

THE INFLUENCE OF COMB TYPE ON
GROWTH RATE IN THE DOMESTIC FOWL

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfilment of the requirements for the degree of
Master of Science.

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April 1964

ACKNOWLEDGEMENTS

Completion of the project on which this thesis has been prepared could not have been accomplished without the generous advice and assistance of many friends and associates.

The author is extremely grateful to Dr. R. O. Hawes under whose excellent supervision the project and thesis preparation was carried out. His encouraging assistance and enthusiastic co-operation is greatly appreciated.

Thanks are also due Professor J. E. Moxley who outlined and assisted immeasurably in the completion of all statistical analyses, and Dr. A. L. Carter who was responsible for much of the organization of apparatus used in the radioactive iodine uptake study and whose advice pertaining to this research was extremely helpful.

Appreciation is also expressed for the assistance and encouragement given by fellow graduate students and by members of the poultry farm staff, in particular Mr. J. P. Roy who provided the pictures which have been included in this thesis.

Financial assistance provided by the Quebec Agricultural Research Council and the Macdonald Agricultural Research Fund is gratefully acknowledged.

Kindest thanks are extended to Miss K. M. Tyrer for her preparation of the manuscript.

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I INTRODUCTION

During the early existence of the science of genetics, the area of single gene effects was the more active area of interest. Throughout the initial development of this science, studies of qualitative traits provided the basis on which the later principles were founded. However, while academic interest in qualitative genetics remained quite popular during subsequent years, researchers with aspirations of applying heredity to the economic improvement of plants and animals were turning to more complex quantitative methods. These are effective during their preliminary applications but their utility appears to decrease with increasing improvement, becoming somewhat ineffective on highly improved populations. As a result, scientists began to seek other means by which genetic improvement of plants and animals could be continued, and qualitative genetics was considered in a new light.

Already numerous associations between single genes and economically important traits of poultry have been recorded. Relationships between plumage colour genes and growth rate and between blood group genes and economic traits have been demonstrated. The possible association between genes controlling comb type and other characteristics, though still not definitely established, would appear to be very probable. However, the research which has been conducted on this subject is not conclusive and numerous complexities have been disclosed.

In view of the fact that results of other workers have differed

and because of the academic interest and possible economic implications pertaining thereto, it was felt that further study on the association between comb type genes and growth rate should be pursued. The present undertaking was, therefore, planned to study not only growth rate per se. but also other physiological traits so as to determine their possible relationship to comb type.

II REVIEW OF LITERATURE

Introduction:

The mode of inheritance of the four common comb types of the domestic fowl was one of the earliest determined examples of Mendelian inheritance in animals. In 1906, only a few years after the rediscovery of Mendel's original work, Bateson and Punnett arrived at a genetic basis for differences in chicken comb types.

Two pair of genes are involved: both pea and rose combs result from dominant alleles, 'P' and 'R', respectively; cushion comb results from the interaction of these two alleles (R-P-) while single results from the presence of the homozygous recessive alleles (rrpp) of both genes. In 1923 the same workers made the only modification that their original scheme has undergone; they introduced a third gene (Bd) for single comb. This gene normally has no effect on the phenotype because it is hypostatic to both the R and P genes. The recessive allele (bd), however, produces a fifth comb type, breda, when all three genes are homozygous recessive.

In addition to controlling the characteristic for which the gene has been named, (i.e. R - rose, P - pea), genes such as those controlling comb type have been shown to have an effect on other superficially unrelated characteristics. A gene with the particular ability to display a multiplicity of effects is one which possesses pleiotropic action. A typical example of pleiotropy is represented by the single gene (ch) for congenital hydrocephalus in the mouse which affects skull shape, development of the nasal septum, the nose and numerous other characteristics. (Grunberg, 1943).

Mendel himself noted that one of the genes possessed by a plant which he studied affected simultaneously the colour of flowers, the colour of seeds and the presence or absence of reddish spots in the axils of the leaves. Since the time of Mendel a multitude of examples of pleiotropy have been reported, (Jaap and Morris, 1937; Jerome et al., 1956; Merat, 1959; Rendel, 1959; Briles and Allen, 1961; Hawes and Buss, 1963). The majority of such examples appear to have no economic importance; there are certain ones, however, in which a practical characteristic has been involved.

A Pleiotropic Gene Action

Pleiotropy in Laboratory Animals:

Feldman (1935) reported that the brown mutation in mice acted secondarily to increase body size. He showed an advantage of from 1.6 to 5.6 percent for brown individuals compared to their black litter-mates. Similar results were obtained by Castle et al. (1936a) who reported that body length was also increased in brown animals. Further studies by Castle et al. (1936b) demonstrated that mice with dilute coat colour were regularly smaller than their intense sibs and that pink-eyed segregates were slightly smaller than their normal sibs. McArthur (1949) also showed relationship between coat colour and body size. Selecting one strain of mice for large and one for small body size he observed, after 21 generations, that they differed genetically with regard to coat colour. Law (1938) repeated Castle's findings and also showed that mice carrying the short-ear gene were distinctly smaller than their normal-ear sibs.

Concurrent work by Castle yielded values of 1 to 5 percent for the retardation in body size for the pink-eye and short-ear genes, respectively.

Plietropy in Poultry:

a) Plietropic Action of Genes Affecting Plumage-

Considerable research has been conducted on the association of various single genes and economic traits in poultry. Jerome and Huntsman (1959) reported that recessive white (cc) chicks were significantly lighter than were coloured (Cc) chicks at nine weeks of age. Smyth and Fox (1961) obtained similar results and also noted the advantage for colour to be greater in males than in female chickens. Buss (1960) observed that recessive white turkeys grew at a slower rate than their coloured sibs.

Jerome et al. (1956) reported an apparent plietropic association between dominant white (I) and reduced rate of growth in chicks at nine weeks of age and Jaap and Grimes (1956) presented evidence to show that in dominant white chickens, interaction between the gene for inhibition of colour (I) and the gene for the extension of black (E) suppressed body growth rate to eight weeks of age by 0.03 to 0.04 pounds. When, in addition to alleles I and E, the allele for sex-linked barring (B) was present, still further growth reduction resulted. Growth differences of 0.06 pounds in favour of coloured over white birds were found by Collins and Hubbard (1958) who used more than 28,000 chicks.

Hays (1951), Hale (1952 - cited in Ram and Hutt, 1956) and Godfrey and Farnsworth (1952) reported that chicks possessing the slow-feathering allele (K) did not differ in rate of

body growth from those that feathered rapidly as the result of possessing the *k* allele. However, numerous other workers have observed a definite positive relationship between rapid feathering (*k*) and growth rate, (Gericke and Platt, 1932; Jaap and Morris, 1937; Jaap and Grimes, 1956). More recently Saeki and Katsuragi (1961) observed that in New Hampshires segregating for rapid and slow feathering, early feathered birds were significantly heavier at two, five and ten weeks of age, the divergence of growth rate increased with age after hatching. Asmundson and Abbott (1961) reported that a dominant sex-linked gene for slow feathering in the turkey caused a similar reduction in the growth rate.

Kabystina and Petrov (1935 - cited in Hutt, 1949) reported that a shortened down condition in chickens was associated with black down colour. Hutt (1951) found a similar condition to that of Kabystina and Petrov in black barred female chicks from a cross between Rhode Island Red males (*bb*) and Barred Plymouth Rock females (*B-*) and also observed the *E* gene to be lethal to about 3.6 percent of the black, non-barred female progeny. The barring gene (*B*) was observed to display a sparing effect on the action of the *E* gene in the male chicks. Similar results had been previously obtained by Landauer (1943). Collins and Hubbard (1958) observed that genes *I* and *E* interacted to reduce embryo viability.

Bernier and Cooney (1954), who obtained a highly significant difference in the incidence of symptoms of riboflavin deficiency between black and non-black embryos and chicks from a cross involving segregation for the *E* and *e* alleles, hypothesized that riboflavin was involved in some way in the process of melanization and that

genes which decreased the intensity or distribution of melanin pigmentation also had a sparing effect on riboflavin requirements for normal embryonic development. They were unable, however, to affect the incidence of deficiency symptoms through administration of riboflavin to the eggs prior to incubation. Similarly, Coles and Cumber (1955) were unsuccessful in preventing the condition through the addition of riboflavin to the breeder ration at a level of 6.4 milligrams per pound and Hawes and Fox (1962) found no difference in the incidence of shortened down between black chicks from dams whose ration was riboflavin deficient and dams fed a riboflavin supplemented ration.

Hawes and Buss (1963) reported a condition in turkeys which was similar to the "clubbed down" of chickens possessing the E allele. Among individuals which were segregating for the black (B) and bronze (b) alleles and the red (R) and buff (r) alleles, abnormal down occurred with very few exceptions in only those embryos with black plumage. There was a significant reduction in the down score (a measure of the severity of "clubbing") of heterozygotes when compared to homozygous black embryos. No increase in mortality of the black embryos was observed such as was reported in black chicken embryos.

Merat (1959) has proposed that the barring allele (B) acted to reduce the duration of survival or the fertilizing ability of sperm carrying it.

b) Plieotropic Action of Genes Controlling Blood Groups-

Whether or not genes controlling blood groups might have secondary effects on other characteristics has become a matter of considerable interest to persons involved in the field of gene plieotropy. Pathological and physiological disease susceptibility in humans has been shown to be associated with the A-B-O agglutinogens and relationships between specific blood group genotypes and performance characteristics of dairy cattle have been demonstrated, (Rendel, 1959; Oosterlee, 1962).

In addition, much data has been accumulated relative to the association of blood group differences with various performance traits of poultry. The B system, because of its advantageous serological characteristics, has been the most extensively investigated, although limited data relative to other systems has been accumulated.

W. E. Briles et al. (1953) observed that two of three inbred lines of White Leghorn males which were heterozygous for B blood group alleles were significantly heavier at nine weeks of age than those which were homozygous. The same worker (W.E. Briles, 1957) reported that ten week old males possessing the B^2B^7 combination were 2.8 percent heavier than those with B^7B^7 ; among the females, those with the former genotype were 4.8 percent heavier than the homozygotes. Weight differences in favour of particular blood group genotypes have also been reported by C.O. Briles (1956). W.E. Briles (1956) observed that hatchability and chick livability were greater among heterozygous B genotypes as compared to homozygotes.

Briles and Allen (1961) compared heterozygous and homozygous

genotypes at the B locus with respect to their effects on livability and egg production. Families were compared as to the survival of homozygotes and heterozygotes on the basis of random segregation and fertilization. The data from chicks alive at 150 days showed that livability differences were associated with certain B locus genotypes in two of seven lines studied. Differences in adult livability were also found to be associated with certain B genotypes in two other lines, and, in general, the homozygous birds laid at a lower rate.

c) Plietropic Action of Genes Controlling Comb Type-

The earliest report of comb type pliety was made by Fisher (1938) who observed that the rose comb allele acted to widen the frontal bone of the skull. He did not establish whether or not the effect was equal in degree in homozygous and heterozygous birds. In 1940, Munro and Kosin reported on 'breast ridge', a peculiar ridge-like formation in the skin of the breast running longitudinally in a median line just over the keel bone and associated with pea comb.

Kan et al. (1959) studied the possible influence of the pea allele on metric traits in the fowl. Traits included were: six week body weight, six month body weight, egg production, percent fertility, and hatchability of fertile eggs. Although none of these traits showed a significant difference between the single and pea comb types, housing weight approached significance at the five percent level and was significant when the variation due to dam differences was removed, indicating an advantage of single over pea

comb birds at seven months of age. Furthermore, even though no significant differences existed among the other traits studied, a consistent trend favouring the single comb birds was apparent.

Smith (1961) compared the relative growth rates of pea and single comb broiler chicks for three separate hatches consisting of more than 11,000 birds. Seventeen different matings of meat-type birds which included eight female and five male lines were used. Pea and single comb progeny were raised intermingled and weighed individually at 62 days. Although matings differed, the average ratio of pea to single comb progeny was approximately 2:1. All but three of the female lines were homozygous for single comb; therefore, with few exceptions all pea comb progeny were Pp. Results indicated that single comb progeny outgrew pea comb individuals by 0.11 pound, the advantage ranging from zero to 0.24 pound. An interaction existed between comb type and mating type.

Collins et al. (1963) studied comb type genotype x environment interaction effects on broiler traits in over 6,000 chickens in five experiments and one field trial. 'Poor' and 'good' brooding environments were provided by allotting 0.5 and 1.0 square foot of floor space per chicken, respectively, in each of the five experiments. In two experiments a low and high energy ration was superimposed on the two floor space regimes. Respiratory infection characterized as 'mild' or 'severe' provided the contrasting environments in the field trial. No significant effect of comb type on body weight was detected in any of the experiments and comb type x space interaction was significant in only one experiment. A significant comb type x environment effect was observed in the field trial. This

work was reported in abstract form and consequently further details were not given.

