Fall 11-2017

Evaluating Long-Term Direct and Correlated Selection Response in White Plymouth Rock Chickens Selected for High or Low 8-Week Body Weight

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EVALUATING LONG-TERM DIRECT AND CORRELATED SELECTION RESPONSE IN WHITE PLYMOUTH ROCK CHICKENS SELECTED FOR HIGH OR LOW 8-WEEK BODY WEIGHT

By

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A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfilment of Requirements

For the Degree of Master of Science

Major: Animal Science

Under the Supervision of Professor

Ronald M. Lewis

Lincoln, Nebraska

November, 2017

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University of Nebraska, 2017

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The increasing demand for poultry meat has led animal breeders to engage in artificial selection of chickens as a way to increase the productivity of poultry. Long-term experiments have been designed to measure rates of genetic response to a trait under selection, and correlated traits, as well as gauge possible selection limits.

Two studies were conducted to evaluate response to selection for body weight (**BW**) in chickens. The chickens were selected for high or low BW at 8 weeks of age. Those that met the criterion were selected as parents for the subsequent generation. In the first study the population structure of the two lines was assessed. Inbreeding coefficients, effective population sizes and relatedness were compared between the lines across the 59 generations of selection. The two lines were parallel in structure, having similar inbreeding levels, founder contributions and family sizes. Such parity allows for reliable comparisons of the performance of the two lines across the selection profile.

In the second study, direct response to divergent selection for BW at 8 weeks of age, and its correlated impact on BW at 4 weeks of age, over 56 generations of selection was evaluated. In the analyses a complete pedigree was used accounting for all familial relationships within and between lines. In the high weight selection (**HWS**) line, both 8- and 4-week BW increased

linearly across generations. Even though selection had occurred over an extend time period, substantial additive variation in BW was retained in the HWS line. In the low weight selection (**LWS**) line, both 8- and 4-week BW decreased in a curvilinear fashion reaching a plateau at around generation 25. Much less variation in BW remained in the LWS than HWS line by generation 56. However, the heritability of BW remained moderately high in both lines. The selection plateau observed in the LWS line therefore likely reflected biological constraints on reproductive fitness rather than the removal of additive variation.

Key words: chicken, long-term experiment, population structure, response to selection

Dedication

In loving memory of my sister, *Laura Harrison*, who always believed in me.

Acknowledgements

I would like to express my sincere gratitude to Dr. Ronald M. Lewis for the continuous support rendered throughout my graduate studies. Your patience, motivation, enthusiasm and immense knowledge provided a learning environment that allowed me to develop professionally. Your vast knowledge in the animal breeding discipline has ignited a curiosity to continuously want to learn more. I could not have imagined a better advisor and mentor.

I am also very grateful to Dr. Paul B. Siegel for giving the opportunity to work on his selection lines. The aspects of this research have allowed me to understand animal breeding in greater detail. It was a great honor to work with one of the greatest poultry geneticists as well as listen to all your valuable stories.

I would also like to thank Dr. Sheila E. Purdum for being in my committee. Your input is truly appreciated.

My sincere gratitude also goes to Christa F. Honaker for helping verify the data and always in a timely manner.

I am thankful for my brother, Gordon, and fiancé, Himatambo, for the continuous support and understanding rendered during this period. I would also like to thank my family and friends back home for the support. Thank you to Celine for the many calls and messages of encouragement.

Finally, I am grateful to the U.S Fulbright program for this opportunity and for funding my studies.

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Chapter I: Review of Literature

GENERAL THEORY

The study of the genetics of quantitative characters is essential for understanding the theory of genetic correlation of traits. This theory entails that if selection for a single character is performed in a breeding program, other characters correlated with the primary character selected are generally found to change too (Lerner, 1950). When two traits are genetically correlated, a change in the mean genotypic value of the selected characteristic (trait X) is associated by a concomitant change in the genotypic value of the unselected characteristic (trait Y). Lerner (1950) expressed this relationship through the following set of equations:

Let ΔG = genetic change in character selected, and

ΔG' = genetic change in correlated character not directly selected. Then:

$$\frac{\Delta G'}{\sigma G'} = r_G \frac{\Delta G}{\sigma G} \quad \text{(Equation 1.)}$$

Given the following definitions of variables:

- $r_{BVx,BVy}$ = r_G = Genetic correlation between breeding values of trait x and trait y
- $r_{BVx,\widehat{BV}x}$ = Accuracy of selection for trait x, where $\widehat{BV}x$ is the estimated breeding value for trait x.
- i_x = Intensity of selection for trait x
- σ_{BVx} = σ_G = Genetic standard deviation for trait x
- σ_{BVy} = $\sigma_{G'}$ = Genetic standard deviation for trait y
- L = average generation interval

If we assume the following:

- i_x = 1
- $r_{BVx,\widehat{BV}x} = \sqrt{h_x^2}$ considering the case of phenotypic selection
- $h^2 = \frac{\sigma_{G_x}^2}{\sigma_{P_x}^2}$ where $\sigma_{P_x}^2$ is the phenotypic variance of trait x, then,

$$\Delta G' = \frac{r_{BVx,BVy} r_{BVx,\widehat{BV}x} i_x \sigma_{BVy}}{L} = \frac{r_{G\sqrt{h^2}\sigma_{G\prime}}}{L} = \frac{r_G\, h\, \sigma_{G\prime}}{L}$$

$$\Delta G = \frac{h\sigma_G}{L}$$

Ignoring generation interval (L), substituting in equation 1:

$$\frac{\Delta G\prime}{\sigma G\prime} = \frac{r_G\, h\sigma_{G\prime}}{\sigma_{G\prime}} = r_G h \quad \text{which is equivalent to } r_G \frac{\Delta G}{\sigma G}$$

ΔG and ΔG' can be directly measured from the observed response to selection. The phenotypic standard deviation (σ_P) can be directly measured. With σ_G and $\sigma_{G\prime}$ then estimated, the h^2 and h'^2 are obtained, since $\sigma_G = h\sigma_P$ and $\sigma_{G\prime} = h'\sigma_{P\prime}$. Thus, for the calculation of the genetic correlation, formula (1) can be rewritten as:

$$r_G = [\frac{\Delta G\prime}{\Delta G}][\frac{h}{h\prime}\frac{\sigma p}{\sigma p\prime}] \qquad \text{(Equation 2.)}$$

If the phenotypic correlation (r_p) between the two characters is also known, the environmental correlation can be calculated from knowledge of the genetic correlation and the heritabilities. The phenotypic correlation can be directly observed and is made up of the genetic and environmental correlations. This gives:

$$r_p = hh'\, r_G + ee'\, r_E \qquad \text{(Equation 3.)}$$

where:

$e^2 = 1 - h^2$ and therefore $e = \sqrt{(1 - h^2)}$, and $e' = \sqrt{(1 - h'^2)}$

This ultimately leads to:

$$r_E = \frac{r_P - hh' r_G}{ee'} \qquad \text{(Equation 4.)}$$

The above derivations provide a way to predict and account for both genetic and environmental correlations between traits. Therefore, with selection for one trait, one can predict correlated response (genetic and environmental) expected in the other trait(s).

SELECTION EXPERIMENTS

High and Low Weight Selection Lines at Virginia Tech

Siegel (1962a) reported initial results from a selection experiment at Virginia Tech for body weight and breast angle at 8 week of age in White Plymouth Rock chickens, which began in 1957, and is still ongoing. Seven inbred lines were crossed to give a heterogeneous foundation stock. The foundation stock was divided at hatch into two subpopulations (body weight or breast angle), which were further divided into two lines where divergent selection was practiced (broad and narrow breast angle, or high and low body weight). The response of the selected and unselected traits was measured by sex as the difference between the upward and downward pair of lines. In addition, using a procedure outlined by Dickerson and Grimes (1947), heritabilities of the selected trait were obtained from the cumulative effect of selection. The heritabilities for the pair of weight lines was estimated to be 0.28 for the females and 0.31 for the males. The corresponding heritabilities for the pair of breast angle lines was estimated to be 0.21 for females and 0.24 for males, indicating that heritability was higher for body weight than for the breast angle trait. Responses between males and females were symmetrical within pairs of lines but did not respond symmetrically between low/narrow selected lines versus the high/broad selected lines. The

asymmetrical response was attributed to unequal heritabilities and variances. This is illustrated in Figure 1.1. and 1.2. reproduced from Siegel (1962a).

Selection for body weight showed larger correlated changes in breast angle (2.4 and 1.8 standard deviation units for males and females, respectively), than correlated response in body weight when direct selection was on breast angle (1.5 and 1.6 standard deviation units for males and females, respectively). This shows that the responses for the unselected traits differed in the two pairs of lines. Body weight had a higher realized heritability and lower standard error than breast angle. This implied that the magnitude of additive genetic effects had more influence on body weight than on breast angle. This is an important conclusion for animal breeders. Genetic correlations between the two traits were observed to be lower than environmental correlations, as also found at an earlier stage of this study (Siegel and Essary, 1959). The positive environmental correlations estimated were similar in size and therefore showed that the environmental influence had similar effects on both trait.

Population Dynamics

Márquez et al. (2010) reported results pertaining to the dynamics of the population of the White Plymouth Rock chickens, from the same long-term selection experiment (Siegel, 1962a). The study aimed at characterizing and quantifying genetic diversity and population structure in the high weight selection (**HWS**) and low weight selection (**LWS**) lines, and to subsequently test the success of the breeding strategy. The breeding strategy was based on keeping inbreeding at low levels and maintaining similar population structures between the two genetic lines. The hypothesis was that if intense artificial selection could be done, individuals and families with favorable traits would have a greater contribution to future generations and thereby influence effective population size and genetic diversity. Konig et al. (2010) reported that estimations of inbreeding are essential

because when high levels are reached, they have deleterious effects on the population by depressing fitness and performance traits. Because breeding programs in chickens typically display intense selection and short generation intervals, increased inbreeding is a risk that has to be mitigated.

In the high and low weight selection experiment, the size of the sire and dam families was kept relatively similar for each generation as a deliberate way to keep inbreeding constrained (Márquez et al., 2010). In both the HWS and LWS, the mean inbreeding coefficients increased linearly from generations 1 to 48. However, the mean inbreeding coefficient in generation 48 was slightly higher in the HWS (0.54 ± 0.02) than in the LWS (0.48 ± 0.01) line. Despite this difference, the rate of change of inbreeding over generations was relatively low (1.3% in LWS and 1.6% in HWS) and fairly constant from year to year. Morris and Pollott (1997) reported that a 1% increase in inbreeding per generation is generally tolerable for commercial chicken production. The rate of change of inbreeding across generations is an important measure because it gives an indication of the reduction in genetic diversity or heterozygosity in a population. This will consequently have an impact on selection response and fitness in the future. The rates of change of inbreeding in this study indicated that the population had enough heterozygosity to allow selection response to continue. This reflected the success in keeping family matings at a minimum.

Charlesworth (2009) reported that the effective population size estimates the extent of genetic drift in large populations. Caballero (1994) reported that the effective population size gives an indication of the effect of management and selection practices on genetic variation. The effective population sizes of the two genetic lines were estimated to be 38.3 (LWS) and 32.1 (HWS) at generation 48. Because the two lines had similar rates of change in inbreeding, the effective population size for both lines was also found to be similar.

The HWS and LWS lines displayed similarity in the parameters investigated implying that they were parallel in population structure and genetic diversity across the different generations (Márquez et al., 2010). This would therefore allow for a more equitable comparison of response in the two lines.

Correlated responses

Correlated responses have been observed in many selection experiments. Dunnington and Siegel (1996) reported results from the same long-term selection experiment introduced previously (Siegel, 1962a). Eight-week body weight was the selected trait. Unselected traits, hypothesized to be impacted through correlated responses, included growth-related traits (body weights at other ages, appetite, anorexia, feed efficiency, and body composition), metabolic factors (thermoregulation, diabetic-like symptoms, growth hormones, thyroid hormones, and digestive enzymes), reproductive traits (embryonic and incubation differences, age at sexual maturity and ovulation, and egg production), and immunological characteristics (histocompatibility complex and antibody responses after being injected with sheep red blood cells).

***Correlated Responses in Growth Traits*.** Dunnington and Siegel (1996) observed that selection for body weight at a specific age caused changes in body weight of the chickens at other ages and to different extents. This was evidence of a correlation. Dietary restrictions and varying amounts of nutrients were also considered lest they influenced the expression of traits. The correlated responses in appetite were more evident in meal number than meal size early in the selection program (generation 5). The HWS line consumed more meals in a 24-hour period than the LWS line. In addition, HWS chickens showed a preference to diets high in protein while LWS chickens preferred diets high in energy. The HWS line was able to go through a day's period without feed and still compensate in feed intake for the fasting period, in comparison to the LWS

line. Plasma treatments were administered to both lines as a way to increase their feed intake (appetite). These treatments were in the form of intracerebroventricular injections of methoxamine and hypotryptamine. These biogenic amines act as neurotransmitters and are active in regulation of blood pressure, elimination, body temperature and other centrally mediated body functions. There was no significant change in the consumption of HWS chickens, but appetite of LWS chickens increased significantly, indicating some property of the plasma stimulated appetite in the LWS line. There was a clear difference in feed intake behavior between the lines. The HWS line displayed hyperphagia (increased appetite) while the LWS line displayed anorexia (appetite loss). This demonstrated a marked difference in eating behavior.

Efficiency of feed utilization was tested in developing embryos from both lines. Embryos from HWS utilized energy and amino acids more than LWS embryos indicating feed utilization efficiency was affected even in early development when body weight was selected for at a fixed age. The HWS line was reported to grow at a faster rate as well as had a higher percentage of body fat than the LWS line. This was attributed to differences in supply and demand organs. Supply organs were those deemed essential in digestion and assimilation of feed. Demand organs were those that made significant use of energy and supplies for body expansion. These two types of organs affected the rate of development of the chickens and subsequently their body composition at a specific age. The HWS line had heavier body organs while the LWS line had heavier feathers. Brain weights were also seen to be heavier in the HWS line further illustrating a correlated response in body organs to selection for body weight.

Correlated Responses in Metabolic Factors. Correlated responses in metabolic factors were also observed when the chickens were selected for body weight at 8 week of age (Dunnington and Siegel, 1996). These changes were conveyed through processes and agents of

thermoregulation, growth hormones, thyroid hormones and digestive enzymes. Foot pad and cloacal temperatures were measured. The HWS line had higher foot pad and cloaca temperatures. However, the cloaca temperature range in the LWS line was extremely narrow. This was presumed to be because of natural selection maintaining intermediate optimal internal temperatures (Dunnington and Siegel, 1985).

The different lines were also examined for glucose tolerance, and for plasma insulin glucagon at 25 day of age. The HWS chicks had high concentrations of glucose, lipids and protein. This was evidence of an association between increased amounts of fat deposition and increased amounts of insulin and glucagon in HWS chickens. Chickens selected for high body weight had higher levels of triiodothyronine, thyroxine and intestinal 5'deiodinase, which resulted in higher intestinal organ weight than the LWS line.

The HWS and LWS lines were also compared for responses in digestive enzyme activity, specifically trypsin, chymotrypsin and amylase in the pancreas, at 25 day of age. Hypertrophy of the pancreas was observed in HWS chicks as compared to the LWS chicks. Results reported by Dunnington and Siegel (1996) indicated higher digestive enzyme levels in the HWS than in the LWS line especially during the early post-hatch period. This showed correlated responses in feed intake in the chickens selected at a specific body weight also regulated digestive enzyme levels. For the HWS chickens, this meant they ate more, had better feed passage and better feed utilization.

Correlated Responses in Reproductive Traits. Dunnington and Siegel (1996) reported that correlated responses with regards to reproductive competence in the HWS and LWS chickens were evident in the early stages of the experiment. The LWS lines displayed a more advanced embryogenesis at oviposition than the HWS line. The HWS line showed a higher percentage of chromosomal abnormalities in their embryos. The relationship between body weight and age at

sexual maturity (age at first egg) indicated a minimum age, minimum body weight and minimum body composition at which the LWS line became sexually mature. This was also reported by Brody et al. (1984) who made comparisons of age, body weight and body composition at the onset of sexual maturity. The LWS chickens reached their lower limit age before the other two factors (body weight and body composition) were adequate for sexual maturity (egg production) indicating that body weight and composition were constraints. This delayed egg production.

A positive correlation was observed between body weight at 8 week of age and percentage of pullets in lay at 275 day in the LWS line. This was attributed to a higher percentage of individuals reaching sexual maturity. However, from the 31st to the 38th generation, body weight reduced consistently but percentage of mature birds increased. That may have been due to the LWS line accommodating a lower body weight to achieve sexual maturity. With regards to egg production, HWS hens produced a larger number of eggs. However, they also produced more defective eggs. The LWS hens produced less quantity of eggs but with fewer defects. Similar results showing that HWS chickens laid more defective eggs but a higher number of total eggs were reported by Udale et al. (1972). Also, multiple-yolked and larger yolks were more frequent in the HWS than LWS line, suggesting a correlation.

Correlated Responses in Immunological Characteristics. Dunnington and Siegel (1996) observed that the LWS line displayed higher persistence of antibodies than HWS line. Similar results from studies involving the same lines have been reported by Miller et al. (1992). Pinardvan der Laan et al. (1998) found that selection for immune responses in chickens can result in correlated responses in production and disease-related traits.

Bidirectional Selection for Juvenile Body Weight

Dunnington et al. (2013) reported results for 54 generations of this same long-term selection experiment (Siegel, 1962a). The focus of this particular study was on the genetic responses in the two weight lines over this extended time frame. The objective of the study was to assess whether long term selection for a single quantitative trait persisted due to sufficient additive genetic variation remaining or due to re-introduction of such variation due to favorable mutations.

In this study, 8-week body weight was the selected trait while 4-week body weight was the unselected correlated trait. Six relaxed lines had been introduced at generations 7, 14, 20, 27, 35 and 44. These lines were established via random sampling of the chickens from within the HWS and LWS lines with selection for 8-week body weight then discontinued. The relaxed lines were maintained using pooled semen from males within the respective relaxed line being inseminated into females of the same line. These lines served as a check on whether stopping selection at various stages of the long-term experiment resulted in regression or return of the performance of the selected lines to original preselected values. This is illustrated in Figure 1.3. extracted and expanded from Dunnington et al. (2013).

The response to phenotypic selection in the HWS and LWS body lines was successful and significant differences in BW4 and BW8 were evident when females and males of the HWS line were compared to the LWS line. The ongoing divergent responses to selection for a single criterion indicated that genetic variation remained throughout the 54 generations of study. In early generations, epistatic deviations appeared to be unimportant (Siegel, 1962b), However, recent QTL analyses have revealed epistatic loci associated with this trait, suggesting that gene complexes may have become more important (P. Siegel, personal communication).

