, F. G. and Gowe, R. S. (1967). The effect of photoperiodism and rearing period feed restriction on the performance of five Leghorn strains. Poult. Sci. 46, 1056.

Purser, A. F. (1960). The use of correction for regression on a second character to increase the efficiency of selection. Biometrical Genetics 210. Ed. Kempthorne, O., Pergamon Press.

Reeve, E. C. R. (1955). The variance of the genetic correlation coefficient. Biometrics 11, 357.

Rendel, J. M. (1954). The use of regressions to increase heritability. Aust. J. biol. Sci. 7, 368.

Rendel, J. M. (1963). Correlation between the number of scutellar and abdominal bristles in Drosophila melanogaster. Genet. 48, 391.

Robertson, A. (1955). Selection in animals: Synthesis. Cold. Spr. Harb. Symp. quant. Biol. 20, 225.

Robertson, A. (1959). Experimental design in the evaluation of genetic parameters. Biometrics 15, 219.

Robertson, A. (1959). The sampling variance of the genetic correlation. Biometrics 15, 469.

Robertson, A. (1961). Selection for several characters. Schr. Reihe Max-Planck-Inst. Tierz. Tierernahr. (Mariensee/Trenthorst) Spec. Vol. 213.

Robertson, F. W. (1955). Selection response and properties of genetic variation. Cold. Spr. Harb. Symp. quant. Biol. 20, 166.

Robertson, F. W. (1962). Changing the relative size of the body parts of Drosophila by selection. Genet. Res. 3, 169.

Robertson, F. W. and Reeve, E. (1952). Studies in quantitative inheritance 1. The effects of selection of wing and thorax length in Drosophila melanogaster. J. Genet. 50, 414.

Saadeh, H. K., Craig, J. V., Smith, L. T. and Wearden, S. (1968). Effectiveness of alternative breeding systems for increasing rate of egg production in chickens. Poult. Sci. 47, 1057.

Saeki, Y., Akita, T., Sekidera, S. and Okawa, Y. (1966). Laying performances and genetic parameters in some breeds of chickens. 2. Genetic and phenotypic correlations between egg weight and some other traits. Japan. Poult. Sci. 3, 201.

Schultz, F. T. (1953). Concurrent inbreeding and selection in the domestic fowl. Heredity 7, 1.

Searle, S. R. (1965). The value of indirect selection. 1. Mass selection. Biometrics, 21, 682.

Sen, B. K. and Robertson, A. (1964). An experimental examination of methods for the simultaneous selection of two characters using Drosophila melanogaster. Genetics 50, 199.

Shoffner, R. N. and Grant, R. E. (1960). Relaxed selection in a strain of White Leghorns. Poult. Sci. 39, 63.

Shoffner, R. N. and Sloan, H. J. (1948). Heritability studies in the domestic fowl. VIII Wld's. Poult. Congr. 1, 269.

Siegel, P. B. (1962). A double selection experiment for body weight and breast angle at eight weeks of age in chickens. Genetics, 47, 1313.

Siegel, P. B. (1962). Selection for body weight at eight weeks of age. 1. Short-term response and heritabilities. Poult. Sci. 41, 954.

Siegel, P. B. (1963). Selection for body weight at eight weeks of age. 2. Correlated responses of feathering, body weights and reproductive characteristics. Poult. Sci. 42, 896.

Siegel, P. B., Van Krey, H. P. and Siegel, H. S. (1968). Pituitary-gonad relationships in weight selected lines differing in sexual maturity. Poult. Sci. 47, 771.

Skaller, F. (1954). Studies on the assessment of egg production in poultry breeding investigations. 2. The correction of hatching date for early selection based on part-annual egg production records. Poult. Sci. 33, 316.

Skaller, F. (1956). The Hagedoorn "nucleus-system" of breeding - a critical evaluation based on an experiment with poultry. Proc. Austr. Soc. Anim. Prod. 1, 165.

Skaller, F. and Sheldon, B. L. (1955). Interactions of genotype and environment in determining sexual maturity in the domestic fowl. Aust. J. agr. Res. 6, 171.

Smith, C. (1967). A note on the improvement of a trait by selecting on its components. Anim. Prod. 9, 125.

Stephenson, A. B., Wyatt, A. J. and Nordskog, A. W. (1953). Influence of inbreeding on egg production in the domestic fowl. Poult. Sci. 32, 510.

Sutherland, T. M. (1965). The correlation between feed efficiency and rate of gain, a ratio and its denominator. Biometrics 21, 739.

Tebb, G. (1958). Intra-generation inbreeding effects in a poultry flock selected for egg production. Heredity 12, 285.

Turner, H. N. (1959). Ratios as criteria for selection in animal or plant breeding, with particular reference to efficiency of food conversion in sheep. Aust. J. agric. Res. 10, 565.

Van Krey, H. P. and Siegel, P. B. (1968). Pituitary-gonadal relationships in lines selected for high and low body weight. Poult. Sci. 47, 480.

Van Vleck, L. D. and Doolittle, D. P. (1964). Genetic parameters of monthly egg production in the Cornell controls. Poult. Sci. 43, 560.

Verghese, Margrith, W. and Nordskog, A. W. (1968). Correlated responses in reproductive fitness to selection in chickens. Genet. Res. 11, 221.