Siegel and Dudley (1963) studied the effects of comb type on behavior and juvenile body weight. Comparisons were made between pea and single comb males raised in flocks where comb types were maintained separately and intermingled. The frequency of encounters (fights, peck-avoidances, threat avoidances) in flocks that consisted of males with single combs was found to be significantly less than the number of encounters in flocks of males with pea combs or in those where males of both comb types were intermingled. In the intermingled flocks, males with pea combs were significantly subordinate to those with single combs. In one of three experiments pea comb males were significantly heavier than their single comb counterparts; in both other experiments there was no significant difference in weight between the two comb type groups.

Crawford and Merritt (1963) reported that subnormal reproductive ability was associated with the rose comb gene but only among homozygous rose comb males. Merat (1962) observed a deficiency of rose comb males among chicks from a cross involving Rr males and rr females. However, Crawford (1963) was unable to show a similar effect of the rose comb gene on sex ratio.

B Interrelationships Between Egg Size, Embryo Size and Chick Growth Rate

Early investigations established a strong relationship between egg weight and day-old chick weight (Halbersleben and Mussehl, 1921; Upp, 1927; Jull and Heywang, 1930).. All of these workers observed that, subsequent to hatching, the correlation between egg weight and chick weight decreased with increasing age of the chick. None found

egg weight to have any substantial effect on chick size beyond five weeks of age. Bray and Iton (1962) observed no significant correlations between egg weight and chick weight after the fourth week of growth in five strains of chickens. The degree of correlation varied between strains to some extent.

The fact that embryo weight and egg weight were related has been supported by Jull and Heywang (1930), Bray and Iton (1962) and others. Bray and Iton concluded that egg size acted as a temporary environmental influence which almost completely determined chick size at hatching. The effect from egg size was observed to begin after eleven days of incubation and to increase up to time of hatching with a rapid decrease after hatching. Byerly (1930) observed differences between White Leghorns and Rhode Island Reds from ten days to hatching time and Byerly et al. (1938) found these differences to be most definite during the 11 to 17 day period. Blunn and Gregory (1935) observed that at 72 hours, 14 days and 19 days of incubation embryos of the White Leghorn breed differed from those of the Rhode Island Red breed with respect to the number of cells and the number of mitoses even though no weight differences existed. Wiley (1950) found no difference in the embryo weights of two strains of Barred Plymouth Rocks selected for large and small body size. McNary et al. (1960) studied the growth of inbred and hybrid embryos and observed genetic differences in embryo growth with respect to the number of somites at 38 hours, and embryo weight after one and two weeks of incubation.

Hamburger and Hamilton (cited in Orlov, 1962) showed the relative appearance of blastodiscs as detected by candling to be associated with the rate of embryonic development and hatchability of the

eggs themselves. Embryos of a particular breed in which blastodiscs could be seen after 14 hours of incubation reached the 9-10 stage of development by 36 hours whereas blastodiscs which became visible by 24 hours had reached only the 5-6 stage during the same period. The respective hatchabilities of the early and late groups were 80-90 percent and 20-60 percent. Orlov (1962) showed that pullets whose blastodiscs could be seen after 8 hours of incubation weighed more than those whose blastodiscs could be seen only after 20 hours.

Bray (1963) mated 15 sires from each of four turkey strains to three dams and weighed embryos after 12, 15, 18, 21 and 24 days of incubation. Significant differences existed between sires within strains for all strains for 18 day embryo weight. Correlations of egg weight with embryo weight increased from about 0.2 at 12 days to about 0.5 at 24 days of incubation. In two strains the correlation between 18-day embryo weight and poult weight from 2 to 24 weeks varied from 0.4 to 0.7 while in the two other strains it was approximately zero.

C The Thyroid Gland and Its Relationship to Growth and Development

The rate of energy exchange is conditioned by the thyroid hormone; that is, the quantity of heat liberated by an organism at relative rest is decreased by deficiencies and elevated by excesses of this hormone. Also, the metabolism of carbohydrates, and probably that of proteins and fats as well is influenced by the functional state of the thyroid gland, (Bodansky, 1938; and others). There have been many reports that thyroidectomy of humans was

followed by an increase in body weight, (Astwood, 1943 - cited in Andrews and Schnetzler, 1946, and others.) Similarly it has been reported (MacKenzie and MacKenzie, 1943) that a large number of compounds related to thiouracil, an antithyroid compound, inhibited thyroid hormone secretion and decreased basal metabolic rate in the rat. Also, Andrews and Bullard (1940) observed that beef steers gained better following the partial thyroidectomy.

Effects of Thiouracil and Protamone:

Protamone, a thyroactive iodinated casein product, when fed to chickens at levels in excess of 0.1 percent of the ration, has been reported by many workers (Turner et al., 1944; Irwin et al., 1943; Mellen and Hill, 1953) to cause a decrease in the size of the thyroid. Irwin et al. (1943) observed a slightly greater rate of growth of Protamone-fed chicks and noted that their carcasses contained decidedly less fat than the controls at twelve weeks of age. Turner et al. (1944) fed 0.1 percent Protamone for periods of six, eight, ten and twelve weeks. The growth rate of the control birds was best although the next heaviest group had received Protamone for the entire twelve week period. Within the treated groups growth rate increased with increasing treatment time.

Glazner and Jull (1946), Astwood et al. (1944), Mixner et al. (1944) have observed thyroid enlargement in the chicken following thiouracil feeding at a level of 0.1 or 0.2 percent of the ration. Andrews and Schnetzler (1946) found the microscopic anatomy as well as the weight of the gland to be proportionately affected by increasing amounts of thiouracil in the ration. Kempster and Turner

(1945) fed 0.2 percent thiouracil to New Hampshires for periods of sixteen and thirty-six days. No growth rate reduction occurred in the former group and grade was improved. The latter group showed a decreased growth rate and feed requirement but also an improvement in grade.

Glazner and Jull (1946) noted that feed efficiency was greater in birds fed 0.1 percent thiouracil than in the controls and also that thiouracil caused a reduction in growth rate during the growing period when fed at levels of 0.1 and 0.2 percent of the ration. Mixner et al. (1946) observed a depression in weight gains but also an improvement in the carcass of heavier, fully grown birds raised on range and fed thiouracil at three levels. Feed efficiency was found to be greatest with the 0.1 percent level of thiouracil as compared to lower levels.

Thyroid Activity Differences Between Species, Breeds and Strains:

Premachandra et al. (1958) compared the thyroxine secretion rates of two strains of New Hampshire chickens which had been selected for high and low response to thiouracil. The birds which showed the greater response to thiouracil by thyroid enlargement were low secretors of thyroxine, whereas the birds which showed a lower degree of response secreted almost three times as much thyroxine per 100 grams of body weight. Though percent I^{131} uptake was similar for both lines, the high secreting group values were slightly higher for both males and females. High secreting yearling males fed 0.1 percent thiouracil in the feed for a period of two weeks had thyroids which were almost two times heavier than those that were low secretors.

Hale and Flipse (1958) have reported that whereas uptake of radioactive iodine by Barred Plymouth Rocks was approximately twenty percent higher than that for New Hampshires, New Hampshire males showed an advantage in winning inter-breed fighting contests. Among the Barred Plymouth Rocks, no significant correlations existed between level of aggression within the breed and individual I^{131} uptake; no correlations were carried out on the New Hampshires.

Lodge et al. (1958) has reported that forty-eight hour uptake of I^{131} by yearling calves was influenced by breed as well as season. Hoersch et al. (1961) found the thyroxine secretion rate of sheep to be correlated with body weight and feed efficiency and according to Howes et al. (1962) the time needed after injection for maximum uptake of I^{131} was greater for Hereford than for Brahman heifers. These workers felt that a lower and slower uptake of iodine by the thyroids of the Brahman cattle indicated a less active thyroid in that breed.

The growth rate of White Pekin ducks has often been shown to be approximately two times faster than that of chickens, (Horten, 1927, and others).

Hoffmann (1950) and Biellier and Turner (1950) observed that the thyroxine secretion rate of growing White Pekin ducklings of both sexes was approximately twice that of chickens of comparable weight.

Biellier and Turner (1950) noted that an addition to the ration of 0.1 percent thiouracil stimulated greater hypertrophy of the thyroid of ducks than any other avian species reported. Thyroid enlargement and a significant reduction in growth rate of ducks

following thiouracil feeding for two weeks was reported by Hoffmann (1950). Thyroxine therapy was successful in reducing the retardation in growth in rough proportion to the amount of thyroxine used. On the other hand, Schultz and Turner (1945) and others have found that more than two weeks of thiouracil supplementation were required to cause a significant reduction in growth rate of chickens; Turner et al. (1944) reported that at least four weeks were required after removal of Protamone treatment of chickens for complete recovery from subcutaneous fat depression. Hoffmann (1950) suggested that the greater thiouracil induced enlargement of the duck thyroid as compared to that of the chicken and the more severe reduction in growth rate of ducks following thiouracil feeding was indicative of a relationship between thyroxine secretion rate and growth rate. Smyth and Fox (1951) observed that the thyroid secretion rates of 3 weeks old Jersey Buff, Broad Breasted Bronze and cross-bred turkey poults were in between the rates for chicks and ducklings of similar weight and ages and that their rates were correlated with growth rate of the three groups. A marked difference occurred in regard to compensatory hypertrophy of thyroids following the feeding of 0.1 percent thiouracil. The females showed greater enlargement in the pure stock compared to the cross, while the males showed the reverse relationship.

The Relationship Between Thyroid Size and Function:

Early investigators reported a relationship between thyroid weight and season, presumably as the result of variation in metabolic activity associated with environmental temperature differences. Enlargement of the thyroids of pigeons and fowl during autumn and

winter as compared to the warmer seasons were observed by Riddle (1927) and Cruickshank (1929), respectively. According to Cruickshank, the iodine content of the thyroids varied directly with seasonal variation in weight. Miller (1939) reported that sparrow thyroids were most active in winter based on histological comparisons and that the increased activity was associated with a higher metabolic rate. On the other hand, Galpin (1938) interpreted data to suggest that thyroid function was inversely related to its mass. Podradsky (1935-cited in Hoffmann and Shaffner, 1950) also postulated that an inverse relationship between thyroid secretion and thyroid weight existed in pigeons and Turner et al. (1944) observed no seasonal decline in thyroxine secretion rate of two year old S.C. White Leghorn hens. However, Hoffmann and Shaffner (1950) significantly increased thyroid weight as well as thyroid secretion rate by maintaining New Hampshire cockerels in a cool environment and Hoersch et al. (1960) reported that hens housed in a fifty degree F. environment had a three-fold higher thyroxine secretion rate than hens maintained at ninety degrees F. The latter workers concluded that in earlier efforts which did not demonstrate a similar relationship, results must have been analyzed in which the correlation between weight and function was obscured by the high degree of inherent variability in the weights of the gland.

III MATERIALS AND METHODS

A General

a) Description of Stocks Used:

The principal stock used in this study was a meat-type strain (Macdonald Large White). It had been maintained at Macdonald College as a closed random-bred population for at least four generations. The strain is composed of S.C. White Leghorns and Barred Plymouth Rocks (single comb - rrpp), Light Brahmas (pea comb - rrPP) and White Wyandottes (rose comb - RRpp). Thus, there is segregation in this stock for four comb types, i.e., single, pea, rose and cushion. The frequencies of these types are approximately equal.

Pure-line S.C. White Leghorn stock homozygous for single (rrpp) comb was used as a tester line in crosses with the Large White strain. This stock had been maintained at the College as a closed population for a minimum of four generations.

The Arkansas White strain used in Experiment C-1 a) is a meat-type Single Comb (rrpp) strain and had been maintained as a closed population at Macdonald College for several generations.

b) Incubation Practices and Management of Birds:

Eggs were stored at 40 degrees F. for a minimum period of two weeks for all hatches; for many of the smaller hatches, however, holding time was considerably less, although in no case were

eggs incubated without having been previously stored for at least twenty-four hours.

All eggs were incubated and hatched in a Bundy Model 6 Incubator and Model 2 Hatcher under similar conditions of temperature and humidity as recommended by the manufacturer.

All chicks except Experiment D-1 were brooded in a windowless brooder house in which the daily light period was constant throughout all growing periods, both within and between individual experiments. Though efforts were made to standardize temperature, a gradual increase accompanied the increased outside temperature. Ventilation was somewhat reduced with increasing temperatures which occurred during the period from March to August, 1963.

All chicks were started on a commercial chick starter ration and transferred to a commercial grower ration at eight weeks of age. Both feed and water were provided ad libitum with the exception of Experiment D-1.

Birds used in Experiment D-2 were managed as described in that section.

All birds were weighed individually to the nearest gram with the exception of those of six and ten weeks of age of hatches four and five (and consequently Experiment D-2). These were weighed to the nearest 0.1 pound.

