AN INVESTIGATION OF MALE TRAITS AS TOOLS TO IMPROVE EGG PRODUCTION IN CHICKENS

By

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Suggested short title

MALE TRAITS TO IMPROVE EGG PRODUCTION

SEGURA

Dedicatoria:

- A mis padres y hermanos

- A mis hijas Aida Annette y Maria Gloria

Ph. D. ABSTRACT Animal Science

AN INVESTIGATION OF MALE TRAITS TO IMPROVE EGG PRODUCTION IN CHICKENS

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Semen yield and wattle size are easily measured in roosters and may be related to egg production. Testes size and ovulation rate are favorably correlated in mammals. Thus, the main objective of this study was to estimate genetic correlations of the above male traits with egg production and other related traits in chickens. Secondary objectives were to estimate genetic parameters of male traits and to examine the effects of lymphoid leukosis virus (LLV) infection and age on semen traits and/or male fertility.

Strains of chickens selected for high egg production to 273 days and other related traits and their respective unselected control strains were used. Semen was collected and evaluated on two consecutive days. The effects of ejaculate sequence, age and LLV infection on semen traits were determined by multiple regression analysis. Heritability of male traits and genetic correlations between male and female traits were estimated by intraclass correlation and regression methods.

Genetic correlations of semen traits measured at 8 months of age with egg weight tended to be favorable (0.02 to 0.36), but unfavorable with egg production (-0.60 to 0.04) and age at first egg (0.03 to 0.40). Wattle weight and

size measured on 14 month old males were favorably correlated with egg production (0.05 to 0.55) and age at first egg (-0.17 to -0.43). Genetic correlations of testes weight and egg production were mostly negative for the control and positive for the selected strains. The genetic correlations of male traits with albumen quality, shell quality and incidence of blood spots were generally of low magnitude or inconsistent between methods of estimation.

Heritability estimates of semen weight, packed sperm volume and total sperm weight were of low to moderate maghitude (0.08 to 0.38). Those of testes and wattle weights were high (0.58 and 0.54, respectively).

Control strains had a significantly higher frequency of LLV-shedding males than the selected strains. LLV infection appeared to be associated with increased semen production and the incidence of abnormal spermatozoa in old males, and appeared to decrease fertility.

Semen weight, packed sperm volume and total sperm weight tended to decrease with advancing age.

UNE ETUDE DES CARACTERES MALES POUR L'AMELIORATION DE LA PRODUCTION D'OEUFS CHEZ LE POULET

La production de sperme et la grosseur des barbillons sont facilemient mesurables chez le coq et pourraient être reliées à la production d'oeufs. La grosseur des testicules et le taux d'ovulation sont favorablement corrélés chez les mammifères. Donc, l'objectif principal de cette étude était d'évaluer les corrélations génétiques des caractères mâles ci-haut mentionnés avec la production d'oeufs et autres caractéristiques reliées chez le poulet. Les objectifs secondaires étaient d'évaluer les paramètres génétiques des caractères mâles et d'examiner les effets de l'âge et d'une infection causée par le virus de la leucose lymphoide (LLV) sur les caractères du sperme et/ou la fertilié du mâle.

Des lignées de poulets sélectionnées pour une production d'oeufs élevée à 273 jours et pour d'autres caractéristiques ainsi que des lignées témoins non-sélectionnés pour chacune descaractéristiques ont servi à l'étude. Pendant deux jours consécutifs, le sperme a été collecté et évalué. Les effets de l'ordre de l'ejaculation, de l'âge et d'une infection causée par LLV sur les caractères du sperme ont été déterminés par analyse de régressions multiples. L'héritabilité des caractères mâles et les corrélations génétiques entre les caractères mâles et femelles ont été évaluées par corrélation à l'intérieur de chaque classe et par des méthodes de régressions.

Les corrélations génétiques des caractéristiques du

sperme, mesurées à l'âge de 8 mois avec le poids de l'oeuf avaient une tendance favorable (0.02 à 0.36), mais non favorable avec la production d'oeufs (-0.60 à 0.04) et l'âge du bébut de ponte (0.03 à 0.40). Le poids et la grosseur des barbillons mesurés chez des mâles agés de 14 mois étaient favorablement corrélés avec la production d'oeufs (0.05 à 0.55) et avec l'âge du début de ponte (-0.17 à -0.43). Les corrélations génétiques entre le poids des testicules et la production d'oeufs étaient surtout négatives pour les lignées témoins et positive pour les lignées sélectionnées. Les corrélations génétiques entre les caractères mâles et la qualité de l'albumen, la qualité de la coquille et l'incidence des taches de sang étaient généralement peu élevées ou contradictoires selon la méthod d'évaluation.

Les évaluations obtenues pour l'héritabilité du poids de la semence, volume de spermatozoides et du poids total du sperme étaient de basses à modérées (0.08 à 0.38). Celles du poids des testicules et des barbillons étaient élevées (0.58 et 0.54, respectivement).

Les mâles des lignées témoins avaient une fréquence de mue reliée au LLV significativement plus élevée que chez les lignées sélectionnées. L'infection causée par le LLV semblait être associée à un accroissement de la production du sperme et de l'incidence de spermatozoides anormaux chez le vieux mâle, et à une baisse de la fertilité.

Le poids de la semence, le volume de spermatozoides et le poids total du sperme avaient tendance à diminuer avec l'âge.

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I INTRODUCTION

Milk production in cattle and egg production in chickens are examples of sex-limited traits in domestic animals; these traits are only expressed in one sex. Males, however, also carry genes for milk and egg production which they transmit to their progeny. This is demonstrated by differences in the reproductive performance of the daughters of different sires (Land and Falconer 1969).

Selection to improve female reproductive performance is complicated because males either have to be chosen at random or on the basis of their female relatives' performance. If males are randomly selected, the expected genetic response to selection is half of that expected based on selection in both sexes (Falconer 1981). In the domestic fowl, males are commonly selected for egg production based on their full- or half- sisters' egg production. Selection based on correlated traits, measured directly in males, as well as the performance of female relatives could increase the accuracy and efficiency of such selection and perhaps allow early culling of some roosters to save feed costs.

It would be desirable to find a trait in males which is correlated with the egg production of their female relatives. If such a trait could be found, more rapid genetic response should be possible and costs of selection programs could be reduced.

One prospective trait could be sperm production of males because this trait and ovulation rate are under

similar physiological control (Sturkie 1976). Evidence from selection experiments and full- sib correlations indicated a favorable genetic association between semen and egg production (Jones and Lamoreux 1942; Nestor 1976, 1977; Marks 1978; Borsting 1980). Therefore, the primary objective of this study was to estimate the genetic correlations of semen production traits with egg production and other related traits.

Ayoub and Merat (1979) reported a positive correlation between wattle length measured on roosters and egg production of their full- sisters. In mammals testes size appeared to be favorably correlated with ovulation rate and litter size (Land and Falconer 1969; Land 1973; Islam et al. 1976; Joakimsen and Baker 1977; Eisen and Johnson 1981). Therefore another objective was to estimate the genetic correlations of testes and male wattle size with egg production and other related traits. In order to accomplish these objectives a series of experiments were conducted. The objectives of each particular experiment were

Experiment I: 1) to establish semen collection and evaluation procedures; 2) to identify the semen trait(s) which characterize semen production and are easy to measure in a large scale experiment, in order to examine their correlation with egg production; 3) to determine the correlated changes in semen traits brought about by selection for high egg production and other related traits.

Experiment II had similar objectives to experiment I but a larger number of males and strains and fewer semen traits were examined.

Experiment III: 1) to estimate the heritability of semen weight, packed sperm volume and total sperm weight; 2) to estimate the genetic correlations among above semen traits; 3) to estimate the genetic correlations between semen traits and egg production and other related traits.

Experiment IV: 1) to determine if there are differences in semen production between breeders and nonbreeders; 2) to estimate the genetic correlations between semen and egg production traits.

Experiment V: 1) to determine if selection for high egg production and other related traits affects wattle and spur size; 2) to estimate genetic correlations between wattle size and egg production and other related traits.

Experiment VI: 1) to determine if selection for high egg production and other related traits has affected testes and wattle weights; 2) to estimate genetic correlations of testes and male wattle weight with egg production and other related traits.

Lymphoid leukosis virus (LLV) infection has economic importance in egg production. Gavora et al (1980) showed that LLV-shedding hens produced 30 eggs less than non-shedding hens and reduced performance in other traits. Therefore, another objective of this study (Experiments I, II and IV) was to examine the frequency of LLV infection and

its effect on semen production and fertility.

An additional objective was to examine the effect of advancing age on semen production traits.

II REVIEW OF LITERATURE

All of us are familiar with the reproductive differences between males and females. However, despite very different reproductive characteristics, the autosomal genes or loci controlling the function of the gonads are common to both sexes (Land 1973). Testes and ovaries, utilize the same set of enzymes for their steroid synthesis (Ohno 1979) and they are under the same physiological control (Sturkie 1976; Bahr and Nalbandov 1977). Furthermore, there are some reports in the literature (Land and Falconer 1969; Eisen and Johnson 1981) suggesting that male and female reproductive characteristics, in mammals, are genetically correlated.

This section will review the information on the correlations between male and female reproductive characteristics. However, to better understand the basis of those associations, the literature on the genetic and hormonal control as well as some environmental factors which may affect egg and/or semen production is reviewed.

2.1 Sex determination and differentiation

Genetic sex is determined by sex chromosomes received from parents.In avians, in contrast to mammals, the male is the homogametic sex (ZZ) and the female the heterogametic sex (WZ). W and Z are the conventional symbols used to identify the sex chromosomes in avians and X and Y are the conventional symbols used in mammals. These sex chromosomes carry the gene(s) involved in sex differentiation of the

embryonic gonads. One of these genes, the H-W antigen gene, has been mapped to the W sex chromosome (Etches and Hawes 1973; Hutt and Rasmusen 1982), and has been associated with ovary organization of the undifferentiated embryonic gonads (Wachtel et al. 1975; Ohno 1979; Mittwoch 1983; Jordanov and Angelova 1984). In mammals, the H-Y antigen gene, believed to be located in the Y chromosome, induces testicular organization (Ohno 1977). The expression of this antigen is hormone dependent (Zaborski et al. 1980). The addition of testosterone to female embryo gonads in organ culture suppressed the expression of this antigen in chickens (Jordanov and Angelova 1984). Nalbandov (1976) indicated that the injection of male or female steroid hormones may reverse the phenotypic sex. Furthermore, the expression of the H-W antigen in experimentally feminized ZZ chicks and African water frogs suggests that the structural gene for the antigen may not be on the W chomosome in these species (Mittwoch 1983). Similarly, in mammals, it has been postulated that the H-Y structural gene(s) could be located in the X chromosome or any of the autosomes; and that the antigen production for this gene is regulated by a gene located in the Y chromosome (Mittwoch 1983).

2.2 Development of male and female reproductive systems

The reproductive system in the two sexes arises from indifferent rudiments in the embryo (Nalbandov 1976). In avians, the primordial germ cells originating in the yolk sac endoderm migrate via the circulatory system to the genital ridge (Basrur 1974; Nalbandov 1976). At the genital ridge, the primordial cells develop into undifferentiated gonads. If a gonad is to become a testis, the cells in the germinal epithelium grow into the underlaying mesenchymal tissue and there they form the seminiferous tubules of the testis. If a gonad is to become an ovary, the primordial cells grow into the mesenchyme, where they differentiate into ovarian follicles containing ova (Nalbandov 1976).

In the male embryo, there is no tubular system laid down per se. The efferent ductules and deferent ducts develop from the mesonephros or urinary system (fowls lack epididymides and accessory glands). Two active agents that are produced by the fetal testis are responsible for differentiation and development of the duct system in males: (1) fetal androgen, produced by the testis, which causes development of the reproductive tract, and (2) Mullerian inhibiting substance responsible for suppression of Mullerian ducts from which oviducts, and vagina develop in the female (Ashdown and Hancock 1980). The anatomical and glandular development of the oviduct in females is under the influence of estrogens (Nalbandov 1976) and androgens (Gilbert 1980).

2.3 Physiological control of reproduction

In comparison with mammals, avian endocrinology is poorly understood and less is known of the male than of the female. Reproduction, in males and females, can be divided into two endocrinologically distinct phases; one in which the physiological mechanisms lead to sexual maturation and the other in which the process results in the production of an egg or semen.

With respect to the first phase, leading to sexual maturation, Sharp (1975) has shown that luteinizing hormone (LH) levels in chicken plasma steadily rise until about 3 weeks before sexual maturity in both sexes. However, he found that the levels of LH, in males, fall at about the onset of sexual maturity (20-23 weeks) and subsequently rise to reach a concentration of approximately 10 ng/ml. In contrast, he observed that the plasma levels began to fall progressively in pullets from 19 weeks of age (5 ng/ml) until 22-25 weeks of age when they began to lay eggs (2 ng/ml). He suggested that the decrease in LH is associated with a raised plasma steroid level brought about by the development of follicles.

The increased secretion of LH at the onset of puberty was believed to be the result of a change in sensitivity of the hypothalamus-hypophyseal complex to the negative feedback of sex hormones (Sharp 1975). However, as birds approach sexual maturity they become photostimulatory and it is this change that is responsible for the future sexual

development (Gilbert 1980). In response to a changing daylength, the hypothalamus alters its output of the gonadotropin-releasing hormone (GnRH) which in turn stimulates the pituitary production of the gonadotropins follicle stimulating hormone (FSH) and LH, (Gilbert 1980; Sharp and Gow 1983). This major activity of the hypothalamus is associated with an increase of functional activity of neurocytes and pertinent nuclei of hypothalamus and gonadotropocytes of adenohypophysis (Novikov 1979; Knight 1983).

Plasma LH levels at the onset of puberty can be increased, in cockerels reared on short days, by increasing the daylength (de Reviers and Williams 1981). Knight (1983) stated that the progressive desensitization of the hypothalamus-hypophyseal system to the negative feedback action of testosterone in cockerels is not the primary mechanism which initiates and sustains the process. The onset of sexual maturation in the cockerel is primarily determined by a central neural mechanism which results in an increased activity of luteinizing hormone-releasing hormone (LHRH) neurones in the hypothalamus (Knight 1983).

The second endocrinological phase of females, the physiological control of ovulation, is a more complex reproductive process . The release of LH from the pituitary is involved and this release may be controlled by feedback mechanisms of steroid hormones (Wilson and Sharp 1973; Etches and Cunningham 1976).

A peak of LH and progesterone at about 4-7 hours occurs normally prior to ovulation in hens (Cunningham and Furr 1972; Furr et al. 1973; Lague et al. 1975; Sturkie 1976). Lague et al. (1975) and Sturkie (1976) suggested that there may be a positive feedback relationship between hypophyseal LH and ovarian progesterone in the laying hen. This relationship was demonstrated by Etches and Cunningham (1976) who observed that progesterone stimulates the secretion of LH and LH stimulates the secretion of progesterone. Small doses of injected progesterone in the hypothalamus have been found to induce ovulation in the hen (Nalbandov 1976).

The role of estrogens in the ovulation of the hen is not clear. Lague et al. (1975) observed that ovulation may occur occasionally in the absence of estrogen peaks and some estrogen peaks appear not to be related to ovulation. Contrary to progesterone, estrogens appear to have a negative feedback effect on gonadotropin production (Gilbert 1980). Other hormones i.e., prostaglandins, are involved in ovulation but their normal role has yet to be clarified.

In cockerels, estradiol but not testosterone is the main hormone in the feedback system which regulates the synthesis and release of LH (Wilson et al 1983). This was suggested by Nalbandov (1976), who observed that estrogen is produced by the testis and that larger than physiological doses of androgen are required to inhibit pituitary function. The negative feedback action of testosterone on

the secretion of LH in cockerels is exerted, at least in part, by means of the product of its aromatization within the brain, estradiol-17B (Wilson et al. 1983).

Androgens are involved in spermatogenesis (Nalbandov 1976). The effect of LH on sperm production in mammals is via its effect on testosterone which is directly or indirectly involved in the maintenance and restoration of spermatogenesis (Steinberger 1976). Other hormones, prolactin, somatotropic hormone and adrenocorticotropic hormone may be implicated in the controlling mechanism of sperm production, but clear evidence for their normal role has yet to be found (Gilbert 1980).

The endocrine control of the reproductive process in males is similar to that of females in that the same two pituitary hormones FSH and LH play the major role in the stimulation of both ovary and testes (Nalbandov 1976). Experiments with hypophysectomized animals clearly show that gonads totally depend on pituitary gonadotropins for support and maintenance (Nalbandov 1976; Novikov 1979). In the hen, FSH and LH are responsible for the development of ovarian follicles, ovulation and steroid production by the ovarian steroid-producing cells (Gilbert 1980). In roosters, FSH is necessary to initiate growth of the seminiferous tubules and LH causes development of the Leydig cells which produce the androgens (Gilbert 1980; Bahr and Nalbandov 1977; Nalbandov 1976).

In summary, most of the hormones which control reproduction in females, also control, directly or indirectly, reproduction in males. This suggests that the quantitative control of the expression of genes controlling the release of gonadotropic hormones (FSH and LH) and steroid hormones is not sex limited; and thus reproductive traits in male and females may be genetically correlated.

2.4 Environmental factors

2.4.1 Age of the bird

Age of the birds has a significant effect on egg production and egg quality. It is known, that older hens produce less eggs of lower quality than hens in their first year of production. It is also known that the thick albumen of normal freshly laid eggs deteriorates with the age of bird, environmental temperature and other factors (Sturkie 1976). Liljedahl et al. (1984) examined 14, 28-day periods in laying hens and observed that the egg number, starting from the day of first egg, increased from the first to the second period and gradually decreased thereafter. Egg weight showed a curvilinear increase with age, while the monthly means of albumen height, shell thickness and shape, generally decreased with the age of the bird. They also observed that age increased the genetic and environmental variance of egg production, egg weight and egg quality traits.

Semen volume and sperm concentration decrease with advancing age (Wheeler and Andrews 1943; Clark and Sarakoon 1967; Marini and Goodman 1969; Ansah et al. 1980; de Riviers and Williams 1981; Van Wambeke et al. 1981; Ansah et al. 1984b). In White Leghorns, Jones and Lamoreux (1942), observed an increase in semen yield from 12 to 45 weeks and a decline from 46 to 52 weeks of age. Wilson et al. (1979) observed an increase in total sperm production and total number of moving spermatozoa with age (20 to 55 weeks) of

broiler breeders.

The effect of age, found in some experiments, but lacking in others, suggests that differences may exist in the persistency of semen production of different strains and breeds. De Riviers and Williams (1981) stated that the efficiency of selecting males based on their daily sperm output is limited by individual variation in the rate at which the daily sperm output declines in the adult.

The age of the rooster does not appear to have any significant effect on sperm motility, pH, or percentage of abnormal spermatozoa (Wheeler and Andrews 1943; Marini and Goodman 1969). In natural matings the reduction in male fertility is due more to the inability to successfully mate or the lack of mating desire than to semen characteristics (Soller et al. 1965a,b; Clark and Sarakoon 1967; Wilson et al. 1979).

Marks (1978) observed that the mean of packed sperm volume of 146 males paralleled the mean daily egg mass curve of 400 full-sib females in 3 out of 5 laying periods. The levels of both packed sperm volume and egg mass were highest in the 3rd period and lowest in the 5th period. If both egg production and semen yield decline with age, probably as a result of an inability of the birds to cope with unfavorable environmental factors, the relationship between semen yield and egg production may change with age within a given population.

2.4.2 Diseases

Diseases cause significant economic losses through mortality of birds and/or through the reduction of egg production and egg quality. It is known that diseases such as Infectious Bronchitis, Newcastle disease, Fowl Pox and Avian Influenza cause a drop in egg production and reduce egg quality (Sturkie 1976; North 1978). Although in most reports nothing is said about the effect on roosters, it could be expected that diseases, such as those mentioned previously, will cause a drop in semen production.

Lymphoid leukosis virus (LLV) disease has been reported to cause only low mortality among adult chickens (Gavora et al. 1975) and thus it has been previously considered a disease of minor economic importance. Gavora et al (1980), however, reported that egg production was significantly reduced (25 to 30 eggs per hen housed and 17 to 24 eggs per surviving hen) in White Leghorn hens shedding LLV into eggs. They also observed that shedders laid significantly smaller eggs with thinner shells. Those findings were further corroborated by Gavora et al. (1982) in meat-type chickens. Egg production to 385 days was lower in shedders than in non-shedders by 10 eggs per hen housed and by 8 eggs per surviving hen. Furthermore, test-positive birds had higher mortality and lower 6 week body weight. Similar effects of LLV on egg production and related traits have been reported by Payne et al. (1982), Romero et al. (1983) and Fairfull et al. (1984).

The effect of LLV on semen production and male fertility has not been reported in the available literature. However, it was of interest to examine whether such effects exist because semen production is economically important for the poultry industry. Furthermore, if the reproductive performance of both sexes is under the same physiological control, it would be expected that LLV affects semen yield and egg production in the same direction.

2.4.3 Frequency of semen collection

The number of ejaculations in a day or per week influences semen volume and concentration of spermatozoa per ejaculate. Both of these semen traits decrease with the frequency of semen collection (McCartney et al 1958; McDaniel and Sexton 1977; Bakst and Cecil 1981;Ansah et al. 1984a). However, when the objective is to obtain a greater amount of spermatozoa in a given period of time, semen yields per male can be increased by more frequent collections (McDaniel and Sexton 1977). These authors have also indicated that such an efficient use of males can be obtained in the early periods of production, but not later on. McDaniel and Sexton (1977) observed that semen yield of males collected five times weekly declined more rapidly after 8 weeks than the semen yield of males collected one or three times a week. Similar results have been reported in turkeys by Lorenz et al. (1955); McCartney et al. (1958) and Ansah et al. (1984a). Ansah et al. (1984a) reported that three ejaculates per

week, in alternate days , will give the maximum sperm production, compared with one or five collections a week.

The frequency of semen collection appears to have no effect on fertility of chickens and turkeys (Lorenz et al. 1955; McCartney et al. 1958; McDaniel and Sexton 1977). However, frequent semen collections increase sperm motility (Swierstra and Strain 1964; de Riviers 1975) and the percentage of live spermatozoa (Ansah et al. 1984a). De Riviers and Williams (1981) concluded that the daily sperm output of the testes is better exploited by the use of frequent semen collections which also improve the quality of ejaculated sperm.

Two to four weekly collections of semen per male would seem sufficient to give a satisfactory measure of the inherent semen yield of a male (Williams and McGibbon 1956). The repeatability estimates of semen traits range from 0.58 to 0.90 for semen volume, from 0.56 to 0.82 for sperm concentration, and from 0.62 to 0.83 for sperm motility (Williams and McGibbon 1956; Siegel and Beane 1960; Soller et al. 1965a, 1965b; Marini and Goodman 1969; Pingel and Schubert 1983). The differences in repeatability values for the same trait are usually a result of the populations used, method of semen collection and probably age of the bird. The high repeatability of semen traits is a desirable characteristic, because any trait selected for to improve egg production, not only has to be correlated with egg production, but also should be easy and inexpensive to

measure.

2.4.4 Other environmental factors

Other environmental factors which are known to affect the reproductive performance of males and females are: light regime, temperature and nutrition. Long photoperiods reduce the age at sexual maturity of pullets, and stimulate egg production (Morris and Fox 1958; Sturkie 1976; Gilbert 1980). It is common practice to keep hens under 14 to 16 hours of light during the egg production period. In cockerels, long day-length also brings about early sexual maturity (Ingkasuwan and Ogasawara 1966; de Riviers and Williams 1981). However, it seems that long (12 to 16 hours) or short (8 to 11 hours) photoperiods do not affect semen yield significantly. Parker and McCluskey (1965), Ingkasuwan and Ogasawara (1966), Siegel et al. (1969) and de Riviers (1980) reported no differences in semen yield between the artificial light regimes they tested.

Ambient temperature has a significant effect on egg production and egg quality, as well as on the reproductive traits of males. Ahvar et al. (1983) reported that pullets at 32°C reached sexual maturity 4 days earlier than birds housed at lower temperature (20 °C) but reduced laying intensity from 71.6 to 66%. They also reported a reduction in egg weight (9.8%), albumen weight (7.2%), yolk weight (13.5%) and shell thickness (9.5%), but an increase in albumen percentage (2.9%). In males, Ingkasuwan and Ogasawara (1966) found that high ambient temperature (32 °C)

accelerated slightly the development of testes and the production of semen in the early stages of their experiment, but depressed production later on. Joshi et al. (1980), reported that males housed at 32 °C produced less semen, with lower sperm concentration and motility, but had higher percentage of live and abnormal spermatozoa, than males under 17 °C.

Low energy diets reduce the rate of egg production and egg weight (Harms and Waldroup 1963; Auckland and Fulton 1973). Auckland and Fulton (1973) also observed that eggs from hens with low energy intake had thinner shells and poor albumen quality. Males fed a low energy diet produced a lower volume of semen and had poorer fertility than those fed a standard diet (Parker and Arscott 1964). In addition, low energy diets reduce the testes and comb weights of cockerels (Parker and Arscott 1964; Engster et al. 1978). Nutritional deficiencies and excessive amounts of certain substances (i.e. drugs) may affect egg and semen production (Gilbert 1980).

2.5 Genetic variation in reproductive traits of males and females

Heritability, the fraction of the total variance attributable to genetic differences, measures the degree of resemblance between relatives, and it is an important tool in making decisions about the best method to obtain maximum genetic improvement.

An extensive review on the heritability and correlations for traits of the chicken have been published by Kinney (1969). The most characteristic feature of studies of this kind is the extreme variability of reported heritabilities and correlations. Kinney stated that "because of the extreme variability, the value of any estimates of these parameters in a specific population is questionable to one interested in a genetically different population". However, the mean of those parameters provides an idea of the overall tending for the heritability or the correlation between traits. A summary of the mean heritability of egg production and related traits from Kinneys's review, and the estimates of heritability of hen traits obtained by Gowe et al. (1973) in some of the strains of birds used in the present study are given in Table 1.

In contrast to females, there are fewer reports on the heritability of semen traits and most of these are based on small sample sizes. The influence of heredity on semen traits was demonstrated by the differences observed between families (Boone 1968), between breeds (Allen and Champion

Table 1. Number (n), mean and range of heritability estimates for some economical traits in hens.*

Trait	Kinney(1969)			Gowe et al. 1973		
	n	mean	range	n	mean	range
Age at first egg	29	0.39	0.07-0.90	6	0.43	0.20-0.61
Hen-housed egg prod.	7	0.15	0.00-0.24	6	0.20	0.09-0.31
Survivors egg prod.	39	0.22	0.02-0.45			
Hen-day rate of egg prod.	8	0.15	0.18-0.51	6	0.34	0.24-0.46
Egg weight	21	0.45	0.15-0.72	6	0.65	0.48-0.92
Egg mass	8	0.26	0.11-0.42			
Specific gravity	6	0.32	0.04-0.47	6	0.53	0.34-0.64
Haugh units	11	0.42	-0.04-0.70	6	0.52	0.20-0.77
Shell shape	7	0.41	0.26-0.74			
Blood spots	3	0.13	0.02-0.23			
Body weight	25	0.52	0.03-0.93	6	0.55	0.24-0.74

* Mean estimates based on sire component of variance of light breeds of chicken. Short term egg production.

1955) and between inbred lines of chickens (Williams and McGibbon 1956). Breed and individual differences in the ultimate size of the gonads and sperm production are dependent somewhat on genetically fixed differences of the level of functional activity of the hypothalamus (Novikov 1979).

The heritabilities of semen traits in the fowl, as those of females, vary extensively from author to author (Table 2). The heritability of semen volume ranges from 0.14 to 0.79; of sperm concentration from 0.01 to 0.65; and of sperm motility from 0.17 to 0.87. Marks (1981b) working with two lines of White Leghorns, obtained realized heritabilities of 0.44 and 0.48 for percentage of packed sperm volume. However, Pingel and Schubert (1983), using intraclass correlation methods, obtained estimates of packed sperm volume as 0.06 and 0.38.

The differences in the estimates of heritability above reported are thought to be due to differences in gene frequency of the populations and methods of estimation used. The mean heritabilities of semen volume, packed sperm volume and sperm concentration calculated from the values reported in Table 2 were moderate (0.42, 0.30 and 0.34, respectively); this indicates that in order to use semen traits as indicators of females' reproductive performance these traits should be positively and highly correlated with egg production.

Table 2. Heritability estimates of semen characteristics in fowl.

Author	Type of fowl*	Heritability	Method**
		SEMEN VOLUME	
Siegel (1963)	1	0.14	Intr. Corr.
Carson et al. (1955)	3	0.50	Intr. Corr.
Soller et al. (1965a)	2	0.41	Intr. Corr.
Chalov (1972)	1	0.35 and 0.41	Regression
Kopylovskaya and Chalov (1973)	1	0.41	Regression
Kurbatov et al.(1974)	2	0.17	Not reported
Mymrin et al. (1973)	3	0.54 and 0.70	"
Nestor (1976)	3	0.35	Selection
Pingel & Schubert(1983)	1	0.58 and 0.79	Intr. Corr.
Ansah et al. (1984b)	2	0.34 and 0.64	Intr. Corr.
		PACKED SPERM VOLUME (%)	
Marks (1981b)	1	0.44 and 0.48	Selection
Pingel & Schubert(1983)	1	0.06 and 0.38	Intr. Corr.
		SPERM CONCENTRATION	
Siegel (1963)	1	0.01	Intr. Corr.
Soller et al. (1965a)	2	0.46	Intr. Corr.
Chalov (1972)	1	0.35 and 0.46	Regression
Kopylovskaya and Chalov (1973)	1	0.46	Regression
Kurbatov et al.(1974)	2	0.18	Not reported
Mymrin et al. (1973)	3	0.34 and 0.42	"
Shishkin (1977)	2	0.28	Regression
Borsting (1980)	2	0.23 and 0.31	Intr. Corr.
Ansah et al. (1984b)	2	0.37 and 0.65	Intr. Corr.
		SPERM MOTILITY	
Siegel (1963)	1	0.29	Intr. Corr.
Soller et al. (1965a)	2	0.87	Intr. Corr.
Chalov (1972)	1	0.26 and 0.41	Regression
Kopylovskaya and Chalov (1973)	1	0.41	Regression
Kurbatov et al. (1974)	2	0.17	Regression
Mymrim et al. (1973)	3	0.17 and 0.51	Regression
Pingel & Schubert(1983)	1	0.07 and 0.20	Intr. corr.

* 1=Egg-type chicken; 2=Meat-type chicken; 3=Turkey;
** Intr. Corr.= Intraclass correlation.

2.6 Phenotypic correlations among male traits

Researchers have always been concerned with the degree of association between different traits, mainly because of the effect that selection on one trait may produce in others. Individual estimates of correlations are usually of little value, except as they relate to a specific study. Nevertheless, the mean of the correlations gives an idea of the overall tendencies.

The phenotypic correlation coefficients among semen traits and between semen traits and other male traits obtained from reports in the literature are given in Table 3. In general, the relationship of semen volume to sperm concentration, and sperm motility in fowl tend to be positive; but the correlation of semen volume, sperm concentration and sperm motility with the percentage of dead or abnormal spermatozoa tends to be negative. The correlation between semen volume and testes size appears to be positive, as that between semen volume and body weight.

Table 3. Phenotypic correlations among semen traits and of semen traits with testes and body weights.