Waring, F. J., Hunton, P. and Maddison, A. E. (1962). Genetics of a closed poultry flock. Br. Poult. Sci. 3, 151.

Wells, O. V. and Clawson, Marion (1933). A study of egg production per hen in central Utah. J. Farm Econ. 15, 633.

Weinland, B. T., Carson, J. R. and King, S. C. (1964). Stability of gene frequencies in a random-bred control population of chickens. Poult. Sci. 43, 985.

Wheat, J. D. and Lush, J. L. (1961). Accuracy of partial trapnest records. 1. Repeatability of daily egg records. Poult. Sci. 40, 399.

Williams, W. (1959). Heterosis and the genetics of complex characters. Nature, Lond. 184, 527.

Williamson, J. H. (1965). Cystic remnants of the right Müllanian duct and egg production in two strains of White Leghorns. Poult. Sci. 44, 321.

Wilson, S. P., Lowe, P. C., Kinney, T. B. and Bohren, B. B. (1966). Estimates of genetic parameters in the regional Cornell control. Poult. Sci. 45, 1138.

Wright, S. (1940). Breeding structure of populations in relation to speciation. Amer. Nat. 74, 232.

Wyatt, A. J. (1954). Genetic variation and covariation in egg production and other economic traits in chickens. Poult. Sci. 33, 1266.

Yamada, Y. (1968). On the realised heritability and genetic correlation estimated from double selection experiments when two characters are measured. Japan. Poult. Sci. 5, 148.

Yamada, Y., Bohren, B. B. and Crittenden, L. B. (1958). Genetic analysis of a White Leghorn closed flock apparently plateaued for egg production. Poult. Sci. 37, 565.

Young, S. S. Y. (1961). A further examination of the relative efficiency of three methods of selection for genetic gains under less restricted conditions. Genet. Res. 2, 106.

APPENDIX

A

Mean performance of Control Populations and Selected Lines

1963-1968

TABLE 1

Mean Performance of Strain 2 Control Population and Selected Lines

(1) Control Line

		(1)	(2)	(3)	(4)	(5)	(6)
Trait	Year	1963	1964	1965	1966	1967	1968
Body Weight							
12 weeks	g.	910.1	984.3	1025.6	975.2	1082.8	994.5
28 weeks	g.	1844.4	1872.8	1900.9	1886.0	2020.4	1966.6
44 weeks	g.	2141.4	1997.4	2018.7	2047.6	2210.9	2101.3
Egg Weight							
28 weeks	g.	48.2	47.7	48.1	49.0	50.7	50.5
44 weeks	g.	57.6	56.2	57.3	57.9	60.0	58.4
Age 1st Egg	wk.	23.4	23.2	24.9	24.7	24.2	23.9
Egg Numbers							
20-44 weeks		47.8	50.4	44.1	44.6	45.1	47.3
44-60 weeks		-	-	27.9	25.9	32.0	27.8

(2) Egg Weight Line

		(1)	(2)	(3)	(4)	(5)
Trait	Year	1963	1964	1965	1966	1967
Body Weight						
12 weeks	g.	934.9	1011.7	1079.2	1035.0	1147.5
28 weeks	g.	1900.7	1951.2	2071.8	2064.8	2149.2
44 weeks	g.	2190.2	2100.1	2203.3	2251.4	2332.3
Egg Weight						
28 weeks	g.	49.7	50.4	53.0	53.9	56.2
44 weeks	g.	60.2	59.5	62.2	63.2	66.5
Age 1st Egg	wk.	23.6	23.4	26.3	24.7	24.4
Egg Numbers						
20-44 weeks		48.1	48.9	40.8	44.9	42.3
44-60 weeks		-	-	28.7	25.8	31.0

TABLE 1 (continued)

Strain 2

(3) Body Weight Line

Trait	Year	(1) 1963	(2) 1964	(3) 1965	(4) 1966	(5) 1967
Body Weight						
12 weeks	g.	857.3	955.7	937.7	833.0	910.9
28 weeks	g.	1767.8	1846.5	1822.9	1692.3	1734.1
44 weeks	g.	2060.7	1970.2	1943.7	1859.8	1907.9
Egg Weight						
28 weeks	g.	47.7	47.6	48.4	47.9	48.3
44 weeks	g.	57.5	56.0	56.5	55.9	57.0
Age 1st Egg	wk.	23.7	23.5	26.1	25.0	24.5
Egg Numbers						
20-44 weeks		46.7	48.1	42.8	46.5	45.8
44-60 weeks		-	-	30.7	27.6	32.9

(4) Ratio Line

Trait	Year	(1) 1963	(2) 1964	(3) 1965	(4) 1966	(5) 1967
Body Weight						
12 weeks	g.	-	930.5	969.1	904.1	970.4
28 weeks	g.	-	1838.1	1731.6	1684.5	1701.3
44 weeks	g.	-	1971.1	1829.8	1801.7	1861.9
Egg Weight						
28 weeks	g.	-	48.9	50.5	51.4	52.5
44 weeks	g.	-	56.9	59.0	59.2	61.2
Age 1st Egg	wk.	-	22.9	23.9	24.0	24.4
Egg Numbers						
20-44 weeks		-	52.6	45.4	45.6	44.7
44-60 weeks		-	-	27.8	25.3	32.0

TABLE 1 (continued)