With the exception of those pertaining to Experiments C-1 a) and D-1, statistical analyses were completed by means of an IBM 1410 computer. The program for least-square analysis was based on methods of analysis for data with disproportionate subclass numbers as presented by Harvey (1960) and Henderson (1953).

The individual mathematical models describing the parameters of each analysis are presented in each relevant section.

Analysis carried out on data from Experiments C-1 a) and D-1 are described therein.

B Determination of Genotype

a) Females:

102 Large White females, representing all four comb types, were mated inter se to S.C. White Leghorn males. Two hatches were incubated (Hatches one and two). Upon hatching each chick was identified on the basis of comb type and classified according to dam. The genotypes of the dams were then determined from the ratio of chicks of the various comb types hatched from each.

b) Males:

Each of 13 Large White males was mated artificially to three Single Comb White Leghorn females confined in individual bird battery-type cages. Eggs were incubated after a two-week collection period (Hatch three). Upon hatching the comb type of each chick was identified and classified with respect to male parentage. Male genotypes were determined from the ratio of offspring of the various comb types sired by each.

C Growth Trials

The progeny from females of the four comb types were compared in six experiments. Three of these compared the growth rate

of chicks grown to ten weeks of age while three others compared embryo weights at thirteen days of incubation.

-1, Hatched Chicks:

Of the three trials on hatched chicks, the final one included a comparison of adrenal and thyroid gland weights, eviscerated weights, and of shank length and breast angle on the ten week old birds.

Data from Trial A were analyzed as outlined therein. Since data from Trials B and C were analyzed for the overall effect of comb type, both of the dam and of the chick, and for comparisons of individual comb types with one another, two mathematical models (Eisenhart, 1947) were arranged for each of the trials.

a); Trial A - Two-Way Crosses:

Eighty-five Large White females, representing the four comb types in approximately equal numbers, were mated inter se to ten Arkansas White (single comb, rrpp) males. The reciprocal cross was made by mating inter se eighty Arkansas White females to thirteen Large White males among which were individuals of the four comb types. Two settings of eggs from both crosses (Hatches four and five) were made at intervals of two weeks. Chicks were grown to ten weeks of age and single, pea, and rose comb individuals were weighed individually at two, six and ten weeks of age.

Data from each of the reciprocal crosses was analyzed as a 4 x 2 randomized complete block in which unequal numbers occurred within experimental units. Two degrees of freedom existed for comb type and one degree of freedom existed for replications where

replications referred to hatch. The model on which the analyses were based is as follows:

$$Y_{ijk} = u + c_i + h_j + e_{ijk}$$

$$(i = 1,3; j = 1,2)$$

Where Y_{ijk} represents the weight of the k th chick of the i th comb type within the j th hatch. 'u' is the theoretical population mean in a case of equal subclass numbers, c_i represents the effect of the i th comb type, h_j represents the effect of the j th hatch; and e_{ijk} is a random error associated with the particular observation and assumed to be NID $(0, \sigma_e^2)$.

Two of three variables measured were two week weight and six week weight; for each sex within each of these weights separate analyses were performed. Analysis of the third variable, ten week weight, was carried out on the males only.

b) Trial B - Pure-line Random-bred Stocks:

Eighty-five Large White females of known genotype were mated inter se to thirteen Large White males. All four comb types were represented among the females; there were, however, no rose comb males. Six hatches were incubated (Hatches 6, 7, 8, 9, 10, 11 and 12). At hatching all chicks were classified according to dam and brooded as outlined above. The birds were grown to ten weeks of age and weighed at two, six and ten weeks.

For purposes of Analysis of Variance of overall effects the model considered appropriate for these data is:

$$Y_{hijklm} = u + dc_h + d_{hi} + h_j + c_k + s_l + cs_{kl} + e_{hijklm}$$

$$(h = 1, 4; i = 1, 68; j = 1, 7; k = 1, 4; l = 1, 2)$$

Where Y_{hijklm} represents the weight of the m th chick of the l th sex, k th comb type and j th hatch and from the i th dam. of the h th dam comb type.

' u ' is the theoretical population mean in a case of equal subclass numbers,

d_{ch} represents the effect of the h th dam comb type,

d_{hi} represents the effect of the i th dam in the h th comb type,

h_j represents the effect of the j th hatch,

c_k represents the effect of the k th comb type,

s_l represents the effect of the l th sex,

cs_{kl} represents the interaction effect of the k th comb type and the l th sex, and

e_{hijklm} is a random error associated with the particular observation and assumed to be NID $(0, \sigma_e^2)$.

For the purposes of this analysis all effects were regarded as fixed.

The above represents the model for a single variable; the analysis was carried out for five variables as follows:

- 1) two week weight,
- 2) six week weight,
- 3) ten week weight,
- 4) six week weight - two week weight, and
- 5) ten week weight - six week weight.

In order to utilize an existing computer program two sets of analysis were carried out. The first analysis ignored the comb type x sex interaction and the second analysis considered each comb type - sex subclass as a separate subgroup. The interaction sum of squares was then calculated by difference.

For the analysis of differences between individual chick comb types, another model was used to show variance differences among the four comb types. This model was similar to the one outlined above for analysis of overall effects except that chick comb type was excluded since separate analyses were carried out for each comb type.

The same variables as outlined for the preceding analysis were analysed for in each of these four analyses. The variances computed, together with their means calculated from the computer-adjusted data, were subsequently used in comparisons of each of the five measured variables by means of a modified 't' test outlined by Goulden (1960).

c) Trial C - Pure-line Pedigreed Stocks:

Four groups of twelve Large White females each were utilized. Within each group the four comb types were represented in approximately equal numbers. One of four Large White males, heterozygous for cushion comb (RrPp), was assigned to each group constituting a completely pedigreed mating. Six settings (Hatches 13, 14, 15, 16, 17, and 18) were made at intervals of two weeks. Chicks were weighed and pedigreed by sire and dam at hatching. They

were again weighed at two, six and ten weeks of age. Following the ten-week weighing all birds were slaughtered and the paired weights of the thyroid and adrenal glands were taken to the nearest 0.0001 gram. An effort was made to remove from each gland any adherent fatty and connective tissue. Breast angle of each bird was measured to the nearest 0.5 degree by means of "West Virginia" calipers; care was taken to apply the instrument to the breast at the same distance from the front of the keel bone in each case. The length of the tarso metatarsus (shank) was taken to the nearest 0.1 inch by partially removing the bone so that the calipers used could be placed directly against the ends of the bone. Sex and comb type were also determined and the weight of the eviscerated carcass was recorded to the nearest 0.10 gram.

For purposes of Analysis of Variance of these data for overall effects the model is as follows:

$$Y_{hijklmn} = u + si_h + dg_{hi} + d_{hij} + h_k + c_l + s_m + cs_{lm} + e_{hijklmn}$$

(h = 1,4; i = 1,6; j = 1,42; k = 1,6; l = 1,4; m = 1,2)

Where $Y_{hijklmn}$ represents the value of the nth chick of the mth sex, lth comb type and kth hatch and from the jth dam of the ith comb type and the hth sire.

'u' is the theoretical population mean in a case of equal subclass numbers,

si_h represents the effect of the hth sire,

dg_{hi} represents the effect of ith dam comb type within the hth sire (i.e. - dam comb type is nested in the sire effect),

d_{hij} represents the effect of the j th dam within the i th dam comb type within the h th sire (dam effect is also nested in the sire effect),

h_k represents the effect of the k th hatch,

c_l represents the effect of the l th chick comb type,

s_m represents the effect of the m th sex,

cs_{lm} represents the interaction effect of the l th chick comb type and the m th sex, and

$e_{hijklmn}$ is a random error associated with the particular observation and assumed to be NID $(0, \sigma_e^2)$.

For the purposes of this analysis all effects were regarded as fixed.

The above represents the model for a single variable; the analysis was carried out for ten variables as follows:

- 1) Hatching weight,
- 2) Two week weight,
- 3) Two week weight - hatching weight,
- 4) Six week weight - two week weight,
- 5) Ten week weight - six week weight,
- 6) Shank length,
- 7) Breast angle,
- 8) Thyroid weight,
- 9) Adrenal weight, and
- 10) Eviscerated weight.

As in C-1 (b) two analysis were carried out. One considered chick comb type x sex interaction and the other ignored it.

The interaction sum of squares was then calculated by difference.

For the four analyses of variance of individual chick comb types a model similar to the one above was used to disclose variance differences except that chick comb type was excluded and the analysis was carried out on each comb type independently.

The same variables as outlined for the preceding analysis were measured in each of these four analyses. As in Experiment C-1 b), the computed variances and calculated means were subsequently used in 't' tests for comparisons between individual comb types.

-2, Embryos:

Three trials, each differing in mating procedure, were conducted.

Jull and Heywang (1930) noted that embryo weight became increasingly dependent on egg weight as incubation progressed. Wiley (1950) observed that embryo size was significantly limited by egg size during the last two or three days of incubation. Bray and Iton (1962) observed that the effect of egg size on embryo weight began after eleven days, increasing rapidly thereafter to hatching. However, for the present study embryos were allowed to incubate for thirteen days. While it was felt desirable to weigh the embryos before egg size would exert an influence, it was, nevertheless, difficult to distinguish comb type prior to thirteen days.

At thirteen days the embryos were removed from the shell, separated from the extra-embryonic membranes, identified with respect to comb type, blotted slightly on absorbent paper and immediately weighed to the nearest milligram.

For analysis, embryo weights were grouped according to the size of egg in which they were contained and statistical corrections were subsequently made for egg size differences.

For trials 1 and 2, the 4 groups were: up to 51 grams, 52 to 56 grams, 57 to 61 grams and 62 grams or greater; for trial 3 the ranges were: up to 46 grams, 47 to 51 grams, 52 to 56 grams, and 57 grams or more.

For purposes of statistical computation, the model used for all embryo growth trials is as follows:

$$Y_{ijkl} = u + h_i + w_j + c_k + e_{ijkl}$$

(ranges of i, j and k are presented for each trial therein)

Where Y_{ijkl} represents the weight of the lth embryo of the kth comb type from an egg of the jth weight and of the ith hatch.

'u' is the theoretical population mean,

h_i represents the effect of the ith hatch,

w_j represents the effect of the jth egg weight,

c_k represents the effect of the kth comb type, and

e_{ijkl} is a random error associated with the particular observation and assumed to be NID $(0, \sigma_e^2)$.

For purposes of this analysis all effects were regarded as fixed.

The above represents the model for a single variable; the analysis was performed for both embryo weight and embryo weight expressed as a percentage of egg weight.

a) Trial D - S.C. White Leghorn x Large White (Random-bred):

Four pens of approximately ten Large White females, each including all four comb types, were mated to S.C. White Leghorn males. Three settings of eggs were made at two week intervals.

With respect to statistical analysis, the respective ranges of i, j, and k were 1,2; 1,4 and 1,4.

b) Trial E - Large White x S.C. White Leghorn (Random-bred):

One each of four heterozygous cushion comb (RrPp) Large White males was mated to one of four lots of approximately ten Single Comb White Leghorn females. Three settings were incubated at two week intervals.

Ranges of i, j, and k were 1,2; 1,4 and 1,4, respectively.

c) Trial F - Large White x S.C. White Leghorn (Random-bred):

Approximately seventy S.C. White Leghorn pullets and ten cushion comb Large White males were mated inter se. Two settings were incubated.

Ranges of i, j and k were 1,3; 1,4 and 1,4, respectively.

D Studies on Thyroid Involvement:

According to Reineke (1954) the average "true thyroxine" content of Protamone is approximately 1 percent. Therefore the level of thyroxine fed when Protomone is added to the ration at a level of 0.02 percent is approximately 0.0002 percent. This level is twice that which Schultz and Turner (1945) found to be equivalent to the endogenous thyroxine secretion rate of chickens.

Mellen and Hill (1953) and others have observed that this level depressed thyroid size, presumably due to the suppression of thyrotropic hormone secretion.

Thiouracil has been shown to be highly goitrogenic when fed to growing chickens at a level of 0.1 percent to 0.2 percent of the ration, (Astwood et al., 1944; Mixner et al., 1944; Adnrews and Schnetzler, 1946; Mellen and Hill, 1953; and others).

-1, Effect of Thiouracil and Protamone:

Males from Hatch one were divided into three groups of approximately 80 chicks, each group containing individuals of the four comb types in approximately equal numbers. Following weighing at hatching, the chicks were brooded in three adjacent pens. All but cushion comb birds were weighed again at four weeks of age after which the following treatments were initiated:

Lot 1 - Thiouracil, as 0.1 percent of the growing ration;

Lot 2 - Protamone, as 0.02 percent of the growing ration;

Lot 3 - Growing ration only.

Thiouracil administration to Lot 1 was continued to completion of the experiment. At six weeks of age the level of Protamone to Lot 2 was increased to 0.04 percent of the ration and this level was continued to completion. All birds in each of the lots were weighed again at six and eight weeks of age.

