

# Genetic diversity and population structure in lines of chickens divergently selected for high and low 8-week body weight

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**ABSTRACT** A long-term selection experiment for high or low 8-wk BW in White Plymouth Rock chickens was conducted to study effects of selection on BW and correlated characters. Two lines [high (HWS), low (LWS) weight] were established and have undergone 48 generations of selection. The lines were managed to curtail inbreeding and to maintain similar population structures; such is necessary for equitable comparison of selection response between lines. Our objective was to test the success of that breeding strategy by characterizing genetic diversity and inbreeding in these lines. A pedigree of 5,998 individuals was assembled, with 68 founders, 2,962 HWS chickens, and 2,968 LWS chickens. Inbreeding coefficients (F) were calculated for each line. Maximum F was 0.53 and 0.61, mean F was 0.26 (SD 0.15) and 0.30 (SD 0.17), and change in F was 1.3 and 1.6% per generation in LWS and HWS lines, respectively. The effective population size was 38.3 in LWS and 32.1 in HWS lines. The effective number of

founders was 15.7 in both lines, and the effective number of ancestors was 17.5 and 15.5 in LWS and HWS lines, respectively. Thirty ancestors accounted for 90% of the genetic makeup of both lines. Seven male and eight female founders still contributed to both lines at generation 48, although some contributed more to one line than the other. Family sizes were similar for males and females of each line, with males having larger family sizes with greater variance. Accumulated inbreeding was high and effective population size was low, as expected in closed lines. Effective number of founders was relatively low compared with actual number of founders, indicating some contributed more than others to the last generation. Family size statistics indicated that fewer males than females were used, leading to the observed levels of inbreeding. Given their similarity in genetic diversity and family size, it can be concluded that breeding decisions throughout the project resulted in similar population structures in the lines.

**Key words:** chicken, divergent selection, genetic diversity, population structure

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## INTRODUCTION

A long-term selection experiment for high and low 8-wk BW in chickens began at Virginia Tech in 1957 and continues to this day. It was conducted to study the effects of selection in meat-type chickens on BW and correlated traits in a closed population (Siegel, 1962). After 46 generations of selection, the high and low weight lines differed more than 8-fold in their 8-wk BW (Le Rouzic et al., 2007). That divergence is clearly delineated in Figure 1. Over 150 publications have been based on this experiment (Taylor and Ashwell, 2009), although genetic diversity and population structure have not been studied in depth in these lines.

As defined by Merriam-Webster (2008), population dynamics is the study of the “pattern or process of

change, growth, or activity” within a population. Patterns of long-term changes in numbers of individuals and their selection characterize a breeding population. With intense artificial selection, individuals and families with desirable attributes are favored; as a consequence, their genetic contribution to future generations is enhanced, influencing effective population size and genetic diversity in the population. With divergently selected lines, as with the high and low weight lines, mapping the process by which genetic change was achieved is central. If dissimilar, the efficacy of line comparisons may be questionable.

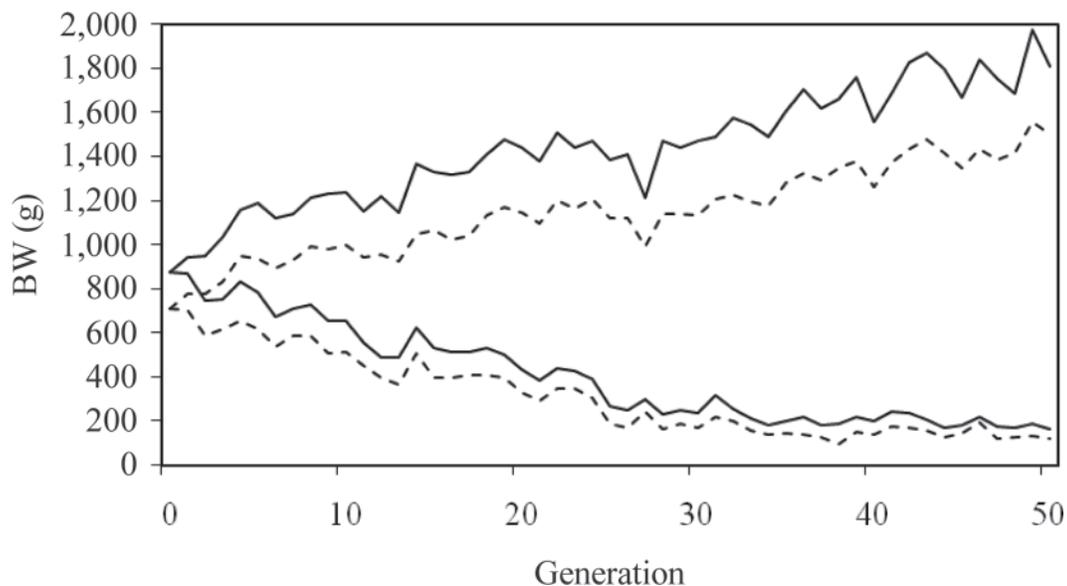
The objective of this study was to quantify genetic diversity and population structure in this long-term selection experiment. Upon selection of the lines, there was a conscious attempt to keep inbreeding at low levels and to maintain similar population structure. Therefore, the current study attempts to test whether this was achieved. Several measures of genetic diversity and population structure were used to explore the dynamics of the lines. Inbreeding and effective population size