Author	Type of fowl*	Semen trait	Correlation coefficients
CORRELATIONS WITH: SEMEN VOLUME			
Siegel & Beane (1960)	2	Concentration	0.42** & 0.56**
Soller et al. (1965a)	2	"	0.52 **
Marini & Goodman(1969)	2	"	-0.09 & -0.05 NS
Kolpakov (1970)	3	"	0.70**
Saeid and Al-Soudi(1975)	4	"	0.04
Nestor and Brown(1976)	3	"	-0.07 NS to 0.32**
Siegel and Beane (1960)	2	Motility	0.27 **
Soller et al. (1965a)	2	"	0.26 NS
Marini and Goodman(1969)	2	"	0.22**
Kolpakov (1970)	3	"	0.67 *
Saeid and Al-Soudi(1975)	4	"	0.09**
Marini & Goodman(1969)	2	% Dead sperm	-0.20* & -0.06 NS
Saeid and Al-Soudi(1975)	4	"	0.04 NS
Marini & Goodman(1969)	2	% Abnormal	-0.16* & -0.12 NS
Saeid and Al-Soudi(1975)	4	"	0.04 NS
Nestor and Brown (1976)	3	"	-0.37** to 0.24**
Burrows and Titus (1939)	4	Testes size	0.78**
Lamoreux (1943)	1	"	0.39*
Ansah et al. (1984b)	2	"	0.31**
Jones and Lamoreux(1942).	1	Body weight	0.32**
Williams & McGibbon(1956)	1	"	0.41**
Saeid and Al-Soudi(1975)	4	"	0.23**
CORRELATIONS WITH: SPERM CONCENTRATION			
Jones & Lamoreux (1942)	1	Motility	Positive
Siegel & Beane (1960)	2	"	0.25 ** & 0.63**
Soller et al. (1965a)	2	"	0.50 **
Marini & Goodman(1969)	2	"	0.48** & 0.42**
Kolpakov (1970)	3	"	0.85 **
Saeid and Al-Soudi(1975)	4	"	0.38**
Marini & Goodman(1969)	2	% Dead sperm	0.07 & -0.01 NS
Saeid and Al-Soudi(1975)	4	"	-0.10**
Marini & Goodman(1969)	2	% Abnormal	0.00 & -0.02 NS
Saeid and Al-Soudi(1975)	4	"	0.06 NS
Nestor and Brown (1976)	3	"	-0.23** to 0.12NS
Ansah et al. (1984b)	2	Testes size	0.35**
Saeid and Al-Soudi(1795)	4	Body weight	0.07 NS
CORRELATIONS WITH: SPERM MOTILITY			
Saeid and Al-Soudi(1975)	4	% Dead sperm	-0.19**
Marini & Goodman(1969)	2	% Abnormal	-0.20* & -0.30**
Saeid and Al-Soudi(1975)	4	"	0.14 NS
Saeid and Al-soudi(1975)	4	Body weight	0.06 NS

\# 1= Egg type chicken; 2=Meat type chicken; 3= Turkeys 4=many breeds

* Significant (P<0.05); ** Highly significant (P,0.01)

2.7 Genetic correlations among male traits

Although phenotypic correlations indicate the degree of phenotypic relationship between two variables, the genetic association and the expected change in one trait by selecting on another is determined by genetic correlations. The genetic causes of correlation are chiefly pleiotropic effects of genes, although linkage can cause transient correlations (Falconer 1981).

Only a few estimates of genetic correlations among semen traits of avians have been reported (Table 4). Semen volume measured in roosters appears to be unrelated to sperm concentration, however, these traits appear to be positively correlated in turkeys. The correlations of sperm motility with semen volume and sperm concentration tend to be positive.

There are no reports in the literature, to the author's knowledge, on the genetic correlation of semen volume, sperm concentration or sperm motility with the percentage of dead or abnormal spermatozoa.

Growth rate of broilers appears to be practically uncorrelated with semen volume (0.08) and sperm concentration (0.04), but negatively correlated (-0.21) with sperm motility. Marini and Goodman (1969) reported a significant decrease in the amount and quality of semen produced by males of two lines selected for fast or slow growth rate. The males of the slow-growth line produced 0.06 cc more semen , 2.4 x 10^9 more spermatozoa, 4.5 % less

Table 4. Genetic correlations among semen traits and between semen traits and other male traits.

Author	Type of fowl*	Traits	Genetic Correlation
CORRELATIONS WITH: SEMEN VOLUME			
Soller et al. (1965b)	2	Concentration	-0.04
Mymrin et al. (1973)	3	"	0.65
Soller et al. (1965b)	2	Motility	0.04
Chalov (1972)	1	"	0.55
Mymrin et al. (1973)	3	"	0.60
Kolpakov (1970)	3	Body weight	0.12
Soller et al. (1965b)	2	Growth rate	0.08
Kolpakov (1970)	3	Testes weight	0.47
CORRELATIONS WITH: SPERM CONCENTRATION			
Soller et al. (965b)	2	Motility	0.51
Kolpakov (1970)	3	"	0.85
Chalov (1972)	1	"	0.63
Mymrin et al. (1973)	3	"	0.54
Soller et al. (1965b)	2	Growth rate	0.04
CORRELATIONS WITH: SPERM MOTILITY			
Soller et al. (1965b)	2	Growth rate	-0.21
Soller and Rappaport (1971)	2	Growth rate	-0.28

\# 1= Egg- type chicken; 2= Meat-type chicken; 3= Turkey

dead spermatozoa and 3.1% less abnormal spermatozoa than the males of the fast-growth line.

Like the heritability estimates, differences in the estimates of genetic correlations may be explained by the method of estimation used, population size and probably the age when the traits were measured.

2.8 Correlations between male and female reproductive traits

2.8.1 Correlations between male and female reproductive traits in mammals

There is experimental evidence that supports Land's (1973) hypothesis that testes size in mammals is genetically correlated with ovulation rate and litter size. Selection for high and low natural and high and low induced ovulation rate in mice caused testes weight to change in the same direction as ovulation rate (Land and Falconer 1969). Eisen and Johnson (1981) observed an increase in testes weight of mice following selection for large litter size. Similarly, selection for large and small litter size in mice changed testes weight in the same direction as litter size (Joakimsen and Baker 1977). Conversely, selection for high and low testes weight in mice led to changes in ovulation rate in the same direction as testes weight (Islam et al. 1976).

In pigs, the results are similar. Selection for high ovulation caused testes size to change in the same direction as ovulation rate (Proud et al. 1976). Males of a line selected over nine generations for ovulation rate had 9 to 15% heavier testes than a control strain, at 120, 141, 162, and 183 days of age (Schinckel et al. 1983). Furthermore, the line selected for ovulation rate had also more rapid testicular development from 120 to 183 days of age than the control line.

Breeds of sheep with high ovulation rate tend to have more rapid growth of the testes than breeds of low ovulation rate (Land 1973; Land et al 1980); On the other hand, selection for high and low testes diameter in sheep caused ovulation rate and litter size per ewe to follow in the same direction as testes size (Land et al. 1980).

It seems feasible, therefore, to change reproductive characteristics in the male by selecting for reproductive trait in the female, and vice versa. However, the magnitude and sign of the genetic correlation between male and female reproductive characteristics must be first established to assess how successful the application will likely be before this approach can be applied satisfactorily.

Eisen and Johnson (1981) estimated the realized partial genetic correlation between testes weight and litter size, holding body weight constant, as 0.42. Land (1973) reported the partial correlation between ovulation rate and testes weight for constant body weight in five strains of mice as 0.82. The genetic correlation of testes weight and ovulation rate was estimated to be 0.50 for primiparous and 0.25 for nulliparous mice (Islam et al. 1976).

In pigs, Schinckel et al. (1983) estimated a positive genetic correlation (0.39 to 0.65) between ovulation rate and testes weight from the correlation of full-sibs. The correlation of testes weight with ovulation rate of dams was less than that between testes weight and ovulation rate of full-sibs (Schinckel et al. 1983).

There are also a few reports on the relationship of testes size with other economically important traits of females. Schinckel et al. (1983) obtained negative estimates for most of the correlations between measures of testis size of boars with age at puberty of full sibs and dams. In sheep, Land et al. (1980) observed that selection for testes size changed the onset of puberty of ewes.

Semen production may be related to ovulation rate and litter size in mammals because both traits are under the same hormonal control and semen production is related to testes size in most species. Indeed, semen production could be the logical trait to examine in species in which the measurement of the testes is not an easy task. This is the case of birds where the testes are inside the body.

2.8.2 Correlations between male and female reproductive traits in fowl

The relationship between semen traits and egg production of fowls is not well understood. Jones and Lamoreux (1942) reported that males of a line selected for high egg production produced more semen at 12, 24 and after 30 weeks of age than males of a line selected for low egg production. However, they did not find differences in the size of the testes in the two strains. Jones and Lamoreux (1942) concluded, based on the greater meiotic activity of the testes and the higher production of semen of the high egg production line, that selection for high or low egg production has been accompanied by relative changes towards

high and low reproductive capacity in male fowl. Recently, Borsting (1980) reported a significant correlation of sperm concentration of broiler breeders selected for body weight and body conformation at 6 weeks, with the rate of lay of their full sisters (0.19). He also reported significant correlations of semen density and with age at first egg (-0.20 and -0.17 respectively).

Frankham and Doornenbal (1972), on the other hand, did not find any advantage in either semen volume or sperm number of two White Leghorn strains selected for high egg production over the control strain. Williams and McGibbon (1956) obtained a non-significant correlation coefficient (r=0.001) between semen production of yearling cockerels and hen housed egg production of inbred White Leghorn strains and crosses. Pingel and Schubert (1983) did not find any significant correlation of semen volume and packed sperm volume of White Leghorn roosters with egg production up to 240 days of age of their full sisters (0.046 and -0.001, respectively). Marks (1981a) selected for percentage of packed sperm volume in males and observed an increase in egg mass after one generation of selection but no further increases in later generations. He concluded that selection for packed sperm volume in males does not result in correlated responses in term of egg mass. Marks (1981a) also observed no correlated changes in age at first egg, percent hen day production from 154 to 294 days, 62-week body weight and 40 week egg weight after three generations of selection

for packed sperm volume. Kopylovskaya et al. (1980) concluded that semen volume and sperm concentration of cockerels are genetically independent of their mother's egg production and egg weight.

Nestor (1976) reported that selection for increased semen yield of toms resulted in an increase in egg production in hens which was established in the first generation of selection and maintained throughout the six generation of selection. Selection for high egg production, likewise, increased semen yield, sperm concentration and total sperm produced per ejaculate (Nestor 1977). The changes occurred in the first generation of selection and were maintained without further changes over a number of generations. Based on his findings Nestor (1976; 1977) concluded that semen yield and egg production may be positively correlated genetically.

Mymrin (1972) in two turkey lines, observed that semen volume was poorly correlated with egg production of the dam, full and half sisters. Similarly, Stenova et al. (1983) found that the correlations of semen volume and sperm concentration of toms with egg-laying rate of the dams were low and non-significant. The correlations between sperm production of toms and the egg laying rate of their daughters were also non-significant.

No reports were found in the literature on the relationship of semen traits of fowl with egg weight or egg quality traits or on the genetic correlation of testes size

and egg production.

Secondary sex traits, e.g. comb and wattles, are influenced by gonadal steroids which are themselves affected by gonadotrophins (Nalbandov 1976). Comb and wattle size may, therefore, be related to egg production and other female reproductive characteristics. Pasvogel et al. (1951) and Pasvogel (1953) have indicated an association between egg production of pullets and comb size of their brothers and sires, and that progeny of males with the fast- and slow-growth combs also differed in testes weight at 3 weeks of age.

Ayoub and Merat (1975) estimated the correlations of wattle length of roosters with egg production of their full or half sisters, as 0.21 and 0.13, respectively; and with age at sexual maturity of their full or half sisters as -0.38 and -0.59, respectively. However, they observed no consistency in the sign of the genetic correlations of wattle length and egg production across years. Ayoub and Merat (1975) obtained an estimate of -0.53 for the genetic correlation of wattle length with age at first egg. They proposed wattle length of cockerels at 10 weeks of age as a criterion of selection for age at sexual maturity and egg production of their sisters. However, Abdel-Warith et al. (1985) reported that, in female Fayoumi chickens, there was no significant relationship between wattle length at 4, 8 and 12 weeks, and either age at sexual maturity or egg production.

There are no reports in the literature either on the genetic correlation of testes size with age at sexual maturity, and egg production of hens or on the genetic correlation of wattle size with egg weight and egg quality traits.

In summary, there is paucity of estimates of genetic correlations for which one trait is measured on females and other in males. It appears that wattle measurements are fair indicators of the female potential for high egg production. However, more and reliable estimates are necessary before final conclusions can be drawn.

III MATERIALS AND METHODS

3.1 Origin and history of the stocks

The origin, development and population size of the strains used in this study have been described by Gowe and Fairfull (1980) and Fairfull *et al.* (1983).

Strains 5 and 3 originated from a within- family division of a narrow common base population of White Leghorn chickens in 1950. Since that year, strain 5 has been maintained as an unselected control strain. Strain 3 has been selected, since 1951, primarely for hen-housed egg production, which was the number of eggs produced up to 273 days of age. In 1970 the selection on strain 3 was relaxed and the strain was divided to develop strain 1, which has been since selected for rate of egg production from age at first egg to 273 days of age.

Strain 4 was started in 1950 by importing hatching eggs from seven unrelated Canadian Records of Performance (R.O.P) stocks that were chosen for their better than average performance. The resulting progeny from a full 7x7 diallel mating were tested for performance in 1951 and selected in the next year and subsequent generations mainly for hen-housed egg production. At that time, space did not permit maintaining an unselected sample of this strain. In 1969 a higher proportion of pullets of strain 4 was selected. These pullets were randomly assigned (within dam and sire families) to two groups to form the base population of females for strains 4 and 2. Strain 2 was

thereafter selected mainly for hen-day rate of egg production.

The control strain 7 originated in 1958 from eggs of four widely used commercial Leghorn stocks being sold in North America. Pedigree matings were begun in 1959 forming two different two-way crosses, using 20 males and 60 females from each of the four commercial strains. In 1960 pedigreed reciprocal crosses between all unrelated two-way crosses were made, using 10 males and 30 females for each of the (two-way) crosses. In 1961 and subsequent generations 80 males were randomly mated with 240 females (3 females/male). Strain 7 has been maintained as an unselected control strain since 1961. In 1968, strains 8 and 9 originated from a within- family division of a large population of chickens from strain 7. Strains 8 and 9 were selected primarely for hen-house egg production and hen- day egg production, respectively.

The unselected control strain 10, originated from four widely used commercial Leghorn-type stocks being sold in North America in 1972. As with strain 7, pedigree matings were made in 1973 by making reciprocal two-way crosses using 20 males and 60 females of each of the 4 strains. In 1974, 4-way crosses were made and the next and subsequent years pedigreed matings of 80 males and 240 females were made as described for strain 7. No selected strains have yet been derived from strain 10 (Table 5).

Table 5. Description of Leghorn strains developed at the ARC, Ottawa.

Strain	Origin		Selection	
	Base population	Year	Primary trait	Secondary trait
1	Derived from strain 3	1971	High egg production rate	Fertility, hatchability viability, egg size, egg quality, low body weight
2	Derived from strain 4	1969	High egg production rate	Fertility, hatchability viability, egg size, egg quality, low body weight
3	Narrow genetic base population(Ottawa)	1950	High hen-housed egg production	Fertility, hatchability viability, egg size, egg quality, low body weight
4	Seven Canadian R.O.P. unrelated stocks crossed	1951	High hen-housed egg production	Fertility, hatchability viability, egg size, egg quality, low body weight
5	Same as strain 3	1950	None	None
7	Four commercial strains crossed	1960	None	None
8	Derived from strain 7	1969	High hen-housed egg production	Fertility, hatchability viability, egg size, egg quality, low body weight
9	Derived from strain 7	1969	High egg production rate	Fertility, hatchability viability, egg size, egg quality, low body weight
10	Four commercial strains crossed	1971	None	None

Since the origin of these strains, no selection has been practised for semen traits.

Egg quality traits refers to specific gravity, Haugh units and incidenceof blood spots.

3.2 Selection procedures

As described above, since 1971 there were six strains under selection in the study, consisting of 3 pairs of strains: 1 and 3, 2 and 4 and 8 and 9. Each pair of strains were derived from a different genetic base and consisted of one strain selected primarily for high number of eggs produced to 273 days (strains 3, 4 and 8), and the other selected primarily for high egg production rate from age at first egg to 273 days of age (strains 1, 2 and 9). A consistent selection procedure (but not a linear selection index) was followed. Differential emphasis was placed on individual and family records depending on the trait (Fairfull and Gowe 1980). McAllister (1977) derived a multiple regression approach to estimate the differential selection attention given to the various traits in the selected lines. He concluded that selection pressure was for the most part directed to egg production (hen-housed egg production or hen-day rate of egg production) and egg weight.

Selection of hens for hen-housed egg production or hen-day rate of egg production was based on individual egg production, and of males based on their full and half sisters performances. For the first three generations (1950 to 1952) no selection for egg size was practised for strains 3 and 4 but after egg size dropped substantially in the first two selected generation, this trait was also put under positive selection (using pedigree or dam and sire records).

In 1960 the selection pressure on egg size was increased using individual and family records taken before the end of the part record period of 273 days. Egg size was included as a selected trait in strains 1,2, 8 and 9 since their origin.

Selection for fertility and hatchability of hens was on the basis of dam and sire records (pedigree selection) using a culling level. Males were selected for fertility, in most years, by pretesting the selected individuals and rejecting sterile males or those with very low fertility records (Fairfull and Gowe 1980).

From 1969 on a limited selection was applied to egg quality traits in all selected strains, particularly specific gravity, Haugh units and the incidence of blood and meat spots. Furthermore, no direct selection was applied to body weight at any age until 1976 when selection for lower mature body size was added to the selection criteria. Also there was no direct selection for sexual maturity at any time (except, of course, that which may have occurred indirectly in selecting for hen-housed egg production to 273 days of age). From 1958, selection was directed entirely at the part-record (to 273 days of age), no older birds being retained as breeders, while prior to this selection was directed at both the part and the complete record (Fairfull and Gowe 1980).

Except for strain 5 which started as a random mated pedigreed population in 1959, the control strains (strains 5, 7 and 10) were reproduced as random mated pedigreed

populations using 80 sires and 240 females per control strain each generation; each male mated to 3 females and as far as possible each sire contributed a sire and each dam a dam, to minimize genetic drift. In the selected strains 28 sires and 244 dams (8 dams/sire) were selected each year until 1982. In 1983, 40 sires from each selected strain were used to reproduce the selected strains.

A important aspect to emphasize here is that no direct selection for semen production was applied at any time in any of the strains used in this study (Table 5). As mentioned before, the selection was primarily on egg production.

3.3 Measurement of female traits

Details of the collection of female data have been given by Gowe and Fairfull (1980) and Fairfull *et al.* (1983). Briefly, egg production was recorded 5 days a week from housing to 497 days of age and converted to 7 day production. Egg weight and egg quality measurements were taken for individual birds at about 240 and 450 days of age with up to 5 eggs being measured for each hen. Body weight of all females was taken at housing and 265 days of age. Body weight of the breeders was taken at 365 days of age. The female traits analysed in this study were:

Age at first egg(days). The age when the first egg of a hen was recorded.

Hen-day rate of egg production(%). The number of eggs produced per hen from first egg to 273 or 497 days of age, divided by the number of days from sexual maturity to death or to the end of a given period (273 or 497 days) and multiplied by 100.

Hen-housed egg production. The number of eggs produced from housing to 273 or 497 days of age.

Survivors egg production. The number of eggs produced per hen surviving from housing to 273 or 497 days of age. Hens with less than 20% egg production en each of the periods: 134 to 273; 274 to 385 and 386 to 497 days were not included.

Egg weight(g). Average egg weight in grams of up to 5 eggs per hen at about 240 or 450 days of age. Measurements of egg quality traits were also made on these eggs.

Egg mass (g). The product of the number of eggs produced per hen surviving from housing to 273 or 497 days and the average egg weight of 5 eggs per hen at about 240 and 450 days of age.

Specific gravity (-1x(1000)). Specific gravity was measured by determining which eggs float in brine solutions of predetermined specific gravity. This is an indicator of shell thickness.

Haugh units. Albumen height corrected for egg weight (Wells 1968). It is an indicator of albumen quality.

Shell shape. Measured the ratio of length to width of the intact egg, multiplied by 10 and reported as a deviation from 10; (L/W - 1)10,to nearest 0.1.

Blood spots percent. Number of eggs with blood spots of any size divided by the number of eggs evaluated. A maximum of 5 eggs were measured for each hen.

Fertility. Number of fertile eggs divided by the number of eggs set and multiplied by 100.

Hatchability. Number of chicks hatched divided by the number of fertile eggs and multiplied by 100.

3.4 General management of the stocks

The management of the flocks has changed throughout the long term selection study and only the conditions from 1979, which correspond to the year of hatch of the first population of birds used in this study, are being described. Since that year, the management of the flock has been similar for each hatch and strain used. Details of the egg production test conditions have been publfshed by Gowe and Fairfull (1980) Fairfull et al. (1983). A brief description of the procedure follows.

3.4.1 Brooding and rearing period

All strains were hatched over a two-day period (half of each strain sire families being hatched each day), and all strains were brooded and reared in a 3-deck cage system in a windowless house. Female chicks of each strains were reared with random assignment of cages in the rearing house so that each strain had a proportionate number of cages in each level and each row of cages. Dam and sire progeny groups were randomized proportionately within families to the cage units. Males were brooded and reared in floor pens of another house. Chicks were identified by wingband, at hatch.

Artificial light (red light) was provided for the first 48 hours (light intensity: approximately 17 lux) after hatching; but during the rearing period, the length of the light period was reduced to 6 hours and the light intensity

to about 1.6 lux. All chicks were dubbed and vaccinated against Marek's disease in the brooding house at the time of transfer to cages/pens and during the growing period they were vaccinated for infectious bronchitis, epidemic tremor and Newcastle disease. From day 0 to day 56, all chicks (male and females) were fed the Ottawa Chick Starter ration and from day 57 to 133 they were fed the Ottawa Grower ration (Appendix Table 1).

3.4.2 Laying period

All pullets were housed in individual 20 x 41 cm cages in a windowless house between 129 and 133 days of age with egg records beginning at 134 days. After being put in cages the females' daylight period was increased one hour the first week and 30 minutes the subsequent weeks until a 16 hour light period was reached. This light period was maintained to the end of the test at 497 days. The light intensity was then about 40 lux.

The conditions and management of the males used in this study are given in the next section. The general conditions of the males during the production period follows:

Males were housed in another building two per cage (30 x 45 cm) between 129 and 133 days of age. They were under a 6 hour period of light and about 1 lux light intensity, until they were 115 days old, but from day 116 after hatching, the males' length of light period and light intensity were increased to 8 hours and and about 11 lux,

respectively.

During the breeding period, the males were also kept in individual cages. The female breeders were fed the Ottawa Hatching ration and the male breeders were fed the Ottawa Grower ration (Appendix Table 1).

3.5 Specific conditions during semen evaluation

In this study, the males were kept in controlled light houses in individual cages. The length of the period of light varied for each particular experiment, to allow a full days work in the house. The males in experiments I and II were under 12 hours light, those in experiment III to V were under 9 hours light and the males in experiment VI were under 14 hours. Males were fed the Ottawa Grower ration *ad libitum* (Appendix Table 1).

3.5.1 Experimental birds and their assignment to blocks

The number of strains and population of males used in each experiment are shown in Table 6. In experiment I, the male breeders hatched in 1979 and a sample of males hatched in 1980 were used. The 1980 sample included 40 males of control strain 7 taken at random, one male from each even-numbered sire family. The 20 strain 8 males and 20 strain 9 males were chosen within each strain by randomly selecting 20 out of 28 sire families and taking one male at random from each of these sire families.

In experiments II, V and VI all males used were breeders that were previously used in reproduction of the strains. In experiment III, the males used were a random sample of males from each dam family. The population structure of the males in experiment III is shown in Table 7. In experiment IV, the control (80 males per strain) and selected (40 males per strain) breeders, plus two males

Table 6. Number of strains and males per strain used in each experiment.

Experiment	Year of hatch	Number of strains		Number of males per strain			Type of bird*
		Control	Selected	Control	Selected	Total	
I	1979	1	2	73	28	129	Breeders
	1980	1	2	40	20	80	Nonbreeders
II	1980	3	6	80	28	408	Breeders
III	1982	3	4	160	336	1684+	Nonbreeders
IV	1982	3	4	80	90	600+	Breeders Nonbreeders
V	1982	3	4	80	40	400	Breeders
VI	1982	2	4	80	40	320	Breeders

* The males breeders and/or a random sample of males (nonbreeders) were used.
+ The difference with respect to the expected value of 1824 was due to mortality and other reason.

Table 7. Population structure of males used in Experiment III.

Type of strain	Number of strains	Sires/ Strain	Dams/Sire	Offspring/ dam	Total
Control	3	80	1	2	480
Selected	4	28	4	3	1344
Total	7				1684*

* The difference with respect to the expected value of 1824 was due to mortality and other reason.

Control strains 5,7 and 10 and selected strains 1,3,8 and 9 were used in the experiment.

randomly selected from each sire family per selected strain were evaluated. If a random male happened to be a breeder, its semen trait value was used twice. In this experiment the difference in semen production between the breeders and the random group of males was tested.

The number of males per block and the size of the semen collection groups within block are shown in Table 8. In general, all males used in each experiment were asigned to large groups (blocks) and within blocks randomly distributed in clusters of 5 to 8 males per strain (in experiment I, males were distributed by strain and year of hatch). The assignment of clusters of cages to the strains and of males to the clusters within strain was at random. In general, one block of males was worked in a day. In experiment III, however, the block of 254 males was divided in two groups of 127 males to allow a full day's work.

3.5.2 Adaptation and training

In general, when males were two per cage before the experimental data collection or had to be moved from one place to another, they were given a period of time to adapt to their new individual cages and environment (Table 9).

In experiment I, the strain 7 males, hatched in 1979, and all the males hatched in 1980 (strains 7, 8 and 9) were moved from their original cages to the new ones in another building where a small laboratory for semen collection and evaluation purposes was set up. Similarly, all males from experiments II, III, IV, V and VI were moved from one place

Table 8. Assignment of males to blocks and size of semen collection groups within block in each experiment.

Experiment	Number of strains		Total of males per block per strain			Number blocks	Size of collection groups
	Control	Selected	Control	Selected	Total		
I	1	2	28	24	52	4	18,18,16
II	3	6	60	42	102	4	4x20,22
III	3	4	66	188	254	6	4x20,2x16
			d	d	160	1	4x18,2x22
							22
IV	3	4	81	120	201	3	9x20,21
V	3	4	120	80	200	2	10x20
VI	2	4	80	80	160	2	8x20

d The number of males per strain was as follows: 18 males for strains 5 and 7; 22 males for strain 10 and 32 and 34 males for strains 3 and 8.

Table 9. Length of the adaptation period and number of ejaculations per male prior to semen collection and evaluation.

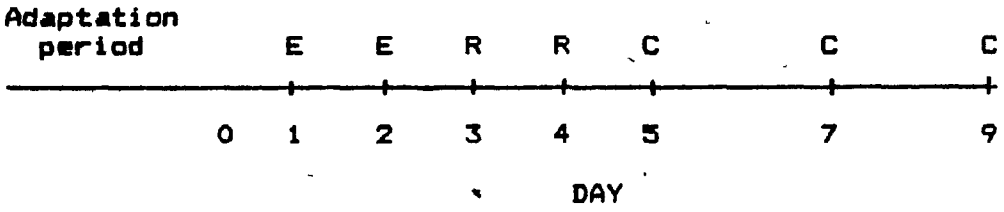
Experiment	Adaptataion and Training	
	Adaptation period(days)	Number of ejaculations
I	5	0
II	8	6
III	18-25	4-6
IV	15	3-6
V	14	5
VI	8	3

to another or rearranged within the same building.

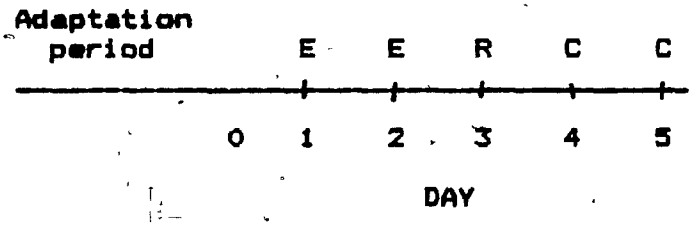
During the period of adaptation, the males were trained (ejaculated)- no semen samples were kept- and the response to the ejaculation training was scored (satisfactory or non-satisfactory). The decision of satisfactory or non-satisfactory status was based on the male's behaviour, not on his semen production. The roosters not capable of being trained were identified and eliminated from the experiment(Appendix Table 2).

The number of ejaculations per male during training varied among and within experiments (Table 9) depending whether or not all or some of the males (breeders or nonbreeders) had been previously ejaculated. After the adaptation period, the males were generally ejaculated in two consecutive days to stabilize the sperm reserve of the deferent ducts, and after one day of rest, semen was collected and evaluated (Figure 1).

Experiment I



Experiments II to VI



E= Emptying (Males were ejaculated but no semen samples were kept).
R= Rest (Males were not ejaculated).
C= Semen was collected and evaluated.

Figure 1. Semen collection program

3.6 Semen collection and evaluation

Semen collection was carried out according to the technique routinely used at the ARC, which is a modification of the abdominal massage technique of Burrows and Quinn (1937). A crew collected the semen in small groups of 16 to 24 males (Table 8), and the semen was immediately taken to the laboratory located in the same building. Semen was always collected and evaluated within half an hour; except for the number of spermatozoa/ml and the percentage of abnormal spermatozoa per ejaculate which were evaluated about 5 hours later. If excreta or blood was seen in the sample, it was noted on the records and those data were not included in the statistical analyses. At the end of each experiment (except experiment I), the males were taken out of the cages and their body weight taken to the nearest 10g.

Semen traits measured:

Semen weight. Semen was collected in 16 X 100 mm pre-weighed plastic vials. Weights were directly marked on each vial. After collection, semen weight was taken on a electronic scale with an accuracy to 0.001 g. Semen weight was then calculated as vial plus semen weight minus the weight of the vial. Semen weight was defined as the weight of semen produced by a rooster in one ejaculate.

Specific gravity of semen. Twenty two 0.1 ml semen samples from each ejaculate of 11 males (two samples per male) were weighed to the nearest μg and the results converted into volume to determine the specific gravity of

semen (µg/ml).

Percentage of packed sperm volume. After gently shaking the vials with semen, one semen sample was taken per vial in a haematocrit tube by capillarity (85 µl), sealed with CRITOSEAL (a vinyl plastic putty) and centrifuged for three minutes in a micro-capillary centrifuge, model MB (International Equipment Company, Needhan Hts, Mass. USA). The percentage of packed sperm volume was measured using a haematocrit set and read from a haematocrit chart reader. One measurement of packed sperm volume per ejaculate was made in experiments I to IV, because of time constraints. In experiments V and VI two measures of packed sperm volume were taken per ejaculate and the average value was used in the statistical analysis. Packed sperm volume was defined as the percentage of sperm mass in the ejaculate.

