Population dynamics of a long-term selection experiment in White Plymouth Rock chickens selected for low or high body weight

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ABSTRACT The population dynamics of 2 lines of chickens from a long-term (59 generations) selection experiment were assessed based on pedigree data. These lines were propagated from phenotypic selection for low and high 8-wk BW in White Plymouth Rock chickens. Our objective was to determine whether the 2 lines maintained similar population structures over the selection horizon to allow meaningful comparisons of their performance data. A complete pedigree of 31,909 individuals, consisting of 102 founders, 1,064 from the parental generation, and 16,245 low weight (**LWS**) and 14,498 high weight (**HWS**) select chickens, was available. Inbreeding (***F***) and average relatedness (***AR***) coefficients were computed. Average F per generation and AR coefficients were 1.3 (SD 0.8) % and 0.53 (SD 0.001) for LWS, and 1.5 (SD 1.1) % and 0.66 (SD 0.001) for HWS. Mean F for the entire pedigree was 0.26 (0.16) and 0.33 (0.19), and maximum F was 0.64 and 0.63, in LWS and HWS, respectively. Based on Wright's fixation index, at generation 59, substantial genetic differences were established between lines. The effective population size was 39 in LWS and 33 in HWS. The effective number of founders was 17 and 15, effective number of ancestors were 12 and 8, and genome equivalents were 2.5 and 1.9 in LWS and HWS, respectively. About 30 founders explained the marginal contribution to both lines. By generation 59, only 7 male and 6 female founders contributed to both lines. Moderately high levels of inbreeding and low effective population sizes were inevitable, as this was a closed population. However, effects on the fitness of the population were expected to be less substantial because founders were a combination of 7 lines. The effective numbers of founders and ancestors were relatively low compared to the actual number of founders, as few ancestors contributed to descendants. Based on these evaluations, it can be inferred that LWS and HWS had similar population structures. Comparisons of selection responses in the 2 lines therefore should be reliable.

Key words: body weight, chicken, divergent selection, inbreeding, genetic structure

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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.com, 2018). Such change is brought about by selection, as individuals that differ in viability and fertility contribute differently to the next generation. Under artificial selection, individuals are chosen to favor those with desirable traits for perpetuation in future generations. A long-term selection experiment in chickens based on low and high BW at 8-wk of age provides a clear illustration of response to artificial selection (Siegel, 1962; Dunnington and Siegel, 1996; Márquez et al., 2010; Dunnington et al., 2013; Lillie et al., 2019). In closed populations such as these, inbreeding is inevitable, which affects the variance of allele frequency from one generation to the next (Konig et al., 2010). There also are impacts on the genetic structure of the population. These are reflected by its effective population size, the contributions of founders and ancestors to their descendants, and genetic drift.

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

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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 continued to maintain similar population structures. Such is necessary to make meaningful comparisons of the performance of the 2 lines over the entire selection profile. Inbreeding, including Wright's F-statistics, average relatedness ($\boldsymbol{AR}$), effective population sizes, effective number of founders, effective number of ancestors, genome equivalents, and family sizes 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 (IACUC-15-136). 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 (hatch years 1957 through 2016). The 2 selection lines were established from a cross of 7 mildly inbred lines of White Plymouth Rock chickens. Fifteen roosters and 87 hens from this cross were the founders of both lines. Their lighter offspring were selected as parents of the low weight select (**LWS**) line, and their heavier offspring were selected as parents of the high weight select (**HWS**) line. From that 1957 hatch, 8 sires and 48 dams were selected to establish the parental generation for each line. There were 3 male and 13 female founders in common to the 2 lines. Thereafter, parentage was distinct to a line.

There were conscious attempts to maintain as many sire and dam families as possible to reduce inbreeding. The strategies implemented were at both hatch and mating. At hatch, chicks were randomly discarded so that dam families rarely exceeded 8. When matings were made to produce the next generation, no more than 2 siblings from a family were chosen as sires. Assignment of dams to sires was such that full and half sib matings were avoided.