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**Figure 1.** Response to selection after 48 generations of directional selection. The high weight selection line is represented by the lines at the top of the figure, and the low weight selection line is represented by the lines at the bottom of the figure. Males are represented by solid lines and females by dashed lines.

were calculated because these are measures of genetic diversity in a population, and high levels of inbreeding have deleterious effects on chicken populations (e.g., Sewalem et al., 1999; Szwaczkowski et al., 2003; König et al., 2010). Relatedness between individuals in the pedigree, which offers a quantitative way to trace relationships, was studied through gene flow and additive relationship coefficients.

## MATERIALS AND METHODS

### Animal Care

Since 1977, the procedures involving animals in the experiment were carried out in accordance with protocols approved by the Institutional Animal Care and Use Committee at Virginia Tech. Before that time, the university lacked stated animal care protocols, although animals were treated in a manner consistent with the currently approved protocols.

### Description of Data

The lines were founded from a population of 68 chickens (13 male, 55 female), which originated from crosses

of 7 inbred lines of White Plymouth Rocks hatched in 1956 (Siegel, 1962). These chickens were the only ancestors common to both lines, serving as the founders to both lines. Offspring of these chickens were selected for high and low 8-wk BW, respectively, to establish the high weight (**HWS**) and low weight (**LWS**) selection lines. A total of 8 sires and 48 dams were selected to establish each line as the parental generation ( $P_0$ ) in 1957. The numbers of chickens used as parents across generations are shown in Table 1.

For each generation, selection was based on high or low 8-wk BW, depending on the line. As a means to constrain inbreeding, efforts were made to restrict the size of sire and dam families. This degree of restriction varied among generations, and efforts were made for representation of sire and dam families in subsequent generations. This did not preclude the deletion of sire or dam families that did not exceed the point of truncation set for BW for each line.

At generation 18, the amount of feed offered to the HWS line was restricted to avoid reproductive problems (Dunnington and Siegel, 1996). However, selection decisions were still based on weight at 8 wk before feed restriction. Hatch dates were the first and third Tuesday in March every year. Husbandry conditions (e.g., hous-

**Table 1.** Number of male and female parents used each generation in each line of selection

Generation (yr)	Low weight		High weight	
	Male	Female	Male	Female
0 (1957)	8	48	8	48
1 (1958)	7	40	8	34
5 (1962)	12	61	12	73
26 (1983)	14	45	14	57
48 (2005)	14	43	14	40

ing, lighting regimen, feed) were unchanged throughout the experiment to avoid confounding of generation (selection) and year (environment) effects.

Data used spanned 50 discrete generations, beginning with the common ancestors (founders) from the 1956 hatch, the establishment of the 2 lines from the 1957 hatch (generation 0,  $P_0$ ), and continuing through the 2005 hatch (generation 48,  $S_{48}$ ). This represented 5,998 chickens: the 68 founders plus 2,962 LWS and 2,968 HWS chickens. Therefore, there was a total of 48 discrete generations of selection within each line. Data included animal, sire, and dam identification numbers, sex, hatch year (generation), and selection line. Pedigree information was complete for each chicken beginning with the founding generation in common to both lines. Only chickens selected as parents of the subsequent generation were recorded in the pedigree. Parentage on 4 chickens from HWS in  $S_{22}$  (1979) was unknown. These chickens and their descendents were removed from the analysis because their information was incomplete.

