Selection for body weight in chickens: Resource allocations and scaling

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ABSTRACT (Academic)

Evaluated were correlated responses to 54-generations of divergent selection for 8-week body weight (BW) and of BW at other ages and reproductive traits. Evaluated first was the influence of scaling on phenotypic responses to selection, phenotypic correlations of means and standard deviations, and unadjusted vs. standardized responses. Measured was BW at 4 (BW4), 8 (BW8), 24 (BW24), and 38 (BW38) weeks of age. Correlations between means and standard deviations were positive and greater in the LWS than HWS. Scaling masked the degree more than the pattern of response and was line specific with the magnitude of response greater in the LWS than HWS. While BW ratios across ages were not influenced by scaling in LWS, they were evident in HWS. Also measured were correlated responses of reproductive traits in selected and relaxed lines. Traits were age at first egg (AFE), body weight at first egg (WFE), their ratio (WAFE), and hen-day normal egg production (HDP). Although sexual maturity was delayed, the effect was more pronounced in the low than high weight lines. Selection for low BW decreased WFE, WAFE and HDP. Selection for high BW resulted in lower HDP, while WFE and WAFE were generally higher. Minimum AFE, WFE and WAFE in relation to sexual maturity were line specific. Opposition between relaxed and artificial selection resulted in a higher reproductive performance and fitness with relaxed than artificial selection. Overall, results demonstrate that correlated responses to long-term divergent selection were masked by scaling and negative correlated reproductive responses.

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ABSTRACT (General audience)

Poultry meat consumption has expanded greatly in the last 50 years. Geneticists and breeders use selection as a tool to measure and change the productivity of chickens to meet demands of an ever increasing human population. The research involved a long-term experiment for growth in chickens. Using selection to change the population involved selecting chicks on their body weight at 8-weeks of age as parents of the next generation. Chicks with higher and lower body weights were selected to reproduce the next generation with those that did not meet the criteria discarded. Body weight at 8-weeks of age and BW at other ages as well as reproductive performance were measured every generation. Interpreting changes associated with selection may be masked by scaling, a population phenomena where there is an association between the change in means and variation. Standardization, a method for removing scaling showed that scaling influenced the size more than the pattern of response.

The second study focused on correlated responses to selection on reproductive performance in these populations as well as when selection was not practiced. The results showed that selection for 8-week body weight negatively influenced sexual maturity and egg production by delaying the former and reducing the latter in the population under selection. Overall, selection changed productivity and standardization was useful in removing scaling and enhancing the interpretability of responses.

DEDICATION

In loving memory of my dad who is my role model.

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ABBREVIATIONS

ACRB	Athens Canadian Random Bred
AFE	Age at first egg
AMC	Alberta Meat Control
BLUP	Best Linear Unbiased Prediction
BW	Body weight
BW4	4-week body weight
BW8	8-week body weight
BW24	24-week body weight
BW38	38-week body weight
d	day
EODES	Erratic oviposition and defective egg syndrome
g	gram
HD	High weight dwarf
HN	High weight normal
HDO	Hen-day ovulation
HDP	Hen-day normal egg production
HWR	High weight relax
HWS	High weight select
LD	Low weight dwarf
LN	Low weight normal
LWR	Low weight relax
LWS	Low weight select
ME	Metabolizable energy
QTL	Quantitative trait loci
S	Generation
SD	Standard deviation
SE	Standard error

VMH	Ventromedial hypothalamus
WFE	Body weight at first egg
WAFE	Body weight and age at first egg ratio

Chapter 1. Introduction

Genetic selection for a particular trait can result in either positive or negative responses in correlated traits. Correlated responses involve changes in the biological functions and the allocation of resources that influence subsequent generations. In closed populations there are changes in gene frequencies for the selected and correlated traits. Long-term divergent selection for BW8 is accompanied by changes in body weights at other ages and reproductive traits. Phenotypic responses to selection for high and low BW8 may be masked by scaling and thus mask the true response. Scaling is a population phenomena that occurs when the phenotypic variances change concomitant with changes in the population means i.e., a correlation of means and variances (Falconer and Mackay, 1996).

Removal of scaling includes transformation to logarithms and coefficients of variations (Falconer and Mackay) and standardization (Baguley, 2009; Hill, 1984). Transformation to remove scaling in programs involving selection may be used as a preprocessing technique to clean data before actual analysis (Carte and Siegel, 1970; Dunnington and Siegel, 1985; Flisar et al., 2014). This is because responses to divergent selection may be asymmetrical and a transformation to logarithms can make the response more symmetrical. Log transformation is a nonlinear conversions of data and is generally applied to correct for heteroscedasticity (Kvalheim et al., 1994), to convert multiplicative relations to additive relations, and to make skewed distributions (more) symmetrical (van den Berg et al., 2006). Scaling transformation enables further regression analysis and/or can enable comparisons of variability (Falconer and Mackay, 1996). Transforming data may be viewed as a standard procedure in genetic investigations to resemble normality because it satisfies one or two of the desired properties of normality, additivity, and variance independent of the mean (Lynch and Walsh, 1998).

Standardizing to remove scaling is one which has been scaled in terms of the variability of the sample or population from which the measure was taken. The aim of standardization is to equate effects measured on different scales (Baguley, 2009). Although this method is more commonly used in preprocessing data for psychological, biomedical, statistical, and functional genomics studies (Baguley, 2009; Gelman, 2008; van den Berg et al., 2006), the aim is to correct for heterogeneity of variances. Such a method of standardization is necessary to increase accuracy and is useful in selection experiments (Hill, 1984).

Reproductive performance associated with long-term divergent selection for BW8 in earlier generations (0-27) included delayed sexual maturity and lowered egg production (Siegel and Dunnington, 1985). These were a consequence of negative correlations between growth and reproductive traits. This is because selection emphasized on body weight is closely associated with growth stages of an individual and thus influenced changes in the biological functioning and allocation of resources during other stages in the life cycle.

Chapter 2. Literature Review

Long-term selection for commercial broilers

Genetic selection for increased growth of broilers is an ongoing process. Since the late 1940s to the early 1950s, breeding companies have specialized in applying quantitative genetics to the selection of chickens specifically for meat characteristics (Havenstein et al., 1994a). These commercial programs have greatly increased body weight (BW) and reduced feed conversion (FC) and yield. Although many of the changes that have occurred were due to genetics, enhanced nutrition, combined with the application and efficiencies of vertical integration, ultimately led to the development of the modern broiler industry (Havenstein et al., 2003b). Concomitant to the profound improvement in productivity of the broiler chicken has been a higher per capita consumption of chicken meat in the United States between 1950 (9.4 kg) and 2005 (39.2 kg) USDA, Economic Research Service (2014).

In the United States, average slaughter weight of meat-type chickens in 2015 was >2.60 kg (Thornton, 2016). Because body weight and breast muscle have moderate to high heritabilities, mass selection and best linear unbiased prediction (BLUP) have had important roles in breeding programs. Thus, today under good husbandry and a high energy diet, a 2.40 kg broiler can be produced in 35 days by using only 3.66 kg of feed. Thus the modern broiler reaches market weight at an early age, has high yield, and efficiently uses feed (Siegel, 2014).

Several studies to measure selection responses over the past 60 years have been conducted by comparing the performance of modern broiler stocks to randombred controls such as the Athens Canadian Random Bred (ACRB) and the Alberta Meat Control (AMC) (Havenstein et al., 2003b; Collins et al., 2014; Zuidhof et al., 2014). Results from these studies to a fixed age show substantially increased BW, yield, and feed efficiency compared to randombred controls.

Havenstein et al. (2003b), reported that broiler stocks grew up to 4.6 times the rate of a 1957 randombred strain. Collins et al. (2014) obtained similar results with the modern broilers outweighing the ACRB line to 10 weeks. Havenstein et al. (2003a, b) and Collins et al. (2014), reported that emerging broiler strains continue to increase in body size but devote a greater percentage of BW to breast muscle, and as a result continue to sacrifice or contribute less to the increase in size of other organs compared to the ACRB. A trade-off to increased breast muscle has been a decrease in the relative size of vital organs (heart, lung, liver, viscera). The smaller heart and lungs then have to support a larger muscle mass while the smaller digestive track must meet the nutritional needs of this increased muscle. Although genetic selection has increased muscle mass of broilers when compared with the ACRB, it has altered the broiler in other ways making feeding and managing this bird for optimum growth and livability challenging (Collins et al., 2014).

Similar comparisons by Zuidhof et al. (2014), for the period 1957 to 2005, showed that broiler growth increased by over 400% with a concurrent 50% reduction in FC. The net result was that over a period of almost 50 years, the broiler industry has been able to reduce the amount of feed required to produce chicken meat by 50%, and increased breast meat by 67%.

Long-term divergent selection experiments for BW in meat-type chickens

Body weight is a polygenic trait with a moderate to high heritability (Marquez et al., 2010). It is a function of chronological age, which was the same for lines selected for high and low body weight and for physiological age which differed between the lines (Dunnington et al., 1983). Single trait long-term selection experiments with closed populations provide information that cannot be obtained from multitrait selection experiments or from analyses of commercial breeding programs where introgression may occur (Siegel and Wolford, 2003).

Divergent selection is selection in opposite directions for the same trait (Tercic, 2013). Two long-term experiments for body weight have been conducted in chickens. They are the Virginia selection lines (Siegel, 1962; Dunnington and Siegel, 1985; Liu et al., 1994; Dunnington and Siegel, 1996; Marquez et al., 2010; Dunnington et al., 2013) and the Slovenia selection lines (Flisar et al., 2014). These selection experiments were designed to study the direct and correlated responses to selection for 8-week body weight (Tečič and Holcman, 2008; Marquez et al., 2010), and have reached 34 (Flisar et al., 2014) and 54 generations (Dunnington et al., 2013), respectively. In both experiments, the common founder populations originated from meat-type crosses and were maintained as closed populations selected for either high or low BW at 8 weeks of age. Various aspects of direct and correlated effects of selection for BW were investigated in depth to understand the mechanisms of selection at organismal, cellular, and molecular levels (Dunnington and Siegel, 1996; Tečič and Holcman, 2008).

Long-term selection for a single trait (BW) can be accompanied by changes in unselected traits (Dunnington and Siegel, 1996; Flisar et al., 2014). Long-term selection experiments provide insights that cannot be obtained in short-term experiments (less than 20 generations) or from commercial breeding programs (Dunnington and Siegel, 1996). This is because genetic factors change over the duration of selection. Responses may be influenced by numerous factors including, initial gene frequencies, rate of allelic fixation, changes in fitness, changes in variance, and genetic and physiological limits (Dunnington and Siegel, 1985; 1996). Divergently selected lines provide valuable tools for studying genetic and physiological basis and consequences of selection pressure on metric traits which are quantitatively inherited (Fisar et al., 2014). Long-term divergently selected lines also provide a unique resource for dissecting the genetic basis underlying the line divergence. Understanding the genetic architecture of traits such as growth and body composition has become a primary focus for biomedical and agricultural research (Tečič and Holcman, 2008).

Genetic factors influencing long-term selection of a quantitative trait are difficult to evaluate because changes occur over the duration of selection. Responses may be influenced by initial population size, initial gene frequencies, rate of allelic fixation, mutation, changes in fitness, inbreeding, changes in variance, and genetic and physiological limits, as well as macro- and microenvironmental changes. The intrinsic value of long-term selection experiments is that they provide insights that cannot be obtained from either short-term experiments or commercial breeding programs (Dunnington and Siegel, 1996).

Selection limits

Artificial selection reaches a genetic limit when no further progress is made because all alleles affecting the trait have been fixed in the population. Namely, additive genetic variance has been exhausted. The time taken to reach the limit may vary from 1-30 generation or 10-20 times the standard deviation (Roberts, 1966a). This is also the case when reverse or relaxed selection at the limit fails to yield any response that is an indication that the additive genetic variance has been exhausted. In contrast, when the line at selection limit regressed slightly towards the base population when selection was relaxed, suggests that loci affecting the trait had therefore not been fixed by selection (Roberts, 1966b).

In a divergent selection experiment, response may be expected to continue for 20-30 generations producing a total divergence between strains selected for high and low expression of trait (Falconer and Mackay, 1996). When it does not occur, one needs to examine reasons for the lack of plateau. This may be the result of nonadditive genetic variation (dominance and epistasis) and/or new variation via spontaneous mutations (Carlborg et al., 2006; Alexander et al., 2015).

Relaxed lines

Relaxed lines that are subpopulations (sublines) of HWS and LWS have been established periodically during the course of the long-term selection experiment to monitor environmental influences of primary and correlated traits (Liu et al., 1994). Relaxation of selection provides a randombred population that may serve as an unselected environmental control for a selected line and, to some extent, provide a measure of effectiveness of artificial selection and natural selection (Liu et al., 1995b). Such sublines were initiated in generations 6, 13, 19, 26, 34, and 43 of HWS and LWS and continued as contemporaries of the selected lines. Comparisons of the selected lines with their contemporary lines in which selection had been relaxed (discontinued) indicated that in the HWS, the relaxed lines generally regressed modestly towards the original (preselection) values suggesting that the linear response to single trait selection was at least partially due to continued genetic variance. Even in the LWS line, a series of plateaus in selection response occurred, but relaxed contemporary lines still regressed modestly towards preselection values for BW8 (Dunnington et al., 2013).

Comparisons of artificial and relaxed selection showed that reproductive complications associated with artificial selection were ameliorated, in part, indicating an opposition between artificial and naturals forces of selection (Dunnington and Siegel, 1985). Namely, more females reach sexual maturity in relaxed than selected lines (Dunnington and Siegel, 1985; Dunnington and Siegel, 1986).

Scaling in selection

Scaling is a population phenomena that occurs when the phenotypic variance changes concomitant with changes in the mean. It is evident in selection programs when the phenotypic variance changes with the population mean, i.e. a correlation of means and variances (Falconer and Mackay, 1996). Scaling is common for body weight traits (Carte and Siegel, 1970; Dunnington and Siegel, 1985; Falconer and Mackay, 1996; Flisar et al., 2014) and can be a problem in the interpretation of selection experiments for body weight (as indeed it can be in the interpretation of experiments conducted for only one generation). Therefore it is important to consider scaling when analyzing long-term responses because this effect may mask the true response of selection (Hill and Bünger, 2004).

Response to 34 generations of divergent selection for 8-week body weight showed scale effects (Flisar et al., 2014) because as the mean of the population changed, so did the variance. This observation was consistent with earlier reports on sexual dimorphism for juvenile body weights that showed the effects of scaling (Carte and Siegel, 1970; Dunnington and Siegel, 1985). Namely, males are heavier than females and the variation for body weight is greater in males than females.

Studies involving the inheritance of juvenile body weight in chickens may be questionable if analyses do not consider a possible correlation between means and variances and/or heterogeneity of variances. Comparisons of heritabilities for males and females may be biased, and the implications in studies of sexual dimorphism and sex-genotype interactions are obvious (Carte and Siegel, 1970).

The effects on the variance (heterogeneity) are likely greatest when directional selection is intense and when selection is on individual phenotypes or within family deviations rather than on family mean performance (Hill and Zhang, 2004). Extremely diverse selected lines may show much higher levels of variation than can be explained by scaling (Falconer and Mackay, 1996). For example, Clayton and Robertson (1957) found that the phenotypic variance for abdominal bristles was higher in both the low and the high selected lines of Drosophila than in the unselected base population. Perhaps a contributing factor to the increased variance was inbreeding concomitant to artificial selection. Namely, with inbreeding there is less “buffering” to environmental insults.

When changes in variance are proportional to the changes in means, then the coefficient of variation is unchanged. As a “rule of thumb” the coefficient of variation of juvenile body weight is about 10% in a wide range of species. One explanation as to what that controls at this level is that selection is acting on the variance per se, and thus cannot just be a consequence of variability in genotypic means. It is worthwhile in analysis of selection experiments and breeding programs to consider the possibility and impact of direct selection on the variance when evaluating selection responses and retained variability (Hill and Zhang, 2004).