Number of spermatozoa/ml. An electronic counter (Coulter counter ZB1; Coulter Electronics of Canada Ltd.) was adapted for sperm counting by calibration using manual heamocytometer sperm counts through manipulation of the amplitude and threshold settings. Sperm counts of 12 semen samples from 12 males were carried out using the haemocytometer (Sorensen 1979) and another 12 samples from the same males were used for sperm counts using the coulter counter. Settings of amplitude to 1 and minimum and maximum thresholds of 10 and 80, respectively, appeared to be appropiate as suggested for the correlation of coulter counter and spermatocrit counts.

Semen samples were prepared for the coulter counter as follows: 0.05 ml of the semen collected in each ejaculate was pre-diluted for conservation in 4.95 ml (dilution rate 1:100) of Isoton in pre-filled vials. Four hours later, these pre-diluted samples were further diluted to 1:50 000, using a dual diluter III, which automatically took 1 ml of the pre-diluted sample and diluted it 500 times.

Motility score. A small drop of semen (about 0.2 ml) was diluted in 0.5 ml of physiological saline (0.9% NaCl), placed on a plain slide and covered with a cover glass. The slide was then examined under the microscope at a magnification of 400X. A subjective estimate of motile spermatozoa, one sample per ejaculate, was obtained according to the following scoring scheme: 0, no movement discernible; 1, slight movement; 2, sluggish movement; 3, vigorous movement; 4, very vigorous movement; and 5, extremely rapid formation of eddies and waves. Motility score and percent motility were always assessed within 30 minutes of collection at room temperature.

Percent motility. Percent motility was evaluated on the same semen sample and under the same microscopic magnification as motility score. Values from 0 to 100 with 5% intervals were used, with the 0 value assigned to the samples with no moving spermatozoa and the 100 value to samples with all spermatozoa moving.

Percentage of abnormal spermatozoa. One drop of stain was added to one drop of semen placed at the end of a

microscope slide and mixed thoroughly. After smearing using a coverslip, the smear was dried on a hot plate. The spermatozoa were stained using EOSIN-B Aniline Blue (Marini and Goodman 1969). No categorization for type of abnormal spermatozoa was done. Three hundred spermatozoa were counted under the microscope (1000x) and the number of abnormal spermatozoa was expressed as a percentage of the total number of spermatozoa counted.

Total sperm weight. The product of semen weight and packed sperm volume.

Number of spermatozoa per ejaculate. The product of semen weight and number of spermatozoa/ml.

3.7 Assessment of testes and secondary sex traits

In experiment V, the males (hatched in 1982) were taken out of the cages and laid down with their head resting on the plane surface of a table. Next, the wattles were unfolded and the length and width of each wattle were measured with a ruler to 1 mm accuracy. The length of the wattle was measured from the base of the beak to the bottom tip of the wattle. The width of the wattle was measured perpendicular to the wattle length at the widest part. The spur length was measured with a flexible ruler, to 1 mm accuracy, from the base of the spur to the end. The spur diameter was also measured to 1 mm accuracy with a caliper at the base of the spur.

In experiment VI, prior to wattle and testes measurements, body weight of the male breeders hatched in 1982 and a sample of males hatched in 1983 was taken to the nearest 10g. Wattle and testes measurements were taken after the males were killed by asphyxiation in a gas chamber, using CO_2. The dead males were transported to the necropsy building where the abdomen of the males was cut open and the testes removed. Wattles were removed by a cut at the base of the beak. Testes and wattles were weighed with accuracy to 0.1 g. After the weighing of wattles of the 1983 hatched males, the length and width of the wattles were taken in a similar way as for the males of experiment V, except that wattles were measured after being removed from the birds.

3.8 Tests for lymphoid leukosis virus

All males from experiment I and a random sample of males from experiments II and IV (Table 10) were tested shortly after collection of semen sample for the presence of LLV in semen or for the presence of the group specific antigen (gsa) in feather pulps within one month after semen collection and evaluation.

In experiment I, each semen ejaculate was collected in a vial with a code number written on and capped immediately. Contamination of the samples by excreta was avoided. After collection the semen samples were submerged in ice water and delivered to the Animal Diseases Research Institute (ADRI) in Nepean, Ontario. The test for the presence of the LLV in semen was made using the phenotypic mixing (PM) test (Okazaki et al. 1975).

In experiments II and IV, feather samples were collected to test for the presence of the gsa in feather pulp. In each experiment 4-6 feathers containing live, vascularized feather pulp were removed from each rooster and placed in a plastic bag identified by wingband number of the bird. The samples were delivered to the ADRI immediately. The gsa in the feathers was detected by the complement fixation (CF) test (Sever 1962; Sarma etal. 1964). Both tests (PM and CF) to detect the presences of the LLV in semen or the gsa in feather pulps were kindly made by Dr. Spencer from the ADRI.

Table 10. Number of males tested for the presence of the lymphoid leukosis virus (LLV) in semen or the presence of the group specific viral antigen in feather pulps.

Experiment	Year of Hatch	Specimen	LLV test*	Number of males
I	1979	Semen	PM	128
	1980	Semen	PM	80
II	1980	Feather pulp	CF	361
IV	1982	Feather pulp	CF	454

* PM= Phenotypic mixing test;
CF= Complement fixation test.

3.9 Statistical Analysis

Data from semen samples that contained blood or faeces and from crippled or sick birds (pale comb and low body weight) were excluded from the statistical analyses. The percentages of semen data excluded are given in Appendix Table 2, by experiment. The statistical analyses included egg production and male fertility data, in addition to semen characteristics, testes weight and secondary sex trait measurements.

3.9.1 Analysis of variance

Analyses of variance are used to test the significance of sources of variation in a statistical model. However, the valid application of the test of significance requires that the experimental error be independently and normally distributed with a common variance. One feature of non-normal distribution is that variance is related to the mean (Snedecor and Cochran 1967). To make data normally distributed and means and variances independent, raw data are normally transformed or a different type of analysis has to be used.

The departure, of the experimental data, from normality was tested by using the Kolomogorov-Smirnov D-statistic. This procedure tests the null hypothesis that the data values are a random sample from a normal distribution. The data are tested against a normal distribution with mean and variance equal to the sample mean and variance.

The data on semen weight and percent motility were

transformed to the natural logarithm and arcsine scales, respectively. The data on total sperm weight, number of spermatozoa per ejaculate and percentage of abnormal spermatozoa were transformed using the square root function, and the data on packed sperm volume (Y) were transformed by the following function: arcsine $(Y + 1/2)^{1/2}$. A new tests of normality for the transformed data indicated no departure of the transformed data from normality.

The semen traits examined in each experiment and the statistical models which described them are presented in Appendix Table 3 and Table 11, respectively. Block by ejaculate interaction was not included in the models, because in a preliminary analysis it was non- significant ($P>0.80$) for any of the semen traits. The effect of lymphoid leukosis virus (LLV) on semen traits and/or fertility of the cockerels was tested only in the control strains of experiments I, II and IV, because the incidence of LLV-shedding birds in the selected strains was very low (Appendix Tables 4, and 5). The statistical models to test the effect of LLV on semen traits and fertility are given in Table 12. The differences between the means of the levels of each main effect were tested by least squares procedures (SAS 1982).

To test the effect of age on semen traits the data from experiments III through VI (8, 16, 20 and 29 months old males, respectively) were combined. The number of males from which data were used in assessment of effects of age were

Table 11. Statistical models and degrees of freedom for the semen traits assessed in each experiment.*

Experiment[1]	Male traits	Degrees of freedom for effects and interactions: Block	Ejaculate (Ejac)	Strain (S)	Block*S	Ejac*S	BW
I	SW,PSV,TSW NSM,NSE,MS MP,PAS	3	2	2	6	4	-
II	SW,PSV,TSW MS,MP	3	1	8	24	8	1
III	SW,PSV,TSW	6	1	6	36	6	1
	MS,MP	6	-	6	36	-	1
IV	SW,PSV,TSW	2	1	6	12	6	1
V	SW,PSV,TSW	1	1	5	5	5	1
	Wattles	-	-	6	-	-	1
	Spurs	-	-	5	-	-	1
VI	SW,PSV,TSW	1	1	5	5	5	1
	Testis,Wattle	-	-	5	-	-	1
	Testis,Wattle	-	-	2	-	-	1
III-VI	SW,PSV,TSW	3	1	5	15	5	1

* All effects were considered to be fixed.
Body weight (BW) was used as a continuous covariable.

[1] In experiment VI testes and wattle measurements were taken in the male breeders hatched in 1982 and in a random sample of males hatched in 1983.

For experiments III-VI block indicates age effect.
SW=Semen weight; PSV=Percentage of packed sperm volume; TSW=Total sperm weight; NSM= Number of spermatozoa in a mililitre; NSE=Number of spermatozoa/ejaculate; MS=Motility score; MP=Motility percent; PAS=Percentage of abnormal spermatozoa.

Table 12. Statistical model and degrees of freedom to test the effect of lymphoid leukosis virus (LLV) on semen traits and fertility* (Experiments I, II and III).

Exp.	Traits	Year of hatch	Degrees of freedom for effects and interaction				
			Strain	Ejaculate	LLV	LLV*Strain	Body weight
I	SW,PSV,TSW	1979	--	2	1	-	-
	NSM,NSE,MS	1980	--	2	1	-	-
	MP, PAS						
II	SW,PSV,TSW	1980	2	1	1	2	1
	MS,MP						
	Fertility	1980	2	-	1	2	-
	Hatchability						
IV	SW,PSV,TSW	1982	2	1	1	2	1
	Fertility	1982	2	-	1	2	-
	Hatchability						

* Test of LLV effect on semen traits and fertility was done only in the control strains,because of the low incidence of LLV-shedders in the selected strains. All effects were considered to be fixed. Body weight was used as a continuous covariable.

SW=Semen weight;PSV=Percentage of packed sperm volume;TSW=Total sperm weight; NSM=Number of spermatozoa in a mililitre of semen; NSE= Number of spermatozoa/ejaculate; MS=Motility score; MP= Percent motility. PAS= Percentage of abnormal spermatozoa.

23, 18 and 58 for strains 1, 3 and 5, respectively, and 66, 28 and 22 for strains 7, 8 and 9, respectively. The statistical model which described the semen traits examined in this study included the fixed effects of age, ejaculate sequence, strain, interactions and body weight as a continuous covariate (see bottom of Table 11). In adddition, the regression lines of semen traits on age of the males were compared as descripted by Snedecor and Cochran (1967). The statistical model used was

$$Y_{ij} = a + bX_{ij} + e_{ij}$$

where: Y_{ij} denotes the ij-th observation of any semen trait in the i-th strain; a and b denote the intercept and slope of the regression lines in the i-th strain, respectively; X_{ij} is the age of the males in the i-th strain; and e_{ij} is the residual error term (0, s^2).

Strain differences in wattle and spur sizes and/or wattle and testes weights in addition to semen traits, were tested in experiments V and VI. The statistical models which described those traits are presented in Table 11.

3.9.2 Chi-square tests

Differences in the frequency of LLV-shedding birds and in the frequency of birds expressing the group specific antigen (gsa) in feather pulps in selected and control strains were tested by chi-square tests. The chi-square test is used in data classified in two classes, e.g., "dead" or "live", or "present" or "absent" and it tests the null hypothesis that there are no differences in the true

proportions of a class between two or more populations (Steel and Torrie 1980).

3.9.3 Estimation of variance components and heritability

Heritabilities of semen weight, packed sperm volume and total sperm weight were estimated based on the first or the mean of two semen ejaculates from the males of experiment III. Heritabilities of semen traits were estimated by intraclass correlation methods. Heritabilities of wattle and testes weights were estimated by regression methods. Heritability of body weight was estimated by intraclass and regression methods. The raw data on semen traits (not the transformed data) were used, because the asumption of normality is not required to estimate components of variance (Steel and Torrie 1980).

3.9.3.1 Intraclass correlation method

In the selected strains of experiment III, semen data were collected from the progeny of 28 sires/strain, each sire mated to 4 dams and each dam contributing three sons. Therefore, it was possible to estimate sire, dam and full-sibs components of variance from a hierarchal design. The statistical model used was

$$Y_{ijkl} = M + L_i + S_{ij} + D_{ijk} + W_{ijkl}$$

where: Y_{ijkl} is the ijkl-th observation of semen weight, packed sperm volume, total sperm weight or body weight; M is the population mean; L_i is the fixed effect of the i-th

strain (i= 1,2,3 and 4); S_{ij} is the random effect of the j-th sire within the i-th strain, asummed to be independently distributed $(0,s^2_s)$ (j=1, 2,...112); D_{ijk} is the random effect of the k-th dam within the j-th sire and i-th strain, asummed to be independently distributed $(0,s^2_d)$ (l=1, 2,... 336); W_{ijkl} is the residual term, associated with the ijkl-th observation, asummed to be independently distributed $(0,s^2_w)$.

The analyses of variance and the expected mean squares for the above model are presented in Appendix Table 6. Equating the appropiate mean squares to their expectations provides the variance component estimates. The coefficients of the components of variance were calculated according to Becker (1975).

For each trait the total phenotypic variance s^2_p was estimated as:

$$s^2_p = s^2_s + s^2_d + s^2_w$$

where: s^2_s is the observed sire component of variance. Sire families consist of half-sibs, so s^2_s is the covariance of half-sibs. s^2_d is the observed dam component of variance. Dam families consist of full-sibs, so s^2_d is the covariance of full-sibs minus the covarfance of half sibs, because the sire effect is removed in the analysis of variance. s^2_w is the residual component of variance. s^2_w is the total variance minus the covariance of full-sibs. The genetic and environmental interpretation of the components of variance is presented in Appendix Table 7.

In the control strains, semen traits and body weight were measured from individuals that were the progeny of 80 sires, each sire mated to one dam. Each dam contributed two sons. Thus it was possible to estimate only full-sib components of variance. The statistical model used was

$$Y_{ijk} = M + L_i + G_{ij} + W_{ijk}$$

where: Y_{ijk} is the ijk-th observation of semen weight, packed sperm volume, total sperm weight or body weight; M is the population mean; L_i is the fixed effect of the i-th strain (i=1, 2 and 3); G_{ij} is the random effect of the j-th full-sib family (j=1, 2, ... 240) within the i-th strain, asummed to be independently distributed $(0,s^2_g)$; W_{ijk} is the random residual term,associated with the ijk-th observation, asummed to be independently distributed $(0,s^2_w)$.

The analysis of variance and the expected mean squares for this analysis are given in Appendix Table 8. For each trait the phenotypic variance (s^2_p) was estimated as:

$$s^2_p = s^2_g + s^2_w$$

where: s^2_g is the observed genetic group variance component. It consists of full-sib families, so $s^2_g = s^2_s + s^2_d$ is the covariance of full-sibs. s^2_w is the residual component of variance and was obtained as $s^2_p - s^2_g$. The genetic and environmental interpretation of the components of variance is given in Appendix Table 7.

The heritability estimates of semen traits and body weight were calculated, in the selected strains, as :

1) $h^2_s = 4s2_{s/s2_p}$

2) $h^2_d = 4s^2_d/s^2_p$

3) $h^2_{s+d} = 2(s^2_s+s^2_d)/s^2_p$

No correction was made for parental relationship; to allow comparison of the results of this study with other reports in the literature, where no correction for parental relationship was made (Pingel and Schubert 1983; Ansah et al. 1984b). The standard error(S.E.) of the heritabilities was estimated using Dickerson's approximation (Becker 1975).

1) S.E. $(h^2_s) = 4\ (Var\ s^2_s)^{1/2}/s^2_p$

2) S.E. $(h^2_d) = 4\ (Var\ s^2_d)^{1/2}/s^2_p$

3) S.E. $(h^2_{s+d}) = 2(Var\ s^2_s + Var\ s^2_d + 2Cov(s^2_s, s^2_d))^{1/2}/s^2_p$

The proportion of the total variance due to maternal plus 1/4 of the dominance effects (m) was estimated as $(s^2_d - s^2_s)/s^2_p$. The proportion of the total variance due to random environmental variance plus 3/4 of the dominance variance (e^2) was estimated as $(s^2_w - 2s^2_s)/s^2_p$.

The heritability estimates of semen traits and body weight were calculated, in the control strains, as:

$$h^2 = 2s^2_g/s^2_p$$

where: s^2_g is the observed full sib variance component and s^2_p is the phenotypic variance.

The standard error (S.E.) of the heritability was estimated as (Becker 1975):

$$S.E.\ (h^2_g) = \frac{2((2(1-t)^2\ (1 + (k-1)t)^2)^{1/2}}{k(k-1)\ (s-1)},$$

where: t is the intraclass correlation, estimated as

s^2_g/s^2_p; k is equal to (N - & n^2_i/N)/(s-1); N is the total number of individuals; n_i is the number of individuals within the i-th mating; and s is the number of sires.

3.9.3.2 Regression method

The estimates of heritability of wattle, testes and body weights were computed in the control and selected strains, from the data of experiments V and VI, using multivariate analysis of variance (SAS 1982). The statistical model for the above traits corrected for age differences of parents (29 months of age) and offspring (14 months of age) was

$$Y_{ijk} = M + A_i + L_j + AL_{ij} + e_{ijk}$$

where: Y_{ijk} is the ijk-th observations of wattle, testes or body weights measured on sire or son; M is the population mean; A_i is the fixed effect of the i-th age (i=1, 2); L_j is the fixed effect of the j-th strain; AL_{ij} is the interaction of age by strain; e_{ijk} is the random error term (0, s^2).

The residual sum of squares and crossproducts from the above model were used to estimate the regression (b) of offspring on parent as:

$$b = RCP/SSP$$

where: RCP is the residual crossproduct of sire - offspring and SSP is the sum of squares of sires.

Heritability was estimated using the regression coefficient multiplied by the inverse of the coefficient of

relationship (a),

$$h^2 = 1/a\ (b) = 1/a\ (s_{po}/s^2_p)$$

where: s_{po} is the covariance of sire-son and s^2_p is the sire variance. When parents are unrelated, the regression of offspring on parent estimates 1/2 of the additive variance plus 1/4 of the additive by additive variance; hence, the heritability can be estimated as twice the regression coefficient. However, when parents are related, the coefficient of relationship is not 1/2 and new coefficients should be estimated.

In this study, the coefficients of relationship were calculated as twice the coefficients of coancestry, (Falconer 1981). The coefficient of coancestry is defined as the probability that a random gene from an individual X is identical by descendent with a random gene from an individual Y (Kempthorne 1973). The coefficient of coancestry (f) for two full-sibs is $f_{XY} = 1/4\ (f_{AA} + f_{BB} + 2f_{AB})$ and for parent-offspring $f_{AX} = 1/2(f_{AA} + f_{AB})$; where: f_{AA}, f_{BB} and f_{AB} are the coefficients of coancestry of each sire with himself, each dam with herself and between sires and dams, respectively.

The coefficients of coancestry for each sire with himself, between sire and dam breeders and for each dam with herself were made available by Drs. Gowe and Fairfull from the ARC. Pedigree information was always recorded for each male of all strains since their origin, except for strain 5 males which started as a pedigreed population in 1959 (Gowe

and Fairfull 1980).

The standard error (S.E.) of heritability was estimated as the reciprocal of the coefficient of relationship (1/a) times the standard error of the regression coefficient.

$$S.E.\ (h^2) = 1/a\ S.E.(b) = (4(s^2_o/s^2_p - b^2)/df)^{1/2}$$

where: s^2_o and s^2_p are the offspring and sire variances, respectively; and df denotes the degrees of freedom.

3.9.4 Estimation of repeatability

Repeatability estimates of semen weight, packed sperm volume and total sperm weight were based on the correlation of two measurements of above traits made in the same rooster in two consecutive days. The statistical model used was,

$$Y_{ij} = M + a_i + e_{ij}$$

where: Y_{ij} is the j-th record on the i-th rooster; M is the population mean; a_i is the effect of the i-th rooster, assumed to be independently distributed $(0, s^2_a)$; e_{ij} is the random environmental effect associated with the j-th record on the i-th rooster$(0, s^2_e)$.

Repeatability (r) was estimated as:

$$r = s_{12}/(s^2_1\ s^2_2)^{1/2}$$

where; s_{12} is the covariance of first and second records; and s^2_1 and s^2_2 are the variances for the first and second records, respectively.

3.9.5 Phenotypic correlations among male traits

The partial correlation coefficients among semen

traits, and between semen traits and testes, wattle and spur measurements were calculated using the residual sum of squares and crossproducts of the statistical models given in Table 11. In calculating the correlations of body weight with above male traits, the effect of body weight was dropped from the statistical models.

The correlation coefficients were calculated as:

$$r = \frac{RCP_{xy}}{(RSS_x \; RSS_y)^{1/2}}$$

where: RCP_{xy} is the residual crossproduct of traits x and y; and RSS_x and RSS_y are the residual sum of squares for traits x and y.

3.9.6 Genetic correlations among male traits

Genetic correlations among semen traits were estimated based on the mean of two semen ejaculates collected in two consecutive days. The components of variance and covariance were estimated, in the selected and control strains, from the hierarchal and single mating designs, used to estimate heritabilities (section 3.9.3.1).

The analyses of covariance with the expected mean crossproducts, for the hierarchal and single mating designs are given in Appendix Tables 9 and 10. Alike the estimates of heritability, equating the appropiate mean crossproducts to their expectations provide the covariance component estimates (Becker 1975). The genetic and environmental interpretation of the components of covariance is presented

in Appendix Table 11.

In the selected strains genetic correlations were estimated based on sire (r_{gs}) and sire plus dam (r_{gd}) components of variances and covariances as:

$$r_{gs} = s_{s(xy)}/(s^2_{s(x)}\ s^2_{s(y)})^{1/2} \quad \text{and}$$

$$r_{gd} = (s_{s(xy)} + s_{d(xy)})/((s^2_{s(x)} + s^2_{d(x)})(s^2_{d(y)} + s^2_{d(y)})^{1/2}$$

where: $s_{s(xy)}$ and $s_{d(xy)}$ are the sire and dam components of covariance; and s^2_s and s^2_d are the sire and dam components of variance for traits x or y.

In the control strains the genetic correlations (r_g) were estimated as:

$$r_g = s_{fs(xy)}/(s^2_{fs(x)}\ s^2_{fs(y)})^{1/2}$$

where: $s_{fs(xy)}$ is the covariance of full-sibs; $s^2_{fs(x)}$ is the full-sib variance component of trait x; and $s^2_{fs(y)}$ is the full-sib variance component of trait y.

3.9.7 Genetic correlations between sex limited traits

Genetic correlations between male semen traits and female egg production and other related traits were estimated only with the data of experiments III and IV; because of the large population of males used in these experiments.

In the selected strains (Experiment III), genetic correlations were estimated by intraclass correlation methods, using dam family means as the observational unit. In the control strains of experiment III and in the control and selected strains of experiment IV, genetic correlations

were estimated by regression methods, using individual or family means as the observational unit.

3.9.7.1 Intraclass correlation method

The statistical model used to estimate the genetic correlations for the selected strains in experiment III was:

$$Y_{ijk} = M + L_i + S(L)_{ij} + d_{ijk}$$

where: Y_{ijk} is the ijk-th observation, based on dam family means, of the dependent variable; M is the population mean; L_i is the fixed effect of the i-th strain; $S(L)_{ij}$ is the random effect of the j-th sire within the i-th strain and d_{ijk} is the effect of dam family means within sire within strain.

The form of the analysis of variance and the expected mean squares based on the model for a full-sib family mean (Appendix Table 12) was given by Kinney and Shoffner (1965). Estimates of sire and dam components of variance and covariance are obtained by equating the observed mean squares to their expectations and solving the resulting equation.

The formula used to estimate the genetic correlations based on family means (r_G) was:

$$r_G = s_{s(mf)} / (s^2_{s(m)} \; s^2_{s(f)})^{1/2}$$

where: $s_{s(mf)}$ denotes the sire component of covariance of male (m) and female (f) traits; $s^2_{s(m)}$ denotes the sire component of variance of the male trait; and $s^2_{s(f)}$ denotes the sire component of variance of the female trait.

3.9.7.2 Regression method

An original approach was developed and used to estimate the genetic correlations between sex limited traits from the correlations of offspring and parent and full-sibs. The statistical models for the multivariate analyses included the population mean, the fixed effect of strain, and the error term.

The genetic correlation (r_g), based on individual observations, between semen traits measured on males and egg production and other traits measured on their female full-sibs or dams can be estimated (See appendix I) as:

$$r_g = r_i / (a\ h_m\ \ h_f)$$

The genetic correlation (r_G), based on dam family means, between male (m) and female (f) traits is given by the following formula (See appendix I):

$$r_G = \frac{r_x\ (1+(n-1)t_m/n)\ \ (1+(m-1)t_f/m)}{a\ h_m\ h_f}$$

where: r_i and r_x are the " phenotypic" correlations of male and female traits, based on individual and family mean observations, respectively; n and m are the average number of relatives (males and females) per family; t_m and t_f are the intraclass correlations of male and female traits; and h_m and h_f are the square roots of the heritabilities of male and female traits, respectively.

To estimate the genetic correlations between male and female sex limited traits, the values of the heritabilities of semen traits used were those obtained in the control and

of semen traits used were those obtained in the control and selected strains (sire plus dam components) of experiment III. The heritabilities used for the female traits were the means of the heritability values reported by Gowe et al. (1973). When no estimates of female traits were available, the means of the heritabilities reported by Kinney (1969) were used (Table 1).

A similar approach was used to estimate the genetic correlations of wattle and testes weights with egg production and other related traits. To estimate the genetic correlations of wattle length, width and index the heritability of these traits was assumed to be similar to that of wattle weight.

IV RESULTS

The results of this study are organized into eigth main sections dealing with: the effect of lymphoid leukosis virus on semen traits and fertility, the effects of age and ejaculate sequence on semen traits, the influence of selection for high egg production on male traits, the heritability and repeatability estimates of male traits, phenotypic and genetic correlations among male traits and genetic correlations between male and female traits. The tables of the analyses of variance showing the significance, sources of variation, coefficients of variation (CV) and determination (r^2) are given in Appendix II. The tables of least squares mean estimates showing the significance of differences among the levels of the main effects of interest are presented in the main text.

4.1 Frequency of lymphoid leukosis virus infection and its effect on semen traits and male fertility

4.1.1 Consistency and frequency of lymphoid leukosis virus infection

The tests for LLV in semen and group specific viral antigen in feather pulps were conducted on the males of experiments I and II (males hatched in 1980). Only in 8 males (4.4%) out of 182 males tested did the results of the phenotypic mixing test (PM) differ from the complement fixation test (CF). In 5 instances, males tested positive with PM tested negative with CF while in 3 instances males negative with PM were positive with CF.

The results of the incidence of LLV infection between the control and selected strains are shown in Tables 13 and 14. The control strains had 15 to 30% higher incidence of LLV-shedders than the selected strains ($P<0.05$).

4.1.2 Effect of lymphoid leukosis virus infection on semen traits and fertility

4.1.2.1 Effect of lymphoid leukosis virus infection on semen traits

The results of the analyses of variance for the effect of LLV status on semen traits are shown in Appendix Tables 13 to 16 by experiment. The least squares mean estimates for LLV-shedders and nonshedders are shown in Tables 15 to 17.

Lymphoid leukosis infection did not affect ($P>0.05$) semen weight (Tables 15a, 16a and 17), motility score or percent motility (Tables 15b and 16b). LLV-shedders had higher packed sperm volume and total sperm weight means than LLV-nonshedders, however, only the differences in experiment II were significant (Tables 15a, 16a and 17). Similarly for the number of spermatozoa/ml and per ejaculate. LLV-shedders produced more spermatozoa than LLV-nonshedders, however, only the differences for the 23 month old roosters were significant (Tables 15a,b and 16a,b). Lymphoid leukosis infection increased the incidence of abnormal spermatozoa (+2.9%) of the 23 month old roosters (Table 15b); however, it did not affect ($P>0.05$) the incidence of abnormal spermatozoa of the 10 month old roosters (Table 16b).

Table 13. Comparison by year of hatch of the frequency of males shedding lymphoid leukosis virus (LLV) into semen of control and selected strains (Experiment I).*

Type of strain	Year of hatch (Age in months) 1979 (23 Mo.) Number tested	% LLV shedders	Chi square	1980 (10 Mo.) Number tested	% LLV shedders	Chi square
CONTROL	69	34.8	6.17*	39	35.9	11.06**
SELECTED	54	14.8		40	5.0	

* Control strain 7 and selected strains 8 and 9;
* P<0.05 ** P<0.01

Table 14. Comparison of the frequency of males shedding the lymphoid leukosis group specific viral antigen (LLV) in feather pulps of selected and control strains (Experiments II and IV)*

Type of strain	Experiment II Number tested	% LLV Shedders	Chi square	Experiment IV Number tested	% LLV Shedders	Chi square
CONTROL	206	24.3	35.6**	221	18.1	27.8**
SELECTED	155	1.9		233	3.0	

* Strains used in experiment II: 1,2,3,4,5,7,8,9 and 10.
Strains used in experiment IV: 1,3,5,7,8,9 and 10.
* P<0.05 ** P<0.01

Table 15a. Least squares mean estimates and standard errors of semen traits (transformed and and untransformed) measured on 23 month old roosters of control strain 7 (Experiment I; 1979 hatch).

Lymphoid leukosis status	n[1]	Semen weight ln(mg)	Semen weight mg	Packed sperm volume arcsine$\sqrt{\ }$	Packed sperm volume %	Total sperm weight $\sqrt{\ }$	Total sperm weight mg	Number of spermatozoa per ml. (x10^7)
NON-SHEDDERS	86	5.49±0.03a	242.7	0.89±0.004a	10.1	4.94±0.15a	26.3	2.20±0.10a
SHEDDERS	41	5.49±0.05a	241.8	0.89±0.006a	10.8	5.17±0.22a	28.6	2.71±0.15b

[1] n Denotes the number of observations for LLV-shedders and nonshedders.
a,b Column means with no letter in common are different (P<0.05).

Table 15b. Least squares mean estimates and standard errors of semen traits (transformed and untransformed) measured on 23 month old roosters of control strain 7 (Experiment I; 1979 hatch).

Lymphoid leukosis status	Number of spermatozoa per ejaculate			Motility score	Percent motility			Abnormal spermatozoa	
	n[1]	$\sqrt{\ }$	(x10⁷)		arcsine	%	n[1]	$\sqrt{\ }$	%
NON-SHEDDERS	86	22.8±0.73a	0.57	4.20±0.06a	0.86±0.013a	75.5	78	0.24±0.008a	6.1
SHEDDERS	41	25.8±1.06b	0.71	4.02±0.08a	0.84±0.018a	74.8	34	0.29±0.012b	9.0

[1] n Denotes the number of observations for LLV-shedders and nonshedders.
a,b Column means with no letter in common are different (P<0.05).

Table 16a. Least squares mean estimates and standard errors of semen traits (transformed and untransformed) measured on 10 month old roosters of control strain 7 (Experiment I; 1980 hatch).

Lymphoid leukosis status	n[1]	Semen weight		Packed sperm volume		Total sperm weight		Number of spermatozoa per ml. ($\times 10^7$)
		ln(mg)	mg	arcsine$\sqrt{\%}$	%	$\sqrt{\text{mg}}$	mg	
NON-SHEDDERS	71	5.89±0.04a	359.6	0.94±0.006a	15.6	7.53±0.20a	59.4	3.16±0.10a
SHEDDERS	41	5.84±0.05a	343.2	0.95±0.008a	16.2	7.50±0.27a	58.9	3.50±0.14a

[1] n Denotes the number of observations for LLV-shedders and nonshedders.
a,b Column means with no letter in common are different ($P<0.05$).