Frequency distributions were also analyzed as a way of determining response to selection and showed that there were dramatic effects of selection. This was because by the 25th generation, the LWS line had no overlap with the base population. Also, by the 54th generation, the HWS line had no overlap with the base population. This showed that selection for 8-week body weight resulted in distinct selected populations. The frequency distributions also suggested that the LWS line approached a selection limit at generation 25 and displayed a plateau with small differences in body weight thereafter. This was primarily because a chicken has a phenotypic limit on size corresponding to survival and successful reproduction. It is not known as to whether this selection plateau was because of reduced additive genetic variance, epistatic networks or presence of mutations. Another notable factor captured by the frequency distributions was that of beneficial mutations in the HWS line. The distributions reflected the presence of outliers at higher and lower ends of the curves. This hinted at the presence of one or more mutation. Martin et al. (1990) reported finding major mutations in chicken lines selected for high and low antibody response to sheep erythrocytes. Additionally, mitogenomic analyses revealed a rapid rate of mitochondrial evolution and evidence of paternal mitochondrial DNA inheritance. These mitochondrial mutations, which occurred exclusively in the LWS line, may have contributed to the divergent phenotypes in the two lines (Alexander et al., 2015).

The ratio of 4-week to 8-week body weight within line and sex was also estimated in order to have an understanding of the developmental growth process of the two lines (Dunnington et al., 2013). The obtained values were within the range 0.31 – 0.37 for LWS:HWS male chickens and 0.33 – 0.44 for LWS:HWS female chickens. This showed that body weight at 4 weeks was just about one third of body weight at 8 weeks of age. By generation 25, it was clear that LWS females ate enough food for survival but not for sexual maturity. Neonatal mortality rates were in the range

5 – 20% and therefore larger hatches were necessary in each generation to allow for continuation of the LWS line.

Neuronal Plasticity

Ka et al. (2009) reported findings pertaining to this same long-term selection experiment (Siegel, 1962) but with regards to different behaviors corresponding to differential expression of genes affecting neuronal plasticity. Neuronal plasticity is a process by which the brain's neural synapses and pathways are altered as an effect of environmental, behavioral and neural changes. This study illustrated that the central nervous system is associated with behavioral differences. The HWS line chickens were seen to be heavy feeders while the LWS line was anorexic. Analysis using complimentary DNA array expression revealed multiple differences in expression profiles. Genes that regulate neuronal plasticity were observed to be differentially expressed. This confirmed that neural systems in charge of feeding behavior in the two lines were different. The study provided further evidence that there were differences in the neural components contributing to the phenotypes of the LWS and HWS. This was attributed to differences in brain plasticity.

Similar Experiments on Direct and Correlated Selection Responses

Falconer (1954) performed a two-way selection experiment with mice, to provide a check on the validity of the theory of genetic correlation. He selected for weight at six week in one pair of lines and for tail length at six week in another pair of lines, from a four-way cross of highly inbred strains. Responses of both characters were observed in both pairs of lines (6 generations in the weight line and 4 generations in the tail line) and genetic correlation estimates between weight and tail length for the pairs of lines were estimated to be 0.62 and 0.57, respectively. This was a good indication that the genetic relationship between the two traits accounted for correlated responses actually observed. However, the environmental correlations did not show perfect

agreement (0.41 in selection for weight and 0.26 in selection for tail length) with differences in phenotypic correlations. The discrepancy indicated that the environmental conditions when selection for weight was done were different from those when selection for tail length was done. This was because selection for tail length was carried out four years after selection for weight, from a repetition of the same four-way cross. Despite the consistency in the genetic resource used between the pair of selection experiments, the discrepancy in time could have led to differences in the environment and this could have altered the measured variables. This was perceived to be the biggest limitation of the experiment. However, the heritabilities and the genetic correlation comparisons were not affected.

Similar correlated responses to selection for body weight and breast width were observed in a study done on 8-week old New Hampshire chickens by Lerner et al. (1950). The genetic correlations across subpopulations were pooled for sexes and found to be 0.51 for males and 0.53 for females. This showed that genetic influence on one trait had a positive effect on the other trait. Environmental correlations were positive and implied that environmental influence on one trait (body weight or breast angle) had a similar size of effect on the other. Phenotypic correlations were reported to be homogenous within pairs of lines but heterogeneous between pairs of lines implying that differences existed between subpopulations.

Aggrey et al. (2010) reported an experiment on genetic properties of feed efficiency parameters in meat type chickens. The objective of this experiment was to determine the genetic inter-relationships between residual feed intake and feed conversion ratio that contribute to feed efficiency. The hypothesis was that selection on feed efficiency or feed conversion ratio would minimize feed required for growth of the chickens, increase growth rate or body weight gain (BWG), and reduce production costs as well as amount of nitrogenous waste produced.

Feed efficiency is used as a measure to determine the chicken's ability to convert feed nutrients into output. It is difficult to quantify and therefore different measures have been developed. It is usually expressed as feed conversion ratio (FCR), which is the amount of feed intake per body weight gain. By its definition, FCR is a ratio trait. The results of this experiment indicated that it is not normally distributed and likely to display skewness and kurtosis. Atchley et al. (1976) reported that the non-normality of a ratio trait is increased when the magnitude of coefficient of variation of the denominator, in this case body weight, is increased. Residual feed intake (RFI) is another measure of feed efficiency, and is defined as the difference between an animal's actual feed intake and its expected feed intake based on its size and growth. It is deemed genetically independent of the level of production. The RFI is ideally the proportion of feed intake not represented by maintenance body weight and BWG.

Aggrey et al. (2010) found that selection based on reduced FCR and subsequently reduced RFI improved feed efficiency, reduced feed intake and increased growth rate. Heritabilities of RFI and FCR were in the range 0.42 to 0.45. This showed that selection on RFI would improve feed efficiency and reduce feed intake. Despite this, correlated responses in both feed intake and BWG could not be predicted accurately because of the ingrained problem of FCR being a ratio trait.

Genetic correlation between RFI and FCR was ascertained at day 28-35 (0.31) and day 35-42 (0.84) of the experiment. A comparison was then made between the two age intervals and suggested that the pleiotropic relationship between RFI and FCR may be dependent on age. Furthermore, the molecular, physiological and nutritional factors that enable RFI and FCR may also depend on time of development. Aggrey et al. (2010) concluded that efficiency of feed utilization is affected by different developmental processes and management practices, all of which

will affect the heritability of the RFI, and subsequently the genetic correlations among the feed intake parameters.

Morris and Pollott (1997) reported results from an experiment on a closed broiler line, done to compare selection response based on phenotype, selection index and best linear unbiased prediction (BLUP). Juvenile body weight, breast meat yield and egg production were measured over a period of 51 weeks. Indices constructed by combining information from half- and full-sibs have been previously used in poultry (Hazel, 1943; Osborne, 1957). However, BLUP has been used more recently; since it combines information from all relatives of an individual, selection decisions are more accurate than from indices based on sib-information alone. The magnitude of the accuracy is highly dependent on the heritability of the trait being measured as well as the amount of data (Sorensen, 1988).

Breeding values estimated for juvenile body weight based on phenotypes showed lower correlations with BLUP breeding values as compared to index scores. Estimates from BLUP and selection indices were more highly correlated. This was attributed to higher accuracies obtained when having more family information considered. BLUP, however, had the more accurate estimates because information on all relatives was used. Only BLUP and selection index estimates were analyzed for breast meat yield and egg production traits because of missing phenotypic records on the birds. A higher correlation was estimated between the two methods for breast meat yield than for egg production; this was attributed to egg production being lowly heritable. Morris and Pollott (1997) reported that for lowly heritable traits, the relative benefit of information provided from increasingly distant relatives is greater than for moderate to highly heritable traits. For all the three traits, BLUP resulted in the highest expected response. Studies done by Belonsky

and Kennedy (1988) gave similar results. The BLUP estimates were also seen to accurately characterize the covariance structure between the parental animals.

Deeb and Lamont (2002) reported results on selection for growth and fitness in a chicken population over a period of 50 generations. Estimates from an outbred meat-type line of chickens were compared to estimates from two inbred lines unselected for growth traits. Effective gene number and heterosis in the chickens was also estimated. Over the years, these meat-type chickens had been selected for growth and fitness and would be expected to have reached selection limits. However, the results of this study indicated that there still was genetic change occurring for growth and meat yield, and that there was a significant distance between inbred lines and the meat-type line in body weight. This was indicative of commercial selection causing evolution of broiler performances beyond the range of genetic variation observed in the founder populations. This has been attributed to a greater allelic diversity determining the phenotype. However, it was reported that meat type chickens had more growth and muscle mass for internal organs and this could be the cause of a higher number of physiological disorders in meat-type chickens.

Closing Remarks on Correlated Responses

A number of factors affect the extent of correlated responses when selection is on a particular trait. Population size, inbreeding, husbandry or management practices, mutations, neuronal plasticity and physiological limits are some of these factors.

ANALYTICAL METHODS

Types of Selection

Phenotypic selection uses information based on the performance of the animal being considered for selection. The phenotype or performance of the animal often gives an indication of its breeding value. The measure of the strength between the two factors is called heritability. A

high heritability shows that the performance of the animal is a good indicator of its breeding value making phenotypic selection very effective.

Selection can also be done using information obtained from the relatives of the animal in question. This is called pedigree information. An increase in the amount of information used increases the accuracy of predictions. A high accuracy is indicative of good predictions of "true" breeding values. This higher accuracy therefore enables the breeder to do a better job at selection.

Selection can also be done between breeds. This is done by determining the breeds from which the parents are selected. Large differences between breeds is used to make genetic change through crossbreeding.

Ways of Evaluating Selection Response

Responses to Selection from Phenotypes. The simplest form of selection is done by choosing individuals based on their phenotypic values. Change produced by selection that results in change of the population mean is called response to selection. In its simplest form, it is measured as the difference in mean phenotypic value between offspring of selected parents and the whole of the parental population before selection.

The amount of selection applied is the mean superiority of selected parents. It is the difference of the base population mean and the mean of the selected parents, and is referred to as the selection differential (S). This parameter is averaged if different proportions of males and females are selected.

$$S = \frac{S_{male} + S_{female}}{2} \qquad \text{(Equation 5.)}$$

Selection intensity (*i*) is a measure of how choosy breeders are in deciding which individuals are selected. It is the number of phenotypic standard deviation units that selected parents are superior

to the mean. In the case of truncation selection, selection intensities are obtained from normal distribution tables depending on the proportion of animals selected as parents. The S is calculated by multiplying the intensities by the phenotypic standard deviation as:

$S = i\sigma_p$ (Equation 6.)

Narrow sense heritability (h^2) is a measure of the genetic component that is contributed by the additive genetic variance. The response to selection is derived by multiplying the heritability by the selection differential.

$R = h^2\mathrm{S}$ (Equation 7.)

From equation 6 above, selection response (R) can also be calculated by:

$R = h^2 i\sigma_p$ (Equation 8.)

This is also called the Breeder's Equation, and is the more classic way to determine genetic response to selection. Because this current study has discrete generations, R can be easily calculated for each year since the generation interval was 1.

Responses to Selection from Breeding Values. Response to selection can also be evaluated by way of estimating breeding values and then regressing the mean breeding values on generation (hatch year). A breeding value is an animal's genetic merit or value of the animal's additive genetic effects, half of which is passed on to its progeny. The true breeding value of an animal is rarely known and therefore estimated. Estimated breeding values ($\widehat{BV}_i$), or **EBV**, can be calculated using the following methods:

a) From an individual animal's own performance record ignoring all other relationships. The performance of the individual animal is directly compared to the average performance of the other animals in the group. The EBV is calculated as:

$\widehat{BV_i} = b_{BV.P}\ (P_i - \bar{P})$ (Equation 9.)

But since heritability is equal to the regression of breeding value on the phenotype:

$h^2 = b_{BV.P}$ (Equation 10.)

this therefore results in:

$\widehat{BV_i} = h^2\ (P_i - \bar{P})$ (Equation 11.)

b) From performance records collected from the individual's relatives. These are termed pedigree and progeny records. Depending on the type of relatives' performance records being used, EBV may be calculated as:

$\widehat{BV_i} = \frac{h^2 nR}{1+(n-1)t^*}(P_i - \bar{P})$ (Equation 12.)

where:

n = number of progeny/sibs.

R = the genetic relationship between the animal being evaluated and where the information is coming from. R differs depending on the type of relatives' performance records being used.

t^* = the intra class correlation which is a measure of family resemblance.

c) From a combination of both the animal's and its relative's information. Information on the animal's own performance records and from all its relatives is combined in a statistical procedure known as BLUP, typically by fitting an animal model that describes gene flow over time. This approach allows the performance records of progeny, cousins, sibs, parents, grandparents and so on to help predict the genetic merit of the individual. This combination

gives the most reliable EBV because it combines information from more sources thereby increasing accuracy.

To obtain BLUP solutions, a linear model is formed and fitted to the performance data. Statistical packages such as ASREML (Gilmour, 2015) or MTDFREML (Boldman, 2017) are used to estimate additive and phenotypic co-variances. These co-variances are then considered as true values, and then plugged back into the BLUP evaluation to predict breeding values.

Response to selection is then calculated by regressing the mean EBV per generation on year:

$R = b_{\overline{BV}.Year}$ (Equation 13.)

This regression can be fitted for individual line, sex, or their combination, as appropriate.

Ways of Evaluating Population Dynamics and Genetic Diversity

Inbreeding. Inbreeding is the mating of individuals more closely related than average for a population. It quantifies the probability that genes in an individual are identical by descent and is therefore a measure of genetic diversity (Wright, 1922). Identity by descent provides the basis for a measure of the dispersive process through the degree of relationship between mating pairs. The measure is the inbreeding coefficient, which refers to an individual and expresses the degree of relationship between the individual's parents. The inbreeding coefficient of a subsequent generation expresses the loss of dispersive process or genetic diversity that has taken place from the time of the base population and compares the degree of relationship between the individuals present currently, with the individuals in the base population. It is calculated by:

$F_t = \frac{1}{2N} + (1 - \frac{1}{2N})F_{t-1}$ (Equation 14.)

where F_t is the mean inbreeding coefficient in generation t and N is the number of individuals in the population.

The rate of change of inbreeding provides a measure of the remaining heterozygosity in a population and therefore the extent of genetic diversity. It is calculated as:

$$\Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}} \qquad \text{(Equation 15.)}$$

where ΔF is the change in mean inbreeding between successive generations.

Effective Population Size. Effective population size (N_e) describes the effective number of breeding individuals. It is the number of individuals that would give rise to the observed inbreeding rates if the population was bred in an ideal manner (randomly mated). Because this parameter describes increase in inbreeding and therefore loss of heterozygosity, it reflects the rate of loss of genetic diversity. Therefore, N_e is inversely related to ΔF by the following equation (Falconer and Mackay, 1996):

$$N_e = \frac{1}{2\ x\ \Delta F} \qquad \text{(Equation 16.)}$$

Effective Number of Founders and Ancestors. Lacy (1989) described the effective number of founders (f_e) as the number of individuals that would be expected to produce the observed genetic diversity in a population if all of the individuals had contributed equally to the population. The f_e is calculated as:

$$f_e = \frac{1}{\Sigma\ q_i^2} \qquad \text{(Equation 17.)}$$

where q_i is the proportion of genes that are contributed by the ith founder.

In populations that have undergone a bottleneck the f_e computed using Lacy's approach is overestimated. Large contributions made by recent ancestors are more important to the population with respect to the loss of genetic diversity than equal contributions made long ago. A second measure of diversity to deal with such situations is the effective number of ancestors (f_a), which considers the genetic contribution of all ancestors in the population, not just founders. The f_a treats all ancestors in the population the same way, and is computed as:

$$f_a = \frac{1}{\Sigma\, p_i^2} \qquad \text{(Equation 18.)}$$

where p_i is the marginal genetic contribution of the ith ancestor. The ancestors with the greatest contributions are selected iteratively. The number of ancestors with a positive genetic contribution is less than or equal to the actual number of founders.

If each founder had the same expected contribution then $f_e = f_a$. The marginal genetic contribution also serves as an indication of which ancestors were most influential in terms of maintaining their genetics in the pedigree.

Gene Flow. Gene flow is the movement of genes between interbreeding populations of a species (Slatkin, 1985). This statistic reflects the proportional contributions of founders. As reported by Kennedy and Trus (1993), gene flow can be obtained from **X'ZTQ** where **X** and **Z** are incidence matrices reflecting line or group and animal, respectively. The **T** matrix is a triangular matrix tracing the flow of genes from one generation to the next while the **Q** matrix is an incidence matrix relating rows of founders and columns of every individual in the pedigree. Each cell in **X'ZTQ** reflects the founder contribution to the line or group, and the sum of elements of the rows of the matrix reflects the total number of animals in each line.

RESEACH OBJECTIVES

- Use more recently established statistical technologies to evaluate the direct response to selection for body weight at 8 week of age by accounting for all individuals and their relationships in the complete pedigree.
- Evaluate correlated responses in body weight at 4 weeks of age when direct selection is done at 8 weeks of age, using information from all individuals in the pedigree, and making a comparison with genetic response when only direct selection on a trait is done.
- Re-evaluate the population dynamics of the selection lines by evaluating genetic diversity and population structure over 59 generations of this study, by quantifying and tracing the relatedness of all individuals in the pedigree and thereby determining inbreeding characteristics, effective population size and number, gene flow, numerator relationships and family sizes.