Removal of scaling

It is important in any analysis to consider the possibility of scaling. Removal of scale effects by transformation helps to interpret responses and draw conclusions to results of selection because scaling may mask the true response to selection (Falconer and Mackay, 1996). Transforming data to resemble normality is a common procedure in genetic investigations because transformation can satisfy the desired properties of normality, additivity, and variance independent of the mean (Lynch and Walsh, 1998). In divergent selection experiments for high and low body weight, transformation is relevant for studying the response to selection. This is because responses may be asymmetrical and transformation is necessary to remove scale effects and make the variance more independent of the mean.

Logarithmic transformation

Logarithmic (to the base 10) transformation is a nonlinear conversions of data and is generally applied to correct for heteroscedasticity (Kvalheim et al., 1994), to convert multiplicative relations to additive relations, and to make skewed distributions (more) symmetrical (van den Berg et al., 2006). In divergent selection experiments for high and low body weight, transformation is relevant for studying the response to selection. This is because response may be asymmetrical and transformation to logarithms makes the response more symmetrical and enables further regression analyses or can enable the comparing of variability (Falconer and Mackay, 1996). Log transformed means may provide a different picture of the late vs. early response rates than do the untransformed means if, for example, the coefficient of variation rather than the standard deviation remains relatively constant (Hill and Bünger, 2004).

Scale effects, commonly due to correlations between means and variances, can be reduced by transformation of data to logarithms. This transformation reduces divergences noted in comparisons between sexes, generations, and populations (Carte and Siegel, 1970). Clearly if a scale transformation such as the logarithmic can substantially reduce the relationship between the mean and variability of the population, then it is appropriate to do so (Hill and Zhang, 2004).

Standardization

Scale effects can also be removed by standardization through placing input variables on a common scale. One method to place input variables on a common scale is to divide each numeric variable by its standard deviation (Gelman, 2008). This standardized measure of effect is one which has been scaled in terms of the variability of the sample or population from which the measure was taken. The aim of standardization is to equate effects measured on different scales (Baguley, 2009). Although this method is more commonly used for preprocessing data in psychological, biomedical, statistical, and functional genomics studies (Baguley, 2009; Gelman, 2008; van den Berg et al., 2006), the aim is to place all variables on a common scale to remove artifacts that may mask responses. In regression analysis, standardizing inputs to a common scale enhances interpretability of the model whose predictors are on difference scales as interpretation of regression coefficients is sensitive to the scale of the input (Gelman, 2008). From an artificial selection point-of-view, Hill (1984) described standardizing by sample standard deviation as an alternative method to correct for heterogeneity of variance when making selection decisions among animals from different environmental groups. Such an alternative method of standardization is necessary to increase accuracy of selection. Scaling by standardization is a robust procedure to correct for heterogeneity of variance and accuracy is high unless groups are very small.

Response to long-term divergent selection for 8-week BW on growth in chickens

Direct responses

Eight-week body weight in chickens changed over the course of 54 generations of divergent selection (Dunnington et al., 2013), resulting in two different lines (HWS and LWS) that differed in growth, feeding behavior, and reproduction (Zelenka et al., 1988). Selection for high body weight subsequently increased the mean BW. Such increases in growth alter feed control mechanisms resulting in chickens eating to gut capacity when fed ad libitum (Denbow, 1994). Burkhart et al. (1983) reported that selection for body weight resulted in a genetic-hypothalamic obesity characterized by the failure of ventromedial hypothalamus (VMH) to diminish appetite. The genetic obesity induced modifications in satiety mechanisms mediated by the hypothalamus. Subsequently, Bokkers and Koene (2003) examined the feeding behavior of broilers and reported that feed intake behavior in these stocks was influenced more by satiety mechanisms than by hunger mechanisms.

Selection for low body weight resulted in reduced mean weights. In generation 25, BW plateaued and further reduction was arrested. The line had reached a physiological limit. Some of these chickens were not consuming enough feed for growth and were anorexic. Mortality ranged from 5 to 20% and those that survived were heavier at selection age than those that did not (Dunnington et al., 2013).

Selection responses during the first 30 generations of selection showed patterns of irregular responses. The phenomenon of irregular response ("waves of response") was characterized by sharp increases of response following a few generations in which there was a cessation of response. Similar patterns of response were reported by Tečič and Holcman (2008) during their selection for high and low 8-week body weight. Considering that the "wave" was relatively longer in the later than in the earlier generations and that there were attempts to minimize macroenvironmental factors, there are two possible explanations. One is that after so many generations of intense selection, genotypes were more sensitive to microenvironmental factors that facilitated irregular responses. Another is spontaneous mutations may have occurred periodically (Dunnington and Siegel, 1996). Recent mitogenomic analysis of 50 generations of selection by Alexander et al. (2015), identified two mutations (*ND4L* and *CYTB*) in LWS that were evidence for paternal mtDNA inheritance and used it to calculate rate of mutation. However, further association analyses demonstrated that neither mutation was significantly correlated with phenotypic differences between the two selection lines.

The limit to response to selection having been reached in the low line appears to involve physiological problems. The LWS showed a quadratic trend in growth whereas the increase in growth in HWS was linear (Dunnington et al., 2013). The continued increase in the HWS may be attributed to continued genetic variance (epistasis) and mutation (Carlborg et al., 2006; Johansson et al., 2010; Pettersson et al., 2013, Alexander et al., 2015). In the Slovania study, a selection limit has been reached in the high line (Flisar et al., 2014).

Comparisons of the selected lines with their contemporary lines in which selection had been relaxed indicated that in the HWS, the relaxed lines generally regressed slightly towards the original (preselection) values. This suggests that the linear response to single trait selection was at least partially due to continued genetic variance. Even in LWS, a series of plateaus in selection response occurred, but relaxed contemporary lines still regressed towards preselection values for BW8 (Dunnington et al., 2013).

Correlated responses to unselected BW traits

Body weight at a specific chronological age is a function of growth of component parts (Dunnington and Siegel, 1996). Selection for BW at a particular age also changes BW at other ages (Dunnington et al., 2013). During the course of long-term selection for growth at 8-weeks of age, considerable changes occurred in the growth patterns from 4-38 weeks of age. Within five generations, selection for both high and low 8-week weight greatly altered the growth patterns of these lines from that of the base population. Deviations thereafter were less dramatic for HWS than LWS (Siegel and Dunnington, 1987).

Correlations analyses between BW at 4, 8, 24, and 38 week of age were moderate to high and positive in both lines from generations 0-18 (Liu et al., 1995b). When feed was restricted in line HWS beginning in generation 18 to address reproductive complications, there were no correlations of BW4 and BW8 with BW24 or BW38. There was a negative regression for HWS pullets from generation 19-36 as a result of feed restriction and this may have masked correlated genetic responses (Liu et al., 1995b). Comparisons of HWS and LWS after 27 generations of selection showed that the former was 4.1, 4.4, 2.8 and 2.4 times heavier than the latter at 4, 8, 24 and 38 weeks of age, respectively. Thus selection for BW8 had a greater effect on juvenile than body weights later in life (Dunnington and Siegel, 1985). Recent findings by Dunnington et al. (2013) show that after 54 generations of selection, the high and low weight lines differed by 10-fold in BW at selection age.

The ratio of BW4/BW8 for HWS and LWS males was 0.33. For LWS females, the ratio increased to 0.44 which implies that the chicks that survived neonatal period were heavier and that may have contributed to the higher ratio. With relaxation of selection in HWS, the relaxed lines generally regressed towards preselected values suggesting existing genetic variance. With LWS, a series of plateaus occurred in selection response. Relaxation of selection show BW4, BW24, and BW38 deviating towards controls.

Correlated responses to long-term divergent selection for 8-week BW on reproduction

Sexual maturity of females defined as age at first oviposition

Sexual maturity and its onset signals to an animal's reproductive life are of profound importance from both evolutionary and economic perspectives (Wright et al., 2012). In chickens, sexual maturity of females is considered as the age when the first egg is oviposited (laid) which is approximately 26 hours from ovulation. Sexual maturity is influenced by chronological age, BW, and body composition (Siegel and Dunnington, 1985) with the relationships involving a specific minimum age, minimum BW, and body composition that are line specific (Dunnington et al., 1983; 1984; Brody et al., 1984; Zelenka et al., 1986a, b; 1987).

Long-term divergent selection for BW8 was accompanied by changes in reproductive performance, including age at sexual maturity and egg production. Correlated responses included delayed sexual maturity and lower egg production in both HWS and LWS (Dunnington et al., 1984, Siegel and Dunnington, 1985; Dunnington and Siegel 1985; Liu et al., 1995b). The delay in sexual maturity was greater for LWS than HWS because the former did not consume sufficient feed required to achieve a minimum body weight for sexual maturity until at an older age. The HWS pullets reached their threshold BW at young ages and sexual maturity was dependent on their achieving a threshold age to begin egg production. Conversely, LWS pullets reached their threshold age before BW and composition were sufficient to allow egg production, causing considerable delays in the initiation of egg production (Dunnington and Siegel, 1996). Thus, chronological and physiological age are not the same.

During the course of 36 generations of divergent selection, several differences were noted regarding the response of sexual maturity in the selected and their respective relaxed lines. For example in the LWS lines, from generations 25 and 26, a considerable number of pullets did not achieve sexual maturity (marked by production of the first egg). From that time on, it was common for a proportion of pullets (it varied depending on generation) to fail to become sexually mature by 275 d of age (Zelenka et al., 1987; Liu et al., 1995b). In generation 31, the proportion of females reaching sexual maturity increased afterwards even though BW8 decreased and plateaued. The increase in generation 31 may be in indication that LWS had adjusted to a new homeostasis (Dunnington and Siegel, 1996).

Correlations between AFE and BW8 were negative in LWS, while positive in HWS (Liu et al., 1995b). For LWS pullets, it reflected that within a population the heavier individuals commenced lay at younger ages. For HWS, restricted feeding may have slowed the faster growing pullets because individuals that reached onset weight commenced lay first (Zelenka et al., 1987).

In another study (Dunnington et al. 1983), with the lines divergently selected for juvenile body weight, pullets of high weight normal (HN) and high weight dwarf (HD) reached sexual maturity soon after 155 days while the low weight normal (LN) and low weight dwarf (LD) began lay at later ages. This difference suggested further that the high weight chickens had apparently reached a minimum body weight and/or composition necessary for sexual maturity and matured after reaching the minimum age. The low weight lines had not achieved an appropriate minimum body weight or composition by 155 days of age and sexual maturity was delayed until they reached a necessary body weight.

When selection was relaxed, more individuals reach sexual maturity at a younger age in the relaxed than selected lines, suggesting an opposition between artificial and natural selection (Dunnington and Siegel, 1985; Dunnington and Siegel, 1986). Also, force-feeding in the LWS resulted in more pullets commencing egg production (Zelenka et al., 1988).

Body weight at first egg (WFE)

Body weight at first egg is the minimum body weight necessary to become sexually mature (Dunnington et al., 1983). As stated previously, there is a minimum age as well as a minimum body weight and/or composition necessary for the onset of egg production. Results from long-term divergent selection for BW8 show that HWS reached minimum body weight and/or composition required for sexual maturity and commence lay shortly after reaching the minimum age. Conversely, the LWS reached the threshold age before they reach the minimum BW necessary for egg production. The time necessary to reach body weight at first egg is displayed in the delay in achieving age at sexual maturity of this line.

Liu et al. (1995b) reported WFE were greater for HWS (2,881 ± 37 g) than HWR (2,774 ± 39 g) pullets and lower for LWS (1,246 ± 21 g) than LWR (1,336 ± 18 g) pullets showing a reversion towards the origin upon relaxing selection. Artificial selection for low BW resulted in chickens with reduced appetites (anorexia) that did not gain sufficient threshold BW necessary to commence egg production. These results were consistent with those of Eitan and Soller (1991) who, after six generations of selection for high and low threshold body weight at first egg, reported that WFE was about 1.4 times greater for the high than low line. Thus, there are thresholds for both age and BW necessary for sexual maturity (Siegel and Dunnington, 1985; Eitan and Soller, 1991). The quantitative trait loci (QTL) analysis by Podisi et al. (2011), revealed overlapping QTL for body weight at first egg and at 9-weeks of age indicating that QTL affecting growth also affect body weight at first egg. Co-localization of QTL for body weight, growth, and sexual maturity suggests that body weight and growth are closely related to the attainment of sexual maturity and that the genetic factors associated with growth have correlated effects on puberty.

WFE varies among populations and appears to be more closely associated with adult than juvenile weight (Dunnington et al., 1983). When comparing BW of sexually immature and mature chickens, the non-layers weighed less and had a lower fat content than those which had commenced lay suggesting that they were under the minimum threshold (Brody et al., 1984).

Body composition

Apart from chronological age and BW, body composition is an important requirement for attaining sexual maturity (Siegel and Dunnington, 1985). Body composition threshold consists of body fat, body lean tissue, and skeletal size (Dunnington and Siegel, 1983; Brody et al., 1984; Zelenka et al., 1987). Accumulation of lean, fat, or both, function as nutrient reserves for the onset of egg production (Zelenka et al., 1987). Fat is an important body constituent in its function with reproduction in chickens (Dunnington et al., 1983). Lean tissue functioned differently in sexually immature and mature pullets suggesting that roles of lean tissues such as breast muscles change from that of nutrient storage in non-layers to nutrient supplier in layer pullets (Zelenka et al., 1986a).

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. There are large energy demands during egg production (Zelenka et al., 1986a). Increases in fat at onset, rather than being general, are directed to a few depots (e.g., clavicular), related, perhaps to selective partitioning of energy with at some point a diversion of energy from growth to egg production (Brody et al., 1984).

Body composition was also influenced by selection (Dunnington and Siegel, 1996). Selection for increased body weight resulted in an increase in percentage abdominal and total carcass fat, due to increasing feed intake and an excess of that required for normal growth and maintenance function (Siegel and Dunnington, 1988).

Body weight and age at first egg ratio (WAFE)

The body weight and age at first egg ratio (WAFE) is calculated by dividing body weight at first egg by the age at first egg. This ratio reflects growth to sexual maturity and it assumes that body composition is constant throughout the growth period to sexual maturity. There is a relationship between minimum thresholds for age and body weight at which the pullets do not become sexual mature that reflects a correlated response to selection for divergent BW8 (Dunnington et al., 1983).

The importance of WAFE is that it can be used to determine if pullets are gaining sufficient BW to reach sexual maturity. This reasoning is consistent with broiler breeder guides which recommend feeding broiler breeders to target weights during the growing period. This measure is population specific with a threshold ratio where sexual maturity will occur. In contrast, a ratio above the minimum threshold may indicate that the pullet is obese and is likely to experience reproductive complications such as erratic oviposition and defective egg syndrome (EODES) as well as associated metabolic and cardiovascular disorders. Early maturity associated with increased juvenile growth has been associated with reproductive problems such as abnormal hierarchies in egg formation (Hocking, 2004). Thus, in the commercial world of feeding programs for breeders, be they for egg or meat production the target weights optimum to achieve high reproductive rates are population specific. One factor that influences growth to sexual maturity is the growth pattern from hatching to sexual maturity. This growth pattern is expressed as a function of time using Logistic, Gompertz, von Bertalanffy growth models and also as a linear regression of BW expressed as a proportion of weight at sexual maturity (Zelenka et al., 1986b).

Egg production

Long-term divergent selection for BW8 is accompanied by changes in reproductive performance including egg production. A decline in egg production was correlated with changes associated with selection for high and low BW (Siegel and Dunnington, 1985). Thus, a strong negative correlation exists between body weight and reproductive efficiency (particularly egg production) as a result of selection for increased growth (McCarthy and Siegel, 1983; Siegel and Dunnington, 1985; Decuypere et al., 2010).