Table 16b. Least squares mean estimates and standard errors of semen traits (transformed and untransformed) measured on 10 month old roosters of control strain 7 (Experiment I; 1980 hatch).

Lymphoid leukosis status	Number of spermatozoa per ejaculate			Motility score	Percent motility		Abnormal spermatozoa		
	n[1]	$\sqrt{\ }$	(x10⁷)		arcsine	%	n[1]	$\sqrt{\ }$	%
NON-SHEDDERS	71	33.9±0.82a	1.19	4.37±0.06a	0.91±0.013a	79.0	70	0.30±0.013a	10.2
SHEDDERS	38	34.8±1.11a	1.26	4.21±0.08a	0.89±0.018a	77.9	38	0.28±0.017a	9.0

[1] n Denotes the number of observations for LLV-shedders and nonshedders.
a,b Column means with no letter in common are different (P<0.05).

Table 17. Least squares mean estimates and standard errors of semen traits (Transformed and untransformed) measured on roosters of control strains 5, 7 and 10 (Experiments II and IV)

Lymphoid leukosis status	n[1]	Semen weight ln(mg)	Semen weight mg	Packed sperm volume arcsine$\sqrt{\ }$	Packed sperm volume %	Total sperm weight $\sqrt{\ }$	Total sperm weight mg
				EXPERIMENT II			
NON-SHEDDERS	289	5.99±0.02a	383.4	0.92±0.002a	13.1	7.11±0.09a	53.1
SHEDDERS	89	6.05±0.04a	411.6	0.94±0.004b	14.9	7.85±0.17b	64.1
				EXPERIMENT IV			
NON-SHEDDERS	299	5.91±0.01a	370.4	0.94±0.002a	14.9	7.44±0.08a	57.3
SHEDDERS	108	5.96±0.03a	387.9	0.96±0.004a	15.3	7.67±0.19a	60.7

[1] n Denotes the number of observations for LLV-shedders and nonshedders
a,b Column means with no letter in common are different (P<0.05).

4.1.2.2 Effect of lymphoid leukosis virus infection on fertility

The results of the analyses of variance to test the effect of LLV status on fertility and hatchability and the least squares means for LLV-shedders and nonshedders are presented in Appendix Table 17 and Table 18, respectively.

Lymphoid leukosis infection decreased fertility by 3.6% in experiment IV; however, it did not affect fertility in experiment II (Table 18). Lymphoid leukosis infection did not affect hatchability in experiment II or in experiment IV (Table 18).

4.2 Effect of age on semen traits

The results of the analyses of variance for the effect of age on semen traits are shown in Appendix Tables 18 and 19. The absence of a significant age by strain interaction suggests that the effect of age on semen production was similar in all strains tested.

Semen weight, packed sperm volume and total sperm weight tended to decline with advancing age (Figures 2 and 3). Selected strain 1 tended to have greater semen weight, packed sperm volume and total sperm weight than strains 5 and 3 at all ages. Strain 5, on the other hand, appeared to have greater semen weight and total sperm weight than strain 3. Unselected control strain 7 tended to have higher semen and sperm production at all ages than selected strains 8 and 9. There was no difference in the slope of the regression lines of semen traits on age in strains 1, 3 and 5 or in strains 7, 8 and 9 (Tables 19 to 24). However, these tables

Table 18. Least squares mean estimates and standard errors of fertility and hatchability (transformed and untransformed) of control strains 5, 7 and 10 (Experiments II and IV).

Lymphoid leukosis status	n[1]	Fertility		Hatchability	
		arcsine	%	arcsine	%
		EXPERIMENT II			
NON-SHEDDERS	143	1.14±0.02a	90.9	0.94±0.02a	80.8
SHEDDERS	46	1.11±0.03a	89.1	0.97±0.03a	82.5
		EXPERIMENT IV			
NON-SHEDDERS	180	1.20±0.01b	93.1	0.98±0.02a	83.1
SHEDDERS	40	1.11±0.03a	89.5	0.99±0.03a	83.8

[1] n Denotes the number of observations for LLV-shedders and nonshedders.

a,b Column means with no letter in common are significantly different ($P<0.05$).

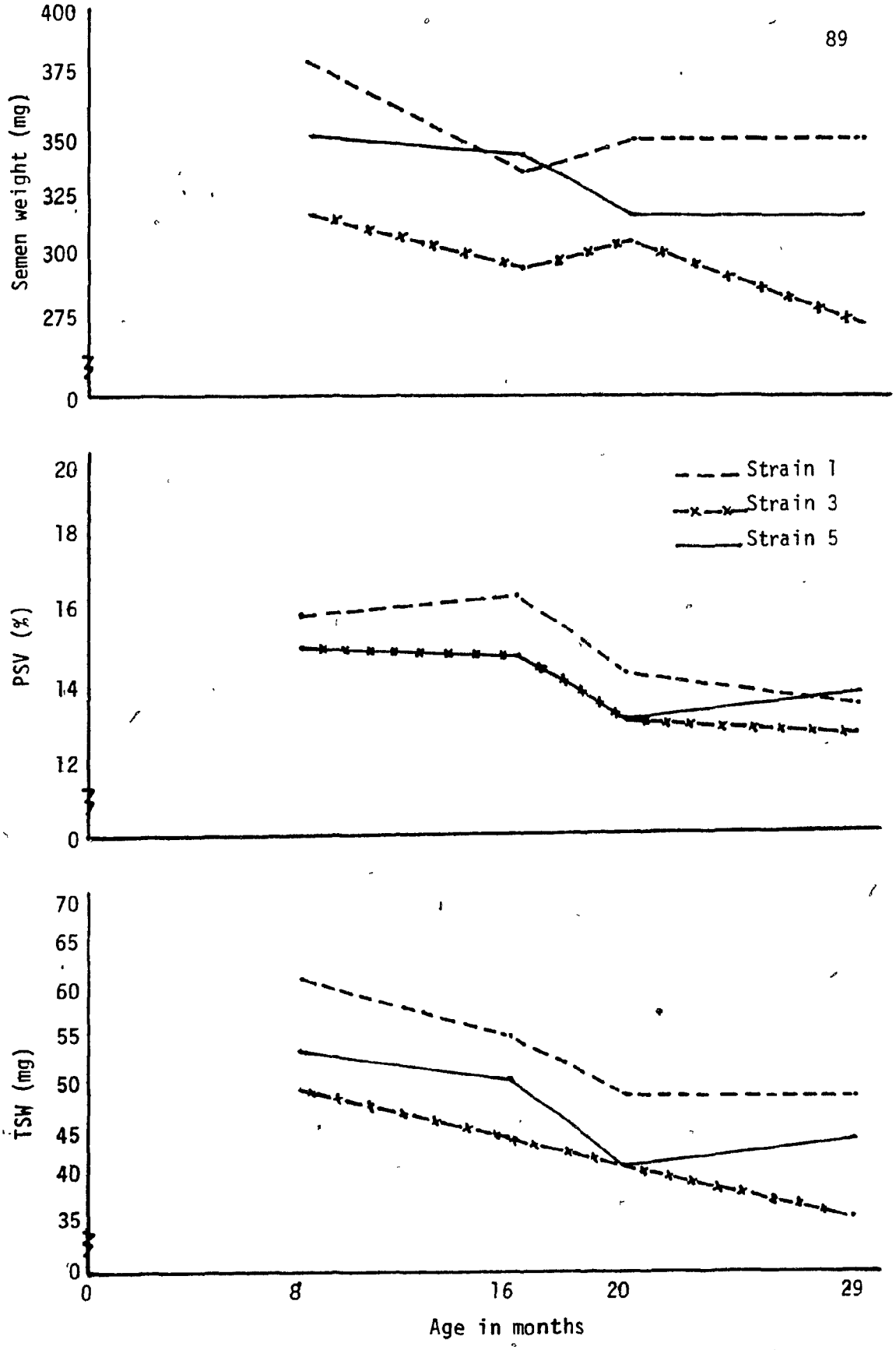


Figure 2. Effect of age on semen weight, packed sperm volume (PSV) and total sperm weight (TSW) of strains 1,3 and 5.

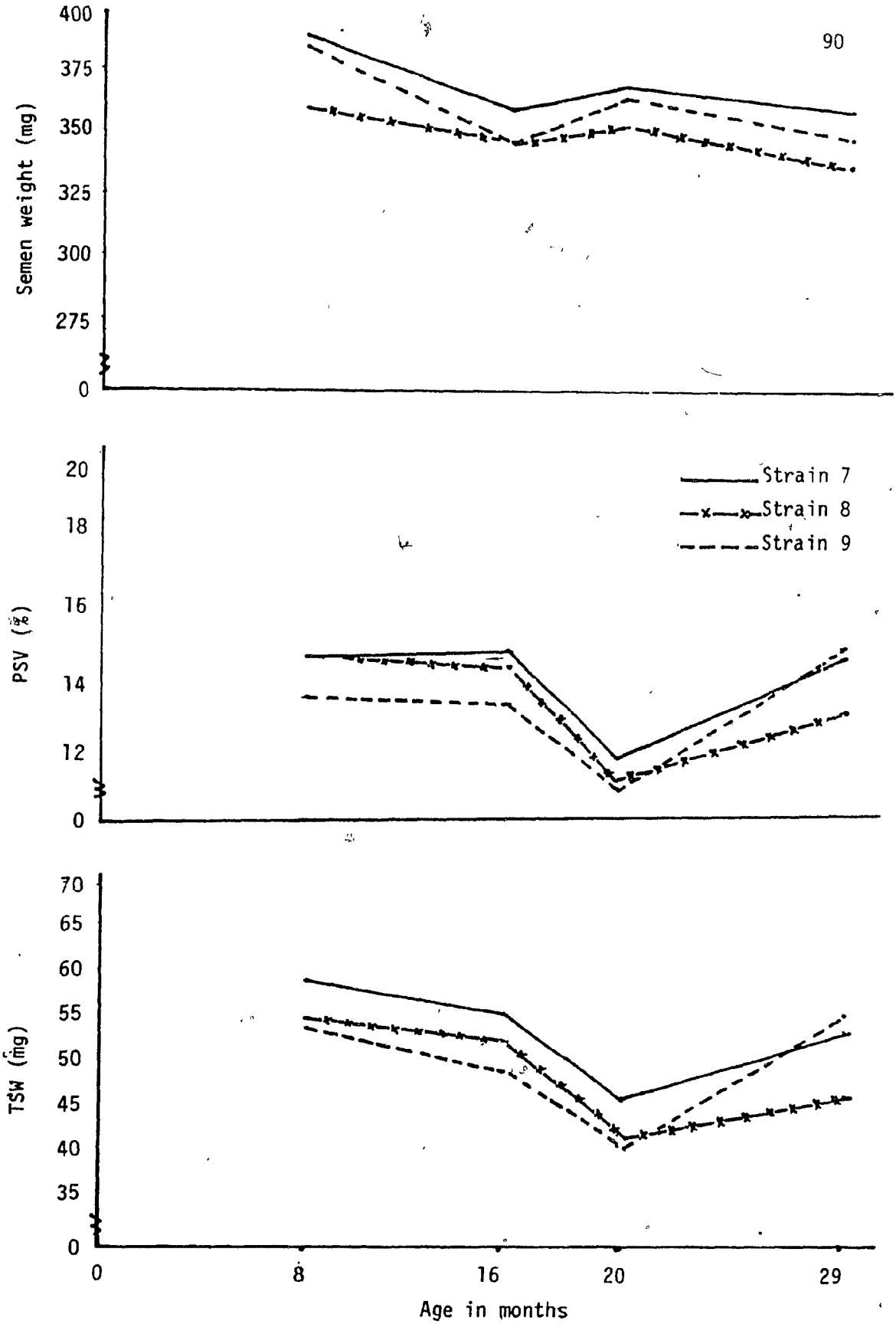


Figure 3. Effect of age on semen weight, packed sperm volume (PSV) and total sperm weight (TSW)of strains 7,8 and 9.

Table 19. Comparison of regression lines of semen weight on age for strains 1, 3 and 5.

	d.f.	Sum of squares of age	Cross-product	Sum of squares of semen weight	Regression coefficient	Deviations from regression d.f.	Deviations from regression Sum of squares	Deviations from regression Mean squares
Within								
Strain 1	94	1.2280	-7.3919	10610.30	-6.0	93	10565.80	113.6108
Strain 3	74	1.2533	-17.1596	7882.97	-13.7	73	7048.03	104.7675
Strain 5	241	1.2126	-13.2798	9419.22	-10.9	240	9273.79	38.6408
						406	27487.62	67.7035
Pooled	409	3.6939	-37.8313	27912.49	-10.2	408	27525.04	67.4633
				Difference of slopes		2	37.42	18.7102
				Comparison of slopes		$F_{2,406}$= 18.7102/67.7035= 0.2764 ns		

Table 20. Comparison of regression lines of packed sperm volume on age for strains 1, 3 and 5.

						Deviations from regression		
	d.f.	Sum of squares of age	Cross-product	Sum of squares of packed sperm volume	Regression coefficient	d.f.	Sum of squares	Mean squares ($\times 10^{-5}$)
Within								
Strain 1	94	1.2280	-0.0120	0.00182	-0.01	93	0.00171	1.8317
Strain 3	74	1.2533	-0.0132	0.00105	-0.01	73	0.00091	1.2479
Strain 5	241	1.2126	-0.0077	0.00168	-0.006	240	0.00163	0.6796
						406	0.00424	1.0448
Pooled	409	3.6939	-0.0329	0.00455	-0.009	408	0.00426	1.0441
				Difference of slopes		2	0.00002	10.0000
				Comparison of slopes	$F_{2,404} = 10.0\times10^{-5}/1.0448\times10^{-5} = 9.57$			ns

Table 21. Comparison of regression lines of total sperm weight on age for strains 1, 3 and 5.

	d.f.	Sum of squares of age	Cross-product	Sum of squares of total sperm weight	Regression coefficient	Deviations from regression d.f.	Deviations from regression Sum of squares	Deviations from regression Mean squares
Within								
Strain 1	94	1.2280	-6.1170	516.566	-5.0	93	486.096	5.2268
Strain 3	74	1.2533	-5.8819	292.502	-4.7	73	264.898	3.6287
Strain 5	241	1.2126	-5.0036	479.430	-4.1	240	458.783	1.9116
						406	1209.777	2.9797
Pooled	409	3.6939	-17.0025	1288.498	-4.6	408	1210.238	2.9663
				Difference of slopes		2	0.461	0.2307
				Comparison of slopes	$F_{2,406}$= 0.2307/2.9797= 0.08		ns	

Table 22. Comparison of regression lines of semen weight on age for strains 7, 8 and 9.

	d.f.	Sum of squares of age	Cross-product	Sum of squares of semen weight	Regression coefficient	Deviations from regression: d.f.	Deviations from regression: Sum of squares	Deviations from regression: Mean squares
Within								
Strain 7	276	1.2433	-17.9895	13586.70	-14.5	275	13326.41	48.4597
Strain 8	109	1.2611	-12.1987	6514.83	- 9.7	108	6396.83	59.2299
Strain 9	87	1.2367	- 4.8495	13116.10	- 3.9	86	13097.08	152.2917
						469	32820.32	69.9794
Pooled	472	3.7411	-35.0377	27912.49	- 9.4	471	32889.48	69.8290
				Difference of slopes		2	69.16	34.5800
				Comparison of slopes	$F_{2,469}$= 34.58/69.94974 = 0.49			ns

Table 23. Comparison of regression lines of packed sperm volume on age for strains 7, 8 and 9.

	d.f.	Sum of squares of age	Cross-product	Sum of squares of packed sperm volume	Regression coefficient	Deviations from regression: d.f.	Deviations from regression: Sum of squares	Deviations from regression: Mean squares ($\times 10^{-5}$)
Within								
Strain 7	276	1.2433	-0.0041	0.00174	-0.003	275	0.00172	0.6264
Strain 8	109	1.2611	-0.0113	0.00090	-0.009	108	0.00080	0.7399
Strain 9	87	1.2367	-0.0016	0.00172	-0.001	86	0.00172	1.9975
						469	0.00424	0.9045
Pooled	472	3.7411	-0.0138	0.00436	-0.004	471	0.00431	0.9141
				Difference of slopes		2	0.00007	6.3000
				Comparison of slopes	$F_{2,469} = 6.3\times10^{-5}/0.9045\times10^{-5} = 6.97$ ns			

Table 24. Comparison of regression lines of total sperm weight on age for strains 7, 8 and 9.

	d.f.	Sum of squares of age	Cross-product	Sum of squares of total sperm weight	Regression coefficient	Deviations from regression		
						d.f.	Sum of squares	Mean squares
Within								
Strain 7	276	1.2433	-4.4069	524.390	-3.5	275	508.770	5.2268
Strain 8	109	1.2611	-5.9294	218.670	-4.7	108	190.791	3.6287
Strain 9	87	1.2367	-0.3210	610.220	-0.3	86	610.137	1.9116
						469	1309.698	2.9797
Pooled	472	3.7411	-10.6573	1353.280	-2.9	471	1322.920	2.9663
				Difference of slopes		2	13.224	6.6112
				Comparison of slopes	$F_{2,469}$= 6.6112/2.7925= 2.37 ns			

indicate that semen weight of strain 1 tended to decline slower than semen weight of males from strain 5 and 3 and semen weight of strains 5 tended to decline slower than semen weight of strain 3. Also, it appeared that the males of strain 9 were less affected by advancing age than strains 8 and 7. The semen weight of strains 7 decreased faster than the semen weight of strain 8, as indicated by the larger coefficient of regression of strain 7.

4.3 Effect of ejaculate sequence on semen traits

In general, ejaculate sequence had a significant ($P<0.05$) effect on semen weight and total sperm weight, but not on packed sperm volume (Appendix Tables 20 to 26). The exceptions were the lack of significant effect of ejaculate sequence on semen weight and total sperm weight of the males of experiment I, hatched in 1980, and semen weight of the males of experiment II (Appendix Tables 21a and 22); also the significant effect of ejaculate sequence on packed sperm volume in experiment II (Appendix Table 22).

In general, semen weight and total sperm weight decreased in consecutive ejaculates (Tables 25 to 28). Number of spermatozoa per ejaculate, measured only in the males of experiment I, was higher in the first than in the second and third ejaculate of the 1979 hatched males (Table 25b). However, no differences were observed in the production of spermatozoa of the males of experiment I hatched in 1980 (Table 26b). Motility score and percent

Table 25a. Least squares mean estimates by ejaculate sequence and range of standard errors of semen traits (transformed and untransformed) measured on 23 month old roosters (Experiment I, 1979 Hatch).

Ejaculate sequence	n[1]	Semen weight ln(mg)	Semen weight mg	Packed sperm volume arcsine$\sqrt{\ }$	Packed sperm volume %	Total sperm weight $\sqrt{\ }$	Total sperm weight mg	Number of spermatozoa/ml (x10^7)
1	89	5.75b	314.8	0.92a	13.7	6.65b	46.2	2.97a
2	94	5.61a	272.9	0.92a	13.2	6.07a	38.8	2.81a
3	95	5.65a	286.6	0.92a	13.0	6.15a	39.8	2.77a
Range of standard errors		0.03 to 0.04		0.004 to 0.005		0.13 to 0.15		0.08 to 0.09

[1] n Denotes the number of observations for each ejaculate.
a,b Column means with no letter in common are different (P<0.05).

Table 25b. Least squares mean estimates by ejaculate sequence and range of standard errors of semen traits (transformed and untransformed) measured on 23 month old roosters (Experiment I; 1979 hatch).

Ejaculate sequence	n[1]	Number of spermatozoa ejaculate √	Number of spermatozoa ejaculate x10⁹	Motility score	Percent motility arcsine	Percent motility %	n[1]	Abnormal spermatozoa √	Abnormal spermatozoa %
1	89	30.8b	0.99	4.15a	0.83a	74.1	85	0.26a	7.7
2	94	28.0a	0.82	4.14a	0.86a	75.7	85	0.26a	7.6
3	95	28.4a	0.85	4.23a	0.89a	77.4	90	0.27a	8.0
Range of standard errors		0.76 to 0.81		0.06 to 0.06	0.01 to 0.01			0.10 to 0.11	

[1] n Denotes the number of observations for each ejaculate.
a,b Column means with no letter in common are different ($P<0.05$).

Table 26a. Least squares mean estimates by ejaculate sequence and range of standard errors of semen traits (transformed and untransformed) measured on 10 month old roosters (Experiment I; 1980 Hatch).

Ejaculate sequence	n[1]	Semen weight		Packed sperm volume		Total sperm weight		Number of spermatozoa/ml (x10⁷)
		ln(mg)	mg	arcsine$\sqrt{\ }$	%	$\sqrt{\ }$	mg	
1	69	5.98a	396.6	0.95a	14.9	7.69a	61.3	3.10a
2	72	5.91a	368.0	0.94a	15.3	7.57a	59.6	3.23a
3	73	5.89a	361.8	0.94a	15.2	7.40a	57.2	3.26a
Range of standard errors		0.04 to 0.04		0.005 to 0.005		0.17 to 0.19		0.09 to 0.10

[1] n Denotes the number of observation for each ejaculate.
a,b Column means with no letter in common are different (P<0.05).

Table 26b. Least squares mean estimates by ejaculate sequence and range of standard errors of semen traits (transformed and untransformed) measured on 10 month old roosters (Experiment I: 1980 hatch).

Ejaculate sequence	n[1]	Number of spermatozoa ejaculate $\sqrt{\ }$	Number of spermatozoa ejaculate x10⁹	Motility score	Percent motility arcsine	Percent motility %	n[1]	Abnormal spermatozoa $\sqrt{\ }$	Abnormal spermatozoa %
1	69	35.2a	1.28	4.15a	0.86a	75.7	69	0.28a	8.6
2	72	34.8a	1.26	4.20a	0.87a	76.5	70	0.27a	8.1
3	73	34.4a	1.23	4.21a	0.89a	77.7	71	0.28a	8.8
Range of standard errors		0.84 to 0.91		0.06 to 0.06	0.01 to 0.01			0.01 to 0.01	

[1] n Denotes the number of observations for each ejaculate.
a,b,c Column means with no letter in common are different (P<0.05).

Table 27. Least squares mean estimates by ejaculate sequence and range of standard errors of semen traits (transformed and untransformed) measured on 18 month old roosters (Experiment II).

Ejaculate sequence	n[1]	Semen weight		Packed sperm volume		Total sperm weight		Motility score	Percent motility	
		ln(mg)	mg	arcsine$\sqrt{\ }$	%	$\sqrt{\ }$	mg		arcsine	%
1	371	5.98a	394.3	0.94b	15.1	7.75b	62.7	4.16a	0.94a	80.9
2	381	5.96a	388.5	0.93a	14.2	7.44a	57.9	4.27b	0.97b	82.5
Range of standard errors		0.02 to 0.02		0.002 to 0.002		0.13 to 0.14		0.03 to 0.03	0.005 to 0.006	

[1] n Denotes the nuber of observations in each ejaculate.
a,b Column means with no letter in common are different (P<0.05).

Table 28. Least squares mean estimates by ejaculate sequence and range of standard errors of semen traits (transformed and untransformed) in experiments III, IV, V and VI.

Ejaculate sequence	n[1]	Semen weight ln(mg)	Semen weight mg	Packed sperm volume arcsine$\sqrt{\ }$ %	Packed sperm volume %	Total sperm weight $\sqrt{\ }$ mg	Total sperm weight mg
				EXPERIMENT III			
1	1492	6.00b	401.7	0.94a	15.5	7.91b	64.9
2	1491	5.88a	358.5	0.94a	15.0	7.33a	56.0
				EXPERIMENT IV			
1	560	5.90b	382.9	0.94a	15.1	7.45b	57.9
2	537	5.84a	356.2	0.94a	15.0	7.12a	53.6
				EXPERIMENT V			
1	292	5.91b	385.2	0.68a	12.7	6.85b	49.7
2	294	5.86a	364.0	0.68a	12.4	6.58a	45.1
				EXPERIMENT VI			
1	275	5.83b	362.9	0.92a	13.7	6.91b	50.1
2	269	5.77a	336.3	0.92a	13.2	6.56a	44.8
Range of standard errors		0.01 to 0.02		0.001 to 0.003		0.04 to 0.10	

[1] n Denotes the nuber of observations in each ejaculate.
a,b Column means with no letter in common are different ($P<0.05$).

motility tended to increase in consecutive ejaculates (Tables 25b, 26b and 27). Ejaculate sequence did not affect the number of spermatozoa/ml, number of spermatozoa per ejaculate and the percentage of abnormal spermatozoa (Tables 25b and 26b).

4.4 Influence of selection for high egg production and other related traits on male traits

Only the comparisons between the means of strains with the same genetic origin (i.e., strains 1 and 3 vs 5; strains 8 and 9 vs 7; and strains 2 and 4) and among the control strains (strains 5, 7 and 10) were considered meaningful.

4.4.1 Influence of selection on semen traits

4.4.1.1 Semen weight, packed sperm volume and total sperm weight

The results of the analyses of variance for the effect of strain on semen traits are also shown in Appendix Tables 20 to 26 by experiment or year of hatch.

The differences between the least squares mean estimates of strains 1, 3 and 5 are shown in Tables 31 to 35. It can be observed that the males of strain 1, in general, had greater semen weight, packed sperm volume and total sperm weight than strains 3 and 5. Furthermore, except for the results of experiment II, control strain 5 tended to produce greater semen weight, packed sperm volume and total sperm weight than selected strain 3.

The results of the differences between the least squares mean estimates of strains 7, 8 and 9 are shown in

Tables 29, 30 and also in Tables 31 to 35. In general, there was no clear indication of a greater semen production of the selected strains 8 and 9 versus the unselected control strain 7 (Tables 30 to 35). The only exception was the results of experiment I which show that the males of control strain 7 hatched in 1979 had lower semen weight, packed sperm volume and total sperm weight than selected strains 8 and 9 (Table 29a). However, as will be explained in the discussion these differences were probably due to the management of the males of strain 7 previous to their use in experiment I. Tables 30 to 34 also show no differences in semen production between males of strains 8 and 9. Strain 9, however, had greater packed sperm volume and total sperm weight than males of strain 8 at 23 and 29 months of age (Tables 29a and 35, respectively). Selected strains 2 and 4 had similar semen production traits (Table 31a).

No differences were found between the semen production traits of the male breeders and nonbreeders of the same strains and generation examined in experiment IV. The mean semen weight, packed sperm volume, and total sperm weight of breeders and nonbreeders, respectively, were 353 and 357 mg; 14.2 and 15.1 %; and 52.0 and 54.7 mg.

With respect to the results of the differences between the means of the control strains, there was a trend for the males of strain 10 to have greater semen weight, packed sperm volume and total sperm weight than males of strains 7 and 5. Also, there was a trend for males of strain 7 to have

Table 29a. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 23 month old roosters (Experiment I; 1979 hatch).

Strain number[1]	n[2]	Semen weight		Packed sperm volume		Total sperm weight		Number of spermatozoa/ ml (x 10^9)
		ln(mg)	mg	arcsine$\sqrt{\ }$	%	$\sqrt{\ }$	mg	
7 C	133	5.49a	242.3	0.89a	10.0	4.91a	26.1	2.31a
8 S	72	5.74b	310.8	0.93b	14.0	6.67b	46.5	3.13b
9 S	73	5.79b	327.3	0.95c	15.9	7.29c	55.1	3.11b
Range of standard errors		0.03 to 0.04		0.04 to 0.05		0.13 to 0.19		0.08 to 0.11

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are different ($P<0.05$).

Table 29b. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 23 month old roosters (Experiment I; 1979 hatch).

Strain number[1]	n[2]	Number of spermatozoa/ ejaculate $\sqrt{\ }$	Number of spermatozoa/ ejaculate $\times 10^9$	Motility score	Percent motility arcsine	Percent motility %	n[2]	Abnormal spermatozoa $\sqrt{\ }$	Abnormal spermatozoa %
7 C	133	23.4a	0.59	4.16a	0.86ab	75.8	119	0.25a	7.2
8 S	72	31.4b	1.03	4.09a	0.83a	73.5	68	0.28a	8.4
9 S	73	32.3b	1.09	4.28a	0.89b	77.9	73	0.27a	7.9
Range of standard errors		0.61 to 0.90		0.05 to 0.07	0.01 to 0.02			0.008 to 0.012	

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are different ($P<0.05$).

Table 30a. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 10 month old roosters (Experiment I: 1980 hatch).

Strain number[1]	n[2]	Semen weight ln(mg)	Semen weight mg	Packed sperm volume arcsine$\sqrt{\ }$	Packed sperm volume %	Total sperm weight $\sqrt{\ }$	Total sperm weight mg	Number of spermatozoa/ ml (x10^9)
7 C	110	5.86a	350.7	0.95a	15.9	7.50a	58.7	3.29a
8 S	53	5.97b	392.3	0.93a	14.5	7.56a	59.7	3.22a
9 S	51	5.95ab	383.4	0.94a	15.0	7.57a	59.7	3.07a
Range of standard errors		0.03 to 0.05		0.004 to 0.007		0.15 to 0.24		0.08 to 0.12

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are different (P<0.05)

Table 30b. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 10 motnh old roosters (Experiment I; 1980 hatch).

Strain number[1]	n[2]	Number of spermatozoa/ ejaculate $\sqrt{\ }$	Number of spermatozoa/ ejaculate x10⁹	Motility score	Percent motility arcsine	Percent motility %	n[2]	Abnormal spermatozoa $\sqrt{\ }$	Abnormal spermatozoa %
7 C	110	34.2a	1.21	4.32b	0.90b	78.6	109	0.29a	9.5
8 S	53	35.9a	1.33	3.99a	0.83a	74.0	52	0.27a	8.0
9 S	51	34.4a	1.23	4.25b	0.88b	77.2	49	0.27a	8.0
Range of standard errors		0.66 to 1.07		0.05 to 0.08	0.12 to 0.19			0.009 to 0.014	

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are different (P<0.05)

Table 31a. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 18 month old roosters (Experiment II).

Strain number[1]		n[2]	Semen weight ln(mg)	Semen weight mg	Packed sperm volume arcsine$\sqrt{}$	Packed sperm volume %	Total sperm weight $\sqrt{}$	Total sperm weight mg
1	S	52	6.00bc	403.4	0.97d	17.7	8.45c	74.5
3	S	52	5.92ab	372.6	0.94bc	15.2	7.55b	59.7
5	C	141	5.85a	348.8	0.93ab	14.0	7.01a	51.8
7	C	148	5.97b	389.7	0.92a	13.7	7.31ab	56.1
8	S	52	6.10c	444.0	0.92a	13.3	7.62b	60.7
9	S	55	5.99bc	399.4	0.93abc	14.1	7.49ab	58.8
2	S	54	5.95ab	382.0	0.94c	15.6	7.72b	62.3
4	S	53	5.91ab	366.9	0.94c	15.5	7.68b	61.7
10	C	141	6.05c	424.6	0.92a	13.2	7.46b	58.3
Range of standard errors			0.02 to 0.04		0.002 to 0.006		0.13 to 0.23	

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are different (P<0.05).

Table 31b. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 18 month old roosters (Experiment II).

Strain number[1]	n[2]	Motility score	Percent motility	
			arcsine	%
1 S	52	4.12ab	0.95a	81.2
3 S	52	4.39c	0.99c	83.7
5 C	141	4.27bc	0.96ab	82.0
7 C	148	4.21b	0.95a	81.3
8 S	52	4.36c	0.98bc	83.3
9 S	55	4.29bc	0.96abc	82.2
2 S	54	4.18ab	0.94a	80.9
4 S	53	4.09ab	0.94a	80.5
10 C	141	4.04a	0.93a	80.2
Range of standard errors		0.03 to 0.06	0.005 to 0.012	

[1] C= unselected control strain; S=selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are significantly different (P<0.05).

