



A Meta-Analysis of Genetic Parameter Estimates for Economically Important Traits in Iranian Indigenous Chickens

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Abstract

This study aimed to perform a meta-analysis to combine genetic parameters for economically important traits of Iranian indigenous chickens. A data set of information related to different growth, reproduction, and egg quality traits including 336 heritability estimates and 433 genetic correlations from 45 articles published between 2007 and 2019 were used. Meta-analysis was performed based on a random-effects model to calculate the effect size for genetic parameters. Also, I^2 statistic and Q test were used to measure the degree of heterogeneity among studies. The mean heritability for growth traits ranged from 0.222 (body weight at hatch) to 0.34 (body weight at 12 weeks of age). The lowest and highest estimates of the heritability for reproductive traits were 0.181 (number of eggs produced) and 0.449 (age at sexual maturity), respectively. The mean heritability estimate for egg internal quality traits varied from 0.211 (yolk weight) to 0.355 (albumin weight) and for external quality traits of eggs in the range from 0.261 (shell strength) up to 0.332 (Shell weight). Also, the mean genetic correlation estimates between growth traits, and between reproductive traits ranged from 0.297 to 0.878 and -0.678 to 0.788, respectively. Also, the genetic correlation between internal and external quality traits of eggs ranged from -0.069 to -0.979 and -0.012 to -0.856, respectively. The estimates reported in the present study are appropriate to be used in breeding programs when reliable genetic parameter estimates are not accessible for economically important traits in native fowls.

Introduction

Native breeds are generally considered as valuable genetic resources in any country and are a useful source of protein for rural families due to their adaptation to the method of breeding in unfavorable and open rural conditions. Therefore, preserving these breeds along with planning for their increase and profitability is essential (Niknafs *et al.*, 2012). Archaeological excavations confirmed the presence of the domestic fowl in the territory of Iran in ancient times (Mohammadabadi *et al.*, 2010). It is known that Persian chickens from the Gilan Province took part in the origin of the Russian Orloff breed (Mohammadabadi *et al.*, 2010). Since 1981, twelve chicken breeding centers were established for reproducing native poultry varieties, and the total number of chickens they maintain is about 8000

birds. Currently, there are eight breeding centers in Fars, West Azarbaijan, Isfahan, Mazandaran, Khorasan, Yazd, Zanjan, and Khuzestan provinces (Mohammadabadi *et al.*, 2010). Research on native chicken populations of Iran has been initiated, and the data on the genetic variability of different loci in these populations have been published (Mohammadifar *et al.*, 2013; Mohammadifar and Mohammadabadi, 2017).

Before designing any breeding program, extensive studies on the genetic characteristics of economic traits should be done and the average production and growth, and the parameters related to these traits should be carefully calculated. Therefore, one of the most effective ways to improve the genetics of these populations in breeding programs and to increase the production capacity of the poultry population is to

estimate accurately the genetic parameters of economically important traits. Over the past few decades, several studies have been performed to estimate genetic parameters using different statistical methods for different traits of the indigenous chicken in Iran. These studies have variable quality in terms of sample size and sometimes have conflicting results. In individual studies, there is uncertainty about estimates, and the results may have been measured with a specific error which can hurt breeding decisions and programs. Accurate estimation of genetic parameters is necessary to increase the accuracy of breeding value estimates, and one of the effective ways to increase the accuracy of estimates is the use of new and scientific methods such as meta-analysis. Many animal studies are replications of past studies. Using meta-analysis to combine results leads to more reliable estimates and reduces the inessential repetition of animal experiments (Hooijmans *et al.*, 2014). Besides, the meta-analysis of animal studies has a greater possibility to find out likely heterogeneity sources because of the more exploratory character of animal experiments than the clinical studies (Lau *et al.*, 1992; Sena *et al.*, 2010). This type of meta-analysis also supplies new facts that were not achievable by analyzing an individual study. Meta-analysis is a method that combines different individual and independent results from studies that have a common field and leads to a report with a single result and higher statistical power (Littell *et al.*, 2008). Because of the variability of the scope of genetic parameter estimates and also the possibility of errors in the literature and published articles, it is necessary to achieve a single range of estimates using meta-analysis, and this single domain will be useful in breeding programs.

To the knowledge of the authors, a specific meta-analysis of the genetic parameters for growth, reproduction, and egg quality traits of Iranian indigenous chickens has not been reported in previous studies. Therefore, the objective of this study was to perform a meta-analysis using a random-effects model to merge different published genetic parameter estimates for the above-mentioned traits in Iranian indigenous chickens.

Material and methods

Collecting required information and inclusion criteria

At first, to find studies related to the research topic, a systematic search of published studies from databases was performed to identify all sources reporting genetic parameter estimates and genetic correlations for growth, reproduction, and egg quality traits in Iranian indigenous chickens; and then, the desired information was extracted from them. Databases used

include ISI Web of Knowledge (<https://apps.webofknowledge.com>), ResearchGate (<https://www.researchgate.net>), Google Scholar (<https://www.scholar.google.com>), and SID (<https://www.sid.ir>). According to Higgins *et al.* (2003), the required and appropriate amount of data is one research, but some other sources consider at least two studies are sufficient. In addition, publication bias decreases with increasing the number of studies. Also, due to the increase in sample size and consequent reduction in standard error, the accuracy of estimates would be increased (Valentine *et al.*, 2010; Turner *et al.*, 2013).

The most comprehensive search was conducted using synonyms and derivatives of the following keywords: meta-analysis, genetic parameters, growth traits, production traits, economically important traits, egg quality traits, genetic correlation, components of variance, Iranian indigenous chickens, heritability, genetic evaluation, reproductive traits.

To summarize the results, a data set of information related to genetic parameters of different growth, reproduction, and egg quality traits of Iranian indigenous chickens, including 336 heritability and 433 genetic correlations from 45 studies were used in the present study. The considered articles were published between 2007 and 2019.

Studied traits

The studied traits were grouped as growth traits [body weight at hatch (BW1), body weight at eight weeks of age (BW8), body weight at 12 weeks of age (BW12)], reproductive traits [age at sexual maturity (ASM), weight at sexual maturity (WSM), egg number during the first three months of laying period (EN), mean egg weight at 28th, 30th, and 32nd weeks (MEW), egg weight at the first day of laying (FEW)] and egg quality traits [shell weight (SHW), shell strength (SHS), shell thickness (SHTH), albumen weight (AW), albumen height (AH), Haugh unit (HU) and yolk weight (YW)].