Liu et al. (1995b) reported that percent hen-day egg production (HDP) declined slightly in both HWS and LWS during earlier generations of selection (Generation 0-36). Regressions of HDP on generation in HWS were .32 ± .38, .46 ± .31, and -.01 ± .12% for Generations 0-18, 19-36, and 0-36, respectively. Thus, there was little evidence for correlated responses in HDP to increased BW8. The change in feeding regimen incorporated to reduce obesity and associated reproductive problems in this line may have masked a response**.** For LWS, there was an overall decline in HDP with a regression of -.28 ± .06% on generation (Generation 0-36). Regressions for the first half and second half of the experiment, however, were not different from zero, being -.10 ± .10 and .19 ± .19%, respectively. The decline in egg production in LWS may be associated with a decrease in energy reserves integral to egg production, a view consistent with the delay in age at sexual maturity observed for this line (Siegel and Dunnington, 1987).

Selection for increased BW resulted in an increase in EODES, a reproductive condition in which obese females produce a high incidence of soft-shelled or membraneous eggs, multiple yolked eggs, extra calcified eggs, multiple egg days, and ovipositions not occurring in sequence (Jaap and Muir, 1968; van Middelkoop, 1971, 1972; van Middelkoop and Siegel, 1976; Siegel and Dunnington, 1985). Embryos in such eggs seldom hatch.

Previously, Udale et al. (1972) reported that although the HW lines produced more eggs than the LW lines, the number of settable eggs was reduced due to erratic oviposition and defective egg syndrome (EODES). The incidences of internal ovulations and defective egg production was greater in HWS than LWS (36% vs. 2%). An increase in the number of defective eggs produced in HWS was due, in large part, to a lack of synchrony in the process of ovulation and subsequent “packaging” of the eggs. Beginning in generation 18, HWS and HWR chickens were feed-restricted, commencing immediately after obtaining 8-week BW (Liu et al, 1995b). Although this feed restriction program precluded valid comparisons with other populations for BW after 8-weeks of age, it was necessary to ensure continued successful reproduction in the lines (Dunnington and Siegel, 1996).

Correlations of BW8 with HDP were not significant during the first 36 generations of selection in HWS (Liu et al., 1995b). After generation 18, the correlation between BW and HDP may have been masked by feed restriction practiced from generation 18 and onwards. Contrariwise, in LWS, correlations between BW and HDP were low, demonstrating different phenotypic relationships of these traits in the two selected lines (Liu et al., 1995b).

Comparisons between selected and relaxed lines from generation 26-36 of selection showed that hen-day ovulations (HDO) were higher for HWR (73 ± 2%) than HWS (68 ± 2%) and higher for LWR (65 ± 2%) than LWS (59 ± 2%) pullets. The ratios of HDP: HDO for HWS (.84) and HWR (.85) were lower than for LWS (.98) and LWR (.99). Similar ratios within a selection direction showed that relaxing selection, while increasing ovulation rate, did not alter the proportion of EODES. An increase in EODES as a correlated response to selection for increased BW observed in this experiment was consistent with that reported for selection for higher BW in turkeys (Nestor, 1985). It is likely that EODES would have been greater in the high weight lines if feed restriction had not been implemented during the later generations. This reasoning is based on reported differences in EODES between feed-restricted and ad libitum broiler breeders (Katanbaf et al., 1989; O'Sullivan et al., 1991).

Comparisons involving artificial and relaxed selection showed that reproductive complications were ameliorated when selection was relaxed as measured by percent normal egg production, indicating an opposition between artificial and natural forces of selection (Dunnington and Siegel, 1985). The opposition between artificial and natural selection for reproductive traits as correlated responses to selection for juvenile BW8 is clearly shown in the antagonistic relationship between growth and reproduction. This is the reason that commercial broiler breeders are fed to a target weight. The target weights are specific for each stock and outlined in the company’s breeder manuals.

Chapter 3. Correlated responses to long-term divergent selection for 8-week body weight in White Plymouth Rock chickens: Standardizing for scaling

Abstract

The influence of scaling on phenotypic responses to long-term selection was evaluated in lines selected for high (HWS) and low (LWS) 8-week body weight (BW8). The focus of the experiment was on phenotypic correlations of means and standard deviations, and unadjusted vs. standardized responses. Traits measured were BW4, BW8, BW24, and BW38 and subsequent BW ratios 4/8, 4/24, 4/38, 8/24, 8/38, 24/38.

Correlations between means and standard deviations for BW8 were positive and greater for the selected trait and body weight at other ages for LWS than HWS. In both lines, scaling masked the degree more than the pattern of response and were line specific. For LWS, the degree of response was greater after standardization. Namely, it influenced the magnitude of response and was higher in the LWS than HWS. While BW ratios 4/8, 4/38, 8/24, 8/38, 24/38 were not influenced by scaling in LWS, they were evident in HWS.

Standardization is a robust method to adjust for scaling thus enhancing the interpretability of responses in long-term divergent selection experiments. Because of changes in variances associated with those in phenotypic means, this method to correct for part-whole correlations was useful.

Introduction

Long-term divergent selection for BW8 is accompanied by changes in unselected traits (Dunnington and Siegel, 1996; Flisar et al., 2014). Such experiments provide insights that cannot be obtained from short-term experiments (less than 20 generations) or from commercial breeding programs. This is because genetic factors change over the duration of selection. Responses may be influenced by numerous factors including initial gene frequencies, rate of allelic fixation, changes in fitness, changes in variance, and genetic and physiological limits (Dunnington and Siegel, 1985; 1996).

A consideration in analyzing the response to selection for BW is that of scaling (Carte and Siegel, 1970; Dunnington and Siegel, 1985; Falconer and Mackay, 1996; Hill and Bünger, 2004; Flisar et al., 2014). Scaling is a population phenomena that occurs when the phenotypic variance changes concomitant with changes in the mean i.e., it is evident upon selection in which the phenotypic variance changes with the population mean (Falconer and Mackay, 1996).

Removal of scaling helps to interpret responses and draw conclusions to results of selection because scaling may contain artifacts that mask the true response to selection (Falconer and Mackay, 1996). This can be accomplished by transformation to logarithms and coefficients of variation (Falconer and Mackay, 1996) or standardization by placing input variables on a common scale by dividing each numeric variable by its standard deviation (Hill, 1984; Gelman, 2008).

Transformation to remove scaling in programs involving selection may be used as a preprocessing technique to clean data before actual analysis (Carte and Siegel, 1970; Dunnington and Siegel, 1985; Flisar et al., 2014). This is because responses to divergent selection may be asymmetrical and a transformation to logarithms can make the response more symmetrical. Log transformation is a nonlinear conversion of data and is generally applied to correct for heteroscedasticity (Kvalheim et al., 1994), to convert multiplicative relations to additive relations, and to make skewed distributions (more) symmetrical (van den Berg et al., 2006). Scaling transformation enables further regression analysis and/or can enable comparisons of variability (Falconer and Mackay, 1996). Transforming data may be viewed as a standard procedure in most genetic investigations to resemble normality as it satisfies one or more of the desired properties of normality, additivity, and variance independent of the mean (Lynch and Walsh, 1998).

On the other hand, standardizing to remove scaling is one which has been scaled in terms of the variability of the sample or population from which the measure was taken. The aim of standardization is to equate effects measured on different scales (Baguley, 2009). Although this method is more commonly used in preprocessing data for psychological, biomedical, statistical, and functional genomics studies (Baguley, 2009; Gelman, 2008; van den Berg et al., 2006), the aim is to correct for heterogeneity of variances. Such a method of standardization is necessary to increase accuracy and is useful in selection experiments (Hill, 1984).

Literature on standardizing for scaling associated with long-term divergent selection experiments for BW8 in chickens is, to my knowledge, lacking. Thus, the objectives of this study are to (i) determine the phenotypic correlations of means and standard deviations of the selected trait (BW8) and correlated body weights (BW4, BW24, and BW38) and (ii) compare unadjusted and standardized responses to long-term divergent selection for BW8 and correlated responses in body weights at other ages as well as BW ratios.

Materials and Methodology

Experimental design

A long-term selection experiment for high and low BW8 in White Plymouth Rock (WPR) chickens began at Virginia Tech in 1957. Foundation stock for the experiment consisted of crosses of 7 moderately inbred lines of WPR (Siegel, 1962). From this segregating gene pool, chickens with heavier BW8 were chosen as parents for the high line (HWS) and those with lighter BW8 were selected as parents for the low line (LWS). Individual selection was then practiced within the respective HWS and LWS lines in all subsequent generations, with BW8 as the single criterion of selection. Numbers of sires and dams selected to produce each line were 8 and 48 through the fourth generation of selection (S4), 12 and 48 from S5 to S25, and 14 and 56 after S25. These parents were selected from within-line groups of approximately 150 to 250 individuals depending on the generation. Pure truncation selection was not used, however, to avoid overrepresentation of sire and dam families (Dunnington and Siegel, 1996; Dunnington et al., 2013). This effort to curtail inbreeding and avoid matings among half sib or close relatives and to avoid selection of particular sire or dam families reduced, yet could not avoid inbreeding from common ancestry. It did result in similar population structures in both lines and by generation 48 inbreeding was moderately high and effective population size was low, as expected, in closed lines (Marquez et al., 2010).

Husbandry

Each generation, chicks were hatched on the first Tuesday in March of every year and wing-banded for individual identification. If adequate numbers were not obtained from this hatch, a second hatch was produced on the third Tuesday in March. Chicks of every generation were reared in identical pens with concrete floors, wood shavings as bedding, continuous light and hot-air brooding until 8-weeks of age (Dunnington and Siegel, 1996; Dunnington et al., 2013). From 8-18 weeks, they were exposed to natural photoperiod, after which they were given artificial light from 0600 to 2000 hours in a light-controlled environment (Liu et al., 1995b). Other than routine husbandry in a rather isolated environment, the only disease preventatives were the addition of a coccidiostat to the diet and vaccination for Marek’s disease, which commenced after the 17th generation of selection. Through generation 13, chickens were maintained in floor pens with wood shavings as litter. Thereafter, they were reared on litter to approximately 126 days of age and then housed individually in wire cages. Throughout the study, feed in mash form and water were provided ad libitum with the same formulations. They were fed chick starter until 8-weeks of age, developer from 8-20 weeks of age, and a breeder diet thereafter. Percentages of crude protein were 20, 16, and 16, and levels of metabolizable energy (ME) were 2,685, 2,761 and 2,772 kcal/kg in the starter, developer, and breeder diets, respectively. Beginning in generation 18, feed intake after 8 weeks was restricted for HWS and its relaxed sublines because of increasing difficulties with reproduction due to obesity (Dunnington and Siegel, 1985; 1996; Dunnington et al., 2013).

Traits

Traits reported here are BW4, BW8 (selected trait), BW24, and BW38. Data were obtained for males and females for BW4 and BW8 and females only for BW24 and BW38. Weights at 4 and 8-week were measured to the nearest gram and 10 gram at later ages.

Statistical analysis

Regressions of mean BW4, BW8, BW24, and BW38 on generation and product moment correlations between these traits were calculated for generation intervals 0-54, 0-18, 19-36, and 37-54. The reason for the 18-generation intervals was to separate the first 18 generations before feed restriction and the subsequent 18-generation intervals to evaluate what happened before and after the feed restriction in HWS. Correlations between means and standard deviations were calculated for generations 0-54 for both sexes and selected lines. Unadjusted generation means were not corrected (adjusted) for scaling.

Standardization for scaling consisted of dividing the mean response in the respective generation by the phenotypic standard deviation for that particular sex and line. Thus, the corrected or adjusted variables were on a common scale of standard deviation units.

$BW_x = \text{Mean } BW_x / SD_x$

where x is either 4, 8, 24, or 38 week BW in each generation

Ratio of BW at different ages;

Unadjusted ratio = $\text{Mean } BW_{xi} / \text{Mean } BW_{yi}$

Where x is the numerator BW in generation *i* and y is the denominator BW in generation *i*

Standardized ratio = $\text{Mean } BW_{xi} / SD\ BW_{xi} \div \text{Mean } BW_{yi} / SD\ BW_{yi}$

Where x is the numerator BW for the mean and standard deviation for generation *i* and y is the denominator BW for mean and standard deviation for generation *i*. All calculations were conducted using regression procedures, correlations, means (standardized and unadjusted), and standard deviations (JMP 11, 2015). Default p value = $P < 0.05$.

Results and Discussion

Correlations of means and standard deviations for body weights

Correlations between means and their respective standard deviations for BW4, BW8, BW24, and BW38 were positive for males and females for all generation intervals (Table 3.1). Although evident in both lines the correlations were consistently higher for LWS than HWS.

For the 0-54 generation interval, the correlation for BW8 in HWS was 0.42 in both sexes. In the LWS line, the correlations for females (0.92) and males (0.90) while also essentially the same were more than twice that for HWS. For BW4, the correlations were 0.62 and 0.48 in HWS females and males, respectively. In contrast, the correlations between means and standard deviations were higher in LWS than HWS being 0.94 and 0.88 for females and males respectively, a pattern consistent with that for BW8. For BW24 and BW38, correlations were 0.25 and 0.44, respectively in HWS during the generation interval of 0-54. Feed restriction practiced after 8 weeks of age from generation 18 onwards may have masked the correlations and responses. In contrast, LWS had higher correlations of 0.84 and 0.86 for BW24 and BW38, respectively.

When the correlations between means and standard deviations were viewed during the first 18-generations of selection in all age groups, they were higher for LWS than HWS (Table 3.1). From generations 19-36, correlations were higher for BW4 and BW8 than the first and last 18 generation intervals in LWS. Correlations for means and standard deviations for BW24 and BW38 decreased over time as seen when comparing values from the first 18 generations to the last 18 generations. In HWS, however, the correlations while positive were not significant for 19-36 and 37-54 generation intervals for BW24. Response of measures after generation 18 for BW24 and BW38 in the HWS may have been influenced by feed restriction.

Overall, selection for BW8 involved positive correlations of means and standard deviations in both lines. There was a consistent pattern where correlations were higher in LWS than HWS.

Response to selection-regression analysis

Unadjusted and standardized regressions of BW8

An overview of unadjusted and standardized trends over the course of selection for BW8 in females of both selected lines is shown in Figure 3.1. Although both unadjusted and standardized trends were similar overall for HWS, the former generally increased while the latter trend was more variable. During the first 20 generations, the standardized measure was generally higher and thereafter lower in HWS. Although the trend in LWS was similar for both the unadjusted and standardized measures as both decreased and plateaued, there was clear separation between them. Similar, but greater responses, were observed with the males for BW8 (Figure 3.2). Scaling influenced the magnitude but not the pattern of response in HWS. The similarities in response between females and males in LWS suggest that scaling was not influential in the pattern of the response which was quadratic for both unadjusted and standardized values. However, the response appeared greater when data were standardized for scale effects.

Regressions of BW on generations are presented by line and sex for unadjusted and standardized values in Table 3.2. In both lines unadjusted values for BW8 (selected trait) were greater in males than females. When standardized, the regressions of the adjusted means on generations were significant for both lines and sexes with HWS having an equal response of 0.06 ± 0.02 for males and females. When responses were adjusted, the pattern while the same was not as extreme as the unadjusted responses. These results suggest that in the unadjusted response, although males had a greater response which may point to the influence of sex-linkage, upon standardizing for scaling the responses are equal between the sexes. Standardization may have removed artifacts due to the greater developmental rate of males. The LWS line had a standardized response of -0.06 ± 0.1 for females and -0.07 ± 0.1 for the males.

Standardized values adjusted for correlations between means and standard deviations by placing the variables on a common scale. Furthermore, the unadjusted and standardized patterns of response for LWS were significant for both linear and quadratic effects. This pattern was consistent with those of Dunnington et al. (2013) who reported a quadratic response to selection in LWS.

Unadjusted and standardized regressions of BW4

In HWS, the correlated response of unadjusted BW4 for males and females increased over the 54 generations of selection. In contrast, standardized responses increased during the first 20 generations and then plateaued (Figures 3.3 and 3.4). The plateau in the standardized measures during the later generations may have been influenced by maternal effects associated with feed restriction because maternal effects influencing juvenile BW dissipate over time (Liu et al., 1993). Scaling may also have influenced the pattern of responses. Clearly, the magnitude differed in both sexes and was lower than the unadjusted response upon standardization during the last 34 generations. In the LWS, both measures showed a similar decline in males and females. Although scaling did not alter the pattern of response, it did influence the degree as seen in a higher responses with standardization. This shows that scaling masked the magnitude of responses in LWS.

