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Comparative analysis of variation in immunity, production, fitness and feed efficiency traits in chicken performing in the tropical environment

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This meta-analysis aimed to assess genetic and environmental effects on humoral immunity in comparison to production, fitness and efficiency trait classes in chicken. Three hypotheses were formulated; associations between heritability with genetic and environmental variances across the trait classes are equal; genetic and environmental effects on the trait classes are equal; study characteristics have no effect on genetic parameters in humoral immunity. Genetic parameters and production system characteristics were extracted from a total of 85 peer-reviewed articles published between 1976 and 2020. Mean standardized genetic variance (CV_A) and environmental variance (CV_R) were used to compare variances of traits measured in different units. Associations between the effect sizes were explored using spearman-rank correlation (non-normal distribution). For heterogeneity tests, hierarchical model was considered while study characteristics influencing genetic parameters in humoral immunity were tested by fitting a meta-regression model; log-transformed effect sizes used as response variables but back-transformed when reporting results. Associations between heritability with CV_A and CV_R was trait dependent. In humoral immunity and fitness traits, heritability was positively ($p<0.05$) associated with CV_A ($r = 0.34$ vs 0.30) For production traits, however, heritability was highly and negatively associated with CV_R than with CV_A ($r = -0.41$ vs 0.11; $p<0.05$). Heterogeneity tests showed significant ($P<0.05$) variation in effect sizes across trait classes. Weighted estimates of effect sizes indicate that humoral immunity had highest genetic (12%) and residual (23%) effects but with low heritability (0.23). In contrast to immunity traits, production traits had the highest heritability ($h^2 = 0.27$) but the least genetic (7%) and residual (9%) effects. Adjusting for moderating factors on humoral immunity, the two arms of humoral immunity, chicken population and production phase were able to explain the 93.1% of the between study variation in heterogeneity in CV_A. Significant differences on genetic parameters across trait classes suggest presence of sub-groups among chicken performing in different production environments. Based on humoral immunity, accounting for these sub-grouping effects gives a better indication of true genetic effects in the different traits.

Key words: genetic parameters, humoral immunity, production, fitness, feed efficiency

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Introduction

Significant advances in chicken productivity have been achieved through breeding for traits that contribute to increased revenues and reduced production costs (Star et al., 2008). However, this has been at the expense of biological functions affecting a chicken's ability to cope with stressors in its environment. For instance, Huber (2018) reported that high producing chicken were highly sensitive to environmental changes due to being forced into early productive life when most critical organs were not adequately developed. Further, altering the allocation and re-allocation of resources towards production resulted to physiological and immunological disorders. These implications have led to gradual inclusion of functional traits in breeding objectives to enhance immunity, fitness and the general well-being of chicken (Star et al., 2008). The goal of this approach is to develop a robust chicken that is capable of producing while maintaining adaptation potential to stressors in its production environment. This meta-analysis aimed at assessing the genetic and environmental influence on humoral immunity, production, fitness and feed efficiency traits in chicken. The study used mean standardized genetic (CV_A) and environmental (CV_R) variances to assess genetic parameters (Houle, 1998). Subsequently, heritability (h^2) was considered to determine its value as a proxy parameter for genetic variance across traits. Therefore, three hypotheses were formulated: 1) associations among the genetic parameters across the trait classes is zero; 2) Heterogeneity on genetic parameters across sampled studies is zero and pooled genetic parameter estimates are equal; 3) Study characteristics have zero effect on genetic parameters in humoral immune traits.