Data editing and preparation

After collecting the required information on genetic parameter estimates for the studied traits, the data were edited and prepared using the Microsoft Excel program. Information required for the analysis included direct heritability, maternal heritability, the genetic correlation between different traits, and their standard errors. However, the information related to data structure included type of breed, number of years for data collection, number of records, estimation method, model and method of analysis, phenotypic mean, standard deviation, and coefficient of variation. Weighted descriptive statistics were estimated using the data set provided. The methods used to estimate the variance components were restricted maximum

likelihood (REML) and Bayesian inference using mixed animal models. Only articles published in valid journals were considered. When the same estimates were published from different articles, only the latest publication information was used in the meta-analysis. Moreover, meta-analysis was conducted solely for traits that had a minimum of two relevant genetic parameter estimates (heritability and or genetic correlation) from different papers. When the standard error of genetic parameter estimates was not reported, the approximate amount of standard error was estimated by the formula of Sutton *et al.* (2000) which used the combined-variance method.

For the meta-analysis of genetic correlations, at first, the published correlation estimates were transformed to the Fisher's Z scale, and then, the estimated parameters were converted to correlations for reporting (Borenstein *et al.*, 2009). The conversion to the Fisher's Z scale would be necessary because the distribution of correlation estimates is usually non-normal. The following formula was used to calculate the approximate normal scale based on the Fisher's Z scale (Borenstein *et al.*, 2009):

$$Z_{ij} = 0.5[\ln(1 + r_{gij}) - \ln(1 - r_{gij})]$$

The r_{gij} is the genetic correlation published for the i^{th} trait in the j^{th} article. The following equation is also used to return to the original scale (Borenstein *et al.*, 2009):

$$r_{gij}^* = \frac{e^{2Z_{ij}} - 1}{e^{2Z_{ij}} + 1}$$

In this equation, r_{gij}^* is the retransformed genetic correlation for the i^{th} trait in the j^{th} article and Z_{ij} is Fisher Z transformation.

Weighted descriptive statistics

Weighted means and standard deviations for all traits were calculated using sample sizes as a weighting factor. The total number of records for each trait was calculated using the total number of records in individual studies reporting the trait. The percentage of coefficient of variation (CV%) for each of the studied traits was calculated using the following formula:

$$CV_i(\%) = \frac{S_i}{\bar{X}_i} \times 100$$

where S_i is the standard deviation for the i^{th} trait and \bar{X}_i is the trait mean.

Estimation of the weighted mean of heritability and correlations

In this study, a meta-analysis was performed based on a random-effects model using CMA software version 2.2 to calculate the effect size for genetic parameters (Borenstein *et al.*, 2009). This software can analyze data using random and fixed-effects models. However, publication bias, effect size summaries,

heterogeneity between different studies, forest plots, and funnel plots were drawn using this software.

The meta-analysis results for each study are summarized and plotted. Overall estimates, the average effect size, and 95% confidence interval are designed in a plot known as a forest plot. In this plot, the horizontal line represents the confidence interval for each study, and the square represents the effect sizes, the size of which is proportional to the inverse variance of the effect size (studied weight) or sample size.

Estimation of heterogeneity

In the present study, I^2 statistic and Q test were used to measure the degree of heterogeneity among studies (Borenstein *et al.*, 2011). Changes between study levels and heterogeneity were assessed using the Q test. The smaller the numerical value of Q, there is less heterogeneity between studies. Increasing the numerical value of this statistic indicated an increase in the degree of heterogeneity in the studied populations. Since the Q test is weak in detecting heterogeneity in studies with a small number of studies, so the numerical value of Q was measured with P-value and the significance level was set at 0.10 (Hardy & Thompson, 1998; Huedo-Medina *et al.*, 2006; Lean *et al.*, 2009). Higgins *et al.* (2003) sought to quantify heterogeneity between studies and defined I^2 statistic as a percentage of the heterogeneity that is part of the total variance of the study because it does not depend on the number of studies, unlike the Q statistic.

Negative values of I^2 were considered equal to zero. Therefore, the range of this index was between zero percent (0%) to one hundred percent (100%). When the I^2 statistic is equal to zero, which means that all variability in estimating the effect sizes is due to sampling errors and is a sign that no heterogeneity is observed. The degree of heterogeneity was considered negligible if the I^2 statistic was in the range of zero percent (0%) to forty percent (40%). A value of 40% to 60% often indicated moderate heterogeneity, and a value of 60% to 100% was considered significant heterogeneity (Higgins & Thompson, 2002; Lean *et al.*, 2009).

Determination of publication bias

Parameter estimates for different traits were examined by Egger's linear regression test if they were found to be homogeneous, provided there were at least three studies to determine the presence or absence of publication bias. According to this test, for each of the parameters of the studied traits, if the publication bias was detected ($P < 0.10$), the trim-and-fill method was used to estimate the number of missing studies, and to correct the final estimate (Duval & Tweedie, 2000). The use of a funnel plot is

a common method for investigating publication bias in studies. In this plot, the effect size is plotted for studies against the standard error of effect size (or other specified indicators). The symmetrical funnel plot indicates the absence of any missing studies.

Results

Weighted descriptive statistics

Table 1 shows the number of studies, unit of measurement, the total number of observations, and

weighted descriptive statistics including mean, standard deviation, and weighted coefficient of variation in the present study for growth, reproduction, and internal and external quality traits of eggs in Iranian native flows. Weighted coefficients of variation for growth traits were estimated to be from 4.89 (for BW1) to 23.03 (for BW12), from 4.86 (for EW) to 14.49 (for EN) for reproductive traits, and from 7.12 (SHW) to 15.48 (SHS) for egg quality traits.