The regression analysis of BW4 over 54 generations of selection (Table 3.2) shows that while the unadjusted responses were greater for males than females in both lines, between lines they were similar (but of opposite signs). The regression of response on generations in HWS for BW4 was 5.0 ± 0.3 g and 4.4 ± 0.2 g for males and females, respectively. In LWS, regressions were -4.2 ±

0.2 g and -3.7 ± 0.2 g for males and females, respectively. Upon standardization, the regressions of the adjusted means on generations were not significant in HWS being 0.02 ± 0.01 for females and 0.02 ± 0.02 for males. Standardization removed the artifacts of scaling due to selection for higher BW. In contrast, regressions for BW4 in LWS were significant being -0.03 ± 0.01 and -0.04 ± 0.01 for females and males, respectively.

Unadjusted and standardized regressions of BW24

The correlated response of unadjusted BW24 increased in HWS during the first 18 generations and plateaued thereafter, whereas overall there was a decreased response in LWS (Figure 3.5). Feed restriction may have influenced both the unadjusted and adjusted responses in HWS. The standardized response prior to feed restriction was lower and then increased prior to reaching a plateau. This may be because feed restriction slowed growth after 8-weeks of age and hence increased in standardized responses. For LWS, the unadjusted response decreased and plateaued after about generation 25. When standardized, responses were consistently lower during the early generations and plateaued after generation 18. It can be seen that scaling may have influenced the degree of response because it was higher than the unadjusted response when values were standardized during the last 27 generations.

Regression analysis for BW24 shows that the unadjusted response was negative and greater in LWS than HWS females, a pattern that was not symmetrical as observed for BW4 and BW8 (Table 3.2). Feed restriction practiced in the HWS after 8 weeks beginning in generation 18 probably influenced the regressions of BW24. Thus, the negative regressions for HWS pullets due to feed restriction may have masked correlated responses (Liu et al., 1995b). Namely, the difference in BW between juvenile and older ages may be due to effects of selection on growth per se as well as alterations in feed intake. Standardization in HWS resulted in significant difference in BW24 of 0.08 ± 0.01 (Table 3.2). The lack of significant differences in unadjusted responses suggests that scaling masked the difference.

Regressions on generation were significant in LWS females for both standardized and unadjusted BW24 (Table 3.2). The response had both significant linear and quadratic effects. Because the regression coefficients were significant for both standardized and unadjusted means for BW24 suggests that scaling was not influential in the pattern of response due to decreases in body weight concomitant to selection. This result may not be uncommon because selected lines may show much higher levels of variation than can be explained by scale effects (Falconer and Mackay, 1996). However, scaling may have influenced the degree of response because it was higher when values were standardized during the last 27 generations (Figure 3.5).

Unadjusted and standardized regressions of BW38

Unadjusted responses of BW38 over the selection period showed an initial increase in body weight during the early generations which plateaued after feed restriction in the HWS (Figure 3.6). The standardized response was lower during the first 18 generation and then plateaued after feed restriction, a trend similar to that for BW24. For LWS, the unadjusted response decreased over time. Upon standardization however, it was generally consistent across the selection period.

In HWS, standardization resulted in a significant pattern for BW38 (Table 3.2). Both unadjusted and standardized responses were significant (although opposite in sign) suggesting that scaling may have an influence on BW38. However, feed restriction may have also masked the response. In contrast, in LWS the regression of BW38 on generations was significant for the unadjusted measure, but not upon standardization. However, scaling influenced the pattern and degree of response as seen in the lack of similarities in the two measures (Figure 3.6) where the degree of response was higher upon standardization suggesting a greater response than when unadjusted.

Regressions of ratios of BW at different ages

Regression of ratios of BW in Table 3.3 show unadjusted and standardized values for the different ages from generation 0-54. Homogeneity of variation was greater in the standardized regression than the unadjusted regression responses. When unadjusted the 4/8 ratios in HWS were not significant for either males or females, results consistent with those reported by Dunnington et al. (2013). Upon standardization, however responses for females were significant and negative while those for males were not significant. The results for females upon standardizing suggests that scaling may have masked the true response because the 4/8 ratio assesses the developmental growth processes in the lines and regression of this ratio measures change in growth process over generations.

The significant differences in regressions of unadjusted BW ratios 4/38, 8/24, 8/38, and 24/38 on generations in HWS females disappeared with standardization. Moreover, there was a change in the sign (direction) suggesting a decreasing change in the direction of response which may have been due to scaling, feed restriction or both.

In LWS, the unadjusted and standardized regressions of BW ratios 4/8, 4/38, 8/24, 8/38, and 24/38 on generation were significant except for 4/24. This suggests that scaling was not influential on the response. The unadjusted regression of 4/8 week ratio was higher in females than males. Dunnington et al. (2013) also reported similar results and standardizing scaling made responses more homogenous.

Conclusion

Correlations between means and standard deviations as a result of selection for BW8 were highly positive and greater for LWS than HWS. In both lines, scaling masked the degree more than the pattern of response and was line specific. Namely, while scaling did not influence the pattern of the response to selection of BW8 in either line, it was population specific with regard to the magnitude of response being higher in the LWS than HWS. In HWS, feed restriction also masked the response at older ages i.e., in BW24 and BW38.

BW ratios 4/8, 4/38, 8/24, 8/38, and 24/38 were not influenced by scaling in LWS. In contrast, scaling influenced 4/8, 4/38, 8/24, 8/38, and 24/38 ratios in HWS females. Also BW24 and BW38 were influenced by the feed restriction practiced post-generation 18 in the HWS precluding ad libitum feeling via human intervention controlled BW after week 8. This result is consistent with the commercial broiler industry where feed intake is designed to meet target body weight for breeders.

Standardization is a robust method to adjust for scaling enhancing the interpretability and direction of long term selection response to selection. Because of the change in variances associated with the change in phenotypic means, this method to correct for the correlation was useful.

Table 3.1. Correlations between means and standard deviations of 4, 8, 24, and 38 weeks BWs for four different generation intervals.

			Generation interval			
Line	**Sex**	**Age (week)**	**0-54**	**0-18**	**19- 36**	**37-54**
HWS	F	4	0.62*	0.25ns	0.33ns	0.08ns
	M		0.48*	0.29ns	0.51*	0.35ns
LWS	F		0.94*	0.69*	0.90*	0.63*
	M		0.88*	0.66*	0.75*	0.58*
HWS	F	8	0.42*	0.32ns	0.26ns	0.02ns
	M		0.42*	0.06ns	0.30ns	0.18ns
LWS	F		0.92*	0.60*	0.95*	0.54*
	M		0.90*	0.62*	0.81*	0.71*
HWS	F	24	0.25ns[1]	0.11ns	0.23ns[1]	0.13ns[1]
LWS	F		0.84*	0.89*	0.63*	0.23ns
HWS	F	38	0.44*[1]	0.03ns	0.50*[1]	0.39ns[1]
LWS	F		0.86*	0.81*	0.41ns	0.28ns

HWS=high weight selected line; LWS=low weight selected line.

F=female; M= male.

[1] The following correlation coefficients were influenced by feed restriction.

*P<0.05; ns= P>0.05 (not significant).

Table 3.2. Regressions ± SE of BW at 4, 8, 24, and 38 weeks of age on generation within lines from generation 0-54 for unadjusted and standardized values.

Line	**Sex**	**Age (week)**	**Unadjusted (g/generation)**	**Standardized (standard deviation unit/generation)**
HWS	F	4	4.4 ± 0.2*	0.02 ± 0.01ns
	M		5.0 ± 0.3*	0.02 ± 0.02ns
LWS	F		-3.7 ± 0.2*	-0.03 ± 0.01*
	M		-4.2 ± 0.2*	-0.04 ± 0.01*
HWS	F	8	13.1 ± 0.5*	0.06 ± 0.02*
	M		16.2 ± 0.7*	0.06 ± 0.02*
LWS	F		-10.8 ± 0.6*	-0.06 ± 0.01*
	M		-13.2 ± 0.7*	-0.07 ± 0.01*
HWS	F	24	-1.9 ± 1.6ns[1]	0.08 ± 0.01*[1]
LWS	F		-29.5 ± 2.0*	-0.06 ± 0.01*
HWS	F	38	-7.5 ± 1.9*[1]	0.08 ± 0.01*[1]
LWS	F		-32.6 ± 2.2*	-0.002 ± 0.01ns

HWS=high weight selected line; LWS=low weight selected line.

F = female; M = male.

[1] The following regressions were influenced by feed restriction.

*Regression significantly different from zero (P<0.05); ns = P > 0.05.

Table 3.3. Regressions ± SE of BW ratios on generation at different ages from generation 0-54 for unadjusted and standardized values.

BW ratio	**Line**	**Sex**	**Unadjusted**	**Standardized**
4/8	HWS	F	0.0002 ± 0.0002ns	-0.003 ± 0.001*
		M	-0.0002 ± 0.0002ns	-0.002 ± 0.001ns
	LWS	F	0.001 ± 0.0004*	0.007 ± 0.002*
		M	0.0008 ± 0.0002*	0.005 ± 0.002*
4/24	HWS	F	0.002 ± 0.0001*[1]	-0.004 ± 0.002*[1]
	LWS	F	-0.0008 ± 0.0001*	0.003 ± 0.002ns
4/38	HWS	F	0.002 ± 0.000009*[1]	-0.005 ± 0.06ns[1]
	LWS	F	-0.0009 ± 0.00009*	-0.003 ± 0.001*
8/24	HWS	F	0.005 ± 0.0003*[1]	-0.002 ± 0.002ns[1]
	LWS	F	-0.003 ± 0.0003*	-0.003 ± 0.001*
8/38	HWS	F	-0.005 ± 0.0003*[1]	-0.002 ± 0.002ns[1]
	LWS	F	-0.003 ± 0.0002*	-0.007 ± 0.001*
24/38	HWS	F	0.001 ± 0.0003*[1]	-0.0004 ± 0.002ns[1]
	LWS	F	-0.004 ± 0.0004*	-0.007 ± 0.001*

HWS=high weight selected line; LWS=low weight selected line.

F=female; M= male.

[1] The following regressions were influenced by feed restriction.

*Regression significantly different from zero (P<0.05).

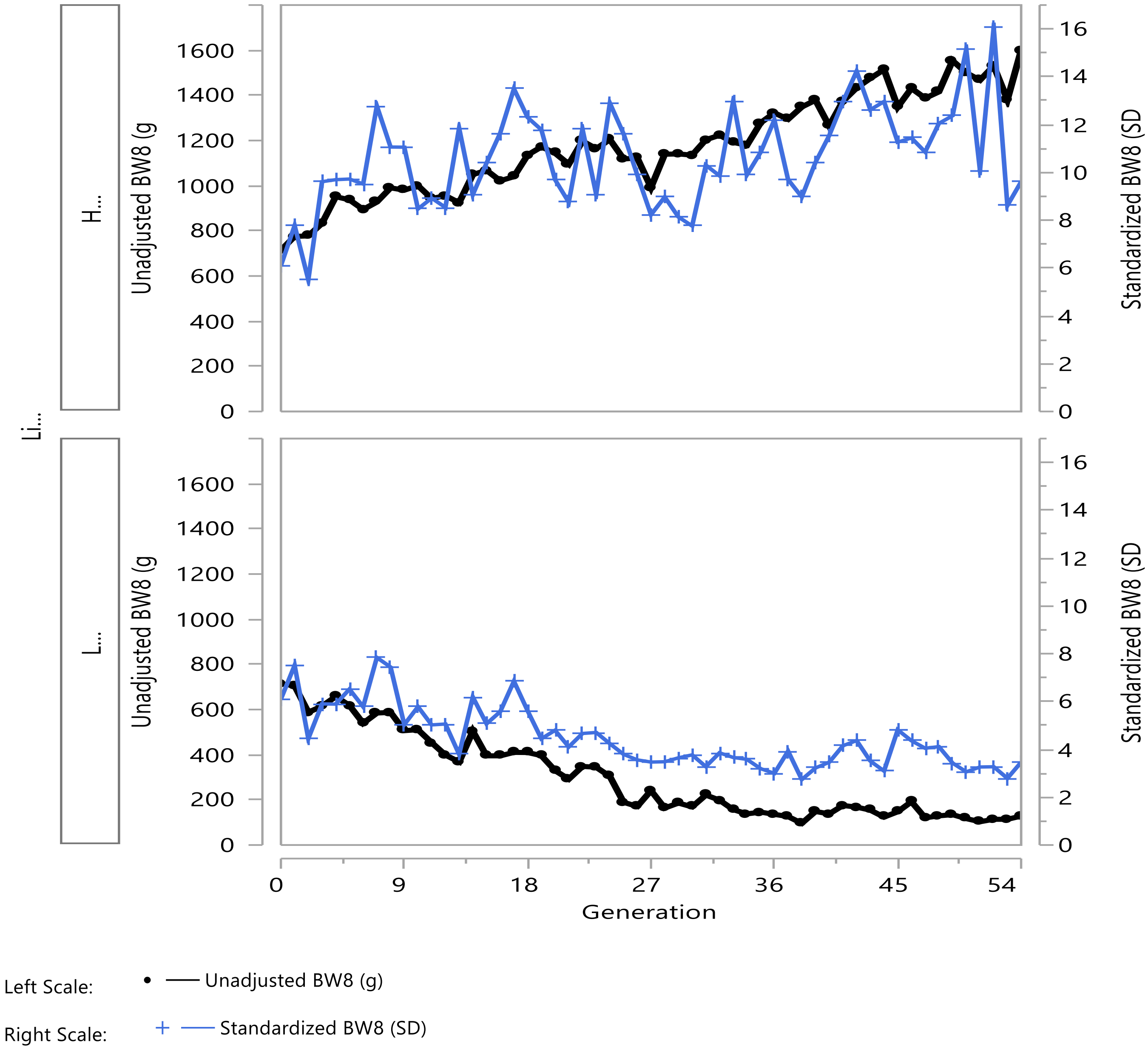

Figure 3.1. Unadjusted and standardized mean BW8 for HWS and LWS females by generation. Unadjusted (•) and standardized response (+) are shown for each line. Regression equation for unadjusted BW8 (HWS) = 821.06 + 13.12*Generation and LWS = 527.35 - 10.82*Generation + 0.26*(Generation)^2. Regression equation for standardized response (HWS) = 9.06 + 0.06*Generation and LWS = 5.76 - 0.06*Generation + 0.001*(Generation)^2.

