GENETIC ANALYSES OF GROWTH, SEXUAL MATURATION, AND OVA PRODUCTION IN CHICKENS

by

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DEDICATION

I would like to dedicate this dissertation to the three people who have given me the most support throughout my college career. They are and , , my parents, and , my grandfather.

The three of you deserve much of the credit for what I have accomplished during my nine years of college. Thank you for understanding the long absences and for knowing deep in your hearts that they were necessary. I hope you can appreciate what this education means to me, even though I am not a real doctor.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

Selection for increased juvenile body weight of chickens results in correlated responses in certain traits that enhance economic worth. These traits include earlier ages to achieve market weight, better feed utilization, and higher carcass yields. Correlated responses to such selection can also be unfavorable, with many of the disadvantages being associated with deleterious effects on fitness. In commercial poultry breeding, decreases in number of offspring produced by nuclear and parental breeding flocks, in many cases, have not outweighed the advantages of improved growth rate. This situation is apparent as many breeders include reproductive traits in their selection programs only after exercising independent culling for growth related traits. In some cases, they attempt to overcome reproductive deficiencies by crossing lines. This procedure is realistic because heterosis of reproductive traits is well documented. In addition, heterotic effects reduce mortality and morbidity. Use of the sex-linked dwarf allele (dw) has also shown promise in reducing some of the reproductive problems observed in breeder flocks of meat-type chickens.

The research reported in this dissertation was designed to determine modes of inheritance and mechanisms associated with growth, sexual maturity, and reproduction of chickens. Such information should further facilitate the use of nonadditive genetic variation in poultry breeding.

REVIEW OF LITERATURE

Growth

Postnatal growth of animals can be viewed as the maturation of an individual from birth or hatching to achievement of maximum weight. This process is usually accompanied by an increase in absolute body size (Ricklefs, 1967a), as well as relative changes in organ to body size (Lilja et al., 1985). These events, in turn, contribute to the dynamic status of body composition during the life cycle. Altering growth of birds and mammals can be accomplished by genetic (Eisen, 1980; Dunnington and Siegel, 1985; Marks, 1985) and nongenetic (Keys et al., 1950; Brody et al., 1980) means. In addition, growth curves can be manipulated as a direct (McCarthy and Bakker, 1979) or correlated (Eisen, 1976; Marks, 1978; Anthony et al., 1986) response to selection for body weight. Recently, there has been increased interest in growth as it relates to topical issues (Andrews, 1982), with areas of interest including the biological (McCance, 1977, Ricklefs, 1985), genetical (McCarthy, 1977, Tierce and Nordskog, 1985), nutritional (Scott, 1977), and physiological (Wise, 1977, Evans, 1977) aspects. The author, therefore, refers the interested reader to these papers for additional information.

Onset of Sexual Maturity

Human studies. Research involving young women suffering from anorexia nervosa which is characterized by a lower than

normal body weight at a given age and a failure to achieve menarche, has generated considerable interest. The major focus of these studies is to determine body characteristics which preclude the menstrual cycle. Many studies have implicated body weight as being a key to the normal menarche (Frisch, 1972; Frisch and Revelle, 1970; Frisch et al., 1971), and support the minimum or "critical" weight hypothesis. Yet, individuals suffering from deafness and cystic fibrosis achieve menarche at a body weight lower than the average for normal controls (Chumlea and Malina, 1979; Moshang and Holsclaw, 1980). Environmental and genetic differences among populations also influence weight at the onset of the reproductive cycle. Johnston et al. (1971) reported lower body weights at menstrual onset for Latin American than for North American girls. These findings may be of interest because of the ease of measuring body weight; however, as pointed out by Marshall and Tanner (1969), body weight and pubertal development is quite variable in adolescents. Body weight may, therefore, be an artifact of other developmental factors such as lean mass, adipose mass, and linear growth.

A relationship between body composition and the onset of sexual maturity is well documented (e.g., Osler and Crawford, 1973; Frisch, 1980). The coefficient of variation of body water/body weight at menarche is lower than that for body weight alone (Frisch, 1980), thereby lending support to the concept that an adipose and/or lean mass requirement is necessary for menarche

(Frisch et al., 1973; Osler and Crawford, 1973; Frisch and McArthur, 1974; Frisch, 1976; 1980). Further support for a minimum body fat content comes from numerous studies in which reproductive function ceased after loss of fat from undernourishment, physical exercise and various clinical or psychological syndromes (e.g., Keys et al., 1950; Parizkova, 1963; Boyar et al., 1974; Frisch and McArthur, 1974; Palmer et al., 1975; Warren et al., 1975; Frisch, 1976; McArthur et al., 1976; Knuth et al., 1977; Vigersky et al., 1977; Boyar et al., 1978; Frisch, 1980; Speroff and Redwine, 1980; Warren, 1980; Schwartz et al., 1981; Vandenbroucke and Valkenberg, 1981; Cohen et al., 1982; Frisch, 1982). In addition, endocrinological studies support the minimum adipose concept because circulating hormone levels required for normal menstrual cycling appear to be associated with body weight (Boyar et al., 1974; Palmer et al., 1975).

In contrast to the literature just reviewed, numerous studies do not support a body weight-composition with onset of maturity relationship. Examples of studies which showed a dissociation of body weight or composition and sexual maturity include Crawford and Osler (1975), Dale et al. (1979) Moshang and Holsclaw (1980), Warren (1980), Baker (1981), Schwartz et al. (1981), Speroff (1981), and Caldwell (1982).

Other Mammals. Body weight and body fat as well as age have been identified as factors necessary for animals other than

humans to achieve a reproductive status (e.g., Ball et al., 1947; Rinaldini, 1949; Mandl and Zuckerman, 1952; Widdowson and McCance, 1960; Kennedy and Mitra, 1963; Dickerson et al., 1964; Widdowson et al., 1964; Monteiro and Falconer, 1966; Arije and Wiltbank, 1971; Glass et al., 1976; Dyrmundsson and Lees, 1972; Frisch et al., 1977; Glass et al., 1979). Although there is an age-weight relationship with endogenous hormonal output and anatomical and behavioral changes associated with hormonal secretion, the specific mechanisms have not been elucidated (Brobeck et al., 1947; Piacsek and Meites, 1967; Howland, 1971; Howland and Ibrahim, 1973; Tartelin and Gorski, 1971; Czaja and Goy, 1975; Ojeda et al., 1976, 1980; Rosenblatt et al., 1980; Wuttke et al., 1980).

Age at the onset of sexual maturity can be influenced by climatic factors. Albino rats exposed to subnormal temperatures achieved vaginal opening at lower body weights and younger ages than those maintained at warmer ambient temperatures (Mandl and Zuckerman, 1952). The mechanism for this occurrence was attributed to adipose tissue turnover. Similarly, in seasonally estrus domestic ruminants (Arije and Wiltbank, 1971; Dyrmundsson and Lees, 1972), individuals born late in the spring tended to have their first ovulation at younger chronological ages and lower body weights than those born earlier in the year.

Undernutrition has been used as means of identifying minimum weight for vaginal opening in rats (Kennedy and Mitra, 1963) and

mice (Monteiro and Falconer, 1966). In these studies, animals whose food intake was limited reached vaginal opening at comparable weights but older chronological ages than their ad libitum controls. Although similar results were obtained with gilts (Dickerson et al., 1964), in rats (Widdowson et al., 1964; Merry and Holehan, 1979) vaginal openings occurred at older chronological ages and lower body weights in restricted than in ad libitum fed animals.

Diets inadequate in a basic nutrient or the underfeeding of nutritionally adequate diets postpone the onset of sexual maturity in rats (e.g., Rinaldini, 1949; Kennedy and Mitra, 1963; Piacsek and Merites, 1967; Bakke et al., 1975; Frisch et al., 1975; Glass et al., 1976; 1979; Kirtley and Maher, 1979; Ronnekleiv et al., 1978; Merry and Holehan, 1979; Glass and Swerdloff, 1980; Ramaley, 1981), and mice (Ball et al., 1947; Monteiro and Falconer, 1966). Feeding high and low fat-supplemented diets tends to bring on an earlier maturity in individuals receiving the higher fat diets (Frisch et al., 1975; Kirtley and Maher, 1979) without substantially influencing body weight or composition. This observation may be explained in terms of general nutrition, as well as growth patterns since body fat percentage increases with age at first estrus in both ad libitum and restricted-fed rats (Frisch et al., 1977; Wilen and Naftolin, 1977; 1978). These findings are not universal among genetic lines, as polygenetically obese rats fed either a

synthetic amino acid diet or normal rat chow entered sexual maturity at variable fat percentages (Glass et al., 1976). The same result was reported for restricted-fed and ad libitum fed polygenic obese mice (Eisen and Leatherwood, 1978). Likewise, genetic background, diet and feeding regime have contributed to conflicting results regarding hormonal and body composition studies (Piacsek and Meites, 1967; Howland, 1971; Howland and Ibrahim, 1973).

One explanation for the general tendency toward a body fat requirement for the onset of sexual maturity is that adipose tissue may function as an extragonadal source of estrogen (Frisch, 1980). In addition, aromatization of androgens to estrogens occurs in adipocytes (Nimrod and Ryan, 1975) and it may be hypothesized that more aromatization occurs when there is more adipose tissue. Although support for this hypothesis is that hyperplastic growth of adipose tissue usually ceases prior to sexual maturity (Hirsch and Han, 1969; Hirsch and Knittle, 1970; Salans et al., 1971; Harris, 1980), there are examples of hyperplastic adipose tissue growth in sexually mature animals (e.g., Johnson et al., 1971; Lemonnier, 1972; Bertrand et al., 1978; Faust et al., 1978). Thus, while there is considerable literature on the subject, the role of body weight and fat percentage in relation to the onset of sexual maturity remains elusive for mammals.

Birds. The manipulation of body weight and age at sexual

maturity is a routine husbandry practice in poultry production suggesting that much is known about sexual maturation and initiating factors. Yet, a survey of the literature shows the same conflicting results for chickens as mammals. Body weight at the onset of lay is usually lower when feed restriction is used as opposed to ad libitum feeding of egg-type pullets (Gowe et al., 1960; Walter and Aitken, 1961; Fuller and Donahoo, 1962; Hollands and Gowe, 1965; Strain et al., 1965), dual purpose breeds (Lister et al., 1966), meat-type stocks (Proudfoot and Lamoreaux, 1973; Brody et al., 1980), turkeys (Hulet and Brody, personal communication), and Japanese quail (Zelenka et al., 1984).

When fed ad libitum, dams of meat-type chickens tend to enter lay when an adequate age is achieved (Leeson and Summers, 1983; Dunnington et al., 1983). In egg-type stocks such as White Leghorns, however, it appears that weight is relatively more important than age in initiating lay. This situation may occur because these birds are selected for early age at maturity and small body size. In both cases, the weight-age pattern exists (Dunnington et al., 1983; Dunnington and Siegel, 1984). Japanese quail exhibit both a minimum age and weight requirement for the onset of lay (Zelenka et al., 1984). Where there is an age but no weight difference at the onset of sexual maturity between restricted and ad libitum fed quail (Morse and Vohra, 1971), it is probable that all groups exceeded the minimum age prior to

reaching their minimum weight. Weight, however, is only a convenient measure and should not be regarded as the sole criterion necessary for lay after a minimum age is achieved. More likely, other growth-related characteristics, such as skeletal development, lean body mass and adipose mass may have a larger impact on lay than body weight per se (Brody et al., 1984; Bornstein et al., 1984; Zelenka et al., 1984), with adipose tissue capable of hyperplastic and hypertrophic growth after sexual maturity (Oruwari et al., 1986) in Japanese quail.

The importance of body composition for egg production has been demonstrated in several avian species. Experienced mallards (McLandless and Raveling, 1981) and Canadian geese (Krapu, 1981) enter breeding groups with more body fat than inexperienced pullets. At the breeding grounds, experienced hens eat more nutrient rich invertebrates and maintain their body weight better than pullets. Fat content is also important in passerines (Ricklefs, 1967b); the energy content per gram of body weight increases from young birds until sexually mature in Red-Winged blackbirds and barn swallows.

Differences in lean tissue exist between birds in reproductive and non-reproductive states (Ward, 1969; Jones and Ward, 1976). Both Yellow-Vented Bulbul and Red-Billed Quilea appear to be dependent upon protein status for the onset and cessation of the breeding season. Other species are regulated by both fat and protein (Fogden and Fogden, 1979). The Grey-Backed

Camaroptera, as would be expected from a dual character control mechanism, have a very irregular breeding season (i.e., they tend to breed during rainy periods when food is readily available). Similarly, chickens selected for low juvenile body weight for 25 generations showed a lower incidence of achieving egg production than those selected in the opposite direction (Dunnington and Siegel, 1984).

In chickens, heterosis has been observed for many traits (e.g., Jeffrey, 1939; Coleman, 1950; Dickerson et al., 1950; King, 1951; King and Bruckner, 1952), with age at onset of lay being among the first traits where heterosis was described (Warren, 1927). Yet, over half a century later, little is known as to why this trait, which is one of the more important ones in the production of commercial poultry, shows such a pronounced heterotic effect.

In summary, it is well documented that diet, feeding regime, and genetic background influence age at sexual maturity. Body weight as well as age at onset of lay can be influenced by these variables. One goal of this dissertation was to elucidate the role of age, body weight and composition on age at sexual maturity in pullets divergently selected for 56-day body weight.

Erratic Ovulation and Defective Egg Syndrome

The occurrence of a pullet laying an egg that contains two eggs with shells (Drew, 1907) and multiple yolked eggs (Curtis, 1914) is not uncommon with the incidence of the latter (multiple

ovulations) greater by several orders of magnitude than that of the former. Multiple ovulations may be simultaneous and/or sequential and are more common in meat than egg-type stocks (Scott, 1940; Jaap and Muir, 1968). In the case of sequential ovulations, the first egg remains in the uterus longer than is necessary and the second ovum enters the occupied uterus (Foster, 1970). The first egg becomes over-calcified (van Middelkoop and Simons, 1970) while the second egg becomes odd shaped from pressing against the already formed egg before plumping has occurred. The second egg was originally termed truncated (Romanoff and Romanoff, 1949), but later it was renamed compress-sided to describe both the cause and shape of the malformation (Foster, 1970; van Middelkoop, 1972). Embryos from both extra-calcified and compress-sided eggs rarely hatch due to faulty air movement through the shell. Yet, the condition is not self-eliminating from the population and may have a positive correlated response to selection for body weight (Reddy and Siegel, 1976).

Other than two shell eggs produced in one day, which is more a function of erratic oviposition (van Middelkoop, 1971), near simultaneous ovulation of two or more yolks can result in double, triple, and quadruple-yolked eggs. This occurrence has been widely described (Curtis, 1914; Lowry, 1967; Sarvella, 1975; van Middelkoop and Siegel, 1976). It appears that, in most cases, both yolks contained in one egg begin the rapid phase of

development and ovulate simultaneously (Buss, 1963). Less often, yolks differ greatly in size. This occurrence may be due to premature ovulations of an underdeveloped yolk, two yolks developing in one follicle (Skalko et al., 1972) or because of a malfunctioning process of oogenesis (Olsen and Frapps, 1950). There is genetic variation for multiple ovulations (Lowry and Abplanalp, 1968, 1984; van Middelkoop, 1972; Sarvella, 1975; Siegel et al., 1978) with heritability estimates considered as moderate.