Strain 2

(5) Regression Line

		(1)	(2)	(3)	(4)	(5)
Trait	Year	1963	1964	1965	1966	1967
Body Weight						
12 weeks	g.	-	974.2	1038.1	983.7	1074.6
28 weeks	g.	-	1986.6	1861.9	1803.7	2027.0
44 weeks	g.	-	2138.9	1988.2	1952.1	2154.7
Egg Weight						
28 weeks	g.	-	52.0	53.1	55.3	57.4
44 weeks	g.	-	60.1	62.2	63.7	68.0
Age 1st Egg	wk.	-	23.8	23.7	24.3	25.3
Egg Numbers						
20-44 weeks		-	49.2	43.0	42.0	39.1
44-60 weeks		-	-	25.4	24.2	29.9

TABLE 2

Mean Performance of Strain 5 Control Population and Selected Lines

(1) Control Line

		(1)	(2)	(3)	(4)	(5)	(6)
Trait	Year	1963	1964	1965	1966	1967	1968
Body Weight							
12 weeks	g.	980.3	986.4	1030.6	1007.5	1056.9	1019.5
28 weeks	g.	1896.7	1786.3	1901.1	1876.4	1969.9	1983.9
44 weeks	g.	2016.5	1820.6	1901.2	1954.2	2062.5	2060.3
Egg Weight							
28 weeks	g.	46.0	47.1	46.9	47.9	48.8	49.6
44 weeks	g.	52.5	55.3	53.8	55.3	56.7	57.4
Age 1st Egg	wk.	25.5	25.6	23.9	25.7	24.3	23.9
Egg Numbers							
20-44 weeks		41.6	41.0	46.6	45.0	48.5	46.0
44-60 weeks		-	25.1	23.3	28.8	26.2	28.2

(2) Egg Weight Line

		(1)	(2)	(3)	(4)	(5)	(6)
Trait	Year	1963	1964	1965	1966	1967	1968
Body Weight							
12 weeks	g.	1018.6	952.9	1049.1	1038.9	1054.0	-
28 weeks	g.	1953.6	1816.2	1933.6	1923.7	1967.0	-
44 weeks	g.	2086.2	1805.4	1928.5	1973.7	2046.5	
Egg Weight							
28 weeks	g.	47.5	49.7	49.6	51.3	53.4	-
44 weeks	g.	55.2	58.2	57.1	58.7	61.8	-
Age 1st Egg	wk.	25.4	27.1	23.8	25.6	24.2	-
Egg Numbers							
20-44 weeks		42.5	30.8	46.2	43.5	46.1	-
44-60 weeks		-	20.8	22.7	28.1	24.1	-

TABLE 2 (continued)

Strain 5

(3) Body Weight Line

		(1)	(2)	(3)	(4)	(5)
Trait	Year	1963	1964	1965	1966	1967
Body Weight						
12 weeks	g.	937.9	865.7	932.7	863.3	867.2
28 weeks	g.	1847.3	1659.1	1735.2	1645.1	1639.0
44 weeks	g.	1972.1	1671.9	1751.0	1693.1	1688.3
Egg Weight						
28 weeks	g.	45.8	46.6	45.1	45.2	45.2
44 weeks	g.	52.9	54.6	52.1	52.0	52.9
Age 1st Egg	wk.	25.8	27.6	24.4	26.2	24.8
Egg Numbers						
20-44 weeks		42.9	36.1	46.6	43.9	46.4
44-60		-	25.8	21.5	27.0	22.9

(4) Ratio Line

		(1)	(2)	(3)	(4)	(5)	(6)
Trait	Year	1963	1964	1965	1966	1967	1968
Body Weight							
12 weeks	g.	-	988.9	-	971.0	954.9	870.6
28 weeks	g.	-	1638.8	-	1735.0	1683.4	1578.4
44 weeks	g.	-	1716.9	-	1811.8	1730.7	1616.8
Egg Weight							
28 weeks	g.	-	46.2	-	48.1	47.8	48.4
44 weeks	g.	-	54.3	-	55.2	54.5	54.8
Age 1st Egg	wk.	-	23.7	-	25.8	23.8	23.7
Egg Numbers							
20-44 weeks		-	46.0	-	44.1	49.6	44.1
44-60 weeks		-	25.8	-	30.3	25.6	23.9

TABLE 2 (continued)

Strain 5

(5) Regression Line

Trait	Year	(1) 1963	(2) 1964	(3) 1965	(4) 1966	(5) 1967	(6) 1968
Body Weight							
12 weeks	g.	-	1060.1	-	1074.8	1054.7	1099.2
28 weeks	g.	-	1774.9	-	1983.4	1940.7	1998.0
44 weeks	g.	-	1882.9	-	2034.5	2008.3	2058.8
Egg Weight							
28 weeks	g.	-	47.9	-	51.3	51.5	53.7
44 weeks	g.	-	56.9	-	59.5	59.7	62.3
Age 1st Egg	wk.	-	23.7	-	25.5	24.0	23.5
Egg Numbers							
20-44 weeks		-	45.0	-	43.9	47.8	46.6
44-60 weeks		-	25.1	-	27.4	22.8	27.8