-2, Measurement of Comparative Uptake of Radioactive Iodine:

Ten single comb and seven rose comb males from the mating Large White x Arkansas White (Hatch four) were selected for this study conducted during the period May 29, to June 4, 1963. Sel-

ection was made on the basis of nearness to the respective mean weight for the two comb type groups. The birds were confined in individual battery-type cages; a growing ration and water were provided ad libitum.

Temperature fluctuated as a function of outside variations and humidity increased slightly with increasing temperatures. Drop-pings which were collected on metal trays beneath the cages were not removed until completion of the experiment.

After an adjustment period of a few days following transfer to the cages, each bird was injected intravenously with 100 uc. of carrier-free radio-active iodine (I^{131}) in Na_2SO_3 diluted to one milliliter in saline. This amount was chosen since it was considered sufficiently high to render one minute counts that could be regarded as an accurate estimate of activity for each counting period and was not so high as to cause physiological damage to the subject.

For counting, each bird was removed from its cage and placed in a special holding device which prevented body movement and which required the bird to hold its neck extended. The holding device was placed a standard distance of 15 inches from the detector such that the rate of emission of radioactivity from the thyroid region of each bird would be determined with a minimum of error. The detector consisted of a 1 inch x 1 inch NaI (Tl) Crystal mounted on a Dumont 6292 Phototube. It was connected to an amplifier with a single discriminator and this section was in turn connected to a Baird-Atomic Scaler, Model 123.

Following injection, the birds were returned to their cages.

and the initial counting was begun at nineteen hours thereafter. Subsequent periodic counts were made at six hour intervals for the first 103 hours and thereafter at intervals of twelve hours to completion at 164 hours. Counting time for each individual within each counting period was one minute. Individuals were counted in the same order during all counting periods. Before and after each counting period, background counts and counts on a 100 uc sample of I^{131} were taken. The latter were used to calculate decay rate and to detect any instrumental drift.

Regression analysis of presumed maximum uptake on body weight was carried out for each comb type group according to the method outlined by Goulden (1960).

IV RESULTS

C Growth Trials

-1, Hatched Chicks- a); Trial A - Two-Way Crosses:

Two lines of meat-type chickens were utilized in this trial. Reciprocal crosses were made between the Arkansas White (A.W.) and Large White (L.W.) strains. Since the Large White strain carried the alleles P and R, there was segregation among the progeny for three comb types (i.e. single, pea and rose). Birds were weighed at two, six and ten weeks of age and the weights of males and females were analysed separately. Hatch effect and comb type x hatch interaction effects were included in the analyses. Two hatches were observed.

In regard to the Arkansas White x Large White cross (Tables 1 and 2, A.W. x L.W.) no significant differences were seen at any age as a result of differences in comb type per se. Significant hatch effects were present at two weeks of age for females and for both males and females at six weeks. A significant interaction between comb type and hatch was seen at two and six weeks for males. In spite of the lack of significance for comb type the rose comb birds were consistently larger in four of the five comparisons while single and pea comb birds were rather similar in weight. However, it is seen that the variance in the rose comb groups was consistently greater (Table 3, A.W. x L.W.).

The cross Large White x Arkansas White showed highly significant comb type differences with respect to body weight at two weeks

of age for both sexes and also for the males at ten weeks of age (Tables 1 and 2, L.W. x A.W.). Hatch differences were highly significant at six and ten weeks for the males. As in the reciprocal cross the rose comb birds were heaviest in three of the five comparisons and were equal to the heaviest group in a fourth comparison (female weights at two weeks). In this cross the variances (Table 3, L.W. x A.W.) were again greatest for the rose comb groups.

All birds in the two crosses with pea or rose combs were heterozygotes.

b); Trial B - Pure-line Random-bred Stocks:

The birds used in this trial were from the Large White strain and were produced as the result of random mating within this population. Weights were taken at two, six and ten weeks of age. Corrections on the absolute weights and weight gains were made for sex differences. Comparison of the absolute weights and weight gains (Tables 4 and 5) for the various comb type groups at each revealed no significant differences. Contrary to the greater weight of rose comb birds which occurred among the strain crosses (Trial A), the rose comb group was consistently lighter in body weight in the present comparison. Single and pea comb birds were again similar in weight to each other and also to the cushion comb birds throughout the entire growing period.

The single comb birds were shown to be significantly less variable (Tables 7 and 8) than pea comb birds at two weeks and ten weeks, than rose comb birds at ten weeks, and cushion comb birds at two and ten weeks.

The only other comparison to show significance was pea vs. rose at two weeks. In regard to six to ten week gain the single comb group was significantly less variable than the other three types. In the previous trial all the birds were heterozygotes; in this trial some homozygotes could be expected although the genotypes were not tested. Assuming the P and R alleles to exert an effect, this might be greater in homozygotes than in heterozygotes and might therefore be assumed to have caused the greater variation among the other comb types as compared to single comb birds which occurred in this trial.

The association between dam comb type phenotype and body weight of progeny was not significant (Table 6) for any of the age groups or weight gain periods. However, the influence of individual dams was highly significant as would be expected. Sex and hatch differences were significant at all ages. Chick comb type was not significant at any age. Comb type x sex interaction was highly significant for the two to six week and six to ten week periods and for ten week weight.

c); Trial C - Pure-line Pedigreed Stocks:

Birds compared in this trial were progeny from a Large White x Large White pedigreed mating which allowed for classification of each chick by both parents. The birds, among which segregation occurred for the four comb types, were weighed at hatching, two weeks, six weeks and ten weeks of age after which they were slaughtered and shank length and breast angle determinations were made and the weights of the thyroid and adrenal glands and the eviscerated carcasses were recorded. Means of each comb type for each of the var-

ables measured are presented in Table 9. Although weight gains from two to six and six to ten weeks were used for analysis rather than the six and ten week weights, the latter have been included in Table 9; gland weights expressed as a percentage of mean body weight have also been included.

None of the statistical comparisons of the means with one another were significant (Table 10). However, examination of the means showed that while the growth rate for the pea and rose comb groups was relatively uniform, that of the single comb group was more rapid than average during the first two weeks of growth and became less rapid than average thereafter. Conversely, the growth rate of the cushion comb group was generally poorer in comparison to the other types during the period of early growth but was the best of all types during the later stages.

Eviscerated weights were not consistent with ten week weight and no relationship between eviscerated weight and either shank length or breast angle was apparent.

Both thyroid and adrenal weight means ranked in the same order of magnitude whether expressed as absolute values or in terms of percentage of body weight. Mean thyroid weight, expressed in either manner was inversely related to ten week weight and also to weight gain from six to ten weeks. No such relationship existed for mean adrenal weight.

Neither dam comb genotype nor chick comb phenotype had a significant effect on any of the variables measured (Table 11). The sire effect was significant for all variables except hatching weight, gain from six to ten weeks, shank length and breast angle;

the dam effect was significant for all but shank length, thyroid weight and adrenal weight. The effect of hatch was significant for thyroid weight and highly significant for all other variables. Sex had a significant effect on all variables except gain from six to ten weeks, breast angle and thyroid weight.

As in Trial B, single comb birds were involved in a substantially greater number of significant variance comparisons (Tables 12 and 13) than were birds of other comb types. However, unlike Trial B, the single comb group had a greater variance in the majority of such cases. The greater variance of the single comb birds for two week weight and gain from hatching to two weeks as compared to pea comb birds was highly significant and the greater variance of pea comb for eviscerated weight as compared to single comb was significant at the five percent level. Single comb birds were also significantly more variable than rose comb birds for two week weight, gain from hatching to two weeks, shank length and adrenal weight although rose comb birds were significantly more variable than single comb birds for gain from two to six weeks (five percent) and in weight at ten weeks, thyroid weight and eviscerated weight (one percent). The variance of single comb was significantly greater than that of cushion comb for gain from hatching to two weeks, while cushion comb was significantly more variable than single comb for hatching weight. Among significant comparisons not involving single comb birds, pea comb was more variable than both rose comb and cushion comb for shank length and rose comb was significantly more variable than cushion comb for gain from six to ten weeks (five percent), and for thyroid weight and eviscerated weight (one percent).

-2, Embryos:

Three trials were conducted to study the possible effect of comb type of embryos on embryo weight at thirteen days of incubation. Each of the three trials differed with respect to the mating by which they were produced. Reciprocal matings of yearling S.C. White Leghorn x Large White provided eggs for Trials D and E. More uniformly sized eggs used in Trial F were from S.C. White Leghorn pullets which had been mated to cushion comb Large White males. In all trials segregation occurred among the embryos for all comb types. Since S.C. White Leghorns were used in each of the trials, all pea, rose and cushion embryos were heterozygotes.

Results from each of the three trials are reported below. In Trial D the effect of egg weight on absolute embryo weight was negligible (Table 14). However, the effect of egg weight on embryo weight in Trial E approached the five percent level of significance (Table 15) and in Trial F its effect on embryo weight was significant (Table 16). Thus in two of the three trials, embryo weight was to some extent influenced by egg size.

a); Trial D - S.C. White Leghorn x Large White (Random-bred):

The weight means of each of the embryo comb type groups, expressed both as absolute values and as percentages of egg weight, and the Analysis of Variance of data from this trial are presented in Table 14. No significant differences in embryo weights were found to be associated with comb type differences.

b); Trial E - Large White x S.C. White Leghorn (Random-bred):

Means of embryo weights, expressed in both forms, and the Analysis of Variance pertaining to these data are presented in Table 15. As in Trial D, no significant effect of comb type on embryo weight was observed.

c); Trial F - Large White x S.C. White Leghorns (Random-bred):

Weight means and the Analysis of Variance of data from this trial are presented in Table 16. Again, no significant effect of comb type on embryo weight was observed.

D Studies on Thyroid Involvement:

-1), Response to Thiouracil and Protamone:

Male chicks produced from a S.C. White Leghorn x Large White cross were divided in three groups consisting of approximately equal numbers of single, pea and rose comb chicks. One group acted as a control, another was fed 0.1 percent thiouracil and the third group was fed 0.02 percent Protamone. The chicks were weighed at hatching, four weeks, six weeks and eight weeks of age. Differences between mean rates of growth of the four comb type groups for the period from hatching to four weeks were not significant with respect to treatment as expected since treatments were not begun until the fifth week (Tables 17 and 18). Each of the comb type groups responded to the thiouracil treatment during the periods from four to six weeks and six to eight weeks (Tables 19 and 20). Response by the

single and pea comb type groups were highly significant (one percent) for the four to six week period; the response by the rose comb birds for this period was significant at the five percent level. Only the single comb birds showed a significant response during the six to eight week period (Table 20). No significant response to Protamone was observed by any of the comb type groups at either of the later periods.