Table 1. Summary statistics for different economically important traits of Iranian indigenous chickens

Trait ¹	Measurement unit	Number of literature estimates	Number of records	Mean	SD	CV (%)
BW1	g	17	559261	36.49	1.78	4.89
BW8	g	28	1082225	639.77	145.82	22.79
BW12	g	29	843359	1051.3	242.18	23.03
ASM	Day	41	834564	167.52	8.62	5.14
WSM	g	14	344891	1683.74	171.97	10.21
EN	Number	35	656778	42	6.09	14.49
FEW	g	8	208204	39.75	2	5.05
MEW	g	34	651416	46.844	2.277	4.861
AW	g	7	7071	28.42	3.27	11.53
AH	mm	6	6416	4.89	0.72	14.82
SHW	g	6	5862	5.04	0.35	7.12
SHS	kg/cm ²	5	5681	3.38	0.52	15.48
SHTH	mm	7	7637	0.35	0.05	15.42
YW	g	9	8952	16.11	2.12	13.2
HU	-	8	7848	70.38	6.19	8.79

¹ BW1, body weight at hatch; BW8, body weight at eight weeks of age; BW12, body weight at 12 weeks of age; ASM, age at sexual maturity; WSM, weight at sexual maturity; EN, egg number during the first three months of laying period; FEW, egg weight at the first day of laying; MEW, mean egg weight at 28th, 30th, and 32nd weeks; AW, albumen weight; AH, albumen height; SHW, shell weight; SHS, shell strength; SHTH, shell thickness; YW, yolk weight; HU, haugh unit.

Table 2. The number of contributing articles (N), Effect size and heterogeneity (I² index and Q statistics) of the direct heritability (h²) (\pm SE) estimates, 95% confidence interval for direct heritabilities for different economically important traits in Iranian indigenous chickens

Trait*	N	h ²	SE	95% CI	P-value	Q	P-value	I ²
BW1	19	0.222	0.041	0.142-0.303	0.000**	7573.3	0.000***	99.762
BW8	30	0.274	0.017	0.241-0.306	0.000**	960.448	0.000***	96.981
BW12	29	0.34	0.025	0.290-0.389	0.000**	2492.833	0.000***	98.877
ASM	41	0.346	0.021	0.305-0.386	0.000**	2764.313	0.000***	98.553
WSM	14	0.449	0.022	0.407-0.492	0.000**	287.394	0.000***	95.477
EN	39	0.186	0.011	0.164-0.208	0.000**	1605.043	0.000***	97.632
FEW	9	0.181	0.027	0.129-0.233	0.000**	480.477	0.000***	98.335
MEW	35	0.387	0.026	0.336-0.438	0.000**	5805.418	0.000***	99.414
AW	7	0.355	0.117	0.127-0.583	0.002**	179.284	0.000***	96.653
AH	6	0.284	0.068	0.150-0.419	0.000**	79.723	0.000***	93.728
SHW	6	0.332	0.091	0.154-0.510	0.000**	87.054	0.000***	94.256
SHS	5	0.261	0.061	0.140-0.381	0.000**	15.098	0.005***	73.506
SHTH	7	0.305	0.062	0.183-0.427	0.000**	33.886	0.000***	82.294
YW	9	0.211	0.064	0.085-0.338	0.001**	500.689	0.000***	98.402
HU	8	0.262	0.086	0.093-0.431	0.002**	311.093	0.000***	97.75

*For traits, see Table 1.

** $P < 0.05$.

*** $P < 0.10$.

Mean estimates of direct heritability

Table 2 presents the mean of direct heritability, 95% confidence interval, standard errors, and heterogeneity test indices obtained from the random-effects model of meta-analysis. Heritability estimates for growth traits showed that the measured traits had moderate heritability and the highest heritability belonged to BW12 (0.34). Heritability estimates for reproductive traits showed that except for WSM which had high heritability (0.449), other reproductive traits had low to moderate heritability. The lowest heritability was observed in EN (0.186) and FEW (0.181). Also, heritability estimates related to egg quality traits showed that all measured traits had moderate heritability and the highest heritability was related to AW (0.355) and the lowest (0.211) for YW. According to Table 2, the standard error for most of the studied traits in this study was low, which indicates the high accuracy of these parameter estimates. Estimates of direct heritability for all studied traits were significant ($P < 0.05$). The 95% confidence interval of direct heritabilities was not zero for all traits, and they generally had a narrow confidence interval which indicated that the estimates related to this parameter were accurate. The Q test was performed to test the heterogeneity of genetic parameter estimates. The value of the Q for all studied traits was estimated to be high, indicating a high degree of heterogeneity.

The significance of the Q test was measured by P-value. According to Table 2, this statistic was significant for all studied traits ($P < 0.10$). Therefore, this confirms the heterogeneity between the studies. Since the number of studies for the internal and external quality traits of eggs was low and the Q statistic is weaker when the number of studies is low, the I^2 statistic was used to determine the heterogeneity of the estimates. Considering that the numerical value of I^2 statistic for all traits was higher than 60%, it can be concluded that there was significant heterogeneity. Given that all traits were detected as heterogeneous, the publication bias test is inappropriate for these estimates and may lead to false-positive claims. Figure 1 provides a forest plot for individual studies and an overall result for estimating the mean direct heritability of the WSM. A forest plot for individual studies and the overall result of the average direct heritability estimates for other traits are presented in the supplementary file. Variability of heritability and standard error along with 95% confidence interval of different studies can be seen schematically in this plot. The effect size of mean direct heritability for WSM has been shown by the diamond shape at the bottom of the plot. Heterogeneity for the direct heritability estimates of the studied traits was evident in forest plots.

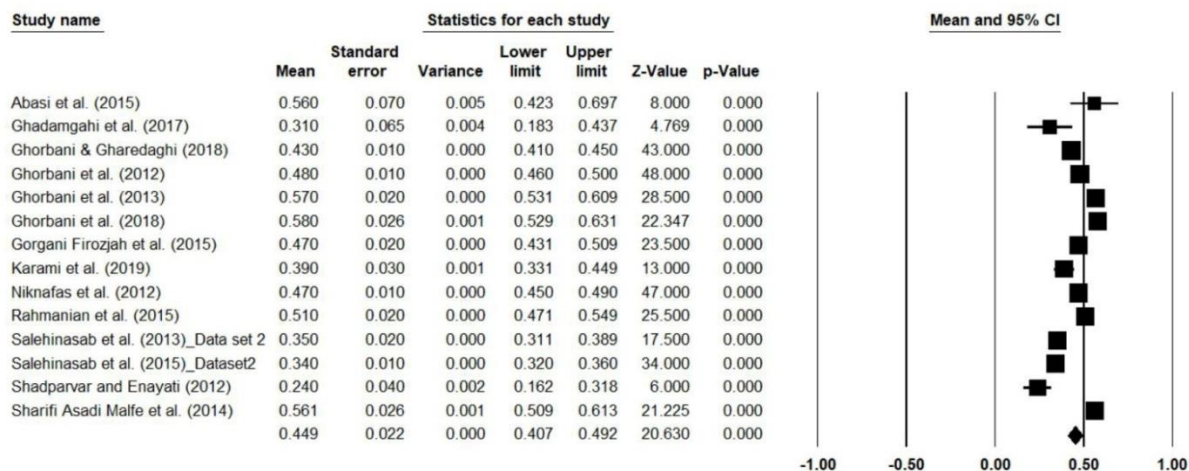


Figure 1. The forest plots for direct heritability estimates of WSM in Iranian indigenous chickens. The average effect size is presented by the diamond at the bottom of the plot. The squares' size indicates the weight for each study with regard to the average effect size. Smaller squares show less weight. The horizontal bars illustrate the 95% confidence intervals for each study.