## Inbreeding

Inbreeding is a measure of genetic diversity, quantifying the probability that 2 genes in an individual are identical by descent (Wright, 1922). To explore genetic diversity within the lines, individual inbreeding coefficients were calculated separately for each line with the R Pedigree package (Coster, 2008; R Development Core Team, 2008) using the algorithm described by Meuwissen and Luo (1992). The founders in common to both lines were considered the base population. Mean inbreeding was calculated for each generation and line to investigate trends and accumulated inbreeding over the generations of selection. Changes in inbreeding over time were calculated as

$$\Delta F_i = \frac{F_i - F_{i-1}}{1 - F_{i-1}},$$

where  $F_i$  was the mean inbreeding coefficient in generation  $i$ . The rate of inbreeding between year  $i$  and  $j$  ( $\Delta F_i - j$ ) was obtained by taking the average of annual rates (Falconer and Mackay, 1992). This calculation reflects changes in inbreeding relative to remaining heterozygosity.

## Effective Population Size

The effective population size ( $N_e$ ) is the number of individuals that would account for the observed inbreeding rates in a population if it were randomly mated. This parameter reflects the rate of loss of genetic diversity in a population, as losses of heterozygosity (increases in inbreeding) are inversely related to  $N_e$  (Falconer and Mackay, 1992). The  $N_e$  was calculated for each line as

$$N_e = \frac{1}{2 \times \Delta F},$$

where  $\Delta F$  is the generational change in mean inbreeding. The population structure (i.e., complete pedigree information, no migration, discrete generations) allowed for this method of calculating  $N_e$ .

## Effective Number of Founders and Ancestors

The effective number of founders ( $f_e$ ) is the number of individuals that would be expected to produce the observed genetic diversity in the population if all of these individuals had contributed equally to the population (Lacy, 1989). This parameter was calculated separately for each line (from the founding generation in common to both lines) as

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

where  $q_i$  is the proportion of genes in the current population contributed by the  $i$ th founder, and  $n$  is the total number of founders. If each founder had the same expected contribution to the population, then the  $f_e$  would equal the actual number of founders.

The  $f_e$  does not account for genetic drift that may occur and ignores potential bottlenecks in the pedigree (Boichard et al., 1997). To account for them, the effective number of ancestors ( $f_a$ ) was calculated for each line as