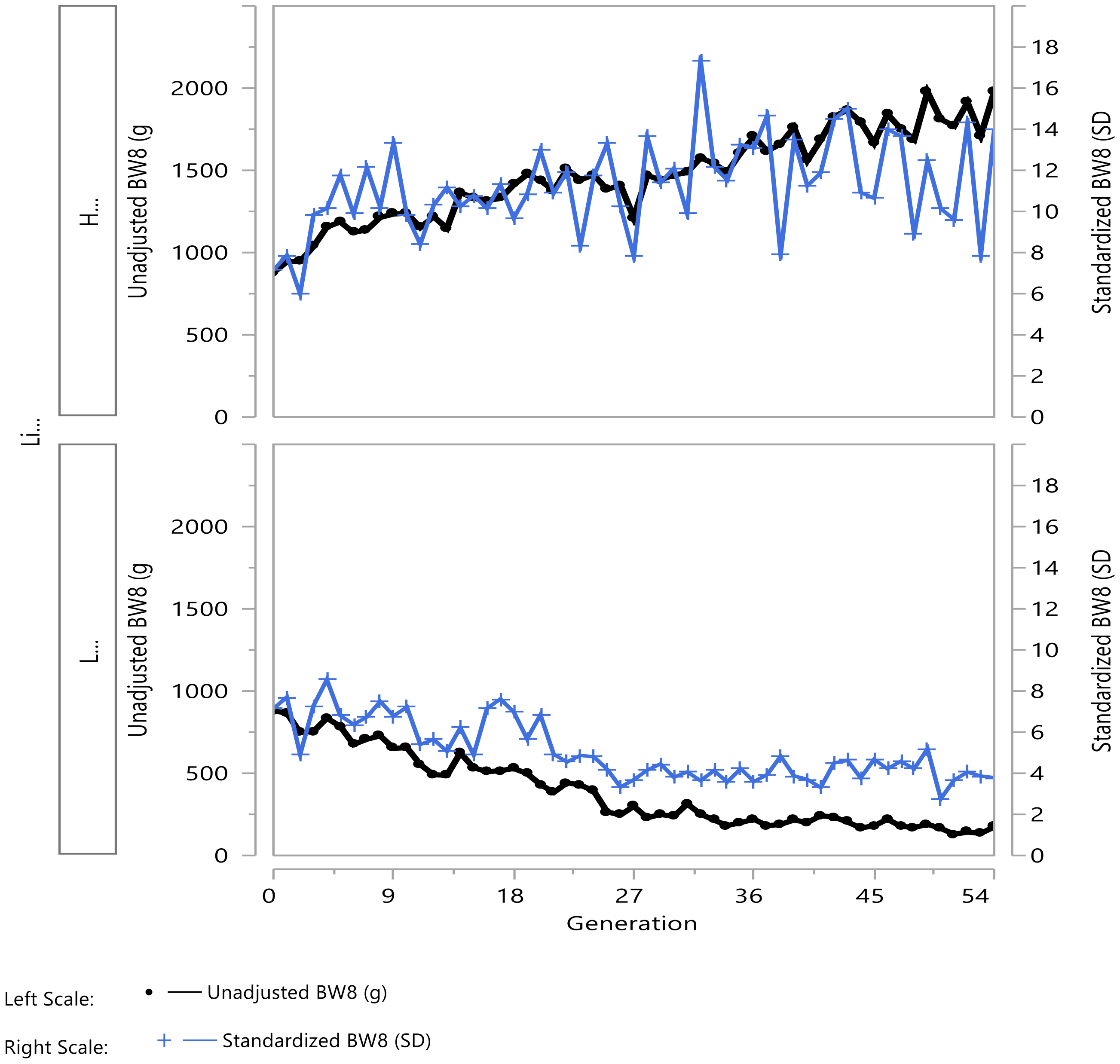

Figure 3.2. Unadjusted and standardized mean BW8 for HWS and LWS males by generation. Unadjusted (•) and standardized response (+) are shown for each line. Regression equation for unadjusted BW8 (HWS) = 1029.21 + 16.25*Generation and LWS= 672.06 - 13.22*Generation + 0.29*(Generation)^2. Regression equation for standardized BW8 (HWS) = 9.73 + 0.05*Generation and LWS= 6.50 - 0.07*Generation + 0.002*(Generation)^2.

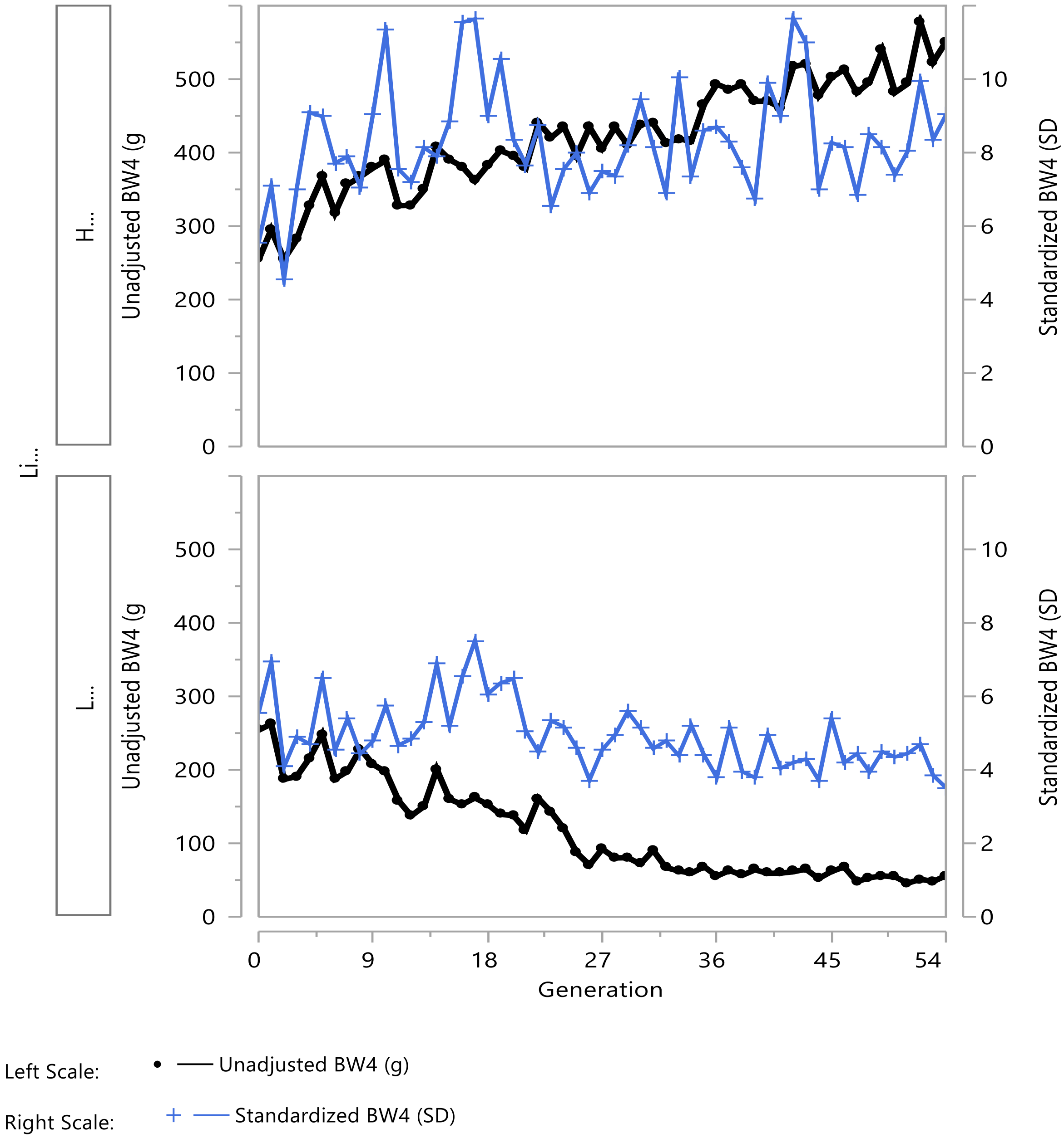

Figure 3.3. Unadjusted and standardized mean BW4 for HWS and LWS females by generation. Unadjusted (•) and standardized response (+) are shown for each line. Regression equation for unadjusted BW4 (HWS) = 303.73 + 4.38*Generation and LWS = 198.82 - 3.74*Generation + 0.07*(Generation)^2. Regression equation for standardized BW4 (HWS): = 7.91 + 0.01*Generation and LWS = 5.73 - 0.03*Generation.

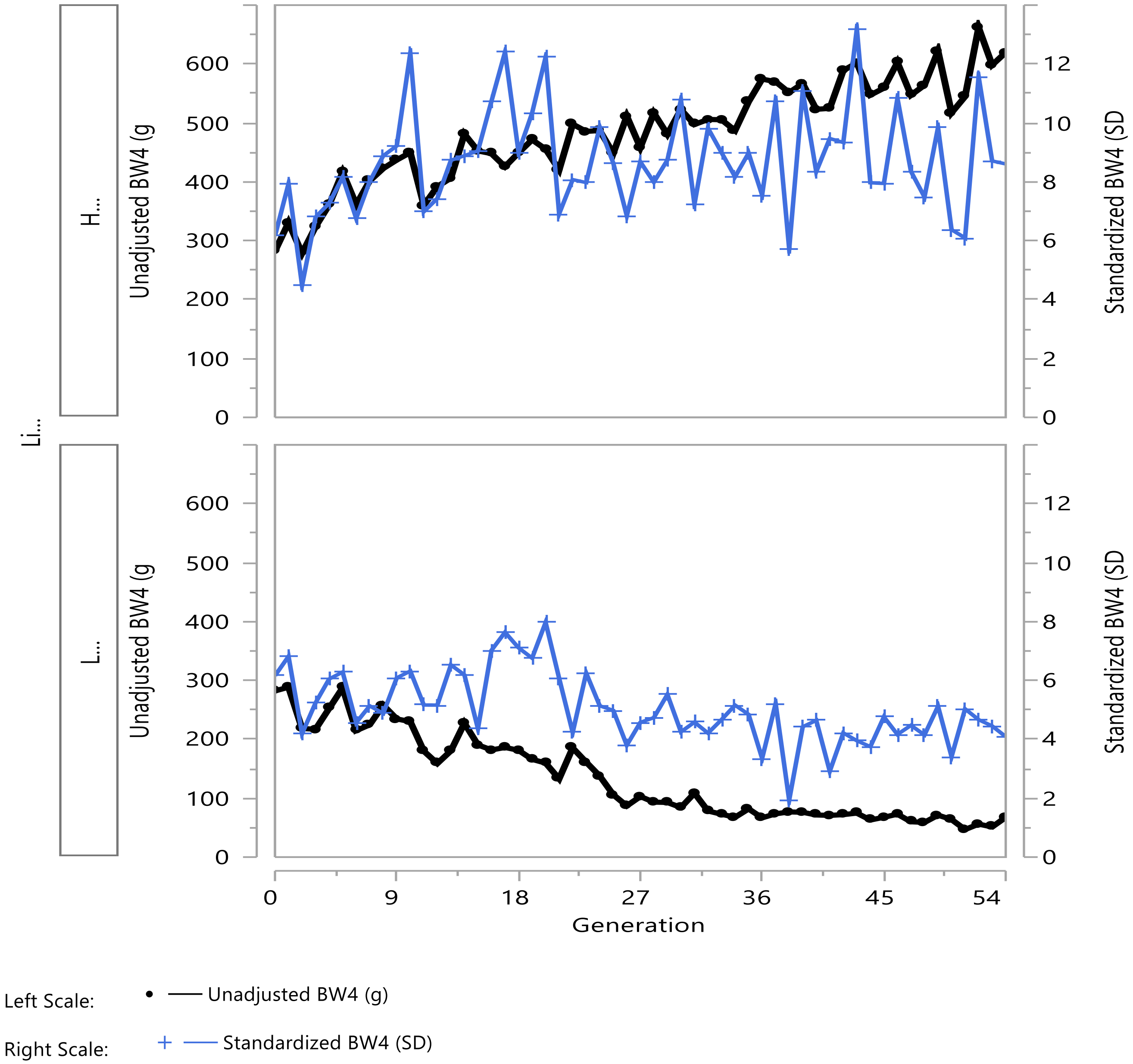

Figure 3.4. Unadjusted and standardized mean BW4 for HWS and LWS males by generation. Unadjusted (•) and standardized response (+) are shown for each line. Regression equation for unadjusted BW4 (HWS) = 349.87 + 4.99*Generation and for LWS = 230.18 - 4.25*Generation + 0.074*(Generation)^2. Regression equation for standardized response (HWS) = 8.16 + 0.02*Generation and LWS = 6.15 - 0.04*Generation.

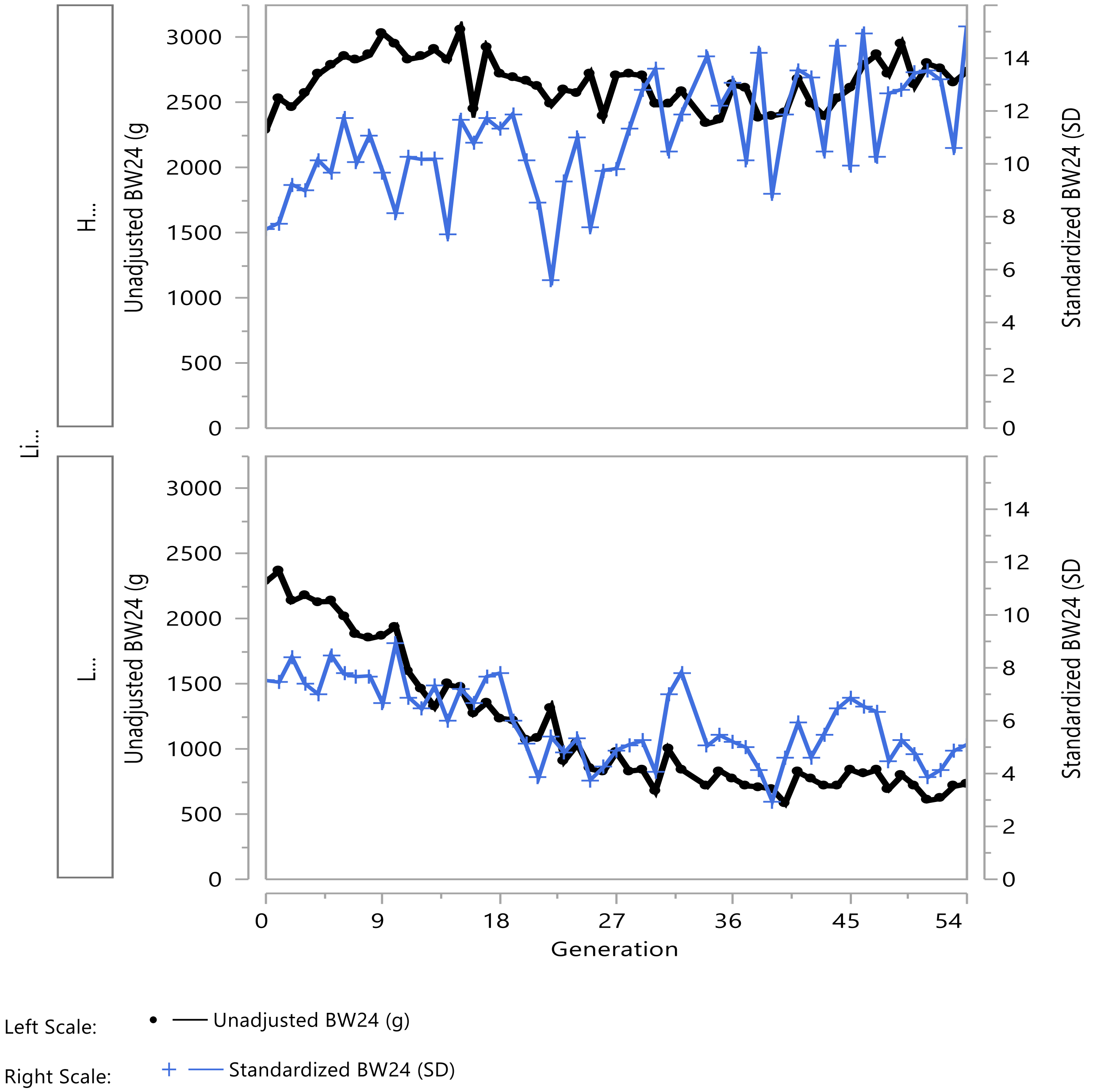

Figure 3.5. Unadjusted and standardized mean BW24 for HWS and LWS females by generation. Unadjusted (•) and standardized response (+) are shown for each line. Regression equation for unadjusted BW24 (HWS) = 2713.13 - 1.88*Generation and LWS= 1726.64 - 29.59*Generation + 0.92*(Generation)^2 .Regression equation for standardized BW24 (HWS) = 8.85 + 0.08*Generation and LWS= 7.03 - 0.06*Generation + 0.002*(Generation)^2.