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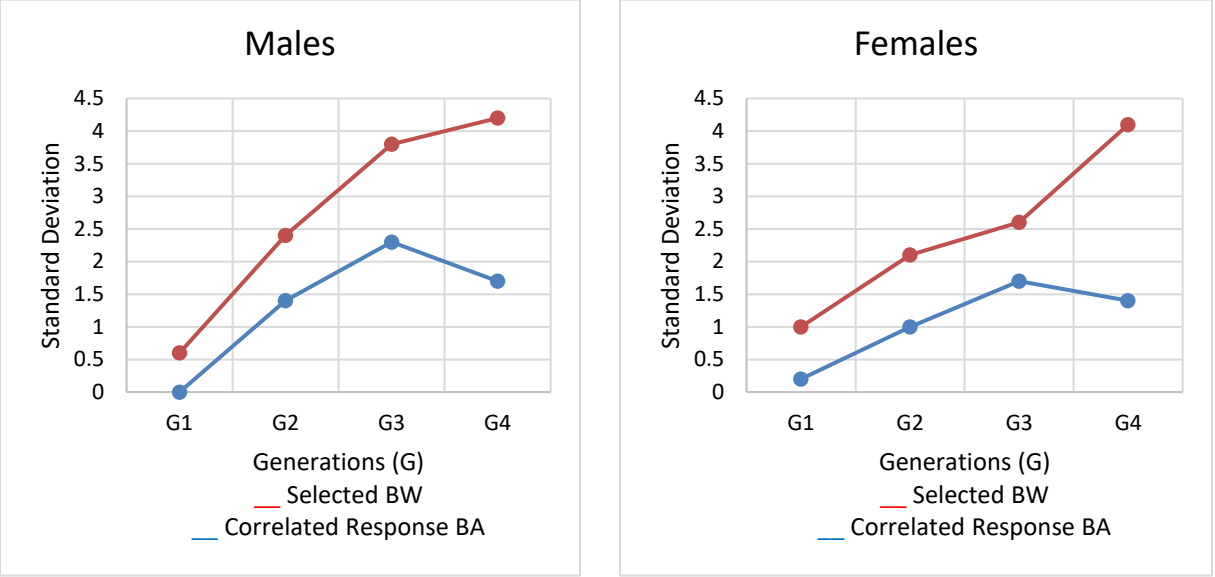

Fig. 1. 1 Differences in standard deviation units between lines selected for body weight at 8 weeks of age (Siegel, 1962a).

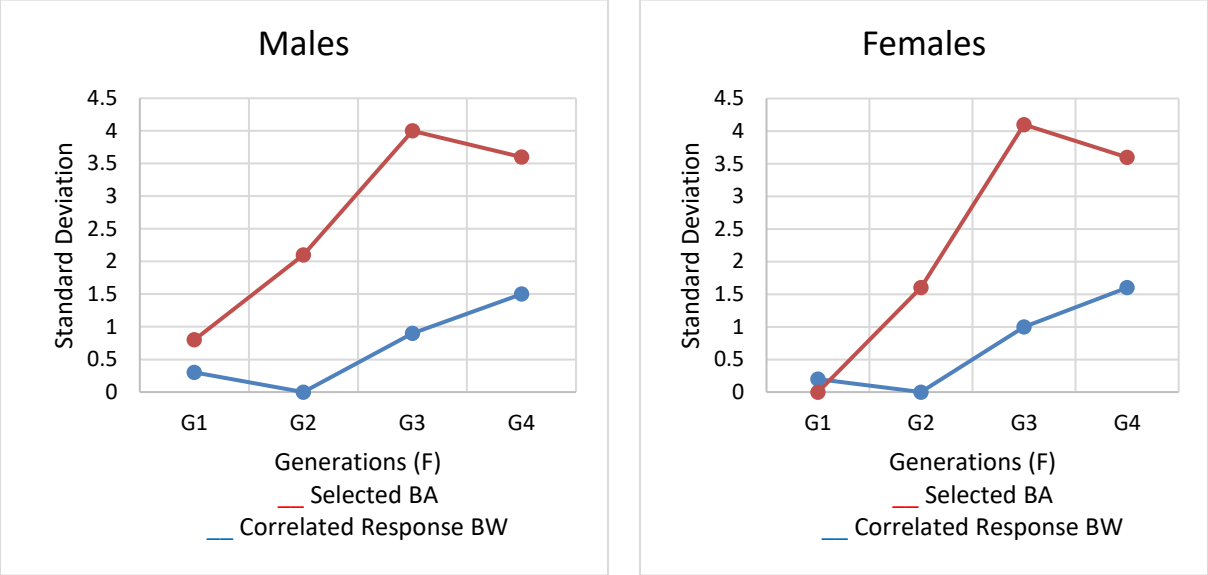

Fig. 1. 2 Differences in standard deviation units between lines selected for breast angle at 8 weeks of age (Siegel, 1962a).

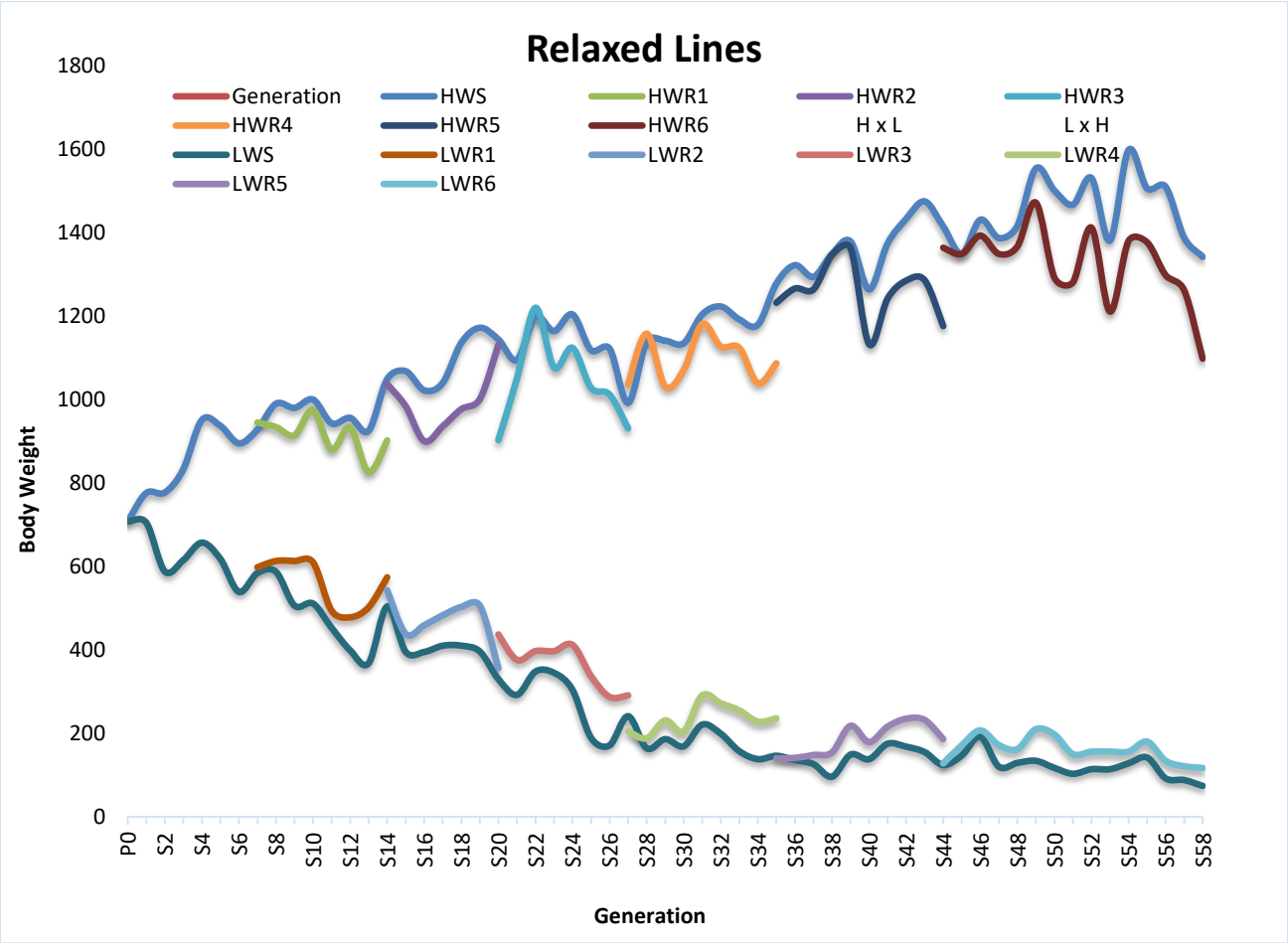

Fig. 1. 3 Mean 8-week body weight for high weight select (HWS) females and low weight select (LWS) females are indicated by solid lines going upward and downward, respectively. Means for the 6 relaxed lines from HWS (dotted line) females are designated by HR1 to HR6 and 6 relaxed lines from LWS (dashed line) females are designated by LR1 to LR6 (Dunnington et al., 2013).

CHAPTER II: Evaluation of Pedigree and Genetic Dynamics in a Long-Term Selection Experiment on White Plymouth Rock Chickens Selected for High or Low Body Weight

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ABSTRACT

The pedigree and genetic structure of two lines of chickens from a long-term (59 generations) selection experiment was studied. These lines were propagated from phenotypic selection for high and low 8-wk BW in White Plymouth Rock chickens. The objective of this study was to evaluate whether the two lines maintained similar population structures, so as to make meaningful comparisons on performance data between them. The total number of animals in the pedigree was 30,943 consisting of 102 founders, 14,549 high weight select (**HWS**), and 16,292 low weight select (**LWS**) chickens. The mean, maximum and average change in inbreeding for the HWS and LWS lines were 0.31 (SD 0.17) and 0.35 (SD 0.19), 0.53 and 0.59, and 1.2 and 1.5% per generation, respectively. The effective population sizes were 40.7 (LWS) and 34.5 (HWS). The effective number of founders was 17.3 (LWS) and 15.2 (HWS). About 30 founders explained the marginal contribution. By generation 59, only 7 male and 8 female founders contributed to both lines. Family sizes were similar between lines and within each sex, reflecting restrictions placed on sizes of sire and dam families to ensure no family predominated over others. Fewer males were used in comparison to females. Based on these evaluations, it can be inferred that the HWS and LWS lines had similar population structures. Comparisons of selection responses in the two lines therefore should be reliable.

Key words: divergent selection, population structure, chicken, heterozygosity, body weight

INTRODUCTION

Population dynamics refer to the way in which the size and age structure of populations change over time, and the characterization of that change in mathematical terms (Encyclopedia of Population, 2003). Such change is brought about by selection, as individuals that differ in viability and fertility contribute differently to the next generation. Under artificial selection, animals are chosen to favor individuals with desirable traits for perpetuation in future generations. A long-term selection experiment in chickens based on high and low BW at 8-wk of age provides a clear illustration of response to artificial selection (Siegel, 1962; Dunnington and Siegel, 1996; Dunnington et al., 2013). In a closed population, such as this one, inbreeding is inevitable, which effects the variance of gene frequency from one generation to the next (Konig et al., 2010). There are also impacts on the structure of the population, manifest in its effective population size, the contributions of founders, genetic drift, and variability in family sizes.

Using pedigree information, Márquez et al. (2010) described the genetic diversity and population dynamics after 48 generations of selection in the lines of chickens selected for divergent BW. In that study, inbreeding trends, effective population sizes and family sizes were evaluated to assess whether the high and low weight selection lines were of similar structure across the selection profile. They were. Gutierreez et al. (2003) reported that genetic variability and evolution can be explained by a well-documented pedigree.

The objective of this study was to reassess the population dynamics and genetic diversity of chickens in this long term selection experiment, given the additional 11 generations of selection since Márquez et al. (2010). This was done to determine whether the lines maintained similar population structures. Such is necessary to make meaningful comparisons of the performance of the two lines over the entire selection profile. Inbreeding rates, effective

population sizes, effective number of founders, family sizes and additive genetic relationships were computed to assess genetic diversity and relatedness among all individuals in the pedigree.

MATERIALS AND METHODS

Animal Use and Care

All procedures and protocols used in this study were approved by the Institutional Animal Care and Use Committee at Virginia Tech as of 1977. Prior to that, the chickens were treated in a like-manner despite the university not having the stated guidelines and protocols.

Data

Data used in this study were from 59 discrete generations. The two selection lines were founded from a cross of 7 inbred lines of White Plymouth Rock chickens. These chickens were founders to both high weight (**HWS**) and low weight (**LWS**) selection lines, established by selecting heavier chickens as parents for the HWS line and lighter chickens as parents for the LWS line. Eight sires and 48 dams were selected to establish the parental generation (P_0) in 1957. Thereafter, there were slight increments in the numbers selected as parents (Table 2.1). In this study, a parent was defined as an individual that had progeny with a known sex and 4-wk or 8-wk BW. Márquez et al. (2010) had slightly more birds identified as parents because they considered pedigree data alone.

A complete pedigree, including sex, generation and selection line, was constructed for each bird beginning with the founders of the two lines. The size of the study is illustrated in Table 2.2.

Husbandry

Each year and in each line, chicks were hatched on the first and third Tuesday of March. The second hatch was done to mitigate for insufficient numbers of chicks from the first hatch. The chicks were reared up to 8 wk in identical pens that had concrete floors, hot air brooding and wood-

shaving beddings. These conditions were maintained throughout the experiment to ensure the same environment for both lines. The chickens were fed a starter (0 to 8wk), developer (8 to 18wk) and breeder (> 18wk) ration containing 20, 16, and 16% CP and 2,685, 2,761, and 2,772 kcal of ME/kg, respectively, in meal form. These rations were as fed. Feed was restricted in the HWS line at generation 18 after 8 wk of age to reduce reproduction problems because of obesity (Dunnington and Siegel, 1996). Coccidiostats were added to the feed throughout all generations and, from generation 17 onwards, the chicks were vaccinated for Marek's disease at hatch.

Statistics

Following the same approach as Márquez et al. (2010), the dynamics and genetic diversity of the population were investigated.

Inbreeding. Inbreeding quantifies the probability that genes in an individual are identical by descent, and is therefore a measure of genetic diversity (Wright, 1922). It is characterized by the inbreeding coefficient (**F**). The F values in this study were obtained for each chicken using the R Pedigree package (Coster, 2008), which uses the algorithm of Meuwissen and Luo (1992). The mean, minimum and maximum inbreeding values for each generation and line were determined and compared. Changes in inbreeding were also calculated to deduce trends and infer the remaining heterozygosity as a measure of genetic diversity over the 59 generations. This was calculated as:

$$\Delta F_t = \frac{F_t - F_{t-1}}{1 - F_{t-1}}$$

where ΔF_t was the change in mean inbreeding between successive generations, and F_t was the mean F in generation t.

Effective Population Size. The effective population size describes the effective number of breeding individuals responsible for the observed inbreeding rates if the population was randomly mated. This parameter describes increases in inbreeding and thereby the loss of genetic diversity, which is inversely related to ΔF_t. It was calculated as:

$$N_{e_t} = \frac{1}{2 \times \Delta F_t}$$

where N_{e_t} was the effective population size at generation t.

Effective Number of Founders. Lacy (1989) described the effective number of founders (f_e) as the number of individuals that would be expected to produce the observed genetic diversity in a population if all the individuals had contributed equally to the population. The f_e for each line was calculated as:

$$f_e = \frac{1}{\sum_{i=1}^{n} q_i^2}$$

where q_i was the proportion of genes that were contributed by the ith founder. The marginal genetic contribution was an indication of which founders were most influential in terms of maintaining their genetic contribution to the population.

Gene Flow. Gene flow reflects the movement of genes between interbreeding populations of a species (Slatkin, 1985). This statistic was calculated to reflect the proportional contributions of founders to the most recent generation (59). It was obtained using the method of Kennedy and Trus (1993). The matrix **X'ZTQ** was computed where **X** and **Z** were incidence matrices reflecting selection line and chicken, respectively. **X'Z** had dimensions 2 x 30,943 with the 2 rows reflecting selection lines and the 30,943 columns reflecting each selected individual in the pedigree. The **T** matrix was a lower triangular matrix tracing the flow of genes from one generation to the next,

while the **Q** matrix was an incidence matrix relating founders (rows) to individuals (columns) in the pedigree. Each cell in **X'ZTQ** reflected the founder contribution to the LWS or HWS lines, and the sum of elements of the rows of the matrix reflected the total number of birds in each line. The proportional contribution of genes by the founders to each line was computed by dividing each element of **X'ZTQ** by the total number of birds in each line. Differences in founder contribution over the entire selection profile were computed by counting the numbers of male and female founders contributing sufficiently (at least 1% to a generation) to each generation.

Numerator Relationships. The additive genetic relationships among the individuals in the pedigree were described by the numerator relationship matrix (Wright, 1922). This matrix was calculated for the full pedigree. The relationship coefficients were then used to determine genetic contributions of the founders to generation 59.

Family Sizes. In each line, the number of sire and dam families were managed and maintained to mitigate the risk of inbreeding. The number of offspring of sires and dams was calculated for each sex and line. In addition, the mean, maximum and variance of these family sizes were calculated.

RESULTS

Inbreeding

Inbreeding statistics are presented in Figure 2.1 and Table 2.3. Mean inbreeding coefficients per generation for the two lines increased in a curvilinear fashion across generations. The fit of the quadratic regression of F on generation in the HWS line had an intercept, slope and quadratic term of -0.024 ± 0.004, 0.018 ± 0.0003, and -0.0001 ± 0.000005, respectively, with R^2 0.997; in the LWS line, those coefficient values were -0.016 ± 0.002, 0.015 ± 0.0002, and -0.0001 ± 0.000003, with R^2 0.999.

At generation 59, the mean inbreeding coefficient in the HWS (0.59 ± 0.0007) was higher ($P < 0.05$) than in the LWS line (0.53 ± 0.001). At that generation, the highest inbreeding coefficient recorded for a chicken was 0.63 in each line. The mean inbreeding coefficients for the entire pedigree was above 0.3 for each line. Average inbreeding rates were similar in both lines at 1.2% (HWS) to 1.5% (LWS) per generation, with the highest rates in generation 13 (>3%).

Effective Population Size

At generation 59, there were 225 chickens in the LWS line and 236 chickens in the HWS line. The N_e in the LWS and HWS lines were 40.7 and 34.5, respectively (Table 2.3). The similar rates of inbreeding in the two lines resulted in their similar N_e.

Effective Number of Founders

There were 102 founders to the pedigree. The f_e for the most recent generation (59) was 15.2 in the HWS line and 17.3 in the LWS line. In the HWS line, the marginal genetic contribution of the highest contributing founder to generation 59 was 15.1%; in the LWS line, the corresponding value was 14.0%. Cumulative marginal contributions to both lines in generation 59 showed that nearly100% of contributions were made by less than 30 founders (Figure 2.2).

Gene Flow

Proportional contributions of male founders to generation 59 chickens are presented in Figure 2.3. The number of founders contributing to different generations is summarized in Table 2.4. Fifteen males formed the founder population; of these, contributions of at least 1% to generation 59 were made by 7 (HWS) and 9 (LWS) males. Of the 87 females that formed the founder population, contributions of at least 1% to generation 59 were made by 16 (HWS) and

16 (LWS) of these females. This indicated less persistence of genetic contributions from female than male founders.

At generation 59, 15 founders (1 male and 14 females) contributed to the HWS line, 17 founders (4 males and 13 females) to the LWS line and 15 founders (7 males and 8 females) to both lines. The number of founders contributing to both lines did not change from 4 to 59 (Table 2.4).