APPENDIX

B

Mean weighted deviations of Selected Lines from the Control

TABLE 1

Weighted Mean Deviations of Selection Lines from Control Line

Strain 2

Year:	(1) 1962-63		(2) 1963-64				(3) 1964-65			
Line:	Egg Weight	Body Weight	Egg Weight	Regression	Ratio	Body Weight	Egg Weight	Regression	Ratio	Body Weight
Trait:										
Body Weight (grams)										
12 weeks	+25**	-52***	+ 17	+ 2	-43***	-39***	+ 69***	+ 2	- 63***	- 77***
28 weeks	+59***	-73***	+104***	+ 83***	-60***	- 1	+158***	-15	-147***	- 95***
44 weeks	+48*	-80***	+160***	+101***	-63**	+29	+157***	+10	-150***	-104***
Egg Weight (grams)										
28 weeks	+1.44***	-0.54	+3.08***	+3.78***	+0.74*	+0.27	+5.16***	+4.97***	+2.36***	+0.60*
44 weeks	+2.54***	-0.18	+3.97***	+3.18***	+0.01	+0.43	+5.04***	+5.02***	+1.79***	-0.75*
Age 1st Egg (weeks)	+0.2	+0.3	+0.1	+0.8***	-0.1	+0.17	+0.17	-0.2	0	+0.1
Egg Numbers (Part Record)										
20-44 weeks	+0.3	-1.0	-0.8	-0.1	+1.3	-1.6	0	-3.9***	-1.2	+1.6
44-60 weeks	-	-	+4.6***	+1.8	+9.0***	+3.0**	-0.4	-1.6*	+0.9	+1.6

* Significant difference at 95.0% level of probability

** Significant difference at 99.0% level of probability

*** Significant difference at 99.9% level of probability

TABLE 1 (continued)

Weighted Mean Deviations of Selection Lines from Control Line

Strain 2

Year:	(4) 1965-66				(5) 1966-67			
Line	Egg Weight	Regression	Ratio	Body Weight	Egg Weight	Regression	Ratio	Body Weight
Trait								
Body Weight (grams)								
12 weeks	+ 66***	+ 3	- 74***	-146***	+ 57***	-14	-118***	-185***
28 weeks	+158***	-54***	-165***	-217***	+127***	-41**	-318***	-300***
44 weeks	+178***	-70***	-213***	-221***	+114***	-67***	-354***	-329***
Egg Weight (grams)								
28 weeks	+4.82***	+6.29***	+2.91***	-1.19***	+5.53***	+6.75***	+1.77***	-2.47***
44 weeks	+4.81***	+6.14***	+1.75***	-2.47***	+6.36***	+7.90***	+1.13***	-3.13***
Age 1st Egg (weeks)	-0.3	-0.1	-0.4**	+0.1	+0.1	+1.0***	+0.2	0
Egg Numbers (Part Record)								
20-44 weeks	+0.1	-2.6**	+0.9	+1.2	-2.3*	-5.5***	0	+1.7
44-60 weeks	+0.3	-2.1**	-0.8	+1.9*	-0.7	-2.1**	+0.1	+1.1

* Significant difference at 95.0% level of probability

** Significant difference at 99.0% level of probability

*** Significant difference at 99.9% level of probability

TABLE 2

Weighted Mean Deviations of Selection Lines from Control Line

Strain 5

Year:	(1) 1962-63		(2) 1963-64				(3) 1964-65			
Line:	Egg Weight	Body Weight	Egg Weight	Regression	Ratio	Body Weight	Egg Weight	Regression	Ratio	Body Weight
Trait:										
Body Weight (grams)										
12 weeks	+38***	-42***	+39***	+ 8	- 69***	-43***	+14	-	-	-101***
28 weeks	+56***	-49**	+61***	-33*	-165***	-86***	+34	-	-	-161***
44 weeks	+69***	-44*	+57**	-4	-179***	-74***	+26	-	-	-148***
Egg Weight (grams)										
28 weeks	+1.51***	-0.15	+2.53***	+0.88***	-0.69*	-0.54*	+2.56**	-	-	-1.84***
44 weeks	+2.65***	+0.39	+3.03***	+1.40***	-1.11**	-0.56*	+3.36**	-	-	-1.75***
Age 1st Egg (weeks)	-0.1	+0.3*	0	-0.3*	-0.2	+0.5***	-0.1	-	-	+0.5***
Egg Numbers (Part Record)										
20-44 weeks	+0.8	+1.2	-5.6***	-0.5	+0.2	-0.4	-0.3	-	-	+0.1
44-60 weeks	-	-	-3.9***	-0.3	+1.1	+1.2	-1.0	-	-	-2.4**

* Significant difference at 95.0% level of probability
** Significant difference at 99.0% level of probability
*** Significant difference at 99.9% level of probability

TABLE 2 (continued)