Márquez et al. (2010) identified an individual as a parent based on pedigree data alone. For this study, records collected at mating, hatch, and at a 4- and 8-wk weighing also were available. An individual was considered as selected if it was mated. It was defined as a parent if it had progeny with a known sex and 8-wk BW. In Table 1, the number of males and females selected and those that were parents are provided for several hatches.

A complete pedigree, including sex, generation, and selection line, was constructed for each individual, beginning with the founders of the 2 lines. The size and structure of the pedigree is provided in Table 2.

Table 1. Number of male and female chickens selected and that produced progeny (in parentheses) by generation and selection line.

	Low weight select		High weight select	
Generation[1]	Male	Female	Male	Female
0 (1957)	8 (8)	48 (39)	8 (8)	48 (43)
1 (1958)	7 (7)	40 (37)	8 (8)	34 (34)
5 (1962)	13 (12)	60 (51)	12 (10)	72 (46)
26 (1983)	14 (14)	42 (41)	14 (13)	53 (39)
48 (2005)	14 (14)	50 (43)	14 (14)	56 (40)
58 (2015)	15 (14)	55 (44)	14 (14)	56 (46)

[1]The generation (year) in which parents hatched.

Husbandry

Each year and in each line, chicks were hatched on the first and third Tuesday of March. The second hatch was produced in case there were insufficient numbers of chicks from the first hatch. The chicks were reared to 8 wk in identical pens that had concrete floors, hot air brooding, and wood-shaving litter. These conditions were maintained throughout all generations to ensure a consistent environment for both lines. The chickens were fed a starter (0−8 wk), developer (8−18 wk), and breeder (>18 wk) ration containing 20, 16, and 16% CP and 2,685, 2,761, and 2,772 kcal of ME/kg, respectively, in mash form. These rations and water were allowed ad libitum. Feed was restricted in the HWS line at generation 18 after 8 wk of age to reduce reproductive problems because of obesity (Dunnington and Siegel, 1996). Coccidiostats were added to the feed throughout all generations. From generation 17 onward, the chicks were vaccinated for Marek's disease at hatch.

Statistics

Following a similar approach as Márquez et al. (2010), the dynamics and genetic diversity of the population were investigated. The analyses were conducted using 2 software packages—Pedigree (Coster, 2008) in R and ENDOG v4.8 (Gutiérrez and Goyache, 2005)—with results cross-validated where possible. Most statistics were expressed relative to a reference population, defined as those chicks hatched in 2016 coinciding with generation 59.

Table 2. Number of chickens, by sex and subpopulation (parent or selection line), in the pedigree data.

	Sex		
Subpopulation	Male	Female	Total
Parents[1]	512	552	1,064
Low weight select[2]	7,713	8,532	16,245
High weight select[3]	7,129	7,369	14,498

[1]Parents of the selection lines were from the 1957 hatch and were the offspring of 15 sires and 87 dams from the founder generation.

[2]Low weight select were from hatches in 1958 through 2016 and were descendants of 8 sires and 39 dams selected for low 8-wk BW in the parental generation.

[3]High weight select were from hatches in 1958 through 2016 and were descendants of 8 sires and 43 dams selected for high 8-wk BW in the parental generation.

Inbreeding and Average Relatedness. Inbreeding quantifies the probability that alleles 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_i), values which were obtained for all individuals in the pedigree. Within lines, changes in inbreeding between successive generations (ΔF_t) were calculated to deduce trends and infer the remaining heterozygosity as a measure of genetic diversity over the 59 generations. It was calculated as:

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

where F_t was the mean F in generation t. The ΔF_t also were averaged across generations.

Another approximation of average rate of inbreeding (ΔF) was proposed by Kempthorne (1957) based on the panmictic index ($P_t = 1 - F_t$) where:

$$P_t = P_0 exp^{(-\Delta F \times t)} = 1 \ \times exp^{(-\Delta F \times t)}$$

in which P_0, the panmictic index in the founder population, equals 1 as the founder population is defined as having no inbreeding. Therefore:

$$1 - F_t = exp^{(-\Delta F \times t)}$$

$$\log(1 - F_t) = \log\left(exp^{(-\Delta F \times t)}\right) = -\Delta F \times t$$

The slope of the regression of $\log(1 - F_t)$ on t was therefore used as an alternative estimate of ΔF across generations for each line.