Several studies were conducted during the late 1960's through the mid 1970's to describe erratic ovulation and defective egg syndrome (EODES). Jaap and Clancy (1968) found upon laparotomy more follicles in rapid development in meat than in egg-type pullets. Yet, oviposits are less in meat than in egg-type chickens. This observation was further illustrated when Jaap and Mohammadian (1969), using fat soluble dyes, a technique developed near the turn of this century (Riddle, 1908), showed that the number of follicles in rapid development of meat-type chickens was about two fewer than was found by autopsy. This may be due to a number of factors including follicular atresia and internal laying. Wood-Gush and Gilbert (1970) estimated the rate of internal ovulation to be over 11% by observing birds which entered nest boxes but did not lay. Follicular atresia is higher in turkeys selected for growth than in those selected for egg production (Bacon et al., 1973), and is greater in chickens

selected for high than for low body weight (Udale et al., 1972; Reddy and Siegel, 1976).

One explanation (Jaap, 1969) for the overproduction of yolk mass by meat-type chickens was that birds selected for rapid growth had metabolic patterns which favored an increased production of lipoprotein precursors in the liver and an increased deposition of yolk material in ovarian follicles. Bacon et al. (1973) later found that the low density factors of plasma lipoproteins did not change with selection for increased body weight of turkey pullets.

Selection to increase normal egg production has been done under continuous lighting (Sheldon and Podger, 1972; Sheldon et al., 1984), and by changing the length of light-dark cycles (Foster, 1972, 1981, 1985; Naito et al., 1985). In addition to making gains due to direct selection and crossing (King and Bruckner, 1952), the dwarfing allele (Abplanalp, 1984) may increase the number of hatching eggs. The former case occurs by increasing ova formation and the latter occurs by reducing defects.

Little is known on the mode of inheritance of yolk formation and the length of time simultaneously ovulated ova are developing. Although methods for determining the duration of yolk formation have been used since the early part of this century (Riddle, 1908), abnormal egg production has been and will continue to be a problem under current selection practices used

in broiler breeding programs. A better understanding of EODES would be of benefit to the broiler and turkey industries which are plagued with reproductive problems in their breeder populations.

CHAPTER I

GROWTH TO SEXUAL MATURITY OF DWARF AND NONDWARF WHITE ROCK CHICKENS DIVERGENTLY SELECTED FOR JUVENILE BODY WEIGHT

INTRODUCTION

Growth, a complex biological phenomenon influenced by genetic and environmental factors, is usually measured in domestic and laboratory animals as change in body weight over time. Such change includes both mass and composition of the individual. Genetic variation of growth has been measured in chickens (Krause et al., 1967), quail (Marks, 1978), and turkeys (Johnson and Gowe, 1962), and selection experiments for body weight at specific ages have been conducted with these species (e.g., Marks, 1985; Nestor, 1985; Siegel and Dunnington, 1985). Similarly, genetic variation in growth rate of rodents has been investigated (e.g., Roberts, 1966; Eisen, 1976, 1980), and selection indices have enabled researchers to directly alter growth curves of mice (e.g., McCarthy and Bakker, 1979).

Growth has been viewed as change in weight over elapsed time (Brody, 1945), at a specific chronological age (Roberts, 1966; Dunnington and Siegel, 1985), at a specific physiological stage in life (Reddy and Siegel, 1977a; Dunnington et al., 1983), and in relation to a final body weight (Ricklefs, 1967). Andrews (1982) related growth to changes in resource allocation during the life cycle. She discussed the patterns of growth in reptiles with respect to relative size at hatching, sexual maturity, maximum size, and as an adult. In female chickens, dramatic changes in body weight and carcass composition occur just prior to the onset of egg production (Zelenka et al., 1986). This

paper compares rate of growth to the onset of egg production (sexual maturity) in dwarf and nondwarf populations of chickens known to differ in age, in body weight, and in carcass composition at this stage in life. Comparisons were based on various equations which describe growth (Ricklefs, 1967), in order to determine whether divergent selection for juvenile body weight caused growth to change in such a way that the growth patterns of the stocks were represented better by different growth equations.

MATERIALS AND METHODS

Stocks. Female chickens from each of five nondwarf and two dwarf populations were used in this experiment. Parental lines were nondwarf White Plymouth Rock chickens divergently selected for 24 generations for high (HN) and low (LN) juvenile body weight (Siegel, 1978; Dunnington and Siegel, 1985). These parental lines were mated to produce the reciprocal F_1 crosses (HL and LH). An F_2 was produced from HL x HL matings. In designation of crosses, the sire population is shown first and the dam second. After 13 generations of divergent selection, the sex-linked recessive allele (dw) for dwarfing (Hutt, 1959) was introduced into samples of the HN and LN lines by mating females from these lines to males of a commercial meat-type stock which carried the dwarf allele (Reddy and Siegel, 1977b). Through repeated backcrossing of heterozygous males to normal females from each selected line, two populations resulted, HD and LD, which were of the same genetic origin as the HN and LN lines, respectively. After ten generations of backcrossing, the HD and the LD populations were maintained for two generations by random mating of dwarf males and females.

Husbandry. Chicks from all mating combinations were produced from age-contemporary parents. On the 22nd day of incubation, chicks were removed from the hatcher, wing-banded, vaccinated for Marek's disease, vent-sexed, and females were placed in litter-floor pens. Lighting was continuous until the

chicks were 14 days of age, after which light was provided from 0600 to 1800 hr. At 57 days, the pullets were moved to a windowed house and exposed to natural lighting until 127 days of age. They were then moved to a windowless house, individually caged, and provided artificial lighting from 0600 to 2000 hr. Starter, developer, and breeder diets (Siegel, 1962) in mash form, and water were provided ad libitum.

Individual body weights were obtained at 1, 8, 15, 22, 29, 42, 57, 71, 85, 99, 113, 127, and 141 days of age. After 141 days of age, each pullet was weighed weekly until all pullets within a mating combination commenced lay.

Analyses. Body weights were measured within mating combinations and expressed as a function of time (Ricklefs, 1967) using the following equations:

Logistic $W = 1/(1 + be^{-ke})$

Gompertz $W = e^{-bk^{-kt}}$

von Bertalanffy $W = (1 - be^{-kt})^3$

where W is body weight expressed as a percentage of body weight at sexual maturity, t is time, b is a constant such that the point of inflection at t = 0 when b = 1 for the Logistic and Gompertz equations and 1/3 for the von Bertalanffy equation, and k is a constant proportional to the specific growth rate (dw/dt) at the point of inflection, with the specific proportions being 4, e, and 4/9 for the Logistic, Gompertz, and von Bertalanffy equations, respectively.

For each mating combination, linear regressions were calculated for body weight expressed as a degree of maturity (DM). The equation was:

$$W = a + bt$$

where W is body weight expressed as a percentage of body weight at sexual maturity, and t is time.

Growth curves were standardized in two fashions to describe age and body weight in terms of degree of sexual maturity. Initially, ages were standardized to age at sexual maturity, resulting in values on the x-axis ranging from 0 to 100% and actual body weight on the y-axis. Subsequently, both age and body weight were standardized so that their respective values at sexual maturity were 100%, because populations differed greatly in age and body weight at sexual maturity (Table 1). This standardization also placed all populations on the same physiological scale.

For genetic analyses, data for lines HN and LN were used both in comparisons of alleles at the dwarf locus and those involving reciprocal F_1 and F_2 crosses. In the latter case, inferences about the modes of inheritance were made from nonorthogonal linear contrasts (Scheffe, 1970).

RESULTS AND DISCUSSION

Growth to sexual maturity. Growth patterns from hatching to sexual maturity are presented for each population in Figure 1. R^2s were largest for DM in all populations except HN where R^2 was slightly higher for the Gompertz equation (Table 2). Weight at maximum growth rate (Wi) differed according to population and method of expressing growth. For DM, age at inflection (Ai) was 50 days for all stocks except LN, which was 120 days of age. Occurrence of the inflection at the same age for dwarf and cross populations was consistent with the suggestion of a stabilizing influence of the dwarf allele in divergently selected weight populations (Reddy and Siegel, 1977b). Also, the relaxing of selection during the last two generations in the dwarf populations may have contributed to stabilization.

Ai occurred earlier for DM and von Bertalanffy than for the logistic and Gompertz equations in all stocks except LN where Ai was intermediate for DM. In all cases, Ai was highest for the logistic equation. Grossman et al. (1985) reported in male and female flocks of Rhode Island Reds and White Leghorns, the logistic equation overestimated Ai for all groups except male White Leghorns.

Degree of maturity. The stocks used in this experiment were, by design, considerably different in age and body weight at sexual maturity (Table 1). When growth was expressed relative to age at sexual maturity, growth of LN pullets differed from that

of LD, HN, and HD in that its early growth was slower and the curve remained concave for an extended period (Figure 2A). As a result, LN pullets were not heavier than the LD birds until attaining a weight of about 400 g. After Ai, growth of LD and HD pullets slowed. Growth from hatching to onset of lay of the F_1 and F_2 crosses approximated the midpoint of the parental lines (Figure 2B).

When ages and body weights were simultaneously standardized for their respective values at sexual maturity, divergence of the curves was greatest between 10 and 90 percent (Figure 4). Patterns for dwarfs were similar to those for the HN chickens (Figure 3A), growth patterns of the crosses were intermediate to those of the parental populations (Figure 3B). Thus, growth relative to body weight and age at sexual maturity, while influenced by additive genetic variation, may have been compensated for by the stabilizing effects of the dw allele (Reddy and Siegel, 1977b).

Genetic analyses. Characterization of growth of normal and dwarf chickens differed depending on whether the criterion was actual or body weight expressed relative to body weight at sexual maturity, and the background genome (Figure 4). Contrast A showed that HN pullets were heavier than HD pullets. When, however, body weight was expressed relative to body weight at sexual maturity, HD pullets were heavier than HN pullets at one day of age but the relationships reversed at 85 days and

subsequent ages. The difference at one day of age, which can be attributed to egg weight (Payne et al., 1957; Reddy and Siegel, 1977b), was overcome at subsequent ages by the faster growth of HN than HD chickens. The minor influence of allele dw on growth at young ages observed here is consistent with previous reports (e.g., Hutt, 1959; Reddy and Siegel, 1977b).

Growth comparisons of normal and dwarf pullets in the low-weight line (Contrast B) were different from those observed in the high-weight line. Although LN chicks were heavier than LD chicks at one day of age due to differences in egg weight, the latter grew faster and for the period from 29 to 57 days of age were heavier than LN ones. After 57 days of age, however, the only difference in body weight between these populations was at 204 days of age when there was a slight decline in the weight of LD chicks. Contrary to results found for absolute body weight relative to body weight at sexual maturity, LD pullets had a higher body weights than those of LN pullets at all ages.

The consistent difference in body weight of the two parental lines (Contrast C) was a function of divergent selection for juvenile body weight and correlated responses in egg weight (Dunnington and Siegel, 1985). Although body weight relative to body weight at sexual maturity was different at all ages except eight days, line LN pullets were relatively heavier at hatch than HN pullets. The faster-growing HN chicks made up this difference by eight days and, after this age, they were proportionately

heavier than those from line LN.

Contrast D, which evaluated weight differences between the dwarf stocks, illustrated additive genetic variation, as was observed with the normal populations. Whereas the dw allele decreased body weight, the extent of the reduction was influenced by the background genome. For example, weights from 1 to 22 days of age represented a greater proportion of body weight at sexual maturity in LD than in HD pullets. After 29 days of age, growth of HD and LD chicks was proportionately similar, indicating that differences at early ages had disappeared. The homeostatic effect of the dw allele was reported for other traits by Reddy and Siegel (1977b).

After some discrepancies at early ages due to effects of egg weight, heterosis was similar and in the same direction for the HL and LH crosses (Contrasts E and F, respectively). This pattern was evident by significance of contrasts for body weight differences at one day of age for HL and LH crosses but not when the crosses were pooled (Contrast G). The difference in hatching weight of reciprocal crosses was because the dams of the HL cross laid smaller eggs than dams of the LH cross. Effects of egg weight on body weight disappeared by 8 and 15 days, respectively, in HL and LH chicks. Contrasts involving either or both HL and LH crosses were not significant until after 57 days of age. Heterosis of body weight relative to body weight at sexual maturity was significant whenever HL and LH crosses were analyzed

simultaneously (Contrast G), and almost always significant when analyzed separately (Contrasts E and F) with the difference again being due to egg weight. These results illustrate that crosses were physiologically more advanced than their parental populations at fixed chronological ages, i.e., the developmental rate was greater for crosses than for the parental lines.

Recombination effects differed depending on whether the F_2 generation was compared to its parental F_1 (Contrast H) or if the parental lines were included (Contrast I). Contrast H was significant at young ages and reflected differences in egg weight. Compensation for these differences occurred during the first few days after hatch for both body weight and body weight relative to body weight at sexual maturity. Recombination effects for body weight were significant at several ages, all prior to the mean age at first egg in cross HL. For contrast H, body weight relative to body weight at sexual maturity was not significant until 15 to 20 days prior to the onset of lay because, shortly before lay began, proportionate growth rate accelerated in HL pullets relative to F_2 pullets. Similar rapid growth was noted in F_2 pullets which commenced lay shortly after HL pullets. Some of this increased growth was likely associated with yolk development (Zelenka et al., 1986). Conversely, no significance was observed at any age when the HN and LN parental lines were included (Contrast I). Recombination and lack of linkage, therefore, brought the F_2 closer to the mean of its

parent and grandparent populations than the HL cross per se.

For body weight at first egg (Table 2), Contrasts A, B, C, and D were significant, indicating that HN, LN, HD, and LD stocks all commenced lay at different body weights. Contrast E, F, G, H, and I were not significant, illustrating that, when weights were compared at sexual maturity, regardless of chronological age, heterosis and recombination for body weight were small (-.4 to -2%). Hence, heterosis and recombination for body weight at younger ages in these populations were associated with different physiological stages at specific chronological ages.

From the data presented herein, heterosis was present for age at first egg. Heterosis for body weight was frequently observed, especially after the age at which selection was made in the parental lines. Such heterosis, however, was not evident when values were standardized according to degree of maturity.

To determine whether directional selection for a trait such as body weight is effective, weights can be compared at the same chronological ages or as days to reach the same body weight. The data presented in this paper demonstrate that patterns of growth exhibited different modes of inheritance in a chronological and in a physiological time frame. Therefore, when comparing stocks, consideration should be given to the biological and physiological importance of the specific characters being studied because resource allocations vary during the life cycle.

SUMMARY

Growth from hatching to the onset of lay (sexual maturity) was studied in White Plymouth Rock pullets from lines selected for high (HN) and low (LN) 56-day body weight, their reciprocal F_1 crosses, an F_2 cross, and two dwarf stocks originating from the HN and LN parental lines. Growth curves of the dwarf populations resembled more those of line HN than LN. The highest R^2s for describing growth for all populations except HN were obtained when body weight was expressed relative to body weight at sexual maturity. Modes of inheritance differed depending on whether patterns of growth were expressed in a chronological or physiological time frame. Heterosis was present for age at sexual maturity and for body weight after the age at which selection was made in the parental lines. When values were standardized according to degree of maturity, however, heterosis was no longer in evidence.

Table 1. Number of individuals, means and standard errors for weight (g) and age (days) at sexual maturity by population

Population	n	Weight	Age
HN	32	2714 ± 36	171 ± 2
HL	25	1969 ± 25	164 ± 2
LH	36	1968 ± 27	165 ± 2
LN	24	1239 ± 25	253 ± 8
F_2	25	1927 ± 49	176 ± 2
HD	28	2184 ± 48	195 ± 4
LD	31	864 ± 18	219 ± 5

Table 2. R^2 of growth curves of various populations expressed by Logistic, Gompertz, von Bertalanffy, and degree of maturity (DM) equations. Weight (Wi) and age (Ai) at the point of inflection were calculated from these equations

	Populations						
Transformation	HD	LD	HN	LN	HL	LH	F_2
R^2							
Logistic	.921	.967	.951	.964	.966	.961	.964
Gompertz	.881	.956	.986	.918	.976	.920	.987
von Bertalanffy	.847	.937	.978	.882	.943	.889	.975
DM	.987	.986	.980	.992	.994	.995	.997
Wi							
Logistic	1092	432	1356	620	964	964	963
Gompertz	808	320	1004	458	728	728	713
von Bertalanffy	655	259	814	572	590	590	578
DM	674	252	970	559	583	564	513
Ai							
Logistic	82	90	70	131	75	78	85
Gompertz	57	62	53	106	57	59	63
von Bertalanffy	49	50	45	91	50	51	53
DM	50	50	50	120	50	50	50

DM = body weight/body weight at first egg, establishing a fixed physiological stage.