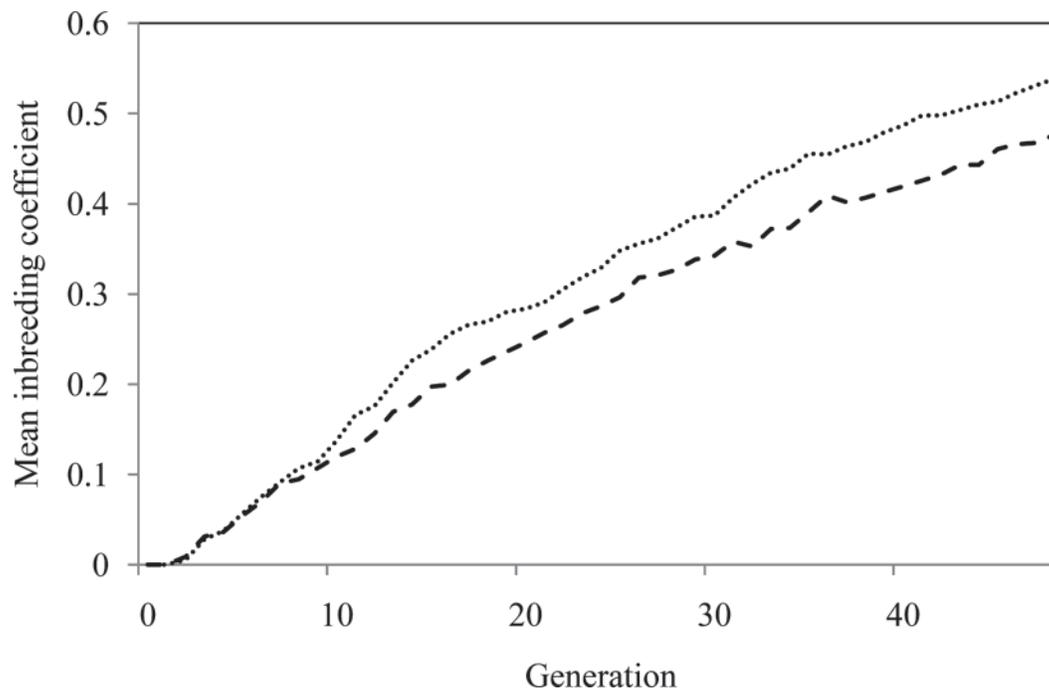
$$f_a = \frac{1}{\sum_{i=1}^n p_i^2},$$

where  $p_i$  is the marginal genetic contribution of the  $i$ th ancestor, and  $n$  is the total number of ancestors (Boichard et al., 1997). An ancestor may or may not be a founder. The marginal genetic contribution also serves as an indication of which ancestors were most influential in terms of maintaining their genetics in the pedigrees.

## Gene Flow

A gene flow approach was used to quantify the genetic contribution of founders to  $S_{48}$ . The method proposed by Kennedy and Trus (1993) was used to compute the proportional contribution of male and female founders to chickens in  $S_{48}$ .

To find the proportional contributions of ancestors, the matrix multiplication  $\mathbf{X}'\mathbf{Z}\mathbf{T}\mathbf{Q}$  was carried out, where  $\mathbf{X}$  and  $\mathbf{Z}$  were incidence matrices relating to se-



**Figure 2.** Mean inbreeding coefficient by generation for the 2 selection lines. The low weight line is represented by the dashed line, and the high weight line is represented by the dotted line.

lection line and chicken, respectively. Therefore, the dimensions of  $\mathbf{X}'\mathbf{Z}$  were  $2 \times 5,998$ , with the 2 rows relating to the selection line, and the 5,998 columns relating to each chicken in the pedigree (including founders). The  $\mathbf{Q}$  matrix was an incidence matrix relating to the founders, with 5,998 columns and 13 or 55 rows relating to male or female founders, respectively. The matrix  $\mathbf{T}$  was a lower triangular matrix that traced the flow of genes from one generation to the next. The sum of the elements of the rows in  $\mathbf{X}'\mathbf{Z}\mathbf{T}\mathbf{Q}$  was the total number of birds in each line. Each cell in the matrix represented the contribution of each founder to the LWS or HWS. The proportion of genes contributed by the founders to each line was obtained by dividing each element of  $\mathbf{X}'\mathbf{Z}\mathbf{T}\mathbf{Q}$  by the total number of birds in each line (or the sum of the elements of each row). To account for differences in founder contributions over the selection horizon, the number of male and female founders that contributed genetically to each generation and each selection line was counted. Only founders that contributed at least 1% to a given generation were considered.

### **Numerator Relationships**

An alternative way to describe relationships among individuals in a pedigree is through the numerator relationship matrix (Wright, 1922). This matrix was calculated using the pedigree for all chickens (LWS and HWS lines simultaneously). From this matrix, numerator relationship coefficients of the founding chickens with all other chickens were extracted. The number of founders related to both the HWS and LWS lines in the

last generation ( $S_{48}$ ), along with their mean relationship to the last generation, was calculated to quantify genetic contributions of the founders.

### **Family Sizes**

Mean, maximum, and variance of family sizes (the number of offspring of sires and dams) were calculated separately for each sex within each line because these are indicative of population dynamics and breeding decisions.