Mean estimates of maternal heritability

Table 3 shows maternal heritability estimates with a 95% confidence interval, standard errors, and heterogeneity test indices of the studied traits. The mean estimates of maternal heritability for growth traits showed that except for BW1 which had moderate heritability (0.236), other estimates of maternal heritability were low and ranged from 0.009

(FEW) to 0.060 (ASM) (Table 3). The estimate of maternal heritability for EN was not significant ($P > 0.05$) which indicates that the estimate of this parameter for EN was not different from zero. The 95% confidence interval in this trait was zero. Estimate of maternal heritability was significant for other traits ($P < 0.05$; Table 3). According to the Q test and I^2 statistic, body weight at different ages,

ASM, EN, and MEW showed significant heterogeneity. The value of the Q test for these traits was high and also the numerical value of this test was estimated to be significant ($P < 0.10$; Table 3). In addition, the value of the I^2 statistic for these traits was higher than 60%, which indicated a high and significant heterogeneity for these traits. The numerical value of the I^2 statistic for WSM was equal to 69.365, which showed moderate heterogeneity. The I^2 statistic for the FEW was equal to zero.

Therefore, the degree of heterogeneity in this trait was zero and the corresponding parameter could be considered homogeneous (Table 3). After detecting homogeneity for this parameter, Egger's linear regression test was used to investigate the publication bias (Table 4). Based on the results of the Egger test, the P-value for FEW was estimated to be 0.309, which was greater than 0.10. Therefore, no publication bias was detected for FEW ($P > 0.10$; Table 4). Figure 2 shows a forest plot for the ASM. The forest plot for individual studies and its overall result for estimates of maternal heritability of other

traits studied in this research are presented in the supplementary file. The estimated effect size along with the 95% confidence interval for this trait is presented in Figure 2. The effect size for the mean maternal heritability of ASM is indicated by the diamond shape at the bottom of the plot. In this plot, the squares represent the sample size, and in fact, the squares' size shows the weight for each study with regard to the average effect size. Smaller squares indicate less weight. The horizontal lines of the plot present a 95% confidence interval for each study. The existing heterogeneity is well evident in this plot (Figure 2). Also, the results of evaluating the publication bias test and the trim-and-fill method to correct the asymmetry of the funnel plot of the FEW are shown in Table 4. As mentioned earlier, Egger's linear regression test for the FEW did not detect any publication bias ($P > 0.10$), but the trim-and-fill method detected two missing studies. This means that two studies were required on the left side of the funnel plot to adjust the plot asymmetry.

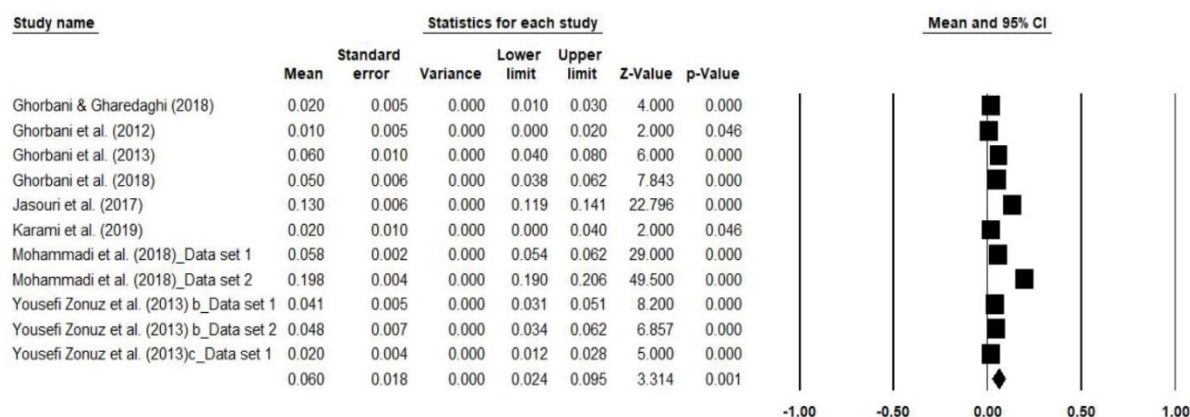


Figure 2. The forest plots for maternal heritability estimates of ASM in Iranian indigenous chickens. Detailed information is provided in Figure 1.

Table 3. The number of contributing articles (N), Effect size and heterogeneity (I^2 index and Q statistics) of the maternal heritability (h^2_m) (\pm SE) estimates, and 95% confidence interval for different economically important traits in Iranian indigenous chickens

Trait*	N	h^2_m	SE	95% CI	P-value	Q	P-value	I^2
BW1	9	0.236	0.036	0.165-0.308	0.000**	474.016	0.000***	98.312
BW8	14	0.053	0.015	0.023-0.082	0.000**	974.867	0.000***	98.666
BW12	9	0.096	0.043	0.013-0.180	0.024**	1628.561	0.000***	99.509
ASM	11	0.06	0.018	0.024-0.095	0.001**	1630.956	0.000***	99.387
WSM	5	0.016	0.003	0.009-0.022	0.000**	13.173	0.01***	69.635
EN	8	0.039	0.022	-0.005-0.083	0.081(ns)	2872.36	0.000***	99.756
FEW	3	0.009	0.003	0.003-0.016	0.004**	0.022	0.989 (ns)	0
MEW	13	0.053	0.014	0.026-0.080	0.000**	1350.851	0.000***	99.112

*For traits, see Table 1.