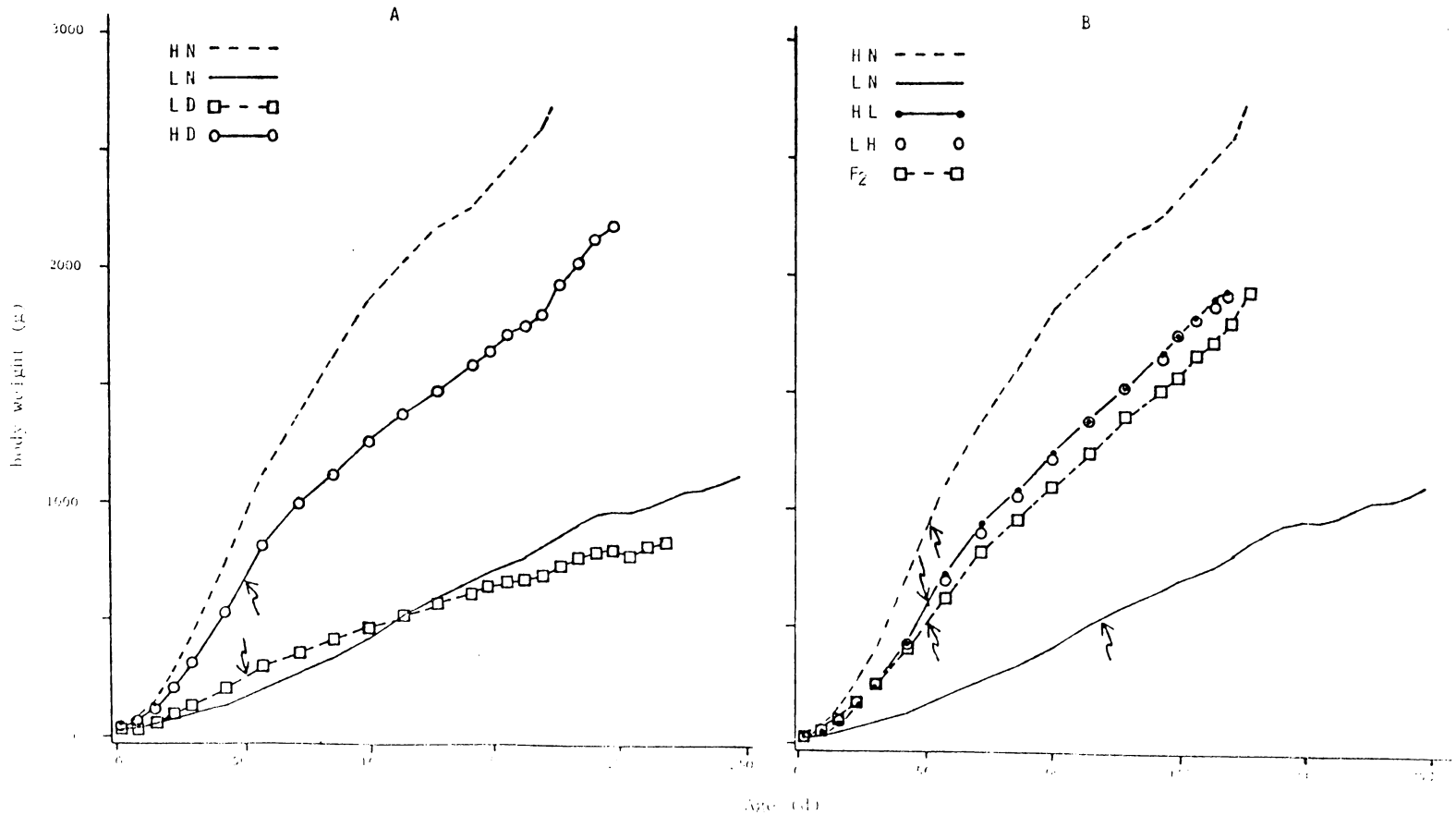

Figure 1. Growth patterns illustrating single allelic (A) and polygenic (B) influences on body weight from hatching to sexual maturity. Arrows show point of inflection.

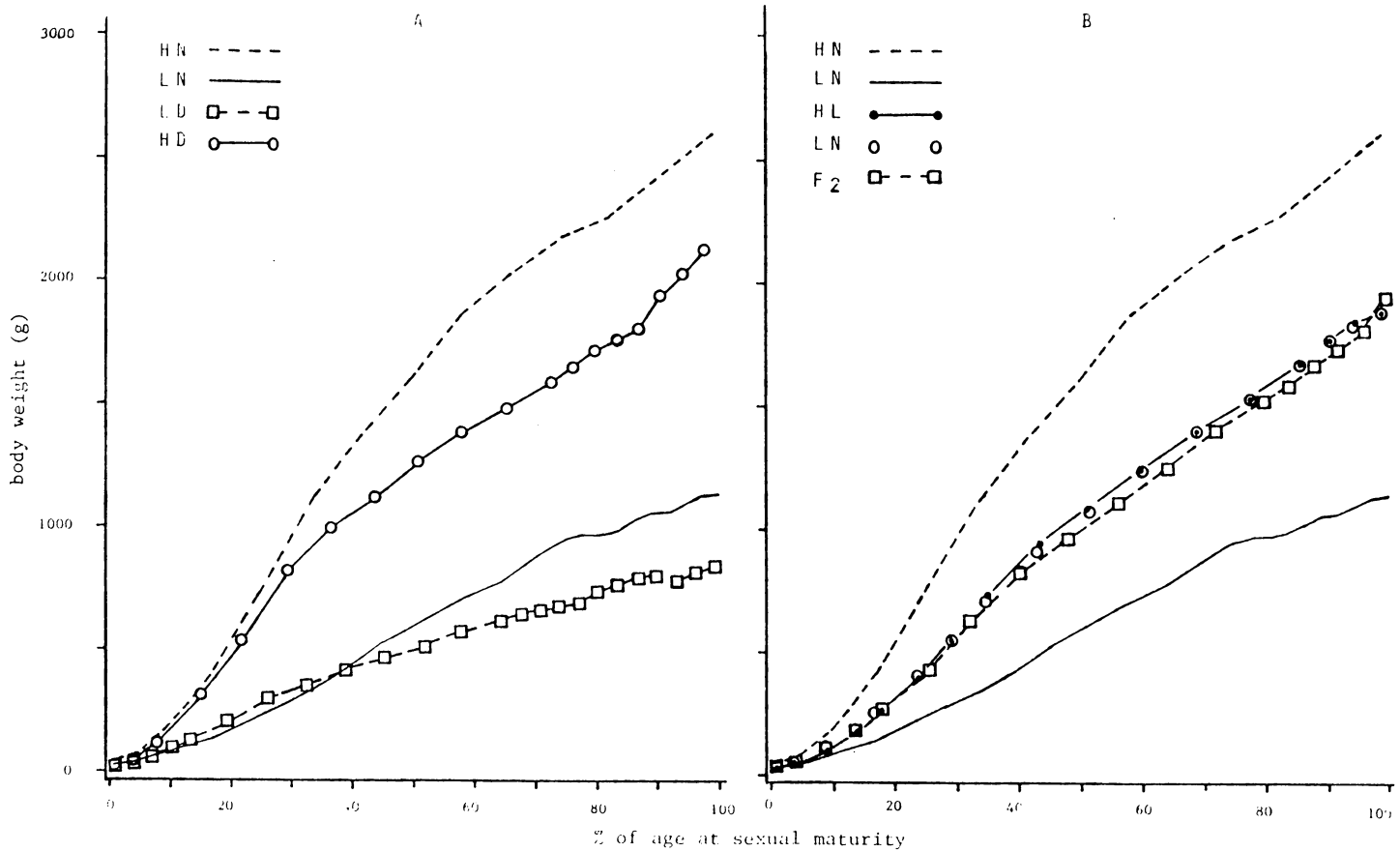

Figure 2. Growth patterns of dwarf and normal chickens (A) and of crosses and parental stocks (B) when chronological age was expressed relative to age at sexual maturity.

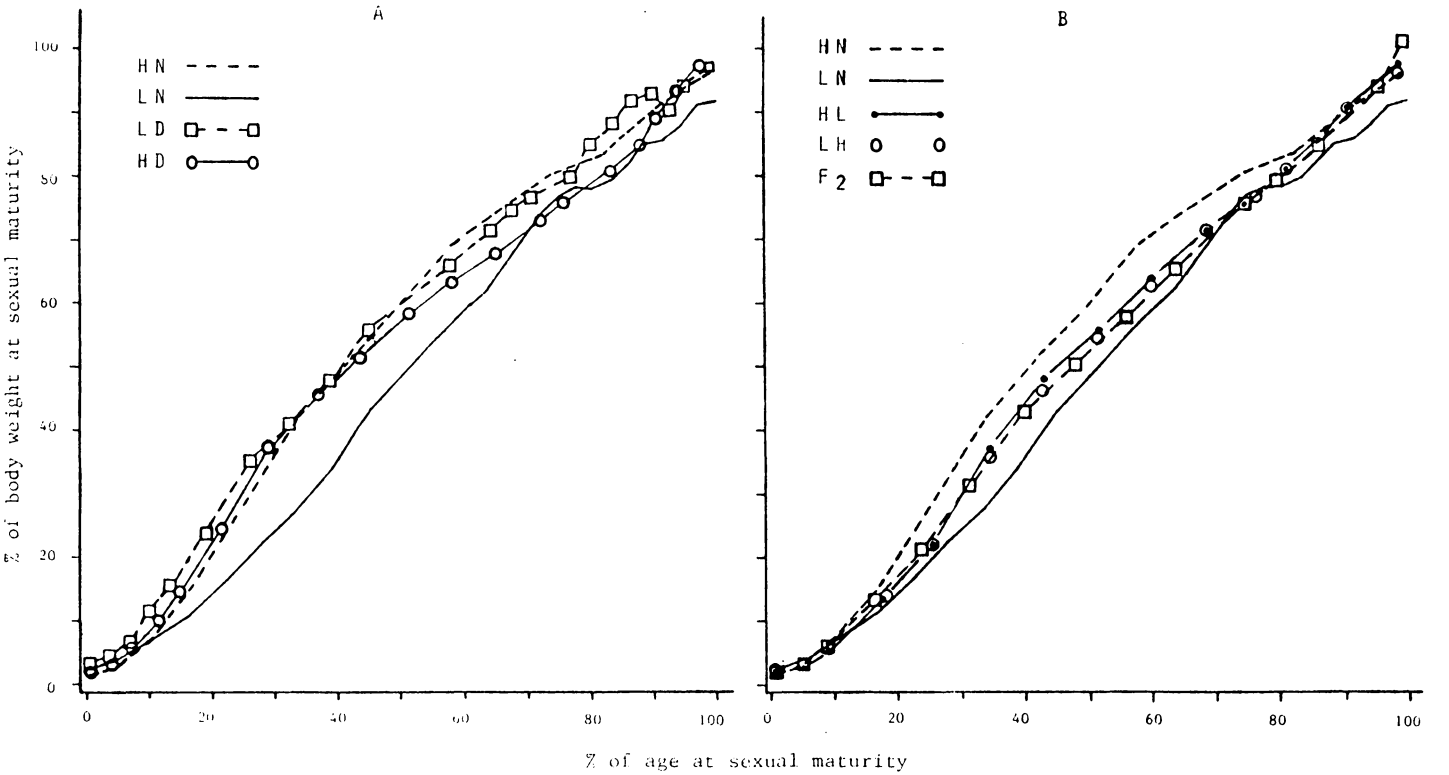

Figure 3. Growth patterns of dwarf and normal chickens (A) and of crosses and parental stocks (B) when chronological age and body weight were expressed relative to age and body weight at sexual maturity.

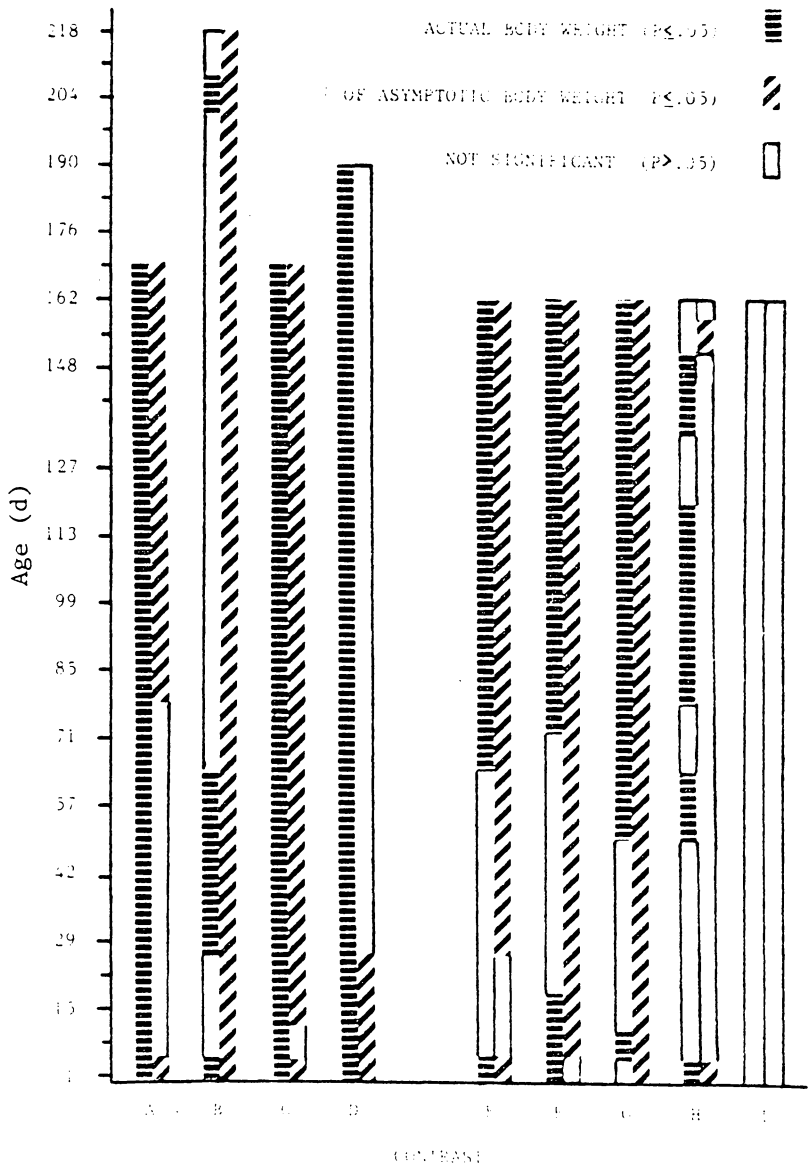

Figure 4. Nonorthogonal linear contrasts of body weights and body weights expressed as a percentage of body weight at sexual maturity (DM).