Weighted Mean Deviations of Selection Lines from Control Line

Strain 5

Year:	(4) 1965-66				(5) 1966-67				(6) 1967-68	
Line:	Egg Weight	Regression	Ratio	Body Weight	Egg Weight	Regression	Ratio	Body Weight	Regression	Ratio
Trait										
Body Weight (grams)										
12 weeks	+28***	+69***	- 34***	-144***	- 5	0	-105***	-190***	+79***	-159***
28 weeks	+34*	+98***	-144***	-242***	-10	-34*	-293***	-340***	+14	-405***
44 weeks	+10	+80***	-142***	-269***	-17	-56**	-336***	-379***	0	-453***
Egg Weight (grams)										
28 weeks	+3.38***	+3.40***	+0.18	-2.71***	+4.69***	+2.76***	-0.96***	-3.49***	+4.10***	-1.59***
44 weeks	+3.45***	+4.24***	-0.10	-3.31***	+5.16***	+3.06***	-2.14***	-3.74***	+4.89***	-2.50***
Age 1st Egg (weeks)	-0.2	-0.5***	0	+0.4	-0.2	-0.4**	-0.6***	+0.4**	-0.5**	-0.1
Egg Numbers (Part Record)										
20-44 weeks	-1.2	-0.6	-0.7	-0.9	-2.2*	-0.4	+1.4	-1.8*	+0.6	-2.6*
44-60 weeks	-0.5	-1.3	+1.5	-1.8	-2.6**	-3.8***	-0.7	-3.8***	-0.5	-5.4***

* Significant difference at 95.0% level of probability

** Significant difference at 99.0% level of probability

*** Significant difference at 99.9% level of probability

APPENDIX

C

Estimates of heritabilities, genetic correlations and phenotypic standard deviations within the Selected Populations over the last 2 generations

TABLE 1

Summary of estimates of heritabilities, genetic correlations and phenotypic standard deviations within the last 2 generations of Egg Weight selection

Strain 2

		Body Weight			Egg Weight		Age 1st Egg	Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks		20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(4)	0.73	0.995	0.950	0.645	0.586	-0.336	0.539	0.690	0.651
	(5)	0.49	0.717	0.642	0.277	0.362	0.384	-0.180	-0.340	-0.163
28 weeks	(4)		0.51	0.916	0.688	0.323	-0.280	0.640	0.423	0.612
	(5)		0.61	0.867	0.976	0.678	0.486	-0.366	-0.240	-0.374
44 weeks	(4)			0.43	0.781	0.383	-0.159	0.495	-0.169	0.271
	(5)			0.70	0.846	0.552	0.430	-0.453	-0.192	-0.403
Egg Weight:										
28 weeks	(4)				0.33	0.811	-0.193	0.409	-1.671	-0.398
	(5)				0.12	1.121	0.116	-0.066	-0.742	-0.329
44 weeks	(4)					0.39	-0.113	0.523	-1.027	-0.058
	(5)					0.48	0.562	-0.511	-0.848	-0.682
Age 1st Egg:	(4)						0.41	-1.016	-0.604	-0.944
	(5)						0.23	-0.868	-0.402	-0.770
Egg Numbers:										
(Part Record)										
20-44 weeks	(4)							0.28	0.649	0.951
	(5)							0.54	0.901	0.975
44-60 weeks	(4)								0.06	0.853
	(5)								0.04	0.739
20-60 weeks	(4)									0.16
	(5)									0.29
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(4)	117.6	211.4	270.7	3.12	3.54	1.63	7.89	9.80	15.32
	(5)	95.9	212.7	246.2	3.19	3.88	2.18	8.16	8.04	14.59

(4) Estimates for 1965/66 generation: d.f. Sires - 15; Dams - 51; Individuals - 153
(5) Estimates for 1966/67 generation: d.f. Sires - 11; Dams - 40; Individuals - 194

TABLE 2

Summary of estimates of heritabilities, genetic correlations and phenotypic standard deviations within the last 2 generations of Body Weight selection

Strain 2

		Body Weight			Egg Weight		Age 1st Egg	Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks		20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(4)	0.40	0.434	0.262	0.211	0.190	-0.818	1.033	0.625	0.622
	(5)	0.67	0.893	0.682	0.495	0.298	-0.408	0.425	0.276	0.437
28 weeks	(4)		0.59	0.879	0.291	0.365	-0.558	0.746	0.359	0.387
	(5)		0.45	0.923	0.437	0.367	-0.103	0.325	0.325	0.405
44 weeks	(4)			0.73	0.195	0.355	-0.411	0.563	0.335	0.335
	(5)			0.53	0.502	0.492	0.021	0.176	0.170	0.211
Egg Weight:										
28 weeks	(4)				0.55	0.910	-0.560	0.772	0.195	0.282
	(5)				0.49	0.914	0.487	-0.128	0.105	-0.008
44 weeks	(4)					0.43	-0.592	0.700	0.049	0.170
	(5)					0.69	0.474	-0.289	-0.282	-0.358
Age 1st Egg:	(4)						0.29	-0.319	-0.562	-0.440
	(5)						0.19	-0.907	0.193	-0.445
Egg Numbers:										
(Part Record)										
20-44 weeks	(4)							0.07	1.937	1.498
	(5)							0.29	0.304	0.798
44-60 weeks	(4)								0.51	1.051
	(5)								0.35	0.816
20-60 weeks	(4)									0.50
	(5)									0.32
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(4)	104.6	162.5	225.3	3.19	3.68	1.91	8.08	9.89	14.87
	(5)	87.0	160.4	186.9	2.77	3.61	2.18	7.58	7.33	12.08

(4) Estimates for 1965/66 generation: d.f. Sires - 15; Dams - 48; Individuals - 151
(5) Estimates for 1966/67 generation: d.f. Sires - 12; Dams - 36; Individuals - 206

TABLE 3

Summary of estimates of heritabilities, genetic
correlations and phenotypic standard deviations
within the last 2 generations of Regression selection