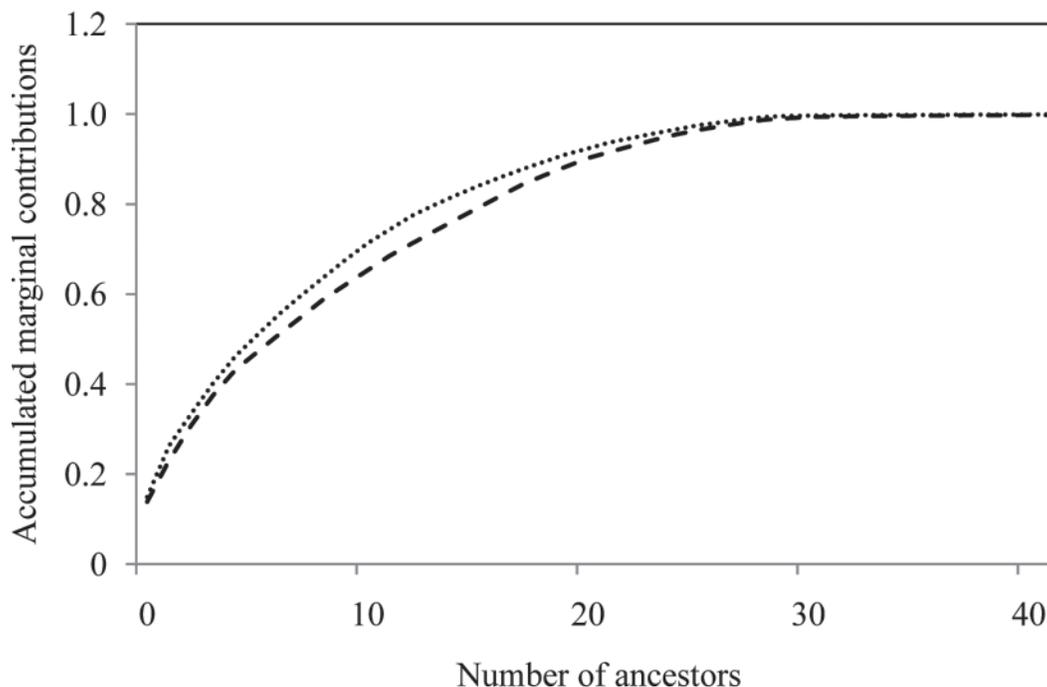
## **RESULTS**

### **Inbreeding**

Inbreeding statistics are shown in Figure 2 and Table 2. Mean inbreeding coefficients increased linearly from  $S_1$  to  $S_{48}$  in both lines. Whereas mean inbreeding coefficient at  $S_{48}$  (year 2005) was numerically higher in the HWS ( $0.54 \pm 0.02$ ) than in LWS ( $0.48 \pm 0.01$ ) line, the rates of change in inbreeding over generations were similar and low (approximately 1% per generation).

### **Effective Population Size**

Effective population size in the LWS and HWS lines was 38.3 and 32.1, respectively (Table 2), at  $S_{48}$ . Due to the similar rates of change in inbreeding,  $N_e$  for both lines was similar. The actual number of animals in  $S_{48}$  was 57 and 54 chickens in the LWS and HWS lines, respectively.



**Figure 3.** Accumulated marginal contribution of ancestors to the last selection generation ( $S_{48}$ ). The low line is represented by the dashed line, and the high line is represented by the dotted line.

### Effective Number of Founders and Ancestors

The effective number of founders ( $f_e$ ) was 15.7 in  $S_{48}$  in both lines. The effective number of ancestors ( $f_a$ ) was 17.5 and 15.5 in the LWS and HWS lines, respectively (Table 2). The most influential ancestor in the LWS line had a calculated marginal genetic contribution of 13.9%; in HWS, that contribution was 14.9%. The rankings of influential ancestors were different in each line. As shown in Figure 3, fewer than 30 ancestors account for the cumulative marginal contribution of ancestors in the pedigree over all generations of selection.

### Gene Flow

The proportional contribution of male founders to  $S_{48}$  is shown in Figure 4, and the number of contributing founders to each generation is shown in Table 3. The number of founders contributing to each generation did not change from  $S_3$  (1960, LWS) and  $S_4$  (1961,

HWS) until  $S_{48}$  (2005). Of the 13 males used to found the lines, 10 (LWS) and 8 (HWS) chickens made genetic contributions of at least 1% to  $S_{48}$ . More male founders contributed to the LWS than the HWS line (Figure 4). Among females, the persistence of contribution of founders was less than in males: 20 (LWS) and 21 (HWS) of the original 48 females.

Some founders contributed to both lines. In  $P_0$ , 8 male and 16 female founders were common across lines. The genetic contribution of 7 of these males, and 8 of these females, continued to both lines at  $S_{48}$ .