Contrast		Genetic Context
A	HN-HD	Influence of dw allele in high line
B	LN-LD	Influence of dw allele in low line
C	HN-LN	Direct effect of selection
D	HD-LD	Influence of selection in genomes containing dw
E	[(HN + LN)/2] - HL	Heterosis
F	[(LN + HN)/2] - LH	Heterosis
G	(HN + LN) - (HL + LH)	Nonadditivity
H	HL - F_2	Recombination
I	[(2HL + HN + LN)/4 - F_2]	Recombination

CHAPTER II

SELECTION FOR BODY WEIGHT AT EIGHT WEEKS OF AGE

COMPARISONS OF MATURE AND IMMATURE PULLETS OF THE SAME WEIGHT AND AGE

INTRODUCTION

Although reproductive maturation of poultry may be modified by environmental factors, the onset of lay is limited by age, body weight, and body composition. Unless thresholds are achieved for these variables, chickens and Japanese quail will not ovulate (e.g., Morse and Vohra, 1971; Brody et al., 1980; Soller et al., 1982; Leeson and Summers, 1983; Bornstein et al., 1984; Dunnington and Siegel, 1984; Zelenka et al., 1984). When 50% of the pullets in a flock commenced lay, heterosis was found for breast weight and body weight in the nonlaying portion of populations but not the laying portion (Chapter III), suggesting that lean tissue functions differently in sexually mature and immature pullets. Although some of the difference may be because, when age-matched, layers are heavier than nonlayers (Brody et al., 1984), information is lacking concerning body composition of sexually mature and immature pullets of the same age and weight. This experiment was conducted, therefore, to evaluate the resource allocation of sexually mature and immature pullets of the same age and body weight in diverse genetic populations.

MATERIALS AND METHODS

Stocks. Female chicks from 5 normal and 2 dwarf populations were used in this experiment. The parental lines had undergone 25 generations of selection for high (HN) and for low (LN) 56-day body weight (Dunnington and Siegel, 1985). Other nondwarf stocks included reciprocal F_1 crosses (HL and LH) of the parental lines, and an F_2 cross (from HL x HL matings). For matings to produce the cross populations, the line of the sire is given first and the dam second. After 13 generations of selection, the sex-linked dwarf allele (dw) was introduced into samples of the parental populations by mating Dw/dw males of a meat-type stock with females from each selected line. Through repeated backcrossing of selected line normal females with heterozygous males, high-weight dwarf (HD) and low-weight dwarf (LD) populations were developed. After 10 generations of such backcrossing, the populations were reproduced by random mating among dwarf males and females. The dwarf chickens used in this experiment had undergone 2 generations of the random mating.

Husbandry. Chicks from age contemporary parents were hatched on the same day, vaccinated for Marek's disease, vent-sexed, and wing-banded. Females were placed in litter-floor, light-controlled pens. Lighting was continuous through 14 days of age, after which it was provided from 0600 to 1800 hr. At 57 days, the pullets were moved to a windowed house and exposed to natural photoperiod until 127 days of age. They were then moved

to a windowless house, individually caged, and provided artificial lighting from 0600 to 2000 hr. Starter, developer, and breeder diets (Siegel, 1962) in mash form, and water were provided ad libitum.

At 140 days of age, at least 5 pullets from each population were designated to be killed by cervical dislocation on the day of their first oviposition. Because of the high frequency of LN pullets which do not reach sexual maturity under ad libitum feeding (Dunnington et al., 1984), all pullets chosen within a stock had 57-day body weights within 1.5 standard deviations of the population mean. When a designated pullet laid its first egg, samples of blood obtained via the brachial vein from her and all nondesignated nonlayers of the same mating combination that were within 10% of her body weight were analyzed for total plasma lipid level (Zoellner and Kirsch, 1962). Pullets with total plasma lipid levels less than 750 mg/100 ml were considered as potential age-weight matches, and from this group the match was selected at random, and killed by cervical dislocation.

Traits measured were weight of the live bird (g), breast (g), retroperitoneal (abdominal) fat pad (.01 g), clavicular fat pad (.01 g), liver (.01 g), oviduct (.01 g), developing yolks (> .3 g), and excised right tarsus-metatarsus length (mm). The contents of the alimentary canal were weighed (.01 g) and discarded. The weight was then subtracted from the live body weight.

All body parts were returned to the carcass except yolks and a 10 g sample of liver. Yolk weights were multiplied by .326 (Romanoff and Romanoff, 1949; p. 317) to estimate their lipid weight. Carcasses were then frozen and stored for subsequent chemical analyses. To prepare carcasses for chemical analyses, each was removed from the freezer, and autoclaved for 4 hr at 1.4 kg/cm^2 pressure and 132 C, ground in a meat grinder, mixed in a blender, and then analyzed for total carcass lipid content (Folch et al., 1957). Liver samples were analyzed for total lipid content (Folch et al., 1957).

Statistical analyses. The statistical model used for analysis of variance was:

$$Y_{ijk} = \mu + P_i + S_j + (PS)_{ij} + e_{ijk}$$

where i = 1, 2 . . . 7 populations and j = 1, 2 physiological stages, and k = 1, 2 . . . n individuals.

Prior to analyses, absolute weights and those expressed as a percentage of body weight were transformed to natural logarithms and arc sines, respectively. Percentages were calculated after correcting body weight for reproductive organ weight by subtracting ovary and oviduct weights. Where significant differences among populations were obtained, comparisons among means were performed by Duncan's multiple range test. When the interaction was significant, comparisons were made between physiological stages within each population.

RESULTS

Comparisons were made to determine if those pullets that reached sexual maturity were representative of their respective populations. Patterns among populations for ages and carcass weights at sexual maturity of the samples (Table 2) were consistent with those reported for these populations in Chapter V. The matching procedure was reliable because there were no significant differences in age or in carcass weight between chickens of the two physiological stages. No differences in plasma lipid levels were found among populations nor for the interaction of population by physiological stage. Plasma lipid levels were dramatically different for layers and nonlayers, with means and standard errors being 1737 ± 123 for the former and 461 ± 34 mg/100 ml for the latter, an expected result, because this was the procedure used to differentiate between reproductive stages.

Tarsus-metatarsus length, clavicular fat pad weight and relative breast weight differed among populations, but not between physiological stages nor for the interaction between the main effects (Table 3). Among the nondwarf populations, the extremes were the HN and LN parental lines with the former having larger values. The HL and F_2 crosses were intermediate and different from the parental lines while the LH cross did not differ from line HN for clavicular fat pad weight and relative breast weight. Heterosis and recombination effects were minor

for these traits. As expected, within each weight line, dwarfs had shorter tarsus-metatarsus bones than nondwarfs. There was no difference between dwarfs and nondwarfs within the high line for either weight of clavicular fat or relative breast weight. In the low line, however, these values were higher in the dwarfs than in the nondwarfs.

Differences were found between physiological stages and populations for liver weight and for lipid-free liver and carcass weights (Table 4), with no interaction of physiological stage by population. Comparisons between physiological stages showed that weights of livers and lean carcasses were heavier in mature than in immature age-weight matches. For liver weight among the nondwarf populations, the parental lines were the extremes with the F_1 and F_2 crosses intermediate and different from the parental lines. The pattern was the same for lipid-free carcass weight except that the mean for the F_2 was greater than that for the HL cross. Within both the high and low-weight lines, values for the dwarfs were smaller than those for their normal counterparts.

The relationship between mature and immature pullets was inconsistent among populations for breast and abdominal fat pad weights and carcass lipid traits as evidenced by significant population by physiological stage interactions for these traits (Tables 5 and 6). Correcting for lipid contained in the ovary did not eliminate the interactions for carcass lipid traits.

Such lipid was only a small part of the total carcass lipid, being greatest (29 g) in the mature HN line pullets. Physiological stage comparisons within lines showed that the deviant population was line LN. This conclusion was made because means for immature pullets were smaller than those for mature ones in this line, while there was no difference between mature and immature pullets in any of the other populations (Tables 5 and 6). When line LN was omitted from the analysis of variance, the physiological stage by population interaction disappeared, demonstrating further that this population was deviant. When comparisons were made for this data subset (i.e., all populations except LN), differences were found among stocks for breast, abdominal fat pad, and carcass lipid weights, but not percent carcass lipid. There was no difference between physiological stage groups for any of these traits (Table 7).

DISCUSSION

Pullets must reach certain minimum body weights and ages for the onset of sexual maturity, with the former exhibiting less variation than the latter (Dunnington et al., 1983; Dunnington and Siegel, 1984). Specific ages and body weights at onset of lay vary with population and may be modified by environmental factors such as photoperiod (Nesheim et al., 1979) and feeding regime (Brody et al., 1980). Age at first egg, which may be considered a measure of developmental age, is influenced by additive and nonadditive genetic variation. It responds readily to artificial selection (Komiyama et al., 1984) and it has been known for decades to exhibit heterosis (Warren, 1927). The data obtained in this experiment showed correlated responses in parental lines to selection for juvenile body weight, heterosis, and the effect of the sex-linked dwarf allele. They also demonstrated that line LN pullets respond differently than those from the other populations. The reason for deviation of line LN may be attributed to feeding behavior and/or metabolic differences (see Siegel et al., 1984).

Results from the remaining 6 stocks where mature and immature pullets were age and weight-matched support the hypothesis that a certain fat to lean ratio is necessary for females to reach sexual maturity (Frisch et al., 1973). Both fat and lean contribute to the nutrient reserves of the individual, and these reserves are essential in determining reproductive

state and clutch size of water fowl (Ankney and MacInnes, 1978; Krapu, 1981; Alisauskas and Ankney, 1985). Similarly, loss of carcass nutrient reserves are observed when molting procedures cause a cessation of lay in chickens (see review by Wolford, 1984). Although immature pullets in this experiment had less lean tissue reserves than mature ones, there were no differences in soluble breast protein levels among populations or between physiological stages. Means were 47 mg/100 g and 50 mg/100 g breast tissue for mature and immature pullets, respectively, indicating breast tissue turnover was not elevated in the former, a situation which was observed in reproductively active red-billed Quelea (Jones and Ward, 1976). Also, the correction of total carcass lipid for yolk lipid had no influence on the general results suggesting that the carcass nutrient reserves were used for more than reproductive organ development. An increase in nutrient reserve at the time of sexual maturity has an evolutionary basis as anorexic behavior has been observed in nesting Jungle fowl (Sherry et al., 1980). Because resource allocation varies with biological functions during the life cycle of an individual, threshold levels of nutrient reserves may be achieved by the accumulation of lean, fat, or both, independent of chronological age or body weight per se. Evidence for this hypothesis is provided by the age-weight matched paradigm used in this experiment.

SUMMARY

Body component and compositional traits of sexually mature and immature pullets of the same age and weight were measured in several genetic backgrounds. Populations included parental lines of White Plymouth Rock chickens selected 25 generations for high and low juvenile body weight, their reciprocal F_1 crosses and an F_2, as well as dwarf and nondwarf pullets from the respective parental lines. Although mature and immature pullets were matched for age and body weight, liver and lipid-free carcass weights were larger for the former than for the latter. Population by physiological stage interactions for breast weight and adiposity traits resulted from the pattern between mature and immature pullets from the low body weight differing from that of the other populations. The data supported the hypothesis that specific compositional requirements, independent of age and body weight, are necessary for the onset of egg production. They also demonstrated physiological buffering properties of heterozygosity and of the sex-linked dwarfing allele (dw).

Table 3. Means and standard errors for age and carcass weight by population and physiological stage[1] at time of sacrifice (sexual maturity)

	Age	Carcass weight[2]
	(d)	(g)
Population		
HN	177 ± 4^{c}	2631 ± 45^{e}
HL	163 ± 3^{ab}	1776 ± 50^{c}
LH	159 ± 2^{a}	1906 ± 40^{cd}
LN	213 ± 7^{e}	1168 ± 32^{b}
F_2	173 ± 2^{c}	1899 ± 70^{cd}
HD	193 ± 6^{d}	1968 ± 62^{d}
LD	208 ± 2^{e}	796 ± 36^{a}
Physiological stage		
Mature	184 ± 4^{a}	1753 ± 92^{a}
Immature	184 ± 4^{a}	1687 ± 96^{a}

a,b,c,d,e Means having the same superscript were not different ($P > .05$).

[1]The population by physiological stage interaction was not significant for these traits ($P > .05$).

[2]Carcass weight = body weight - (ovary wt + oviduct wt).

Table 4. Means and standard errors for tarsus-metatarsus (TM) length (mm), clavicular fat pad (g) and breast weight[1] by population and physiological stage[2]

	Length	Weight	
	TM	Clavicular fat	Breast
Population			
HN	83 ± 1^{e}	13 ± 1^{c}	17.3 ± .3^{c}
HL	79 ± 1^{d}	7 ± 1^{b}	15.5 ± .4^{b}
LH	79 ± 1^{d}	10 ± 1^{bc}	16.3 ± .3^{bc}
LN	70 ± 1^{c}	2 ± 1^{a}	14.3 ± .4^{a}
F_2	79 ± 1^{d}	8 ± 1^{b}	15.7 ± .4^{b}
HD	60 ± 1^{b}	8 ± 2^{bc}	16.7 ± .3^{bc}
LD	45 ± 1^{a}	5 ± 1^{b}	16.5 ± .7^{bc}
Physiological stage			
Mature	71 ± 2^{a}	7 ± 1^{a}	16.3 ± .3^{a}
Immature	71 ± 2^{a}	7 ± 1^{a}	15.7 ± .3^{a}

^{a,b,c,d,e}Means having the same superscript were not different ($P > .05$).

[1]Breast = (breast wt/carcass wt) x 100.

[2]The population by physiological stage interaction was not significant ($P > .05$).

Table 5. Means and standard errors for liver weights and lipid-free liver and carcass weights (g) by population and physiological stage[1]

	Weight	Lipid-free wt[2]	
	Liver	Liver	Carcass
Population			
HN	46 ± 3^{d}	42 ± 3^{d}	2189 ± 32^{e}
HL	33 ± 2^{c}	32 ± 2^{c}	1489 ± 47^{c}
LH	37 ± 2^{c}	35 ± 2^{c}	1609 ± 36^{cd}
LN	21 ± 1^{b}	20 ± 1^{b}	1029 ± 28^{b}
F_2	39 ± 3^{c}	33 ± 3^{c}	1639 ± 61^{d}
HD	34 ± 4^{c}	30 ± 3^{c}	1672 ± 50^{d}
LD	14 ± 1^{a}	14 ± 1^{a}	673 ± 32^{a}
Physiological stage			
Mature	35 ± 2^{b}	32 ± 2^{b}	1567 ± 54^{b}
Immature	28 ± 2^{a}	26 ± 2^{a}	1472 ± 45^{a}

a,b,c,d,e,f Means having the same superscript were not different ($P > .05$).

[1]The population by physiological stage interaction was not significant ($P > .05$).

[2]Lipid-free carcass weight determined from carcass weight including oviduct.

Table 6. Means and standard errors by population-physiological stage subclass for breast (g) and abdominal fat pad (g) weights

	Weight (g)			
	Breast		Abdominal fat pad	
	Mature	Immature	Mature	Immature
Population				
HN	442 ± 16	468 ± 10	63 ± 5	81 ± 10
HL	295 ± 15	253 ± 5	39 ± 7	34 ± 2
LH	319 ± 16	302 ± 9	47 ± 7	43 ± 7
LN	188 ± 8*	148 ± 8	32 ± 6*	9 ± 1
F_2	305 ± 18	289 ± 9	56 ± 14	33 ± 7
HD	330 ± 24	328 ± 9	53 ± 6	46 ± 3
LD	137 ± 7	128 ± 6	16 ± 2	17 ± 4

*Identifies that the mature pullet means were significantly ($P \leq .05$) different from the immature pullet means.

[1]The population by physiological stage interaction was significant ($P \leq .05$).

Table 7. Means and standard errors by population-physiological stage subclass for carcass lipid traits[1]

	Carcass lipid wt (g)		Carcass lipid/ carcass wt[2]	
	Mature	Immature	Mature	Immature
Population				
HN	436 ± 24	564 ± 61	15.8 ± 0.7	20.9 ± 1.9
HL	314 ± 14	305 ± 39	16.1 ± 0.7	17.8 ± 1.8
LH	314 ± 13	322 ± 31	15.5 ± 0.5	17.5 ± 1.4
LN	188 ± 16*	125 ± 7	14.2 ± 1.1*	11.5 ± 0.6
F_2	311 ± 26	274 ± 22	15.1 ± 0.7	14.7 ± 0.9
HD	342 ± 41	327 ± 23	15.7 ± 1.2	17.0 ± 1.0
LD	145 ± 13	125 ± 14	17.3 ± 0.9	15.7 ± 1.5

*Identifies that the mature pullet means were significantly ($P \leq .05$) different from the immature pullet means.