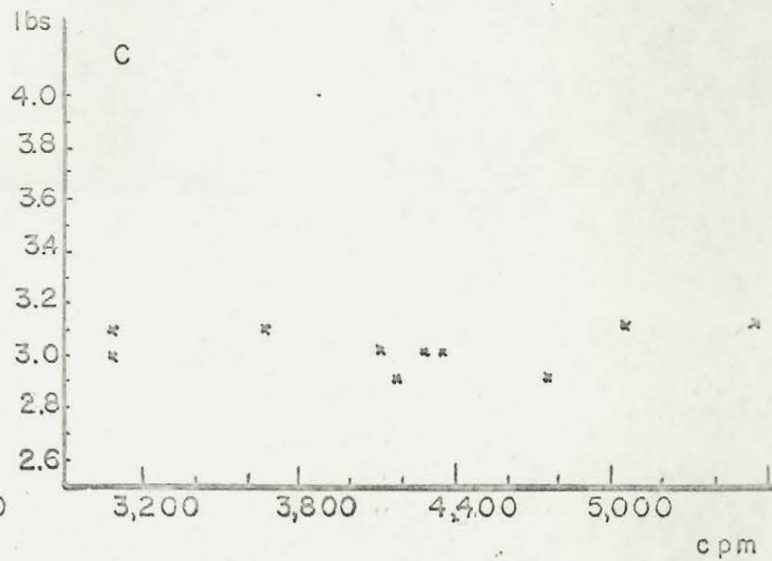
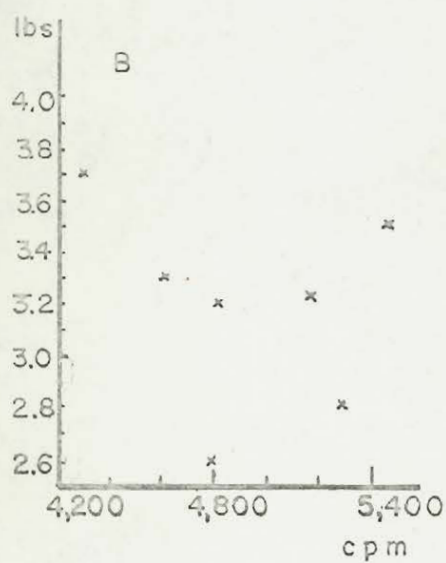
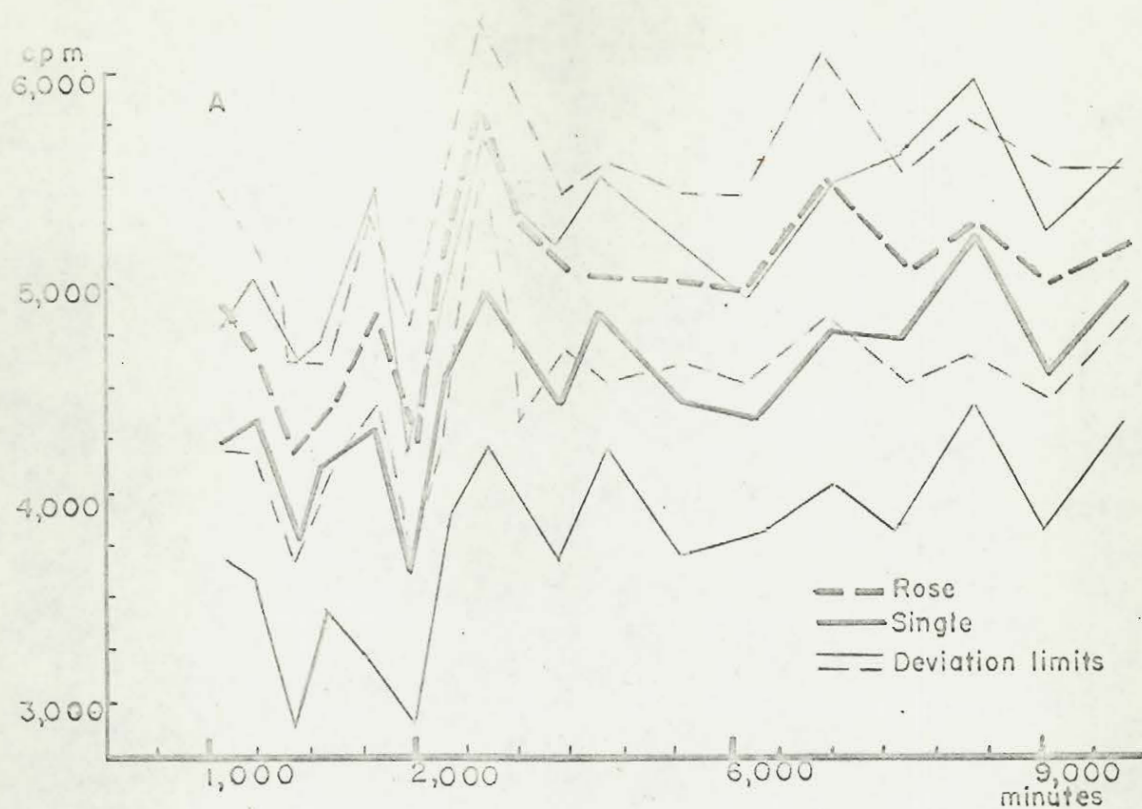
-2), Measurement of Comparative Uptake of Radioactive Iodine:

Ten single and seven rose comb males of approximately thirteen weeks of age were injected with radioactive iodine (I^{131}) and uptake of the isotope by the thyroid gland of each bird was traced by measuring counting rate individually at regular intervals.

The mean counting rate at each of the eighteen counting periods are presented graphically on the following page. The relationship between body weight and counting rate at the point of presumed maximum uptake for both comb type groups is presented in the form of two scatter diagrams on the same page.

It can readily be seen that the mean counts are consistently higher for the rose comb birds of the larger mean body weight (3.2 vs. 3.0 pounds) throughout the entire experimental period. However, it is also apparent that the deviation limits (the mean standard deviation of counts for all birds within each group) overlap at all points.

Both of the scatter diagrams would appear to show an inverse relationship between body weight and presumed maximum uptake, although the regression analysis in each case was nonsignificant (Table 21).



A- Mean uptake of radioactive iodine (I^{131}) by rose and single comb groups
 B, c- Relationship between presumed maximum uptake and body weight -
 B, rose comb; C, single comb

V DISCUSSION

A Variability in Comb Shape and Similarities in Appearance of Different Comb Types

A major problem confronted in carrying out this project was that of accurately identifying comb type. Though the ease with which the various comb types could be distinguished was greater among the older birds, there were a considerable number of cases where arrival at a conclusive decision was difficult. Generally, the difficulty existed between the single and pea comb types and between the rose and cushion comb types; with very few exceptions single and pea comb birds could quite easily be distinguished from rose and cushion comb birds.

Within all types considerable variation existed, a situation which was probably in part the result of the presence of both homozygous and heterozygous pea, rose and cushion comb birds (in those trials where segregation occurred) within each of these comb type groups. Incomplete dominance of the pea comb gene, which has been reported by Bateson (1902) and Pearl and Pearl (1909), would account for further variability in the shape of pea and cushion combs (the latter possessing at least one P allele). Attempts to distinguish between birds possessing the P allele (pea and cushion) and those lacking it (single and rose) on the basis of a breast ridge (Crawford, 1961) were not successful because breast ridge was not consistent in its degree of expression. When difficulty was encountered in distinguishing comb type, similar difficulty was usually encountered in detecting breast ridge.

For purposes of illustrating the nature of the various comb types and the variation which occurred within each type used in this

study, pictures of Large White adult females, the major stock used, are presented on the following pages. These have been arranged according to comb type genotype in order to illustrate the manner in which similarities between comb types occurred.

According to Bateson (1902), homozygous and heterozygous pea combs normally were not easily distinguishable in newly hatched chicks and the distinction between the two types was not fully evident, especially in females, until birds reached the adult age. For the research reported on here, the comb type of birds on which growth comparisons were made were identified at not later than ten weeks of age and in the case of Trial A, at two weeks of age. Bateson (1902) implied that differentiation is easier in the unhatched chick than it is in the newly hatched chick; although comb structures were found to be very small in embryos studied here, they were, nevertheless, probably more easily distinguishable than in the growing birds. Bateson (1902) described the homozygous pea comb of adult birds as having three distinct and well-marked ridges laterally aligned with the length of the head. He stated that, in the heterozygote, the ridges were often somewhat less distinct. Among the majority of pea comb birds used in this study, including both homozygotes and heterozygotes which are pictured, few had distinct ridges. Nevertheless the presence of ridging was one of the most dependable means of distinguishing between pea and single comb birds.

Bateson (1902) and Pearl and Pearl (1909) found the comb to stand upright in homozygous pea comb birds while in the heterozygous birds it often fell to one side as single combs often do. This characteristic of the heterozygous pea comb genotype is well illustrated in

PICTORIAL DESCRIPTION OF FEMALE COMB TYPES

Single (rrpp):



Pea (Pp):



FEMALE COMB TYPES, continued-

Pea (PP):



Rose (RR):

Rose (Rr):



FEMALE COMB TYPES, continued-

Cushion (R-P-):



several of the heterozygous pea comb birds pictured.

A high degree of variability in the shape of pea combs similar to that reported by Pearl and Pearl (1909) is evident in the Large White stock. The combs pictured in the uppermost row of heterozygous pea comb females are quite similar to those of some of the single comb birds. Progressing through the heterozygous pea comb group, comb shape becomes less similar to that of the single comb birds and more like that of the two homozygous pea comb birds.

Bateson (1902) described the rose comb as consisting of a number of papilliform elevations standing on the same horizontal plane and with a point or spike at the rear. Bateson (1902) found that, among birds from a S.C. White Leghorn x White Dorking cross, the rose comb was recognizable from about nine days of incubation onward and thereafter could not be confused with single comb embryos. He also reported that single progeny from the same cross were reduced in height in comparison to those of pure S.C. White Leghorns. He felt that otherwise homozygous and heterozygous rose combs were quite similar.

The only homozygous rose comb pictured had a noticeably smaller, more refined comb than most of the heterozygous rose comb birds and especially those in the last three rows of pictures. These progressively became more bulky and less refined in shape.

The cushion comb was described (Bateson and Punnett, 1905) as being wide similar to the rose comb, but much less papillose and without a posterior spike. Its most distinct feature, however, was the presence of small bristles or minute feathers near the rear of the comb which often formed a narrow band crossing it about two-thirds

of the way back. These workers reported that bristles were found only in cushion combs. Among cushion combs examined in this work, bristles were often but not always apparent in cushion comb birds and in many cases there was a close resemblance between the rose and cushion comb types.

There is more than strong likelihood that comb shape is influenced by the residual genotype of each individual bird. Pearl and Pearl (1909) felt that such was the case among birds in which they studied. Their contention was that while basic comb type is controlled by single genes, gross modifications in shape may be caused by other genes of the residual genetic milieu or modifiers which act specifically on comb shape. Munro (1962) has suggested the possibility of multiple alleles at comb type loci. These could account for such shape differences as have been observed here. While the variation in shape of the combs of birds used in these experiments appeared to be too extensive to support his proposal, no conclusive results have shown otherwise.

B Growth Trials

Results from chicken growth trials showed that the effect of comb type on growth and other metric traits was either nonexistent or at least unpredictable. This finding is in agreement with that of other workers who have studied the comb type-growth rate relationship (Kan et al., 1959; Smith, 1961; Collins et al., 1963; Siegel, et al., 1963). In this project comb type was not consistent with respect to its influence on weight nor did the variances always rank in the same order among the various trials. Both Smith (1961) and

Siegel et al. (1963) mentioned the existence of an interaction between comb type and mating type in their results. A similar situation was seen in the results from these trials.

The degree of variability of growth rate for each comb type did not seem to be associated with growth rate nor was it greater among pea, rose and cushion comb birds where there was a possibility of both homozygous and heterozygous birds being present than where birds of all these types were known to be heterozygotes. However, while the variances were not consistent between trials, there was some indication that significant comparisons between the variances of individual comb types were reasonably consistent for some comb types within trials. The fact that significant comparisons occurred seems to offer proof that comb types differed with respect to their variability even though it was in an unpredictable manner.

The only instance of a significant effect from comb type per se on weight was observed in Trial A among birds which differed in residual genetic constitution (reciprocal strain crosses) from the pure-line Large White birds studied in other trials. In this trial, rose comb birds were heaviest at most ages among birds from both crosses. No comparisons with results of other workers pertaining to this observation are possible because no published studies have been conducted in which rose comb birds were considered.

In no case was a particular comb type observed to be significantly heavier than any other. Kan et al. (1959) observed that seven month old single comb birds were heavier than pea comb birds of the same age and Smith (1961) reported a similar result in birds of approximately nine weeks of age. However, Collins et al.

(1963) observed no difference in the growth rates of pea and single comb birds and Siegel et al. (1963) observed that pea comb birds were heavier than single comb birds in one of three comparisons while in the other two there was no difference between comb types groups. In all of the growth trials carried out here single comb birds were heavier than pea comb birds at ten weeks of age albeit differences were not significant. To this extent, results of these trials are in agreement with those of Kan et al. (1959) in which a consistent trend in both growth and fertility favouring single comb birds was observed.

The interaction between comb type and hatch observed in Trial A suggested an interrelationship between environment and comb type similar to that in ~~the~~ single and pea comparisons of Collins et al. (1963). The occurrence of a highly significant sex x comb type interaction which occurred in Trial B is not readily explainable and suggests that greater numbers would probably have been beneficial.

In all of these trials, birds were grown intermingled as were those of the aforementioned workers. The suggestion by Siegel et al. (1963) that differences in social order of pea and single comb birds might be a reason for growth differences gives special significance to the embryo weight comparisons made here where the possibility of social competition was absent. The negative results from these trials would support the suspicion that, in the absence of social competition, the growth rates of birds with different comb types are likely to be quite similar. Crawford and Smyth (1961) have shown that barred chickens were subordinate on the basis of peck-order to chickens of the same breed with columbian pattern and

Hale and Buss (1960) reported that social rank was associated with colour-determining genes in turkeys. Because of the positive relationship which may exist between pre- and post-hatching growth rate (Bray and Iton, 1962), it is recommended that further studies concerning the genetic differences in growth rate be carried out by embryo comparisons, correlations between pre- and post-hatching growth rate having previously been determined for each individual strain. The main advantage of such studies would be the elimination of social interactions. By randomization of eggs within the incubator, other physical environmental differences could also be overcome.

C Response to Thiouracil and Protamone

The decision to conduct a study comparing the response of different comb types to thiouracil and Protamone was based on the assumption that growth rate differences which might exist between comb types might possibly be related to differences in thyroid activity and that, if such was the case, their response to compounds which influence thyroid activity would differ in relation to the 'natural' levels of activity of each group (Biellier and Turner, 1950). It was felt that if birds of a particular comb type had 'normal' thyroid activity, their growth response to thyroactive Protamone would be negligible and that, conversely, thiouracil, a thyroid inhibiting compound, would affect most adversely the growth rate of these birds. On the same basis, birds of another comb type whose thyroid state was one of mild hypothyroidism would respond in a positive manner to Protamone treatment and would be least adversely affected by thiouracil treatment. Since it was felt that the comparative change in

growth rate rather than weight per se. would be more likely to reveal dynamic effects, the results were reported on this basis.