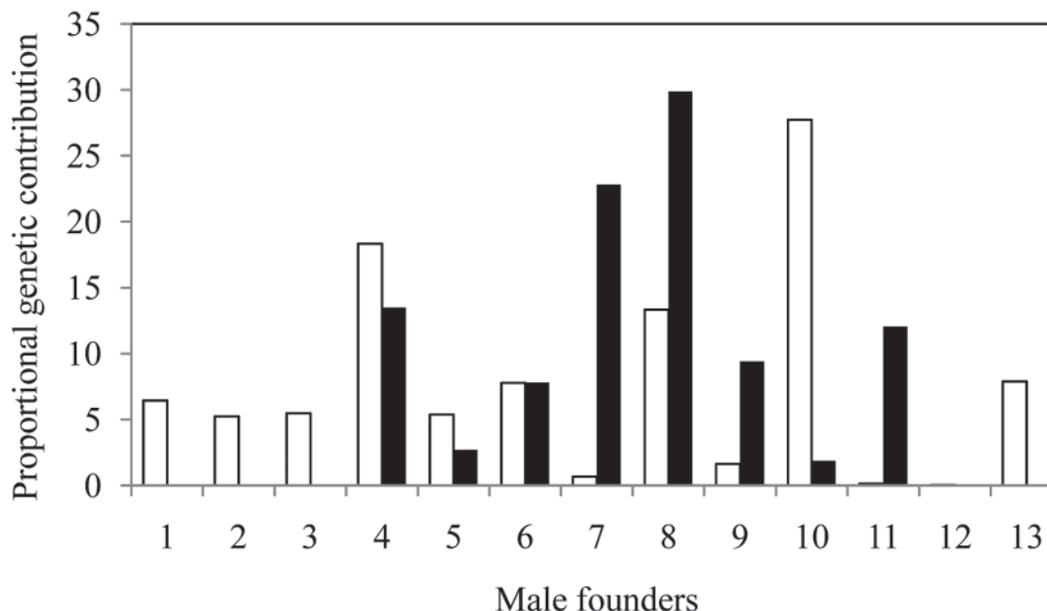
### Numerator Relationships

Using a numerator relationship matrix approach, the contribution of the same 7 male and 8 female founders detected earlier to both lines in  $S_{48}$  was corroborated. The average of the numerator relationship coefficients of these founders to  $S_{48}$  chickens was 4.1% (LWS) and 4.2% (HWS). The average of the numerator relationship coefficients of all founders to chickens in  $S_{48}$  was

**Table 2.** Summary statistics for genetic parameters in the 2 lines of selection at generation 48

Parameter <sup>1</sup>	Low weight	High weight
No.	2,962	2,968
Maximum F	0.53	0.61
Mean F (SD)	0.26 (0.15)	0.30 (0.17)
Change in F per generation (%)	1.3	1.6
$N_e$	38.3	32.1
$f_e$	15.7	15.7
$f_a$	17.5	15.5

<sup>1</sup>F = inbreeding;  $N_e$  = effective population size;  $f_e$  = effective number of founders;  $f_a$  = effective number of ancestors.



**Figure 4.** The proportional contribution of male founders to chickens in the last generation of selection ( $S_{48}$ ). White bars represent low weight selection line, and black bars represent the high weight selection line.

1.5% in both lines. The chickens most related to the LWS and HWS had a numerator relationship coefficient with  $S_{48}$  of 13.9 and 15.1%, respectively.

### Family Sizes

Family size statistics are detailed in Table 4. Family sizes of males were larger than females. Means and variances of family sizes were similar in both lines for each sex.

## DISCUSSION

By  $S_{48}$ , inbreeding in both lines was moderately high (Table 2, Figure 2). Further increases in inbreeding could compromise fitness in the lines because inbreeding depression influences a wide array of fitness and performance traits in meat and egg type chickens (e.g., Sewalem et al., 1999; Szwaczkowski et al., 2003; König et al., 2010). Chicken breeding is characterized by intense selection and short generation intervals, which can lead to rapid increases in inbreeding, unless population sizes are large. In the current study, where intensive

single trait selection was practiced within a line, genetic diversity was invariably lost; high levels of inbreeding were to be expected in such closed lines. The effort to avoid matings among half sib or closer relatives and to avoid selection of particular sire or dam families undoubtedly reduced, yet could not avoid, inbreeding. In future research, it will be of interest to analyze the effects of inbreeding on fitness and other phenotypic measures in these lines.