Table 32a. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 8 month old roosters (Experiment III).

Strain number[1]		n[2]	Semen weight		Packed sperm volume		Total sperm weight	
			ln(mg)	mg	arcsine$\sqrt{\ }$	%	$\sqrt{\ }$	mg
1	S	544	5.93b	374.3	0.96e	16.7	7.96d	65.6
3	S	503	5.82a	336.9	0.94b	14.9	7.10a	52.7
5	C	253	5.86a	350.7	0.95de	16.3	7.61bc	60.2
7	C	269	5.97bc	391.8	0.94bc	15.4	7.80cd	63.1
8	S	580	6.00c	405.0	0.92a	13.6	7.44b	57.6
9	S	546	5.99c	400.8	0.93a	14.0	7.48b	58.3
10	C	288	5.99c	402.7	0.95cd	15.8	7.98d	65.9
Range of standard errors			0.01 to 0.02		0.001 to 0.003		0.04 to 0.12	

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b, c,d Column means with no letter in common are significantly different (P<0.05).

Table 32b. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 8 month old roosters (Experiment III).

Strain number[1]		n[2]	Motility score	Percent motility	
				arcsine	%
1	S	271	4.15a	0.91a	79.1
3	S	255	4.15a	0.91a	78.9
5	C	128	4.19a	0.93ab	80.1
7	C	131	4.21a	0.92ab	79.6
8	S	288	4.24a	0.94b	80.7
9	S	271	4.25a	0.94b	81.0
10	C	144	4.24a	0.93ab	80.1
Range of standard errors			0.03 to 0.05	0.006 to 0.010	

[1] C=unselected control strain; S=selected strain.
[2] n Denotes the number of observations per strain.
a,b Column means with no letter in common are significantly different (P<0.05).

Table 33. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 16 month old roosters (Experiment IV).

Strain number[1]		n[2]	Semen weight		Packed sperm volume		Total sperm weight	
			ln(mg)	mg	arcsine$\sqrt{\ }$	%	$\sqrt{\ }$	mg
1	S	157	5.88b	375.5	0.96c	17.0	7.88d	64.6
3	S	157	5.73a	318.5	0.93ab	14.6	6.72a	46.9
5	C	128	5.84b	359.4	0.94b	15.2	7.24bc	54.8
7	C	145	5.90b	377.0	0.94b	15.0	7.41c	56.9
8	S	178	5.86b	364.7	0.93a	14.0	7.03b	50.7
9	S	181	5.88b	374.2	0.93a	14.0	7.10bc	53.0
10	C	151	6.00c	417.5	0.94b	15.4	7.86d	63.4
Range of standard errors			0.01 to 0.03		0.002 to 0.003		0.06 to 0.13	

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b, c,d Column means with no letter in common are significantly different ($P<0.05$).

Table 34. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 20 month old roosters (Experiment V).

Strain number[1]		n[2]	Semen weight ln(mg)	Semen weight mg	Packed sperm volume arcsine$\sqrt{\ }$	Packed sperm volume %	Total sperm weight $\sqrt{\ }$	Total sperm weight mg
1	S	74	5.92b	384.8	0.71d	14.7	7.39c	56.8
3	S	73	5.79a	339.1	0.68bc	12.8	6.46ab	43.1
5	C	148	5.73a	319.6	0.68c	13.0	6.30a	42.1
7	C	143	5.93b	394.8	0.67ab	11.8	6.69b	47.7
8	S	77	5.95b	395.7	0.66a	11.3	6.55ab	44.7
9	S	71	5.99b	413.5	0.67ab	11.7	6.87b	50.6
Range of standard errors			0.02 to 0.04		0.003 to 0.007		0.10 to 0.20	

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b, c,d Column means with no letter in common are significantly different (P<0.05).

Table 35. Least squares mean estimates by strain and range of standard errors of semen traits (transformed and untransformed) measured on 29 month old roosters (Experiment VI).

Strain number[1]		n[2]	Semen weight		Packed sperm volume		Total sperm weight	
			ln(mg)	mg	arcsine$\sqrt{\ }$	%	$\sqrt{\ }$	mg
1	S	65	5.88b	382.6	0.92c	13.6	7.06c	52.1
3	S	66	5.67a	303.5	0.91a	12.3	6.02a	37.8
5	C	126	5.70a	314.4	0.92c	13.5	6.39bc	43.1
7	C	140	5.84b	364.2	0.93c	14.4	7.10c	52.4
8	S	73	5.85b	355.8	0.91ab	12.4	6.55b	43.8
9	S	74	5.87b	377.3	0.93c	14.5	7.26c	55.5
Range of standard errors			0.02 to 0.04		0.002 to 0.004		0.09 to 0.18	

[1] C= unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b, c,d Column means with no letter in common are significantly different (P<0.05).

larger semen production than those of strain 5 (Tables 31a, 32a, 33, 34 and 35).

4.4.1.2 Number of spermatozoa/ml and per ejaculate

The numbers of spermatozoa/ml and per ejaculate were assessed only on the semen of the males from experiment I. Strain differences were significant only for the data of the males hatched in 1979 but not for those hatched in 1980 (Tables 29a,b and 30a,b). Males of strain 7 (hatched in 1979) produced lower number of spermatozoa/ml and per ejaculate than males of strains 8 and 9. However, as mentioned earlier the differences were probably due to the management of the males of strain 7 previous to their use in experiment I.

4.4.2 Influence of selection on semen quality

Except for the results of experiment II, in which males of selected strain 3 had higher sperm motility (score and percent) than males of selected strain 1 and control strain 5, no differences in sperm motility or percentage of abnormal spermatoza were observed between the selected and their respective control strains. Also, there were no differences in the quality of the semen of control strains 5, 7 and 10 (Tables 29b, 30b, 31b and 32b).

4.4.3 Influence of selection on wattle, testes and spur measurements

The results of the analyses of variance of wattle weight and/or size are shown in Appendix Tables 27, 28 and 29, by experiment and age of the roosters. Wattle size and

weight were measured on a random sample of males (14 months of age; 1983 hatch) of three control strains and on males of selected and control strains hatched in 1982 (20 and 29 months of age, respectively).

In the 14 month old population, males of strain 7 had similar wattle length, width, index and weight as strain 10. Strain 7, on the other hand, had significantly ($P<0.05$) greater wattle size and weight than strain 5. Strain 10 had longer and heavier but similar wattle width and index to strain 5 (Table 36).

In the 20 month old populations, males of strain 3 had wider ($P<0.05$) wattles and tended to have longer wattles and greater wattle index than strains 1 and 5 (Table 37). Males of strain 8, on the other hand, tended to have longer and wider wattles than strains 7 and 9, and had significantly greater wattle index than strain 9 (Table 37). Males of control strain 7 had longer wattles than control strains 5 and 10, however, only the differences with strain 5 were significant (Table 37).

In the 29 month old populations, males of strain 3 had similar wattle weight as strain 1, but heavier wattles than strain 5 (Table 38). Males of strain 1 had similar wattle weight as strain 5. The weight of wattles of males of strain 7 was similar to those of strains 8 and 9 (Table 38). Males of control strain 7 had heavier wattles than those of control strain 5 (Table 38).

Table 36. Least squares mean estimates by strain and range of standard errors of testes and wattle measurements on 14 month old roosters from three unselected control strains (Experiment VI: 1983 hatch).

Strain number	n[1]	Testes weight (g)	Wattle weight (g)	Wattle length (cm)	Wattle width (cm)	Wattle index (cm^2)
5	41	20.7a	20.2a	7.0a	6.0a	43.08a
7	41	27.4b	27.8b	7.8b	6.8b	54.45b
10	50	25.4b	24.9b	7.5b	6.7ab	48.75ab
Range of standard errors		1.03 to 1.14	1.26 to 1.38	0.16 to 0.18	0.14 to 0.16	2.12 to 2.32

[1] n Denotes the number of observations per strain.
a,b Column means with no letter in common are significantly different ($P<0.05$).

Table 37. Least squares mean estimates by strain and range of standard errors of wattle size measured on 20 month old roosters (Experiment V).

Strain number[1]	n[2]	Wattle length (cm)	Wattle width (cm)	Wattle index (cm^2)
1 S	40	7.3 a	6.4 a	47.7 ab
3 S	38	7.7 ab	6.9 b	53.4 bc
5 C	76	7.4 a	6.3 a	47.1 a
7 C	79	8.3 c	7.2 bc	60.9 de
8 S	39	8.7 c	7.4 c	65.3 e
9 S	38	8.2 bc	7.0 bc	58.3 cd
10 C	90	7.9 b	7.0 b	56.5 cd
Range of standard errors		0.01 to 0.02	0.01 to 0.02	1.6 to 2.5

[1] C=unselected control strain; S=selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are different ($P<0.05$).

Table 38. Least squares mean estimates by strain and range of standard errors of testes and wattle weights measured on 29 month old roosters (Experiment VI; 1982 hatch).

Strain number[1]	n[2]	Testis(g) right	Testis(g) left	Wattle(g) right	Wattle(g) left	Testes (g)	Wattles (g)
1 S	40	11.7b	11.8b	11.1ab	11.3ab	23.5b	22.4ab
3 S	37	9.3a	9.6a	12.9b	13.0b	18.9a	25.9b
5 C	78	10.9b	10.9ab	10.4a	10.6a	21.8b	21.0a
7 C	75	14.5c	14.1c	15.1c	15.5c	28.6c	30.5c
8 S	40	14.2c	14.1c	15.6c	15.7c	28.3c	31.2c
9 S	37	14.8c	14.4c	14.9bc	14.9bc	29.2c	29.8bc
Range of standard errors		0.37-0.53	0.36-0.52	0.53-0.76	0.55-0.78	0.75-1.00	1.07-1.53

[1] C=unselected control strain; S= selected strain.
[2] n Denotes the number of observations per strain.
a,b,c Column means with no letter in common are significantly different (P<0.05).

The results of the analyses of variance of testes weight measured on 14 and 29 month old males are shown in Appendix Tables 27 and 29, respectively. The least squares means of testes weight of the 14 month old males are shown in Tables 36 and 38. The differences in the means of testes weight of strains 5, 7 and 10 were similar to those of wattle weight; i.e., males of strains 7 and 10 had heavier testes than males of strain 5 (Table 36). In the 29 month old populations, however, males of strain 3 which had heavier wattles than strains 1 and 5, had the smallest testes (Table 38). Males of strains 7, 8 and 9 had similar testes weight (Table 38). Males of strain 7 had heavier testes than those of strain 5 (Table 38).

The results of the analyses of variance of spur sizes measured on 20 month old males are shown in Appendix Table 30. Males of strain 1 had longer spurs than strains 3 and 5, but these strains had similar spur diameter and index (Table 39). Strain 7, on the other hand, had longer spurs and greater spur index than strain 8, which had similar spur sizes as strain 9.

Table 39. Least squares mean estimates by strain and range of standard errors of spur size measured on 20 month old roosters (Experiment V).

Strain number[1]		n[2]	Spur length (cm)	Spur diameter (cm)	Spur index (cm^2)
1	S	39	4.1 bc	0.82 a	3.36 ab
3	S	38	3.7 a	0.83 a	3.11 a
5	C	75	3.7 a	0.84 ab	3.16 a
7	C	78	4.5 c	0.90 c	4.03 c
8	S	39	4.0 ab	0.88 bc	3.50 b
9	S	38	4.3 c	0.92 c	3.97 c
Range of standard errors			0.07 to 0.10	0.010 to 0.015	0.08 to 0.12

[1] C=unselected control strain; S=selected strain.
[2] n Denotes the number of observations per strain.
a,b, c Column means with no letter in common are significantly different ($P<0.05$).

4.5 Heritability and repeatability estimates of male traits

Heritability estimates of semen weight, packed sperm volume, total sperm weight, based on the first or the mean of two ejaculates, and body weight of the selected and control strains are shown in Tables 40, 41 and 42. The use of the average of two ejaculates of semen weight and total sperm weight did not increase significantly the heritability of those traits compared to estimates based on a single ejaculate. However, the heritability estimates of packed sperm volume based on the mean of two ejaculates were higher than those based on the first ejaculate alone (Tables 40 and 41).

Heritability estimates based on dam components of variance were higher than those based on sire components of variance; except the heritability for packed sperm volume, based on one semen ejaculate, which was lower than the heritability estimate based on the sire component of variance (Tables 40 and 41). Estimates for the control strains based on full-sib components of variance were higher than those for the selected strains, based on sire plus dam components of variance (Tables 40, 41 and 42).

The proportion of the phenotypic variance due to maternal plus one quarter of the dominance variance was low (<11%) for semen traits and body weight (Tables 40 and 41). The proportion of the total phenotypic variance due to environmental effects plus three quarters of the dominance deviation was high (0.60 to 0.77) for semen traits and

Table 40. Genetic, maternal and environmental proportions of the total phenotypic variance of semen traits measured on 8 month old males from four selected strains (First ejaculate; Experiment III).+

Male trait	Genetic h^2_a	Genetic h^2_d	Genetic h^2_{a+d}	m	e^2
Semen weight	0.18 (±0.10)*	0.52 (±0.18)	0.35 (±0.10)	0.09	0.73
Packed sperm volume	0.29 (±0.10)	0.17 (±0.15)	0.23 (±0.07)	-0.02	0.60
Total sperm weight	0.08 (±0.08)	0.43 (±0.17)	0.26 (±0.06)	0.10	0.77
Body weight	0.51 (±0.13)	0.46 (±0.14)	0.49 (±0.09)	-0.02	0.49

+ Number of strains=4; sires=112; dams= 336. Average number of offspring/dam=2.5; average number of dams/sire=2.7; and average number of offspring/sire=10.1

* Standard errors of the heritabilities, were estimated by Dickerson's approximation (Becker 1975).

m Estimates the proportion of the phenotypic variance due to maternal variance plus 1/4 of the dominance effects.

e^2 Estimates the proportion of the phenotypic variance due to random environmental variance plus 3/4 of the dominance effects.

Table 41. Genetic, maternal and environmental proportions of the total phenotypic variance of semen traits measured on 8 month old males from four selected strains (Mean of two ejaculates;Experiment III).+

Male trait	Genetic			m	e^2
	h^2_a	h^2_d	h^2_{a+d}		
Semen weight	0.18 (±0.10)*	0.54 (±0.16)	0.36 (±0.08)	0.09	0.73
Packed sperm volume	0.38 (±0.12)	0.45 (±0.15)	0.42 (±0.08)	0.02	0.60
Total sperm weight	0.13 (±0.09)	0.51 (±0.16)	0.32 (±0.06)	0.10	0.77
Body weight	0.51 (±0.13)	0.46 (±0.14)	0.49 (±0.09)	-0.02	0.49

+ Number of strains=4; sires=112; dams= 336; average number of progeny/dam=2.5; average number of dams/sire=2.7; and total number of progeny/sire=10.1

* Standard errors of the heritabilities, were estimated by Dickerson's approximation (Becker 1975).

m Estimates the proportion of the phenotypic variance due to maternal variance plus 1/4 of the dominance effects.

e^2 Estimates the proportion of the phenotypic variance due to random environmental variance plus 3/4 of the dominance effects.

moderate for body weight (0.49).

Heritability estimates of testes and wattle weights measured on males from two control strains were calculated by regression of offspring on parent data. Heritability estimates of testes and wattle weights corrected for age effect were slightly lower than those uncorrected (Table 43).

The repeatability estimates of semen weight, packed sperm volume and total sperm weight were high. The repeatability estimates for semen weight, packed sperm volume and total sperm weight, in experiment III, were 0.66, 0.67 and 0.67, respectively, and in experiment IV, the estimates were 0.65, 0.76 and 0.75, respectively.

4.6 Phenotypic correlations among male traits

The coefficients of correlation among semen traits are shown in Tables 44 to 48. The correlations between semen weight and packed sperm volume tended to be positive but mostly not significant and of low magnitude (0.02 to 0.25). The part -to- whole correlations of semen weight and packed sperm volume with total sperm weight were positive and high (0.63 to 0.80). The phenotypic correlations of semen weight, packed sperm volume and total sperm weight with motility score and percent motility were, in general, low and inconsistent in sign (-0.25 to 0.20). Males that produced greater semen weight, packed sperm volume and total sperm weight tended to produce a large number of spermatozoa/ml and per ejaculate (Table 44). Also, semen of males that

Table 42. Heritabilities and standard errors of semen traits, based on one or the mean of two ejaculates, and body weight of 8 month old roosters from three control strains (Experiment III).*

Male trait	First Ejaculate	Mean of two Ejaculates
Semen weight	0.38 ± 0.15	0.42 ± 0.15
Packed sperm volume (%)	0.56 ± 0.15	0.50 ± 0.15
Total sperm weight	0.40 ± 0.15	0.41 ± 0.15
Body weight	0.86 ± 0.13	----------

* Heritabilities were estimated from full-sib components of variance and the standard error according to Becker (1975). Number of strains=3; number of sires= 156; total=312; number of offspring per mating= 2.0.

Table 43. Heritability and standard errors of testes wattle and body weights in two control strains estimated by regression of offspring on parent.*

Male trait	Heritability	
	Age corrected	Uncorrected
Testes weight	0.58±0.11	0.60±0.11
Wattle weight	0.54±0.10	0.62±0.10
Body weight	0.49±0.10	0.46±0.10

* Strains 5 and 7. Age of the parent 29 months. Age of the offspring 14 months. The number of observations was 72.

Table 44. Phenotypic correlations among semen traits (Experiment I).-

Male trait	SW	PSV	TSW	MS	MP	CCB	TNS	ABN
Semen weight (SW)		0.25 **	0.78 **	−0.08	−0.12	0.16 **	0.74 **	0.12
Percentage of packed sperm volume (PSV)	0.04		0.78 **	0.20 **	0.17 **	0.52 **	0.49 **	0.00
Total sperm weight (TSW)	0.68 **	0.74 **		0.05	−0.03	0.41 **	0.79 **	0.06
Motility score (MS)	−0.15 *	−0.02	−0.13		0.83 **	0.30 **	0.15 *	0.01
Percent motility (MP)	−0.18 *	0.01	−0.13	0.83 **		0.28 **	0.06	0.01
No. sperm/ ml (CCB)	0.11	0.39 **	0.34 **	0.07	0.03		0.75 **	−0.04
Total number sperm/ejac (TNS)	0.74 **	0.29 **	0.70 **	−0.06	−0.10	0.73 **		0.03
Percentage of abnormal sperm (ABN)	0.08	0.17 *	0.18 *	−0.09	−0.03	0.10	0.10	

- Above the diagonal, the partial correlation coefficients of the males hatched in 1979. Below the diagonal, the partial correlation coefficients of the males hatched in 1980. The number of pairs of observations for the 1979 and 1980 populations were 287 and 214 respectively; except for the ABN where there were 263 and 210 observations respectively.

* $P<0.05$ ** $P<0.01$

Table 45. Phenotypic correlations among semen traits and between semen traits and body weight, (Experiment II).*

Male trait	PSV	TSW	MS	MP	BW
Semen weight (SW)	0.07	0.73**	0.01	0.03	0.16**
Percentage of packed sperm volume (PSV)		0.70**	-0.25**	-0.21**	-0.04
Total sperm weight (TSW)			-0.16**	-0.15**	0.09*
Motility score (MS)				0.91**	-0.04
Percent motility (MP)					-0.03

* The number of pairs of observations was 752.
* P<0.05 ** P<0.01

Table 46. Phenotypic correlations among male traits of selected and control strains (Experiment III).+

Male trait	SW	PSV	TSW	BW
Semen weight (SW)		0.09*	0.72**	0.10*
Percentage of packed sperm volume (PSV)	0.02		0.64**	0.01
Total sperm weight (TSW)	0.76**	0.63**		0.05
Body weight (BW)	0.19**	0.00	0.03	

+ Above the diagonal, the partial correlation coefficients of the selected strains. Below the diagonal the partial correlation coefficients of the control strains. The number of pairs of observations for the selected and control strains were 2173 and 810, respectively.

Table 47. Phenotypic correlations among male traits (Experiments IV and V).+

Male trait	Semen weight	Packed sperm volume	Total sperm weight	Body weight
Semen weight		0.07*	0.74**	0.07*
Packed sperm volume	0.13**		0.72**	-0.08*
Total sperm weight	0.71**	0.77**		0.00
Body weight	0.23**	0.07	0.19**	

+ Above the diagonal partial correlation coeficients for experiment IV. Below the diagonal partial correlation coefficients for experiment V. The number of pairs of observations in experiments IV and V was 1097 and 596, respectively.

* P<0.05 ** P<0.01

Table 48. Phenotypic correlations among male traits (Experiment VI).+

Male trait	Packed sperm volume	Total sperm weight	Body weight
Semen weight	0.07	0.80**	0.16**
Packed sperm volume	—	0.63**	0.00
Total sperm weight			0.12**

+ The number of pairs of observations was 526.
* P<0.05 ** P<0.01

Table 49. Phenotypic correlations among semen traits and between body weight and wattle size (Experiment V).+

Male trait	Semen weight	Packed sperm volume	Total sperm weight	Body weight
Wattle length	0.11**	0.08	0.11**	0.27**
Wattle width	0.11**	0.06	0.10*	0.26**
Wattle index	0.10*	0.07	0.10*	0.28**

+ The number of pairs of observations was 582.
* P<0.05 ** P<0.01

produced large number of spermatozoa/ml tended to have better sperm motility. In Tables 44 and 45 it can be observed that semen samples with good motility score had high percentage of motile spermatozoa. Packed sperm volume and total sperm weight were positively correlated with the percentage of abnormal spermatozoa of the 10 month old males but not of the 23 month old males (Table 44).

Body weight appeared to be positively correlated with semen weight (0.07 to 0.23) and total sperm weight (0.00 to 0.19), but unrelated with packed sperm volume (-0.08 to 0.07). Males with a heavy body weight tended to have poor motility score and percent motility (Tables 44 and 45).

The phenotypic correlations of wattle size with semen traits, testes weight and body weight are shown in Tables 49 and 50. Those of wattle size with spur size are shown in Table 51. The correlations of wattle size with semen weight, packed sperm volume and total sperm weight were positive although of low magnitude (0.06 to 0.11); those with body weight, however, were of moderate magnitude (0.20 to 0.28). The correlations of wattle measurements with testes weight were positive but of low magnitude (0.13 to 0.19). The correlations between wattle size and spur length were close to zero but those between wattle size and spur diameter were slightly moderate (0.20 to 0.24). The phenotypic correlations of testes weight and body weight were low but those of wattle weight and size were high (Table 50).

Table 50. Phenotypic correlations among wattle measurements and of wattle measurements with testes and body weights (Experiment VI).+

Male trait	Testes weight	Wattle weight	Wattle length	Wattle width	Wattle index	Body weight
Testes weight		0.19*	0.13	0.13	0.14	0.08
Wattle weight	0.04		0.91**	0.88**	0.94**	0.20**
Wattle length				0.87**	0.96**	0.24**
Wattle width					0.96**	0.24**
Body weight	0.17**	0.17**				

+ Above the diagonal correlations of traits for the males hatched in 1983 (n=132); strains 5,7 and 10. Below the diagonal correlations for the males hatched in 1982 (n=307); strains 1,3,5,7, 8 and 9.

* P<0.05 ** P<0.01

Table 51. Phenotypic correlations among wattle and spur sizes (Experiment V).+

Male trait	Wattle width	Wattle index	Spur length	Spur diameter	Spur index
Wattle length	0.87**	0.97**	-0.04	0.21**	0.14*
Wattle width		0.96**	0.01	0.24**	0.19**
Wattle index			-0.02	0.23**	0.11
Spur length				0.20**	0.66**
Spur diameter					0.87**

+ The number of pairs of observations was 400 and 307 for wattle and spur traits, respectively.
* P<0.05 ** P<0.01

4.7 Genetic correlations among male traits

The estimates of genetic correlations (mean of two semen ejaculates) for the selected and control strains are presented in Table 52. In the selected strains, the estimates of genetic correlations, based on sire components of variance and covariance, between semen weight and packed sperm volume and of body weight with semen weight, packed sperm volume and total sperm weight were negative (-0.33 to -0.67). The part-to-whole correlations of total sperm weight with semen weight and packed sperm volume were positive (0.37 and 0.74, respectively). Estimates, from sire plus dam components of variance and covariance of total sperm weight with semen weight and packed sperm volume were also positive (0.80 and 0.72, respectively). Body weight was negatively correlated with packed sperm volume and total sperm weight (-0.24 and -0.16, respectively). The genetic correlations between semen weight and packed sperm volume and between semenweight and body weight were close to zero(0.01 and 0.01).

In the control strains, the genetic correlation estimates were consistent with those of the selected strains, based on sire plus dam components of variance and covariance. Genetic correlations between semen weight and packed sperm volume and of body weight with packed sperm volume and total sperm weight were of low magnitude (-0.25 to 0.13). Semen weight and packed sperm volume were positively correlated with total sperm weight (0.71 and 0.77, respectively).

Table 52. Estimates of genetic correlations among semen traits and between semen traits and body weight of selected and control strains(Experiment III)

Male trait	Type of strain: Selected* Sire	Selected* Dam	Selected* Sire+Dam	Control** Full-sib
Semen weight- Packed sperm volume	-0.38	0.23	0.01	0.09
Semen weight- Total sperm weight	0.37	0.80	0.69	0.71
Semen weight- Body weight	-0.37	0.26	0.01	0.13
Packed sperm volume- Total sperm weight	0.74	0.72	0.70	0.77
Packed sperm volume - Body weight	-0.33	-0.15	-0.24	-0.25
Total sperm weight - Body weight	-0.67	0.11	-0.16	-0.09

* In the selected strains, the genetic correlation were estimated by a hierarchal analysis, using sire, dam within sire and sire plus dam components of variance and covariance. The number of strains, sires and dams were 4, 112 and 336, respectively; the average number of offspring/dam was 2.5.

** In the control strains, the genetic correlations were estimated by a single mating design, using full- sib componenets of variance and covariance. The number of strains, mating pairs and average number of offspring/ mating were 3, 156 and 2.0, respectively.

4.8 Estimates of genetic correlations between male and female traits

4.8.1 Genetic correlations between semen traits and egg production and other related traits

The means of the coefficients of relationship between parent- offspring and between full- sibs, estimated to calculate the genetic correlations by regression method were 0.72 for the control strains and 0.76 for the selected strains. The sampling variances of the estimates of genetic correlations are unknown but presumed high.

The estimates of genetic correlations of semen weight, packed sperm volume and total sperm weight measured on 8 month old males with age at first egg, egg production up to 273 and 497 days of age and egg quality traits assessed at 240 and 450 days are shown in Tables 53, 54 and 55, by semen trait.

Semen production traits tended to be favorably correlated with egg weight as indicated by the magnitude of the genetic correlations (0.02 to 0.36) . The exceptions were the correlations between packed sperm volume of control strain males and egg weight of their full- sisters, assessed at 240 days and 450 days (-0.19 and 0.0, respectively). Semen production traits were, in general, unfavorably correlated with age at first egg (0.03 to 0.40), hen- housed egg production (-0.60 to 0.04), survivors egg production (-0.08 to -0.52) and hen-day rate of egg production (-0.36 to 0.14). Egg mass production up to 273 days of age was unfavorably correlated with semen weight, packed sperm

volume and total sperm weight (-0.34, -0.05 and -0.34, respectively).

Semen weight was unfavorably correlated with specific gravity, Haugh units, and the incidence of blood spots; however, most of the correlation coefficients were of low magnitude (Tables 53). The genetic correlations of packed sperm volume with specific gravity, Haugh units and the incidence of blood spots were in the undesirable direction (Table 54). The negative correlation of semen weight and packed sperm volume with shell shape indicates that selection for those semen traits may decrease the ratio of egg length to egg width (Tables 53 and 54). The genetic correlations of total sperm weight with the egg quality traits were of low magnitude (-0.22 to 0.15); except the genetic correlation between total sperm weight and incidence of blood spots, from the half-sib analysis, which were moderate (Table 55).

The estimates of genetic correlations of semen production traits measured on 16 month old males with egg production and other related traits are shown in Tables 56, 57 and 58, by semen trait. In the selected strains, semen weight, packed sperm volume and total sperm weight were generally unfavorably correlated with age at first egg and egg production. However, in the control strains, the genetic correlations estimated by full- sib analysis were inconsistent with those estimated by dam- son analysis.

Similar to the correlations of semen traits and egg

Table 53. Estimates of genetic correlations by Full-sib, Half-sib and Dam-son analysis between semen weight of 8 month old roosters and egg production and other related traits in selected and control strains (Experiment III).

Female traits	Type of strain: Selected — Half-sib[a]	Control — Full-sib[b]	Control — Dam-son[b]
Age at first egg	0.27	0.29	0.26
Hen-housed egg production			
to 273 days	-0.30	-0.22	-0.12
to 497 days	-0.29	-0.01	-0.10
Survivor egg production			
to 273 days	-0.44	-0.12	-0.12
to 497 days	-0.39	-0.20	-0.10
Hen-day rate of egg production			
to 273 days	-0.10	-0.16	0.14
to 497 days	-0.25	0.07	-0.02
Egg weight			
at 240 days	0.19	0.20	0.20
at 450 days	0.20	0.30	0.28
Specific gravity			
at 240 days	-0.19	0.07	-0.25
at 450 days	0.01	-0.04	-0.10
Haugh units			
at 240 days	-0.09	-0.16	-0.14
at 450 days	-0.18	-0.33	-0.16
Shell shape			
at 240 days	-0.18	0.20	0.06
at 450 days	-0.04	-0.07	-0.05
Blood spots			
at 240 days	0.45	0.08	0.20
at 450 days	0.41	0.14	0.40

Number of pairs of observations: a=450; b=419

Table 54. Estimates of genetic correlations by Full-sib, Half-sibs and Dam-son analysis between packed sperm volume of 8 month old roosters and egg production and other related traits in selected and control strains (Experiment III).

Female traits	Type of strain		
	Selected	Control	
	Half-sib[a]	Full-sib[b]	Dam-son[b]
Age at first egg	0.26	0.03	0.33
Hen-housed egg production			
to 273 days	-0.42	0.04	-0.29
to 497 days	-0.18	-0.12	-0.38
Survivor egg production			
to 273 days	-0.18	-0.08	-0.29
to 497 days	-0.09	-0.13	-0.38
Hen-day rate of egg production			
to 273 days	-0.01	-0.01	-0.01
to 497 days	-0.03	-0.12	-0.36
Egg weight			
at 240 days	0.26	-0.19	0.10
at 450 days	0.07	0.00	0.09
Specific gravity			
at 240 days	-0.07	0.06	0.08
at 450 days	0.11	0.23	0.25
Haugh units			
at 240 days	0.07	0.12	-0.06
at 450 days	0.23	0.15	-0.25
Shell shape			
at 240 days	-0.10	-0.03	-0.11
at 450 days	-0.07	0.04	-0.01
Blood spots			
at 240 days	0.20	-0.24	-0.23
at 450 days	-0.09	-0.08	-0.16

Number of pairs of observations: a=450; b=419

Table 55. Estimates of genetic correlations by Full-sib, Half-sib and Dam-son analysis between total sperm weight of 8 month old roosters and egg production and other related traits in selected and control strains (Experiment III).