[1]The population by physiological stage interaction was significant ($P \leq .05$).

[2]Carcass weight including oviduct.

Table 8. Means and standard errors of traits which had significant population by physiological stage interactions[1]

	Weight (g)			Percent[2]
	Breast	Abdominal fat pad	Carcass lipid	Carcass lipid
Population				
HN	455 ± 10^{e}	72 ± 6^{c}	500 ± 39^{c}	18.4 ± 1.3^{a}
HL	274 ± 10^{b}	37 ± 5^{b}	310 ± 20^{b}	17.0 ± 0.9^{a}
LH	310 ± 9^{cd}	45 ± 5^{b}	318 ± 17^{b}	16.5 ± 0.8^{a}
F_2	297 ± 10^{bc}	45 ± 8^{b}	292 ± 17^{b}	14.9 ± 0.6^{a}
HD	329 ± 12^{d}	49 ± 5^{b}	334 ± 22^{b}	16.4 ± 0.7^{a}
LD	130 ± 5^{a}	17 ± 2^{a}	135 ± 9^{a}	16.5 ± 0.9^{a}
Physiological stage				
Mature	304 ± 17^{a}	46 ± 4^{a}	300 ± 17^{a}	15.9 ± 0.3^{a}
Immature	292 ± 18^{a}	42 ± 5^{a}	320 ± 27^{a}	17.3 ± 0.6^{a}

a,b,c,d,e Means having the same superscript were not different ($P > .05$).

[1]Line LN was not included because its presence resulted in a significant ($P \leq .05$) physiological stage by population interaction.

[2]Carcass weight including oviduct.

CHAPTER III

INHERITANCE OF TRAITS ASSOCIATED WITH SEXUAL MATURITY WHEN POPULATIONS OF CHICKENS REACH 50% LAY

INTRODUCTION

Onset of egg production in ground nesting birds is dependent on several interrelated factors including chronological age, body weight, lean mass, adiposity, and skeletal size (Brody et al., 1980, 1984, Krapu, 1981; Dunnington et al., 1983, Leeson and Summers, 1983; Dunnington and Siegel, 1984, Zelenka et al., 1984). Although 50% of lay is a common index of sexual maturity in commercial flocks, descriptions of characteristics associated with onset of lay at this level of production are not available. Also, while heterosis for age at first egg has been documented for over half a century (e.g., Warren, 1927), there is a lack of information concerning the mode of inheritance of variables associated with this trait. This experiment supplied information on the mode of inheritance of body weight, lean carcass traits, shank length, and fat depots of sexually mature and immature pullets when 50% of populations had laid.

MATERIALS AND METHODS

Stocks and husbandry. Female chickens from 8 populations were used in this experiment. Parental lines consisted of White Plymouth Rock lines bidirectionally selected for 25 generations for high (HH) and low (LL) 56-day body weight (Siegel, 1978, Dunnington and Siegel, 1985) and a closed population of Jersey Black Giants (JJ). Mating combinations (sire line presented first and dam line second) were HH, LL, JJ, HL, LH, JH, JL, and F_2 (HL x HL). Chicks from all matings were hatched on December 8th, wingbanded, vaccinated for Marek's disease, sexed, and raised in unisexual flocks in floor pens under natural photoperiod. At 126 days of age, pullets were moved into individual cages in a windowless room and exposed to artificial light from 0600 to 2000 hr. Starter, developer, and breeder diets (Siegel, 1962) in mash form and water were provided ad libitum. The number of pullets in each population differed due to differential mortality and sexing errors.

Traits measured. Individual body weights (g) were obtained at 91 and 126 days of age without fasting. When half of the pullets within a population had laid, all individuals from that population were weighed (g) and killed by cervical dislocation without fasting. Traits measured were: length of right shank (mm), and weights of breast (g), retroperitoneal (abdominal) fat pad (.01 g), clavicular fat pad (.01 g), oviduct (.01 g), and ova in excess of .3 g. Using number of rapidly developing ova,

pullets were classified as layers or nonlayers. Individuals which would not have ovulated within the next 7 days were considered nonlayers.

Statistical analyses. Organ weights listed above were analyzed by analysis of variance as absolute values and as a percentage of body weight. Percentages were calculated after correcting for reproductive organ weight by subtracting ovary and oviduct weights from live body weights. Prior to analysis, absolute weights and percentages were transformed to natural logarithms and arc sine square roots, respectively. Where significant differences were obtained among populations, differences among means were tested by Duncan's multiple range test. Inferences about the mode of inheritance were based on comparisons of specific means and combinations of means within layer-nonlayer categories (Scheffe, 1970). The statistical model was:

$$Y_{ijk} = \mu + P_i + S_j + PS_{ij} + e_{ijk}$$

where $i = 1, 2 \ldots 8$ populations and $j = 1, 2$ physiological stages. The division of populations into layer-nonlayer physiological stages by ovarian development precluded valid ANOVA of ovarian measurements.

RESULTS

Reproductive organs. As expected due to assignment of pullets to layer-nonlayer classifications by ovarian development, ovary and oviduct weights plus number of rapidly developing ova (ova > .3 g) were influenced significantly by population, physiological stage, and the population by physiological stage (layer and nonlayer) interaction. Differences in physiological stage were expected since pullets had been separated into these respective groups by ovarian development. Similarly, differences among populations were expected since oviduct and ovary weights represent a relatively constant proportion of body weight in sexually mature pullets (Brody et al., 1984). The population by physiological stage interaction was due to LL nonlayers having fewer rapidly developing ova and less oviduct development than those from the other combinations. Nonlayers from all other populations had more reproductive organ development, and thus were closer to the onset of lay than the LL pullets.

Body weight. From reproductive organ development at time of killing, retrospective analyses showed that pullets classified as mature at 50% of lay were significantly heavier than those classified as immature at 91 days of age (Table 8). At 126 days of age, the general pattern among stocks and potential layers was similar to that observed at 91 days with an important exception, the interaction of population by physiological stage was significant. This interaction was caused by weight dimorphism

between LL and F_2 layers and nonlayers being disproportionately greater than that for the other populations. Although the interaction was not significant at 91 days of age, this trend was evident (Table 9).

Body weight when 50% of the individuals within a stock had commenced lay was influenced by population, physiological stage, and the interaction between them. The pattern was the same regardless of whether or not weights included reproductive organs (Table 8). As with body weight at 126 days of age, the interaction was due to nonlayers being disproportionately smaller than their laying counterparts in LL and F_2 than in the other populations (Table 9).

Chronological age at 50% production could not be analyzed statistically because it was a single value for a population. As seen in Table 8, it took approximately one third longer for LL pullets to reach 50% lay than the heavier HH and JJ parental populations. Crosses reached 50% lay at ages equal to or younger than their parental lines. Moreover, the outcrosses (JH and JL) were the first stocks in which 50% of the pullets laid. For reciprocal crosses of the high and low weight lines, LH reached 50% lay 5 days before HL, which reached this level at the same age as its HH parental line. The F_2 population attained 50% of lay later than any stock except LL.

Adiposity. There were no population by physiological stage interactions for any adiposity traits, suggesting a similar

relationship across populations. Layers were significantly fatter than nonlayers (Table 9). The relative pattern across stocks for weight of these depots was consistent, as rank correlations between abdominal and clavicular depot weight were .86** and .81* on an absolute and relative to body weight basis, respectively. The pattern of differences among populations was marked. HL pullets had the highest percentage of fat expressed on an adjusted body weight basis (ovary and oviduct weight removed) with JL pullets being the lowest (Table 10). HH, LH, and F_2 pullets were not different than those from the HL cross. JJ pullets had a lower percentage of fat in the abdominal fat depot and a similar amount in the clavicular fat depot as those from HL. As with absolute amounts of fat, there was no difference between populations LL and JL in either percentage abdominal or combined fat. Unlike the absolute clavicular fat depot weight, the JL cross did not differ from LL line in percentage clavicular fat. Moreover, the JL cross had the lowest percentage abdominal and combined fat weights and was not different from JH for these traits. Therefore, while absolute fat depot weight increased concomitantly with body weight, the increase was not proportional.

Breast weight and shank. Breast weight was significantly influenced by population, physiological stage, and the interaction between them. The pattern of layer to nonlayer ratios of the stocks was similar to that for body weight at 50%

lay. Accordingly, the interaction was caused by LL nonlaying pullets having disproportionately smaller breasts than their laying counterparts (Table 9).

Expressing breast weight as a percentage of body weight corrected for ovary and oviduct weight eliminated the population by physiological stage interaction and physiological stage effects. Stock differences persisted with LL pullets having the lowest breast weight per 100 g body weight (Table 11). The mean for the JH cross was highest while those for the other populations were intermediate and not different from each other. Means for JL, JH, and F_2 pullets were also not different from each other.

Population, but not physiological stage differences, were observed in shank length (Table 11). JJ and JH pullets had the longest shanks. While shanks of HH, JL, and LH pullets were significantly shorter than those of JJ and JH, they were significantly longer than those of the F_2, HL, and LL. LL pullets had the shortest shanks.

Modes of inheritance. Differences were observed among purelines for all traits and there were no significant reciprocal effects. This section, therefore, will deal primarily with heterotic and recombination effects.

Heterosis for body weight followed the same pattern regardless of physiological classifications at 91 and 126 days of age, being present in the HL, LH, and JL crosses and not present

in the JH cross (Table 12). Although significant heterosis for body weight at 50% of lay persisted for nonlayers in HL, LH, and JL crosses, it disappeared in the layers of these populations. Recombination values, while generally negative, were not significantly different from zero.

Although age at 50% of lay was not statistically analyzed for reasons mentioned earlier, all F_1 crosses reached 50% lay at younger ages than the average of their parental populations. Crosses involving parental line LL exhibited greater heterosis than those which did not involve LL (contrasts A and B vs contrast C). Recombination percentages were small, inconsistent in sign, and dependent on whether the F_2 was compared solely to its parental line (Contrast D) or if grandparental lines were included (Contrast E).

Contrasts testing for heterosis and recombination were not significant for the adipose depots measured. More important, however, were the percentages and signs of heterosis observed. Regardless of physiological stage, percentage heterosis of the HL and LH crosses was generally large and positive with the greatest effect observed for the clavicular fat depot. JH and JL crosses, unlike those previously mentioned, exhibited negative heterosis. This dichotomy indicates that there is specific combining ability for adiposity. Percentage recombination was generally negative and numerically larger in the nonlayers than layers.

Breast weight at 50% of lay followed a pattern similar to

that for body weight at 50% lay with significant heterosis only observed in HL, LH, and JL nonlaying pullets. Recombination was small but positive in the laying population, and negative and numerically larger for the nonlayers. Percentages of heterosis and recombination for shank length while positive were small (0 to 6%) and not significant (Table 12).

DISCUSSION

Phenotypic correlations between body weight at various ages and age at sexual maturity are variable (see Hutt, 1949), and environmental and genetic correlations may be of like or opposite signs (e.g., Peeler et al., 1955). The data obtained from the purelines and their crosses and reported in this paper showed that when 50% of a flock has commenced egg production, body, breast, and fat depot weights were greater for those pullets which had commenced lay than those which were not in lay. These differences may be due, in part, to differences observed between the layer and nonlayer LL stock. Shanks were of similar lengths. The differences between layers and nonlayers for variables measured were consistent with those reported between reproductively and nonreproductively active individuals in a variety of vertebrate species (e.g., Dickerson et al., 1964, Widdowson et al., 1964; Monteiro and Falconer, 1966; Ward, 1969; Jones and Ward, 1976; Frisch, 1980; Bornstein et al., 1984, Zelenka et al., 1984) including man (Frisch and Revelle, 1970; Frisch et al., 1973; Crawford and Osler, 1975).

Heterotic effects are well documented for age at sexual maturity in the chicken (e.g., Warren, 1927; King, 1951; King and Bruckner, 1952). The degree of heterosis for the onset of lay is a function of traits associated with sexual maturation. At 50% lay when the LL population was a parental line, significant heterosis was noted for body and breast weight in pullets which

had not matured, while values for the laying segment were not significant. This discrepancy suggested that body and breast weight function as different traits in the sexually mature and immature pullets. Although heterotic effects were not significant for fat deposition, the negative heterosis in outcrosses (JH and JL) and the positive heterosis of the HL and LH crosses indicate the importance of specific combining ability in fat deposition. The magnitude and sign reversal between the laying and nonlaying individuals for contrasts A vs B and C were indicative of a genotype by microenvironmental interaction (McBride, 1958).

Loss of heterosis in traits associated with the onset of sexual maturity can be explained in terms of the natural history of the fowl. Gallus gallus spadiceus (Burmese Jungle fowl) females lose body weight throughout the incubation process whether food is plentiful or sparse (Sherry et al., 1980). Thus, natural selection should favor offspring survival of females which enter the breeding season with sufficient nutrient reserves to survive incubation. This thesis has been substantiated in several species of water fowl (Ankney and MacInnes, 1978; Krapu, 1981; Alisauskas and Ankney, 1985). Females which entered the breeding grounds with greater nutrient reserves produced more offspring than those which were in poorer condition.

The deposition of fat and protein prior to the onset of lay should be viewed in its role during the reproductive cycle of the

fowl, that is, egg production, incubation, and care of the young. Although incubation and brooding behavior are no longer required in commercial poultry production, the biological bases have not been precluded in domestic animals (Price, 1984). Since there are large energy demands during egg production and there is evidence of anorexia in Jungle fowl (Sherry et al., 1980) during incubation, the life history of the fowl has placed selection pressure on storage of adequate nutrients prior to the onset of egg production (Ankney and MacInnes, 1978). This reasoning may explain the loss of heterosis for breast weight in the reproductively active portion of the population, as well as why an absolute amount of breast tissue is necessary before breast expressed as a percentage of body weight becomes important as a threshold trait for reproduction.

SUMMARY

In order to study the mode of inheritance of traits associated with the onset of sexual maturity, data from stocks differing in genetic background were analyzed when populations achieved 50% lay. Parental lines were White Plymouth Rocks bidirectionally selected for high (HH) and low (LL) 56-day body weight, and a closed populations of Jersey Black Giants (JJ). Crosses were produced from reciprocal matings of the White Rock lines (HL and LH), their F_2 (HL x HL), and Jersey males mated to weight-line females (JH, JL). When 50% of the pullets within a population had laid, traits were measured for each individual in that group. Retrospective analyses showed that sexually mature pullets were heavier at 91 days of age than those which had not commenced lay, while the layer-nonlayer dimorphism between LL and F_2 pullets was greater than in other populations at 126 days of age, i.e., a population by physiological stage interaction. Fat depots were heavier and percentages of fat higher in layers than nonlayers. Evidence was obtained suggesting that an absolute quantity of breast tissue was necessary before lean tissue percentage became meaningful as a threshold trait for the onset of lay. Modes of inheritance for body weight and compositional characteristics were different in sexually immature and mature pullets, suggesting that muscle functioned differently in laying pullets than those that had not reached this physiological stage.