Inbreeding rate, rather than the absolute level of inbreeding, is often of greater interest because it represents reductions in genetic diversity (heterozygosity) within a population and thus may limit future selection response and reduce fitness. Young and Seykora (1996) reported that although estimates of inbreeding coefficients were downward biased when more recent years were defined as the base, the rate of change in inbreeding was not significantly affected. In our experiment, the pedigree information was complete and the base population was defined as the founders. Therefore, estimates of inbreeding were not expected to be downward biased. The base population (founders) was assumed to be unrelated and non-inbred for computing

**Table 3.** Number of male and female founders still contributing to the population over generations calculated using probabilities of gene origin

Generation (yr)	Low weight		High weight	
	Male	Female	Male	Female
0 (1957)	13	38	9	35
1 (1958)	12	28	8	26
2 (1959)	11	22	8	23
3 (1960)	11	21	8	23
4 (1961)	11	21	8	22
48 (2005)	10	20	8	21

**Table 4.** Maximum, mean, and variance in family sizes by line and sex across all generations

Sex	Line	Maximum	Mean	Variance
Male	High	21	5.0	10.3
	Low	16	5.0	7.0
Female	High	10	2.2	2.3
	Low	7	2.0	1.2

purposes given that they originated from crosses of 7 inbred lines.

Whereas inbreeding coefficients were relatively high and increasing, the rate of change of inbreeding was relatively low and nearly constant across generations (Figure 2). Rates of inbreeding ranging from 0.13 to 1.5% have been reported in chickens (König et al., 2010), and a 1% increase in inbreeding per generation has been considered generally tolerable for commercial poultry production (Morris and Pollott, 1997). Avoidance of family matings in the selection lines was successful in avoiding high rates of change of inbreeding, which suggests that sufficient heterozygosity remains in the population to allow continued selection response (Figure 1).

Effective population size is inversely proportional to the rate of inbreeding. It is an estimate of genetic drift when populations are large and is valid after sufficient time has elapsed since the foundation of a population, as in the current study (Charlesworth, 2009). The  $N_e$  can also characterize the effect of management and selection practices on genetic variation (Caballero, 1994). Boichard et al. (1997) found, by simulation, that when pedigree information was complete,  $N_e$  was similar to its theoretically expected value; when pedigree information was incomplete, the  $N_e$  was upward biased. Pedigree information was complete in these data. Therefore, the estimated  $N_e$  is expected to be an accurate approximation to its true value.

The similarity between  $N_e$  and actual numbers of chickens in  $S_{48}$  (approximately 60% of the actual population in  $S_{48}$ ) is noteworthy given amounts of inbreeding and the intensive selection practiced in the lines. Although this may partly reflect pedigree recording (animals that were not selected were not recorded in the pedigree, thus overestimating  $N_e$  in  $S_{48}$ ), the result was nonetheless remarkable.

Probabilities of gene origin offer a different way to study the evolution of genetic diversity and population dynamics. As suggested by Lacy (1989), there is no clear relationship between  $N_e$  and parameters derived from probabilities of gene origin. The relationship between inbreeding and genetic variation is complicated in these lines because inbreeding is theoretically different for neutral and selected loci (Verrier et al., 1991). Studying probabilities of gene origin removes the concern of biases due to inbreeding from the analysis and allows the genetic contributions of founders to the current population to be better quantified. This method allows for verification of how the gene pool, and thus

genetic diversity, has been maintained (or not) over generations of selection (Boichard et al., 1997).