The response to thiouracil by the different comb type groups indirectly suggested a relationship between comb type and growth rate of birds used in this trial. Thiouracil had the predicted effect of reducing growth rate. A significant response to this compound was shown by all comb types over the four to six week period. Single comb birds showed a significant negative response again for the six to eight week period which may be indicative of a different level of thyroid activity by this group for this period. It could be argued that single comb birds could just as easily have had the lowest level of thyroid activity and that they showed the greatest negative response to thiouracil simply by virtue of the activity of their less active thyroids having been almost completely inhibited by thiouracil. However, they were the heaviest group among the non-treated birds. Also, Hoffman (1950) has reported that, in ducklings whose growth rate is more rapid, the effect of thiouracil in ducklings is more marked than in chicks. Whether or not the fact that growth rate of the single comb bird was greater for this period is secondary; the fact remains that comb types differed with respect to thyroid activity for this period. While there is strong likelihood, as Glazner et al. (1949) have reported, that thyroid activity is related to the difference in the growth rates of the non-treated birds, no definite conclusions can be drawn at this time. At the same time, differences in thyroxine secretion rates between strains of chickens selected for high and low response to thiouracil (Premachandra et al., 1958) and differences in thyroxine secretion

rates between ducklings and chicks which also differ in growth rate (Hoffmann, 1950) and in response to thiouracil (Biellier and Turner, 1950) have been previously discussed.

The level of Protamone fed in this trial was concluded to be too low to cause any differences in growth rate. Since Turner *et al.* (1944) found Protamone at a level of one percent of the ration to be excessive and Mellen and Hill (1953) and others have reported that 0.02 percent did not affect growth rate, it was decided that the level chosen should lie within these values. A level of 0.02 percent was initiated at four weeks of age and increased to 0.04 percent at six weeks of age so as to avoid outright damage to the glands of the young birds (four to six weeks of age). According to Mellen and Hill (1953) the latter level should have provided at least twice as much thyroxine activity as the normal endogenous level of thyroid hormone secreted at this age. There is the possibility that the threshold level for response to Protamone by different stocks is quite variable; also the fact that S.C. White Leghorns, whose thyroid activity is probably greater than that of heavier birds, since their basal metabolism is greater, were used in this trial may be a factor in explaining the absence of response to Protamone.

D Comparative Uptake of Radioactive Iodine

The purpose of comparing radioactive iodine uptake differences of single and rose comb birds was to investigate the possibility that the thyroid gland was involved in growth rate differences which occurred between comb types in growth trials in which the rose comb birds were heavier than the other types (Trial A).

The fact that comparative uptake was used as a basis for study may be open to question since in most present-day studies on thyroid activity in poultry the thyroxine secretion rate is the usual measurement (Pipes et al., 1958; Premachandra et al., 1958; Mellen and Wentworth, 1960; and others). However, it was felt that for a preliminary study such as this, comparison of uptake means by the two comb type groups would be satisfactory. In fact, Edwards (1962) reported that uptake differences existed between mice selected for large and small body size though the thyroxine secretion rates were similar for both lines. Premachandra et al. (1958) have pointed out that I^{131} uptake can be greatly influenced by the amount of dietary iodine and by variation in the size of the gland. Feed intake was considered sufficiently similar for all birds used in this trial. The possibility that weight differences would be confounded with the uptake values was not considered as a weakness because the difference in thyroid activity was the criterion for comparison irrespective of factors which determined it. As is apparent from the deviation limits for each group plotted, variability within birds was extensive; the means, however, are quite consistently different.

While uptake values are most frequently expressed in terms of percentage uptake of the total dose, they have been expressed here simply as counting rate per se. for two reasons: all injections were of equal activity, and individual absolute uptake was considered quite secondary to the mean counting rate of each group.

Counting was not begun until 19 hours post-injection rather than at six hours as planned because of the development of unforeseen problems in technique. Premachandra et al. (1958) have

observed that I^{131} activity from the thyroid of chickens decreased at an exponential rate following maximum uptake. It is suspected that the reason for the considerably less rapid decline in activity among birds in this trial was the result of reutilization of I^{131} from metabolized hormone. However, since this fact was not definitely established, the term 'maximum uptake', when used here, has been preceded by the qualification 'presumed'.

On the assumption that the procedure which has been followed is experimentally sound, it can be said that the higher counting rate for the rose comb birds as a group for all counting periods is a direct indication of a greater mean uptake of radioactive iodine by the thyroid glands of these birds as compared to the single comb birds. The mean weight of the rose comb birds used in this experiment was approximately 0.03 pounds greater than the single comb birds although the 'F' values for the regression analyses of presumed maximum uptake on body weight were not significant, it is probable that an inverse relationship existed between body weight and maximum uptake existed among these birds (see Draper and Firth, 1957). Turner (1948) observed that thyroxine secretion rate decreased in fowls with increasing body weight and age, and that it could be prevented by feeding protamone. If such is the case among these birds and if thyroxine secretion rate and uptake are correlated, then Protamone would be expected to have acted as an exogenous substitute for a less than optimum thyroid hormone output in the single comb group had it been used in the present study.

E General

The results observed in this project, while they do not demonstrate definite repeatable effects of various comb types, have nevertheless shown that sporadic differences in the weights, variability in weights and probably thyroid activity are associated with genes controlling comb type. These effects appeared unpredictable in both their occurrence and in the direction which they followed.

Various factors may have contributed to or altered comb type differences and the variability associated with them. Based on differences in results between trials, it would appear as though the residual genotype in cases where parent stock differed might have had an effect on comb type gene expression, not only in terms of its shape but also with regard to secondary effects associated with them. Briles et al. (1953) pointed out that background genotype influenced the expression of blood genes in relation to their pleiotropic effects. However, variation in expression also existed between trials in which stocks of identical background genotype were used.

Seasonal differences may have influenced the effect of comb type on thyroid activity which in turn may have caused differences in both weights and variance in weights. It is recalled that, disregarding the absence of statistical support, comb type and thyroid activity were shown to be related (Experiments D-1 and D-2) and in both of these cases thyroid activity was positively related to weight. It is possible that an interrelationship exists between environment, background genotype and thyroid activity whereby the background genotype determines thyroid activity which is in turn influenced by

environment. Depending on the level of thyroid activity these combined effects induce, increased or decreased activity brought about by comb type genes may or may not result in growth differences. The background genotype may also affect the expression of comb type genes directly through modification by other genes acting exclusively on those controlling comb type. A further possibility is that of multiple alleles for comb type genes (Munro, 1962) which has been considered as a reasonable explanation for the differences in the results of Merat (1962) and Crawford (1963) on the effect of rose comb on sex ratios. Such a situation would also account for the variation in response to comb type genes under varying physiological conditions.

The actual manner in which comb type genes could effect growth rate (or possibly, more accurately, thyroid activity) cannot be resolved in simple terms. Grunberg (1943) felt that genuine pleiotropy did not exist and postulated that the primary action of genes was either cell specific or tissue specific and never organ specific. Supporting this view was his description of the manner in which the gene causing congenital hydrocephalus and many other pleiotropic effects in the mouse acted primarily on the cartilage. However, the possibility of genuine pleiotropy cannot be as easily discarded in numerous other cases. Coleman (1960) has shown that phenylalanine hydroxylase, which converts phenylalanine to tyrosine, had only fifty percent of normal activity in mice homozygous for the dilute (d) allele and 14 percent of normal activity in mice homozygous for the dilute lethal allele (d^1). Any explanation for these results

other than genuine pleiotropy is difficult to reconcile at this time. Similarly, the effect of colour genes on body weight in mice (Feldman, 1935; Law, 1938; and others) and in poultry (Smyth and Fox, 1961; Jerome et al., 1956) are equally difficult to explain on other grounds. Of course, there is the possibility that very close linkage between comb type genes and other genes influencing growth rate may exist. No definite conclusion can be made with respect to this possibility at this time.

VI SUMMARY AND CONCLUSIONS

Six growth trials which consisted of three comparisons on growing birds and three on embryos at thirteen days of incubation were conducted for the purpose of studying the association between genes controlling the comb type of chickens and growth rate. One of the three trials on growing birds included a comparison of thyroid and adrenal gland weights, shank length and breast angle. Two additional experiments investigated the possible involvement of the thyroid gland as the physiological means by which comb type genes might alter the growth rate. The following conclusions were based on results from these experiments:

1- Significant effects on growth rate could be attributed to comb type differences; however, the occurrence of these effects was not consistent.

2- Significant variance differences between comb types in which single comb birds were most often involved but which were otherwise quite unpredictable in occurrence indicated that genes controlling comb type affected weight variability.

3- The complete absence of significant weight differences among embryos of different comb types suggested that among growing birds a social advantage associated with certain comb types may be an explanation for growth differences which have been reported by other workers and which were also observed to occur here.

4- An apparent greater negative response to thiouracil by single comb birds from a particular cross in which they were also heavier in weight suggested that the thyroid gland may be the

target organ on which comb type genes act to induce growth differences. Greater uptake of radioactive iodine by rose comb birds from another cross in which they were also significantly heavier was considered as further support.

The inconsistency in results between and even within experiments has been discussed on the basis of the following: social advantage of certain comb types; a background genotype-thyroid activity-environment interrelationship by which the background genotype must provide for a particular level of thyroid activity under specific environmental conditions if comb type effects are to be realized; and a system of multiple alleles for comb type genes, which might further be confounded in the above interrelationship.

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APPENDIX

TABLE NO. 1

C-1 a); (Trial A)

(i) Mean Weights (in Grams) of Comb Type Groups:

Arkansas White x Large White				
Age		Single (n)	Pea (n)	Rose (n)
2 weeks	males	159 (99)	158 (36)	170 (42)
	females	156 (98)	157 (37)	150 (36)
6 weeks	males	849 (82)	858 (36)	881 (41)
	females	735 (98)	726 (36)	740 (35)
10 weeks	males	1757 (82)	1734 (36)	1784 (40)
Large White x Arkansas White				
2 weeks	males	166 (80)	166 (28)	177 (23)
	females	163 (82)	153 (32)	163 (28)
6 weeks	males	849 (78)	890 (28)	881 (24)
	females	772 (83)	763 (31)	790 (28)
10 weeks	males	1743 (75)	1712 (27)	1902 (23)

TABLE NO. 2

C-1 a); (Trial A)

(ii) Analyses of Variance¹:

Arkansas White x Large White

<u>Males</u> <u>Age</u>	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>
Two Weeks	Comb Type	2	3,438	1,719	2.40
	Hatch	1	2,631	2,631	3.67
	Comb Type x Hatch Interaction	2	6,263	3,132	4.37*
	Error	151	108,126	716	
Six Weeks	Comb Type	2	14	7	1.36
	Hatch	1	44	44	8.49**
	Comb Type x Hatch Interaction	2	2	1	2.51
	Error	153	792	5.18	
Ten Weeks	Comb Type	2	22	11	1.33
	Hatch	1	5	5	.60
	Comb Type x Hatch Interaction	2	51	26	3.13*
	Error	152	1,266	8.3	

1 - d.f., degrees of freedom; S.S., Sum of Squares; M.S., Mean Square

*Significant at the 5 percent level; **Significant at the 1 percent level

TABLE NO. 2, continued

Arkansas White x Large White

Females

<u>Age</u>	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>
Two Weeks	Comb Type	2	1,240	620	1.20
	Hatch	1	2,652	2,652	5.12*
	Comb Type x Hatch Interaction	2	7	3.5	.0068
	Error	165	85,471	518	
Six Weeks	Comb Type	2	1	.5	.128
	Hatch	1	28	2.8	7.2**
	Comb Type x Hatch Interaction	2	2	1	1.11
	Error	163	37	3.91	

TABLE NO.2, continued

Large White x Arkansas White

<u>Males</u>						
<u>Age</u>	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>	
Two Weeks	Comb Type	2	2,154	1,077	6.69**	
	Hatch	1	2,953	2,953	18.34**	
	Comb Type x Hatch Interaction	2	911	456	2.83	
	Error	125	20,121	161		
Six Weeks	Comb Type	2	16	8	.74	
	Hatch	1	256	256	23.7**	
	Comb Type x Hatch Interaction	2	103	52	4.81**	
	Error	124	1,345	10.8		
Ten Weeks	Comb Type	2	258	129	5.92**	
	Hatch	1	85	85	3.90	
	Comb Type x Hatch Interaction	2	215	108	4.95**	
	Error	119	259	21.8		

TABLE NO. 2, continued

Large White x Arkansas White

Females

<u>Age</u>	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>
Two Weeks	Comb Type	2	2,314	1,157	5.67**
	Hatch	1	1,689	1,689	8.28**
	Comb Type x Hatch	2	1,118	559	2.74
	Interaction				
	Error	136	27,764	204	
Six Weeks	Comb Type	2	5	2.5	.30
	Hatch	1	53	53	5.76**
	Comb Type x Hatch	2	2	1	.11
	Interaction				
	Error	136	1,250	9.2	

TABLE NO. 3

C-1 a); (Trial A)

(iii) Variances of Comb Types:

Arkansas White x Large White						
	Single	(n)	Pea	(n)	Rose	(n)
Two Week Weight	2,553	(180)	2,545	(73)	2,639	(75)
Six Week Weight	14,119	(180)	14,119	(72)	14,619	(76)
Ten Week Weight	68,100	(82)	66,965	(36)	70,642	(40)
Large White x Arkansas White						
Two Week Weight	2,712	(162)	2,572	(60)	2,901	(51)
Six Week Weight	15,118	(161)	15,164	(59)	15,799	(52)
Ten Week Weight	66,738	(75)	68,009	(27)	77,316	(23)

TABLE NO. 4

c-1 b); (Trial B)*

(1) Mean Weights (in Grams) of Comb Type Groups:

	Single n=48	Pea n=46	Rose n=42	Cushion n=49
Two Week Weight	161 ^{a*}	161 ^a	154 ^a	158 ^a
Six Week Weight	744 ^a	747 ^a	720 ^a	744 ^a
Ten Week Weight	1407 ^a	1368 ^a	1363 ^a	1405 ^a
Six Week Weight - Two Week Weight	583 ^a	586 ^a	572 ^a	595 ^a
Ten Week Weight - Six Week Weight	663 ^a	621 ^a	638 ^a	640 ^a

*Means with similar superscripts a,b,c within any age group are not significantly different from one another at the five percent level.