Strain 2

		Body Weight			Egg Weight		Age 1st Egg	Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks		20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(3)	0.50	0.589	0.449	0.297	0.284	-0.166	-0.256	0.249	0.113
	(4)	0.59	0.852	0.845	0.526	0.492	0.320	-0.691	-0.321	-0.522
28 weeks	(3)		0.50	1.010	0.373	0.274	0.440	-0.041	-0.162	-0.124
	(4)		0.87	0.986	0.592	0.537	0.129	-0.528	-0.316	-0.428
44 weeks	(3)			0.43	0.252	0.364	0.287	0.117	-0.075	-0.024
	(4)			0.83	0.492	0.501	0.078	-0.596	-0.381	-0.490
Egg Weight:										
28 weeks	(3)				0.44	0.779	-0.150	-0.489	0.144	-0.017
	(4)				0.44	0.948	-0.059	-0.187	-0.173	-0.236
44 weeks	(3)					0.39	-0.428	0.471	0.503	0.467
	(4)					0.77	-0.270	-0.190	-0.386	-0.323
Age 1st Egg:	(3)						0.22	-0.088	-0.291	-0.226
	(4)						0.17	-0.570	-0.090	-0.323
Egg Numbers:										
(Part Record)										
20-44 weeks	(3)							0.08	1.319	1.168
	(4)							0.25	0.932	0.989
44-60 weeks	(3)								0.38	1.022
	(4)								0.22	0.966
20-60 weeks	(3)									0.35
	(4)									0.31
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(3)	101.3	201.0	244.3	3.09	3.82	1.18	8.22	11.01	16.47
	(4)	104.6	227.6	263.2	3.31	4.36	1.54	6.38	8.06	12.10

(3) Estimates for 1965/66 generation: d.f. Sires - 14; Dams - 37; Individuals - 139
(4) Estimates for 1966/67 generation: d.f. Sires - 13; Dams - 36; Individuals - 220

TABLE 4

Summary of estimates of heritabilities, genetic
correlations and phenotypic standard deviations
within the last 2 generations of Ratio selection

Strain 2

		Body Weight			Egg Weight			Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks	Age 1st Egg	20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(3)	0.23	0.883	0.852	0.607	0.234	0.299	0.837	1.024	0.896
	(4)	0.50	0.882	0.902	0.868	0.539	-0.145	0.685	0.759	0.712
28 weeks	(3)		0.69	1.023	0.851	0.786	0.624	0.256	0.085	0.174
	(4)		0.38	0.964	1.148	0.848	0.120	0.481	0.739	0.595
44 weeks	(3)			0.51	0.951	0.725	0.514	0.211	0.035	0.127
	(4)			0.59	0.940	0.728	0.143	0.364	0.482	0.415
Egg Weight:										
28 weeks	(3)				0.71	0.977	0.568	-0.236	0.234	-0.022
	(4)				0.19	0.629	0.038	1.075	1.631	1.321
44 weeks	(3)					0.41	1.146	-0.745	-1.132	-0.895
	(4)					0.33	0.578	0.127	1.118	0.583
Age 1st Egg:	(3)						0.38	-0.733	-0.564	-0.638
	(4)						0.42	-0.696	-0.158	-0.440
Egg Numbers:										
(Part Record)										
20-44 weeks	(3)							0.21	1.119	1.024
	(4)							0.19	1.042	1.009
44-60 weeks	(3)								0.08	1.035
	(4)								0.10	1.012
20-60 weeks	(3)									0.18
	(4)									0.20
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(3)	93.0	156.4	187.9	3.12	3.32	1.34	8.83	11.56	17.81
	(4)	84.2	171.7	212.2	3.33	3.51	2.16	7.59	9.14	14.19

(3) Estimates for 1965/66 generation: d.f. Sires - 14; Dams - 40; Individuals - 166
(4) Estimates for 1966/67 generation: d.f. Sires - 11; Dams - 31; Individuals - 196

TABLE 5

Summary of estimates of heritabilities, genetic correlations and phenotypic standard deviations within the last 2 generations of Egg Weight selection

Strain 5

		Body Weight			Egg Weight		Age 1st Egg	Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks		20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(4)	0.83	0.806	0.822	0.189	0.352	-0.035	0.123	0.142	0.148
	(5)	0.44	0.624	0.394	0.603	0.219	0.014	-0.054	0.302	0.134
28 weeks	(4)		0.86	0.990	0.134	0.221	0.322	-0.044	-0.151	-0.115
	(5)		0.47	0.982	1.015	0.630	0.163	0.036	-0.116	-0.044
44 weeks	(4)			0.52	0.076	0.134	0.372	0.042	-0.059	-0.016
	(5)			0.30	0.955	0.504	0.240	-0.171	-0.596	-0.400
Egg Weight:										
28 weeks	(4)				0.45	1.051	0.115	0.050	0.250	0.178
	(5)				0.11	1.500	-0.030	0.145	-0.125	0.004
44 weeks	(4)					0.24	0.006	-0.322	-0.265	-0.321
	(5)					0.26	0.240	-0.361	-0.544	-0.464
Age 1st Egg:	(4)						0.36	-0.420	-0.018	-0.218
	(5)						0.32	-0.491	-0.621	-0.568
Egg Numbers:										
(Part Record)										
20-44 weeks	(4)							0.30	0.629	0.878
	(5)							0.29	0.934	0.982
44-60 weeks	(4)								0.27	0.924
	(5)								0.20	0.985
20-60 weeks	(4)									0.29
	(5)									0.29
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(4)	130.2	220.8	239.9	2.98	3.82	1.22	8.18	10.66	16.91
	(5)	114.8	204.2	240.9	3.35	3.84	1.34	7.61	10.13	15.67