Numerator Relationships

The average additive genetic relationship of the 15 founders in common to both lines with chickens in generation 59 was 4.2%. Such was the case both across and within the two lines. The average additive genetic relationship of all founders with chickens in generation 59 was 3.2%, and just over 3.0% for each line. The relationship of the 15 founders contributing exclusively to the HWS line was 2.6%, while the relationship of the 17 founders contributing only to the LWS line was 2.2%, with those chickens in the most recent generation.

Family Sizes

Means, standard deviations and maximum values of family sizes were calculated and presented in Table 2.5. The family sizes were presented for: (i) a full pedigree, encompassing all individuals with a known sex and weight, and (ii) all parents, encompassing individuals selected to be parents, and had progeny with a known sex and weight. A similar structure for each sex was observed across lines.

DISCUSSION

Inbreeding

A gradual increase in inbreeding coefficients in the HWS and LWS lines was observed. Because inbreeding increases the frequency of homozygous genotypes in a closed population,

expression of deleterious recessive alleles can lead to inbreeding depression, which may have negative effects on fertility and survivability. Other studies have shown that increased inbreeding tends to reduce egg number and delay sexual maturity in poultry (Meleg et al., 2005; Sewalem et al., 1999). Inbreeding depression has the most severe effects in small and closed livestock populations undergoing selection, with coefficients reported as being higher than 20% (Gutiėrrez et al., 2003). These populations were propagated by shorter generation intervals as is the case with chickens. The moderately high levels of inbreeding identified in this study were inevitable; in such a closed population, individuals became more closely related with increasing generations. However, the effects of inbreeding depression were less drastic in this study because the founders were entirely unrelated, and selection and mating decisions consciously avoided accumulating inbreeding.

The rate of inbreeding is the rate at which homozygosity increases in a population. Increased rates of inbreeding reduce heterozygosity which in turn reduce opportunities for hybrid vigor to be expressed. Consequently, traits show a decline in performance as these rates increase. In this study, average inbreeding rates were relatively low and similar in the two selection lines across generations. Other studies on chicken breeds have reported rates of inbreeding in the range 0.03% to 25% (Larivière at al., 2011). Simon and Buchenauer (1993) reported that chicken populations of over 50 generations with inbreeding rates of < 5% offer less risks of inbreeding depression and extinction, 5 to 15% are potentially at risk, 25 to 40% are endangered, and > 40% are at a critical status. With the approximately 1% increase in inbreeding per generation found in these lines, there is a low risk of inbreeding depression and extinction.

Effective Population Size

The N_e is a lower limit for the number of breeding individuals required for a population to be of a viable size (Soulė, 1987). In closed populations, N_e can be negatively impacted by inbreeding in the short term, and affect selection response in the long term, because of loss of genetic variation. The N_e is therefore indirectly proportional to the rate of inbreeding. It is a good estimate of the actual population size when the pedigree is well defined and complete, as was the case in this study.

The N_e observed was similar to that reported by Márquez et al (2010), with only slight variations. This similarity can be attributed to a relatively constant rate of inbreeding across generations. At generation 59, the N_e was about 68% and 60% of the actual population size (number of selected parents) in the HWS and LWS lines, respectively. The small difference in N_e found in this study [40.74 (LWS); 34.45 (HWS)] as compared to the Márquez et al (2010) study [38.30 (LWS); 32.10 (HWS)] could be because only birds with progeny with a known BW and sex now were defined as parents. Other studies have reported that the critical N_e necessary for maintenance of adequate genetic variation is 500 (Franklin and Frankham., 1998; Soulė, 1980). Based on those guidelines, this population falls short and could be at a potential risk. However, the cited studies do not indicate whether that threshold is only specific to a particular species or breed, or due to biological differences such as reproductive rate.

Effective Number of Founders

The f_e is used to detect significant changes in breeding strategies and maintenance of gene pools. In generation 59 of this study, the f_e [17.25 (LWS); 15.24 (HWS)] was relatively low compared to the actual number of founders (102). This result could be attributed to unequal contributions of founders.

Most male founders (11 LWS and 8 HWS out of 15) contributed, although in varying proportions, to generation 59. Clearly, male founders persisted in their genetic impact on the population. However, this persistence was less in female founders (21 LWS and 22 HWS out of 87). The marginal contribution of founders to generation 59 was explained by about 30 of the 102 founders. The f_e was also calculated for generation 48 and yielded similar results to those of Márquez et al. (2010).

Gene Flow

Probabilities of gene origin and flow offer perspective when describing population structure, and better quantify losses in genetic variability due to selection, because they remove biases accrued by inbreeding (Boichard et al., 1997; Márquez et al., 2010). Gene flow also is useful when trying to ascertain maintenance of genetic diversity and consequences of selection (Gutiėrrez et al., 2003).

In this study, the HWS and LWS lines were established from a single panmictic base population. It was nearly inevitable that these lines would share genes in common. From a base population of 15 males and 87 females, 7 male and 8 female founders contributed, in varying degrees, to both lines in generation 59. The contribution of male founders was higher in the LWS line while that of female founders was about the same in both lines. These varying contributions indicate differences in genetic potential for growth or heavy use of certain founders through their descendants within a line or both.

Numerator Relationships

The relatedness of the founders to all chickens in both lines offers insight on the closeness of additive genetic relationships in the population. Using pedigree-based relationships, founders common to both lines at generation 59 had about the same degree of relationship across

and within both lines. The additive genetic relationships among founders exclusive to either the LWS or HWS lines were similar. As anticipated, the strength of those relationships decreased as selection progressed. This is evident from results of these percentages from generation 48 (13.9% LWS and 15.1% HWS) reported by Márquez et al. (2010) and results from this study (2.2% LWS and 2.6% HWS) after an additional 11 generations of selection. The average relatedness corresponding to founders common to both lines in the numerator relationship matrix did not change over time, as was also evident from the results at generation 48 reported by Márquez et al. (2010).

Family Sizes

Family sizes and their variances reflect breeding decisions, with larger variances in family sizes resulting in higher inbreeding levels in the population. Variation in family size results when parents, typically males bred to females via artificial insemination, are used in higher proportions than others, or as a result of differential fertility among individual males and females as was the case in this study. The family sizes in this study were similar between lines and within each sex. That stability reflected the design of the breeding program: restrictions were placed on sizes of sire and dam families to ensure no family predominated over others and to mitigate inbreeding.

CONCLUSION

Based on various statistics that characterize the dynamics and diversity of a population, the HWS and LWS lines were found to be similar in their genetic architecture. Robust comparisons of the performance of these two lines over the entire selection profile therefore can be made with confidence. Furthermore, despite losses of genetic diversity due to the continuing

gradual accumulation of inbreeding, adequate levels of heterozygosity still remain to allow further selection.

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Table 2. 1 Number of male and female parents in each line

	Low weight		High weight	
Generation	Male	Female	Male	Female
0 (1957)	8	48	8	48
1 (1958)	7	37	8	34
5 (1962)	12	51	10	46
26 (1983)	14	41	13	39
48 (2005)	14	43	14	40
59 (2016)	14	44	14	46

Table 2. 2 Number of chickens by sex, line and sub-population

	Sex		
Line	Male	Female	Total
Founders	15	87	102
High	7,138	7,411	14,549
Low	7,721	8,571	16,292

Table 2. 3 Genetic diversity summary statistics in the selection lines across 59 generations

Parameter[1]	Low weight	High weight
n	18,164	15,284
Max F	0.53	0.59
Mean F (SD)	0.31 (0.17)	0.35 (0.19)
Change in F per gen (%)	1.23	1.45
N_e	40.74	34.45
f_e	17.25	15.24

[1]F = inbreeding coefficient; N_e = effective population size; f_e = effective number of founders.

Table 2. 4 Number of male and female contributing founders to different generations across the selection profile by weight line

	Low weight		High weight		Common founders	
Generation (yr)	Male	Female	Male	Female	Male	Female
1 (1958)	12	34	8	31	8	15
2 (1959)	12	27	8	26	8	10
3 (1960)	11	22	8	23	7	8
4 (1961)	11	21	8	23	7	8
5 (1962)	11	21	8	22	7	8
48 (2005)	11	21	8	22	7	8
59 (2016)	11	21	8	22	7	8

Table 2. 5 Family sizes by line and sex across 59 generations

Sex	Weight line	n	Maximum	Mean	SD
Full pedigree[1]					
Male	High	758	95	20.2	12.7
	Low	751	92	24.2	14.8
Female	High	2333	26	6.6	4.3
	Low	2518	24	7.2	4.5
Parents[1]					
Male	High	703	18	4.3	2.6
	Low	721	14	4.5	2.3
Female	High	1513	9	2.0	1.3
	Low	1708	9	1.9	1.1

[1]Pedigree = all individuals with a known sex and 4-wk or 8-wk BW; [1]Parents = individuals with progeny with a known sex and 4-wk or 8-wk BW.

FIGURES

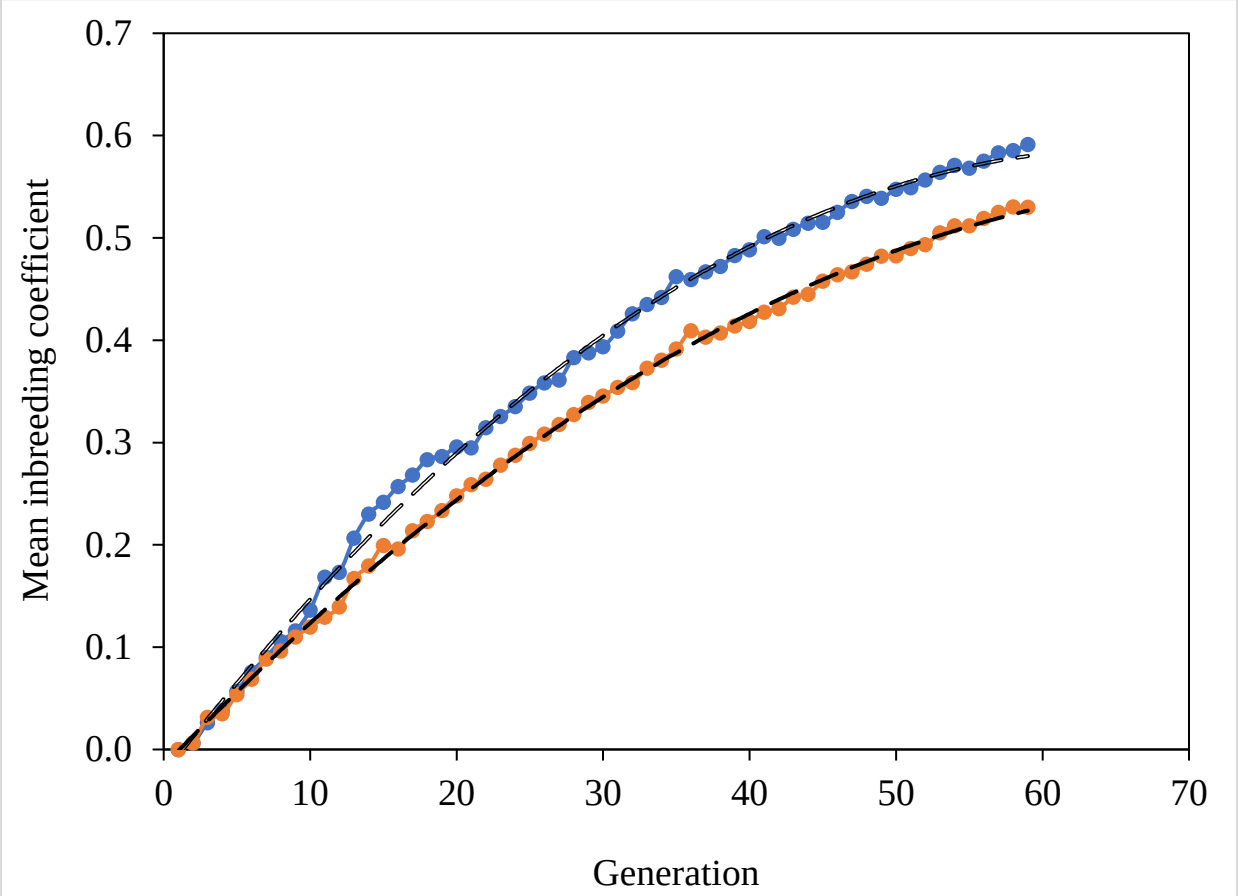

Fig. 2. 1 Mean inbreeding coefficient across 59 generations for the high weight selection (HWS) and low weight selection (LWS) lines. HWS = blue dots and LWS = red dots.

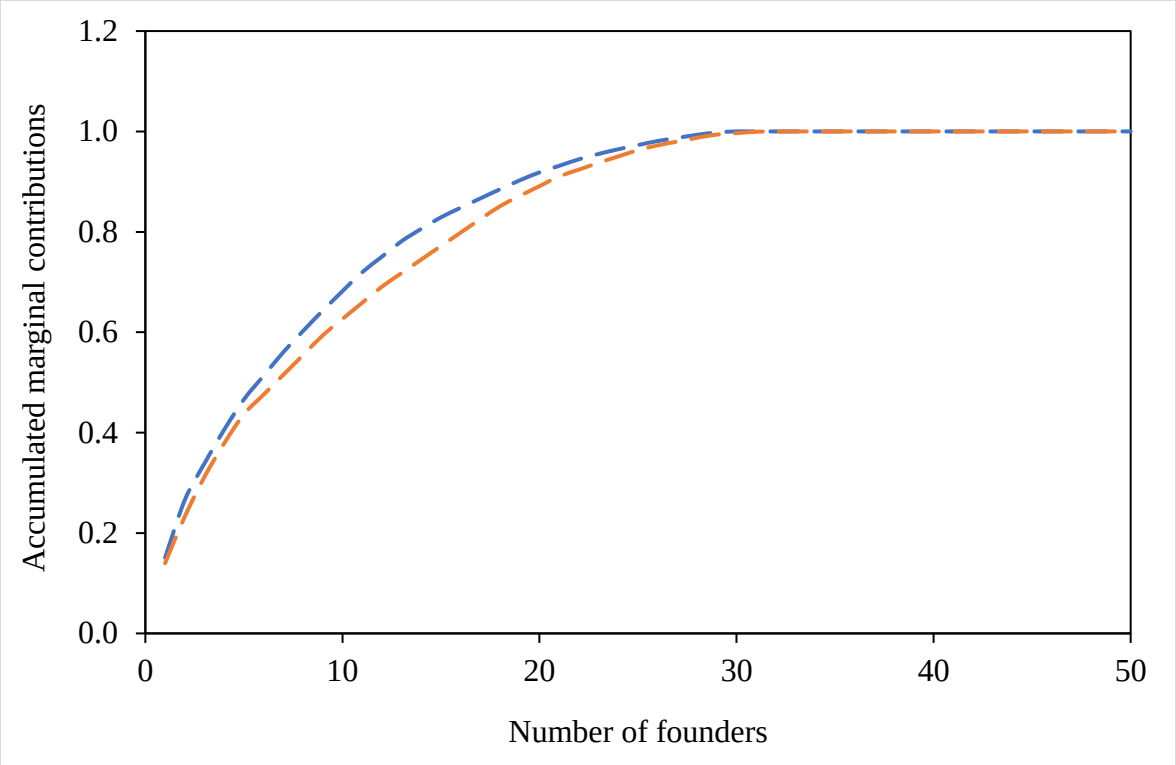

Fig. 2. 2 Accumulated marginal contribution of founders to generation 59. Red line = low weight selection line; Blue line = high weight selection line.

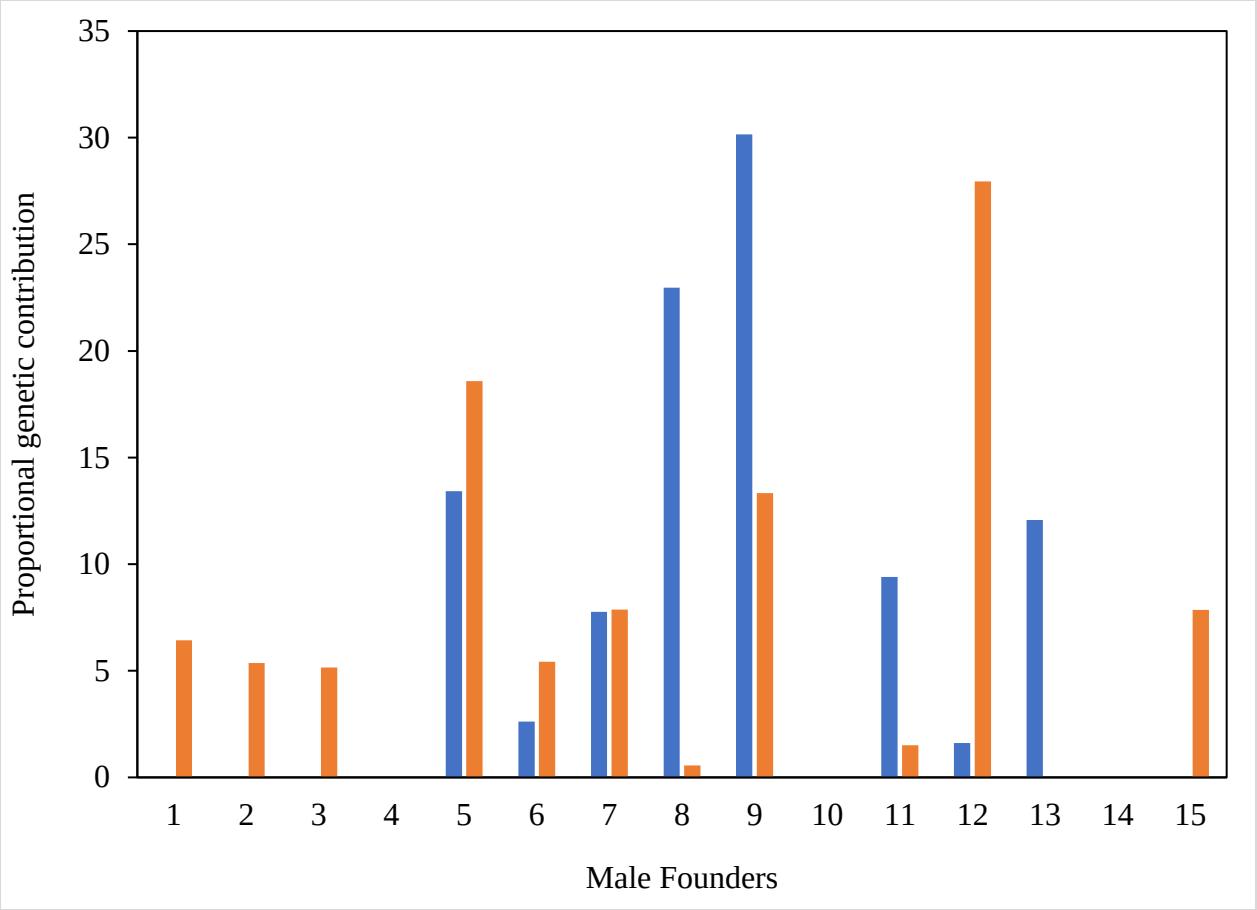

Fig. 2. 3 Proportional contribution of male founders to generation 59. Red bars = low weight selection line; Blue bars = high weight selection line.