Material and Methods

To drive the literature-search process, keywords related to the objectives were defined. Identified studies were reviewed and screened for eligibility. This resulted to 85 studies published between 1976 and 2020 being used to extract data on study characteristics and parameter estimates. Study characteristics included: author, publication year, country, population, age, sex, selection status, production system, sample size, model fitted. Parameters included: mean (and standard deviation), heritability, phenotypic variance, additive genetic variance, residual variance and standard errors (SE) associated with each parameter. Coefficient of variation measures (CV_A, CV_R) were estimated and log-transformed (to correct for non-normal distribution) as described by Nakagawa et al. (2015). Heritability estimates, on the other hand, were log transformed directly. Associations between the parameters were explored using spearman-rank correlation (untransformed data). A hierarchical model was considered to account for possible correlated structures that may arise from several parameters originating from a single study. Log-transformed parameters were used as response variables while results were back transformed. First, the model was fitted on the whole data set with trait class fitted as a fixed factor to allow for comparison of global estimates across the trait classes. Thereafter, treating each trait class as a separate data set, an intercept only model was fitted to test for heterogeneity. To determine the effect of the study characteristics on genetic parameters in humoral immunity, a meta-regression model was fitted.

Results and Discussion

Associations among the genetic parameters show that CV_A and CV_R were positively and highly (r_s = 0.54 to 0.83; $p<0.05$) correlated across all traits, suggesting parallels between processes shaping the genetic and environmental effects on these traits (Houle, 1998). Being a component of genetic and residual variances, heritability was positively associated with CV_A and negatively with CV_R in the traits studied. However, the weight and significance of associations was trait dependent. In the case of humoral immunity (0.34; $p<0.05$) and fitness (0.30; $p<0.05$) traits, heritability could be used as an indicator for genetic variance. For production traits, however, heritability was highly and negatively associated with CV_R (-0.41; $p<0.05$) than with CV_A (0.11; $p<0.05$), indicating large environmental influence on heritability compared to genetic effect.

Heterogeneity test statistics, prediction intervals and pooled estimates for the genetic parameters are presented in Table 1. In each of the trait class, there was significant (p<0.05) differences in the genetic parameters across sampled studies, suggesting presence of sub-grouping among the sampled studies. Fitness traits were more heterogeneous across all parameters (CV_A, CV_R and h^2) while production and immune traits had the least variance in CV_A and h^2, and CV_R, respectively. Comparing sources of variation, in fitness (CV_A and CV_R) and production (CV_R and h^2) traits, a higher proportion of variation was due to between-study variance which could be attributed to differences in study characteristics (Hoffman et al., 2016). On the other hand, a higher proportion of variation in immune and efficiency traits (CV_A and CV_R), and production traits (CV_A) was due to within-study variance, indicating that traits falling into the same class within a study may not necessarily be highly correlated (Hoffman et al., 2016). Consequently, prediction intervals of genetic parameters were broad across the trait classes implying wider dispersion of estimates and could be related to the high heterogeneity among sampled studies.

Table 1: Heterogeneity statistics, prediction interval and pooled estimates on genetic effect, residual effect and heritability across trait classes

Trait class	**Test statistics and pooled parameters[1]**								
	K (N)	Q_E	df	Tau^2	I^2_{bs} (%)	I^2_{ws} (%)	95% PI[3] LCI	UCI	Pooled estimates[3]
	Coefficient of variation of additive genetic effect (logs)								
Efficiency	11 (52)	170275***	51	1.53	31.66	68.30	0.01	1.58	0.10
Fitness	22 (99)	3588149***	98	2.14	69.73	30.27	0.00	1.32	0.07
Immune	29 (145)	280775.2***	144	1.70	38.40	61.56	0.01	1.61	0.12
Production	39 (328)	5108407***	327	1.47	46.47	53.53	0.01	0.72	0.07
	Coefficient of variation of residual effect (logs)								
Efficiency	11 (52)	166176***	51	1.77	6.45	93.5	0.01	2.47	0.18
Fitness	22 (99)	3825197***	98	2.83	94.17	5.82	0.00	3.27	0.11
Immune	29 (145)	159029.6***	144	0.87	48.43	51.50	0.04	1.49	0.23
Production	39 (328)	5831278***	327	1.48	52.46	47.53	0.01	1.04	0.09
	Heritability(logs)								
Efficiency[2]	11 (52)	3484.31***	51	0.01	99.90	-	-0.03	0.44	0.18
Fitness[2]	22 (99)	9165.53***	98	0.02	99.25	-	-0.06	0.53	0.19
Immune[2]	29 (145)	2210.09***	144	0.01	96.20	-	0.12	0.35	0.23
Production	39 (328)	397.3**	327	0.01	46.37	7.04	0.07	0.52	0.27