** $P < 0.05$.

*** $P < 0.10$.

ns non-significant ($P > 0.05$, $P > 0.10$).

Table 4. Results from Egger’s test and the trim-and-fill method for maternal heritability estimate of FEW in Iranian indigenous chickens

Trait*	Egger’s test <i>P</i> -value	Trim-and-fill method		
		Missing	Mean	95% CI
FEW	0.309	2	0.009	0.003-0.014

*For traits, see Table 1.

Missing: Number of missing studies.

Table 5. The number of contributing articles (N), effect size and heterogeneity (I2 index and Q statistics) of the genetic correlation estimates between different traits (r_g) estimates, and 95% confidence interval for different economically important traits in Iranian indigenous chickens

Trait 1*	Trait 2*	N	r_g	95% CI	<i>P</i> -value	Q	<i>P</i> -value	I ²
AH	AW	5	0.354	-0.034-0.649	0.073 (ns)	20.533	0.000***	80.52
AH	HU	4	0.979	0.955-0.990	0.000**	1.36	0.715 (ns)	0
AH	SHW	4	0.176	-0.063-0.396	0.148 (ns)	4.165	0.244 (ns)	27.975
AH	YW	5	0.06	-0.064-0.181	0.344 (ns)	5.744	0.219 (ns)	30.357
ASM	EN	20	-0.687	-0.772- -0.579	0.000**	4335.486	0.000***	99.562
ASM	EW	22	0.234	0.155-0.311	0.000**	1003.644	0.000***	97.908
ASM	FEW	4	0.398	0.167-0.587	0.001**	160.354	0.000***	98.129
ASM	WSM	4	0.216	-0.012-0.423	0.063 (ns)	196.523	0.000***	98.473
AW	HU	5	0.134	-0.323-0.540	0.574 (ns)	14.84	0.005***	73.045
AW	SHS	4	0.024	-0.176-0.222	0.818 (ns)	5.571	0.134 (ns)	46.15
AW	SHTH	4	0.149	-0.100-0.381	0.24 (ns)	2.352	0.503 (ns)	0
AW	SHW	5	0.669	0.473-0.802	0.000**	1.364	0.85 (ns)	0
AW	YW	5	0.139	-0.140-0.398	0.329 (ns)	5.647	0.227 (ns)	29.165
BW1	ASM	9	0.08	0.050-0.110	0.000**	25.018	0.002***	68.023
BW1	BW8	11	0.369	0.301-0.433	0.000**	276.353	0.000***	96.381
BW1	BW12	11	0.297	0.246-0.346	0.000**	111.252	0.000***	91.011
BW1	EN	8	-0.024	-0.112-0.065	0.602 (ns)	241.375	0.000***	97.1
BW1	EW	10	0.446	0.342-0.540	0.000**	878.71	0.000***	98.976
BW1	FEW	5	0.361	0.091-0.581	0.01**	549.658	0.000***	99.272
BW1	WSM	6	0.309	0.209-0.403	0.000**	202.751	0.000***	97.534
BW8	ASM	10	-0.075	-0.135- -0.015	0.015**	71.299	0.000***	87.377
BW8	BW12	12	0.878	0.745-0.944	0.000**	1938.673	0.000***	99.433
BW8	EN	11	-0.041	-0.078- -0.005	0.026**	57.897	0.000***	82.728
BW8	EW	13	0.264	0.200-0.326	0.000**	113.283	0.000***	89.407
BW8	FEW	5	0.273	0.219-0.325	0.000**	19.232	0.001***	79.202
BW8	WSM	7	0.503	0.374-0.614	0.000**	421.62	0.000***	98.577
BW12	ASM	19	-0.04	-0.077- -0.003	0.032**	132.9	0.000***	86.456
BW12	EN	19	-0.062	-0.115- -0.008	0.024**	283.244	0.000***	93.645
BW12	EW	21	0.339	0.281-0.394	0.000**	328.929	0.000***	93.92
BW12	FEW	5	0.35	0.279-0.417	0.000**	31.849	0.000***	87.441
BW12	WSM	9	0.662	0.542-0.756	0.000**	492.679	0.000***	98.376
EN	EW	21	-0.278	-0.361- -0.191	0.000**	1859.111	0.000***	98.924
EN	FEW	4	-0.534	-0.693- -0.325	0.000**	150.262	0.000***	98.004
EW	FEW	5	0.788	0.685-0.860	0.000**	80.671	0.000***	95.042
EW	AW	4	0.931	0.829-0.973	0.000**	0.151	0.985 (ns)	0
EW	HU	4	-0.331	-0.560- -0.055	0.02**	5.045	0.169 (ns)	40.536
EW	SHS	5	-0.012	-0.166-0.142	0.876 (ns)	1.206	0.877 (ns)	0
EW	SHTH	5	0.113	-0.281-0.474	0.581 (ns)	14.587	0.006***	72.579
EW	SHW	6	0.779	0.755-0.801	0.000**	1.523	0.91 (ns)	0
EW	YW	4	0.528	0.257-0.721	0.000**	1.031	0.794 (ns)	0
SHS	SHW	4	0.356	0.099-0.568	0.008**	2.582	0.461 (ns)	0
SHS	SHTH	4	0.571	0.377-0.717	0.000**	2.615	0.455 (ns)	0
SHW	HU	4	0.037	-0.163-0.234	0.718 (ns)	3.126	0.373 (ns)	4.019
SHW	SHTH	4	0.856	0.706-0.933	0.000**	0.052	0.997 (ns)	0
WSM	EN	7	-0.348	-0.477- -0.205	0.000**	276.998	0.000***	97.761
WSM	EW	8	0.48	0.390-0.560	0.000**	102.181	0.000***	93.149
WSM	FEW	4	0.504	0.403-0.593	0.000**	68.091	0.000***	95.594
YW	HU	5	-0.069	-0.108- -0.031	0.000**	3.226	0.521 (ns)	0
YW	SHS	4	-0.057	-0.405-0.305	0.764 (ns)	9.295	0.026 (ns)	67.725
YW	SHTH	4	0.051	-0.294-0.384	0.778 (ns)	9.047	0.029 (ns)	66.841
YW	SHW	5	0.126	-0.155-0.388	0.382 (ns)	7.548	0.11 (ns)	47.009

*For traits, see Table 1.