The population had a hierarchical structure with the divergent lines drawn from the founders. Wright's (1978) F-statistics can usefully describe such a dynamic. Coancestry coefficients (f_{ij}) between each pair of individuals, i and j, were obtained and used to calculate Wright's F-statistics: $\boldsymbol{F_{IS}}$, the inbreeding coefficient of an individual relative to its own line; and $\boldsymbol{F_{ST}}$, the average inbreeding of a line relative to the total population.

The AR coefficient is a complementary statistic to F_t because it accounts for both inbreeding and coancestry coefficient. Defined as the probability that an allele randomly chosen from the whole pedigree population belongs to a given individual, it was calculated within each line as:

$$x' = \left(\frac{1}{n}\right) 1' A$$

where x was a row vector with x_i corresponding to the average of AR coefficients in the row for individual i, A was the numerator relationship matrix with dimensions $n \times n$, and n was the number of individuals in the pedigree (Dunner et al., 1998). Beyond serving as an alternative measure of homozygosity, the AR of a founder is indicative of its genetic contribution to a population.

Effective Population Size. The effective population size ($\boldsymbol{N_e}$) 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 the rate of change in inbreeding. It was calculated in 2 ways. First, within each line, the realized effective size based on inbreeding ($\overline{N}_e$; Cervantes et al., 2008) was obtained for chickens hatched in the reference population (2016 hatch):

$$\overline{N}_e = \frac{1}{2 \times \Delta\overline{F}}$$

where $\Delta\overline{F}$ was the average:

$$\Delta F_i = 1 - \sqrt[t-1]{1 - F_i}$$

of the individuals within the reference population, F_i was an individual's inbreeding coefficient, and t was the number of equivalent complete generations (Gutiérrez et al., 2009). With the discrete generations in this flock, t was 59 for all chicks hatched in 2016.

An alternative estimate of realized N_e is based on coancestry ($\overline{N}_{ec}$; Cervantes et al., 2011). Like $\overline{N}_e$, it was obtained as:

$$\overline{N}_{ec} = \frac{1}{2 \times \Delta\overline{c}}$$

where $\Delta\overline{c}$ was the average:

$$\Delta c_{jk} = 1 - \sqrt[\left(\frac{g_j+g_k}{2}\right)]{1 - c_{jk}}$$

of the chickens within the reference population, with c_{jk} the inbreeding corresponding to an offspring of j and k, and g_j and g_k were the number of equivalent complete generations of individual j and k. For the reference population, $g_j = g_k = \left(\frac{g_j+g_k}{2}\right) = 58$.

Effective Number of Founders, Ancestors, and Genome Equivalents. 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:

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

where q_i was the proportion of alleles originating with the ith founder, and f was the total number of founders. The f_e provided an indication of which founders were most influential in terms of maintaining their genetic contribution to the population.

Although capturing founder contributions, f_e does not account for unbalanced use of potential parents resulting in losses in genetic diversity producing bottlenecks (Boichard et al., 1997). Such effects, however, are accounted for by determining the effective number of ancestors (f_a), which was calculated for each line as:

$$f_a = \frac{1}{\sum_{j=1}^{a} p_j^2}$$

where p_j was the marginal genetic contribution of the jth ancestor, and a was the total number of ancestors (Boichard et al., 1997). Note that an ancestor may or