CHAPTER III: Evaluation of Long-Term Direct and Correlated Response to Selection on White Plymouth Rock Chickens Selected for High or Low Body Weight

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ABSTRACT

Response to selection was evaluated in 56 generations of a long-term experiment in White Plymouth Rock chickens divergently selected for 8-wk BW. Results yielded a fourteen-fold difference in BW between the high weight select (**HWS**) and low weight select (**LWS**) lines that originated from a common founder population. Several analytical approaches were used to estimate response to selection at 8-wk of age. These were based on regression of mean phenotypes on generation number, products of selection differentials and estimates of heritabilities, and regression of estimated breeding values (**EBV**) on generation number, with EBV obtained fitting an animal model. Eight-wk BW increased linearly in HWS over the selection horizon, with retention of substantial amounts of additive variation. In the LWS line, the decrease in 8-wk BW followed the pattern of quadratic polynomial, suggesting a possible selection plateau. Estimates of heritabilities and selection response based on the fit of an animal model, which was unique to this study, were consistent with earlier values on these lines. Estimated genetic trends obtained by regressing EBV on generation number were similar to responses estimated by phenotypic regression. Estimates of heritabilities across-lines for 8-wk BW were: gen 1-18; 0.38 (±0.02), gen 19-25; 0.56 (±0.04), gen 26-36; 0.53 (±0.03), and gen 37-56; 0.44 (±0.03). Corresponding estimates for 4-wk BW were 0.42 (±0.02), 0.52 (±0.04), 0.55 (±0.03) and 0.51 (±0.02). Within lines, heritability estimates also were fairly constant across generations. Although additive variation in BW remained in both selection lines, a selection plateau was observed in the LWS likely reflecting biological constraints on reproductive fitness. Still, direct and correlated responses to selection for increased BW has continued throughout the 56 generations suggesting genetic mechanism for maintaining additive variation exist even in long-term selection scenarios.

Key words: body weight, meat-type , divergent selection, heritability, long-term response

INTRODUCTION

Selective breeding entails choosing individuals as parents based on some criterion to directionally change a population. A long-term selection experiment in chickens based on high and low BW at 8 wk of age, which began in 1957 and still continues, has provided a clear illustration of response to such artificial selection (Siegel, 1962; Dunnington and Siegel, 1996; Dunnington et al., 2013). Due to pleiotropic effects, selection for one characteristic also may result in changes in others. As reported by Dunnington and Siegel (1985), correlated responses have occurred in 4-wk BW, along with a plethora of efficiency and reproductive traits, in these same selection lines. Such observations cannot be easily obtained from short-term experiments; they reflect gradual changes in allele frequencies that may lead to losses in fitness and in genetic and physiological limits or plateaus in performance. Long term experiments therefore provide insights into the broader impacts of directional selection on correlated responses.

Studies that have been conducted previously in these selection lines have evaluated response to selection based on phenotypic means for each generation (Siegel, 1962; Liu et al., 1994; Dunnington and Siegel, 1996; Dunnington et al., 2013). In those studies, additive variances were estimated from 8-wk BW on individual chicks by intra-class correlation and parent-offspring regression accounting for sex and line. Heritability estimates were then used to compute effects of selection in divergent directions. An alternative predictive approach to determining selection response is to account for all pedigree relationships by fitting an animal model, thereby more intimately modelling the genetic structure of the population. This has been done in other poultry experiments (Morris and Pollott, 1997; Aggrey et al., 2010) but, as of yet, not in the long-term selection study underway at Virginia Tech.

The population structure of the high and low BW selection lines was evaluated up to generation 48 by Márquez et al. (2010). They determined that levels of inbreeding and family sizes were similar in the two lines across generations and, at least at generation 48 of selection, considerable heterozygosity remained in both lines. Although additional inbreeding has accumulated since with further loss in genetic diversity (Chapter 2), that analogous population structures for the two lines has continued. This design of the study predicates its value for evaluating direct and correlated responses to long-term selection.

We had two main objectives in this study: to estimate co-variances and their ratios (heritabilities, correlation), and to predict direct and correlated responses to selection, in chickens divergently selected for BW. For these analyses we used 8-wk (directly selected trait) and 4-wk (correlated trait) BW collected on both lines, and on their corresponding relaxed lines, collected over 56 generations of selection. These entire data, as well as partitions thereof (generation 1-18, 19-25, 26-36, and 37-56), were evaluated. Because complete pedigree data were assembled, parameter values were obtained fitting an animal model; those analyses benefitted from our accounting for familial relationships tracing back to the foundation of the lines. Among other approaches explored, Best Linear Unbiased Prediction (**BLUP**) of breeding values were obtained and used to assess selection responses.

MATERIALS AND METHODS

Animal Use and Care

All procedures and protocols used in this study were approved by the Institutional Animal Care and Use Committee (IACUC) at Virginia Tech as of 1977. Prior to that, the chickens were treated in a like-manner despite the university not having the stated guidelines and protocols.

Selection Lines

A long-term experiment began in 1957 with selection for high or low 8-wk BW in chickens (Siegel, 1962). The experiment is ongoing. The two selection lines were founded from a cross of 7 inbred lines (13 males and 55 females) of White Plymouth Rock chickens. The 68 chickens were founders to both a high weight selection (**HWS**) and low weight selection (**LWS**) line, with heavier chickens chosen as parents for the HWS line and lighter chickens chosen as parents for the LWS line. Eight sires and 48 dams were retained for the parental generation (P_0) in 1957. Thereafter there were slight increments in the numbers selected as parents. A parent was considered an individual with progeny of known sex and a 4-wk or 8-wk BW, or both BW.

Relaxed Lines

In generations 7, 14, 20, 27, 35 and 44, random samples of chickens were selected from within each line. These chickens served as parents for establishing relaxed lines. Relaxed lines originating from the HWS line were designated **HWR** while those from the LWS line were designated **LWR**. These lines were reproduced by artificial insemination using pooled semen from the males within a line to inseminate the females within that line. Each relaxed line was maintained for 7 to 15 generations, and were overlapped by one generation.

Husbandry

Each year and in each line, chicks were hatched on the first and third Tuesday of March. The second hatch was done to mitigate for insufficient numbers of chicks from the first hatch. All chicks were hatched in the same incubators, kept in identical pens and fed the same diet. Further details of the flock husbandry were provided earlier (Chapter 2).

Data

Data used in this study were from 56 discrete generations starting with the founders in 1956, formation of the parental lines in 1957, and continuing until 2013. Four- and 8-wk BW, sex, hatch (first or second), and generation were available. A full pedigree was constructed beginning with the founder chickens common to the two lines.

Statistical Analyses

Estimation of Co-variances. A linear mixed model was defined as

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Zu} + \boldsymbol{e}$$

where **y** represented a vector of observations (either 4-wk or 8-wk BW), $\boldsymbol{b}$ was a vector of fixed, systematic environmental effects with incidence matrix $\boldsymbol{X}$, $\boldsymbol{u}$ was a vector of random direct additive effects with incidence matrix $\boldsymbol{Z}$, and $\boldsymbol{e}$ was a random vector of residuals. The fixed effects considered were sex and contemporary group (generation-hatch combinations). The variance structure of the model was $var(u) = \boldsymbol{A}\sigma_a^2$ and $var(e) = \boldsymbol{I}\sigma_e^2$, where $\boldsymbol{A}$ was the numerator relationship matrix among animals in the pedigree, $\boldsymbol{I}$ was the identity matrix, σ_a^2 was the direct additive variance, and σ_e^2 was the residual variance.

Initially, a univariate animal model was fitted using ASREML (ASREML v4.1; Gilmour et al., 2015) to estimate the direct additive and residual variance for 4-wk and 8-wk BW separately. Subsequently, a bivariate analysis of the pair of BW was conducted to also estimate their genetic co-variance. Using these co-variance estimations, heritabilities ($\boldsymbol{h^2}$) for each BW, their genetic correlations and respective SE, were obtained.

Additionally, a sire model was also fitted and the results were largely similar to the fit of the animal model. For conciseness, those results will not be included.

Response to Selection. Response to selection for the entire selection profile (generation 1 to 56), and for specified intervals (generation 1 – 18, 19 – 25, 26 – 36 and 37 – 56), was evaluated in 3 ways: (i) regression of 8-wk BW on generation number (phenotypic regression); (ii) weighted selection differentials; and, (iii) regression of BLUP estimated breeding values (**EBV**) of 8-wk BW on generation number (genetic regression). The generations were partitioned as such because: (i) there was a feed restriction imposed on the HWS line at generation 18 (generation 1-18); (ii) monitoring genetic change after the feed restriction was imposed until about mid-way through the selection profile was deemed useful (generation 19-25); (iii) there appeared to be a selection plateau in the LWS line after generation 25 (Dunnington et al., 2013; generation 26 – 36); and, (iv) monitoring genetic change over the most recent years of selection was also considered valuable (generation 37-56).

Firstly, response to selection (***R***) was obtained within line and sex by regressing the mean BW for the generation on generation number. A quadratic polynomial of the form $y = a + b_1x + b_2x^2$ was fitted where y was the mean BW and x was the generation number (1 to 56). Frequency distributions also were computed for females and for males for 4-wk and 8-wk BW to illustrate the effects of selection on phenotypic variation in BW.

Secondly, R was computed as the product of weighted selection differentials and heritability estimates. Selection differentials (***S***) were obtained by generation as the difference between the base population mean within sex and line, and the mean of the respective selected parents. The values were weighted based on parental contribution to those progeny that themselves were selected as parents in the following generation. As a comparison, unweighted selection differentials (values weighted based on parental contribution to all progeny in the following generation) were also computed. Response within each generation was obtained as

h^2S. The h^2 specific to a time (generational) interval was used in the calculation. The R were then averaged for the interval.

Thirdly, R was obtained from the quadratic regression of mean BLUP estimated breeding values (**EBV**) for the generation on generation number. The EBV were obtained from the fit of the bivariate animal model to the full data. However, only EBV for those animals with either a 4-wk or 8-wk BW were used when constructing the mean. Regressions were fit separately by line.

Lastly, correlated response to selection (**CR**) for 4-wk BW was obtained within line and sex as $i_{BW8}h_{BW8}h_{BW4}r_{BW8,BW4}\sigma_{p_{BW4}}$ where i_{BW8} was the selection intensity for 8-wk BW, $r_{BW8,BW4}$was the genetic correlation between 8- and 4-wk BW, and $\sigma_{p_{BW4}}$ was the phenotypic standard deviation for 4-wk BW. The CR were calculated using the within-line parameter estimates specific to a year (i_{BW8}) and generation interval (h_{BW8}, h_{BW4}, $r_{BW8,BW4}$, $\sigma_{p_{BW4}}$), which were then averaged for the respective intervals.

RESULTS

Effects of Selection

Changes in BW in chickens selected for high and low BW at 8 wk of age over 56 generations are shown in Figure 3.1 and 3.2 for males and females, respectively. The divergence between the HWS and LWS lines indicated about a fourteen-fold difference in BW by generation 56 (Table 3.1). Mean 8-week BW in the foundation population (P_0) was 880 (121) g for the males and 711 (114) g for the females. After 56 generations of selection, mean 8-wk BW in HWS and LWS males was 1852 (149) g and 131 (22) g, respectively. Corresponding values in females were 1510 (88) g and 93 (25) g.

Discontinuing selection resulted in the regression of the BW towards original values. As illustrated in Figures 3.1 and 3.2, BW in HWR were less than the HWS lines and, conversely, the BW in the LWR were greater than in LWS, over corresponding intervals.

Co-variances and their Ratios

Estimates of (co)variance components obtained fitting a bivariate animal model for combined data are summarized in Table 3.2 and 3.3. The estimates of additive variance for both 8-wk and 4-wk BW increased in the progressive intervals. Across lines, the heritabilities for both traits increased between the first (generation 1 – 18; 8-wk: 0.38 ± 0.02; 4-wk: 0.42 ± 0.02) and second generational interval (generation 19 – 25; 8-wk: 0.56 ± 0.04; 4-wk: 0.52 ± 0.04), remained relatively similar in the third interval (generation 26 – 36; 8-wk: 0.53 ± 0.03; 4-wk: 0.55 ± 0.03), and reduced modestly in the final interval (generation 37 – 56; 8-wk: 0.44 ± 0.03; 4-wk: 0.51 ± 0.02). Across these partitions both the additive and phenotypic variances increased gradually. However, since the heritability is the ratio between these variances, their change in values were less systematic.

Similarly, the estimates of additive and phenotypic covariances for both 8-wk and 4-wk BW increased across intervals (Table 3.3). Across lines, the genetic correlations of both traits increased between the first (generation 1 – 18; 0.81 ± 0.02) and second generational interval (generation 19 – 25; 0.89 ± 0.02), remained fairly similar in the third interval (generation 26 – 36; 8-wk: 0.84 ± 0.02), and reduced to a slight degree in the final interval (generation 37 – 56; 0.79 ± 0.02).

Within-line estimates of variances for 8-wk BW, and their heritabilities, are summarized in Table 3.4. In the LWS line, additive and phenotypic variances decreased substantially while in the HWS line those values increased moderately. However, heritabilities were fairly stable across generations in both lines.

Response to Selection

Phenotypic Regression. The fit of the quadratic regressions of mean BW for a generation on generation number for 8-wk and 4-wk BW in the HWS line by sex are illustrated in Figures 3.3 to 3.4. Both across and within generational intervals, and in both sexes, the estimate of the quadratic coefficients did not differ from zero ($P < 0.05$). Therefore, a simpler model including only the intercept and slope was fitted for HWS, suggesting gain was relatively linear and consistent across all generation intervals. The exception was the 6-yr time interval (gen 19-25), which showed some incompliancy in its fit (Table 3.5). This may have been a residual effect of the feed restriction imposed in generation 18 on BW in the HWS line. With adult hens being less obese, different molecular mechanisms affecting the various components of growth (e.g., muscle, fat) may have come into play. Genetic gain per generation in males was about 16.1 (± 0.70) and 4.9 (± 1.04) g/yr for 8-wk and 4-wk BW, respectively. In females these values were about 12.9 (± 1.96) and 5.4 (± 0.83) g/yr, respectively

Conversely, in the LWS, the quadratic model provided a better fit for the regression of mean BW on generation number across all generations ($P < 0.001$). There was a clear curvilinear pattern, with the reduction in BW decreasing across generations (Figures 3.5 and 3.6). However, within a generational interval, the quadratic coefficient was not significant. Therefore, a simpler model was fitted to each data partition including only the intercept and

slope (Table 3.6). In the later generations, the slope became less negative showing that the reduction in BW was slowing perhaps reaching a lower plateau. This trend was similar across all generation intervals except gen 19-25. However, the general trend was that the slope became closer to zero, coincident with the observation that the rate of change was slowing. Minimum 8-wk BW for the LWS line were observed around generation 38 in females and generation 51 in males.

Weighted Selection Differentials. The weight selection differentials for the HWS and LWS lines for 8-wk BW by generation are summarized in Figure 3.9. In HWS, the *S* varied appreciably by generation yet remained substantial (90.5 (29.26) g). However, in the LWS, the *S* decreased across generations first approaching zero at generation 35; thereafter, *S* oscillated close to zero. Weighted and unweighted selection differentials are summarized by generational interval in Table 3.8.

Frequency distributions of BW for females and males at 8- and 4-wk of age are shown in Figures 3.7 and 3.8 for three generations in the selection profile (0, 36 and 56). As a consequence of selection, the two lines diverged from the panmictic founder population into 2 distinctly different populations. By generation 56, there was very little overlap in BW in both lines with the founder population.

Response estimated from the product of weighted selection differentials and heritability estimates by interval is summarized in Table 3.8. Response in the HWS line appeared to fall in generation 19 – 25 and increased modestly in generation 26 – 36 and 37 – 56. In the LWS line, response decreased over time.

Genetic Regression. Genetic trends in 8-wk BW were obtained from the regression of mean EBV for a generation on generation number as shown in Figure 3.10 for each line. As with the phenotypic regressions, the estimates of the quadratic coefficients within each generational interval did not differ from zero in either line ($P < 0.05$). However, in the LWS line, the regression of mean EBV on generation number across the entire selection profile was improved by including the quadratic term in the model fitted.

The average EBV within line for 8-wk BW are presented by generation interval in Table 3.7 Following a similar pattern to the BW, the EBV increased linearly across generations in the HWS line (Figures 3.10 and 3.11). The gain per generation was about 16.8 (± 0.64) and 5.9 (±0. 30) g/yr for 8- and 4-wk BW, respectively. In the LWS, EBV decreased in a curvilinear fashion.

Correlated Responses. Correlated responses estimated from the product of the selection intensity for 8-wk BW, the genetic correlation between and selection accuracies of 8- and 4-wk BW, and the phenotypic standard deviation of 4-wk BW are summarized in Table 3.9. Correlated response in the HWS line appeared to decrease in generation 19-25 and increase modestly in generation 26-36 and 37-56. Conversely, correlated responses decreased across the selection horizon in the LWS line.

DISCUSSION

Effects of Selection

The effectiveness of divergent selection over 56 generations of continuous selection pressure on 8-wk BW was tested. Two lines, extremely distinct in BW, were produced from a single founder population. Still, additive genetic variation remained in both lines. Previous experiments on earlier generations of these lines suggested variation remained due to the effects

of multiple loci and epistatic networks on BW, and possible spontaneous mutations in the population (Dunnington and Siegel, 1996; Pettersson et al., 2011; Dunnington et al., 2013).

Relaxed lines were randomly selected and maintained over 6 time-phases across the generations. The BW of chickens in the HWR lines were less than that of the HWS lines; conversely, the BW of chickens in the LWR lines were greater than that of the LWS lines. While this phenomenon explained the effectiveness of selection, the relaxed lines did not fully regress to the founder population means. This can be attributed to the adaptation period of the relaxed chickens to their new physiological state (Dunnington et al., 1996). Furthermore, selection had focused on additive effects impacting BW, likely with allelic fixation at many loci. Therefore, even with relaxation of selection, dominance interactions were not overly impacted. This also may have reduced the extent of the regression of the BW in the relaxed lines toward the founder means.