(4) Estimates for 1965/66 generation: d.f. Sires - 12; Dams - 45; Individuals - 196
(5) Estimates for 1966/67 generation: d.f. Sires - 10; Dams - 32; Individuals - 152

TABLE 6

Summary of estimates of heritabilities, genetic
correlations and phenotypic standard deviations
within the last 2 generations of Body Weight selection

Strain 5

		Body Weight			Egg Weight			Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks	Age 1st Egg	20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(4)	0.21	0.265	0.245	0.282	0.079	-0.108	0.275	0.622	0.495
	(5)	0.47	0.544	0.602	0.454	0.312	-0.409	0.300	0.334	0.348
28 weeks	(4)		0.48	0.797	0.536	0.454	0.248	0.029	0.553	0.337
	(5)		0.71	0.972	0.736	0.605	0.083	-0.159	0.151	0.018
44 weeks	(4)			0.32	0.658	0.476	-0.220	0.231	0.606	0.465
	(5)			0.63	0.735	0.592	0.099	-0.052	0.258	0.134
Egg Weight:										
28 weeks	(4)				0.56	0.765	-0.387	0.225	0.345	0.310
	(5)				0.66	0.917	-0.002	-0.188	-0.100	-0.150
44 weeks	(4)					0.55	0.052	-0.108	0.170	0.047
	(5)					0.50	0.388	-0.574	-0.230	-0.413
Age 1st Egg:	(4)						0.51	-0.715	-0.378	-0.564
	(5)						0.69	-0.894	-0.340	-0.633
Egg Numbers:										
(Part Record)										
20-44 weeks	(4)							0.51	0.763	0.926
	(5)							0.37	0.680	0.892
44-60 weeks	(4)								0.44	0.950
	(5)								0.39	0.938
20-60 weeks	(4)									0.54
	(5)									0.42
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(4)	95.4	144.1	178.6	2.98	2.99	1.37	8.17	10.75	16.62
	(5)	100.9	161.9	230.2	2.93	3.58	1.70	9.02	11.38	17.91

(4) Estimates for 1965/66 generation: d.f. Sires - 11; Dams - 43; Individuals - 181
(5) Estimates for 1966/67 generation: d.f. Sires - 11; Dams - 32; Individuals - 190

TABLE 7

Summary of estimates of heritabilities, genetic correlations and phenotypic standard deviations within the last 2 generations of Regression selection

Strain 5

		Body Weight			Egg Weight			Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks	Age 1st Egg	20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(3)	0.47	0.891	0.774	0.442	0.692	-0.241	0.490	0.101	0.273
	(4)	0.76	0.964	0.727	0.449	0.856	-0.197	0.034	-0.175	-0.068
28 weeks	(3)		0.64	0.997	0.611	0.707	0.012	0.315	-0.037	0.117
	(4)		0.57	0.919	0.256	0.761	-0.051	0.008	-0.136	-0.055
44 weeks	(3)			0.50	0.646	0.740	-0.074	0.157	-0.160	-0.022
	(4)			0.47	0.167	0.540	0.108	-0.140	-0.003	-0.067
Egg Weight:										
28 weeks	(3)				0.65	0.885	0.249	-0.036	-0.213	-0.133
	(4)				0.23	0.523	0.128	-0.249	-0.559	-0.460
44 weeks	(3)					0.44	-0.123	0.251	-0.169	0.020
	(4)					0.34	-0.276	-0.268	-0.298	-0.383
Age 1st Egg:	(3)						0.33	-0.792	-0.354	-0.548
	(4)						0.51	-0.618	-0.249	-0.441
Egg Numbers:										
(Part Record)										
20-44 weeks	(3)							0.39	0.997	1.001
	(4)							0.54	0.997	0.997
44-60 weeks	(3)								0.33	1.000
	(4)								0.28	1.008
20-60 weeks	(3)									0.47
	(4)									0.51
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σ_p	(3)	93.8	198.2	251.5	3.25	4.41	1.37	7.91	10.90	16.33
	(4)	92.8	197.6	231.8	2.98	3.22	1.90	9.53	9.54	16.43

(3) Estimates for 1966/67 generation: d.f. Sires - 9; Dams - 38; Individuals - 154

(4) Estimates for 1967/68 generation: d.f. Sires - 5; Dams - 30; Individuals - 128

TABLE 8

Summary of estimates of heritabilities, genetic
correlations and phenotypic standard deviations
within the last 2 generations of Ratio selection