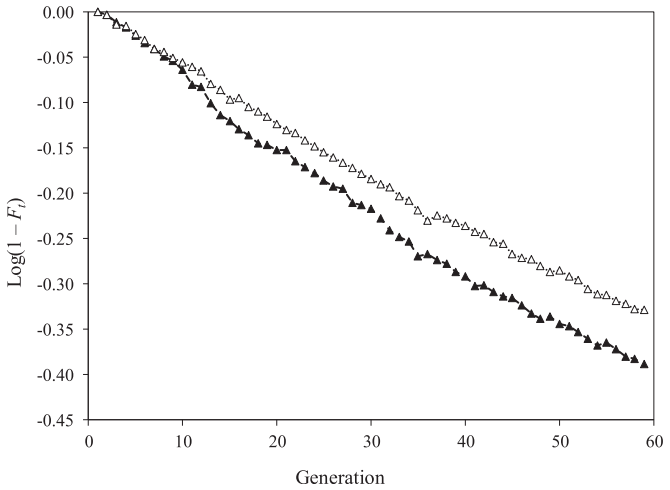

Figure 1. Regression of log(1 − F_t) on t across 59 generations by line, where F_t was the mean inbreeding coefficient at generation t for the low weight select (△, dotted line) and high weight select (▲, dashed line) lines. The slopes approximated the rate of inbreeding per generation within a line: 0.58 ± 0.19% in the low weight select and 0.68 ± 0.32% in the high weight select lines.

may not be a founder. The f_a indicated which ancestors were most influential in genetic contribution to descendants.

As a final measure of effective number, founder genome equivalents (f_g) were obtained as the inverse of twice the average coancestry of individuals (Caballero and Toro, 2000) within a line. This statistic quantifies the number of equally contributing founders that would lead to the same level of genetic diversity as seen in the population under study assuming there were no random losses of founder alleles (Lacy, 1989).

Family Sizes. 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 and Average Relatedness

Mean inbreeding coefficients per generation are shown in Figure 1 as the regression of log(1 − F_t) on t ($R^2 >$ 0.98). The slope for LWS of −0.58 ± 0.19% and for HWS of −0.68 ± 0.32% approximated the $-\Delta F$ for each line. When based on the average of the ΔF_i per generation, ΔF were again similar in both lines; however, the estimates were more than twice as large [1.3 (SD 0.8) % in LWS and 1.5 (SD 1.1) % in HWS]. The highest ΔF_i were in generation 13 (3.2% in LWS and 4.0% in HWS).

Estimates of Wright's fixation index values are summarized in Table 3. For the entire population, including the founder (1956 hatch) and parent (1957 hatch) generations, F_{ST} was 0.1202. This F_{ST} at the population-level was 6- to over 9-fold of that between the parent and LWS and HWS subpopulations, respectively. This suggests substantial variation in the population was due to line differences. Furthermore, the population-level F_{ST} was consistent with the pairwise F_{ST} between lines (0.1215). The F_{IS} values suggest appreciable accumulation of inbreeding within lines, consistent with the average F_i within line. Based on this evidence, there was substantial divergence between the selected lines.

At generation 59, mean F_i in LWS [0.53 (SD 0.016) %] and HWS [0.59 (SD 0.011) %] were similar, as shown in Table 4. Such also was the case for the entire pedigree [0.26 (0.16) in LWS and 0.33 (0.19) in HWS]. The maximum F_i at generation 59 were nearly equivalent between lines (0.64 in LWS and 0.63 in HWS). Differences in AR were more pronounced (0.53 and 0.66 in LWS and HWS, respectively), but with little variation within either line (CV% < 0.04; Table 4).

Effective Population Size

At generation 59, there were 193 LWS and 185 HWS chickens. The realized N_e, whether based on inbreeding ($\overline{N}_e$) or coancestry ($\overline{N}_{ec}$), were approximately 39 in LWS and 33 in HWS (Table 4). The similar rates of inbreeding in the 2 lines resulted in their similar N_e.

Effective Number of Founders, Ancestors, and Genome Equivalents

Both selection lines were established from generation 0 (1957 hatch), which consisted of 1,064 chickens. There were 102 founders to this generation, of which 15 were male. The f_e and f_a were both 34, with 13 of these founders explaining 50% of the genetic variation. In both lines, the most substantial decrease in effective founder and ancestor contributions occurred by generation 3, with f_e of 16 (HWS) to 17 (LWS), and f_a of 13 (LWS) to 14 (HWS). Reductions thereafter were small (Table 5). The exception was the effective number of ancestors to HWS. Between generation 10 and 15, f_a decreased from 12 to 8.