TABLE NO. 5

C-1 b); (Trial B)

(ii) Statistical Comparisons of Means of Individual Comb Types:Comparison of Single and:

	Pea		Rose		Cushion	
	<u>t* values</u>		<u>t values</u>		<u>t values</u>	
	<u>calcu-</u> <u>lated</u>	<u>required</u>	<u>calcu-</u> <u>lated</u>	<u>required</u>	<u>calcu-</u> <u>lated</u>	<u>required</u>
two week weight	.024	2.02	.333	2.02	.119	2.01
six week weight	.033	2.01	.177	2.01	.079	2.01
ten week weight	.990	2.02	.208	2.02	.012	2.01
six week - two week weight	.029	2.01	.117	2.01	.135	2.01
ten week - six week weight	.398	2.02	.230	2.02	.225	2.01

Comparison of Pea and:Comparison of

	Rose		Cushion		Rose and Cushion	
	<u>t values</u>		<u>t values</u>		<u>t values</u>	
	<u>calcu-</u> <u>lated</u>	<u>required</u>	<u>calcu-</u> <u>lated</u>	<u>required</u>	<u>calcu-</u> <u>lated</u>	<u>required</u>
two week weight	.278	2.02	.116	2.02	.333	2.01
six week weight	.213	2.02	.030	2.02	.194	2.01
ten week weight	1.127	2.02	.900	2.02	.232	2.02
six week - two week weight	.152	2.02	.101	2.02	.265	2.02
ten week - six week weight	.132	2.02	.153	2.02	.016	2.02

*For significance, calculated 't' must exceed required 't'

TABLE NO. 6

C-1 b); (Trial B)

(iii) Analyses of Variance¹:

<u>Age</u>	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>
Two Week Weight	Dam Comb Type	3	2,106	702.0	.91
	Dam	64	49,404	771.9	2.19**
	Hatch	6	154,361	25,727	73.07**
	Chick Comb Type	3	732	244.1	.69
	Sex	1	9,910	9,910.2	281.50**
	Chick Comb Type x Sex Interaction	3	2,102	700.6	2.00
	Error	345	121,471	352.1	
Six Week Weight	Dam Comb Type	3	22,540	7,513	.66
	Dam	64	733,940	11,468	1.83**
	Hatch	6	2,493,170	415,528	66.21**
	Chick Comb Type	3	15,460	5,153	.82
	Sex	1	1,011,681	60,789	9.69**
	Chick Comb Type x Sex Interaction	3	182,369	6,079	.97
	Error	345		6,276	

1 d.f., degrees of freedom; S.S., Sum of Squares; M.S., Mean Squares.

**Significant at the 1% level.

TABLE NO. 6, continued

<u>Age</u>	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>
Ten Week Weight	Dam Comb Type	3	122,480	40,827	1.31
	Dam	64	1,989,090	31,080	1.88**
	Hatch	6	1,528,277	254,713	15.40**
	Chick Comb Type	3	41,890	13,963	.84
	Sex	1	7,094,054	7,094,054	428.98**
	Chick Comb Type x Sex Interaction	3	1,831,383	277,128	16.76**
	Error	345	5,705,312	16,537	
Six Week Weight - Two Week Weight	Dam Comb Type	3	21,030	7,010	1.35
	Dam	64	552,980	8,640	1.67**
	Hatch	6	2,214,052	369,009	71.15**
	Chick Comb Type	3	13,365	4,455	.86
	Sex	1	821,318	821,318	158.37**
	Chick Comb Type x Sex Interaction	3	175,297	58,432	11.27**
	Error	345	1,789,356	5,186	
Ten Week Weight - Six Week Weight	Dam Comb Type	3	42,660	14,220	1.00
	Dam	64	912,830	14,263	20.78**
	Hatch	6	1,401,066	233,511	34.02**
	Chick Comb Type	3	23,035	7,678	1.12
	Sex	1	2,747,782	2,747,782	400.32**
	Chick Comb Type x Sex Interaction	3	373,371	124,457	18.13**
	Error	345	2,367,953	6,684	

TABLE NO. 7

C-1 b); (Trial B)

(iv) Variances of Comb Type Groups:

	Single d.f.=38	Pea d.f.=54	Rose d.f.=58	Cushion d.f.=63
Two Week Weight	170 ^{a*}	464 ^b	245 ^{a,c}	347 ^{b,c}
Six Week Weight	5,580 ^a	5,130 ^a	4,597 ^a	4,622 ^a
Ten Week Weight	9,658 ^a	16,363 ^b	16,560 ^b	16,265 ^b
Six Week Weight - Two Week Weight	5,041 ^a	4,322 ^a	4,003 ^a	3,556 ^a
Ten Week Weight - Six Week Weight	3,762 ^a	7,380 ^b	8,010 ^b	6,671 ^b

*Variances with similar superscripts a,b,c within any age group
are not significantly different from one another at the five per-
cent level.

TABLE NO. 8

C-1 b); (Trial B)

(v) Statistical Comparisons of Variances, ('F' values):

Comparison of Single and:						
	Pea		Rose		Cushion	
Two Week Weight	2.73**	P/S ¹	1.44	R/S	2.04*	C/S
Six Week Weight	1.09	S/P	1.21	S/R	.83	C/S
Ten Week Weight	1.69*	P/S	1.72*	R/S	1.68*	C/S
Six Week Weight - Two Week Weight	1.17	S/P	1.26	S/R	1.42	S/C
Ten Week Weight - Six Week Weight	1.96*	P/S	2.13**	R/S	1.77*	C/S
Comparison of Pea and:				Comparison of		
	Rose		Cushion		Rose and Cushion	
Two Week Weight	1.89*	P/R	1.33	P/C	1.42	C/R
Six Week Weight	1.12	P/R	1.10	P/C	1.01	C/R
Ten Week Weight	1.01	R/P	1.01	P/C	1.02	R/C
Six Week Weight - Two Week Weight	1.08	P/R	1.22	P/C	1.13	R/C
Ten Week Weight - Six Week Weight	1.09	R/P	1.11	P/C	1.20	R/C

¹ indicates that the numerator is greater than denominator,
i.e. - the variance of pea is greater than that of single.

TABLE NO. 9

C-1 c); (Trial C)

(i) Mean Weights (in Grams) and Means of Other Measurements of Comb Type Groups:

	Single n=52	Pea n=90	Rose n=90	Cushion n=135
Weight at Hatching	43.26	42.25	43.55	41.85
Two week Weight	130.45	124.00	128.42	126.12
Two week weight - Hatching weight	87.19	81.75	84.86	84.27
Six week Weight	564.40	578.39	587.94	597.47
Six week weight - two week weight	433.95	454.39	459.52	471.35
Ten week Weight	1312.8	1305.9	1379.3	1402.9
Ten week weight - six week weight	748.4	727.5	791.4	805.44
	n=53	n=85	n=97	n=137
Shank Length (inches)	3.263	3.268	3.266	3.045
Breast Angle (degrees)	74.251	74.505	82.18	75.21
Thyroid Weight (grams)	.12096	.14466	.11543	.11367
Thyroid Weight x 100/ Ten Week Weight	.009212	.011077	.008371	.008102
Adrenal Weight (grams)	.12589	.11460	.11154	.14062
Adrenal Weight x 100/ Ten Week Weight	.009588	.008375	.008088	.010023
Eviscerated Weight	936.35	861.57	930.64	867.89

TABLE NO. 10

C-1 c); (Trial C)

(ii) Statistical Comparisons of Individual Comb Types:

	Comparison of Single and:					
	Pea		Rose		Cushion	
	t* values		t values		t values	
	calcu- lated	required	calcu- lated	required	calcu- lated	required
Weight at Hatching	.319	2.04	.095	2.04	.390	2.04
Two Week Weight	.23	2.05	.073	2.05	.154	2.05
Two Week Weight - Hatching Weight	.193	2.05	.079	2.05	.104	2.05
Six Week Weight - Two Week Weight	.255	2.04	.255	2.04	.552	2.04
Ten Week Weight - Six Week Weight	.142	2.14	.269	2.04	.180	2.04
Shank Length	.0172	2.04	.0012	2.04	.908	2.04
Breast Width	.0485	2.04	1.40	2.01	.167	2.03
Thyroid Weight	.523	2.03	.107	2.04	.182	2.04
Adrenal Weight	.286	2.04	.379	2.01	.368	2.04
Eviscerated Weight	.534	2.04	.039	2.04	.547	2.03

*For significance, calculated 't' must exceed required 't'

TABLE NO. 10, continued

	Comparison of Pea and: Rose t values		Cushion t values		Comparison of Rose and Cushion t values	
	Calcu- lated	required	Calcu- lated	required	Calcu- lated	required
Weight at Hatching	.394	2.04	.108	2.01	.447	2.01
Two Week Weight	.611	2.03	.102	2.02	.095	2.03
Two Week Weight - Hatching Weight	.425	2.03	.117	2.02	.083	2.03
Six Week Weight - Two Week Weight	.054	2.03	.675	2.03	.143	2.03
Ten Week Weight - Six Week Weight	.361	2.03	.293	2.03	.111	2.03
Shank Length	.007	2.03	.851	2.03	1.04	2.03
Breast Width	.128	2.03	.125	2.02	1.08	2.03
Thyroid Weight	.552	2.04	.069	2.03	.036	2.04
Adrenal Weight	.0927	2.04	.722	2.02	.843	2.02
Eviscerated Weight	.404	2.04	.0583	2.03	.606	2.03

TABLE NO. 11

C-1 c); (Trial C)

(iii) Analyses of Variance:¹

	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>
Hatching Weight	Sire	3	186.0	62.0	1.69
	Dam comb type ²	15	544.5	36.3	1.81
	Dam	32	641.6	20.1	2.91**
	Hatch	5	153.1	30.6	4.44**
	Chick comb type	3	31.1	10.4	1.50
	Sex	1	45.9	45.9	6.65*
	Chick comb type ³ x Sex Interaction	3	13.1	4.4	.63
	Error	302	2,084.0	6.9	
<hr/>					
Two Week Weight	Sire	3	4,520	1,507	4.00*
	Dam comb type	15	5,657	377	.80
	Dam	32	15,065	471	1.63*
	Hatch	5	5,739	1,148	3.96**
	Chick comb type	3	929	310	1.07
	Sex	1	1,891	1,891	6.53
	Chick comb type x Sex Interaction	3	975	325	1.12
	Error	302	87,503	290	

1 - d.f., degrees of freedom; S.S., Sum of Squares; M.S., Mean Square

2 - Dam comb type genotype

3 - Chick comb type phenotype

*significant at the 5 percent level; ** significant at the 1 percent level

TABLE NO. 11, continued

	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>
Two Week Weight - Hatching Weight	Sire	3	4,538	1,513	4.00*
	Dam comb type	15	5,670	378	.83
	Dam	32	14,506	453	1.61*
	Hatch	5	4,581	916	3.25**
	Chick comb type	3	904	301	1.07
	Sex	1	1,348	1,348	4.78*
	Chick comb type x Sex Interaction	3	1,062	354	1.26
	Error	302	85,056	282	
<hr/>					
Six Week Weight - Two Week Weight	Sire	3	181,705	60,568	5.87*
	Dam comb type	15	154,726	10,315	1.35
	Dam	32	243,695	7,615	1.86**
	Hatch	5	232,256	46,451	11.37**
	Chick comb type	3	1,723	574	.14
	Sex	1	317,218	317,218	77.7**
	Chick comb type x Sex Interaction	3	8,160	2,720	.67
	Error	302	1,233,542	4,085	
<hr/>					
Ten Week Weight - Six Week Weight	Sire	3	101,300	33,767	1.43
	Dam comb type	15	35,426	23,617	1.13
	Dam	32	671,310	20,978	1.83**
	Hatch	5	107,143	21,429	1.87
	Chick comb type	3	28,042	9,347	.81
	Sex	1	1,843,801	1,843,801	160.74
	Chick comb type x Sex Interaction	3	22,032	7,344	.64
	Error	302	3,464,360	11,471	