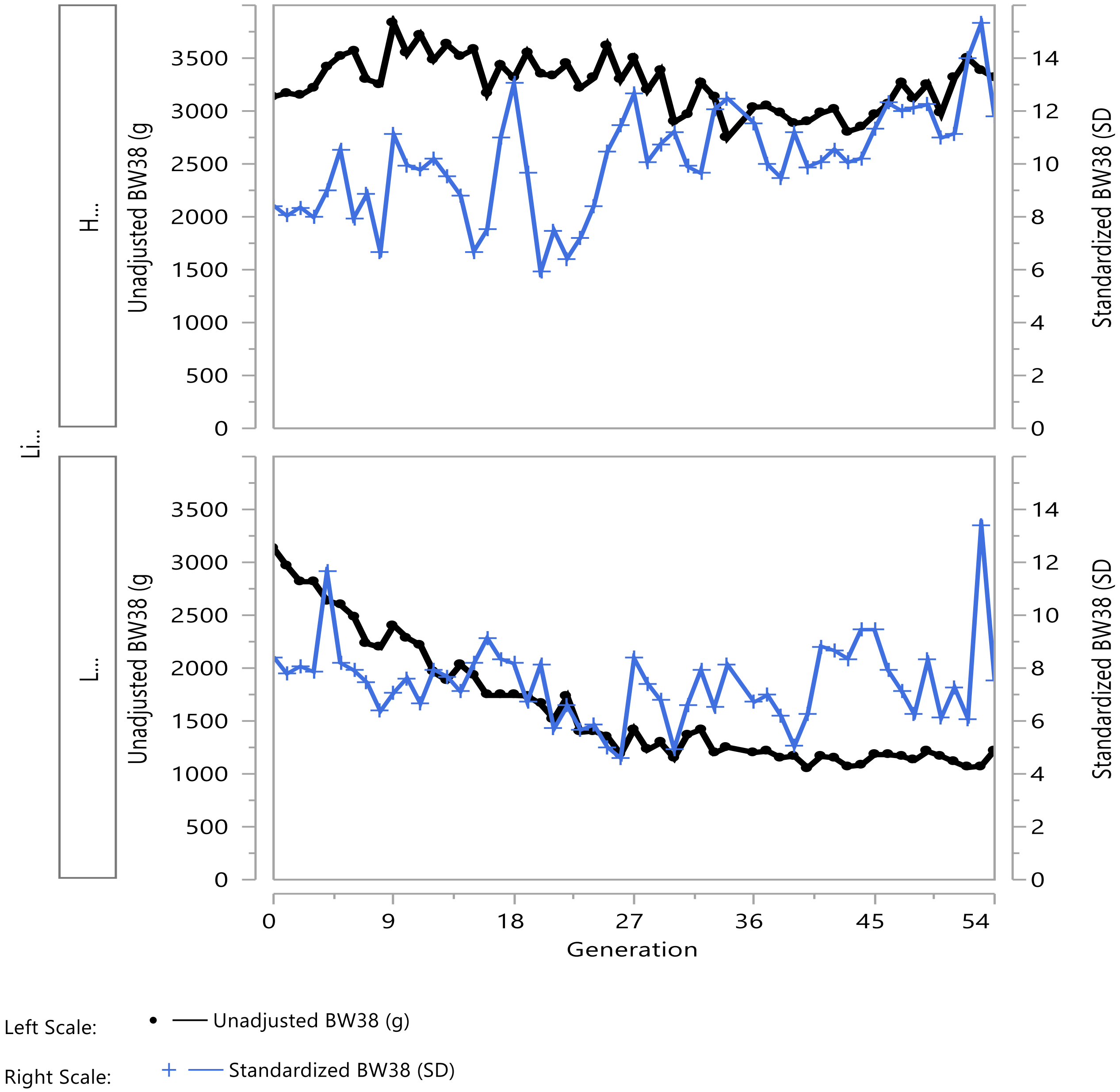

Figure 3.6. Unadjusted and standardized mean BW38 for HWS and LWS females by generation. Unadjusted (•) and standardized response (+) are shown for each line. Regression equation for unadjusted BW38 (HWS) = 3456.72 - 7.48*Generation and LWS= 2239.58 - 32.64*Generation + 1.04*(Generation)^2. Regression equation for standardized BW38 (HWS) = 8.07 + 0.07*Generation and LWS= 6.82 - 0.002*Generation + 0.002*(Generation)^2.

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Chapter 4. Correlated responses to long-term divergent selection for 8-week body weight in female White Plymouth Rock chickens: Sexual maturity and egg production.

Abstract

Reported here are correlated responses for reproductive traits to long-term divergent selection (54 generations) for 8-week body weight (BW). Comparisons involved both selected and relaxed lines. Traits measured were age at first egg (AFE), body weight at first egg (WFE), ratio of body weight and age at first egg (WAFE), and hen-day normal egg production (HDP). Although sexual maturity was delayed in the selected lines, the effect was more pronounced in the low than high selected and relaxed lines. Selection for low BW resulted in decreases in WFE, WAFE, and HDP. Correlated responses to selection for high BW were lower HDP and higher WFE and WAFE. Minimum AFE, WFE, and WAFE in relation to sexual maturity were line specific and influenced by selection for BW8. WAFE provided a "yardstick" for target body weights that were optimum for successful attainment of sexual maturity and higher reproductive rates. There was opposition between relaxed and artificial selection resulting in a higher reproductive performance and fitness for the former than latter.

Introduction

Long-term divergent selection for BW8 is accompanied by changes in reproductive performance. Correlated responses associated with selection for high and low BW from an earlier generation period (Generation 0-27) included delayed sexual maturity and lower egg production (Siegel and Dunnington, 1985). These were a consequence of negative correlations between growth and reproductive traits. A strong negative correlation exists between body weight and reproductive efficiency (particularly egg production) as a result of selection for increased growth (McCarthy and Siegel, 1983; Decuypere et al., 2010).

Sexual maturity and its onset to an animal's reproductive life are of profound importance from both evolutionary and economic perspectives (Wright et al., 2012). Onset of sexual maturity is influenced by chronological age, BW, and body composition (Dunnington and Siegel, 1985; Eitan and Soller, 2001). Namely, for a chicken to commence egg production there is a specific minimum age, minimum BW, and body composition that are line specific (Dunnington et al., 1983, 1984; Brody et al., 1984; Zelenka et al., 1986a, b; 1987). The QTL analysis by Podisi et al. (2011) revealed overlapping QTL for body weight at first egg and at 9-weeks of age indicating that QTL affecting growth also affected body weight at first egg. Co-localization of QTL for body weight, growth, and sexual maturity suggests that body weight and growth are closely related to the attainment of sexual maturity and that the genetic factors associated with growth have correlated effects on puberty.

During the earlier generations of selection (Generation 0-36) there was a slight decline in hen-day egg production of HWS and LWS (Liu et al., 1995b). The decline in egg production in LWS may have been associated with a decrease in energy reserves integral to egg production, a view consistent with the delay in age at sexual maturity observed for this line (Siegel and Dunnington, 1987). In the HWS, there was an increased incidence of defective eggs due, in large part, to a lack of synchrony between ovulation and subsequent "packaging" of the egg. There are dramatic changes in relationships between a selected trait and traits associated with fitness which imply an opposition between artificial and natural selection that demonstrates a strong effect of the latter on the traits regardless of how long artificial selection has been practiced.

The objectives of this study are (i) to measure the correlated responses of long-term selection for BW8 on sexual maturity and percent hen-day normal egg production for 54 generations of selection, (ii) to determine the response of body weight at first egg (WFE) from generation 27-54 and relationships of growth to sexual maturity, and (iii) compare the reproductive performance of selected and relaxed lines.

Materials and Methodology

Experimental design

Fifty-four generations of selection were conducted for high or low BW8 in chickens. The foundation stock consisted of crosses of 7 moderately inbred lines of White Plymouth Rock (WPR) chickens (Siegel, 1962). From this segregating gene pool, chickens with heavier BW8 were chosen as parents for the high line (HWS) and those with lighter BW8 were selected as parents for the low line (LWS). Individual selection was then practiced within the respective HWS and LWS lines in all subsequent generations, with BW8 as the single criterion of selection. Numbers of sires and dams selected to produce each line were 8 and 48 through the fourth generation of selection (S4), 12 and 48 from S5 to S25, and 14 and 56 after S25. These parents are selected from within-line groups of approximately 150 to 250 individuals depending on generation. Pure truncation selection was not used, however, so that overrepresentation of sire and dam families would be avoided (Dunnington and Siegel, 1996; Dunnington et al., 2013). This effort to curtail inbreeding from common ancestry and avoid matings among half sib or close relatives and to avoid selection of particular sire or dam families reduced, yet could not avoid inbreeding from common ancestry and also resulted in similar population structures in the lines. By generation 48, inbreeding in both lines was moderately high and effective population size was low, as expected, in closed lines (Marquez et al., 2010).

Relaxed lines

In S6, S13, S19, S26, S34, and S43 of chickens from lines HWS and LWS were chosen at random before selection of breeders for the selected lines to establish sublines in which selection for BW8 was relaxed. Each subline (designated HR1, HR2, HR3, HR4, HR5, and HR6 for line HWS and LR1, LR2, LR3, LR4, LR5, and LR6 for line LWS) was maintained as a contemporary of its corresponding selected line and reproduced by random matings each generation. The relaxed lines were produced by using pooled semen within a subline to artificially inseminate females in that line. The same husbandry procedures and environments were employed for the relaxed lines as those practiced in the selected lines. A relaxed line was maintained for 7 to 11 generations. Each subsequently relaxed line was initiated one generation before the previous relaxed line was discontinued (Dunnington et al., 2013).

Husbandry

Each generation, chicks were hatched on the first Tuesday in March of every year and wing-banded for individual identification. If adequate numbers were not obtained from this hatch, a second hatch was produced on the third Tuesday in March. Every generation, chicks were reared in identical pens with concrete floors, wood shavings as bedding, continuous light, and hot-air brooding until 8-weeks of age (Dunnington and Siegel, 1996; Dunnington et al., 2013). From 8-18 weeks, they were exposed to natural photoperiod, after which they were provided artificial light from 0600 to 2000 hours in a light-controlled environment (Liu et al., 1995b). Other than routine husbandry in a rather isolated environment, the only disease preventatives were the addition of a coccidiostat to the starter and developer diets and vaccination for Marek's disease, which commenced after the 17th generation of selection. Through generation 13, chickens were maintained in littered floor pens. Thereafter, they were reared on litter to approximately 126 days of age and then housed individually in wire cages. Throughout the study, feed in mash form and water were provided ad libitum with the same formulations. Chicks were fed the starter until 8-weeks of age, developer from 8-20 weeks and a breeder diet thereafter. Percentages of protein were 20, 16, and 16, and levels of metabolizable energy (ME) were 2,685, 2,761 and 2,772 kcal/kg in the starter, developer, and breeder diets, respectively. Beginning in generation 18, feed intake after 8 weeks was restricted for HWS and its relaxed sublines because of increasing difficulties with reproduction due to obesity (Dunnington and Siegel, 1985; 1996; Dunnington et al., 2013).

Traits

Traits reported here are age at first egg (AFE), percent hen-day normal egg production, (HDP), body weight at first egg (WFE), and ratio of body weight and age at first egg (WAFE). Data for the WFE and WAFE were collected only since the 27th generation of selection.

The AFE was defined as age when the first egg was laid, provided that a second egg was laid within the next 9 d. In the later generations of selection, age at first egg in LWS was biased downward because an increasing number of pullets did not begin to produce eggs by 240 days of age (Dunnington and Siegel, 1985). Subsequently, the period was extended to 275 days of age.

Body weight at first egg (to the nearest 10 g) were obtained on the first day of lay. Ratio of body weight and age at first egg (WAFE) was calculated by dividing the mean of WFE by AFE for each generation. This ratio reflects growth to sexual maturity and assumes that body composition is constant throughout the growth period to sexual maturity.

Egg production, from AFE to a fixed age, was recorded for each female that produced eggs and percentage HDP was calculated (total number of normal eggs laid during that period/total number of days for that period) x 100 (Liu et al., 1995b). From generation 0 through 13, egg production was calculated as the percentage of ovipositions per hen-day from sexual maturity to a fixed date. Because egg production data were obtained by trap- nesting, floor eggs reduced accuracy. Maintenance of pullets in individual cages for generations 14 through to 54 enabled classification of each egg (van Middlekoop and Siegel, 1976) as normal, extra calcified, compressed, broken, double yoked, or otherwise defective (e.g., membraneous, soft-shelled, rough shelled). Percentage hen-day normal egg production was then used as the measure of production (Dunnington and Siegel, 1985).

Statistical analysis

Regressions of mean AFE, HDP, WFE and WAFE on generations were calculated in the selected lines from generation 0-54 for the first two and from generation 27-54 for the last two traits. Divisions of generations into overlapping intervals corresponding to the propagation of the relaxed lines (6-14, 13-20, 19-27, 26-35, 34-44, and 43-54) provided regressions where selected and relaxed lines could be compared. Six groups of relaxed-selection lines (initiated every 7 to 11 generations) were analyzed separately for each line (HWS, LWS) to compare linear slopes of selected vs. relaxed lines for mean AFE and HDP and three groups for WFE and WAFE. The results provided information on whether relaxation (cessation) of selection at different stages of the selection experiment resulted in changes in regressions of the correlated response to selection for BW8. Prior to analysis WFE was transformed to common logarithms and HDP percentages to arc sine square root. All calculations were conducted using regression procedures in JMP software (JMP 11, 2015). Default p value = $P < 0.05$.

Results and Discussion

Age at first egg (AFE)

Sexual maturity of females is defined here as the age when the first egg is oviposited (laid). There is a time lapse of approximately 26 hours from ovulation to oviposition. A complete overview of the correlated response of AFE in the selected and their respective relaxed lines is seen in Figure 4.1. There was little change from the increase in HWS between the earlier and later generations. Moreover, the relaxed lines responded similarly to HWS from environmental factors throughout the experiment. The AFE increased in LWS throughout the experiment while its relaxed lines generally reached sexual maturity at younger ages. Means and standard errors for age at sexual maturity were 212.64 ± 3.15 d in LWS and 180.57 ± 1.98 d in HWS from generation 0-54. It is evident from Figure 4. 1 that there were similarities and differences between the selected and their respective relaxed lines. To ascertain what occurred overall and during time periods the regressions are presented in Table 4.1. The overall regression of AFE on generation (Gen 0-54) was 0.63 ± 0.09 d in the HWS and 1.25 ± 0.10 d for the LWS. Although HWS became sexually mature at a younger age than LWS, over the course of the selection experiment there was a delay of 34 and 68 d in HWS and LWS, respectively. Thus, while both selected lines experienced delays in reaching sexual maturity, the delay was greater for LWS than HWS suggesting a lower efficiency in body weight conversion concomitant to a decrease in feed intake with the direction of selection.

When viewed within periods of selection, the regression of AFE on generation was positive and higher (4.01 ±1.35 d) as early as the generation interval 6-14 in LWS, whereas response in HWS were also positive but lower (0.86 ± 0.54 d) indicating an earlier onset of sexual maturity.

During generation periods 13-20, 19-27, and 26-35 regressions were positive and higher in HWS than HWR. Although the response in LWS was similar to HWS being positive, all regressions for LWR were negative as they were sexually maturing at younger ages than LWS. The differences between LWS and its relaxed counterparts became obvious as early as the 13-20 generation interval. The lack of difference between the selected and relaxed HW lines may be attributed to controlling the onset of lay by restricting feed intake (Liu et al 1995b).

During the generation interval 34-44, AFE decreased in both the selected and their respective relaxed lines as shown by the negative regressions of AFE on generation (Table 4.1). Although none was significant, regressions were less for the selected than their respective relaxed line. This pattern suggests that there were environmental factors that caused the selected and relaxed lines to respond similarly during this period. Also, it is obvious that the effects of relaxing selection on AFE was greater in the low than high lines. This pattern was consistent with those reported by Dunnington and Siegel (1985) that relaxation of selection decreased AFE. The direction of response changed to positive in generations 43-54 for HWS, LWS, and LWR, but not HWR. High weight lines reached sexual maturity at younger ages than the LW lines which was consistent with those reported by Liu et al. (1995b) that the regression of AFE on generation was higher in LWS than HWS.

Body weight at first egg (WFE)

For a complete overview of the correlated responses of WFE in the selected and their respective relaxed lines from generation 27-54, see Figure 4.2. WFE, which was not measured prior to generation 27, was greater in the HW than LW lines. HWS commenced egg production at a heavier BW than its relaxed lines and LWS commenced lay at a lower BW than its relaxed lines. WFE ranged from 2,735 to 3,291 g in HWS and 1,078 to 1,329 g in LWS. The overall means and standard errors for WFE were 2,939 ± 26 g for the HWS and 1,183 ± 14 g in the LWS, a 2.5 fold difference in WFE between the two lines. Similarities in both lines include declining WFE from generation 27-44 which increased thereafter. The increase, however, was greater in the HWS than LWS concomitant to direction of selection.