Table 3. Summary of Wright's F-statistics.[1]

	F_{ST}			
Subpopulation[2]	Parent	Low weight select	High weight select	F_{IS}
Parent	-	0.0200	0.0127	−0.0153
Low weight select		-	0.1215	0.0788
High weight select			-	0.1030

[1] F_{ST} is the average inbreeding of a line to the total population; F_{IS} is the average inbreeding of an individual relative to its own line.
[2] The parents of selection lines were from the 1957 hatch; the low and high weight selection lines were from the 1958 through 2016 hatches.

Table 4. Summary statistics for genetic diversity measures at generation 59 by selection line.

Parameter[1]	Low weight select	High weight select
n	193	185
Mean F_i (SD)	0.53 (0.016)	0.59 (0.011)
Maximum F_i	0.64	0.63
Mean AR (SD)	0.53 (0.001)	0.66 (0.001)
$\overline{N}_e$	39.3	33.2
$\overline{N}_{ec}$	38.6	32.9

[1] F_i is individual inbreeding coefficient; AR is average relatedness coefficient; $\overline{N}_e$ is realized effective population size based on inbreeding; $\overline{N}_{ec}$ is realized effective population size based on coancestry.

At generation 59, 32, and 30 founders, respectively, contributed at least 1% genetically to LWS and HWS (Figure 2). In LWS, the highest contribution of a founder to that generation was 14.0%; in HWS, the corresponding value was 15.1%. Both were males. The proportional contributions of the 15 male founders are presented in Figure 3. Eleven and 8 of these male founders contributed to the LWS and HWS, respectively; 7 contributed to both lines. Of the 87 females in the founder population, 19 contributed to LWS and 20 to HWS at generation 59; only 6 contributed to both lines. This indicated less persistence of genetic contributions from female than male founders.

In Figure 4, the cumulative marginal contributions of ancestors to genetic diversity in each line at generation 59 is plotted. Thirty-three ancestors contributed to LWS, while 15 ancestors contributed to HWS. In LWS, 5 males and 1 female ancestor explained 50% of the genetic variation. In HWS, 3 male ancestors explained that same amount of variation. There were no common ancestors to both lines.

Founder genome equivalents were 2.5 and 1.9, respectively, in LWS and HWS. If all founders had contributed equally to each generation of descendants, and with no alleles lost by drift due to bottlenecks (Lacy, 1989), approximately 2 founders would have defined the allelic diversity observed in each line at generation 59.

Table 5. Observed and effective numbers of founders and ancestors contributing to a generation in the low weight (LWS) and high weight (HWS) select line[1].

Line	Generation (yr)	n[2]	Founders[3] n	Founders[3] f_e	Ancestors[4] n	Ancestors[4] f_a	Ancestors[4] n 50% var.
LWS	1 (1958)	432	46	22	45	19	7
	2 (1959)	312	39	18	32	15	6
	3 (1960)	473	33	17	27	13	5
	4 (1961)	417	32	17	28	14	6
	5 (1962)	447	32	17	30	13	5
	10 (1967)	335	32	17	24	13	5
	15 (1972)	356	32	17	24	13	5
	20 (1977)	194	32	17	25	13	5
	40 (1997)	197	32	17	31	12	5
	48 (2005)	195	32	17	32	12	5
	59 (2016)	193	32	17	33	12	5
HWS	1 (1958)	467	39	18	41	18	7
	2 (1959)	373	34	16	32	15	6
	3 (1960)	393	31	16	30	14	5
	4 (1961)	306	31	15	28	13	5
	5 (1962)	362	30	15	29	13	5
	10 (1967)	184	30	15	30	12	5
	15 (1972)	338	30	15	15	8	3
	20 (1977)	218	30	15	15	8	3
	40 (1997)	139	30	15	15	8	3
	48 (2005)	210	30	15	15	8	3
	59 (2016)	185	30	15	15	8	3

[1] Both selection lines were established from generation 0 (1957 hatch). It consisted of 1,064 chickens. The actual (equivalent) and effective number of founders to generation 0 were 103 and 34, respectively. The actual and effective number of ancestors to generation 0 were 102 and 34, respectively, with 13 ancestors explaining 50% of the genetic variation.

[2] Number of chickens in generation.