TABLE NO.11, continued

	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>
Shank Length	Sire	3	.2022	.0674	1.08
	Dam comb type	15	.9393	.0626	1.62
	Dam	32	1.2339	.0386	1.37
	Hatch	5	1.7662	.3532	12.61**
	Chick comb type	3	.0246	.0082	.29
	Sex	1	7.7183	7.7183	275.65**
	Chick comb type x Sex Interaction	3	.1776	.0592	2.11
	Error	309	8.6866	.0281	
<hr/>					
Breast Angle	Sire	3	316.8	105.6	3.23
	Dam comb type	15	491.0	32.7	1.03
	Dam	32	1,018.2	31.8	1.58*
	Hatch	5	2,119.4	423.8	21.1**
	Chick comb type	3	59.9	20.0	.99
	Sex	1	.22	.22	.001
	Chick comb type x Sex Interaction	3	.60	.20	.001
	Error	309	6,196.1	20.1	
<hr/>					
Thyroid Weight	Sire	3	.0195	.00650	4.01*
	Dam comb type	15	.0244	.00162	1.05
	Dam	32	.0497	.00155	1.40
	Hatch	5	.0138	.00280	2.52*
	Chick comb type	3	.0024	.00078	.70
	Sex	1	.00078	.00078	.70
	Chick comb type x Sex Interaction	3	.00012	.00004	.036
	Error	309	.3431	.00111	

TABLE NO.11, continued

	<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F.</u>
Adrenal Weight	Sire	3	.0072	.00239	4.43*
	Dam comb type	15	.0081	.00054	.56
	Dam	32	.0310	.00097	1.39
	Hatch	5	.0309	.00618	8.83**
	Chick comb type	3	.0005	.00017	2.43
	Sex	1	.0501	.05010	71.6**
	Chick comb type x Sex Interaction	3	.0034	.00110	1.57
	Error	309	.2198	.00070	
<hr/>					
Eviscer- ated Weight	Sire	3	429,240	143,080	3.58*
	Dam comb type	15	600,150	40,010	1.56
	Dam	32	820,370	25,637	2.24**
	Hatch	5	1,613,335	322,667	28.21**
	Chick comb type	3	7,769	2,590	.23
	Sex	1	2,519,233	2,519,233	220.23**
	Chick comb type x Sex Interaction	3	13,886	4,629	.40
	Error	309	3,534,700	11,439	

TABLE NO. 12

C-1 c); (Trial C)

(iv) Variances of Comb Types:

	Single n=21	Pea n=47	Rose n=51	Cushion n=87
Weight at Hatching	4.40	5.41	5.72	8.47
Two Week Weight	537.0	216.0	296.0	244.0
Two Week Weight - Hatching Weight	549.6	234.0	292.0	224.0
Six Week Weight - Two Week Weight	2,360	4,099	4,665	3,238
Ten Week Weight - Six Week Weight	8,076	13,684	17,495	10,458
	n=19	n=44	n=59	n=89
Shank Length	.03796	.04693	.02365	.0217
Breast Width	12.89	14.63	21.36	20.57
Thyroid Weight	.00084	.001205	.001628	.000791
Adrenal Weight	.00095	.000614	.000475	.000713
Eviscerated Weight	6,381	13,317	16,009	9,366

TABLE NO. 13

G-1 c); (Trial C)

(v) Statistical Comparisons of Variances, ('F' values):

	Comparison of Single and:		
	Pea	Rose	Cushion
Hatching Weight	1.23 P/S ¹	1.30 R/S	1.93* C/S
Two Week Weight	2.49**S/P	1.81* S/R	2.20* S/C
Two Week Weight - Hatching Weight	2.35**S/P	1.88* S/R	2.46**S/C
Six Week Weight - Two Week Weight	1.74 P/S	1.98* R/S	1.37 C/S
Ten Week Weight - Six Week Weight	1.69 P/S	2.17**R/S	1.29 C/S
Shank Length (inches)	1.24 P/S	1.61* S/R	1.75 S/C
Breast Angle (degrees)	1.13 P/S	1.66* R/S	1.60 C/S
Thyroid Weight (grams)	1.43 P/S	1.94**R/S	1.06 S/C
Adrenal Weight (grams)	1.56 S/P	1.98* S/R	1.34 S/C
Eviscerated Weight	2.09* P/S	2.51**R/S	1.47 C/S

1 indicates that numerator is greater than denominator,
i.e. - the variance of pea is greater than that of single.

TABLE NO. 13, continued

	Comparison of Pea and:		Comparison of	
	Rose	Cushion	Rose and Cushion	
Hatching Weight	1.06 R/P	1.57* C/P	1.48 C/R	
Two Week Weight	1.37 R/P	1.13 C/P	1.21 R/C	
Two Week Weight - Hatching Weight	1.25 R/P	1.04 P/C	1.30 R/C	
Six Week Weight - Two Week Weight	1.14 R/P	1.27 P/C	1.44 R/C	
Ten Week Weight - Six Week Weight	1.28 R/P	1.31 P/C	1.67* R/C	
Shank Length (inches)	1.98**P/R	2.16**P/C	1.09 R/C	
Breast Angle (degrees)	1.46 R/P	1.41 C/P	1.04 R/C	
Thyroid Weight (grams)	1.14 R/P	1.53 P/C	2.06**R/C	
Adrenal Weight (grams)	1.27 P/R	1.16 C/P	1.48 C/R	
Eviscerated Weight	1.20 R/P	1.42 P/C	1.71**R/C	

TABLE NO. 14

C-2 a); (Trial D)

(i) Weight Means of Comb Type Groups:

	Embryo Weight	Embryo Weight as Percentage of Egg Weight
Single	6.445 grams	11.335 percent
Pea	6.308 "	11.105 "
Rose	6.215 "	11.068 "
Cushion	6.601 "	11.657 "

(ii) Analysis of Variance of Embryo Weights:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Hatch	1	23.76	23.76	25.72**
Comb Type	3	1.79	.60	.65
Egg Weight	3	.58	.19	.21
Error	123	113.68	.92	

(iii) Analysis of Variance of Embryo Weights Expressed
As A Percentage of Egg Weight:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Hatch	1	56.66	56.66	22.05**
Comb Type	3	3.89	1.30	.51
Egg Weight	3	45.45	15.51	6.04
Error	123	315.70	2.57	

TABLE NO. 15

C-2 b); (Trial E)

(i) Weight Means of Comb Type Groups:

	Embryo Weight	Embryo Weight as Percentage of Egg Weight
Single	6.746 Grams	11.538 percent
Pea	6.565 "	11.626 "
Rose	6.897 "	12.319 "
Cushion	6.828 "	12.253 "

(ii) Analysis of Variance of Embryo Weights:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Hatch	1	17.73	17.73	28.51**
Comb Type	3	2.49	.83	1.33
Egg Weight	3	4.95	1.65	2.65
Error	172	106.93	.62	

(iii) Analysis of Variance of Embryo Weights Expressed
As A Percentage of Egg Weight:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Hatch	1	53.36	53.35	26.05**
Comb Type	3	11.99	4.00	1.88
Egg Weight	3	91.60	30.53	14.34**
Error	172	367.04	2.13	

TABLE NO. 16

C-2 c); (Trial F)

(i) Weight Means of Comb Type Groups:

	Embryo Weight	Embryo Weight as Percentage of Egg Weight
Single	6.587 grams	12.938 percent
Pea	6.467 "	12.696 "
Rose	6.453 "	12.615 "
Cushion	6.650 "	13.146 "

(ii) Analysis of Variance of Embryo Weights:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Hatch	2	1.39	.69	1.88
Comb Type	3	.95	.32	.86
Egg Weight	3	3.06	1.02	2.77*
Error	274	100.95	.37	

(iii) Analysis of Variance of Embryo Weights Expressed
As A Percentage of Egg Weight:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Hatch	2	2.44	1.22	.61
Comb Type	3	12.31	4.10	1.37
Egg Weight	3	222.08	74.03	24.08**
Error	274	842.27	3.07	

TABLE NO. 17

D-1; (Response to Protamone and Thiouracil)*

(1) Growth Rate Means:

Hatching to Four Weeks

Comb Type	Control (n)	Protamone (n)	Thiouracil (n)
Single	337 ^{a,b} (12)	354 ^a (13)	334 ^b (17)
Pea	339 ^{a,b} (7)	322 ^a (9)	337 ^b (13)
Rose	351 ^{a,b} (6)	366 ^a (9)	359 ^b (7)

Four to Six Weeks

Comb Type	Control (n)	Protamone (n)	Thiouracil (n)
Single	337 ^a (12)	338 ^a (13)	286 ^b (17)
Pea	321 ^a (7)	322 ^a (9)	273 ^b (13)
Rose	357 ^a (6)	324 ^a (9)	303 ^b (7)

Six to Eight Weeks

Comb Type	Control (n)	Protamone (n)	Thiouracil (n)
Single	1014 ^a (7)	944 ^a (13)	8759 ^b (17)
Pea	7487 ^{a,b} (7)	1001 ^a (9)	9081 ^b (9)
Rose	9995 ^{a,b} (6)	1012 ^a (9)	9486 ^b (7)

*Values with similar superscripts indicate no significant differences in comparing control vs. protamone and control vs. thiouracil. No comparison was made between protamone vs. thiouracil.

TABLE NO. 18

D-1; (Response to Protamone and Thiouracil)

(ii) Analyses of Variance of Weight Gains From Hatching to Four Weeks:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Single - Control - vs - Protamone				
Treatment	1	1,276	1,276	.51
Error	22	54,594	2,482	
Single - Control - vs - Thiouracil				
Treatment	1	226	226	.10
Error	27	58,536	2,168	
Pea - Control - vs - Protamone				
Treatment	1	1	1	.00009
Error	4	45,086	11,222	
Pea - Control - vs - Thiouracil				
Treatment	1	77	77	.04
Error	18	35,637	1,980	
Rose - Control - vs - Protamone				
Treatment		788	788	1.63
Error		5,819	485	
Rose - Control - vs - Thiouracil				
Treatment		248	248	.42
Error		6,583	598	

TABLE NO. 19

D-1; (Response to Protamone and Thiouracil)

(iii) Analyses of Variance of Weight Gains From Four to Six Weeks:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Single - Control - vs - Protamone				
Treatment	1	4,394	4,394	2.42
Error	24	43,564	1,815	
Single - Control - vs - Thiouracil				
Treatment	1	20,406	20,406	13.05**
Error	32	50,036	1,564	
Pea - Control - vs - Protamone				
Treatment	1	3	3	.001
Error	15	44,876	2,991	
Pea - Control - vs - Thiouracil				
Treatment	1	10,813	10,813	8.55**
Error	19	20,027	1,265	
Rose - Control - vs - Protamone				
Treatment	1	2,932	2,932	3.53
Error	13	10,799	831	
Rose - Control - vs - Thiouracil				
Treatment	1	9,982	9,982	5.33*
Error	12	22,477	1,873	

TABLE NO. 20

D-1; (Response to Protamone and Thiouracil)

(iv) Analyses of Variance of Weight Gains From Six to Eight Weeks:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Single - Control - vs - Protamone				
Treatment	1	29,400	29,400	3.78
Error	22	171,293	7,786	
Single - Control - vs - Thiouracil				
Treatment	1	128,043	128,043	16.81**
Error	25	190,417	7,617	
Pea - Control - vs - Protamone				
Treatment	1	11,431	11,431	1.26
Error	15	136,358	9,090	
Pea - Control - vs - Thiouracil				
Treatment	1	6,492	6,492	.67
Error	14	135,115	9,651	
Rose - Control - vs - Protamone				
Treatment	1	486	486	.11
Error	13	55,738	4,288	
Rose - Control - vs - Thiouracil				
Treatment	1	8,380	8,380	.80
Error	11	115,145	10,468	

TABLE NO. 21

D-2; (Uptake of Radioactive Iodine)

(i) Analyses of Variance of Regressions:

Single

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Regression	1	281,794	281,794	.34
Error (deviations from regression)	7	5,872,581	838,940	

Rose

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Regression	1	61,494	61,494	.32
Error (deviations from regression)	5	967,352	193,470	