The difference between the effective (16) and actual (68) number of founders indicates that their genetic contribution to  $S_{48}$  differed. However, most male founders (10 LWS and 8 HWS out of 13) continued to contribute genetically throughout the selection profile to  $S_{48}$  (Table 3), although to different extents in each line (Figure 4). A shortcoming of using  $f_e$  as a diversity measure is that it does not account for bottlenecks and is upwardly biased under intensive selection (Boichard et al., 1997). Although  $f_e$  accounts for selection rate and variation in family size, it does not account for the probability of gene loss. The effective number of ancestors ( $f_a$ ) may be a more appropriate measure for describing a population that has gone through bottlenecks. This parameter gives the number of ancestors (founders or otherwise) necessary to explain the diversity levels of the population. The  $f_e$  and  $f_a$  of the LWS and HWS lines were similar (Table 2), indicating low bias in  $f_e$ . In establishing the 2 lines, the “tails” were selected to produce the respective lines, with few chickens selected from near the mean of the population. This procedure, although more extreme for males than females, does not appear to have strongly limited genetic diversity in the lines. The accumulated marginal contribution of ancestors (Figure 3) is indicative of the influence of ancestors in the population. Of these, few were needed to explain most of the ancestral contribution, consistent with other results regarding founders.

Both lines originated from the same population, and it therefore was expected that they would share common genes. In  $S_{48}$ , 7 male and 8 female founders contributed to both lines, although to different extents (Figure 4). For males, more founders contributed to LWS than to HWS, and except for 1 bird, the contributions were not equivalent for each line. Similar results were observed for females (results not shown), with some birds contributing primarily to one line and not the other. This differential contribution of founders to the lines likely corresponds with differences in genetic potential for growth. The numerator relationship matrix quantified relatedness between birds in the pedigree. A similar number of chickens were found to be related to  $S_{48}$  based on numerator relationship coefficients and gene flow approaches. The founders most related to the LWS and HWS lines also had similar relationship percentages using both approaches, and the rankings of the most related individuals were the same up to the 4th most related chicken within each line. The average nu-

erator relationship coefficient of founders to chickens in  $S_{48}$  was low as expected because 48 nonoverlapping generations of selection had taken place. The average relatedness did not change over generations, indicating that founder contributions were steady, corroborating gene flow results.

The size of families is highly indicative of mating decisions. Large variances in family sizes can lead to higher inbreeding because some animals are used more widely than others, increasing the probabilities of matings between related individuals. This also leads to decreased  $N_e$ . Family size statistics (Table 4) indicate that males were used more widely than females in both lines. This was due to the use of AI for breeding. The mean family sizes were similar in both lines for each sex, reflecting success in avoiding predominance of certain families.

Response to selection in this experiment was high (Figure 1), and divergence in 8-wk BW was certainly achieved. This is not unique; strong genetic gains have been observed for other traits in selection experiments (Miller, 2006). Body weight is a polygenic trait with moderate to high heritability. Had selection been based on a different trait, for instance one of lower heritability, response may have reached a plateau or been slower. In the LWS and HWS lines, the pattern of response has been characterized by waves (Dunnington and Siegel, 1996) in which substantial changes were observed following generations with little change. This cyclicity in selection response may be due to spontaneous backward and forward mutations that occurred periodically in the lines, as well as other factors interacting at the molecular level.

On a molecular level, Johansson et al. (2010) found that the lines were fixed for alternate alleles in 50 regions of the genome and that there were more polymorphic alleles in LWS than HWS. Johansson et al. (2010) reported that the number of fixed SNP increased by 75% from generation 40 to 50 in each line. Those results indicate wide divergence between the lines and loss of genetic diversity within each line, in accordance to the current study. There are several examples of the lines diverging for other traits that have been studied. Included are gene networks (Le Rouzic et al., 2007), developmental gene expression (Mott et al., 2008), differences in proviral integrations (higher in LWS than HWS line; Ka et al., 2009a), differentially expressed genes (Ka et al., 2009b), and loss of function of genes (Rubin et al., 2010).

The similarity between the 2 lines in all measures of population dynamics investigated is important. This implies that the lines are parallel in structure and, likely, in extent of genetic diversity across generations. Comparisons of performance between lines can therefore be appropriately made. Chickens that reach sexual maturity in the LWS tend to be heavier, with the lightest chickens failing to reproduce. This may lessen selection pressure in this line. Still, both lines appear to have retained substantial genetic diversity, particularly as small closed populations under considerable selec-

tion pressure. Sufficient genetic variation in both lines therefore remains to allow selection for high and low 8-wk BW to continue for more generations. It can be concluded that although the breeding decisions conducted throughout the course of the study were successful in maintaining similar population structure in the lines, the underlying structure is dynamic and allows for integration of population studies at the phenotypic and molecular levels.

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