[3] Observed (n) and effective number (f_e) of founders.

[4] Observed (n) and effective number (f_a) of ancestors, and the number of ancestors defining 50% of the genetic variation (n 50% var.).

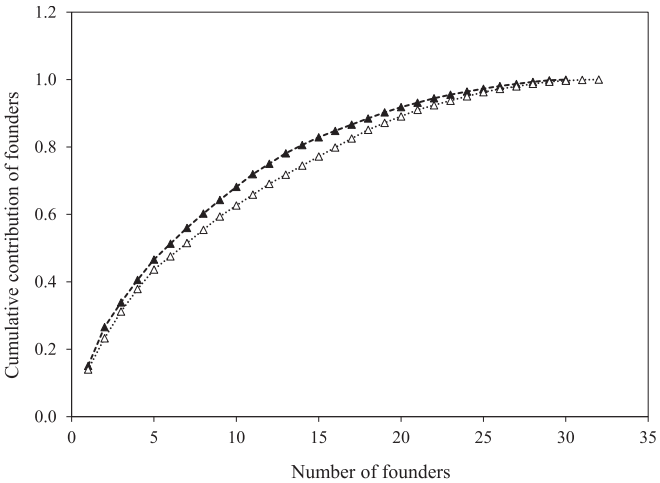

Figure 2. Cumulative contribution of founders to generation 59 for the low weight select (△, dotted line) and high weight select (▲, dashed line) lines. Founder contributions were based on average relatedness. Thirty-two and 30 founders, respectively, contributed at least 1% genetically to the low weight select and high weight select lines.

Family Sizes

Means, standard deviations, and maximum values of family sizes were calculated and presented in Table 6. 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. Family sizes of males were larger than

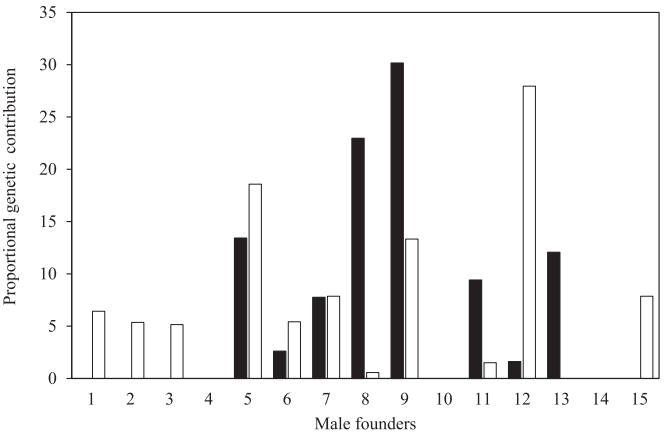

Figure 3. Proportional genetic contribution of the 15 male founders to generation 59 (white bars—low weight select; black bars—high weight select). Seven founders contributed to both lines.

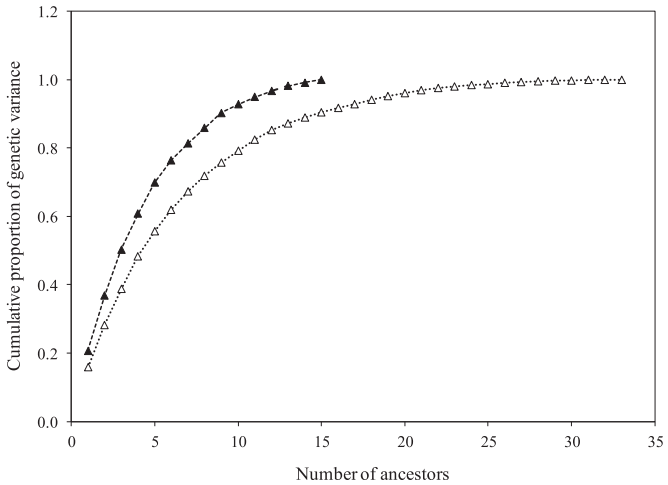

Figure 4. Cumulative proportion of genetic variance explained by ancestors at generation 59 for the low weight select (△, dotted line) and high weight select (▲, dashed line) lines. Thirty-three and 15 ancestors, respectively, contributed to the low weight select and high weight select lines.

females both in the complete pedigree and the population of selected parents. Additionally, the family sizes were larger in the complete pedigree than in the population of selected parents. A similar structure for each sex was observed across lines.