Female traits	Type of strain		
	Selected	Control	
	Half-sib[a]	Full-sib[b]	Dam-son[b]
Age at first egg	0.40	0.22	0.35
Hen-housed egg production			
to 273 days	-0.60	-0.11	-0.26
to 497 days	-0.43	-0.11	-0.27
Survivor egg production			
to 273 days	-0.52	-0.13	-0.26
to 497 days	-0.47	-0.21	-0.27
Hen-day rate of egg production			
to 273 days	-0.17	-0.13	0.06
to 497 days	-0.32	-0.07	-0.24
Egg weight			
at 240 days	0.36	0.02	0.11
at 450 days	0.24	0.18	0.12
Specific gravity			
at 240 days	-0.16	0.06	-0.18
at 450 days	0.04	0.11	0.11
Haugh units			
at 240 days	0.00	0.00	-0.06
at 450 days	0.09	-0.16	-0.18
Shell shape			
at 240 days	-0.22	0.15	-0.01
at 450 days	-0.14	-0.04	0.00
Blood spots			
at 240 days	0.56	-0.08	-0.04
at 450 days	0.25	0.01	0.06

Number of pairs of observations: a=450; b=419

Table 56. Estimates of genetic correlations by Full-sib and Dam-son analysis between semen weight of 16 month old roosters and egg production and other related traits in selected and control strains (Experiment IV).

Female traits	Type of strain: Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	0.10	0.22	-0.06	0.18
Hen-housed egg production				
to 273 days	-0.13	-0.33	0.00	-0.10
to 497 days	-0.11	-0.32	0.24	-0.04
Survivor egg production				
to 273 days	-0.09	-0.33	0.14	-0.10
to 497 days	-0.06	-0.32	0.26	-0.04
Hen-day rate of egg production				
to 273 days	-0.24	-0.24	0.20	0.23
to 497 days	-0.11	-0.13	0.36	0.08
Egg weight				
at 240 days	0.16	0.24	0.28	0.01
at 450 days	0.14	0.22	0.23	0.06
Specific gravity				
at 240 days	-0.04	-0.04	0.13	-0.21
at 450 days	0.01	0.19	0.14	-0.30
Haugh units				
at 240 days	-0.24	-0.03	-0.06	-0.07
at 450 days	-0.05	-0.13	0.11	-0.13
Shell shape				
at 240 days	0.03	-0.02	0.09	0.36
at 450 days	-0.01	-0.10	0.01	0.12
Blood spots				
at 240 days	-0.31	-0.20	0.23	0.16
at 450 days	0.11	-0.29	0.17	0.32

Number of pairs of observations: a=330; b=210

Table 57. Estimates of genetic correlations by Full-sib and Dam-son analysis between packed sperm volume of 16 month old roosters and egg production and other related traits in selected and control strains (Experiment IV).

Female traits	Type of strain: Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	0.03	0.35	-0.36	0.29
Hen-housed egg production				
to 273 days	-0.12	-0.38	0.24	-0.43
to 497 days	0.03	-0.29	0.07	-0.30
Survivor egg production				
to 273 days	-0.03	-0.38	0.04	-0.43
to 497 days	0.04	-0.29	0.21	-0.30
Hen-day rate of egg production				
to 273 days	-0.17	-0.08	0.02	-0.19
to 497 days	0.01	-0.10	0.13	-0.23
Egg weight				
at 240 days	-0.09	-0.12	-0.24	-0.34
at 450 days	-0.07	-0.13	0.11	-0.19
Specific gravity				
at 240 days	-0.11	0.22	0.23	0.05
at 450 days	0.15	0.04	0.15	0.03
Haugh units				
at 240 days	-0.03	-0.06	0.36	0.13
at 450 days	-0.14	-0.12	0.20	0.05
Shell shape				
at 240 days	0.17	0.06	-0.06	-0.19
at 450 days	-0.09	0.11	-0.24	-0.18
Blood spots				
at 240 days	-0.25	0.12	0.07	-0.47
at 450 days	-0.08	-0.12	0.05	-0.38

Number of pairs of observations: a=330; b=210

Table 58. Estimates of genetic correlations by Full-sib and Dam-son analysis between total sperm weight of 16 month old roosters and egg production and other related traits in selected and control strains (Experiment IV).

Female traits	Type of strain: Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	0.04	0.39	-0.37	0.40
Hen-housed egg production				
to 273 days	-0.18	-0.48	0.18	-0.33
to 497 days	-0.08	-0.33	0.16	-0.25
Survivor egg production				
to 273 days	-0.09	-0.48	0.08	-0.33
to 497 days	0.03	-0.33	0.29	-0.25
Hen-day rate of egg production				
to 273 days	-0.34	-0.19	0.11	0.05
to 497 days	-0.12	-0.16	0.25	-0.13
Egg weight				
at 240 days	0.07	0.04	0.02	-0.23
at 450 days	0.07	0.04	0.27	-0.08
Specific gravity				
at 240 days	-0.13	0.20	0.23	-0.06
at 450 days	0.11	0.17	0.11	-0.13
Haugh units				
at 240 days	-0.18	-0.08	0.33	0.14
at 450 days	-0.11	-0.21	0.24	-0.01
Shell shape				
at 240 days	0.16	-0.12	-0.06	0.03
at 450 days	-0.07	-0.12	-0.19	-0.09
Blood spots				
at 240 days	-0.44	-0.08	0.21	-0.36
at 450 days	-0.03	-0.27	0.14	-0.04

Number of pairs of observations: a=330; b=210

production, there were also some discrepancies in the magnitude and sign of the genetic correlations of egg weight with semen traits. The genetic correlations between egg weight and semen weight were generally favorable (0.01 to 0.28). Those between egg weight and packed sperm volume were mostly unfavorable (-0.34 to 0.11) and those between egg weight and total sperm weight were mostly positive, except the correlations of the control strains, based on dam-son analysis which were negative (Table 58). The estimates of genetic correlations of semen production traits with egg quality traits were in general inconsistent and of low magnitude.

4.8.2 Genetic correlations of testes and wattle weights with egg production and other related traits

4.8.2.1 Testes weight and egg production and other related traits

The genetic correlations between testes weight measured on 14 month old males and egg production and other related traits are shown in Table 59. The genetic correlations between testes weight and egg production to 273 days of age were mostly negative (-0.33 to 0.29). The genetic correlations estimated by full-sib analysis between testes weight and egg production to 497 days were inconsistent with those estimated by dam-son analysis. Low and inconsistent estimates were observed for the correlations of testes weight with age at first egg, egg weight and egg quality traits (Table 59).

The correlations of testes weight of the 29 month old

Table 59. Estimates of genetic correlations by Full-sib and Dam-son analysis between testes weight of 14 and 29 month old roosters and egg production and other related traits in control and selected strains (Experiment VI).

Female traits	Type of strain (Age in months)					
	Control (14)		Selected (29)		Control (29)	
	Full-sib[a]	Dam-son[b]	Full-sib[a]	Dam-son[b]	Full-sib[a]	Dam-son[b]
Age at first egg	0.02	-0.01	0.0	-0.17	0.29	0.32
Hen-housed egg production						
to 273 days	-0.06	-0.08	0.04	0.20	-0.17	-0.52
to 497 days	0.29	-0.12	0.39	0.47	0.06	-0.44
Survivor egg production						
to 273 days	-0.06	-0.08	0.01	0.20	-0.44	-0.52
to 497 days	0.29	-0.12	0.28	0.47	0.07	-0.44
Hen-day rate of egg production						
to 273 days	0.04	-0.33	0.08	0.11	-0.09	-0.39
to 497 days	0.29	-0.23	0.35	0.48	0.11	-0.41
Egg weight						
at 240 days	0.06	0.06	-0.11	0.05	0.25	0.26
at 450 days	-0.09	-0.29	-0.07	-0.27	0.35	0.50
Specific gravity						
at 240 days	-0.13	0.08	0.30	0.21	0.00	-0.28
at 450 days	-0.08	0.08	0.30	0.06	0.06	-0.21
Haugh units						
at 240 days	-0.27	-0.21	0.22	-0.01	0.10	0.28
at 450 days	-0.26	0.04	0.18	0.15	0.16	0.18
Shell shape						
at 240 days	0.08	0.13	0.36	0.05	-0.13	0.11
at 450 days	-0.16	0.11	0.04	0.00	-0.29	0.27
Blood spots						
at 240 days	-0.06	0.26	0.27	0.38	-0.30	0.13
at 450 days	0.00	-0.02	0.09	-0.02	0.24	0.03

Number of pairs of observations: a=265; b=132; c=154; d=150

males with egg production and other related traits are also shown in Table 59. In general the estimates obtained in the selected strains were inconsistent in sign and size with those of the control strains. In the selected strains for example, the correlations of testes weight with hen-housed egg production, survivor egg production and hen-day rate of egg production were positive but they were mostly negative for the control strains.

4.8.2.2 Wattle size and egg production and other related traits

The estimates of genetic correlations of wattle weight and index (product of wattle length and width) measured on 14 month old males of three control strains with egg production and other related traits are presented in Table 60. Wattle weight and index appear to be favorably correlated with age at first egg (-0.17 to -0.43) hen-housed egg production (0.26 to 0.55), survivor egg production (0.26 to 0.55), and hen-day rate of egg production (0.05 to 0.44).

Wattle weight and index were unfavorably correlated with egg weight (-0.16 to -0.48). The estimates of genetic correlations of wattle weight and index with specific gravity, Haugh units, shell shape and blood spots were generally inconsistent and of low magnitude. The results of the correlations of wattle length and width with egg production traits were similar to those obtained for wattle weight and index and are shown in Table 61.

Wattle length, width and index measured on 20 month

Table 60. Estimates of genetic correlations by Full-sib and Dam-son analysis between wattle weight and index (product of length and width) of 14 month old roosters and egg production and other related traits in three control strains (Experiment VI).

Female traits	Wattle weight		Wattle index	
	Full-sib[a]	Dam-son[b]	Full-sib[a]	Dam-son[b]
Age at first egg	-0.17	-0.36	-0.27	-0.43
Hen-housed egg production				
to 273 days	0.26	0.35	0.35	0.35
to 497 days	0.26	0.51	0.28	0.55
Survivor egg production				
to 273 days	0.26	0.35	0.35	0.35
to 497 days	0.26	0.51	0.28	0.55
Hen-day rate of egg production				
to 273 days	0.17	0.10	0.17	0.05
to 497 days	0.26	0.44	0.27	0.39
Egg weight				
at 240 days	-0.16	-0.23	-0.22	-0.23
at 450 days	-0.18	-0.43	-0.20	-0.48
Specific gravity				
at 240 days	0.20	0.03	0.11	0.00
at 450 days	0.12	-0.25	0.07	-0.18
Haugh units				
at 240 days	-0.03	0.37	-0.03	-0.32
at 450 days	0.05	0.17	0.10	0.23
Shell shape				
at 240 days	-0.05	-0.08	-0.13	-0.08
at 450 days	0.01	0.20	0.00	0.19
Blood spots				
at 240 days	0.29	-0.24	0.29	-0.06
at 450 days	0.38	0.07	0.50	0.25

Number of pairs of observations: a=265; b=132

Table 61. Estimates of genetic correlations by Full-sib and Dam- son analysis between wattle length and width of 14 month old roosters and egg production and other related traits in three control strains (Experient VI).

Female traits	Wattle length		Wattle width	
	Full-sib[a]	Dam-son[b]	Full-sib[a]	Dam-son[b]
Age at first egg	-0.34	-0.39	-0.17	-0.43
Hen-housed egg production				
to 273 days	0.43	0.29	0.26	0.32
to 497 days	0.31	0.46	0.27	0.53
Survivor egg production				
to 273 days	0.43	0.29	0.26	0.32
to 497 days	0.31	0.46	0.27	0.53
Hen-day rate of egg production				
to 273 days	0.13	0.01	0.20	-0.04
to 497 days	0.27	0.35	0.29	0.40
Egg weight				
at 240 days	-0.20	-0.20	-0.25	-0.23
at 450 days	-0.22	-0.45	-0.18	-0.48
Specific gravity				
at 240 days	0.17	0.08	0.11	-0.08
at 450 days	0.13	-0.17	0.04	-0.16
Haugh units				
at 240 days	-0.08	0.37	0.06	0.35
at 450 days	-0.09	0.31	0.20	0.22
Shell shape				
at 240 days	-0.15	-0.03	-0.08	-0.10
at 450 days	0.00	0.18	-0.03	0.20
Blood spots				
at 240 days	0.35	-0.06	0.29	0.03
at 450 days	0.53	0.25	0.46	0.27

Number of pairs of observations: a= 265; b=132

old males and wattle weight measured on 29 month old males appeared to be uncorrelated with hen-housed egg production, survivor egg production and hen-day rate of egg production. This statement is based on the inconsistency between the estimates of genetic correlations calculated by full-sib and dam-son analysis and also in the low magnitude of the estimates (Tables 62, 63, 64 and 65). Similarly, the correlations of wattle size with egg weight and egg quality traits were in general inconsistent and of low magnitude.

4.8.2.3 Spur size and egg production and other related traits

It was not possible to estimate genetic correlations between spur measurements and egg production traits from dam-son and full-sib analysis because heritability estimates for spur length, spur diameter or spur index (product of length and diameter) were neither estimated in this study nor were they available in the literature. The "phenotypic" correlations of spur measurements of males with egg production to 273 days and other related traits of their dam and full-sisters are shown in Tables 66, 67 and 68 by spur measurement. In general, the correlation estimates of full-sibs, of both the selected and control strains, were inconsistent with the dam-son correlation estimates. However, the correlations of spur sizes measured on the males of the control strains with shell shape were significant and positive.

Table 62. Estimates of genetic correlations by Full- sib and Dam-son analysis between wattle length of 20 month old roosters and egg production and other related traits in selected and control strains (Experiment V)

Female traits	Type of strain			
	Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	-0.37	0.06	0.18	0.27
Hen-housed egg production				
to 273 days	0.26	-0.17	-0.27	-0.07
to 497 days	0.00	-0.12	-0.18	-0.05
Survivor egg production				
to 273 days	0.31	-0.17	-0.22	-0.07
to 497 days	0.16	-0.12	-0.04	-0.05
Hen-day rate of egg production				
to 273 days	-0.14	-0.14	-0.28	0.12
to 497 days	-0.13	-0.16	-0.09	0.05
Egg weight				
at 240 days	0.02	-0.02	0.01	0.12
at 450 days	0.01	0.08	-0.06	0.14
Specific gravity				
at 240 days	0.00	-0.20	0.02	0.02
at 450 days	0.29	0.20	-0.31	-0.14
Haugh units				
at 240 days	0.02	-0.14	0.08	0.11
at 450 days	-0.06	-0.15	0.14	0.02
Shell shape				
at 240 days	-0.11	-0.01	0.13	-0.04
at 450 days	-0.05	0.05	0.05	-0.05
Blood spots				
at 240 days	0.12	-0.09	0.29	-0.31
at 450 days	0.44	-0.09	0.27	-0.06

Number of pairs of observations: a=152; b=233

Table 63. Estimates of genetic correlations by Full- sib and Dam- son analysis between wattle width of 20 month old roosters and egg production and other related traits in selected and control strains (Experiment V).

Female traits	Type of strain			
	Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	-0.37	-0.02	0.12	0.22
Hen-housed egg production				
to 273 days	0.16	0.08	-0.16	-0.04
to 497 days	-0.10	-0.25	-0.06	-0.01
Survivor egg production				
to 273 days	0.23	0.08	-0.15	-0.04
to 497 days	0.08	-0.25	0.06	-0.01
Hen-day rate of egg production				
to 273 days	-0.26	0.08	-0.16	0.13
to 497 days	-0.33	-0.34	0.01	0.07
Egg weight				
at 240 days	0.13	-0.08	-0.04	0.13
at 450 days	0.14	0.13	-0.03	0.17
Specific gravity				
at 240 days	-0.13	-0.15	-0.11	-0.07
at 450 days	0.17	0.29	-0.29	-0.27
Haugh units				
at 240 days	-0.02	-0.35	0.15	0.15
at 450 days	-0.20	-0.33	0.16	0.11
Shell shape				
at 240 days	0.01	0.07	0.04	-0.08
at 450 days	-0.04	-0.08	0.02	-0.13
Blood spots				
at 240 days	0.08	0.08	0.29	-0.35
at 450 days	0.36	-0.05	0.17	-0.11

Number of pairs of observations: a=152; b=233

Table 64. Estimates of genetic correlations by Full-sib and Dam-son analysis between wattle index (product of length and width) of 20 month old roosters and egg production and other related traits in selected and control strains (Experiment V).

Female traits	Type of strain			
	Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	-0.38	0.00	0.15	0.25
Hen-housed egg production				
to 273 days	0.22	-0.05	-0.22	-0.06
to 497 days	-0.05	-0.19	-0.13	-0.04
Survivor egg production				
to 273 days	0.29	-0.05	-0.19	-0.06
to 497 days	0.10	-0.19	0.01	-0.04
Hen-day rate of egg production				
to 273 days	-0.20	-0.04	-0.23	0.12
to 497 days	-0.23	-0.26	-0.05	0.06
Egg weight				
at 240 days	0.08	-0.05	-0.01	0.12
at 450 days	0.08	0.11	-0.04	0.15
Specific gravity				
at 240 days	-0.06	-0.16	-0.04	-0.02
at 450 days	0.22	0.22	-0.25	-0.19
Haugh units				
at 240 days	0.00	-0.21	0.11	0.12
at 450 days	-0.12	-0.22	0.14	0.06
Shell shape				
at 240 days	-0.06	0.04	0.08	-0.06
at 450 days	-0.05	-0.01	0.04	-0.09
Blood spots				
at 240 days	0.10	0.01	0.25	-0.29
at 450 days	0.42	-0.07	0.21	0.08

Number of pairs of observations: a=152; b=233

Table 65. Estimates of genetic correlations by Full-sib and Dam-son analysis between wattle weight of 29 month old roosters and egg production and other related traits in selected and control strains (Experiment VI).

Female traits	Type of strain			
	Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	-0.28	0.17	0.13	0.12
Hen-housed egg production				
to 273 days	0.08	-0.18	-0.24	0.12
to 497 days	-0.11	-0.16	0.00	-0.27
Survivor egg production				
to 273 days	0.18	-0.18	-0.12	0.12
to 497 days	0.02	-0.16	0.13	-0.27
Hen-day rate of egg production				
to 273 days	-0.23	0.05	-0.44	0.22
to 497 days	-0.32	-0.20	0.18	-0.25
Egg weight				
at 240 days	-0.07	-0.01	0.14	-0.04
at 450 days	0.04	0.17	0.18	0.00
Specific gravity				
at 240 days	-0.18	-0.25	0.01	-0.10
at 450 days	0.14	0.10	-0.21	-0.25
Haugh units				
at 240 days	-0.13	-0.06	0.08	0.10
at 450 days	-0.12	-0.06	0.00	-0.12
Shell shape				
at 240 days	-0.22	0.06	-0.08	0.03
at 450 days	-0.16	-0.22	-0.18	0.00
Blood spots				
at 240 days	-0.13	-0.20	0.10	-0.16
at 450 days	0.05	0.04	0.11	-0.32

Number of pairs of observations: a=154; b=150

Table 66. Correlations between spur length of 20 month old roosters and egg production to 273 days and other related traits of their sisters (Full- sib) and dams (Dam-son) in selected and control strains (Experiment V).

Female traits	Type of strain			
	Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	-0.16	0.11	-0.01	0.01
Hen-housed egg production to 273 days	0.15	-0.02	0.06	-0.02
Survivor egg production to 273 days	0.14	-0.02	0.08	-0.02
Hen-day rate of egg production to 273 days	0.02	0.09	0.06	-0.05
Egg weight at 240 days	-0.04	-0.12	-0.02	-0.04
Specific gravity at 240 days	-0.11	-0.10	-0.03	0.12
Haugh units at 240 days	-0.10	0.01	-0.08	-0.01
Shell shape at 240 days	0.06	-0.02	0.24**	0.22**
Blood spots at 240 days	0.01	-0.06	-0.06	-0.15

Number of pairs of observations: a=152; b=233
** P<0.01

Table 67. Correlations between spur diameter of 20 month old roosters and egg production to 273 days and other related traits of their sisters (Full-sib) and dams (Dam-son) in selected and control strains (Experiment V).

Female traits	Type of strain			
	Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	-0.03	0.06	0.08	0.07
Hen-housed egg production to 273 days	-0.02	-0.07	-0.11	-0.11
Survivor egg production to 273 days	0.03	-0.07	-0.09	-0.11
Hen-day rate of egg production to 273 days	0.00	-0.05	-0.09	-0.11
Egg weight at 240 days	0.10	-0.05	0.08	0.09
Specific gravity at 240 days	-0.11	-0.10	0.10	0.10
Haugh units at 240 days	0.04	0.09	-0.08	0.03
Shell shape at 240 days	0.02	0.07	0.17	0.08
Blood spots at 240 days	0.04	-0.03	-0.02	0.08

Number of pairs of observations: a=152; b=233

Table 68. Correlations between spur index (product of length and width) of 20 month old roosters and egg production to 273 days and other related traits of their sisters (Full- sib) and dams (Dam- son) in selected and control strains (Experiment V).

Female traits	Type of strain			
	Selected		Control	
	Full-sib[a]	Dam-son[a]	Full-sib[b]	Dam-son[b]
Age at first egg	-0.13	0.11	-0.03	0.04
Hen-housed egg production to 273 days	0.09	-0.06	-0.02	-0.07
Survivor egg production to 273 days	0.12	-0.07	0.03	-0.07
Hen-day rate of egg production to 273 days	0.00	0.03	0.01	-0.10
Egg weight at 240 days	0.04	-0.10	0.03	0.01
Specific gravity at 240 days	-0.15	-0.08	0.02	0.14
Haugh units at 240 days	-0.04	0.03	-0.11	0.01
Shell shape at 240 days	0.06	0.01	0.28**	0.20*
Blood spots at 240 days	0.03	-0.07	-0.06	-0.14

Number of pairs of observations: a=152; b=233
** P<0.01

V DISCUSSION

5.1 Frequency of lymphoid leukosis virus infection and its effect on semen traits and fertility

5.1.1 Consistency in the results of tests for LLV and group specific viral antigen and frequency of LLV infection

The close agreement between the results of tests for LLV in semen and the group specific viral antigen in feather pulp was expected. Spencer et al. (1979; 1983) reported a close agreement between the results of these two tests in the albumen of eggs or feather pulps of birds of the same strains used in this study.

Males shedding the LLV in semen or the group specific viral antigen in feather pulps were less frequent in the strains selected for high egg production and other related traits than in the unselected control strains. Similar findings have been reported by Spencer et al. (1979; 1980) and Gavora et al. (1980) for females and males of the same strains used in this study. Spencer et al. (1979) and Gavora et al. (1980) attributed the lower frequency of LLV-shedding birds in the selected strains to a correlated effect of selection for high egg production. LLV infection affects egg production as well as other economic traits (Gavora et al. 1980; Gavora and Spencer 1985); thus LLV-shedding hens tended to be eliminated during the process of selection for high egg production. The identification and elimination of LLV-shedding males has practical importance because, although sires do not contribute to vertical

(congenital) transmission of LLV disease, they may lead to horizontal (bird to bird) transmission of the virus which frequently results in persistent low level infection that is difficult to detect (Spencer 1984). Furthermore, the culling of the LLV-shedding males may improve the fertility of the flock and reduce the number of abnormal spermatozoa in old males (Tables 15b and 18).

5.1.2 Effect of LLV infection on semen traits and male fertility

The absence of a significant strain by LLV status interaction suggests that the effect of LLV on semen and fertility was similar in all strains tested. The positive effect of LLV infection on semen production, observed in this study, was unexpected. Lymphoid leukosis virus infected roosters and hens develop infections in their reproductive tracts that persist over a prolonged period of time (Spencer et al. 1980). Therefore, the reproductive processes of males and females could be affected through a wide range of endocrine functions. LLV infection has been shown to decrease egg production and egg quality in hens (Gavora et al. 1980, 1982; Payne et al. 1982; Romero et al. 1983; and Fairfull et al. 1984). Therefore, from the results of this study, it could be speculated that the unfavorable effect of LLV on egg production could be through a stress produced on the synthesis and/or release of gonadotropins (FSH and LH) that affect the peak of LH necessary for ovulation. However, sperm production, being a continuous process, may not be

affected by the presence of LLV. It is, therefore, possible that LLV may affect the reproductive processes of males and females in a different direction.

Fertility of eggs from hens mated to males shedding the LLV tended to be lower (0.2 and 3.6% lower) than the fertility of eggs from hens mated to non- shedder males (Table 18). Reduction in egg fertility and hatchability of hens shedding the LLV has been reported by Gavora et al. (1980) and Romero et al. (1983).

5.2 Effect of age on semen traits

Semen weight, packed sperm volume and total sperm weight tended to decrease with advancing age (Figures 2 and 3). This is also indicated by the negative regression coefficients of semen traits on age (Tables 19 to 24). The causes of reduction in sperm production with advancing age in the domestic fowl may be similar to those reported in other species. These causes are 1) the thickening of the basement membrane of seminiferous tubules (fibrosis); 2) decline in the Leydig cell population; and 3) reduction in gonadotropins and steroids production (Johnson et al. 1984; Meites 1984; Ottinger et al. 1985). Leydig cells are the site of steroid production in the testes and a reduction in the number of these cells will reduce the production of testosterone. LH is required for steroid production in the testis and testosterone and FSH are indispensable for the initiation of spermatogenesis and the completion of maturation of spermatids to mature spermatozoa, respectively

(Steinberger 1976; DiZeraga and Sherins 1981). On the other hand, fibrosis of the testes will reduce the supply of blood to it and this will affect sperm production.

A reduction in semen and sperm production with advancing age has been reported in the domestic fowl by Wheeler and Andrews (1943); Clark and Sarakoon (1967); Marini and Goodman (1969); Ansah et al. (1980; 1984b); de Reviers and Williams (1981); Van Wambeke et al. (1981). Bakst and Cecil (1984) observed a decline in the testicular sperm number and deferentis sperm number in mature turkeys (32 to 52 weeks of age) and reported a negative relationship of above traits with age (-0.32 and -0.46, respectively).

The absence of significant strain by age interaction suggests that the effect of age on semen and spermatozoa production was similar in all strains tested. Non-significant age by strain interaction was reported by Ansah et al. (1984b) in two lines of meat-type chickens; one selected for fertility of frozen-thawed semen and an unselected control strain.

5.3 Effect of ejaculate sequence on semen traits

The decrease in total sperm weight with ejaculate sequence was due to a reduction in ejaculate volume. This is indicated by the smaller semen weight means of the second ejaculate compared with the first ejaculate, and the fact that ejaculation in two consecutive days did not affect packed sperm volume per ejaculate. It is well established

that increased frequency of semen collection reduces semen volume first and concentration of spermatozoa second (Lorenz et al. 1955; McCartney et al. 1958; McDaniel and Sexton 1977; Bakst and Cecil 1981; Ansah et al. 1984a);

Motility score and percent motility assessed in this study tended to increase with ejaculate sequence. These results agree with those in the literature indicating that frequent semen collections improve the quality of the ejaculated spermatozoa (Swierstra and Strain 1964; de Riviers 1975; de Riviers and Williams 1981; Ansah et al. 1984a)

5.4 Influence of selection for high egg production and other related traits on male traits

5.4.1 Correlated responses in semen production and sperm quality

Selection for high egg production and a complex of economic traits has been successful in increasing egg number of the strains used in this study (Gowe and Fairfull 1980). However, selection for high egg production did not change semen production. The overall results of this study are well illustrated by Figures 2 and 3. These figures show that males of strain 7 tended to have greater semen weight, packed sperm volume and total sperm weight than males of selected strains 8 and 9. Also, males of unselected control strain 5 tended to have greater semen production than strain 3.

The only significant indication of a correlated response in semen production from selection for high egg production came from the semen data of the males of

experiment I hatched in 1979. In this experiment, the males of strain 7 (but not the males of strains 8 and 9) were used in force feeding trials to determine the total metabolize energy of feeds (Sibbald and Morse 1983) the week before the experimental data collection. A brief description of the feeding trial procedure follows: the males of strain 7 (1979 hatch) were starved in two consecutive days; the third day some of the birds were fed a small amount of feed and all birds were starved again the fourth day. On the next day the birds were moved to another building and given one week adaptation period to their new cages and environment, before semen collection and evaluation. It is possible then, that this feeding regime may have had an effect on the semen production of the males of strain 7.

The results of this study tended to agree with findings of Frankham and Doornenbal (1972) who reported no differences in semen volume of two strains of Single Comb White Leghorns (SCWL) selected for high egg production and the corresponding unselected control strain. The results of this study also tended to agree with the findings of Marks (1981a) who after successful selection for packed sperm volume found no correlated response in egg mass, except in the first generation of selection. In turkeys, Nestor (1976) observed that selection for large semen volume caused a correlated response in egg production during the fist generation of selection but no further improvement in egg production was observed after this. Nestor (1976) indicated

that the improvement in egg production was due to a reduction in broodiness of the hens. Nestor (1977), also in turkeys, observed that selection for high egg production increased semen yield in the first generation of selection and this difference was mantained after six generations of selection.

The results of this study and those cited above failed to support the hypothesis of Jones and Lamoreux (1942) that semen and egg production are examples of comparable genotypes in the domestic fowl.

Sperm quality and egg production may not be correlated with each other. This is indicated by the lack of correlated response of motility and the incidence of abnormal spermatozoa to the selection for high egg production and other related traits in the strains used in this study.

5.4.2 Correlated responses on wattle, testes and spur measurements

Selection for high egg production and other related traits tended to increase wattle index and weight. This is particularly evident in the strains selected for hen- housed egg production, most of which had significantly larger and heavier wattles than their respective control strains. It is possible then that wattle size and egg production are favorably correlated.

The differences in wattle size between the strains selected for hen- housed egg production and those selected

for hen- day rate of egg production suggest that selection for those two egg production traits is affecting two different physiological mechanisms. In the strains selected for hen- housed egg production, most of the improvement in egg production was due to a reduction in the age at first egg, whereas the improvement in egg production for the strains selected for hen- day rate of egg production was basically an increase in the rate of ovulation (Appendix Table 31).

The absence of significant differences in testes weight between the control strain 7 and selected strains 8 and 9, and the smaller testes of the males of selected strain 3 versus those of control strain 5, indicate that testes and egg production may not be correlated. This finding agrees with the results of Jones and Lamoreux (1942) who reported no differences in testes weights of 12, 24 and 30 week old males from two SCWH strains selected for high and low female fertility which differed in egg production. The results of this study appear to contradict those of similar investigations in mammals, where selection for ovulation rate or litter size in females produced changes in testis weight of the males in the same direction as those in the female trait and vice versa (Land and Falconer 1969; Eisen and Johnson 1981; Islam et al. 1976; Joakimsen and Baker 1977; Proud et al. 1976; Schinckel et al. 1983). However, ovulation rate in mammals and avians may be under different types of genetic and physiological control.

Ovulation rate in multiparous mammals is a simultaneous process (a number of ova are shed at one time) whereas ovulation rate in avians is a sequential process (ova are usually shed one at a time).

The similar spur sizes of the selected and control strains found in this study indicate that no correlated responses to selection for high egg production occurred in spur size of the males. However, there appear to be some differences in the size of spurs of males from strains selected for hen- housed egg production and those selected for hen- day rate of egg production, although Fairfull and Gowe (1985) have recently reported that there were no differences in the spur length of hens of the same strains used in this study.