Regressions of WFE on generation 27-54 were 9.82 ± 2.70 g and -5.20 ± 1.27 g for HWS and LWS, respectively (Table 4.2). The increase in WFE in the HWS was greater during the last generation interval (generation 43-54) than the two previous intervals where the regressions of WFE on generation were negative. The difference may be attributed to the feed restriction and its effects on weight after selection age. In contrast, the decrease in WFE for LWS was influenced more during the two earlier intervals (generations 27-35 and 34-44) where the regressions of WFE on generations were negative other than positive during the last generation interval. The magnitude of decrease was higher in LWS than HWS in the two earlier intervals. In contrast, regression coefficients for the last generation interval were higher in HWS than LWS (30.02 ± 8.94 vs. 0.48 ± 4.57 g) indicating an increase in WFE.

For selected and relaxed lines, regressions of WFE on generation during the first two generation intervals (27-35, 34-44) decreased in both the HWS and HWR, although WFE was lower in the latter than former. HWR commenced egg production at a lower BW than HWS, however, both responses increased during the last generation interval (generation 43-54). The increased regression response was significant for HWS but not HWR (30.02 ± 8.94 vs. 7.24 ± 11.10). The similarity in response on the intervals for HWS and HWR demonstrate that feed restriction practiced in the high weight lines influenced the pattern of response.

In LWS, there was a similar trend of decreasing WFE in the earlier generations before increasing during the last generation interval. This increase in WFE during generation 43-54 occurred in both LWS and LWR. Selection for low BW has resulted in a threshold body weight below which pullets do not reach sexual maturity. For the LWS, the minimum of 1,000 g below which pullets did not commence egg production (Dunnington et al., 1983) continues to the present. This threshold may be due to anorexia because by force feeding, non-layers reached the threshold body weight necessary for the attainment of sexual maturity as measured by producing eggs (Zelenka et al., 1988).

When selection was relaxed, WFE was lower for the HWR than HWS. For the low weight lines, LWR was heavier than LWS at sexual maturity (Figure 4.2). Thus, there was an opposition between the forces of artificial and natural selection where selection increased WFE in HWS and decreased WFE in LWS implying that minimum WFE is line (population) specific.

Ratio of WFE and AFE (WAFE)

The correlated response of WAFE in the selected and their respective relaxed lines from generation 27-54 is seen in Figure 4.3. WAFE was higher in HW than LW lines reflecting a higher growth to sexual maturity in HWS with differences of >3 fold in the selected lines. The ratio of body weight and age at first egg in HWS decreased during the earlier generations and increased during later generations. In contrast, WAFE in LWS decreased throughout. Upon comparing the relaxed and selected lines, WAFE was generally greater in the selected than in relaxed HW lines. On the other hand, WAFE was consistently higher in LWR than LWS. Upon relaxation of selection, there was a decrease in WAFE for HWR and an increase in LWR.

It is evident from Figure 4.3 that there are similarities and differences between the selected and their respective relaxed lines. Regressions of WAFE that occurred overall and during time periods are presented in Table 4.3. The regressions of the ratio between WFE and AFE from generation 27-54 were 0.03 ± 0.02 g/d and -0.02 ± 0.01 g/d in HWS and LWS, respectively.

Means and standard errors for daily weight gain from hatch to sexual maturity were 15.60 ± 0.19 and 5.15 ± 0.08 g/d in HWS and LWS, respectively.

Although the difference in WAFE between the selected lines was >3 fold, there was a small but consistent difference with HWR being generally lower than HWS. This may be due to the restriction of their feed intake after 8-week of age and thus a steady growth to reduce reproductive complications. The difference in patterns between the high and low weight lines show that the HW lines were more variable in response than the LW lines which were decreasing overall. In contrast, WAFE was consistently higher in LWR than LWS, thus delaying the onset of sexual maturity in the latter. The difference in WAFE between relaxed and selected lines was greater and obvious from the beginning in the LW than the HW lines (Figure 4.3).

That the regressions of WAFE on generations were negative throughout all the generation intervals in LWS (Table 4.3) suggested slower growth to maturity than LWR which was always positive. The importance of WAFE (assuming body composition is constant) is it can be used to evaluate whether or not pullets are gaining sufficient BW to reach sexual maturity. This reasoning is consistent with breeder guides which recommend feeding broiler breeders to a target weight during the growing period. A WAFE lower than the threshold ratio such as ratio of <4g/d in LWS may be an indication that pullets in these lines are unable to commence lay and may be anorexic. Feeding programs such as force-feeding have been successful in bringing non-laying pullets with lower WAFE into egg production. Namely, anorexia was restricting them from reaching threshold BW required for sexual maturity (Zelenka et al., 1988).

From a selection point-of-view, this growth information may be monitored in young ages as most likely, an individual with a lower body weight gain as early as 4-8 weeks of age may not consume sufficient feed to meet the threshold BW to commence lay. Namely, WFE is more closely tied to adult than to juvenile BW (Dunnington et al., 1983). A low but positive genetic correlation between WFE and early growth suggests that continued selection for rapid growth should produce only minor further increases in WFE (Soller et al., 1984b). Thus, feed restriction practiced in HW during the rearing period will further control growth and keep BW at a constant requirement for sexual maturity and reproductive success. A WAFE higher than the target may indicate that the chicken is obese with possible reproductive complications such as EODES as well as associated metabolic and cardiovascular disorders. Selection for increased BW has resulted in heavier WFE and negative effects on reproductive performance in adults when fed ad libitum. Early maturity associated with increased juvenile growth has been associated with reproductive problems such abnormal hierarchies in egg formation (Hocking, 2004). Accordingly from a practical aspect, human intervention is realistic in monitoring the growth of breeders.

The relationship between age and body weight showed that there are minimum thresholds for ages and body weights at which the chickens cannot reach sexual maturity as a correlated response to selection for BW8 (Dunnington et al., 1983). WAFE showed that there is a minimum average daily growth at which sexual maturity will occur and below that LWS pullets will not commence egg production. For the HWS, a higher WAFE above the minimum of approximately 15-17g/day contributes to obesity and associated reproductive complications. Anorexia associated with selection for low body weight reduces growth and delay or preclude sexual maturity. Thus, in the commercial world of feeding programs for breeders, be they for egg or meat production stocks, we are dealing with population specifics to achieve the target weights optimum for high reproductive rates.

Hen-day normal egg production (HDP)

A complete overview of the correlated response of HDP in the selected and their respective relaxed lines is seen in Figure 4.4. The response of HDP to selection was more variable in the earlier generations for the HW than LW lines. HDP decreased during the first 6 generations of selection and was more variable during the first 23 generations than thereafter. In contrast, the initial higher HDP production in LWS steadily decreased over generations. That is, HDP was higher during the first 18 generations in LWS and decreased steadily thereafter. On the other hand, LWR had a lower HDP in the earlier generations and increased from generation 18 onwards being consistently higher than LWS. In contrast, HWR performed similarly to its selected line. Thus, the difference in performance between the selected and relaxed lines was greater in LW than HW line. The overall means and standard errors of percent hen-day normal egg production during this period was 55.08 ± 0.94 % and 58.78 ± 0.82 % for HWS and LWS, respectively.

There were similarities and differences between the selected and their respective relaxed lines over the 54 generations as seen in Figure 4.4. Regressions of percent HDP that occurred overall and during time periods are presented in Table 4.4. For generation 0-54 the means and standard errors of normal egg production decreased in the selected lines being -0.12 ± 0.06 % in HWS and -0.28 ± 0.03 % in LWS. The correlated decrease in HDP with selection may be attributed to the antagonistic relationship between juvenile growth and normal egg production in these divergently selected lines of chickens (Siegel and Dunnington, 1985). The negative regression response of HWS, although similar to LWS was probably masked by feed restriction to address reproductive complications associated with obesity.

HDP increased in both the selected and relaxed lines from generation 6-14 and decreased from generation 13-20. From generation 0-13, eggs were not classified as normal and some abnormal eggs (e.g. extra calcified) were considered in hen-day production. This may have influenced the response in the earlier generations. From generation 14 onwards, eggs of both lines were classified and percentage of normal egg productions decreased from generations 13-20.

There was little difference between relaxed and selected HW lines as feed restriction was practiced in both lines. Namely both HWS and HWR responded similarly to environmental factors including the restriction of feed. This may have also masked correlated responses to increased BW in HWS.

In the LW lines, responses were generally less variable across the generations, however, the difference in HDP between LWS and LWR became obvious after generation 18 with consistently higher HDP in LWR than LWS (Figure 4.4). Relaxation of selection caused an increase in HDP in LWR. Furthermore, during generations 34-44, there was a significant decrease in HDP in LWS (-0.54±0.23) while it increased in LWR (0.88±0.33) (Table 4.4).

Regressions of hen-day normal egg production during the last generation interval (43-54) was negative in the low lines and positive in the high lines (Table 4.4). Again, feed restriction may play a part in the increase in normal egg production because it decreases the incidence of EODES. Excessive follicle development that disrupts normal ovarian function resulting in EODES due to selection for increased growth can be ameliorated by feed restriction (Decuypere et al., 2010). Feed restriction limits excessive body weight gains and EODES during initial pullet growth and during lay (Eitan and Soller, 2009). In the low weight lines, however, when feed intake is insufficient, they do not ovulate and have to be force-fed to commence lay (Zelenka et al., 1988).

Although there was a decrease in egg production for both LWS and LWR during generations 43-54, the magnitude of decrease was higher in the former than latter. Since generation 19, HDP was generally higher in the relaxed than the selected lines. Normal egg production increased when selection was relaxed is evidence of the opposition between the delicate balance of natural and artificial selection in the response associated with reproductive fitness traits.

Conclusion

Long-term divergent selection for BW8 resulted in changes in AFE, WFE, WAFE, and HDP. Although sexual maturity was delayed in both selected lines, it was more pronounced in LWS than HWS. Selection for low body weight resulted in correlated decreases in WFE, WAFE, and HDP. Sexual maturity and egg production declined more in the low than the high selected lines. Selection for heavier body weights also resulted in a lower HDP, however WFE and WAFE were generally higher and the feed restriction program may have influenced responses.

Minimum AFE, WFE and WAFE in relation to sexual maturity were specific for each line and influenced by selection for BW8. An important measure for assessing growth to reach sexual maturity was WAFE. This measure provides a “yardstick” to which sexual maturity is likely or unlikely to occur and the possibility of reproductive complication or a case of anorexia. There are likely economic advantages for this measure from the point-of-view of selection experiments or commercial breeding program. Lastly, an opposition between relaxed and artificial selection is seen in the difference in response between selected and relaxed lines. Namely, there is a higher reproductive performance and fitness with relaxed than artificial selection on the high and low extremes of body weight.

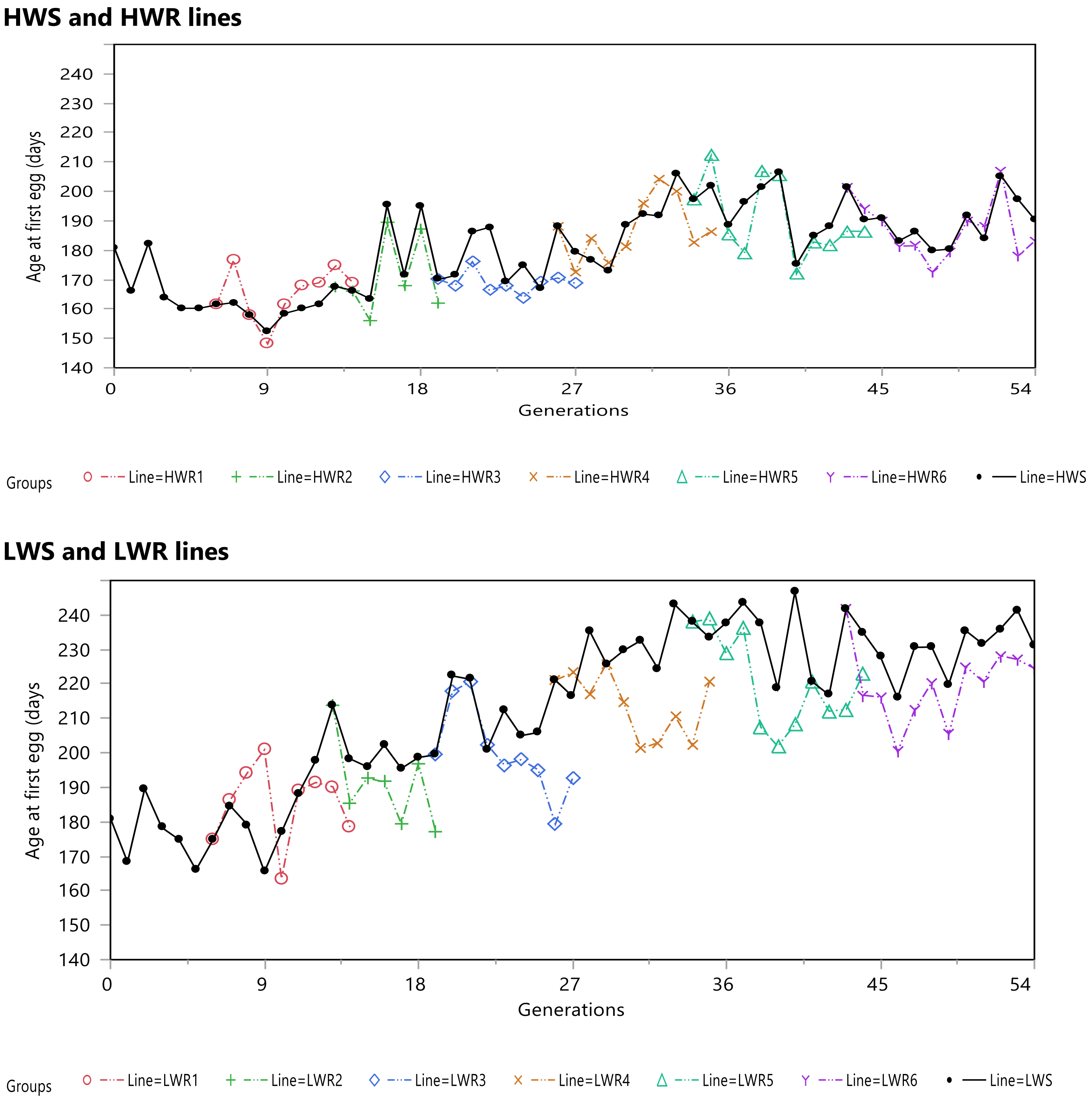


Figure 4.1. Mean age (days) at first egg for all lines across generations. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line (numbers following letters for HWR and LWR related to chronology of when selection was relaxed).