DISCUSSION

Inbreeding and Average Relatedness

A gradual increase in inbreeding coefficients in the LWS and HWS 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 pigeons (Meleg et al., 2005) and chickens (Sewalem et al., 1999).

Inbreeding depression has the most severe effects in small and closed livestock populations undergoing selection. In beef cattle, effects of inbreeding depression have been most severe in populations with rapid inbreeding, with coefficients reported as being higher than 20% (Burrow, 1993; Gutiérrez et al., 2003). These beef cattle populations were propagated by short generation intervals (3.7−6.1 yr). In chickens, the generation interval is even shorter, with one generation per year in this selection experiment. The inbreeding that accumulated by generation 59 was inevitable; in such a closed population, individuals became more closely related with increasing generations. However, the effects of inbreeding were less drastic in these lines because selection and mating decisions were consciously made to reduce accumulating inbreeding.

Recently, Restoux et al. (2022) described their survey of genetic diversity of 18 local French populations of chicken based on both molecular and pedigree data. These were small populations managed similarly with an aim to limit inbreeding rates while applying selection. Rates of inbreeding were consistent with the current study (0.8−1.9% per generation based on ΔF). Pedigree-based estimates of N_e ($\overline{N}_{ec}$) in their reference populations (chickens hatched in 2013), however, were in general larger (22−285), likely in part reflecting fewer generations (4−24). Although the extent of diversity within a breed varied according to its history and selection protocols, genetic diversity levels remained high. Even with small, closed populations, as in the selection lines considered in our study, inbreeding levels can be controlled through planned mating strategies thereby preserving genetic variability.

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 per generation were similar in the 2 lines, at approximately 1.5%. Larivière et al. (2011) also evaluated inbreeding per generation in traditional Belgian breeds of chickens. In breeds with N_e similar to the LWS and HWS, they reported rates of inbreeding ranging from 1.1 ($N_e = 44$) to 1.5% ($N_e = 34$).

Simon and Buchenauer (1993) considered the consequences of accumulated inbreeding in livestock populations over 50 yr. When the inbreeding accumulated over that timeframe was <5% there was little risk of inbreeding depression and extinction. However, populations with accumulated inbreeding of 5 to 15% were potentially at risk, of 25 to 40% were endangered, and of >40% were at a critical status. With nearly 60 generations of selection in our chicken lines, with one generation per year, accumulated inbreeding exceeded 50%. Reproductive efficiency therefore may have been reduced because of inbreeding. That supposition is based on correlated responses in traits associated with reproduction in these lines, which included erratic ovulation and defective egg syndrome in the HWS and anorexia in the LWS (e.g., Siegel and Dunnington, 1987; Dunnington et al., 2013; Jambui et al., 2017).

Table 6. Family sizes in the low weight (LWS) and high weight (HWS) select line by sex across 59 generations.

Sex	Line	n	Maximum	Mean	SD
Full pedigree[1]					
Male	LWS	751	92	24.2	14.8
	HWS	758	95	20.2	12.7
Female	LWS	2518	24	7.2	4.5
	HWS	2333	26	6.6	4.3
Parents[1]					
Male	LWS	721 (723)[2]	14 (16)	4.5 (5.1)	2.3 (2.6)
	HWS	703 (716)	18 (20)	4.3 (5.2)	2.6 (3.0)
Female	LWS	1708 (1820)	9 (9)	1.9 (2.0)	1.1 (1.2)
	HWS	1513 (1683)	9 (10)	2.0 (2.2)	1.3 (1.5)

[1]Full pedigree are all individuals with a known sex and BW; parents are individuals with progeny with a known sex and BW.

[2]In parentheses, values of statistics for selected parents including those that did not produce progeny.

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 indirectly proportional to the rate of inbreeding. It therefore is a good estimate of the actual population size when the pedigree is well defined and complete, as was the case in our study.