Co-variances and their Ratios

Additive and residual variation in 8-wk BW tended to increase over generations for data combined across lines, although in a proportional fashion as heritabilities remained relatively similar. Within the individual lines, heritabilities also remained fairly constant over time. Therefore, in theory, opportunity for continued selection response in both lines seems possible. However, in the HWS line, the amount of additive and residual variation increased across the selection horizon, while that in the LWS decreased substantially. Therefore, the rate of any further genetic change in the LWS line is clearly curtailed.

Heritabilities in other meat type chicken breeds at 8-wk BW have been reported to be in the range 0.24 ± 0.00 to 0.47 ± 0.01 (Niknafs et al., 2012). Those estimates are consistent with those obtained in the current study across lines and generations (0.30 ± 0.01).

Selection Response

Phenotypic and Genetic Regression. Selection response was evaluated by the quadratic regression of mean BW on generation number for each line by sex combination. In the HWS line, BW effectively increased linearly across generations (in males, 16.1 (± 0.70) and 4.9 (± 1.04) g/yr for 8-wk and 4-wk BW, respectively; in females, 12.9 (± 1.96) and 5.7 (± 0.83) g/yr for 8-wk and 4-wk BW, respectively). This suggests additive genetic variation was being maintained despite the long-term selection.

However, in the LWS line, the decrease in 8- and 4-wk BW was curvilinear with little further reduction in BW in later generations of the selection. Although additive genetic variation was still present, the phenotypic variance decreased giving evidence of a selection plateau in the LWS line. This likely supports the selection plateau reflecting a biological barrier manifesting itself as a constraint. Typically, a selection plateau refers to running out of genetic variation for a selected trait. In this case, this biological constraint caused a loss in reproductive fitness as smaller birds had difficulty reaching sexual maturity and, as such, were not able to produce offspring (Dunnington and Siegel, 1996; Zelenka et al., 1988). This indirectly affects selection for lower BW because some birds selected to be parents in successive generations will not produce progeny, making their selection irrelevant.

Response to selection from genetic regression showed a similar trend as that of the phenotypic regression. The HWS lines had more gain per annum than the LWS lines.

Weighted Selection Differentials. The weighted selection differential for the HWS line varied, but oscillated around a mean of 91 g, while the LWS line decreased and oscillated close to zero. Larger negative values in the LWS line implied larger negative differentials between the population and parental means. With successive generations, this difference became smaller.

This evidence of the biological constraint on fitness, with the pattern reflecting LWS line birds overcoming reproductive limits as their BW continued to fall.

The frequency distributions in the LWS line became narrower over time, which coincided with the reduction in additive variation. In the HWS line, the width of the distribution seemed to increase slightly. These results also are indicative of the tremendous response to selection in both lines. By generation 56, both lines had very little overlap with the founding population.

The selection response computed from the product of the selection differentials and the heritabilities was higher when weighted rather than unweighted selection differentials were used. Differences in fertility cause some parents to contribute more offspring to the next generation than others. Weighting the selection differentials enables measuring joint effects of natural and artificial selection (Falconer and Mackay, 1996). The computed selection responses for the partitioned data confirmed that there was substantial amounts of additive variation in both lines. The pattern of reduced response in the LWS line is as a result of smaller selection differentials as BW fell coupled with losses in reproductive fitness.

Correlated Response to selection

Correlated responses in 4-wk BW from selection for increased 8-wk BW in both lines achieve about 30-40% of the response that would be anticipated from selecting directly for 4-wk BW. Double selection experiments are not always consistent in the estimates of genetic correlations that they give (Falconer and Mackay, 1996). This may lead to low predictability of correlated responses. Another possible reason for low predictability could be sensitivity of genetic correlations to gene frequency changes during the course of selection.

CONCLUSION

Response to selection in the long-term selection experiment was evaluated using different analytical strategies. Substantial response was achieved from selecting chickens on 8-wk BW, with that annual rate of response relatively constant in the HWS line throughout the 56 generations. Such can only occur in a population where additive genetic variation remains or if mutations reintroduce additive variation. A genomic analysis of the population would reveal possible mutated regions influencing the continued genetic variation in the HWS line. The LWS line showed decreased responses to selection caused in part by physiological barriers affecting viability.

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Table 3. 1 Means and numbers of chickens within line and sex at 8-wk BW

			Generation				
	Sex	Line	0	1	18	36	56
Means[1](SD)	Male	HWS[2]	880.8(121)	943.6(119.7)	1412.3(146)	1704(130)	1852(149)
		LWS[3]		867.7(112.6)	526(58)	214.9(64)	130.6(22)
		(H - L)[4]		75.9	886	1489.1	1721.4
	Female	HWS	711.7(114)	774.8(99.3)	1135.9(92)	1319.1(103)	1510(88)
		LWS		705.2(93.8)	409.9(72)	135.7(43.5)	92.7(25)
		(H - L)		69.6	726	1183.4	1417.3
Numbers	Male	HWS	491	235	106	156	126
		LWS		214	150	96	63
	Female	HWS	498	193	146	146	100
		LWS		193	170	128	102

[1]Mean weights (g); [2]High weight selection line; [3]Low weight selection line; [4]Difference between high and low weight selection lines

Table 3. 2 Estimates of additive, environmental and phenotypic variances, and heritabilities, for 8-wk and 4-wk BW

	σ_a^2 [1]	σ_e^2 [2]	σ_p^2 [3]	h^2 [4]
8-wk BW				
All generations	4560.3	10488.6	15049.0	0.30 ± 0.01
Generation interval				
1 - 18	4523.6	7376.4	11900.0	0.38 ± 0.02
19 – 25	9517.8	7629.7	17148.0	0.56 ± 0.04
26 – 36	10441.0	9223.1	19664.0	0.53 ± 0.03
37 - 56	10548.1	13569.8	24118.0	0.44 ± 0.03
4-wk BW				
All generations	873.3	1460.7	2334.0	0.37 ± 0.01
Generation interval				
1 - 18	795.7	1093.1	1888.8	0.42 ± 0.02
19 – 25	1137.4	1047.3	2184.7	0.52 ± 0.04
26 – 36	1625.8	1322.4	2948.1	0.55 ± 0.03
37 - 56	1925.5	1835.4	3760.9	0.51 ± 0.02

[1]Additive variance for 8 and 4-wk BW (g^2); [2]Residual variance for 8 and 4-wk BW (g^2); [3]Phenotypic variance for 8 and 4-wk BW (g^2); [4]Heritabilities of 8 and 4-wk BW (σ_a^2/σ_p^2).

Table 3. 3 Estimates of additive, environmental and phenotypic covariances and correlations between 8- and 4-wk BW

	$\sigma_{a_{x,y}}$ [1]	$\sigma_{e_{x,y}}$ [2]	$\sigma_{p_{x,y}}$ [3]	r_G [4]	r_e [5]	r_p [6]
All generations	1572.9	2697.6	4270.6	0.79±0.01	0.69±0.01	0.72±0.00
Generation interval						
1 - 18	1529.7	1935.7	3465.4	0.81±0.02	0.68±0.01	0.73±0.01
19 – 25	2942.3	1772.3	4714.5	0.89±0.02	0.63±0.03	0.77±0.01
26 – 36	3441.0	2367.6	5808.6	0.84±0.02	0.68±0.01	0.76±0.01
37 - 56	3546.4	3365.5	6911.9	0.79±0.02	0.67±0.01	0.73±0.01

[1]Additive covariance for 8 and 4-wk BW (g); [2]Residual covariance for 8 and 4-wk BW (g);

[3]Phenotypic covariance for 8 and 4-wk BW (g); [4]Genetic covariance of 8 and 4-wk BW; [5]

Residual covariance of 8 and 4-wk BW; [6]Phenotypic covariance of 8 and 4-wk BW.

Table 3. 4 Within line estimates of additive, environmental and phenotypic variances, and heritabilities, for 8-wk BW

	σ_a^2 [1]	σ_e^2 [2]	σ_p^2 [3]	h^2 [4]
All generations	7484.4	10932.7	18417.0	0.41 ± 0.02
High weight selection				
Generation interval				
1 - 18	8385.3	6217.4	14603.1	0.57 ± 0.04
19 – 25	14606.0	6184.8	20791.0	0.70 ± 0.06
26 – 36	12399.9	8616.3	21016.0	0.59 ± 0.05
37 - 56	18581.7	11695.7	30277.0	0.61 ± 0.04
All generations	7857.4	2198.5	10056.0	0.78 ± 0.01
Low weight selection				
Generation interval				
1 - 18	5433.2	4860.4	10294.0	0.53 ± 0.02
19 – 25	3447.2	3638.4	7085.6	0.49 ± 0.07
26 – 36	2585.3	2064.5	4649.4	0.56 ± 0.05
37 - 56	1930.8	1315.6	3245.9	0.59 ± 0.04

[1]Additive variance for 8 and 4-wk BW (g^2); [2]Residual variance for 8 and 4-wk BW (g^2);

[3]Phenotypic variance for 8 and 4-wk BW (g^2); [4]Heritabilities of 8 and 4-wk BW (σ_a^2/σ_p^2).

Table 3. 5 Parameter estimates, standard errors, t-statistics and p-values for comparisons of the slopes for the regression of 8-wk BW on generation for the high weight selection line

	Slope				
	Estimate (g/yr)	SE	R^2	t-stat	P-value
Female					
All	12.85	0.49	0.92	25.98	< 0.001
Generation interval					
1-18	15.48	2.23	0.75	6.96	< 0.001
19-25	2.09	7.97	0.01	0.26	0.80
26-36	20.48	5.08	0.64	4.03	0.002
37-56	10.98	2.29	0.56	4.78	0.0001
Male					
All	16.14	0.70	0.91	22.92	< 0.001
Generation interval					
1-18	21.63	2.76	0.79	7.83	< 0.001
19-25	-5.23	9.49	0.05	-0.55	0.61
26-36	30.79	7.16	0.67	4.3	0.001
37-56	11.79	3.78	0.35	3.12	0.006

Table 3. 6 Parameter estimates, standard errors, t-statistics and p-values for comparisons of the slopes for the regression of 8-wk BW on generation for the low weight selection line

	Slope				
	Estimate (g/yr)	SE	R^2	t-stat	P-value
Female					
Generation interval					
1-18	-17.55	2.11	0.81	-8.31	< 0.001
19-25	-23.76	9.77	0.54	-2.43	0.05
26-36	-5.77	2.86	0.31	-2.01	0.07
37-56	-1.68	0.96	0.15	-1.75	0.09
Male					
Generation interval					
1-18	-20.87	22.54	0.81	-8.21	< 0.001
19-25	-40.08	10.22	0.75	-3.92	0.01
26-36	-6.90	3.23	0.34	-2.15	0.05
37-56	-3.48	0.92	0.44	-3.78	0.001

Table 3. 7 Average estimated breeding values and corresponding standard errors for 8-wk body weight, for the different generation intervals for selected animals within line

Gen	Av EBV HWS	Av EBV LWS
1 – 18	289.5 (±48.5)	-203.0 (±48.3)
19 – 25	521.9 (±49.6)	-401.6 (±50.1)
26 – 36	657.9 (±50.0)	-465.5 (±50.8)
37 - 56	904.7 (±50.9)	-531.3 (±52.2)

Table 3. 8 Weighted and unweight selection differentials, and selection response, for 8-wk BW by line and sex

	High weight select				Low weight select			
Gen.	Male	Female	Avg.	R[1]	Male	Female	Avg.	R
Weighted selection differential (g)								
1 – 18	130.3	58.6	94.4	53.8	-128.5	-51.7	-90.1	-47.8
19 – 25	105.6	34.7	70.1	49.1	-92.8	-28.9	-60.8	-29.8
26 – 36	151.9	27.5	89.7	52.9	-72.9	-0.3	-36.6	-20.5
37 - 56	142.5	46.3	94.4	57.6	-38.7	2.2	-18.2	-10.7
Unweighted selection differential (g)								
1 – 18	121.2	56.1	88.6	50.5	-124.8	-49.2	-87.0	-46.1
19 – 25	98.6	29.3	64.0	44.8	-87.9	-29.3	-58.6	-28.7
26 – 36	143.8	28.5	86.2	50.9	-70.8	0.38	-35.2	-18.7
37 - 56	141.5	43.7	92.5	56.4	-35.6	-16.8	-16.8	-9.9

[1]Response was obtained as the product of the heritability (Table 2) and average selection differential by interval (g/yr).

Table 3. 9 Correlated selection response, for 8-wk BW by line and generation interval

	i_{BW8}[1]	$r_{BW8,BW4}$[2]	h_{BW8}[3]	h_{BW4}[4]	$\sigma_{p_{BW4}}$[5]	CR[6]	CR/R[7]
High weight selection							
1 – 18	0.78	0.88	0.75	0.75	49.9	19.3	0.4
19 – 25	0.49	0.90	0.84	0.79	58.1	17.0	0.3
26 – 36	0.62	0.79	0.77	0.76	66.6	19.1	0.4
37 - 56	0.54	0.85	0.78	0.82	83.7	24.6	0.4
Low weight selection							
1 – 18	-0.88	0.91	0.73	0.75	39.8	-17.4	0.4
19 – 25	-0.72	0.95	0.70	0.64	27.9	-8.5	0.3
26 – 36	-0.54	0.93	0.75	0.79	20.9	-6.2	0.3
37 - 56	-0.32	0.88	0.77	0.78	19.2	-3.2	0.3

[1]selection intensity of 8-wk BW; [2]Genetic correlation between 8 and 4-wk BW; [3]accuracy of 8-wk BW; [4]accuracy of 4-wk BW; [5]phenotypic standard deviation of 4-wk BW (g); [6]Correlated response was obtained as the product of the selection intensity for 8-wk BW, the genetic correlation between the two traits, accuracies of the two traits, and the phenotypic standard deviation of 4-wk BW (g/yr); [7]efficiency of indirect selection.

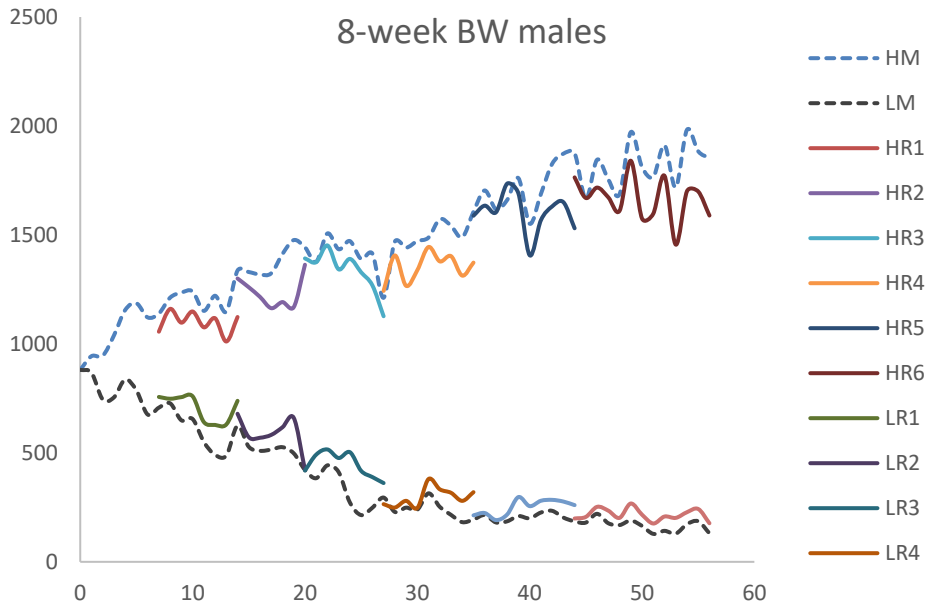

Fig. 3. 1 Mean 8-wk BW for males in the high and low weight select lines (dotted lines), and in the high and low weight relaxed lines (smooth lines)

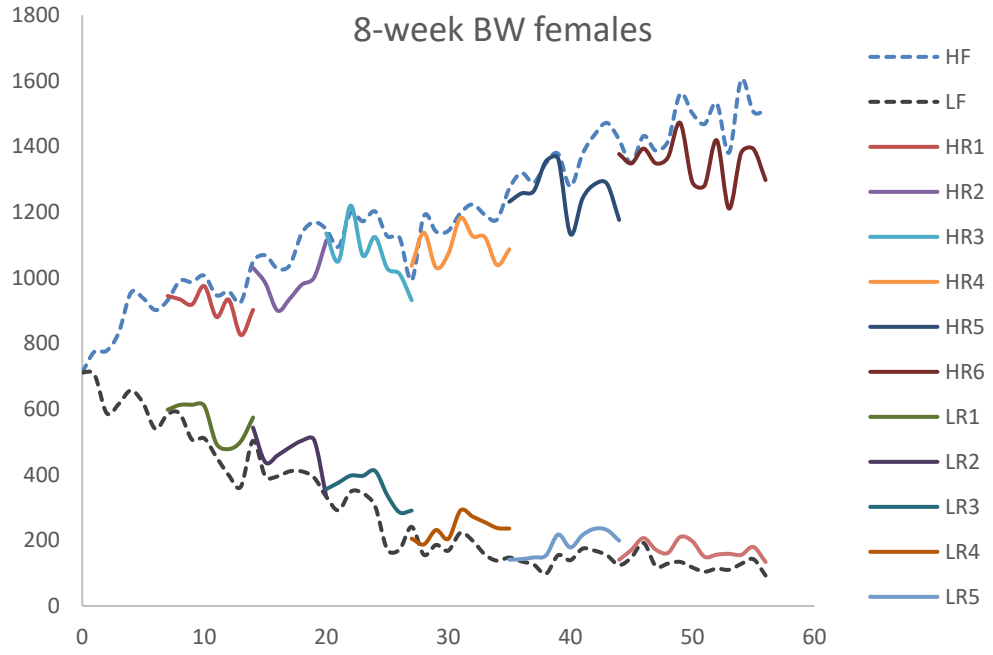

Fig. 3. 2 Mean 8-wk BW for females in the high and low weight select lines (dotted lines), and in the high and low weight relaxed lines (smooth lines)

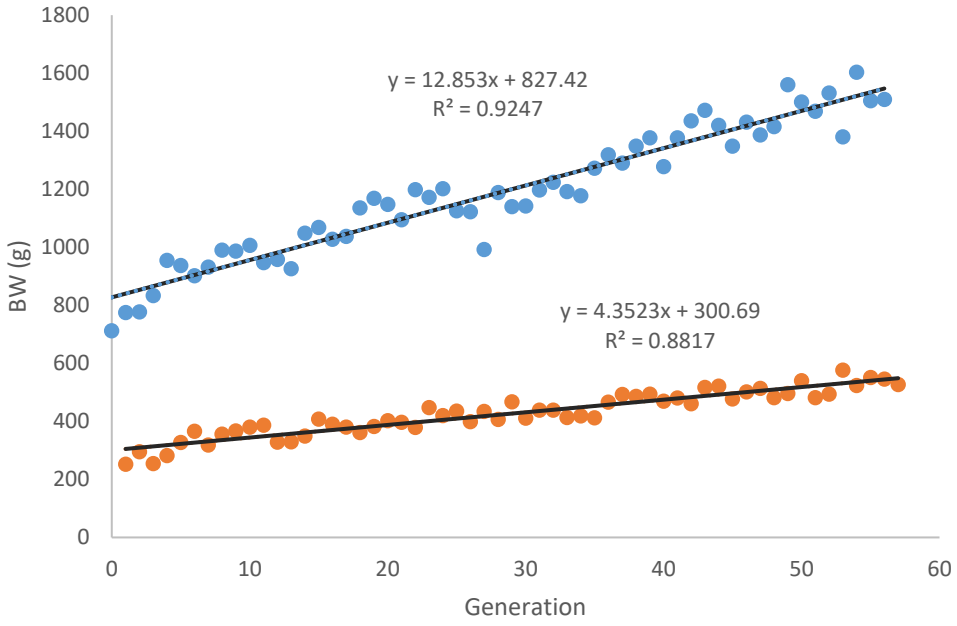

Fig. 3. 3 Regression of 8-wk or 4-wk BW on generation number in females in the HWS line across 56 generations. Regression equation for 8-wk BW was 827.4 (±16.06) + (12.85 (±0.49) x Gen), R^2 = 0.92; and for 4-wk BW was 300.7 (±10.08) + (5.35(±0.83) x Gen), R^2 = 0.88. (8-wk = blue dots; 4-wk BW = red dots.)