5.5 Heritability estimates of male traits

5.5.1 Heritability of semen traits

It appears that with the semen collection and evaluation technique used in this study, it was not necessary to collect more than one semen ejaculate for semen trait assessment. Except for the heritabilities of packed sperm volume based on dam and sire plus dam components of variance (Tables 40 and 41) there were no major differences in the heritability estimates of semen weight, packed sperm volume and total sperm weight based on one or the mean of two ejaculates. One reason for taking repeated measurements of a trait is to reduce the environmental variance and to

obtain better estimates of heritability (Falconer 1981). However, for traits with high repeatability, the gain in accuracy is expected to be very small (Becker 1975). The repeatability estimates of semen weight calculated in this study were high (0.65 and 0.66). They were within the range of repeatability estimates (0.42 to 0.95) for semen volume measured on alternate days, twice or three times a week (Williams and McGibbon 1956; Siegel and Beane 1960; Soller et al. 1965a,b; Pingel and Schubert 1983). The repeatabilities of packed sperm volume calculated in this study (0.66 and 0.75) were similar to those reported for packed sperm volume collected twice a week (Pingel and Schubert 1983).

In this study, the heritability estimates for semen weight calculated from the sire components of variance were similar to the estimates of semen volume calculated by Siegel (1963) and Kurbatov et al. (1974), but lower than the heritabilities estimated by Kopylovskaya and Chalov (1973), Soller et al. (1965a), Pingel and Schubert (1983) and Ansah et al. (1984b). The heritability estimates for packed sperm volume (0.29 and 0.38) were within the range of heritability estimates calculated by Marks (1981b) and Pingel and Schubert (1983) using selection and intraclass correlation methods, respectively. The heritability estimates for total sperm weight (0.08 and 0.13) were lower than the estimates of heritability for sperm concentration reported by Soller et al. (1965a), Chalov (1972), Kopylovskaya and Chalov (1973),

Borsting (1980) and Ansah et al. (1984b). The heritabilities for body weight of the males of the selected strains was similar to those reported by Kinney (1969).

The low heritability estimates, based on sire components of variance, for semen weight and total sperm weight suggest that these traits are influenced mainly by nonadditive genetic and environmental factors. Also, the low heritability estimates of above semen traits may exclude them as prospective traits to be used in selection for improved egg production.

The heritability estimates of semen weight, packed sperm volume and total sperm weight based on dam components of variance, except that of packed sperm volume based on the first ejaculate, were higher than those based on sire components of variance. This suggests that maternal and nonadditive genetic effects may be important for those semen traits. However, in this study, the estimates of the proportion of the total variance due to maternal effects plus 1/4 of the dominance effects were small ($m < 11\%$). Therefore, maternal and dominance effects may explain only partially the discrepancy between heritability estimates based on sire or dam components of variance. There were, to the author's knowledge, no reports available in the literature on the proportion of the total phenotypic variance due to maternal effects. However, the inconsistency in the heritability estimates, based on sire and dam components of variance, for packed sperm volume, observed by

Pingel and Schubert (1983) indicates that maternal effects may not be important for semen traits.

Another factor that could lead to discrepancies between sire and dam components of variance and to under- or over-estimates of heritability is parental relationship, i.e. relationship between parents (Fujishima and Tredeen 1972). Heritability estimates are normally estimated under the assumption that parents are unrelated. In this study, however, selected strains 1, 3, 8 and 9 have been reproduced since their origin using 28 sires and 224 dams each generation, therefore, after 14 to 30 generations of selection for high egg production the assumption of no parental relationship may not be valid. Parental relationship may have also led to low estimates of the maternal and dominance proportions here calculated.

The larger estimates of heritability for packed sperm volume and body weight of the control strains versus those of the selected strains (Tables 40, 41 and 42) could have been caused by differences in the degree of inbreeding and LLV infection in those strains. The average coefficients of inbreeding, calculated from pedigree records by Gowe and Fairfull (1980) were low. They ranged from 8.0 to 20.6% (mean= 14.5%) for the selected and from 0.8 to 7.7% (mean=4.0%) for the control strains. Corrections for the effect of inbreeding, using Falconer's (1981) formula, however, did not increase the heritability estimates of the control strains and only increased the magnitude of the

heritabilities for the selected strains by about 4%. Also the heritability of semen weight and total sperm weight of the selected strains (sire plus dam components) was similar to those of the control strains. Therefore, inbreeding was not the main cause of the differences in the heritability estimates. Differences in the heritability estimates of selected and control strains may also be due to lymphoid leukosis infection. Effect of LLV infection on mean performance and variation of female traits have been reported by Gavora et al. (1983). In this study, the frequency of LLV- shedding males was higher in the control (18.1 to 35.9%) than in the selected strains (1.9 to 14.8%). However, the extent of the effect of LLV infection on the heritability of semen traits estimated here could not be assessed. Thus, the differences between the heritabilities of semen traits of the control and selected strains could be due to LLV infection, as well as to differences in population size and structure of the control and selected strains.

5.5.2 Heritability of wattle and testes weights

The large heritability estimates of wattle (0.54) and testes (0.58) weights calculated in this study indicate that these traits are influenced mainly by additive genes. A large heritability estimate is desirable when surveying secondary traits for a potential use to improve egg production in chickens.

The heritability for wattle weight (0.54) estimated in this study is within the range of heritability estimates reported in the literature. Ayoub and Merat (1975), using intraclass correlation methods, reported heritabilities for wattle length of 10 week old males of 0.31 and 0.64. Ayoub et al. (1979) reported the heritability of wattle length of 22-week pullets as 0.25. The heritability for testes weight (0.58) estimated in this study was lower than the estimates (0.81 and 0.87, respectively) calculated in 1 and 11 day old chicks by Jaap et al. (1961).

Difference in the heritabilities of wattle and testes weights estimated here and those reported in the literature, are probably due to age differences, methods of estimation and size and structure of the populations used.

5.6 Correlations among male traits

The extent and direction of correlated selection responses are determined by genetic correlations between the pertinent traits. Genetic correlations among semen traits and between semen traits and body weight, for the control

and selected strains (sire plus dam components) were consistent in sign (Table 52). However, from the selection point of view, the genetic correlations based on sire components are most important. These genetic correlations are discussed in this section together with phenotypic correlations.

The phenotypic correlations of semen weight with packed sperm volume and body weight were positive but of low magnitude (0.04 to 0.25). This positive association, however, was due to non-additive genetic and/or environmental effects because estimates of genetic correlations (based on sire components) of semen weight with packed sperm volume and body weight were negative (-0.38 and -0.37, respectively). The negative genetic correlations of body weight with semen weight and packed sperm volume, although undesirable for broiler breeders, is a desirable relationship for the egg production breeder because, selection for semen production is expected to decrease body weight. However, if selection to improve semen production is applied it should be based in both semen weight and packed sperm volume because these traits appear to be unfavorably correlated with each other (-0.38).

Selection for semen weight and packed sperm volume may also improve the motility of spermatozoa in the domestic fowl. This is indicated by the positive genetic association of semen weight and packed sperm volume with percent motility reported in the literature (Table 4). The

correlations (phenotypic and genetic) of semen weight and packed sperm volume with total sperm weight are part- to-whole correlations; therefore these semen traits were expected to be highly correlated.

The phenotypic correlations of semen weight, packed sperm volume and total sperm weight with motility score and percent motility obtained in this study were generally negative (-0.25 to 0.20) whereas the correlations of semen volume and sperm concentration with sperm motility reported in the literature are all positive (0.09 to 0.85). These results could be attributed to population size, type of strains and species differences. For example, Jones and Lamoreux (1942) indicated a positive correlation between sperm concentration and the percentage of motile spermatozoa in White Leghorn chickens. The strains of chickens they used, however, were selected for high and low fertility; whereas the strains used in this study were unselected control strains and strains selected for high egg production and other related traits. All other estimates reported in the literature (Table 3) were calculated in broilers and turkeys.

The phenotypic correlations of semen weight, packed sperm volume and total sperm weight with the percentage of abnormal spermatozoa of the 1979 birds of experiment I were of low magnitude (-0.12 to 0.18). This agrees with the low phenotypic correlations of semen volume and sperm concentration with the percentage of abnormal spermatozoa

reported by Marini and Goodman (1969) and Saeid and Al-Soudi (1975).

Wattle size was positively but low correlated with semen weight, total sperm weight and packed sperm volume (0.06 to 0.11). The correlation between wattle weight and semen weight obtained in this study was similar to that reported between wattle index (product of wattle length by width) and semen volume by Burrows and Titus (1939). In this study, wattle size was also positively correlated with body weight, spur size and testes weight, which indicates that these traits are under similar environmental and physiological control. A positive phenotypic and genetic correlation between wattle length and body weight at sexual maturity has been reported in pullets by Ayoub et al. (1979).

Males with large wattles had heavy wattles. This is indicated by the highly significant and positive phenotypic correlations of wattle weight with wattle length, width and index (0.88 to 0.96).

5.7 Estimates of genetic correlations between male and female traits

In general, the genetic correlations between male traits and female reproductive traits for the partial and the whole year of egg production (273 and 497 days of age, respectively) were consistent in sign. Therefore, the discussion involving egg production and egg quality traits will refer to both periods of egg production unless

indicated, otherwise.

5.7.1 Genetic correlations between semen traits and egg production and other related traits

5.7.1.1 Methods of estimation

The genetic correlations between semen production and egg production estimated in the selected strains of experiment III, using one way analysis of variance, based on family means as the observational unit were consistent in sign with the estimates of genetic correlations calculated by regression methods. Also, estimates by the regression method using full- sib or dam- son analysis were consistent in sign. Differences in the magnitude of the genetic correlations estimated by the various methods may be due to the large standard errors associated with this type of estimates and to differences in population size.

No corrections for parental relationship were necessary for the genetic correlations estimated by intraclass correlation method because the coefficients of relationship cancelled each other in this type of analysis (Becker 1975). The genetic correlations estimated by regression methods (dam-son and full-sib analysis) were estimated using the coefficients of relationship of 0.72 and 0.76 obtained for the control and selected strains used in this study. The use of a coefficient of relationship of 0.5 for parent- offspring or full- sibs analysis could have lead

to over- estimates of the genetic correlations. The genetic correlations estimated in this study may be over-estimated if sex linked effects were important.

5.7.1.2 Genetic correlations between semen traits and egg production

The genetic correlations between semen and egg production for the control and selected strains were in agreement independently of the type of analysis. Differences in the magnitude of the estimates of genetic correlations may be due to differences in the population size and structure, differences in gene frequency of the control and selected strains and large standard errors.

The genetic correlations of semen traits with age at first egg and egg production were unfavorable; i.e. the greater the semen produced, the later the age the pullets will start laying and less eggs will be produced. These findings were very surprising because, as mentioned earlier, LH and FSH control ovulation and semen production in chickens (Sturkie 1976) and these hormones are under similar genetic control (Land 1973). One possible explanation for this result could be that the complement of autosomal genes controlling a quantitative trait (e.g., semen or egg production) may be expressed differently depending on whether the genes are expressed in the male or female environment. The internal physiological and external

environment of roosters and hens may differ considerably (e.g. the type and quantity of hormone present, light regime etc.). Sharp (1975) has reported that males have higher levels of LH than females; therefore, a sex by genotype interaction is possible.

Another possible explanation could be that although many of the structural genes involved in female reproduction (e.g. the genes for FSH, LH, progesterone, testosterone and estrogens synthesis) are present also in males, these genes represent only a small fraction of the hundreds of genes that control egg and semen production. Regulatory genes may play a role in the synthesis of these hormones, and their frequency may be different in males and females. For example, the synthesis of steroid hormones in males and females has the same biosynthetic pathway (Figure 4). Both males and females produce progesterone, testosterone and estrogens. However, the genes controlling the production of testosterone are more active in males than in females. Similarly, higher levels of progesterone and estrogens are found in female blood plasma than in males. Therefore, a negative or zero correlation between semen and egg production could be expected.

The unfavorable relationship between semen and egg production obtained in this study is further supported by the following findings:

1) lack of correlated response in semen production to selection for high egg production in the strains studied.

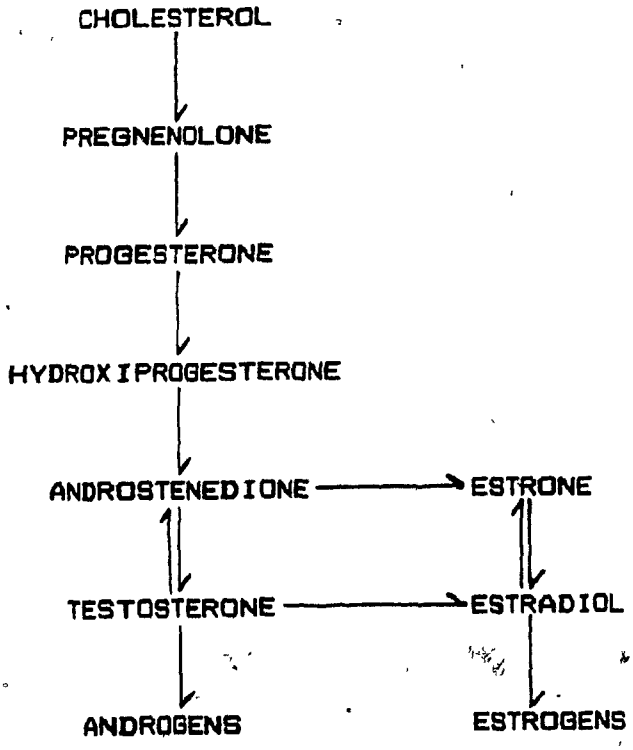


Figure 4. Biosynthesis of gonadal steroids from cholesterol (Nalbandov 1976).

2) LLV did not affect semen production of roosters, although it has been shown to reduce egg production of LLV-shedder hens (Gavora et al. 1980).

The results of this study on the relationship of semen and egg production traits tended to agree with findings in the literature supporting a zero correlation between these traits (Pingel and Schubert 1983; Mymrin 1972; Stenova et al. 1983). Thus, in general, it can be stated that semen and sperm production are not good indicators of the potential of females for high egg production.

5.7.1.3 Genetic correlations of semen traits with egg weight and egg quality traits

Female relatives of males which produced large semen weight and had greater total sperm weight at 8 months of age, tended to produce larger eggs. This is indicated by the positive genetic correlations of semen weight and total sperm weight with egg weight (0.02 to 0.36); and by the consistency of the sign of the genetic correlations calculated by intraclass and regression methods. Therefore, selection for semen weight or total sperm weight may increase egg size in chickens. However, selection for semen weight or total sperm weight in turkeys may not increase egg size. This is supported by experimental results of Nestor (1976), who observed that selection for semen yield resulted in an increase in average egg weight in the first generation but no further improvement throughout the sixth generation of selection. Also, Kopylovskaya et al. (1980) have

indicated that semen yield of toms and egg weight of their sibs were uncorrelated.

The genetic correlations between packed sperm volume and egg weight tended to be positive (0.00 to 0.26), however the correlations, for the control strains, between packed sperm volume and egg weight assessed at 240 days were negative (Table 54). Thus, packed sperm volume and egg weight may be genetically unrelated. This is supported by the experimental evidence of Marks (1981a), who observed no correlated changes in egg weight after three generations of selection for high packed sperm volume.

In general, the genetic correlations of semen traits with egg quality traits were inconsistent and mostly of low magnitude; therefore, selection for semen traits is not expected to change egg quality.

5.7.2 Genetic correlations of testes and wattle measurements with egg production and other related traits

The low and mostly negative genetic correlations between testes weight measured at 14 months of age and egg production are consistent with the lack or negative correlations of semen traits and egg production. Also, the estimates of genetic correlations between testes weight measured at 29 months of age and egg production were inconsistent between control and selected strains. This indicates that testes weight may not be a good indicator of female potential for high egg production.

The unfavorable genetic correlations between testes

weight and egg production found in control strains used in this study, appear to contradict the results reported in mammals, which suggest a positive correlation between testes size and ovulation rate and litter size (Land and Falconer 1969; Land 1973; Islam et al. 1976; Joakimsen and Baker 1977; Eisen and Johnson 1981). Eisen and Johnson (1981) reported a genetic correlation of 0.42 between testes weight and litter size in mice. Islam et al. (1976) estimated the genetic correlation of testes weight and ovulation rate of primiparous and nulliparous mice as 0.50 and 0.25, respectively. However, as mentioned earlier, ovulation rate in mammals and avians may be under different type of genetic and physiological control.

In this study, wattle weight and size measured on 14 month old roosters were favorably correlated with egg production of their female relatives. This result together with the fact that wattle size is easily measured, it is not sex limited and had a high heritability indicates that selection for wattle size measured at 14 months of age could increase egg production. In addition, wattle size can be measured at an early age and could be used as a pre-selection trait.

Wattle size and weight measured at 20 and 29 months of age, respectively, were mostly negative but low correlated with egg production. These results suggest that wattle size is controlled by somewhat different physiological systems at 14 and at 20 and 29 months of

age.

Favorable correlations between comb size (another secondary sex trait) and egg production have been suggested by Pasvogel (1953) and Pasvogel et al. (1951). Also, Ayoub and Merat (1975) reported the correlation of wattle length of 10 week old roosters with egg production of their full- or half- sisters, as 0.21 and 0.13, respectively. They also observed no consistency in the sign of the genetic correlations of wattle length and egg production across years. Nevertheless, the positive correlation between wattle length of males and egg production of their full- and half-sisters (0.21 and 0.31, respectively), and the negative genetic correlation (-0.53) between wattle length and age at sexual maturity reported by Ayoub and Merat (1975), suggest a positive correlation between wattle length and egg production.

The results of this study and those from the literature appear to indicate that it may be possible to achieve more rapid genetic progress, by selecting for wattle size, than selecting by egg production alone. One condition under which indirect selection is expected to be superior to direct selection is when the secondary characteristic (in this case wattle size) has a higher heritability than the desirable characteristic (in this case egg production), and the genetic correlation between the two is high; i.e. $h^2_e < h^2_w r_g$ (where: h^2e and h^2_w are the heritabilities of egg production and wattle size, respectively and rg is the

genetic correlation between those two traits).

Substituting, in above formula, the values of the heritability of wattle weight (0.54) and the mean of the genetic correlations between wattle weight and hen-housed egg production to 497 days (0.40) estimated in this study and the heritability of egg production (0.20) estimated by Gowe et al. (1973) it can be observed that the response of egg production by indirect selection for wattle weight is slighly greater than the expected genetic gain by selection for egg production. i.e., $0.20 < 0.54(0.40) = 0.22$. Further genetic gain would be expected by increasing the intensity of selection for wattle size at an earlier age. The genetic gain in egg production by selecting males with large wattles may result from a reduction in age at first egg, as well as from an increase in the rate of egg production. This is indicated by the favorable genetic correlations of wattle weight or size with age at first egg (-0.17 to -0.43) and hen-day rate of egg production (0.05 to 0.55).

Female relatives of males with large wattles tended to mature at an early age. This is indicated by the negative correlation of wattle weight or size measured on the 14 month old males with age at first egg. A favorable genetic correlation between these traits (-0.53) was reported by Ayoub and Merat (1975), who proposed the use of wattle length of males as a criterion of selection for age at sexual maturity and egg production in females.

Female relatives of males with large wattles tended to produce smaller eggs. This is indicated by the unfavorable genetic correlations of wattle weight or size with egg weight (-0.16 to -0.48). However, in commercial egg production, selection is done on a complex of economic traits (number, weight and quality of the egg, as well as fertility). Therefore, the unfavorable effect of wattle weight or size on egg weight could be overcome by the selection on egg weight. Selection for large wattles, on the other hand, is not expected to change egg quality because wattle size and egg quality traits appear to be unrelated. This is indicated by the low and usually inconsistent genetic correlations between wattle size and egg quality traits.

The significant and positive correlations between spur length and index of males and shell shape of their full-sisters and dams, observed in the control strains indicate that selection for spur size may increase the length to width ratio of the egg. However, this result may have occurred by chance because the correlations for the selected strains were low and not significant.

VI SUMMARY AND CONCLUSIONS

Selection to improve egg production in chickens is a long and costly process. Males are commomly selected for high egg production based on their full- and half- sisters' performance. Selection based on correlated traits, measured directly on males, as well as the performance of female relatives could increase the efficiency of selection for high egg production. Therefore, the main objectives of this study were to obtain estimates of genetic correlations of male semen traits, testes and wattle weights with egg production, as well as to examine the influence of selection for high egg production and other related traits on semen traits, testes weight and wattle and spur size. Secondary objectives of this study were 1) to obtain heritability estimates of semen traits, testes weight, wattle weight and genetic correlations among semen traits; 2) to examine the frequency of lymphoid leukosis virus infection and its effects on semen traits and fertility; and 3) to examine the effect of advancing age on semen production.

From this study the following conclusions were drawn.

6.1 Genetic correlations of semen traits, wattle and testes measurements with egg production and other related traits.

6.1.1 Female relatives of males that produced greater semen weight, packed sperm volume and total sperm weight at 8 months of age matured later and produced fewer eggs. This is indicated by the unfavorable genetic correlations of the above semen traits with age at first egg (0.03 to 0.40),

hen- housed egg production (-0.60 to 0.04), survivors egg production (-0.08 to -0.60) and hen- day rate of egg production(-0.36 to 0.14). Therefore, semen production is not a good indicator of female potential for high egg production.

6.1.2 Female relatives of males that produced large amounts of semen and spermatozoa at 8 months of age tended to produce larger eggs. This is indicated by the favorable genetic correlations of semen production with egg weight (0.02 to 0.36). Therefore, semen traits may be of assistance in selecting for large egg size. However, except for semen weight, the favorable relationships of packed sperm volume and total sperm weight tended to disappear with age of the males.

6.1.3 There was, in general, no consistency in the results of the genetic correlations of semen traits and egg quality traits. In addition, the estimates of the genetic correlations were of low magnitude. Therefore, selection for semen production is not expected to change egg quality.

6.1.4 Female relatives of males with large wattles at 14 months of age matured earlier and tended to produce more eggs. This is based on the favorable genetic correlations of wattle weight or size with age at first egg (-0.17 to -0.43) and egg production (0.05 to 0.55). Therefore, wattle size measured at 14 months of age could be of assistance in selecting for high egg production. The genetic correlations of wattle size of males measured at 20 months of age and egg

production were generally inconsistent in sign.

6.1.5 Female relatives of males with large wattles tended to produce smaller eggs. This is indicated by the unfavorable genetic correlations of wattle weight or size with egg weight(-0.16 to -0.48). The genetic correlations between wattle size and egg quality traits were mostly low and inconsistent. Therefore, selection for wattle size alone may decrease egg weight and maintain unchanged the shell and albumen quality of the egg, the shape of the egg and the incidence of blood spots in the egg.

6.1.6 The genetic correlations between testes weight measured on 14 and 29 month old males and egg production and other related traits for the data of the control and selected strains were mostly inconsistent. Therefore, selection for testes weight is not expected to increase egg production.

6.1.7 Selection for high egg production and a complex of economic traits did not change semen production. This is indicated by the similarity of the mean semen traits of the selected and control strains used in this study.

6.1.8 The results of this study on the genetic correlations of semen production or testes weight with egg production contradict those found in mammals, where selection for ovulation rate increased testes size and vice versa. Therefore, it may be some genetic and physiological differences in the control of ovulation in mammals and avians.

6.2 Estimation of genetic parameters of male traits.

6.2.1 The low magnitude of the heritabilities for semen weight and total sperm weight (0.08 to 0.18) indicates that these traits are controlled mainly by non-additive genetic and environmental factors. The heritabilities for packed sperm volume were moderate (0.29 to 0.38)

6.2.2 One semen ejaculate appears to be sufficient to estimate the heritability of semen traits. This is indicated by the similar magnitude of the heritability estimates of semen traits, particularly semen weight and total sperm weight, based on one or the mean of two semen ejaculates.

6.2.3 Maternal effects are not very important for semen traits. This is supported by the low maternal and dominance ratio of the total phenotypic variance estimated for semen traits (<0.11%). This ratio, however, may be under- or over estimated because the parents used in this studywere related.

6.2.4 The high heritability estimates of testes and wattle weights (0.58 and 0.54, respectively) indicate that these traits are controlled mainly by additive genes.

6.2.5 Males with large body weight tended to produce more semen. This is indicated by the positive but low phenotypic correlations between semen traits and body weight. However, selection for body weight may reduce semen production because the genetic correlations between semen traits and body weight were negative (-0.33 to -0.67). This negative association between semen traits and body weight may be

the broiler breeder.

6.3 Frequency of lymphoid leukosis virus (LLV) infection and its effect on semen traits and fertility.

6.3.1 The results of the tests for LLV in semen and group specific viral antigen in feather pulps were consistent. The frequency of LLV-shedding males was higher in the control (18.1 to 35.9%) than in the strains selected for high egg production (1.9 to 14.9%).

6.3.2 Males shedding the LLV or the group specific viral antigen tended to have lower fertility, and higher incidence of abnormal spermatozoa at older ages than nonshedders. Therefore, culling of males carrying the LLV may reduce horizontal transmission of the disease and improve fertility of the flock.

6.3.3 Males shedding the LLV or the group specific viral antigen tended to produce more semen and spermatozoa. Results in females showed that LLV infection decreased egg production (Gavora et al. 1980). Therefore, the findings in this study suggest that LLV infection may affect the reproductive processes of males and females in a different direction.

6.4 Effect of age on semen production.

Semen weight, packed sperm volume and total sperm weight tended to decline with advancing age. Therefore, more males will be needed when they are intended to be used over a longer period of reproduction.

6.5 Effect of ejaculate sequence on semen production.

Semen weight, but not packed sperm volume, decreased with ejaculate sequence. Therefore, the reduction in total sperm weight of the first ejaculate compared with the second ejaculate was a consequence of a reduction in semen weight. Sperm motility tended to increase with ejaculate sequence.

VII STATEMENT OF ORIGINALITY

To the best of the author's knowledge, the following information contained in this thesis constitutes an original contribution to the scientific literature.

1) The estimation of genetic correlations between sex limited traits by regression methods was an original approach. The results obtained by this method were consistent with those using intraclass correlation.

2) This is the first study to report genetic correlations between semen and egg production for selected and control strains. Full-sib and dam-son correlations have been reported in the literature. The genetic correlations of semen weight, packed sperm volume and total sperm weight with egg weight and other important egg quality traits are also reported for the first time.

3) This is the first report of the genetic correlation of wattle weight and size with egg production. Ayoub and Merat (1975) indicated that the genetic correlations between wattle length and egg production were inconsistent with year of hatch, but they do not report the values of the correlations.

4) In this study, genetic correlations between testes weight and egg production and egg quality traits were for the first time obtained in chickens.

5) This is the first study to report the heritability of total sperm weight and the genetic relationship of total sperm weight with semen weight and packed sperm volume. The proportions of the total variance due to maternal and environmental effects were estimated for first time for these traits.

6) This is the first study to examine the effect of LLV on semen and sperm production and on male fertility.

7) This is the first report on the effect of age on semen production of strains from a long term selection for the improvement of egg stocks of poultry.

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IX. APPENDIX I

THE COMPUTATION OF THE GENETIC CORRELATION OF SEX LIMITED TRAITS BY REGRESSION METHODS.

The genetic correlations of sex limited traits, can be calculated from the correlations of dam- son, full-sibs or half-sibs, using simple algebric manipulation. In this section, the formulae to calculate genetic correlations of sex limited traits are given for the following situations: 1) the correlation of male and female traits based on individual observations; 2) the correlation of male and female traits based on family means as the observational unit; and 3) the correlation of a male trait value and the mean value of his female relatives.

1) The correlation of a male trait (e.g. testes size) with a female trait (e.g. egg production) based on individual observations is given by,

$$r_m = Cov_p(m,f)/(s_{pm}\, s_{pf}) \qquad (1)$$

where: r_m is the correlation of male(m) and female(f) traits; Cov_p is the covariance of the pertinent traits; and s_{pm} and s_{pf} denote the square roots of the phenotypic variances of male and female traits, respectively.

Assuming no environmental effects and that only additive effects are important,

$$Cov_p(m,f) = a\ Cov_g(m,f) \qquad (2)$$

where: a is the coefficient of relationship; and Cov_g is the genetic covariance of male and female traits. From (1) and (2)

$$r_m = a\ Cov_g(m,f)/(s_{pm}\, s_{pf}) \qquad (3)$$

Multiplying the numerator and denominator of formula (3) by s_{Am} and s_{A+}, the square roots of the additive variance of male and female traits, respectively; formula (3) reduces to

$$r_a = a\, r_g\, h_m\, h_+$$

from above formula the genetic correlation (r_g) of two sex limited traits can be calculated as:

$$r_g = r_a/(a\, h_m\, h_+)$$

where: h_m and h_+ are the square roots of the heritabilities of male and female traits, respectively.

The genetic correlation of male and female sex limited traits based on family means as the observational unit can be calculated as follows:

$$r_g = Cov_p(M,F)/(s_M\, s_F)$$

where: r_a is the correlation of relatives of different sex based on family mean values; $Cov_p(M,F)$ is the covariance of male (M) and female (F) traits based on family means; and s_M and s_F are the square roots of the phenotypic variance of male and female traits, respectively.

Assuming no environmental effects and that only additive effects are important,

$$Cov_p(M,F) = a\, Cov_a(M,F) = a\, Cov_a(M,F) \qquad (4)$$

because the covariance based on mean values is equal to the covariance based on individual observations: i.e.,

$$Cov(M,F) = Cov(M_1+M_2+\ldots+M_n/n\ ,\ F_1+F_2+\ldots F_m/m)$$

$$= 1/nm\ [Cov(M_1,F_1) + Cov(M_1,F_2) + \ldots + Cov(M_2,F_1) + \ldots + Cov(M_n,F_m)]$$

If we assume that $Cov(M_1,F_1) = Cov(M_1,F_2) = \ldots = Cov(M_n,F_m)$,

$$Cov(M,F) = nm\ Cov(M_i,F_i)/nm = Cov(M,F)$$

However, the variance of a mean s^2_M is different from the variance of individual observations s^2_m, i.e.,

$s^2_M = (1+(n-1)t_m)s^2_m/n$; as shown below

$$s^2_M = s^2_{(m_1+m_2+\ldots+m_n/n)} = s^2_{m_1}+s^2_{m_2}+\ldots+s^2_{m_n}+2Cov(M_1,M_2)$$
$$+2Cov(M_1,M_3)+\ldots+2Cov(M_{n-1},M_n)/n^2 =$$
$$= ns^2_m/n^2 + n(n-1)Cov(M_1,M_2)/n^2 \qquad (A)$$

Assuming that: $s^2_{m_1} = s^2_{m_2} = \ldots = s^2_{m_n}$ and

$Cov(M_1,M_2) = Cov(M_1,M_3) = \ldots = Cov(M_{n-1},M_n)$; and knowing that the intraclass correlation (t) is equal to:

$t = Cov(M_1,M_2)/s_{m_1}s_{m_2}$; thus $Cov(M_1,M_2) = t_m s^2_m$ (B)

From (A) and (B) we have:

$$s^2_M = ns^2_m/n + n(n-1)t_m s^2_m/n^2 = s^2_m/n + (n-1)t_m s^2_m/n$$
$$= (1/n + (n-1)t/n)s^2_m \qquad (5)$$

Similarly, $s^2_F = (1 + (m-1)t_f/n^2)s^2_f$

From (4) and (5) we have,

$$r_B = Cov_B(M,F)/(s_M\ s_F) = aCov_G(M,F)/(s_m\ s_f\ n_m\ n_f) =$$

where $n_m = [1+(n-1)t_m/n]$ and $n_f = [1+(m-1)t_f/m]$

multiplying the numerator and denominator by the square roots of the additive variance of male and female traits (s_{Af} and s_{Am}, respectively).

$$= aCov(M,F)s_{Am}s_{Af}/s_m s_f n_m\ s_{Am}s_{Af}$$

$$r_B = ar_G h_m h_f/(n_m\ n_f)^{1/2}$$

$$r_G = r_B n_m n_f/a h_m h_f$$

This is the general formula to estimate genetic correlations, from which other particular cases derive.