Table 9. Number of birds, age at 50% lay, and means and standard errors for body weight at various ages by population and physiological stage

	No. birds[3]		Age at 50% lay	Body weight			
						At 50% lay	
	L	NL		91 days	126 days[1]	Total[1]	Adjusted[1] [2]
Population							
HH	11	11	168	2220 ± 20	2410 ± 32	2790 ± 38	2745 ± 35
HL	15	9	168	1577 ± 21	1783 ± 22	2195 ± 31	2142 ± 27
LH	14	10	163	1652 ± 24	1856 ± 27	2163 ± 38	2126 ± 36
LL	6	3	224	628 ± 47	732 ± 47	1330 ± 79	1300 ± 73
F_2	13	10	177	1420 ± 55	1589 ± 64	1968 ± 83	1925 ± 75
JH	14	6	157	2109 ± 38	2331 ± 43	2645 ± 58	2580 ± 54
JL	11	10	161	1569 ± 32	1763 ± 36	2097 ± 42	2053 ± 41
JJ	7	7	170	1864 ± 40	2084 ± 35	2672 ± 51	2603 ± 48
Physiological stage[3]							
L				1729 ± 44[b]	1921 ± 46	2346 ± 45	2275 ± 44
NL				1659 ± 53[a]	1847 ± 58	2199 ± 54	2175 ± 52

[1]The population by physiological stage interaction was significant ($P \leq .05$), hence Duncan's multiple range test was not performed on these data.

[2]Live wt - (ovary wt + oviduct wt).

[3]L = layer, NL = nonlayer.

[ab]Means having the same superscript were not different ($P > .05$).

Table 10. Layer to nonlayer ratios x 100 by population for various traits

Trait	Population							
	HH	HL	LH	LL	F_2	JH	JL	JJ
Body wt.								
91 days	98	106	100	118	114	106	104	108
126 days[1]	98	102	100	122*	116*	104	102	104
Wt. at 50% lay								
Total[1]	103	108	104	134*	118*	113	106	108
Adjusted[1] [2]	100	105	102	130*	116*	110	104	106
Actual adipose depot wt.								
Abdominal	113	115	123	221	150	141	119	130
Clavicular	118	116	120	180	135	137	111	147
Combined	113	115	123	213	147	140	118	133
Adipose per 100 g body wt.								
Abdominal	111	112	120	170	136	127	114	125
Clavicular	116	112	118	140	119	127	104	141
Combined	112	112	120	164	133	127	112	128
Breast wt.								
Actual[1]	100	99	94	136*	116	102	102	109
Per 100 g body	98	97	91	103	99	90	96	102
Shank								
Length	99	99	98	106	102	100	101	100

[1]Population by physiological stage interaction was significant ($P \leq .05$).

[2]Live wt - (ovary wt + oviduct wt).

*Population where layers and nonlayers were different ($P \leq .05$) when the population by physiological stage interaction was significant.

Table 11. Means and standard errors for adiposity traits by population and physiological stage[1]

	Adipose depot wt (g)			Adipose depot wt. (g/100 g body wt.)[2]		
	Abdom.	Clav.	Total	Abdom.	Clav.	Total
Population						
HH	85 ± 7^{d}	14 ± 1^{cd}	99 ± 7^{d}	3.1 ± .2de	0.5 ± .04^{abc}	3.6 ± .2^{cd}
HL	67 ± 3^{c}	14 ± 1^{cd}	81 ± 3^{c}	3.2 ± .1^{e}	0.6 ± .04^{c}	3.8 ± .2^{d}
LH	52 ± 3^{bc}	14 ± 1^{cd}	66 ± 4^{bc}	2.5 ± .1^{bcd}	0.6 ± .04^{c}	3.1 ± .1^{cd}
LL	24 ± 6^{a}	6 ± 1^{a}	30 ± 7^{a}	1.8 ± .1^{a}	0.4 ± .04^{a}	2.2 ± .4^{a}
F_2	58 ± 5^{bc}	11 ± 1^{bc}	69 ± 7^{bc}	2.9 ± .2^{cde}	0.6 ± .06^{bc}	3.5 ± .3^{cd}
JH	50 ± 4^{b}	12 ± 1^{bc}	63 ± 5^{b}	1.9 ± .1^{ab}	0.5 ± .04^{ab}	2.4 ± .2^{ab}
JL	33 ± 2^{a}	9 ± 1^{b}	42 ± 3^{a}	1.6 ± .1^{a}	0.4 ± .03^{a}	2.0 ± .1^{a}
JJ	63 ± 7^{bc}	15 ± 2^{d}	78 ± 9^{bc}	2.4 ± .2^{bc}	0.6 ± .06^{bc}	3.0 ± .3^{bc}
Physiological stage[3]						
L	61 ± 3^{b}	13 ± 1^{b}	74 ± 3^{b}	2.7 ± .1^{b}	0.6 ± .02^{b}	3.2 ± .1^{b}
NL	50 ± 3^{a}	11 ± 1^{a}	61 ± 4^{a}	2.2 ± .1^{a}	0.5 ± .02^{a}	2.7 ± .1^{a}

[1]Population by physiological stage interaction was not significant ($P > .05$).

[2]Percentages were calculated using [body wt - (ovary wt + oviduct w)] as the denominator.

[3]L = layer, NL = nonlayer.

^{abcde}Means having the same superscript were not different ($P > .05$).

Table 12. Means and standard errors for breast weight and tarsus-metatarsus (TM) length by population and physiological stage

	Breast wt.		TM
	g[1]	g/100 g body wt.[2]	mm
Population			
HH	451 ± 8	16.5 ± 0.3^{b}	87 ± 1^{c}
HL	344 ± 6	16.1 ± 0.2^{b}	81 ± 1^{b}
LH	349 ± 8	16.4 ± 0.2^{b}	85 ± 1^{c}
LL	188 ± 12	14.5 ± 0.2^{a}	76 ± 1^{a}
F_2	325 ± 14	16.8 ± 0.2^{bc}	82 ± 1^{b}
JH	457 ± 11	17.6 ± 0.3^{c}	91 ± 1^{d}
JL	345 ± 8	16.8 ± 0.3^{bc}	87 ± 1^{c}
JJ	422 ± 14	16.2 ± 0.4^{b}	91 ± 1^{d}
Physiological stage[3]			
L	373 ± 9	16.4 ± 0.1^{a}	85 ± 1^{a}
NL	364 ± 10	16.7 ± 0.2^{a}	85 ± 1^{a}

[1]The population by physiological stage interaction was significant ($P \leq .05$), hence Duncan's multiple range test was not performed on these data.

[2]Breast percentages were calculated using [body wt - (ovary wt + oviduct wt)] as the denominator.

[3]L = layer, NL = nonlayer.

^{abcd}Means having the same superscript were not different ($P > .05$).

Table 13. Nonorthogonal contrasts[1] and percentages of heterosis and recombination[2] for various traits for layers (L) and nonlayers (NL) when the population reached 50% lay

Trait		Heterosis A[3]	Heterosis B	Heterosis C	Recombination D	Recombination E
Body weight						
91 days	L	14**	22**	4	-6	-1
	NL	14**	32**	0	-14	-11
126 days	L	16**	22**	5	-6	0
	NL	13**	31**	0	-17	-12
Wt. at 50% lay						
Total	L	4	2	-1	-6	-4
	NL	10*	11*	-7	-15	-11
Adjusted[4]	L	4	3	-1	-6	-4
	NL	10*	11*	-7	-14	-11
Age at 50% lay		-16	-18	-7	5	-3
Adipose						
Abdominal	L	7	-30	-33	-4	3
	NL	13	-13	-38	-27	-17
Clavicular	L	30	-22	-21	-13	-1
	NL	52	-8	-19	-25	-10
Total	L	11	-29	-31	-6	3
	NL	19	-10	-35	-26	-16
Shank length	L	1	4	3	3	2
	NL	4	6	1	0	1
Breast weight	L	5	8	1	1	3
	NL	15*	23*	7	-14	-8

[1]Contrast A is (HL + LH) - (HH + LL).
B is JL - [(JJ + LL)/2].
C is JH - [(JJ + HH)/2].
D is F_2 - HL.
E is F_2 - [(2HL + HH + LL)/4].

[2]Percentages heterosis and recombination were calculated as the deviation of the first from the second combination in the contrast.

[3]Since contrasts testing for reciprocal effects (HL - LH) were not significant (P > .05), an average heterosis value is presented.

[4]Live weight - (ovary wt + oviduct wt).

*(P ≤ .05), **(P ≤ .01).

CHAPTER IV

OVA FORMATION AND MULTIPLE OVULATIONS IN LINES OF WHITE PLYMOUTH ROCKS AND F_1 AND F_2 GENERATION CROSSES

INTRODUCTION

Studies of avian ova nuclear development have appeared in the literature throughout this century (e.g., Harper, 1904). The phenomenon of multiple ovulation patterns has also received considerable attention. The inheritance of multiple ovulation patterns has been investigated via direct selection (Lowry and Abplanalp, 1967, 1984; Abplanalp et al., 1977) and as a correlated response to selection for increased body weight in chickens (Udale et al., 1972; Reddy and Siegel, 1976) and in turkeys (Nestor et al., 1970). There appears to be two major categories of multiple ovulation, sequential and simultaneous, with the former resulting in extra-calcified compressed-sided eggs (Foster, 1970; van Middelkoop, 1971), and the latter in eggs with more than one yolk (Romanoff and Romanoff, 1949). Reported in this paper is information on the inheritance of yolk formation and double-yolked eggs, as well as an observation which would result in formation of a double-yolked egg from a single ovarian follicle.

MATERIALS AND METHODS

Pullets from parental lines selected 25 generations for high (HH) and low (LL) 56-day body weight (Dunnington and Siegel, 1985), their reciprocal F_1 crosses (HL and LH), and an F_2 cross (from HL x HL matings) were used in this experiment. For all matings, the sire line is listed first and the dam line second. Pullets from all mating combinations were hatched April 6th, vaccinated for Marek's disease, and reared on wood shavings until 127 days of age. Lighting was continuous through 14 days of age and from 0600 to 1800 hr to 57 days. Chicks were then moved to a windowed house, exposed to natural lighting until 127 days of age, and then placed in individual cages in a windowless house and subjected to a photoperiod from 0600 to 2000 hr. Feed and water were available ad libitum throughout.

Each pullet received 1 ml of corn oil containing Sudan IV (red) or Sudan Black (.05 g/ml) for 30 days commencing on the day of first egg by inserting a 12 in tube attached to a syringe into the crop. Dyes were alternated daily. Each egg laid during the 30-day period was collected, hard-cooked, bisected, and the concentric layers of yolk counted. Number of days required for rapid yolk development was established by number of concentric dye rings (Udale et al., 1972). Double-yolked eggs were also noted and the number of dye rings recorded for each yolk. The one triple-yolked egg that was laid was not used in the analyses.

Statistical analyses. Data for number of eggs laid,

duration of the rapid growth phase of yolk development in single-yolked eggs, and the percent of double-yolked eggs for the first 30 days of production were analyzed by one-way analysis of variance. The statistical model was:

$$Y_{ij} = \mu + G_i + e_{ij}$$

where i = 1, 2 . . . 5 genotypes and j = 1, 2 . . . n individuals per genotype. Prior to analyses, percentages were transformed to arc sines. Comparisons among specific means and combinations of means were made by nonorthogonal linear contrasts (Scheffe, 1970).

Contrasts	Genetic Inference
HL - LH	Reciprocal differences
(HL + LH) - (HH + LL)	Heterosis
F_2 - [(2 HL + (HH + LL)/4]	Recombination
HH - LL	Parental line differences

Data concerning time differential between paired yolks for rapid growth phase of yolk development within double-yolked eggs were analyzed by analysis of variance using a five by four block arrangement. Blocking factors were mating combination and difference in number of days of the rapid growth phase of yolk development. The statistical model was:

$$Y_{ij} = \mu + G_i + D_j + (GD)_{ij}$$

where i = 1, 2 . . . 5 genotypes, and j = 0, 1 . . . 3 days separations. Because data were not normally distributed, the number of yolks within a mating combination and days difference in rapid growth phase subclass were analyzed as arc sines of percent double-yolked eggs.

RESULTS

During the first 30 days of lay, there were highly significant differences between parental lines, as well as positive heterosis (12%) for number of eggs laid (Table 13). Differences between reciprocal crosses and recombination effects were not evident. There were no differences between parental lines or between reciprocal crosses for duration of the rapid growth phase of yolk development (Table 13). Correspondingly, heterosis and recombination effects were small (-1% and -5%, respectively) and not significant, indicating little, if any, nonadditive genetic variation for yolk formation in these populations.

The rate at which double-yolked eggs were produced did not differ between parental lines or reciprocal crosses (Table 13). However, because there were differences among populations for number of eggs laid, those that produced more eggs also had a higher number of double-yolked eggs. Heterosis and recombination effects for the percentage of double-yolked eggs produced were not significant, with percentages being negative (-26% and -60%, respectively), though much larger than those values exhibited for yolk formation.

In double-yolked eggs, both yolks usually underwent rapid development for the same number of days or differed by only one day (Table 14). Those differing by more than one day comprised 8% of the double-yolked eggs and the incidence was less frequent

than for the former. There were no double-yolked eggs with a yolk-age differential of more than three days.

Upon autopsy, one HH pullet had two rapidly developing ova within one follicular membrane (Plate 1). If this had not been observed prior to ovulation, it would have been identified at lay as a double-yolked egg with the smaller yolk differing from the larger yolk by more than one day of rapid development.

DISCUSSION

The slow response to selection for reduced oviposition interval (Foster, 1972, 1985) may have been, in part, because of little genetic variation for time required for yolk formation. If there is relatively little genetic variation for time required for a yolk to complete the period of rapid development, then more yolks must be undergoing rapid development at any one time to sustain a shorter oviposition period. Romanoff and Romanoff (1949) suggested that crossbreds may have more yolks undergoing rapid development than their parental lines. Thus, nonadditive genetic variation for the number of yolks undergoing rapid development may be a means of reducing oviposition intervals (Foster, 1985). Our data support this thesis since heterosis for number of eggs laid during the first 30 days of lay was 12%.

Foster (1972, 1981) discussed how light-dark cycle length imposed certain constraints on egg production, assuming one oviposition per cycle. For example, limits of 86 and 114 eggs per 100 days were imposed with light-dark cycles of 28 and 21 hours, respectively. Since it requires approximately 25 hours to produce a normal-shelled egg, the latter light-dark cycle may have imposed limits on this physiological barrier while the former did not. Pullets from a line selected for short laying interval were found to ovulate prior to oviposition and still produce normal eggs (Sheldon and Podger, 1972); however, Sheldon et al. (1984) presented data which indicates that they have

broken through the barrier of an ovulation per 24 hr cycle in a normal light regime and the response in interval is due to the egg spending less time in the oviduct. In lines of birds not selected, as were those of Sheldon and Podger (1972) and Naito et al. (1985), long-short oviposition patterns resulted in a higher incidence of soft-shelled eggs and other egg shell deformations because of two eggs being in the uterus at the same time (van Middelkoop, 1971; Siegel and Dunnington, 1985).

Double-yolked eggs were observed at a frequency of 2.4% for the first 30 days of lay. Yolks within the double-yolked eggs were relatively uniform in that 92% of the yolks did not differ by more than one day of rapid development. This result is consistent with that initially reported by Buss (1963), who proposed that the main cause of double-yolked eggs was that two ova "reach maturity and are released at the same time."

Double-yolked eggs with yolks differing substantially in both size and age, as seen in this experiment, represent a relatively unique situation. This pattern was observed in three eggs where the smaller yolk differed by three days of rapid development from the larger one. As shown in Plate 1, such double-yolked eggs are probably the result of dual oocytes being released from a single ovarian follicle.

The occurrence of dual ova within a single follicle could be simply the result of two separate and distinct oocytes being encapsulated by granulosal layer cells during the initial stages

of follicular development. An alternative explanation could be an incomplete separation of oocytes following meiotic cytokinesis. In immature chickens and chicken embryos, as in a number of other vertebrates, intracellular bridges have been observed between developing oocytes in early meiotic prophase (Skalko et al., 1972). Thus, if the normal separation of such conjoined oocytes were delayed, dual oocytes within a single follicle might result. The yolk-age differential that we observed is probably related to relative oocyte vascularity and rate of vitellogenesis. In either instance, however, double-yolked eggs with yolks differing considerably in size and age are the result of aberrant oogenesis.