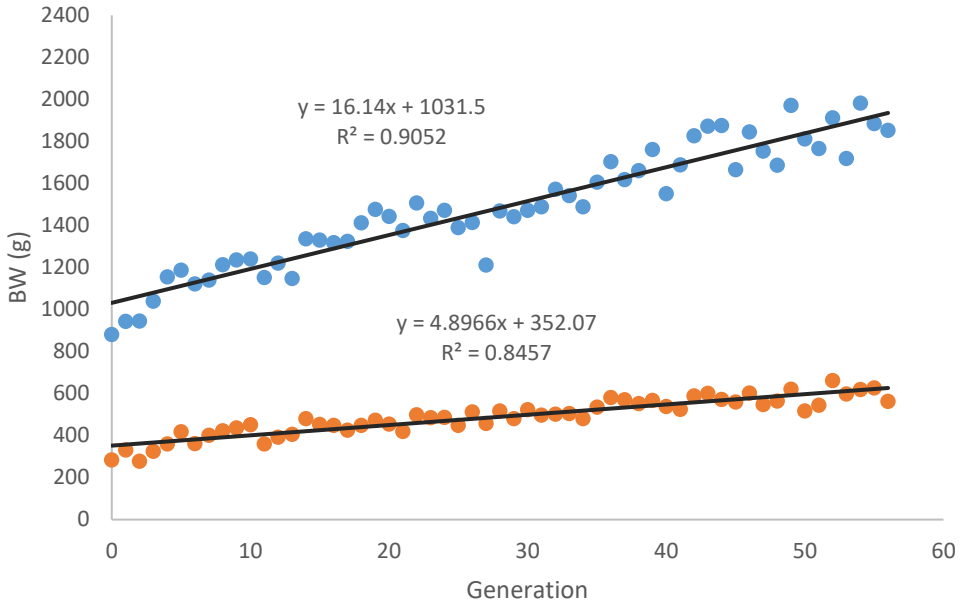

Fig. 3. 4 Regression of 8-wk or 4-wk BW on generation number in males in the HWS line across 56 generations. Regression equation for 8-wk BW was 1031.5 (±22.87) + (16.14 (±0.70) x Gen), R^2 = 0.91; and for 4-wk BW was 352.1(±12.64) + (4.89(±1.04) x Gen), R^2 = 0.87. (8-wk = blue dots; 4-wk BW = red dots.)

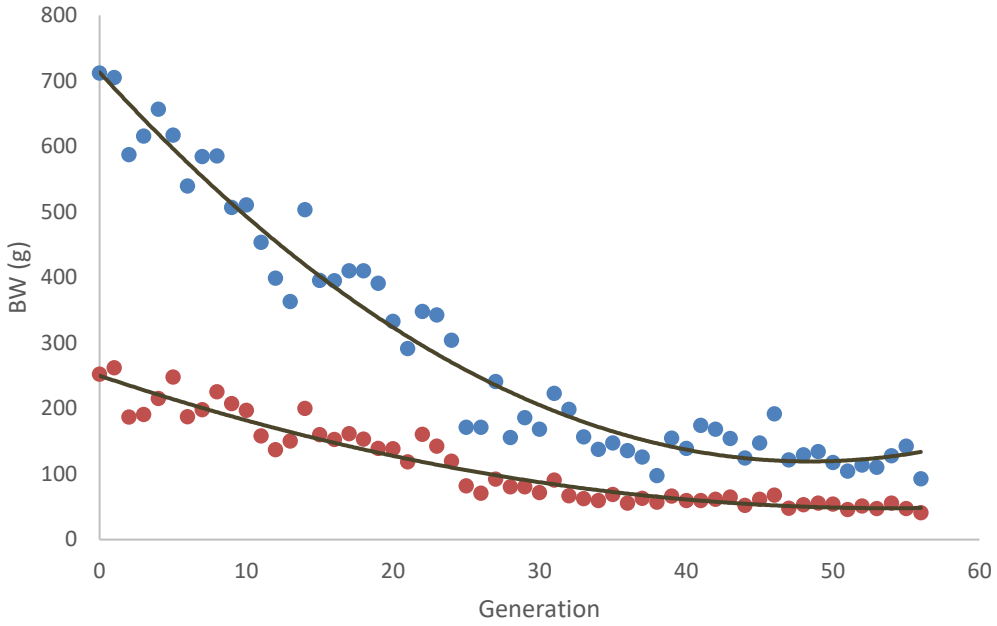

Fig. 3. 5 Regression of 8-wk or 4-wk BW on generation number in females in the LWS line across 56 generations. Regression equation for 8-wk BW was 712.9 (±15.15) + (-24.51 (±1.21) x Gen) + (0.25 (±0.02) x Gen^2), R^2 = 0.96; and for 4-wk BW was 250.0 (±6.79) + (-7.51(±0.54) x Gen) + (0.07(±0.01) x Gen^2), R^2 = 0.92. (8-wk = blue dots; 4-wk BW = red dots.)

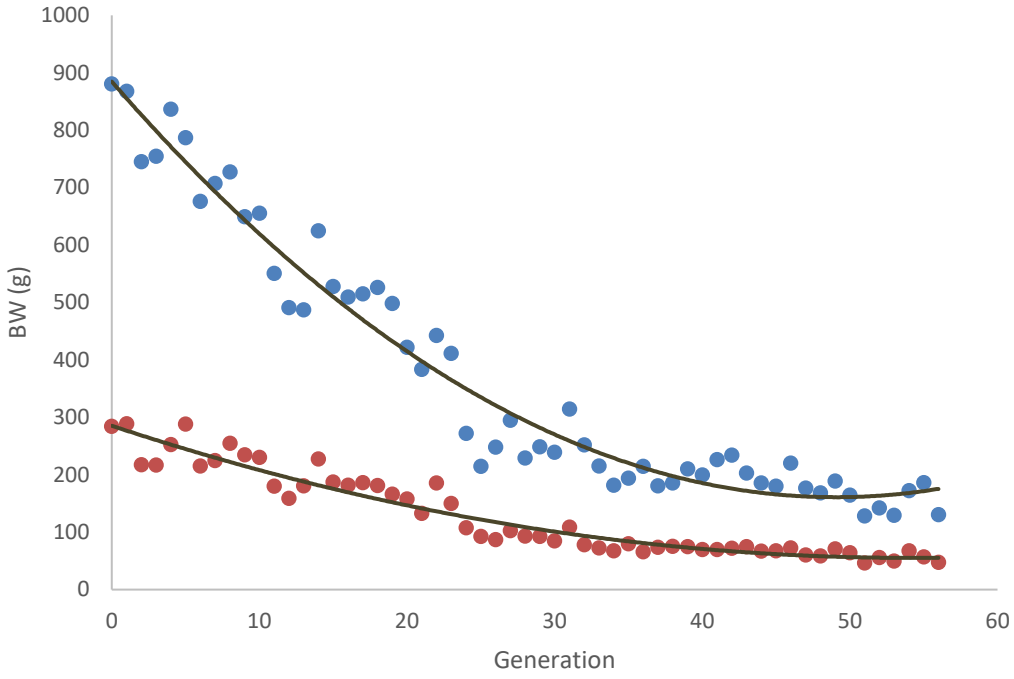

Fig. 3. 6 Regression of 8-wk or 4-wk BW on generation number in males in the LWS line across 56 generations. Regression equation for 8-wk BW was 884.6 (±18.01) + (-29.50 (±1.49) x Gen) + (0.30 (±0.03) x Gen^2), R^2 = 0.96; and for 4-wk BW was 285.3 (±7.84) + (-8.50(±0.65) x Gen) + (0.08(±0.01) x Gen^2), R^2 = 0.93. (8-wk = blue dots; 4-wk BW = red dots.)

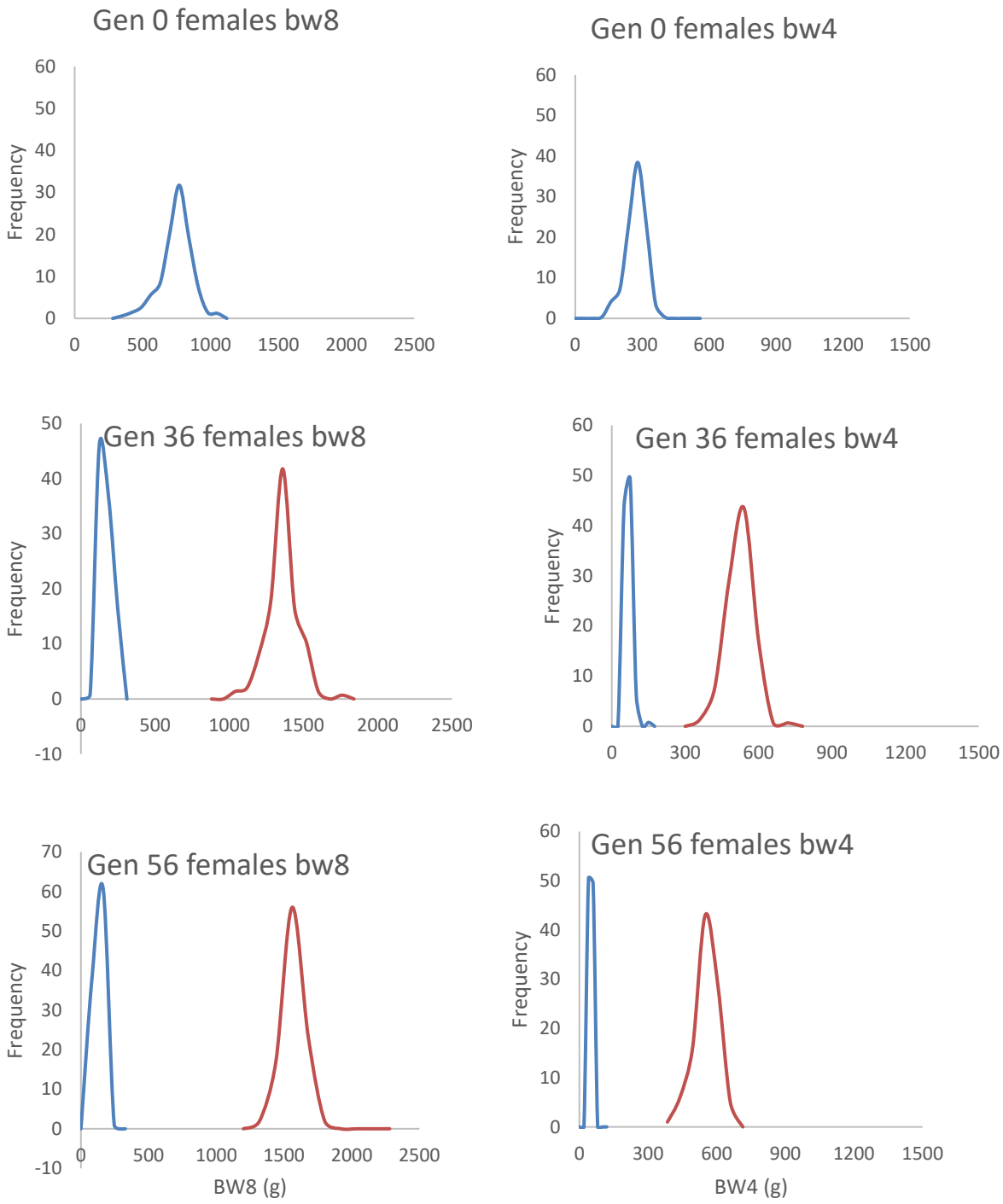

Fig. 3. 7 Frequency distributions for 8 and 4-wk BW of females in the base population, generation 36 and generation 56 of selection. Blue plot = low weight selection line; Red plot = high weight selection line

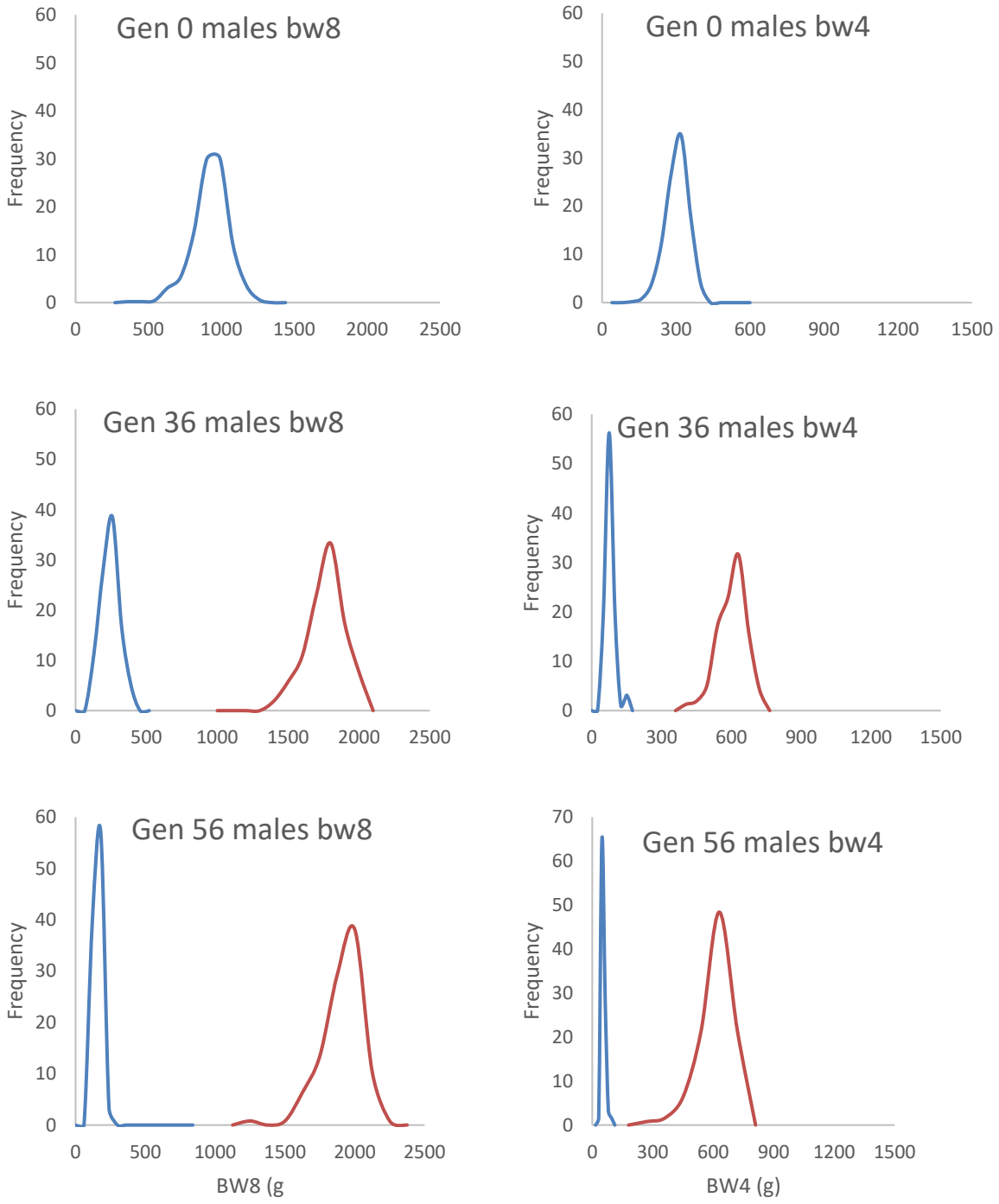

Fig. 3. 8 Frequency distributions for 8 and 4-wk BW of males in the base population, generation 36 and generation 56 of selection. Blue plot = low weight selection line; Red plot = high weight selection line

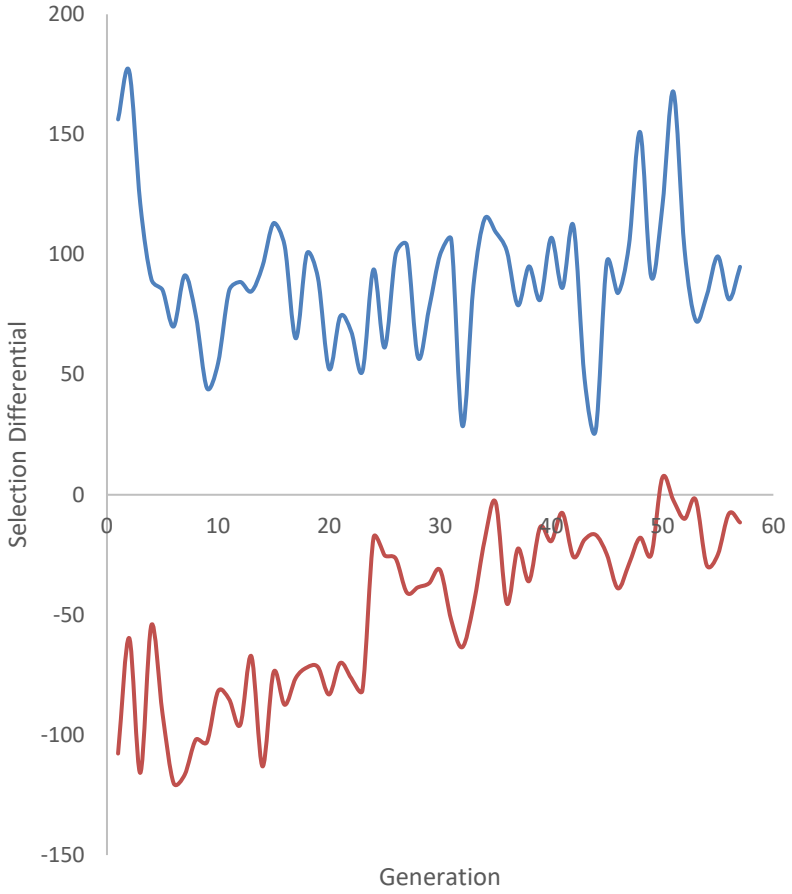

Fig. 3. 9 Weighted selection differentials in the high weight (blue line) and low weight (orange) selection lines for 8-wk BW