For the case of the genetic correlation of a male trait (individual observation) with the mean trait value of his female relative; i.e, when $n_m=1$

$$r_g = r_s[1+(m-1)t_f/m]^{1/2}/a\ h_m h_r$$

X. APPENDIX II

Appendix Table 1. Calculated composition of rations.

	Ration		
	Chick Starter	Ottawa Grower	Ottawa Hatching
Total Metabolize energy(MJ/Kg)	12.1	12.3	11.9
Protein (N x 6.25)g/Kg	18.2	13.1	15.5
Lysine(g/Kg)	9.6	5.6	7.8
Methionine + cystine (g/Kg)	6.2	4.6	5.4
Calcium(g/Kg)	6.0	6.0	28.0
Phosphorous*	3	3	4

* 30% of plant phosphorous was assumed to be available.

Appendix Table 2. Percentage, with respect to the total number of observations, of semen data excluded for various reasons from the statistical analysis.

Experiment	Percentage of					Total Number of data
	Sick birds	Nervous birds[1]	Bad samples[2]	No semen	Total	
III	0.002	4.36	4.00	1.05	9.41	3344
IV	0.003	5.00	0.74	0.56	6.30	1206
V	1.50	3.05	0.002	1.30	6.32	800
VI	0.07	3.65	0.01	0.13	4.85	640

1 Percentage of males that did not respond to the ejaculate training.
2 Semen samples contaminated with faeces, urate or blood.

Appendix Table 3. Male traits measured in each experiment.

Male trait	Experiment I	II	III	IV	V	VI
Semen weight(mg)	Yes	Yes	Yes	Yes	Yes	Yes
Packed sperm volume(%)	Yes	Yes	Yes	Yes	Yes	Yes
Total sperm weight(mg)	Yes	Yes	Yes	Yes	Yes	Yes
Number of spermatozoa/ml (x 10^9)	Yes	No	No	No	No	No
Number of spermatozoa per ejaculate (x 10^9)	Yes	No	No	No	No	No
Motility score	Yes	Yes	Yes	No	No	No
Percent motility	Yes	Yes	Yes	No	No	No
Abnormal spermatozoa(%)	Yes	No	No	No	No	No
Testes weight (g)	No	No	No	No	No	Yes
Wattle size (cm)	No	No	No	No	Yes	Yes
Wattle weight(g)	No	No	No	No	No	Yes
Spur size(cm)	No	No	No	No	Yes	No

Appendix Table 4. Numbers of males shedding the lymphoid leukosis virus into semen (Experiment I).

Lymphoid leukosis status	Year of hatch (Age in months) 1979 (23 Mo.) 7 c*	8 s	9 s	1980 (10 Mo.) 7 c	8 s	9 s	TOTAL
NON-SHEDDERS	45	24	22	25	18	20	154
SHEDDERS	24	4	4	14	2	0	48
TOTAL	69	28	26	39	20	20	202

* c= unselected control strain; s= selected strain
Males were tested for LLV by the Phenotypic mixing test.

Appendix Table 5. Numbers of males shedding the lymphoid leukosis virus into feather pulps of selected and control strains (Experiments II and IV).

Lymphoid leukosis status	Strain number and type									
	1 s*	2 s	3 s	4 s	5 c	7 c	8 s	9 s	10 c	TOTAL
EXPERIMENT II										
NON-SHEDDERS	25	26	25	24	55	50	27	25	51	308
SHEDDERS	1	0	1	0	14	16	0	1	20	53
TOTAL	26	26	26	24	69	66	27	26	71	361
EXPERIMENT IV										
NON-SHEDDERS	39	37	37	37	58	68	39	37	55	407
SHEDDERS	1	3	1	1	22	14	1	0	18	53
TOTAL	40	40	38	38	80	82	40	37	73	460

* c= unselected control strain; s= selected strain.
Semen tested for the presence of the group specific antigen by the complement fixation test

Appendix Table 6. Hierarchal analysis of variance based on individual values with expected mean squares.

Sources	Degrees of freedom	Mean squares	Expected mean squares
Strain	l−1	MS_L	Not relevant
Sire within strain	s−l	MS_S	$s^2_w + k_2\, s^2_d + k_3\, s^2_s$
Dam within sire	d−s	MS_D	$s^2_w + k_1\, s^2_d$
Progeny within dam	N−d	MS_R	s^2_w

l=number of strains; s= number of sires; d=number of dams; N=total number of progeny.
MS_L, MS_S, MS_D and MS_R= Mean squares of strain, sire within strain, dam within sire within strains and and residual, respectively.
s^2_w=the residual component of variance; s^2_d= the dam component of variance; s^2_s= the sire component of variance.
$k_1 = (N - E(\ E\ n^2_{i,j}/n_{i.}\ ))/(d-s)$.
$k^2 = (EEn^2_{i,j}/n_{i.} - EEn^2_{i,j}/N)/(s-1)$.
$k_3 = (N - E\ n^2_{i.}/N)/(s-1)$.
$n_{i,j}$=number of progeny/dam; $n_{i.}$=number of progeny/sire.

Appendix Table 7. The genetic and environmental interpretation of the components of variance.

Variance components	Covariance	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_M	V_E
s^2_s	Cov_{HS}	1/4	0	1/16	0	0	0	0
s^2_d	$Cov_{FS}-Cov_{HS}$	1/4	1/4	3/16	1/6	1/16	1	0
s^2_w	$s^2_p-Cov_{FS}$	1/2	3/4	3/4	7/8	15/16	0	1
$s^2_s+s^2_d$	Cov_{FS}	1/2	1/4	1/4	-1/8	1/16	1	0

s^2_s= sire component of variance; s^2_d= dam component of variance; s^2_w=residual; s^2_p=total variance; Cov_{HS}=covariance of half sibs; Cov_{F-H}= covariance of full sibs.
V_A= additive variance; V_D= dominance variance; V_{AA}=additive by additive variance; V_{AD}=additive by dominance variance; V_{DD}= dominance by dominance variance.
V_M= maternal variance; V_E= environmental variance.

Appendix Table 8. Single pair mating analysis of variance based on individual values with expected mean squares.

Sources	Degrees of freedom	Mean squares	Expected mean squares
Strain	l-1	MS_L	Not relevant
Among matings	m-1	MS_M	$s^2_w + k\ s^2_g$
Among progeny within mating	N-m	MS_R	s^2_w

l= number of strains; m=number of matings; N= total number of individuals; MS_L, MS_M and MS_R= mean squares of strains, matings and residual, respectively; s^2_w= the residual component of variance; s^2_g= the genetic group component of variance.
$k = (N - \sum n^2_i/N)/(m-1)$; n_i= number of individuals within the ith mating.

Appendix Table 9. Hierarchal analysis of covariance based on individual values with expected mean cross products.

Sources	Degrees of freedom	Mean cross products	Expected mean cross products
Strain	l-1	MCP_L	Not relevant
Sire within strain	s-l	MCP_s	$Cov_w + k_2 Cov_D + k_3 Cov_s$
Dam within sire	d-s	MCP_D	$Cov_w + k_1 Cov_D$
Progeny within dam	N-d	MCP_R	Cov_w

l=number of strains; s= number of sires; d=number of dams; N=total number of progeny; MCP_L, MCP_s, MCP_D, MCP_R= Mean cross products of strain, sire within strain, dam within sire within strain and residual, respectively.
Cov_s, Cov_D, Cov_w = sire, dam and residual components of covariance.
$k_1=(N - E(E n^2_{i,j}/n_{i.})/(d-s)$.
$k_2=(EEn^2_{i,j}/n_{i.} - EEn^2_{i,j}/N)/(s-1)$.
$k_3=(N - E n^2_{i.}/N)/(s-1)$.
$n_{i,j}$=number of progeny/dam; $n_{i.}$=number of progeny/sire.

Appendix Table 10. Single pair mating analysis of covariance based on individual values with expected mean cross products.

Sources	Degrees of freedom	Mean cross products	Expected mean squares
Strain	l-1	MCP_L	Not relevant
Among matings	m-l	MCP_M	$Cov_w + k\ Cov_a$
Among progeny within mating	N-m	MCP_R	Cov_w

l= number of strains; m=number of matings; N= total number of individuals; MCP_L, MCP_M and MCP_R=mean cross products of strain, mating within strain and residual, respectively. Cov_a and Cov_w= components of covariance of genetic group and residual respectively.
$k = (N - \sum n^2_i/N)/(m-1)$; n = number of individuals within the i-th mating.

Appendix Table 11. The genetic and environmental interpretation of the components of covariance.

Component of covariance	Cov_A	Cov_D	Cov_{AA}	Cov_{AD}	Cov_{DD}	Cov_M	Cov_E
Cov_S	1/4	0	1/16	0	0	0	0
Cov_D	1/4	1/4	3/16	1/8	1/16	1	0
Cov_W	1/2	3/4	3/4	7/8	15/16	0	1
Cov_S+ Cov_D	1/2	1/4	1/4	1/8	1/16	1	0

Cov_S, Cov_D, Cov_W= sire, dam and residual components of covariance; Cov_A= additive genetic covariance; Cov_D= dominance covariance; Cov_{AA}= additive by additive covariance; Cov_{AD}= additive by dominance covariance; Cov_{DD}= dominance by dominance covariance; Cov_M= maternal covariance; Cov_E= environmental covariance.

Appendix Table 12. Analysis of variance and covariance among and within sire based on full-sib family means (After Kinney and Shoffner 1965).

Sources	Degree of freedom	Expected mean square	Expected mean product
Strain	l-1	Not relevant	Not relevant
Among sires within strain	s-l	$k_2 s^2_w + s^2_d + k_3 s^2_s$	$CovD_{m\bullet} + k_3 CovS_{m\bullet}$
Among dam family means within sire	d-s	$k_1 s^2_w + s^2_D$	$CovD_{m\bullet} = \overline{CovD}_{m\bullet}$

l=number of strains; s=number of sires; d=number of dams;
s^2_w= residual variance component; s^2_D= dam component of variance;
s^2_s=sire component of variance; $CovD_{m\bullet}$=dam component of covariance,

based on individual observations; $\overline{CovD}_{m\bullet}$= dam component of covariance based on family means;

$k_1 = (\sum\sum 1/n_{ij} - \sum 1/n_i \sum 1/n_{ij})/(N-s)$;

$k_2 = (\sum 1/n_i \sum 1/n_{ij} - 1/N \sum\sum 1/n_{ij})/(s-1)$;

$k_3 = (N - \sum n^2_i/N)/(s-1)$; n_{ij}= number of progeny per dam;
n_i= number of dams per sire; N= total number of dams.

Appendix Table 13a. Analyses of variance (Mean squares) to test the effect of lymphoid leukosis virus on semen traits measured on 23 month old males of control strain 7(Experiment I;1979 hatch).

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine$\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg	Number of spermatozoa per ml (x10^9)
EJACULATE	2	0.3428*	0.0630	2.9920	0.3529
LYMPHOID LEUKOSIS STATUS	1	0.0047	0.1142	1.4427	7.3167**
RESIDUAL	123	0.0877	0.1673	1.9300	0.8925
CV		5.4	4.6	27.8	40.1
r^2		6.0	1.2	3.1	6.7

* P<0.05 ** P<0.01

Appendix Table 13b. Analyses of variance (Means squares) to test the effect of lymphoid leukosis virus on semen traits measured on 23 month old males of control strain 7 (Experiment I; 1979 hatch).

Sources of variation	d.f.	Number of spermatozoa per ejaculate $x10^9$ $\sqrt{\ }$	Motility score	Percent motility (arcsine)	Percent of Abnormal spermatozoa $\sqrt{\ }$ $x10^{-2}$
EJACULATE	2	49.6804	0.7040	0.0415	0.5811
LYMPHOID LEUKOSIS STATUS	1	257.8555*	0.8541	0.0038	7.0510**
RESIDUAL	123	45.5078	0.2884	0.0137	------
	109	-------	------	------	0.4716
CV		28.4	12.9	13.7	27.0
r^2		6.0	5.8	4.9	13.8

* P<0.05 ** P<0.01

Appendix Table 14a. Analyses of variance (Mean squares) to test the effect of lymphoid leukosis virus on semen traits measured on 10 month old roosters of control strain 7 (Experiment I; 1980 hatch).

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine$\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg	Number of sperm/ml x10^{7}
EJACULATE	2	0.0832	0.0569	1.8920	0.7255
LYMPHOID LEUKOSIS STATUS	1	0.0544	0.1066	0.0211	2.7289
RESIDUAL	105	0.0912	0.2278	2.7275	0.7051
CV		5.1	5.0	21.9	25.6
r^2		2.3	1.0	1.3	5.5

* P<0.05 ** P<0.01

Appendix Table 14b. Analyses of variance (Means squares) to test the effect of lymphoid leukosis virus on semen traits measured on 10 month old roosters of control strain 7(Experiment I;1980 hatch).

Sources of variation	d.f.	Number of spermatozoa/ ejaculate $x10^9\sqrt{\ }$	Motility score	Percent motility (arcsine)	Percent of Abnormal spermatozoa $\sqrt{\ } x10^{-2}$
EJACULATE	2	36.6601	0.2116	0.0297	1.0255
LYMPHOID LEUKOSIS STATUS	1	19.5467	0.6209	0.0072	1.1128
RESIDUAL	105	47.1782	0.2214	0.0129	------
	104	-------	------	------	1.0962
CV		20.1	10.9	12.5	35.5
r^2		1.8	4.4	4.8	2.7

* P<0.05 ** P<0.01

Appendix Table 15. Analyses of variance (Mean squares)to test the effect of lymphoid leukosis virus (LLV) on semen traits measured on 18 month old roosters of control strains 5, 7 and 10 (Experiment II).

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine $\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg	Motility score	Percent motility (arcsine)
EJACULATE	1	0.0382	1.4154**	16.7492**	0.6390	0.0216
STRAIN	2	0.4864**	0.8670**	2.5507	1.2762**	0.0260
LLV	1	0.3340	2.3038**	35.7887**	0.0087	0.0007
STRAIN * LLV	2	0.1968	0.2794	8.0492*	0.3268	0.0063
BODY WEIGHT	1	1.7042**	0.1241	3.9738	0.0252	0.0004
RESIDUAL	370	0.0984	0.1746	2.5259	0.2700	0.0107
CV		5.3	4.5	21.9	12.4	10.9
r^2		7.9	8.0	6.9	5.4	2.9

* P<0.05 ** P<0.01

Appendix Table 16. Analyses of variance (Mean squares) to test the effect of lymphoid leukosis virus (LLV) on semen traits measured on 20 month old roosters of control strains 5, 7 and 10 (Experiment IV).

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine $\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg
BLOCK	2	0.0759	225.1311**	8.9818**
EJACULATE	1	0.2286*	0.0857	3.0456
LLV	1	0.0927	4.2964	2.1744
STRAIN	2	0.5073**	47.3399*	16.2299**
BLOCK*STRAIN	4	0.1339	35.0361	3.7383
EJACULATE * STRAIN	2	0.0293	7.6267	0.5557
STRAIN*LLV	2	0.0260	117.4014**	9.0687**
BODY WEIGHT	1	0.2643*	160.5972**	1.5770
RESIDUAL	341	0.0605	16.7660	1.8422
CV		4.2	27.1	18.1
r^2		11.0	15.1	11.0

* P<0.05 ** P<0.01

Appendix Table 17. Analyses of variance (Mean squares)to test the effect of lymphoid leukosis virus (LLV) on fertility and hatchability of control strains 5, 7 and 10 (Experiments II and IV)

Sources of variation	d.f.	Experiment II		Experiment IV	
		Fertility arcsine(%)	Hatchability arcsine(%)	Fertility arcsine(%)	Hatchability arcsine(%)
STRAIN	2	0.2877**	0.0761	0.0145	0.0407
LLV	1	0.0316	0.0386	0.2573**	0.0049
STRAIN * LLV	2	0.0053	0.0155	0.0234	0.1130
RESIDUAL	183	0.0342	0.0412	------	------
	215	------	------	0.0312	0.0434
CV		16.3	10.2	15.0	21.1
r^2		10.2	4.1	5.6	2.5

* P<0.05 **P<0.01

Appendix Table 18. Analyses of variance (Mean squares) to test the effect of age on semen traits of strains 1, 3 and 5.

Source of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine $\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg
AGE	3	0.8214**	1.6252**	33.5726**
EJACULATE	1	0.8127**	0.0771	17.3708**
STRAIN	2	1.7301**	0.4302	35.4232**
AGE*STRAIN	6	0.0725	0.1381	0.9783
EJACULATE * STRAIN	2	0.0010	0.1591	0.0416
BODY WEIGHT	1	4.1310**	0.8981	24.8622**
RESIDUAL	775	0.0894	0.1924	2.4369
CV		5.1	4.7	22.4
r^2		11.3	7.7	10.5

* P<0.05 **P<0.01

Appendix Table 19. Analyses of variance (Mean squares) to test the effect of age on semen traits of strains 7, 8 and 9.

Source of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine$\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg
AGE	3	0.4413**	4.2234**	30.0376**
EJACULATE	1	0.7844**	0.1480	17.8005**
STRAIN	2	0.0319	1.0716**	10.2911*
AGE*STRAIN	6	0.0125	0.2618	1.6649
EJACULATE * STRAIN	2	0.0009	0.1820	1.3356
BODY WEIGHT	1	0.9759**	1.5530**	0.0035
RESIDUAL	913	0.0956	0.1603	2.4066
CV		5.2	4.3	21.9
r^2		11.3	12.9	7.5

* P<0.05 **P<0.01

Appendix Table 20a. Analyses of variance (Mean squares) of semen traits measured on 23 month old roosters of strains 7, 8 and 9 (Experiment I; 1979 hatch).

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine $\sqrt{\ }$	Total sperm weight $\sqrt{\ }$mg	Number of spermatozoa/ ml (x 10^9)
BLOCK	3	0.9795**	0.1370	7.5597*	2.8980*
EJACULATE	2	0.4463*	0.1211	8.2612*	0.9255
STRAIN	2	2.5019**	9.3743**	145.2933**	21.4926**
BLOCK*STRAIN	6	0.3410*	0.2953	10.5175**	4.0659**
EJAC*STRAIN	4	0.0502	0.0378	0.9005	0.1813
RESIDUAL	260	0.1017	0.1568	1.9792	0.7551
CV		5.7	4.3	23.4	31.5
r^2		29.1	33.4	42.1	27.9

* P<0.05 ** P<0.01

Appendix Table 20b. Analyses of variance (Mean squares) of semen traits measured on 23 month old roosters of strains 7, 8 and 9 (Experiment I; 1979 hatch).

Sources of variation	d.f.	Number of spermatozoa/ ejaculate $x10^{9}\sqrt{\ }$	Motility score	Percent motility (arcsine)	Percent of abnormal spermatozoa $\sqrt{\ } x10^{-2}$
BLOCK	3	0.0407**	0.2828	0.0249	0.6577
EJACULATE	2	0.1923**	0.2098	0.0539	0.2745
STRAIN	2	0.2335**	0.7183	0.0801*	1.0670
BLOCK*STRAIN	6	0.3302**	0.7779*	0.0449	3.2746
EJACULATE * STRAIN	4	0.0017	0.1563	0.0020	0.5340
RESIDUAL	260	0.0044	0.3378	0.0183	------
	242	-------	------	------	0.7329
CV		23.7	13.9	15.8	32.3
r^2		40.7	9.1	12.0	13.2

* P<0.05 ** P<0.01

Appendix Table 21a. Analyses of variance (Mean squares) of semen traits measured on 10 month old roosters of strains 7, 8 and 9 (Experiment I; 1980 hatch).

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine $\sqrt{\ }$	Total sperm weight $\sqrt[3]{\ }$ mg	Number of spermatozoa/ ml (x10^9)
BLOCK	3	0.2945*	0.1066	4.2803	3.3783**
EJACULATE	2	0.1441	0.0276	1.1381	0.4523
STRAIN	2	0.2711*	0.4515	0.1100	0.8332
BLOCK*STRAIN	6	0.3925**	0.1918	10.1353**	1.4382*
EJAC*STRAIN	4	0.0729	0.4952	3.1353	1.0146
RESIDUAL	196	0.0885	0.2124	2.4531	0.6762
CV		5.0	4.9	20.8	25.6
r^2		18.5	10.0	14.8	18.0

* P<0.05 ** P<0.01

Appendix Table 21b. Analyses of variance (Mean squares) of semen traits measured on 10 month old roosters of strains 7,8 and 9(Experiment I; 1980 hatch).

Sources of variation	d.f.	Number of spermatozoa/ ejaculate $x10^{9}\sqrt{\ }$	Motility score	Percent motility (arcsine)	Percent of abnormal spermatozoa $\sqrt{\ } x10^{-2}$
BLOCK	3	0.2228**	0.1734	0.0253	3.9550**
EJACULATE	2	0.0010	0.0697	0.0154	0.3071
STRAIN	2	0.0054	1.9531**	0.0888**	1.8970
BLOCK*STRAIN	6	0.0130*	0.8384**	0.0400*	0.8422
EJACULATE * STRAIN	4	0.0030	0.0616	0.0088	0.8170
RESIDUAL	196 192	0.0048 ------	0.2880 ------	0.0153 ------	------ 0.8747
CV		20.1	12.7	14.1	33.2
r^2		15.9	15.9	18.3	13.6

* P<0.05 ** P<0.01

Appendix Table 22. Analyses of variance (Mean squares) of semen traits measured on 18 month old roosters of control and selected strains (Experiment II).+

Sources of variation	d.f.	Semen weight (ln)	Packed sperm volume % arcsine$\sqrt{}$	Total sperm weight $\sqrt{}$mg	Motility score	Percent motility (arcsine)
BLOCK	3	0.6700**	0.3624	4.2700	1.4834**	0.0857**
EJACULATE	1	0.0320	1.3984**	14.7054*	1.8337**	0.1273**
STRAIN	8	0.4418**	1.5541**	10.6713**	1.1007**	0.0306**
BLOCK* STRAIN	24	0.1336	0.2634	3.8326	0.3725*	0.0154**
EJACULATE * STRAIN	8	0.0212	0.0394	0.3334	0.3173	0.0102
BODY WEIGHT	1	1.5860**	0.1520	13.1647*	0.1985	0.0053
RESIDUAL	706	0.0970	0.1836	2.6231	0.2069	0.0080
CV		5.2	4.6	21.7	10.8	9.4
r^2		12.4	15.0	10.4	16.9	17.8

+ Control strains 5, 7 and 10; selected strains 1, 2, 3, 4, 8 and 9.
* P<0.05 ** P<0.01

Appendix Table 23. Analyses of variance (Mean squares) of semen traits measured on 8 month old roosters of control and selected strains (Experiment III).+

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine√	Total sperm weight √mg	Motility score	Percent motility (arcsine)
BLOCK	6	3.0818**	3.1069**	27.6776**	1.8091**	0.0576**
EJACULATE	1	8.5304**	1.8203**	224.3675**	------	------
STRAIN	6	2.2339**	6.4005**	40.5875**	0.4466	0.0408**
BLOCK * STRAIN	36	0.1613**	0.4041**	4.2010**	0.3747*	0.0178*
EJACULATE * STRAIN	6	0.0284	0.0371	0.2219	------	------
BODY WEIGHT	1	2.0489**	6.2969**	0.0629	0.1704	0.0009
RESIDUAL	2926	0.0806	0.1725	2.2977	------	------
	1438	------	------	------	0.2535	0.0113
CV		4.8	4.4	20.0	12.0	11.5
r^2		17.8	14.3	10.6	7.5	7.0

+ Control strains 5, 7 and 10; selected strains 1, 3, 8 and 9.
* P<0.05 ** P<0.01

Appendix Table 24. Analyses of variance (Mean squares) of semen traits measured on 16 month old roosters of control and selected strains (Experiment IV).*

Source of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine$\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg
BLOCK	2	0.2266*	2.5862**	4.5584
EJACULATE	1	1.1142**	0.0079	18.9805**
STRAIN	6	1.0275**	1.9328**	28.7909**
BLOCK*STRAIN	12	0.1516*	0.3194*	4.1222*
EJACULATE * STRAIN	6	0.0247	0.0962	1.0416
BODY WEIGHT	1	0.4239*	1.0919*	0.0078
RESIDUAL	1068	0.0749	0.1733	1.9924
CV		4.6	4.4	19.3
r^2		11.9	10.3	10.7

* Control strains 5,7 and 10; selected strains 1,3,8 and 9.
* P<0.05 **P<0.01

Appendix Table 25. Analyses of variance (Mean squares) of semen traits measured on 20 month old roosters of control and selected strains (Experiment V).+

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine$\sqrt{\ }$	Total sperm weight $\sqrt{\ }$ mg
BLOCK	1	0.6788*	0.0653	3.6445
EJACULATE	1	0.3305*	0.2247	9.5826*
STRAIN	5	0.9628**	2.0960**	12.1923**
BLOCK*STRAIN	5	0.1158	0.0956	1.8819
EJACULATE * STRAIN	5	0.0203	0.1338	1.2784
BODY WEIGHT	1	2.6289**	0.6597	50.4933**
RESIDUAL	567	0.0841	0.2668	2.3422
CV		4.9	7.6	24.1
r^2		15.0	8.4	7.9

+ Control strains 5,7 and 10; selected strains 1,3,8 and 9.
* P<0.05 ** P<0.01

Appendix Table 26. Analyses of variance (Mean squares) of semen traits measured on 29 month old roosters of control and selected strains (Experiment VI).*

Sources of variation	d.f.	Semen weight ln(mg)	Packed sperm volume % arcsine $\sqrt{}$	Total sperm weight $\sqrt{}$ mg
BLOCK	1	0.0001	0.1090	1.2862
EJACULATE	1	5.5635*	0.2286	14.9724**
STRAIN	5	0.6330**	0.7670**	18.3740**
BLOCK*STRAIN	5	0.1936	0.0887	3.9053
EJACULATE * STAIN	5	0.0377	0.0189	0.4893
BODY WEIGHT	1	1.5351**	0.0088	13.8329**
RESIDUAL	307	0.1111	0.1232	1.9623
CV		5.7	3.8	20.7
r^2		9.0	7.0	12.4

* Control strains 5,7 and 10; selected strains 1, 3, 8 and 9.

* P<0.05 **P<0.01

Appendix Table 27. Analysis of variance (Mean squares) of testes weight and and wattle weight and size measured on 14 month old roosters of strains 5,7 and 10(Experiment VI; 1983 hatch).

Sources of variation	d.f.	Testes weight (g)	Wattle weight (g)	Wattle length (cm)	Wattle width (cm)	Wattle index (cm^2)
STRAIN	2	475.3219**	598.0984**	707.6900**	580.3263**	1321.8131**
BODY WEIGHT	1	30.3961	433.9732*	1195.3087*	600.5802*	1816.3648**
RESIDUAL	128	52.0215	76.9898	127.8697	99.2947	217.1004
CV		29.4	36.1	15.2	15.6	30.2
r^2		12.5	12.5	12.9	11.9	13.4

* P<0.05 **P<0.01

Appendix Table 28. Analyses of variance (Mean squares) of wattle size measured on 20 month old roosters of control and selected strains (Experiment V).*

Sources of variation	d.f.	Wattle length (cm)	Wattle width (cm)	Wattle index (cm^2)
STRAIN	6	12.2135**	9.3546**	2314.87**
BODY WEIGHT	1	45.2391**	28.0404**	8428.51**
RESIDUAL	392	1.2020	0.9002	224.74
CV		13.9	13.8	27.0
r^2		18.4	17.7	18.6

* Control strains 5, 7 and 10; selected strains 1,3,8 and 9.

* P<0.05 ** P<0.01

Appendix Table 29. Analysis of variance (Mean squares) of testis and wattle weights measured on 29 month old roosters of control and and selected strains (Experiment VI; 1982 hatch).+

Sources of variation	d.f.	Testis(g)		Wattle(g)		Testes (g)	Wattles (g)
		right	left	right	left		
STRAIN	5	228.987**	184.926**	247.938**	252.121**	824.867**	999.306**
BODY WEIGHT	1	50.225*	126.168**	188.380**	203.942**	335.601**	784.335**
RESIDUAL	300	10.509	9.898	21.467	22.425	37.014	86.435
CV		25.7	25.1	35.2	35.5	24.2	35.1
r^2		26.6	24.3	16.3	15.9	27.2	16.3

+ Control strains 5 and 7; selected strains 1, 3, 8 and 9.
* P<0.05 ** P<0.01

Appendix Table 30. Analyses of variance (Mean squares) of spur size measured on 20 month old roosters of control and selected strains (Experiment V).*

Sources of variation	d.f.	Spur length (cm)	Spur diameter (cm)x10^{-2}	Spur index (cm^2)
STRAIN	5	5.4219**	7.4484**	8.8996**
BODY WEIGHT	1	5.8120**	34.0442**	20.0447**
RESIDUAL	300	0.3512	0.8452	0.4971
CV		14.6	11.1	19.9
r^2		23.8	21.4	31.0

* Control strains 5,7 and 10; selected strains 1,3,8 and 9.
* P<0.05 ** P<0.01

Appendix Table 31. Mean performance of six selected (s) and three control (c) strains of SCWL chickens hatched in 1982.

Trait		Strain number and type								
		1 s*	3 s	5 c	2 s	4 s	7 c	9 s	8 s	10 c
Number of hens housed		1183	980	788	990	854	736	1000	821	832
Fertility	%	92.4	93.6	86.0	88.0	85.5	88.1	87.2	89.1	92.4
Hatchability	%	74.8	72.5	82.2	67.8	69.9	76.5	69.0	71.0	80.5
Age at fist egg(AFE)	days	153.9	142.0	176.2	167.5	143.3	166.6	168.7	149.8	166.6
Hen-housed egg production	No.	110.4	115.9	82.5	95.8	116.2	89.5	96.5	111.6	89.4
Survivors egg production	No.	119.9	118.4	84.8	97.7	117.7	91.1	98.1	112.9	92.4
Rate of lay from AFE to 273 days	%	91.6	88.2	84.3	90.2	88.7	83.5	91.4	89.6	83.8
Egg weight at 240 days	g	56.4	55.8	50.7	55.5	55.6	52.2	55.8	55.4	54.2
Specific gravity at 240 days	(1.0)	87.0	85.9	83.6	85.3	85.0	83.6	88.8	87.0	84.4
Haugh units at 240 days		90.9	88.2	86.5	90.6	90.0	86.0	90.5	92.0	87.7
Blood spots at 240 days	%	3.2	2.2	5.4	2.9	2.0	4.8	2.3	2.1	3.7
Body weight at 365 days	g	1680	1650	1800	1660	1650	1690	1650	1490	1570

* c= unselected control strain; s= selected strain.
Means for traits other than fertility, hatchability and hen-housed egg production are survivors values. Survivors are defined as hens that lived to the end of test and laid at a rate of at least 20% in all three egg production periods, and had a 240 day egg weight.