Population Genetics of Egg laying Chickens: The Patterns of Nucleotide Diversity, Linkage Disequilibrium and Demographic History

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Many decades of intensive selection for increased egg production and more efficient feed conversion have strongly affected the genome of egg laying chickens. The aim of this study was to systematically characterize genome-wide statistics and determine the current status of effective population size (Ne) in breeding lines of layers. To this purpose we used different sources of information and methods. In the first step, 36 k and 57 k genotypes from two independent genotyping chips were used to characterize nucleotide diversity and structure of linkage disequilibrium (LD) in the genome of 454 birds from four populations of commercial vs., experimental and white vs., brown egg laying chickens. In general, brown layers showed a higher level of genetic variability than the white Leghorn populations. We observed a large difference of LD between the lines of white and brown layers (Figure 1). A mean value of r^2 =0.73 ± 0.36 was observed in pair-wise distances of <25 Kb for commercial white layers, and it dropped to 0.60 ± 0.38 with distances of 75 to 120 Kb, the interval which includes the average inter-marker space in this line. In contrast, an overall mean value of $r^2 = 0.32 \pm 0.33$ was observed for SNPs less than 25 Kb apart from each other and dropped to 0.21 ± 0.26 at a distance of 100kb in commercial brown layers. There was a remarkable similarity of the LD patterns within the populations of white and brown layers, while the LD pattern between white and brown layers was clearly different. Inferring the population demographic history from LD data resulted in a larger effective population size in brown than white populations, reflecting less inbreeding among brown compared to white egg layers (Figure 2). In a further step, we used three approaches based on both demographic (sex ratio) and genetic data (inbreeding coefficient and marker assisted temporal sampling) to compare Ne estimates in four populations. To this purpose pedigree data along with the composite genotype of 30 microsatellites from 468 individuals were analysed. For each population data from a present and a historical generation separated by 9 generations were available. Ne estimates from the number of parents revealed a size of ≈36 over a period of 10 years in experimental population. In the case of commercial lines Ne was estimated as 49.5 and 63.8, for brown and white layers, respectively. With pedigree-based inbreeding coefficients the harmonic mean of Ne over 10 years was less than 20 for experimental lines while commercial lines were maintained at higher values. Using microsatellite analyses the harmonic mean Ne ranged from 12.4 (95% CI: 9.7-15.7) to 31.1 (95% CI: 22.4-43.4) for commercial and experimental brown layers, respectively (Table 1).

Overall, the patterns of diversity and LD were found to be consistent between analyses based on the parallel SNP chips and across different populations within the brown and the white layers. Although the *Ne* is consistently < 70, it behaves roughly contradictory across method vs., population classes. The discrepancies highlight the sensitivity of estimates on their underlying assumptions. If a precise value of *Ne* is needed, for example, to define number of sampled individuals to be genotyped for a genomic selection scheme, different metrics would result in different conclusions. Therefore, it is strongly recommended to use various *Ne*

estimators to increase the information value. Since these analyses are based on different sources of information and independent method/line classes, the results can be validated across populations.

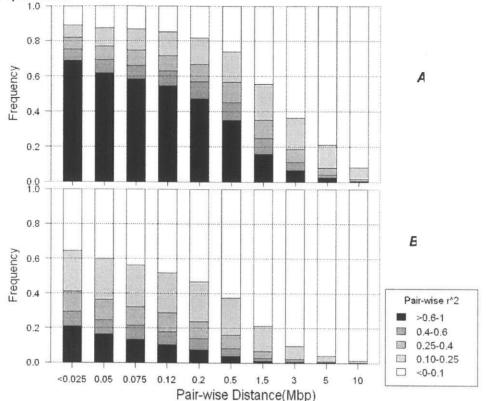


Figure 1. Comparison of the fraction of marker pairs with different LD levels (<0.1, 0.1-0.25, 0.25-0.4, 0.4-0.6 and >0.6, depicted by different colors) in different distance bins between commercial white (A) and brown (B) egg laying lines.

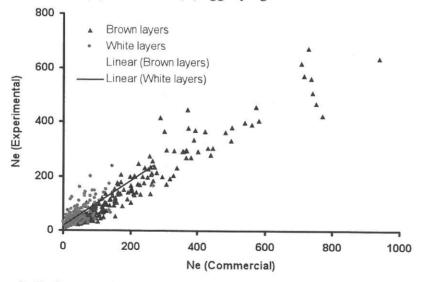


Figure 2. Estimates of historical Ne from experimental white and brown layers are plotted against the commercial lines. R^2 of fitted lines were estimated as 0.92 and 0.57 for brown and white layers, respectively.

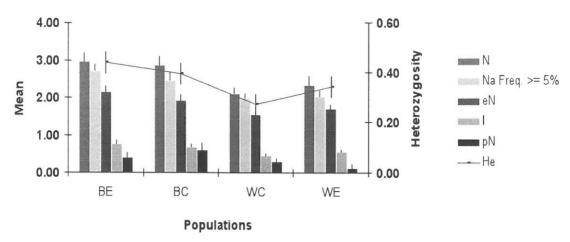


Figure 3. Microsatellites allelic pattern across populations (N: number of alleles; Na Freq. >= 5%: number of alleles with frequency >= 5%; eN: effective number of alleles; I: Information index; pN: number of private alleles; He: expected heterozygosity).

Table 1. Current effective population size estimates from different models.

Population ¹	Sex ratio ²	Inbreeding ²	Temporal sampling ³
BE	36.3	9.4	31.1 (22.4-43.4)
WE	36.3	17	25.6 (16.7-39.1)
BC	49.5	28	12.4 (9.7-15.7)
WC	63.8	27.2	19.1 (12.9-27.4)

¹Experimental (E) and commercial (C) populations, each comprising a white (W) and a brown (B) layer breed.

²Harmonic mean of *Ne* values between 1996 and 2007.

³Ne values extracted from the lower and upper confidence/credible limits. Values are based upon 10'000 iterations with priors values estimated from demographic model and 30 loci genotyped from 468 diploid individuals sampled 9 generations apart.