SUMMARY

The duration of the rapid growth phase of yolks was measured in single and double-yolked eggs in parental lines of White Plymouth Rock chickens selected for high (HH) and low (LL) juvenile body weight, reciprocal F_1 crosses, and an F_2 cross. Commencing with the day of first egg, each pullet was intubated daily with a fat soluble dye for 30 consecutive days. There was little genetic variation for the rapid growth phase of yolk development. The frequency of multiple-yolked eggs was similar among populations. Yolks within a double-yolked egg usually were in the rapid growth phase for a similar length of time. Large discrepancies in yolk size were observed in three double-yolked eggs with the smaller yolks differing from the larger ones by three days of rapid development. On rare instances, a single follicle contained two yolks. It is hypothesized that such eggs result from dual ootids being released from a single follicle or from an incomplete separation of oocytes following meiotic cytokinesis.

Table 14. Means and standard deviation for number of eggs laid, duration of the rapid growth phase of yolk development, and percent double-yolked eggs by mating combination during the first 30 days of lay

Mating Combination	No		Yolks	
	Pullets	Eggs	Days develop.	% double
HH	26	26 ± 3	7.4 ± 1.0	4.5 ± 6.9
HL	18	23 ± 3	7.6 ± 1.1	3.0 ± 5.2
LH	28	24 ± 3	7.5 ± 1.1	1.6 ± 3.0
LL	12	16 ± 5	7.8 ± 0.7	1.7 ± 3.3
F_2	16	22 ± 5	7.2 ± 1.2	1.2 ± 2.4

Table 15. Percentage of double-yolked eggs observed by mating combination and number of days yolks differed in rapid development

Mating Combination	Days yolks differed				Pooled
	0	1	2	3	
HH	22.4	15.6	0.0	2.0	40.0
HL	14.6	9.8	2.0	0.0	26.4
LH	9.8	6.8	2.0	1.0	19.6
LL	5.9	1.0	1.0	0.0	7.9
F_2	4.9	1.0	0.0	0.0	5.9
Pooled	57.6^{b}	34.2^{b}	5.0^{a}	3.0^{a}	

[1]Percentages calculated from 103 double-yolked eggs.

^{a,b}Values having the same superscript were not different ($P > .05$). Comparisons were made for means.

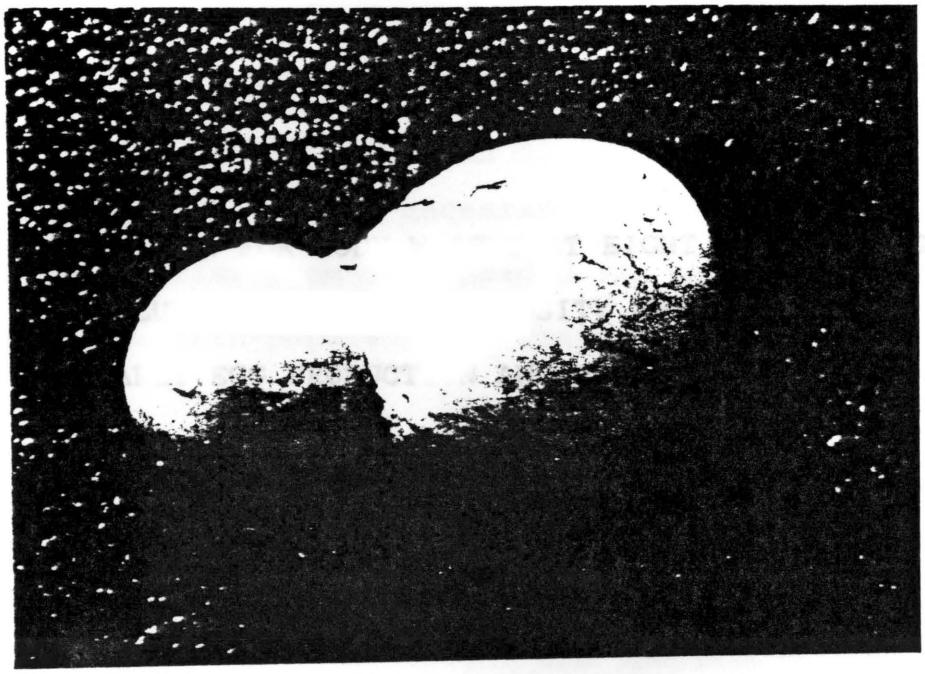

Plate 1. Ovarian follicle containing two developing yolks.

EXPERIMENT V

SELECTION FOR BODY WEIGHT AT EIGHT WEEKS OF AGE INFLUENCES OF HETEROZYGOSITY AND DWARFISM ON EARLY EGG PRODUCTION AND ASSOCIATED TRAITS

INTRODUCTION

The interface of age, body weight, and carcass composition for the onset of sexual maturity of poultry is population-dependent and subject to environmental influences (e.g., Soller et al., 1982, Dunnington et al., 1983, Leeson and Summers, 1983, Bornstein et al., 1984; Brody et al., 1984). Body weight and compositional requirements necessary for the onset of lay, however, may differ from that needed for maintenance of lay since considerable within-population variation exists in spent hens (Giles et al., 1982, 1984). Lacking are data on the association between early egg production and changes in carcass traits. The research reported in this paper addresses this void through comparisons of dwarf and normal chickens from lines divergently selected for juvenile body weight and specific F_1 and F_2 crosses during the first 60 days of lay.

MATERIALS AND METHODS

Stocks. Female chickens from each of 2 dwarf and 5 normal White Plymouth Rock populations were used in this experiment. Parental lines were nondwarf chickens selected 25 generations for high (HN) and low (LN) 56-day body weight (Dunnington and Siegel, 1985). These parental lines were mated to produce reciprocal F_1 crosses (HL and LH) and an F_2 cross from HL x HL matings. In matings to produce crosses, the sire population was identified first and the dam line second. After 13 generations of divergent selection, the sex-linked recessive allele for dwarfing (dw) was introduced into samples of the selected lines by mating pullets from these lines to males of a commercial meat-type stock which carried the dw allele (Reddy and Siegel, 1977b). Through repeated backcrossing to heterozygous (Dw/dw) males to normal females from each selected line, two populations resulted, HD and LD, which were the same genetic origin as the HN and LN lines, respectively. After 10 generations of backcrossing, dwarf males were randomly mated to dwarf pullets for 2 generations to perpetuate the HD and LD populations.

Husbandry. All chicks used in the experiment were hatched on the same date and produced from age-contemporary parents. Upon hatching, chicks were vaccinated for Marek's disease, vent-sexed, wing-banded, and the females were placed in litter-floor, light-controlled pens. Lighting was continuous until the chicks were 14 days of age, after which the photoperiod was from 0600 to

1800 hr. At 57 days, pullets were moved to a windowed house and exposed to natural lighting until 127 days of age. They were then transferred to individual cages in a windowless room, and provided artificial lighting from 0600 to 2000 hr. Starter, developer, and breeder diets (Siegel, 1962) in mash form, and water were provided ad libitum.

Traits measured and statistical analyses. A sample of females from each population was removed to measure developmental changes at the onset of sexual maturity in age-weight matches (Chapter II). For the birds used in the experiment reported here, individual body weights were obtained on the day of first oviposition and 60 days later. All oviposits during this period were classified as either normal or defective (van Middelkoop and Siegel, 1976), and expressed both as number and as percentage hen-day production of yolks, normal eggs and defective eggs. Actually, the percentage is a coding since the denominator was 60. Each pullet was killed by cervical dislocation 60 days after her first oviposit and measurements obtained for tarsus-metatarsus length (mm) and breast, liver, and retroperitoneal (abdominal) fat pad weight (g). When these carcass characteristics were expressed as a percentage of body weight, body weight - (ovary weight + oviduct weight) was used as the denominator.

Comparisons among populations were by one-way analysis of variance. Prior to analyses, percentages and weights were

transformed to arc sines and to natural logarithms, respectively. Where significance was obtained, differences among means were determined by Duncan's multiple range test. In addition, nonorthogonal linear contrasts (Scheffe, 1970) were used for comparisons among specific means and groups of means. The contrasts were: [(HL + LH) - (HN + LN)] for heterosis, [4(HLHL) - (2HL + HN + LN)] for recombination, and [HL - LH] for reciprocal effects.

Stepwise multiple regressions were calculated within populations to evaluate the effects of age and body weight at the onset of lay and change in body weight during the laying period on hen-day normal egg and yolk production. Similarly, the effects of age and body weight at the onset of lay and of hen-day yolk production on breast and abdominal fat pad weight after the 60 days of lay were assessed.

RESULTS

Carcass traits. Populations differed for age and body weight at the onset of lay (Table 15) with high-weight line females maturing at younger ages and with heavier body weights than those from the low line. At maturity, HN pullets were younger and heavier than HD ones, while LD pullets reached maturity at younger ages and lighter body weights than LN pullets. Although the F_1 crosses did not mature at younger ages than parental line HN, heterosis was highly significant (-21%) and recombination loss was -5%. There was no evidence of heterosis (1%) or recombination loss (-3%) for body weight at the onset of lay.

Changes in body weight during the 60-day laying period were greater for HN than for HD pullets both on an absolute and relative basis (Table 15). In the low line, differences between normals and dwarfs while present for absolute weight change, disappeared when expressed as a percentage of onset weight. Among nondwarfs, line HN pullets gained more weight both on an absolute and relative basis than those from line LN. Crosses did not differ from the HN parental population with heterosis being 21% for actual weight change and 35% when expressed relative to onset body weight. Respective values for recombination loss were 0% and 5%.

Within line means for tarsus-metatarsus length and for breast, abdominal fat pad, and liver weight were larger for

nondwarf than for dwarf pullets (Table 16). When expressed as a percentage of body weight, however, breast and liver weights of HN and HD pullets were not different, while abdominal fat pads were larger for the former than the latter. In the low-weight line, relative breast weight was larger and abdominal fat pad weight was smaller for dwarf than normal pullets. There were no differences in relative liver weights.

Among nondwarfs, crosses were intermediate and different from parental lines for tarsus-metatarsus length and breast and liver weights (Table 16) with heterotic and recombination effects being small. When expressed as a percentage of body weight minus reproductive organ weight, no differences were found among nondwarfs for liver weight. Relative breast weights of HN, HL, LH, and F_2 stocks were greater than those for line LN. The LH pullets had a smaller mean for this trait than HN and HL but not F_2 pullets. Heterosis for breast weight was 7% when expressed on a relative body weight basis and 5% on an absolute basis with recombination effects being minor in both instances.

Abdominal fat pad weight among nondwarfs was lowest for LN pullets both on an absolute and as a percent of body weight basis (Table 16). Although reciprocal crosses did not differ in abdominal fat pad weight, the mean for the F_2 was similar to HL and smaller than LH. Also, while differences existed among reciprocal crosses and HN pullets for abdominal fat pad weight, when expressed as a percent of body weight, HN pullets had

smaller pads than those from the LH cross. Heterosis was 30% and 33% for abdominal fat on an absolute and relative body weight basis, respectively; both were highly significant. Recombination loss was -8% for the former and -2% for the latter.

Egg production traits. Differences among populations for number and percent hen-day production of yolks, normal eggs, and defective eggs, followed the same pattern (Table 17). Since the percentage is a coding for number because only the latter will be discussed subsequently. Although HN and LN pullets produced more yolks than their respective dwarfs, normal egg production was the same for HN and HD pullets, while the LN pullets had higher values than LD ones. This dichotomy occurred because while both LN and LD pullets laid few defective eggs, the frequency of such eggs was considerably greater for HN than for HD pullets. Neither the reciprocal crosses nor the F_2 differed from the HN parental population for yolk production, although all were higher than those for line LN. Normal egg production, while similar for reciprocal F_1 crosses, was higher than for either parental population. The F_2 was intermediate to the F_1 and the parental lines. Heterosis was smaller (14%) for number of yolks produced than for number of normal eggs, 21%, and recombination loss was small, being 4% and -3%, respectively. The 50% heterosis for reducing defective eggs reflected a correction via crossing for the high incidence of defective eggs produced by HN pullets.

Regression analyses. Influences of independent variables on

production of yolks and of normal eggs were population-dependent. Although body weight at the onset of lay had a major effect on normal egg production of both HN and LD pullets, the effect was negative for HN and positive for LD pullets (Table 18). Age at the onset of lay negatively influenced normal egg production of LN pullets, while for F_1, F_2, and HD pullets, no single variable had a major influence. Similarly, weight at the onset of lay positively influenced yolk production in LD pullets and age at the onset of lay negatively influenced this trait in line LN, a pattern consistent with that observed for normal egg production. No single variable significantly influenced ovulation frequency in the remaining stocks.

Body weight positively influenced breast and abdominal fat pad weight weight in all populations except LN and HL (Table 18). In LN pullets, age at onset negatively influenced breast weight while both body weight and yolk production positively affected breast weight in HL pullets. There was a positive influence of yolk production on abdominal fat pad weight in line LN, while no one variable influenced this trait in the HL cross.

DISCUSSION

Body weight and age differences among populations at sexual maturity observed in this experiment were consistent with those reported for these populations (Chapter III). Similarly, the lack of and considerable heterosis for body weight and age at sexual maturity, respectively, were consistent with the data presented in Chapter II. The heterosis for age would suggest that developmental rate is a fitness trait because if the chance of becoming prey were random, those individuals which matured at younger ages would have a better chance of producing offspring. Heterosis observed for absolute and for relative change in body weight during the 60-day laying period was large, as was that for weight of the abdominal fat pad. In all cases, the crosses showed a propensity toward the high-weight parental line.

Normal egg production was highest among reciprocal F_1 crosses, although they did not differ from the HN parental line for yolk production. The frequency of defective eggs was reduced in dwarfs with the effect more pronounced in the high line than in the low line. These results are consistent with the thesis that crossing (King and Bruckner, 1952) and the dwarf allele (Jaap and Mohammadian, 1969; Kuit and van Middelkoop, 1972; Reddy and Siegel, 1977b, Abplanalp, 1984) enhance regularity in ovulation patterns of chickens. The negative relationship between body weight and normal egg production (Jaap and Muir, 1968, Kinney, 1969, Nestor and Bacon, 1972, Siegel and

Dunnington, 1985) was also observed in this experiment. Line HN pullets produced normal eggs from only 78% (38/49) of their observed ovulations while comparable values for the other stocks ranged from 92% to 100%.

It may be hypothesized that heterosis for normal hen-day egg production is due more to regularity of ova development and synchrony in ovulation than to a production of yolks. The same picture emerges for the mode of action of the dwarfing allele, since while dwarfs ovulated less often than their nondwarf counterparts, they produced fewer defective eggs. Finally, the lack of a single major influence on number of observed yolks in the crosses and HD pullets suggests that homeostatic properties of these genotypes precluded the phenotypic expression of the influences of these traits on the number of yolks and normal eggs produced.

SUMMARY

Body weight and body components were measured 60 days after the onset of lay in pullets from lines selected for high and low juvenile body weight, their reciprocal F_1 crosses and an F_2 cross, and dwarfs from the parental lines. Both relative and absolute changes in body weight of nondwarfs during the first 60 days after onset of lay were similar for crosses and the high-weight parental line. Values for the low-weight parental line, however, were considerably less. Absolute and relative body weight gains were less for dwarf than for nondwarf pullets in the high-weight line, while in the low-weight line there were differences in absolute but not relative weight gains. Although the crosses produced more normal eggs than either parental population, numbers of ovulations were the same as for the high-weight parental line. Rate of normal egg production was influenced mainly by variation in body weight at onset in the high-weight normals and low-weight dwarfs, and by age at first egg in low-weight normal pullets. None of the variables measured had a major influence on normal egg production in the crosses and high-weight dwarf populations.