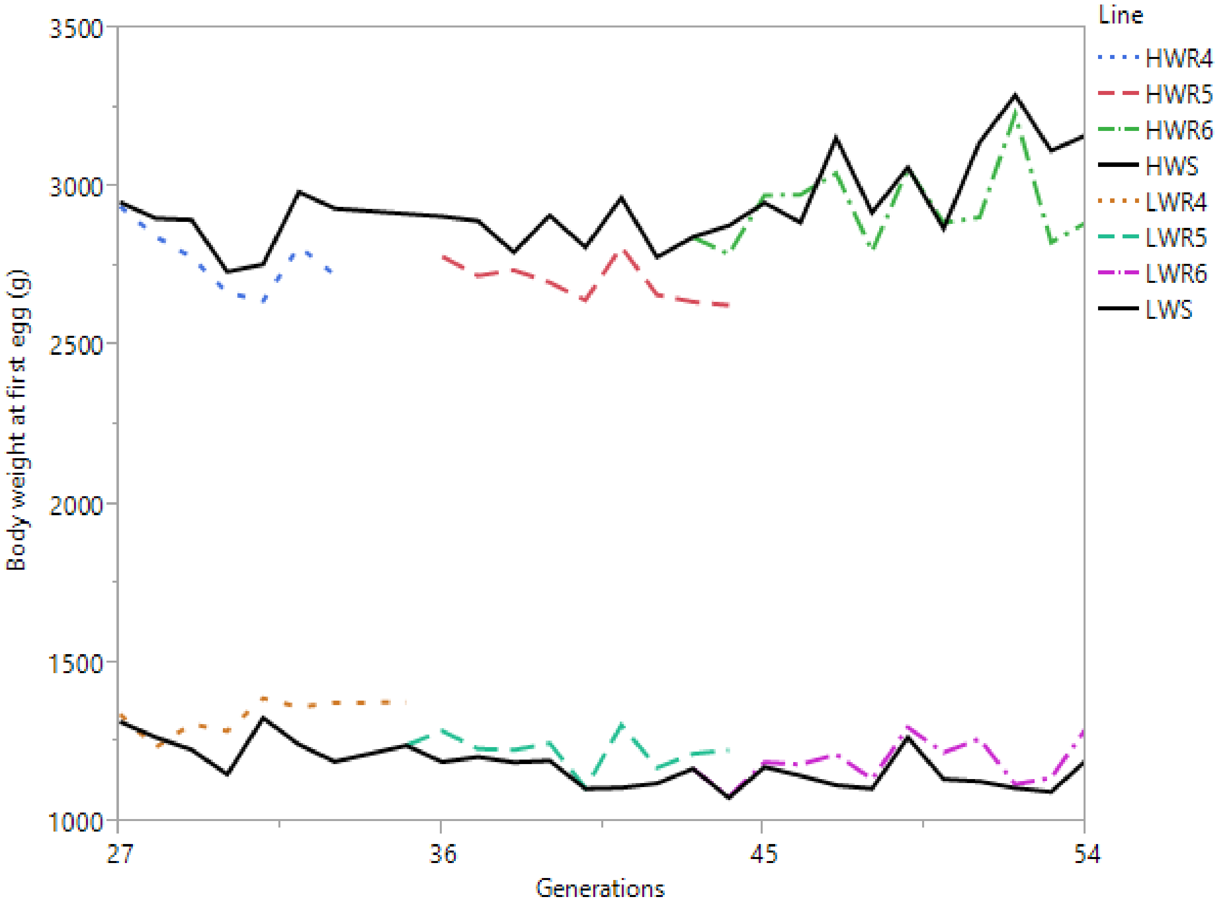


Figure 4.2. Mean body weight (g) at first egg for all lines across generations. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line (numbers following letters for HWR and LWR related to chronology of when selection was relaxed).

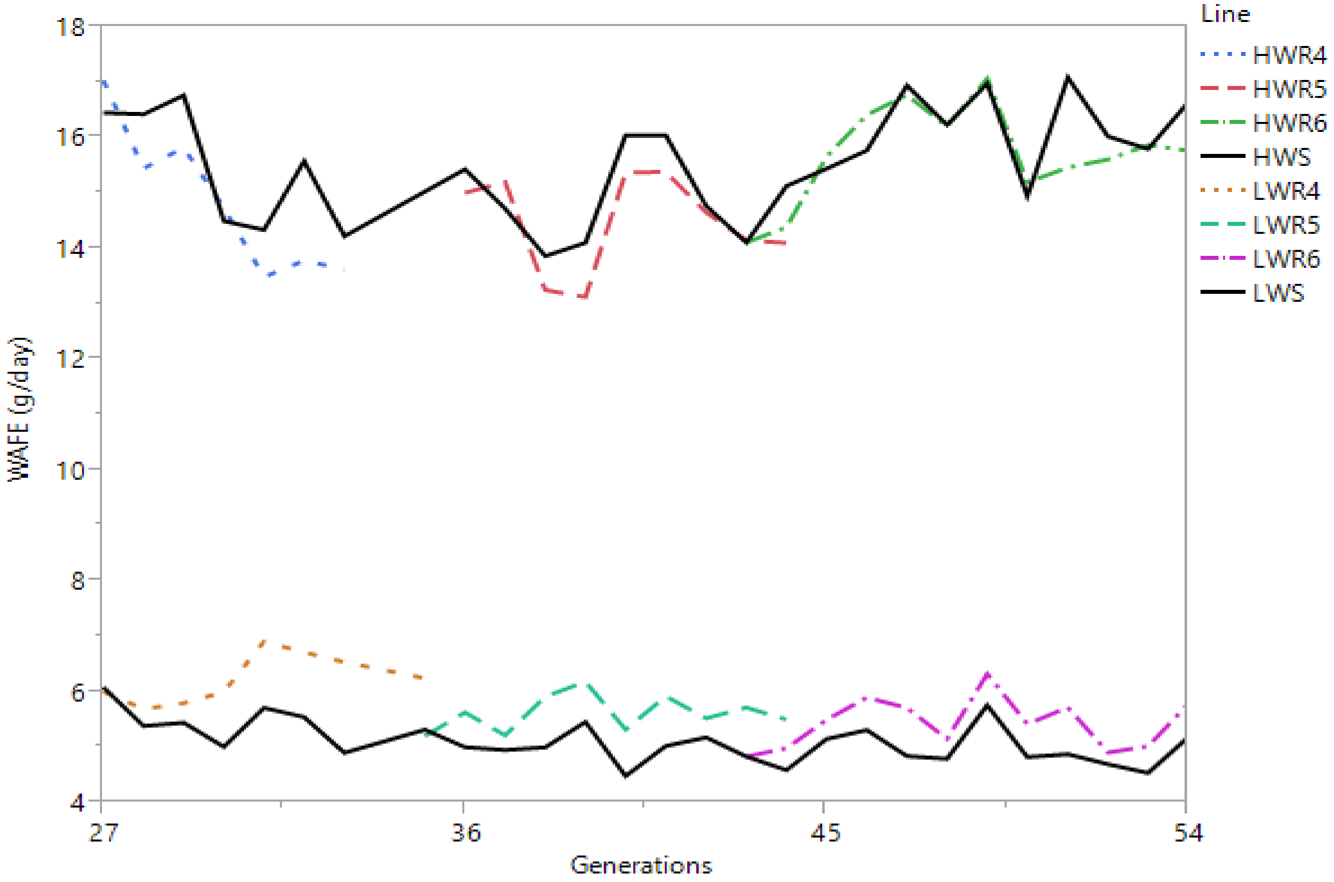
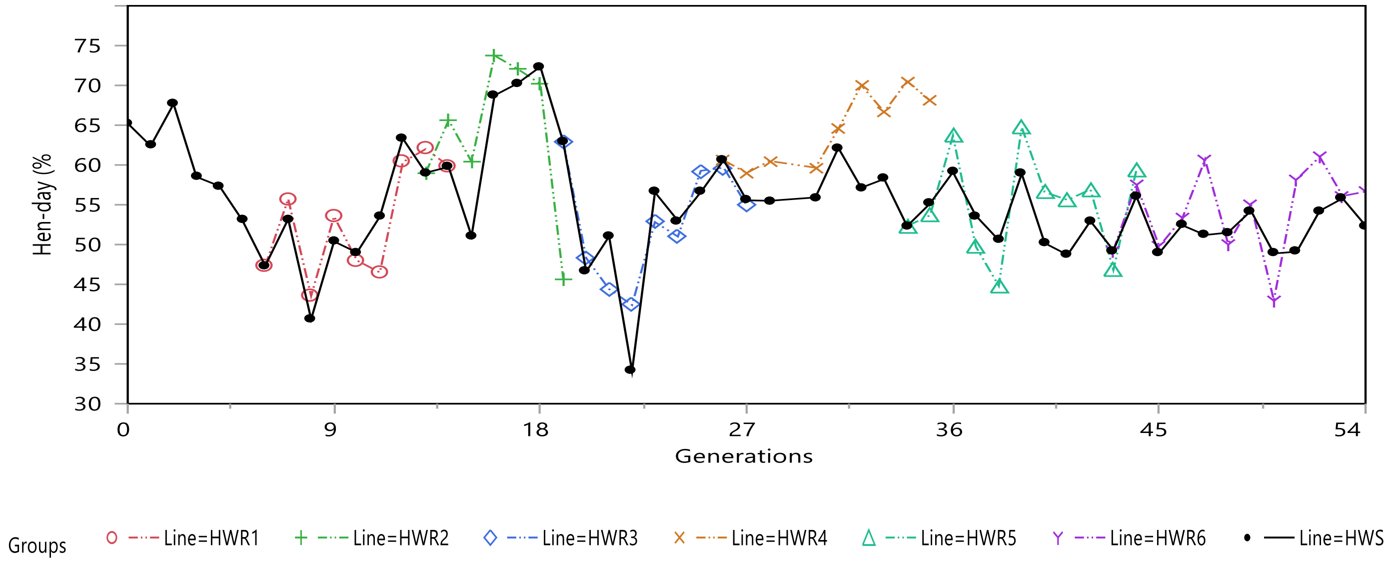


Figure 4.3. Mean ratio of body weight and age at first egg (WAFE) for all lines across generations. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line (numbers following letters for HWR and LWR related to chronology of when selection was relaxed).

HWS and HWR lines



LWS and LWR lines

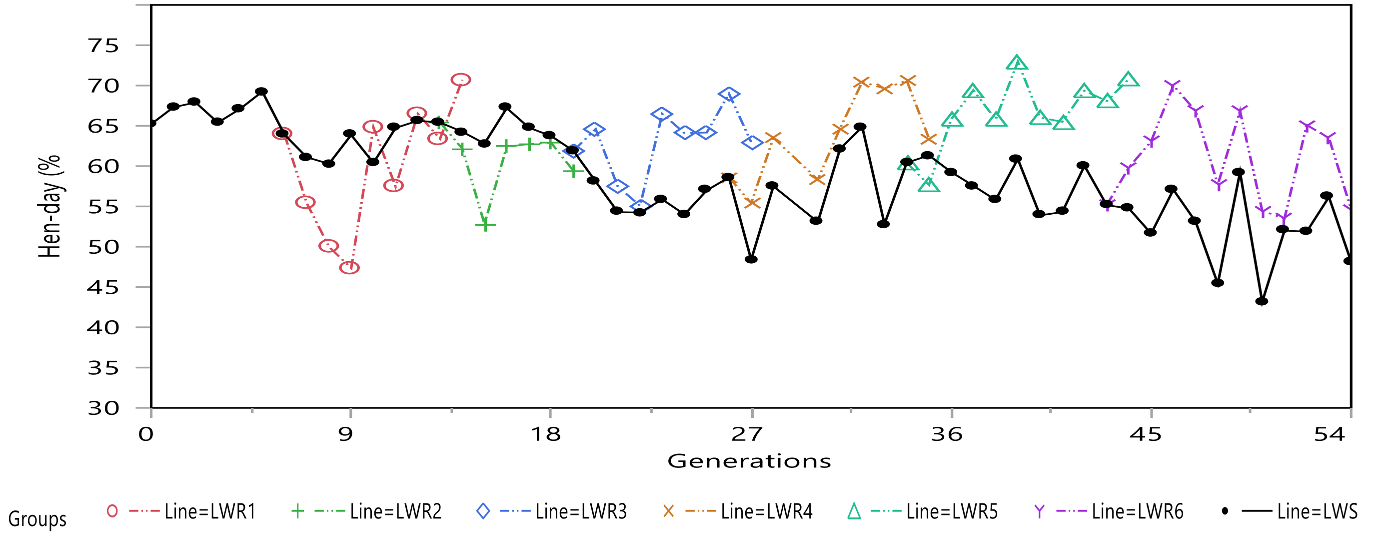


Figure 4.4. Mean percentage hen-day normal egg production for all lines across generations. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line (numbers following letters for HWR and LWR related to chronology of when selection was relaxed).

Table 4.1. Regressions of age (days) at first egg (AFE) on generation.

Line	**Generation interval**						
	0-54	**6-14**	**13-20**	**19-27**	**26-35**	**34-44**	**43-54**
HWS	0.63±0.09*	0.86±0.54	1.38±2.04	0.61±1.15	2.77±0.80*	-0.79±0.89	0.20±0.70
HWR		1.106±1.15	1.34±2.53	-0.23±0.45	1.43±1.08	-1.78±1.16	-0.55±0.86
LWS	1.25±0.10*	4.01±1.35*	0.80±1.57	0.62±1.23	1.81±0.70*	-0.75±1.01	0.28±0.66
LWR		0.15±1.56	-3.56±1.99	-3.32±1.21*	-1.62±0.91	-2.36±1.07	0.39±0.95

*(P<0.05) regressions which were significantly different from zero. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line.

Table 4.2. Regressions of body weight at first egg (g) on generation.

Line	**Generation interval**			
	27-54	**27-35**	**34-44**	**43-54**
HWS	9.82±2.70*	-1.21±20.06	-4.05±8.44	30.02±8.94*
HWR		-30.36±16.80	-15.06±7.07	7.24±11.10
LWS	-5.20±1.27*	-6.95±8.64	-14.35±3.58	0.48±4.57
LWR		13.14±6.22	-5.15±6.28	7.23±5.66

*(P<0.05) regressions which were significantly different from zero. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line.

Table 4.3. Regressions of WAFE (g/day) on generation.

Line	**Generation interval**			
	27-54	**27-35**	**34-44**	**43-54**
HWS	0.03±0.02	-0.39±0.15	0.01±0.11	0.14±0.07
HWR		-0.57±0.11*	-0.03±0.12	0.08±0.07
LWS	-0.02±0.01*	-0.07±0.05	-0.05±0.03	-0.004±0.03
LWR		0.10±0.06	0.02±0.04	0.02±0.04

*(P<0.05) regressions which were significantly different from zero. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line.

Table 4.4. Regressions of hen-day normal egg production (%) on generation.

Line	**Generation Interval**						
	0-54	**6-14**	**13-20**	**19-27**	**26-35**	**34-44**	**43-54**
HWS	-0.12±0.06*	1.93±0.64*	-0.07±1.53	0.71±1.15	-0.32±0.34	-0.30±0.35	0.17±0.23
HWR		1.59±0.73	-0.69±2.00	0.68±0.94	1.26±0.28*	0.10±0.64	0.43±0.45
LWS	-0.28±0.03*	0.43±0.24	-0.75±0.33	-0.79±0.43	0.73±0.57	-0.54±0.23*	-0.37±0.40
LWR		1.57±0.91	-0.24±0.83	0.67±0.54	1.29±0.46*	0.88±0.33*	-0.24±0.50

*(P<0.05) regressions which were significantly different from zero. HWS=high weight selected line; LWS= low weight selected line; HWR= high weight relaxed line; LWR=low weight relaxed line.

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Chapter 5: General conclusion

Responses to long-term divergent selection for BW8 involved positive correlations between means and standard deviations for BW8 and for BW at other ages. These correlations were consistently greater in LWS than HWS. In both lines, scaling masked the degree more than the pattern of response. Namely, while scaling did not influence the pattern of the response to selection of BW8 in either line, it did influence the magnitude of response and was line specific. Removal of scaling by standardization was robust and thus enhanced the interpretability of long-term responses.

Correlated responses associated with sexual maturity and egg production involved AFE, WFE, WAFE, and HDP. Although sexual maturity was delayed in both selected lines, the delay was more pronounced in LWS than HWS. Selection for low body weight resulted in a decrease in WFE, WAFE, and HDP. Selection for high body weight also resulted in a correlated response of a lower HDP, however WFE and WAFE were generally higher and the feed restriction program instituted in this line may have influenced the response. Minimum AFE, WFE, and WAFE in relation to sexual maturity were line specific. A measure for assessing growth to reach sexual maturity is WAFE because it provides a “yardstick” to which sexual maturity is likely or unlikely to occur in addition to possible reproductive complications. There are likely economic advantages for this measure from the point-of-view of selection experiments and commercial breeding programs. Also, an opposition between relaxed and artificial selection was seen in differences in responses among selected and relaxed lines. Namely, there was a higher reproductive performance and fitness with relaxed than artificial selection on the high and low extremes of body weight. Continuous divergent selection for a single trait reduces fitness. The magnitude of the correlated response can be masked by scaling.

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