[1]k=number of studies; n=number of effect sizes; q_e=total sum of squares of observed effects; df=degrees of freedom; tau^2=variance due to random effect of study; I^2 bs (%)=proportion of total variance due to random effect of between study variance; I^2 ws (%)=proportion of total variance due to random effect of within study variance; 95% PI = Prediction intervals; LCI= lower credible interval; UCI = upper credible interval. [2]two level model was fitted. [3]Estimates back-transformed. ***p<0.001; **p<0.01; *p<0.05

Generally, pooled estimates of CV_A, CV_R and h^2 were significantly (p<0.05) different across the trait classes. Humoral immunity had the highest CV_A and CV_R than other trait classes, however, its heritability was low. Similarly, efficiency and fitness traits had low heritability estimates despite the moderate CV_A and CV_R. Production traits had the highest heritability but with the least CV_A and CV_R. Based on these heritability estimates, the lowly heritable traits could be interpreted as traits under strong directional selection resulting to depletion of genetic variation while the high heritability in production traits would be attributed to weak or stabilizing selection and thus, maintained genetic variation. In contrast, using CV_A, immune traits had the highest additive genetic variation followed by fitness and efficiency traits. Considering that immunity, fitness and efficiency traits are expressed throughout an individual's life time, Houle (1998) explains that these traits depend on many underlying physiological and morphological traits such that they sum genetic variation over many loci. Furthermore, this multitude of loci provide a large mutational target that is able to counter the effects of directional natural selection. On the other hand, these traits tend to integrate environmental variability an individual is exposed to during its life-time, subjecting the traits to low repeatability and hence, the low heritability.

Study characteristics significantly ($p<0.01$) influenced genetic effect on humoral immunity. These included the arm of humoral immunity, population type, age and sex. Genetic variance between the two arms of humoral immunity differed significantly ($p<0.05$) with adaptive immunity (0.19) having a higher CV_A than innate immunity (0.10). Pinard-van Der Laan (2002) indicates that the two arms of immune system may be influenced by different genetic components considering they carry out different functions. Across chicken populations, exotic chicken had the highest CV_A (0.20) while indigenous chicken had the least (0.06). Zhang et al. (2020) indicates that these populations are under different forces of selection, mutation and environment effects resulting to variations in gene frequencies. In regard to age, there was a higher genetic variance (CV_A = 0.89) during the mid-lay period compared to other production phases. Houle (1998) explains that a trait expressed later in life is likely to display more variance than the same trait expressed early in life due to cumulative effects of the same allelic variants. Comparing the effect of sex on CV_A, females had a higher level of CV_A (0.17) compared to males (0.03). Differences between sexes on immunological responses are germline encoded and therefore, regulation of responses are controlled by the level of expression of sex chromosomes (Klein and Flanagan, 2016).

Conclusions and Outlook

Heritability was positively and negatively associated with additive genetic and residual variance, respectively, however, the weight and significance of association was trait dependent. Heterogeneity tests indicated significant differences (between and within studies) in the genetic parameters across sampled studies. Weighted average genetic and residual variances, and heritability significantly differed across trait classes. Study characteristics significantly influenced genetic variance in humoral immunity and adjusting for these factors improved the prediction interval. Weighted average genetic parameters provide critical information to breeding programs on the current genetic status of traits in chicken populations, however, correlations among these trait classes would be more informative on the expected correlated responses.

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