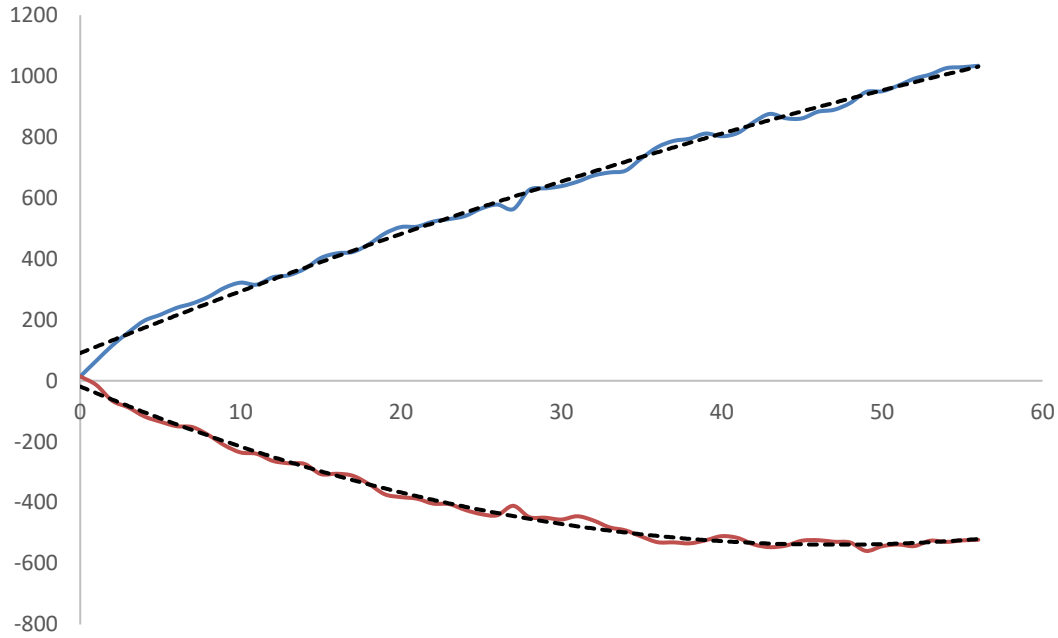

Fig. 3. 10 Regression of mean estimated breeding value (EBV) on generation number for 8-wk high weight (HWS) and low weight (LWS) selection line. Regression equation for HWS was 130.01 (±11.89) + (16.79 (±0.64) x Gen), R^2 = 0.99; and for LWS was -18.81 (±5.45) + (-22.07 (±0.45) x Gen) + (0.23 (±0.01) x Gen^2), R^2 = 0.99 . HWS = blue line and LWS = orange line.

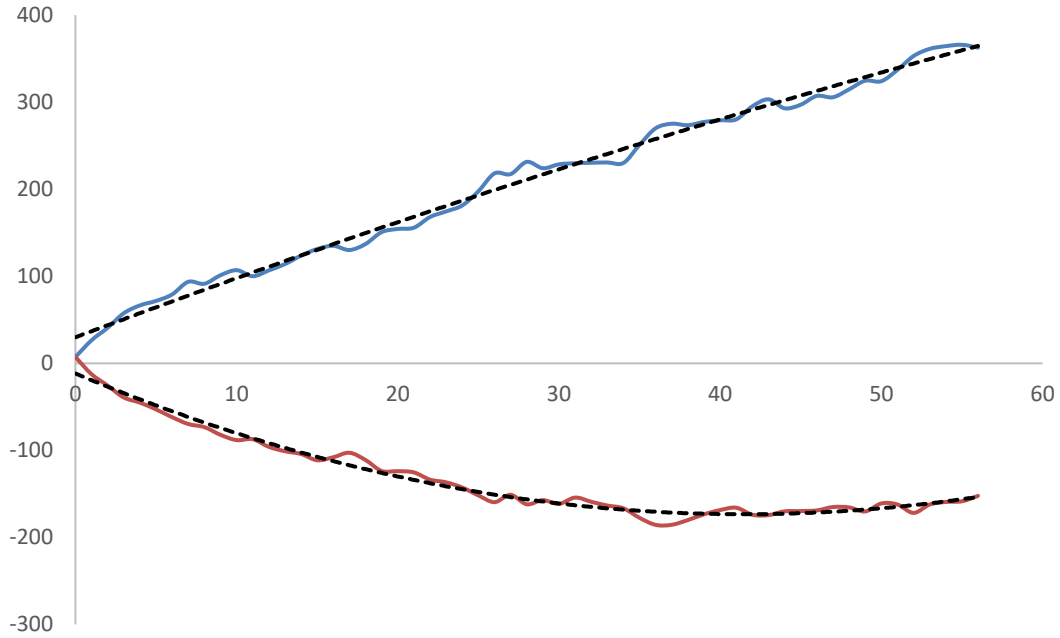

Fig. 3. 11 Regression of mean estimated breeding value (EBV) on generation number for 4-wk high weight (HWS) and low weight (LWS) selection line. Regression equation for HWS was 39.02 (±3.64) + (5.90 (±0.30) x Gen), R^2 = 0.99; and for LWS was -11.62 (±2.54) + (-7.79 (±0.21) x Gen) + (0.09 (±0.00) x Gen^2), R^2 = 0.98. HWS = blue line and LWS = orange line.

CHAPTER IV: Synthesis of Learning from Research Project

INTRODUCTION

Chickens are the most widely eaten poultry species in the world, utilized for both meat and egg production. In the United States, the value of production from broilers and eggs in 2016 was $25.9 billion and $6.5 billion, respectively, while the total numbers of broilers and eggs produced were 8.7 billion and 102 billion, respectively. This was a considerable decline from the year 2015 (USDA Poultry production and value 2016 summary report). The poultry industry is therefore a large business and poultry breeding is where it all starts.

Poultry breeding is an aspect of artificial selection, which selectively develops phenotypic traits of interest, by choosing which animals will be mated to produce offspring. To evaluate the effects of artificial selection in a long-term selection experiment, one must measure the amount of variation in the traits of interest, for instance high and low body weight, over the duration of selection. Substantial amounts of variation retained present opportunity to improve on the traits. Understanding the population structure of the developed selected lines enables one to comparatively measure the change produced by artificial selection, termed ‘response to selection’.

Chapter 2 of this thesis considers the effects of diversity and structure in the pedigree of this study from 1957 to 2016. This is followed by evaluation of performance data on the same animals, in chapter 3. The limitations of the study have also been presented.

POPULATION STRUCTURE

This study had an objective to assess the population structure and genetic diversity of the complete pedigree and to determine if tangible comparisons could be made on performance data in the two lines. The inbreeding and effective population size were computed in the two lines as a way to measure genetic diversity in the pedigree. Relatedness of individuals was then measured by quantifying gene flow, additive genetic relationships and family sizes.

RESPONSE TO SELECTION

This second study was designed to estimate additive genetic variances, and direct and correlated responses to selection on performance data. Three analytical approaches were reviewed to understand the genetic trends and response to selection: (1) phenotypic regression; (2) product of weighted selection differentials and estimated heritabilities; and (3) genetic regression.

The response to selection study revealed substantial genetic variation retained in the lines, more so in the high weight line than the low weight line which was constrained by biological factors.

LIMITATIONS AND POSSIBLE IMPROVEMENTS

To accurately measure selection, poultry producers must have accurate information and efficient record-keeping techniques. Using exploratory data analysis, some extreme outliers in the performance data had been identified. This was likely due to incorrect entry of data.

Data Entry

During the course of this long-term experiment, almost all pedigree and performance information collected was recorded on paper and by different individuals over the years. While this is a tangible method of record-keeping, it is inevitable to incorrectly enter data when one is occupied or has been working long hours. This may have been what resulted in the few extreme outlier values that were identified. Incorrect data affects the accuracy of the analysis results. Additionally, this paper recording approach is time consuming and allows for a form of redundancy as records will have to be electronically entered at a later date, for easy analysis. It also makes it difficult to retrieve animal-specific information. Additionally, some entered records would be difficult to identify, as was the case in this experiment.

A computer software package that allows one to keep track of individual animals, their ancestors, siblings, progeny and all matings, would be an ideal record keeping system. Such a system would also keep track of groups of individuals used to set up the next generation of matings. Any performance data on all individuals would be recorded. This would reduce variation caused by human error. Ideally, these records would have to be maintained in a format that is easily accessible, easily determines the relationships between any components of the population and easily inputted into a software analysis program.

Programs such as the Animal House Manager (AMAN) facilitate data entry with automatic cross referencing and extensive error checking. Data are entered through a series of queries and answers or pointing and clicking protocols. Users are able to retrieve animal-specific information from a breeding population (Silver, 1993). Programs like this provide ability to maintain control over a complex breeding program with instant access to each record, current and past.

Farm Managers

Farm managers in this study were consistent for the most part, with regards to keeping the environment unchanged. However, there were a few variations between managers with regards to format of data entry. This constraint affected ease of reading and entering the data electronically. This may have been as a result of differences in protocol interpretations. This was identified as a minor potential source of error. Data checking and validation, as was carried out in this study, is a good way to mitigate this risk.

Unbalanced Samples

Some generations had substantially bigger sample sizes, within line and sex, than others. Ideally, a second and sometimes third batch of birds was hatched in order to mitigate for risks like mortality or sickness. Larger sample sizes would be preferred because they represent smaller standard errors and therefore smaller sampling errors.

ESTABLISHING A FORMAL POULTRY BREEDING PROGRAM IN ZAMBIA USING IDEAS FROM RESEARCH AND COURSEWORK

Agriculture is an important component of Zambia's economy and is largely encompassed by crop farming. The livestock industry is currently characterized by cattle, poultry, pigs, sheep and goats. This industry is a major source of income for many Zambians and especially those living in rural areas. The Zambian poultry sector is one of the fastest growing sectors in the livestock industry with an annual growth rate of 3.3%, despite the setbacks attributed to high prices for poultry feed and limited animal breeding knowledge (Zambia Agriculture Sector Profile, 2011; Indaba Agricultural Policy Research Institute proceedings, 2013). Poultry is currently the main meat consumed in Zambia, totaling an estimated 50 per cent of total meat

consumption, followed by beef at 28 per cent, pork and fish at 16 per cent and the other meat products at six per cent. This industry contributes around 4.8 per cent to agricultural gross domestic product (GDP) and livestock value addition is estimated at 48 per cent (African farming and food processing report, 2014). This sector therefore has substantial potential to contribute towards Zambia's wealth creation and economic development.

A breeding program is likely to increase the output per animal after generations of selection. Establishing an interactive breeding program would require me to carry out an assessment of the production systems in Zambia, understand or establish livestock policies governing breeding programs, survey market information and access, and assess environmental conditions, available infrastructure and financial resources. A successful breeding program needs to be integrated and would be highly reliant on farmer involvement. The following points explain some steps I would undertake.

Understand Livestock Breeding Policies

The Zambian Government is currently in the process of drafting a livestock breeding policy for the implementation of breeding centers. In establishing my program, I would make effort to understand these guidelines. Poultry breeding programs should be viewed as long-term development programs that will subsequently increase food production and improve livelihoods of poultry farmers/breeders. This will in turn improve the food production and income of communities and the country at large. Creating awareness of these policies will enable involved parties to refute possibilities of short-term gains, as an ideal breeding policy should have a long-term vision.

Identify Socio-Economic and Cultural Values.

Identifying the roles that poultry play, in different communities will gauge the relative importance placed on poultry. This may have an impact on the breeding objective if the economic potential of poultry is not fully understood. In some Zambian communities, livestock is a symbol of identity and their economic value and improvement may not be a priority.

Assess Environment Production System and Market

Having an understanding of the environmental conditions and production systems under which chickens would be bred is important. Zambia is divided into 3 ecological zones. Therefore identifying the best environment to breed poultry is essential. In addition, having a sense of the possible markets to which the poultry products would be sold is important. I would also assess whether approved disease control programs and good feed systems are present or can easily be set up. These factors would intensify having a successful program. Part of the success of the long-term selection experiment was as a result of keeping the feed, vaccines, hatcheries, pens and management the same, through the generations. Having variations in the environmental conditions would greatly alter the breeding program.

Reports have shown that in most developing countries, breeding programs are initially developed by respective governments in partnership with donor agencies (Ahuya et al., 2005). This enables required structures to be put in place, after which cooperatives get involved in maintaining the structures and programs. If this would be the case, I would work with the government to make sure the above conditions are met.

Characterize Populations

I would carry out phenotypic characterization of poultry breeds. This would entail identifying distinct poultry breed populations and describing their internal and production

characteristics in the Zambian environment. This is essential for planning, inventorying and monitoring trends and associated risks in the breeding program. Accurate records and geographic distribution are vital in the success of a breeding program.

Define my Breeding Program Objectives

I would then set primary breeding objectives. These would elaborate the importance of improving my selected trait(s) of interest in the applicable production environment. For instance, understanding that Zambia has a tropical climate would likely place weight on traits associated with parasite resistance, physiological adaptability and survivability. Other possible objectives would be to obtain genetic parameters for traits of economic importance and construct selection indices for them. Following this, the relative economic importance of traits would be calculated, either by placing restrictions on the change in specific traits or defining the desired gain in each trait. I would place focus on the most important traits improving productivity and fitness rather than placing focus on too many traits at once. Additionally, awareness of these objectives to farmers and industry would be equally important because conflict may arise if involved parties are interested in short-term benefits. Having an idea of the duration of the program is equally essential. My breeding objectives would also be reviewed based on what has been achieved in similar production environments.

Decide on Breeding Strategy

This would entail deciding whether the characterized breeds have potential to be improved through pure or cross breeding. I would evaluate the level of performance of indigenous breeds as well as the performance and adaptability of exotic breeds in the Zambian environment. Viability of both strategies would need to be investigated. Additionally, weighing the importance of heterosis on my selected traits would be essential. Typically, in tropical

regions, crossbreeding has been adapted in other livestock species such as cattle, to make use of breed complementarity (Cunningham and Syrstad, 1987).

Identify Possible Recording and Data Processing Methods

This would entail setting up a system where accurate information on individual animals is recorded. Accurate information on the animals, their use and performance is essential for the breeding program. This may differ depending on different production systems but efforts can be made to put a uniform, simplistic and cost-effective system in place. An electronic system would be my preference.

Identify Feasible Reproductive Methods

Analyzing which reproductive method would be most feasible is important. Initially, I would use natural mating, as artificial insemination in chickens is not the norm. However, artificial insemination may be of value as a strategy to mitigate some problems (e.g., competition among roosters) and to overcome other obstacles (e.g., introduction of novel genetic types or lines). In other poultry (Turkey) and livestock species, artificial insemination has been widely used. Still, this may not be as feasible in Zambia because of costs of transportation and storage of semen (e.g., liquid nitrogen).

Carry Out Selection, Performance Testing and Mating

For a start-up program, I would recommend phenotypic selection as a preferred approach because performance records on all individuals would be collected. Mass selection is a good method to screen animals for the initial nucleus population. Because phenotypes for a trait are assumed to be related to breeding values for that trait, they are good indicators of underlying breeding values. High or low heritabilities then give an indication of the effectiveness of phenotypic selection. Alternatively, if resources and methods allow, selection can be done using

information on individuals and their relatives (complete pedigree). The accuracy of selection increases with more available information. I would then compare heritability estimates for each generation of selection. Typically for poultry, each generation interval would be one year.

I would then carry out performance testing so as to have a systematic measurement of records for the particular traits of interest. Following that, I would put in place a mating system to determine which selected males are mated to which selected females, and in what proportions. Because of the effects of inbreeding depression, I would keep inbreeding at a minimum.

Genetic Analyses and Estimation of Breeding Values

Genetic improvement for a breeding program can be evaluated by analyzing the amount of variation. Tropical breeds may be likely to have substantial variation within breeds and high estimates of heritabilities because these breeds have been subjected to very mild artificial selection pressures (Rege et al., 1992; Mpofu and Rege, 2002).

I would measure genetic improvement by regressing phenotypic performance on generation number. This would give an indication of the amount of variation in my population. If resources allow, I would also obtain estimated breeding values by fitting appropriate animal models and getting best linear unbiased prediction (**BLUP**) solutions. This method separates genetic and environmental effects, as was done in the long-term selection experiment.

DNA analyses and marker information may be very useful for a program as they would predict breeding values for new-born animals and this would save on time. However, this would be impractical for a start-up program in Zambia because of the complexity of the method and available resources.

Monitoring Genetic Progress

I believe this is a significant part of a breeding program as it analyses the impact of the program. Inputs and outputs of products would be economically assessed. Monitoring would also give opportunity to make improvements in the breeding program. This would be essential for collaborations and future support of the program.

I believe setting up a breeding program entails considerable research on the targeted areas, species and resources. It would also require carrying out some scientific research and practical experiments to develop appropriate methods to set up the program. Farmer and industry involvement would equally enrich the breeding program. Awareness programs to all involved parties is essential for a successful program, especially for the end-user. Additionally, keeping up with trends of breeding programs in other developed places, such as molecular genetics and marker assisted selection, would help advance the program.

CONCLUSION

Long-term selection experiments provide methods to study the genetics of traits and influences of artificial selection. Modern approaches like the BLUP give indications of genetic and environmental variation retained. This provides useful information but more work is needed to be done at a molecular level to understand the drivers of variation and constraints thereof. This long-term selection experiment has also provided clear guidelines on how to set up a poultry breeding program. This is a significant contribution to developing countries where agriculture has a growing potential.

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