***P* < 0.05.

****P* < 0.10.

ns non-significant (*P* > 0.05, *P* > 0.10).

Mean estimates of genetic correlation between growth, reproduction, and egg quality traits

Table 5 presents genetic correlation estimates, 95% confidence interval, and heterogeneity of estimates based on Q test and I^2 statistics. The mean genetic correlation between AH and other internal and external egg quality traits was positive. The estimates varied from 0.06 (YW) to 0.979 (HU). The genetic correlation between AH-HU was positive, high (0.979), and significant ($P < 0.05$). But its correlation with AW was moderate (0.354) and non-significant ($P > 0.05$; Table 5). Also, the 95% confidence interval covered a wide range that included zero. Table 5 shows the genetic correlation between ASM-EN was negative and high (-0.687). The genetic correlation between ASM with MEW, FEW, and WSM was moderate and positive. Apart from the genetic correlation between ASM-WSM, its correlation with other production traits was significant ($P < 0.05$).

The genetic correlation between AW-SHW was positive, high (0.669), and significant ($P < 0.05$). Also, the genetic correlation between this trait and HU, SHS, SHTH, and YW was low, positive, and non-significant ($P > 0.05$). The genetic correlation between body weight at different ages was positive and varied from moderate to high. The means of genetic correlation between BW1 with BW8 and BW12 were 0.369 and 0.297, respectively. Also, the genetic correlation between BW8 and BW12 was positive and high (0.878). Estimates of genetic correlation between BW1 with reproductive traits ranged from -0.24 (EN) to 0.446 (MEW) (Table 5). Except for the genetic correlation between BW1 with EN which was low and non-significant, the genetic correlation of this trait with other traits was significant ($P < 0.05$).

Genetic correlation estimates between BW8 with reproductive traits ranged from low to high and ranged from -0.075 (ASM) to 0.503 (WSM). All genetic correlation estimates between BW8 with reproductive traits were significant ($P < 0.05$). Also, the genetic correlation estimates between BW12 with reproductive traits varied from -0.062 (EN) to 0.662 (WSM). The genetic correlations between BW12 with reproductive traits were significant ($P < 0.05$; Table 5).

The genetic correlation between EN with MEW was low and negative (-0.278) and with MEW was negative and high (0.534). Estimates of genetic correlation between EN with these two traits were also significant. The weighted genetic correlation between MEW with FEW was positive and high (Table 5).

The genetic correlations between MEW with AW, HU, and YW were positive and high (0.931), negative and moderate (-0.331), and positive and moderate (0.528), respectively. Also, all these estimates were significant ($P < 0.05$). The mean genetic correlation between MEW and egg quality traits ranged from -0.012 (SHS) to 0.779 (SHW), which were significant only for the correlation between EW and SHW.

The heterogeneity test of genetic correlation estimates was performed by the Q test and I^2 statistic. Based on these tests, the genetic correlation between AH with HU, SHW, and YW and also the genetic correlation between AW with SHS, SHTH, SHW, and YW had negligible Q values and were homogeneous. The value of the I^2 statistic for these traits ranged from 0% to 40%; therefore, the degree of heterogeneity in these traits was negligible and non-significant. Also, the Q test value was not significant for these traits ($P > 0.10$).

Table 6. Results from Egger's test and the trim-and-fill method for genetic correlations between different traits in Iranian indigenous chickens

Trait 1*	Trait 2*	Egger's test P -value	Trim-and-fill method		
			Missing	Mean	95% CI
AH	HU	0.711	2	0.975	0.950-0.987
AH	SHW	0.046	2	0.306	0.055-0.521
AH	YW	0.808	1	0.056	-0.052-0.165
AW	SHS	0.746	0	0.023	-0.176-0.221
AW	SHTH	0.772	1	0.104	-0.133-0.331
AW	SHW	0.396	1	0.678	0.496-0.803
AW	YW	0.653	1	0.044	-0.233-0.314
EW	AW	0.215	2	0.927	0.827-0.970
EW	HU	0.352	2	-0.489	-0.692- -0.213
EW	SHS	0.095	2	0.015	-0.130-0.159
EW	SHW	0.741	0	0.779	0.755-0.801
EW	YW	0.095	1	0.557	0.331-0.723
SHS	SHW	0.068	2	0.259	-0.007-0.492
SHS	SHTH	0.086	0	0.57	0.377-0.716
SHW	HU	0.269	1	0.099	-0.149-0.336
SHW	SHTH	0.418	1	0.858	0.717-0.932
YW	HU	0.859	0	-0.069	-0.108- -0.030
YW	SHW	0.432	1	0.037	-0.249-0.317

*For traits, see Table 1.

Missing: Number of missing studies.

In addition, the genetic correlation between MEW with AW, HU, SHS, SHW, YW, and also the genetic correlation between SHS with SHW and SHTH were homogeneous due to the low values of the Q test and I^2 statistic. The Q test was not significant for the correlation between these traits ($P > 0.10$; Table 5). Based on the heterogeneity test presented in Table 5, estimates of the genetic correlation between SHW with HU and SHTH, and the genetic correlation between YW with HU and SHW, showed a low heterogeneity for these traits which could be considered homogeneous. The value of the Q test and I^2 statistic for other traits were significant and high. The estimate of the Q value for these traits was also significant ($P < 0.10$). Therefore, the genetic correlations between these traits were considered to be heterogeneous. Because of the homogeneous genetic correlations between the aforementioned traits, Egger's linear regression test was used to investigate the publication bias (Table 6). As shown in Table 6, Egger's linear regression test indicated no publication bias ($P > 0.10$) for the mean correlation between AH with HU and YW, the genetic

correlation between AW with SHS, SHTH, SHW, YW, and also the genetic correlation between EW with AW, HU, SHW. In addition, for the genetic correlation between SHW with HU, SHTH, and genetic correlation between YW with HU, SHW, no publication bias was detected. On the other hand, the presence of publication bias was detected ($P < 0.10$) for genetic correlation between AH with SHW, EW, SHS, and EW with YW, SHS, and SHW, as well as the genetic correlation between SHS, SHTH. Figure 3 shows a forest plot for the genetic correlation between ASM with EN. Estimated effect sizes and 95% confidence intervals for genetic correlation between ASM and EN are shown in this plot. Table 6 presents the results of the evaluation of the publication bias test and the trim-and-fill method for correcting the asymmetry of funnel plots of traits that were found to be homogeneous. Based on the trim and fill method, the number of missing studies for genetic correlation estimation between AW-SHS, EW-SHW, SHS-SHTH, as well as YW-HU was equal to zero. The funnel plots for these traits were perfectly symmetric.