The N_e observed was similar in both lines and to that reported by Márquez et al. (2010), with only slight variations. This similarity may be attributed to a relatively constant rate of inbreeding across generations. The small difference in N_e found here [39.3 (LWS); 33.2 (HWS)] as compared to Márquez et al. (2010) [38.3 (LWS); 32.1 (HWS)] could be because only chickens with progeny with a known BW and sex now were defined as parents.

Genomic diversity in the LWS and HWS lines was evaluated by Lillie et al. (2019) at generations 40, 50 and 55. Heterozygosity and nucleotide diversity was assessed using sequence data (approximately 7.6 million SNP) from pooled blood samples from 9 to 30 chickens sampled from each line. The consistency of their results and ours, viewing the same lines from different vantage points, shows a general decline in heterozygosity and nucleotide diversity across generations. Genomic diversity was somewhat higher in the LWS than HWS line. Lillie et al. (2019) suggested this may reflect more fixation events in the HWS line and biological limits impeding selection to further reduce BW in the LWS. Around generation 30, there was a plateau in selection response in the LWS line with fewer chickens achieving sexual maturity; they hypothesized relatively more genomic diversity was therefore maintained in that line.

In natural populations, it was reported that the critical N_e necessary for maintenance of adequate genetic variation was 500 (Soulė, 1980; Franklin and Frankham, 1998). Based on those guidelines, our lines fall short and could be at potential risk. However, they did not indicate whether that threshold was specific to a particular species or breed or due to biological differences such as reproductive rate and generation interval. In livestock, smaller population sizes (e.g., $N_e > 100$) have been considered viable to maintain long-term selection responses (Goddard, 1992; Weigel, 2001).

Effective Number of Founders, Ancestors, and Genome Equivalents

The f_e measures the expected founder contributions to descendants across generations. However, the f_a is more befitting for a population that has undergone bottlenecks, which risks a potential loss of alleles. In generation 59 of our study, the f_e [17 (LWS); 15 (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 contributed to generation 59 (out of 15, 11 and 8, respectively, to LWS and HWS), although in varying proportions. Clearly, male founders persisted in their genetic impact on the population. However, this persistence was less in female founders (19 to LWS and 22 to HWS out of 87). These varying contributions may indicate differences in genetic potential for growth, heavy use of certain founders through their descendants within a line, or both. 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 with similar results to those of Márquez et al. (2010).

The f_a in generation 59 [12 (LWS); 8 (HWS)] also was low compared to the actual number of founders (102), taking note that an ancestor was not necessarily a founder. The cumulative marginal contribution of the ancestors showed that few ancestors were most influential in genetic contribution to descendants, as was the case with founders.

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. Still, between lines, the mean and variability in family sizes were similar. That stability reflected the design of the breeding program: restrictions were placed on sizes of sire and dam families to ensure that no family predominated over others and to mitigate inbreeding.

General Comments

To fairly compare the performance of selection lines, 3 factors are crucial: i) the lines must be connected genetically through common founders; ii) systematic effects must be consistent (e.g., management, housing, nutrition); and iii) inbreeding rates, and thereby losses in heterozygosity, should be similar across the selection horizon (generations). The focus of this study was on the third of these factors. However, as touched on in this manuscript, all 3 were achieved in this selection experiment. If inbreeding had appreciably varied between lines, beyond differential effects on fitness, there would be risk of heterogeneity in genetic (additive) and phenotypic variances. Possible accommodations would be fitting inbreeding as a covariate, and to correct variances for heterogeneity, in the data analysis. To be comprehensive, the influence of applying such adjustments will be tested in the next phase of this research. However, based on the results of this study, presumably neither will be needed.

CONCLUSIONS

Using statistics that characterize the dynamics and diversity of a population, the LWS and HWS were

similar in their genetic structure. Robust comparisons of the performance of these 2 lines over the entire selection profile therefore can be made with confidence. Furthermore, despite losses of genetic diversity due to the gradual accumulation of inbreeding, heterozygosity remains to allow further response to selection.

DISCLOSURES

The authors declare that there is no conflict of interest regarding the publication of this article.

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