Table 16. Means and standard errors for age (d) and body weight (g) at first oviposition and changes in body weight (g and %) during the first 60 days of lay, by population

	(n)	At first egg		Change in body wt	
		Age	Body wt	Absolute	%
Population					
HN	(16)	171 ± 4[a]	2602 ± 64[e]	499 ± 55[c]	19 ± 2[c]
HL	(17)	164 ± 3[a]	1966 ± 27[c]	349 ± 21[c]	18 ± 1[c]
LH	(28)	164 ± 2[a]	1948 ± 29[c]	392 ± 26[c]	20 ± 1[c]
LN	(13)	245 ± 12[d]	1283 ± 46[b]	112 ± 48[b]	9 ± 3[b]
F_2	(15)	177 ± 3[a]	1887 ± 66[c]	326 ± 46[c]	17 ± 2[c]
HD	(15)	196 ± 7[b]	2199 ± 75[d]	71 ± 27[ab]	3 ± 1[a]
LD	(26)	219 ± 5[c]	860 ± 21[a]	68 ± 13[a]	8 ± 2[ab]

[a,b,c,d,e]Means in a column having the same superscript were not significantly different (P > .05).

[1]Percent change in body weight =

(body wt after 60 days of lay - body wt at 1st egg)/body wt at 1st egg

Table 17. Means and standard errors for length of tarsus-metarsus (TM) and weight of breast, abdominal fat pad (AFP), and liver after 60 days of lay, by population

	TM	Breast		AFP		Liver	
	mm	g	%[1]	g	%[1]	g	%[1]
HN	84±1[e]	502±15[d]	16.4±.3[c]	117±9[e]	3.8±.3[c]	58±3[d]	1.9±.1[a]
HL	78±1[d]	366± 8[c]	16.2±.2[c]	95±4[de]	4.2±.2[cd]	43±1[c]	1.9±.1[a]
LH	79±1[d]	351± 7[c]	15.4±.2[b]	108±5[e]	4.7±.2[d]	47±2[c]	2.1±.1[a]
LN	70±1[c]	180± 7[b]	13.3±.3[a]	39±4[b]	2.9±.2[b]	30±2[b]	2.2±.1[a]
F_2	79±1[d]	340±15[c]	15.8±.3[bc]	80±9[cd]	3.7±.4[c]	43±3[c]	2.0±.1[a]
HD	61±2[b]	362± 8[c]	16.5±.3[c]	65±6[c]	2.9±.2[b]	40±3[c]	1.8±.1[a]
LD	45±1[a]	137± 4[a]	15.3±.2[b]	18±1[a]	2.0±.2[a]	18±2[a]	2.0±.1[a]

[a,b,c,d,e]Means in a column having the same superscript were not significantly different ($P > .05$).

[1]Percentages were calculated using [body wt - (ovary wt + oviduct wt)] as the denominator.

Table 18. Means and standard errors for the number of yolks, normal eggs, defective eggs and hen-day production for these traits for the first 60 days of lay, by population

	Number			Percent hen-day		
	Yolks	Normal eggs	Defective eggs	Yolks	Normal eggs	Defective eggs
Population						
HN	49 ± 2^{d}	38 ± 2^{b}	9 ± 2^{c}	82 ± 4^{d}	63 ± 3^{b}	15 ± 4^{c}
HL	49 ± 2^{d}	45 ± 2^{c}	2 ± 1^{ab}	82 ± 3^{d}	75 ± 4^{c}	3 ± 1^{ab}
LH	51 ± 1^{d}	47 ± 1^{c}	3 ± 1^{b}	85 ± 2^{d}	78 ± 1^{c}	5 ± 3^{b}
LN	39 ± 2^{b}	38 ± 2^{b}	1 ±<1^{ab}	66 ± 4^{b}	63 ± 3^{b}	1 ±<1^{ab}
F_2	45 ± 2^{cd}	43 ± 2^{bc}	2 ± 1^{ab}	75 ± 4^{cd}	72 ± 4^{bc}	3 ± 4^{ab}
HD	40 ± 2^{bc}	39 ± 2^{b}	1 ±<1^{ab}	67 ± 3^{bc}	65 ± 3^{b}	2 ± 1^{ab}
LD	21 ± 2^{a}	21 ± 2^{a}	<1 ±<1^{a}	35 ± 4^{a}	35 ± 3^{a}	<1 ±<1^{a}

^{a,b,c,d}Means in a column having the same superscript were not significantly different ($P > .05$).

Table 19. Percent of total variation of dependent variables accounted for by independent variables

Dependent variable	Independent variable code[2]	Populations						
		HN	HL	LH	LN	F_2	HD	LD
Hen-day normal egg production	1	<1	3	5	↓43**	1	<1	<1
	2	↓28*	1	1	1	6	12	↑33**
	3	4	<1	9	<1	5	4	4
Hen-day yolk production	1	5	<1	2	↓37*	<1	6	<1
	2	1	2	<1	2	8	11	↑20*
	3	3	1	4	<1	1	9	9
Breast wt	1	<1	3	<1	↓52**	<1	3	1
	2	↑80**	↑39**	↑45**	<1	↑70**	↑55**	↑60**
	4	<1	↑24**	4	<1	1	12	2
Abdominal fat pad wt	1	3	2	5	10	3	1	9
	2	↑55**	6	↑21*	1	↑27*	↑74**	↑41**
	4	2	5	<1	↑57**	<1	3	<1

[1] *(P < .05), **(P < .01).
↑Positive slope.
↓Negative slope.

[2] Independent variables:

1. Age at onset
2. Body weight at onset
3. Change in body weight during the first 60 days of lay
4. Hen-day yolk production

GENERAL SYNTHESIS

Long-term artificial selection for traits which ultimately affect individual fitness results in a lowering of the reproductive capabilities (Clayton et al., 1957, Falconer, 1981). Selection for juvenile body weight in meat-type chickens has increased the growth rate and improved the feed efficiency to a fixed weight. Concomitantly, this selection has increased fat deposition, contributed to leg problems (Pierson and Hester, 1982), and lowered reproduction of parental populations. Accordingly, most of the desirable correlated responses to selection for body weight at early ages are observed prior to sexual maturity, while many of the undesirable responses are associated with a lowering of reproductive performance.

The experiments reported in this dissertation were designed to investigate nonadditive genetic influences on growth, sexual maturity, reproduction, and related traits in lines of chickens divergently selected for 56-day body weight (Dunnington and Siegel, 1985). The vehicle for accomplishing this goal was by studying growth patterns from hatching to sexual maturity, and carcass characteristics at several physiological stages in diverse populations of chickens. Populations used in most experiments included parental White Plymouth Rock lines, their reciprocal F_1 crosses, and an F_2 cross, as well as the dwarf allele (dw) in the genome of the parental lines. Chapter III included a population of Jersey Black Giants which were proported

to be a large slow-growing lean stock.

Growth in a chronological frame is different from growth in a physiological context. Although heterosis for body weight was observed at some chronological ages, because of the faster developmental rate associated with hybrid vigor, heterosis for body weight in physiological time was minimal. Similarly, dwarfs, which grow slower and weigh less at sexual maturity than nondwarfs, grew as fast or faster than nondwarfs when growth was expressed in a physiological time frame.

Genetic analyses of carcass characteristics at several physiological stages revealed little nonadditive genetic effects for lean carcass traits; there was evidence of general heterosis for weight gain after 57 days of age and specific combining ability for fat deposition. Qualitatively, the dw allele stabilized growth of the body and its components since carcass components on a relative body weight basis were more similar among dwarf than nondwarf chickens. The stabilizing effects of dw may vary depending on whether it is acting in a population that has undergone selection for body weight (Merat, 1982).

There was little genetic variation among parental lines and hybrids for time required for the rapid development of yolks. The implication of this finding infers that increasing egg production should be accomplished through selection for more yolks in the rapid phase of development at one time or through utilization of nonadditive genetic effects. Selection for more

developing ova may result in more multiple-yolked eggs since it was reported by Buss (1963) and confirmed in an experiment in this dissertation that yolks in a double-yolked egg usually begin the rapid stage of yolk development within one day of each other. Although heterotic effects for yolk formation were minimal, there was marked heterosis for normal egg production. This heterosis was a result of a more regular ova development and synchrony in ovulation patterns. Similarly, the allele, dw, reduced erratic ovulation and defective egg production in the high-weight line.

A reduction in reproductive fitness of highly selected meat lines of chickens can be partially overcome by crossing and through the incorporation of the dw allele. Two distinct mechanisms appear to be involved. Hybrids had an accelerated and synchronous growth rate, resulting in an earlier age at sexual maturity than parental stocks. This effect could be because of hybridization per se and/or removal of inbreeding depression. Since the crosses showed a preponderance to the high weight line, the latter may be important in the context of its analogy with directional dominance. The dwarf allele appeared to have a stabilizing influence in particular genomes which enhanced uniformity between the divergently selected lines.

This dissertation provided empirical evidence of minimum values for age, body weight, and carcass composition for the onset of lay. Use of age, and age-weight matching procedures in several populations contributed to the hypothesis that was

developed. A flaw was in not obtaining empirical evidence from techniques that accelerate the body weight and carcass composition minimums so that reducing age minimums could be investigated. Such experiments should include use of high nutrient density rations and force feeding.

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APPENDIX

Appendix Table 1. Correlations for various traits measured during the first 60 days of lay for line LN (n=13) above the diagonal and line HN (n=17) below the diagonal, (Chapter V)

Trait Code[1]	A	B	C	D	E	F	G	H	I	J
A		-.54	-.24	.11	-.54	-.72**	.72*	-.66*	-.61	-.18
B	.40		.28	.70**	.39	.28	.07	.19	.09	-.29
C	.51*	.53*		.27	.72**	.57*	.35	.24	.21	.02
D	.21*	.28	.59*		.38	.25	.41	.09	.18	.44
E	.40	.85**	.70**	.67**		.66	.63*	.38	.36	.20
F	.37	.87**	.52*	.63**	.79**		.48	.60*	.50	-.24
G	.37	.73**	.34	.44	.62**	.78**		.73**	.75**	.51
H	-.33	.53*	-.60*	-.33	-.59*	.58*	.70**		.94**	-.38
I	.22	.03	.00	-.14	-.14	.07	.10	.46		-.33
J	.38	.28	.62*	.28	.35	.44	.49	-.64**	.27	

[1]Trait codes:
A = Age at onset
B = Weight at onset
C = Tarsus-metatarsus length after 60 days of lay
D = Weight change after 60 days of lay
E = Body weight after 60 days of lay
F = Breast weight after 60 days of lay
G = Abdominal fat pad weight after 60 days of lay
H = Hen-day normal egg production
I = Ovulation rate
J = Rate of defective egg production

Appendix Table 2. Correlations for various traits measured during the first 60 days of lay for reciprocal F_1 crosses (n=17) above the diagonal and the F_2 cross (n=15) below the diagonal, Chapter V

Trait Code[1]	A	B	C	D	E	F	G	H	I	J
A		.44	.11	-.40	.11	.24	.13	-.04	.01	-.14
B	-.22		.43	-.03	.75**	.65**	.23	-.02	.04	.05
C	-.28	.53*		.14	.43	.60**	.08	.07	.12	.10
D	-.51	.51*	.33		.63**	.33	.41	.16	-.06	.36
E	-.40	.93**	.52*	.79**		.72**	.42	-.11	.17	.26
F	.22	.84**	.58*	.71**	.89**		.31	.16	.19	.07
G	-.29	.52*	.39	.44	.58*	.55*		-.02	.11	.30
H	.20	.13	-.04	-.19	.00	.12	.01		.88**	.55*
I	-.04	.28	.24	.06	.22	.30	.15	.92		-.18
J	-.66**	.36	.67**	.68**	.56*	.46	.30	-.38	.00	

[1]Trait codes:
A = Age at onset
B = Weight at onset
C = Tarsus-metatarsus length after 60 days of lay
D = Weight change after 60 days of lay
E = Body weight after 60 days of lay
F = Breast weight after 60 days of lay
G = Abdominal fat pad weight after 60 days of lay
H = Hen-day normal egg production
I = Ovulation rate
J = Rate of defective egg production

Appendix Table 3. Correlations for various traits measured during the first 60 days of lay for line LD (n=26) above the diagonal and line HD (n=16) below the diagonal, Chapter V

Trait Code[1]	A	B	C	D	E	F	G	H	I	J
A		-.49*	-.55**	.25	-.51**	-.43**	-.58**	-.25	-.15	.11
B	.67**		.59**	.12	.87**	.77**	.64**	.57**	.45*	.45*
C	.19	.69**		.24	.60**	.43*	.36	.14	.06	-.33
D	-.44	-.55*	-.24		.61**	.48*	.34	-.15	-.30	-.05
E	.57*	.93**	.70**	-.19		.86**	.68**	.37	.20	-.39
F	.25	.74**	.69**	-.21	.75**		.43*	.32	.20	-.33
G	.47	.86**	.48	-.54*	.70**	.57*		.45*	.30	-.06
H	-.25	-.09	.10	.50	.06	.11	.22		.95**	-.41*
I	-.38	-.14	.17	.49	.01	.15	.13	.93**		-.33
J	-.29	-.10	.09	-.05	-.09	.01	-.25	-.26	.08	

[1]Trait codes:
A = Age at onset
B = Weight at onset
C = Tarsus-metatarsus length after 60 days of lay
D = Weight change after 60 days of lay
E = Body weight after 60 days of lay
F = Breast weight after 60 days of lay
G = Abdominal fat pad weight after 60 days of lay
H = Hen-day normal egg production
I = Ovulation rate
J = Rate of defective egg production

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GENETIC ANALYSES OF GROWTH, SEXUAL MATURATION, AND OVA PRODUCTION IN CHICKENS

by

Daniel J. Zelenka

(ABSTRACT)

Five experiments were conducted to study genetic influences on growth and early egg production in chickens. Parental lines included White Plymouth Rocks divergently selected 25 generations for high (H) and for low (L) 56-day body weight and a closed population of Jersey Black Giants (JJ). F_1 generation crosses (sire listed first) included HL, LH, JL, and JH, and an F_2 generation from HL x HL matings. Comparisons also include dwarf and nondwarf chickens from the H and L lines. Symbols for dwarfs and nondwarfs within the high line were HD and HN and within the low line were LD and LN.

Growth patterns of dwarfs more closely approximated that of the H than that of the L line, regardless of whether measured in a chronological or physiological context. Although body components were usually smaller for dwarfs than their within-line nondwarf counterparts, on a relative body weight basis, dwarfs were more uniform than nondwarfs. Dwarfs were also more uniform than normals for age at first egg. The dw allele reduced yolk formation and ovulation rate, resulting in less erratic ovulation and lowering the incidence of defective eggs.

Differences between reciprocal crosses were minor as were

recombination effects for the traits measured. There was little, if any, evidence of heterosis for body weight and skeletal and lean traits prior to 57 days of age, at sexual maturity, or 60 days after the onset of lay. When present, heterosis was general for most traits measured with the exception of those associated with adiposity which were population dependent. Modest heterosis was observed for the age of inflection of the growth curve, age at sexual maturity, egg production traits, and body weight change during a 60-day laying period. Hybrid vigor for egg production traits resulted in more normal eggs via regularity of yolk development and synchronization of ovulation.

The onset of sexual maturity was accompanied by the achievement of a population-dependent body composition, which was generally independent of age and body weight. Under ad libitum feeding, lean carcass traits appeared to be more critical to the onset of sexual maturity than adiposity, as evidenced by greater differences between mature and immature pullets for the former than for the latter traits. The exception to this pattern was the line selected for low juvenile body weight where adiposity traits appeared to be primary.