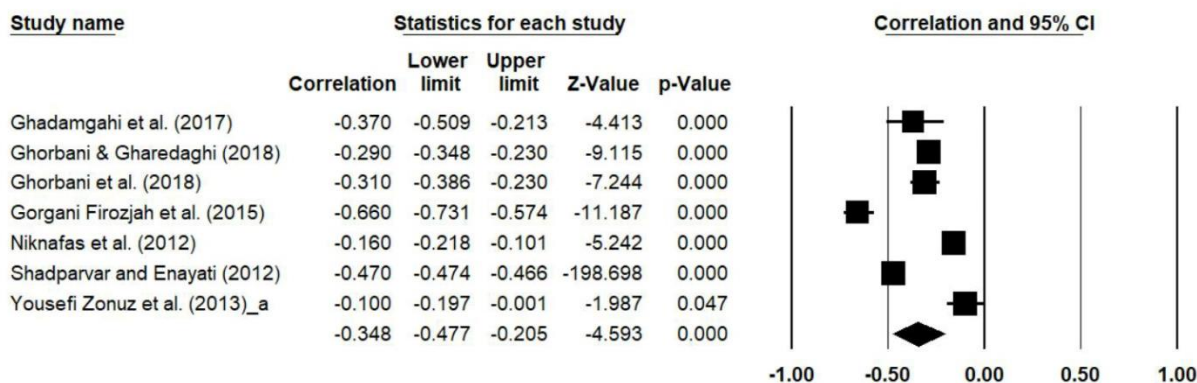


Figure 3. The forest plots for genetic correlation estimates between ASM and EN in Iranian indigenous chickens. Detailed information is provided in Figure 1.

According to Table 6, genetic correlation estimates between AH-HU, EW-AW, EW-HU as well as SHS-SHW required two missing studies on the left side of the plot to correct the asymmetry of these plots. Two missing studies on the right side of the plot were needed to correct the funnel plots of genetic correlation estimates between the AH-SHW, as well as the EW-SHS (Table 6). In addition, as shown in Table 6, based on the trim-and-fill method, the estimates of genetic correlation between AH-YW, AW-SHTH, AW-YW, as well as the genetic correlation between YW-SHW require one missing study on the left side of the plot. Genetic correlation estimates between AW-SHW, EW-YW, SHW-HU, and genetic correlation between SHW-SHTH needed one missing study on the right side of the plot to correct the asymmetry of the respective funnel plots.

Discussion

The importance of preserving native genetic resources and the use of optimal production methods and new breeding methods play an effective role in increasing the livestock production quality in any country (Jasouri *et al.*, 2017). Therefore, there is an urgent need to provide accurate estimates of genetic parameters including heritability and genetic correlation traits. Definition of genetic goals helps us a lot in setting long-term goals, designing breeding programs, better understanding of the genetic mechanisms of traits, and predicting the expected response from selection programs (Matika *et al.*, 2003). A review of the relevant literature provides different genetic parameter estimates of the important economic traits in different breeds of Iranian indigenous chickens. The difference between

estimates reported in various studies may be due to variations in environmental and managerial conditions, genetic structure differences in the study population, type and size of the study population, and different approaches applied for estimating heritability. Meta-analysis using a random-effect model allows the integration and combination of heritability estimates and correlation for economically important traits (Safari *et al.*, 2005; Akanno *et al.*, 2013; Diaz *et al.*, 2014).

The number of articles on the genetic basis of growth and reproduction traits was high, which indicates the greater importance of these traits for breeding programs of Iranian indigenous chickens. The amount of weighted coefficient of variation for body weight at different ages increased with age. The weighted coefficient of variation for all studied traits was less than 25%, which indicates relatively good control of the factors that cause differences and diversity. Further, the dispersion of these traits was low. The lowest weighted coefficient of variation for growth traits was for BW1 (4.89%), which demonstrates that the phenotypic diversity of these traits is biologically low and indicates good control of these traits.

The highest estimate of heritability was related to WSM and MEW, which showed a large impact of genes with additive action on these traits and indicates a more appropriate response of these traits to selection programs. It also indicates a significant contribution of the genes in creating phenotypic diversity. As a result, the use of breeding methods will improve these traits more quickly in the next generations. This indicates that WSM and MEW are under additive genetic effects control and satisfactory genetic responses would be expected if these traits are included in the breeding goals of Iranian indigenous chickens. The lowest estimate of heritability was related to FEW and EN, which indicates that the effect of non-genetic factors, such as environmental factors, on these traits is greater than the genetic ones, and genetic progress would be slower for these traits. Also, the effect of management on the manifestation of such traits would be much greater. The mean estimate of heritability for growth traits was moderate; therefore, the response to selection for these traits is expected to be moderate as well. Genes affecting body growth often have an additive effect and the collection of these genes in one breed is one of the breeding program's goals. Generally, when a trait has a high heritability, it can be improved quickly by selection programs. Although the rate of genetic improvement depends on heritability, other variables such as genetic variation, generation interval, and selection intensity would also influence the genetic gain (Ghavi Hossein-Zadeh, 2021). In this study, standard errors and 95% confidence interval for estimates of direct heritability of growth and

reproductive traits were low, which showed the high accuracy of the estimates being reported in this study. Due to the smaller number of observations for the internal and external egg quality traits, their standard error and 95% confidence interval were slightly higher than other traits. Except for BW1, the maternal heritability estimates were generally low for other traits (Table 3). Besides, maternal heritabilities were lower than direct ones, indicating the slow rate for the genetic improvement of maternal effects for such traits. The maternal genetic effect can be defined as the effect of maternal genotype on the studied traits that can affect the offspring's function (Dobson, 1991). It was suggested that the removal of any maternal effects from the model of analysis would lead to overestimation of the direct additive genetic variance and would finally lead to overestimation of the direct heritability. Thus, considering the maternal effects would contribute to a more accurate estimation of the (co) variance components as well as genetic parameters of fowl's performance traits. Accordingly, making selections based on direct breeding values, without any notice of additive maternal effects, would lead to the reduction of effective maternal potentials for some reproductive traits in the course of each generation.