Strain 5

		Body Weight			Egg Weight		Age 1st Egg	Egg Numbers		
	h^2	12 weeks	28 weeks	44 weeks	28 weeks	44 weeks		20-44 weeks	44-60 weeks	20-60 weeks
Body Weight:										
12 weeks	(3)	0.71	0.688	0.623	0.598	0.477	-0.053	0.237	0.328	0.303
	(4)	0.35	0.524	0.509	0.633	1.018	-0.176	0.426	0.186	0.326
28 weeks	(3)		0.81	0.924	0.638	0.734	-0.044	0.463	0.571	0.547
	(4)		0.66	0.977	1.010	1.069	0.228	-0.019	-0.259	-0.143
44 weeks	(3)			0.75	0.564	0.572	-0.013	0.453	0.489	0.489
	(4)			0.79	0.879	0.793	0.252	-0.008	-0.139	-0.076
Egg Weight:										
28 weeks	(3)				0.57	1.044	0.039	0.145	0.468	0.362
	(4)				0.66	1.164	0.147	0.037	-0.344	-0.154
44 weeks	(3)					0.23	0.295	-0.096	0.411	0.237
	(4)					0.35	-0.066	0.299	-0.003	0.161
Age 1st Egg:	(3)						0.68	-0.558	-0.131	-0.291
	(4)						0.71	-0.884	-0.570	-0.772
Egg Numbers:										
(Part Record)										
20-44 weeks	(3)							0.32	0.888	0.953
	(4)							0.74	0.812	0.956
44-60 weeks	(3)								0.56	0.986
	(4)								0.65	0.947
20-60 weeks	(3)									0.55
	(4)									0.82
		g.	g.	g.	g.	g.	wk.	eggs	eggs	eggs
σp	(3)	98.0	164.7	179.7	2.95	4.02	1.21	7.63	10.46	15.94
	(4)	70.4	150.5	169.3	3.49	3.56	2.44	12.27	12.16	21.39

(3) Estimates for 1966/67 generation: d.f. Sires - 12; Dams - 40; Individuals - 205
(4) Estimates for 1967/68 generation: d.f. Sires - 5; Dams - 32; Individuals - 99

APPENDIX

D

Numbers of breeders used to reproduce the Selected Lines

TABLE 1

Numbers of effective breeders in selected lines and predicted increase in average inbreeding

Strain 2

	Egg Weight Line			Body Weight Line		
Year Mated	Sires	Dams	ΔF*	Sires	Dams	ΔF*
1962	33	33	.008	35	35	.007
1963	14	54	.011	15	48	.011
1964	15	60	.010	15	59	.010
1965	16	66	.010	16	62	.010
1966	12	52	.013	13	49	.012
Cumulative inbreeding:			0.052			0.050

	Regression Line			Ratio Line		
Year Mated	Sires	Dams	ΔF*	Sires	Dams	ΔF*
1963	15	48	.011	15	47	.011
1964	15	64	.010	15	61	.010
1965	14	52	.011	15	55	.011
1966	14	47	.012	12	43	.013
Cumulative inbreeding:			0.044			0.045

$$*\Delta F \text{ (approximately)} = \frac{1}{8N_m} + \frac{1}{8N_f}$$

TABLE 2

Numbers of effective breeders in selected lines and predicted increase in average inbreeding

Strain 5

	Egg Weight Line			Body Weight Line		
Year Mated	Sires	Dams	ΔF*	Sires	Dams	ΔF*
1962	26	26	.010	27	27	.009
1963	15	57	.011	15	56	.011
1964	15	42	.011	16	48	.010
1965	13	58	.012	12	55	.013
1966	11	43	.014	12	44	.013
Cumulative inbreeding:			0.058			0.056

	Regression Line			Ratio Line		
Year Mated	Sires	Dams	ΔF*	Sires	Dams	ΔF*
1963	15	59	.010	15	50	.011
1965	11	46	.014	10	37	.016
1966	10	48	.015	13	53	.012
1967	6	35	.024	6	38	.024
Cumulative inbreeding:			0.063			0.063

*ΔF (approximately) $= \frac{1}{8N_m} + \frac{1}{8N_f}$

ABSTRACT OF THESIS

Name of Candidate JOHN MITCHELL MANSON

Address 34 Comely Bank, Edinburgh 4.

Degree Doctor of Philosophy Date 31st July, 1970.

Title of Thesis "Inter-relationship of body weight and egg weight in the domestic fowl".

Egg weight and body weight in the fowl are genetically positively correlated so that a change in one of the traits in a given direction is expected to be accompanied by a change in the same direction in the other. It is probably to the net economic advantage of the poultry breeder, however, to attempt to select these two traits in opposing directions, i.e. reduced body weight but increased egg weight, provided rate of lay is not impaired in the process.

This thesis is concerned with describing the results of a 5-year selection experiment which set out to test the feasibility of selecting for lower body weight or higher egg weight without incurring the expected associated change in the correlated trait.

Four sub-lines were established within each of 2 strains (S2 and S5) of White Leghorns, while a pedigreed, random-bred population also derived from the same base population was maintained as a control line within each strain. The selection lines comprised:-

1. Selection for increased egg weight (Egg Weight line).
2. Selection for decreased body weight (Body Weight line).
3. Selection on the value of the ratio of the individual hen's egg weight to body weight (Ratio line).
4. Selection on an index taking the form, I = Egg Weight - (b) Body Weight (Regression line), b in this instance being the calculated average genetic regression of egg weight on body weight in the base populations.

Both body weight and egg weight had estimated heritabilities of approximately 0.50 from variance analyses in the base populations and a genetic correlation between the 2 traits of the order of +0.3 to +0.4.

Selection for high egg weight or low body weight in lines 1 and 2 over 5 generations was apparently equally effective (realised heritabilities around 0.40). Body weight selection was accompanied by /

Use other side if necessary.