The genetic correlations between body weights at different ages were positive, moderate, and somehow high. The genetic correlation between BW8 and BW12 was positive and high, indicating that similar genes are responsible for controlling these traits. In addition, it can be argued that their genetic structure is highly similar and selection for body weight at younger ages would lead to greater body weight in older ages. The genetic correlations between BW1 with both MEW and FEW were reported as positive and moderate. The value of this genetic correlation indicates that selection for increased BW1 would positively lead to higher values reported for MEW and FEW. The genetic correlation of this trait with ASM has been estimated as positive and low, indicating that selection to increase BW1 wouldn't have a significant effect on improving ASM. The genetic correlation between BW8 and BW12 with both MEW and FEW was positive and moderate as well. Thus, as a result of selection to increase body weight, it can be expected that correlated response would be incurred in MEW and FEW traits upon making the selection. In other words, heavier fowls are expected to lay bigger eggs. Usually, the existence of a genetic correlation between traits shows that selection for a particular trait would lead to variations in other traits. This phenomenon is known as a correlated response to selection. Considering the negative and low correlation between BW8 and BW12 with ASM, it seems that selection to increase body weight at 8 and 12 months of age may decrease ASM to some extent. Therefore, the

simultaneous selection of indigenous fowls for ASM reduction and increase in BW8 and BW12 and their use in the selection index may lead to increased genetic progress for these traits. Although much reduction in ASM is not favorable because this would lead to a higher number of produced eggs which is a favorable outcome, due to the negative correlation between EN and EW, one can expect that attempts toward increased EN would lead to reduced egg weight and production of smaller-than-normal eggs. These small eggs are not suitable for incubation purposes. Besides, fowls store a sufficient amount of calcium before hatching. Therefore, as a result of their premature puberty, they lack sufficient reservoirs for hatching. That's why their produced eggs have a very thin eggshell. Thus, it can be expected that the co-presence of these two traits in the selection index would lead to lowered genetic progress for each trait. Moreover, in case the fowl's growth rate at pre-sexual maturation and sexual development would be lower than optimal, selection for body weight increase would favorably lead to lower ASM; however, in case the fowls have proper pre-sexual maturation body development indices, selection for increased body weight not only wouldn't lead to earlier maturation but also would delay the maturation stage among indigenous chicken.

The correlation between body weight at different ages and WSM was positive and average. Thus, selection to increase body weight at different ages would lead to increased WSM. Selection for increased body weight throughout native fowl's life cycle leads to reaching an appropriate body weight at sexual maturity. Consequently, this would result in the development of the required physical prerequisites for the production of heavier birds with high-quality eggs. Because egg weight would affect the survival potential and final weight of the chicks, it can be considered a critical trait. In other words, medium-sized to large eggs are endowed with higher incubation potential compared with smaller eggs (King'ori, 2011). Although increased egg weight is considered an important objective in the breeding programs of fowls, the proportion of different contents of the egg is important as well. That's because cholesterol and fat would make a major portion of the eggs yolk, which is arguably noticed in terms of health-related issues. Lower yolk weight is positively correlated with the amount of cholesterol in eggs. Besides, it seems that the lower weight of the albumen is due to different factors including breed, environmental issues, and their diet.

There was a positive correlation between WSM and ASM and it seems that early sexual maturity of the fowls would lead to lower weight at the age of sexual maturation. Thus, in the case of selection to reduce ASM, maturation weight must be simultaneously controlled as well. The negative

correlation between WSM and EN suggests that upon any increase in body weight during maturation, the number of produced eggs would be decreased. The mean genetic correlation between WSM and MEW illustrates that the heavier fowls at maturation, the higher MEW would be expected. This may be due to the finalization of fowl's reproductive nature in terms of hormone and physiological conditions. The correlation between the mean eggs weight and traits including AW and SHW was positive and high. Furthermore, the genetic correlation between MEW and SHTH has been estimated as positive, and the correlation between MEW and YW was estimated to be moderate and positive as well. The genetic correlations between these traits suggest that those genes responsible for controlling the egg weight contribute a lot to the emergence of AW, SHW, SHS, and finally YW. However, enhanced SHW and AW, as a result of selection based on egg weight, can't be regarded as favorable. That's because the quality of the day-old chick is highly dependent upon the weight of the egg yolk as well as the ingredients of the yolk. Though the selection based on the egg weight would result in increased YW, as a relevant trait for day-old chicks, at the same time, it may affect the incubation potential due to the observed increase in AW, SHW, and SHTH. To put it differently, due to the higher heritability of eggs weight as well as the positive genetic correlation with AW and YW, a higher mean for these traits is to be expected as a result of selection for eggs weight; however, due to the observed negative correlation with SHTH, thinner eggshells are to be expected in next generations. Thus, it is necessary to pay attention to SHTH for the prevention of side effects associated with thin eggshells in the breeding programs. The genetic correlation between SHTH and SHS was positive. Besides, as expected, after selection for increased SHTH, the resultant eggshell would be stronger (Table 5).

The mean genetic correlation between egg weight and AW was positive and high. On the contrary, the genetic correlation between egg weight and HU was estimated to be negative and moderate. These correlation estimates lead us to the following conclusion: although selection for egg weight among indigenous chickens of Iran would lead to higher values being reported for AW, its quality would be lowered likely. The mean genetic correlation between AH and other traits including AW and HU was positive and medium to high. This fact suggests that in the case of selection for increased AH, an improvement in egg quality traits is expected due to the moderate heritability and its optimal correlation with other traits concerning egg quality. The positive but low correlation of the albumen with HU leads us to conclude that larger albumen doesn't necessarily lead to high-quality eggs. Considering the positive

and high genetic correlation between FEW and MEW, one can argue that attempts toward increased FEW would finally lead to higher MEW throughout the whole breeding period. The wide confidence interval estimated for genetic correlations between some traits indicates a relatively smaller data set and diversity between studies.

In conclusion, the proposed meta-analysis using a random-effects model provides the pooled estimates of heritability as well as genetic correlations for

growth, reproduction, and egg quality traits in Iranian indigenous chickens. Because of the importance of accurate genetic parameter estimates for improving economic traits in the breeding programs, the estimates reported in the present study are appropriate to be used in breeding programs when accurate genetic parameter estimates are not obtainable for economically important traits in Iranian indigenous chickens.

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