

Estimation of genetic trends and parameters for some economic traits using different linear models in Mazandaran native chickens

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At the Mazandaran native fowl breeding center we have developed a breeding scheme in order to produce dual purpose birds for rural areas. In this way, fully pedigreed records were applied to estimate variance components of some economic traits in a population of Mazandaran native fowl. The number of animals in the pedigree programme were 74351 and the number of records in data were 47452 to 72547. In the present study direct and maternal genetic and maternal common environmental effects were estimated for some economic traits including body weight at day 1 of age (BW1), body weight at 8 weeks of age (BW8), body weight at 12 weeks of age (BW12), weight at sexual maturity (WSM), age at sexual maturity (ASM), egg number (EN), egg weight at day 1 of laying (EW1) and mean egg weight (MEW). Data analysis was conducted by a series of six various animal models accompanied by maternal effects for the above-mentioned traits. Estimates of direct heritability ranged from 0.04 (BW1) to 0.54 (MEW) on the basis of most best fitted models. The maternal heritability estimates were in the range from 0.01 to 0.16, while the maternal common environmental variance ranged from 0.01 (EW1) to 0.21 (BW1) according to the fitted models. Our study demonstrated that model choice is an important factor in an accurate estimation of production and reproduction traits. A negative correlation was found between direct and maternal additive genetic effects (ram). The predicted genetic gains by the regression of breeding value on the generation number amounted to 9.99, 1.32, 0.06 and -1.44 for BW12, EN, MEW and ASM, respectively. Regarding the program of the Mazandaran native fowl breeding center in producing dual purpose chickens, despite the negative correlations between some of the selected traits (BW12, EN, ASM, and MEW), the genetic gain was observed in all selected traits of MNF during 23 generations. Taken together, it was concluded that including the direct genetic effect and maternal effects in the model will result in improving the selection efficiency for production and reproduction traits in fowl.

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Native fowls have been known as valuable genetic resources that are well adapted to harsh environments in rural areas [Kheirkhah *et al.* 2017]. In some countries many efforts have been made to preserve native breeds of chickens from extinction. Furthermore, some strategies have been developed for decades to increase productivity in village production systems [Teklewold *et al.* 2006]. Indigenous fowls exhibit greater disease resistance and higher performance potential under poor nutritional and environmental conditions compared to commercial strains in rural areas [Horst 1989]. Thus, breeding schemes need to be implemented in order to improve growth rate and egg production traits. Among domestic chickens, Iranian native fowls (INFs) have also been included in these debates. INFs are used in a large part of rural poultry farming throughout the country and are most popular providers of high quality and antibiotic-free protein sources for consumers.

Mazandaran native fowls (MNFs) are one of the major fowl populations in Iran that are naturally reared all over the Mazandaran province in northern Iran. These are dual purpose birds producing both eggs and meat. Hence, it is of importance to estimate the (co)variance components of economic traits in MNF. Understanding these relationships would be beneficial in maintaining genetic diversity, improving production and designing breeding programs for the MNFs. Previous reports have highlighted the significance of other genetic effects in poultry performance traits and livestock [Albuquerque *et al.* 1998, Mannen *et al.* 1998, Wei and van der Werf 1993]. A genetic model that includes non-additive and maternal (indirect) effects provides a more precise prediction of breeding values [Wei and van der Werf 1993]. The direct additive genetic component of the trait may be assessed through a single observation in each animal. However, similarities between relatives may result from the effects of shared environments as much as genetic effects [Kruuk and Hadfield 2007]. In order to comprehend the maternal effect (common phenotypes shared by all offspring of the same dam) in a population, it is necessary to have data for the number of offspring produced by a given dam, the number of recorded dams and the number of generations with data [Heydarpour *et al.* 2008, Maniatis and Pollott 2003]. At the presence of maternal genetic effects, which are neglected, the resulting overestimation of direct heritability may sometimes be as high as over 2-fold [Clement *et al.* 2001]. In poultry the maternal common environmental effect is different than this in mammals. This is because more than one egg from different hens is hatched and raised together under the same environmental conditions [Ghorbani *et al.* 2013]. Unfortunately, knowledge regarding existing potential productivity and production characteristics of native chickens is limited [Hoffmann 2005]. This may to some extent be related to the low production performance of native chickens and their inability to economically compete with commercial chickens. It is important to take into account appropriate breeding plans to obtain better production and reproduction potential of INFs.

The overall objective of this study was to estimate the (co)variance components and genetic parameters using appropriate animal models for economic traits in MNF.

In addition, we evaluated the results of long term selection based on genetic merits of production and reproduction traits in a population of MNFs.

Material and methods

Geographical location and management

MNFBC is located in the Mazandaran province of northern Iran at the southern coast of the Caspian Sea and it was established in 1986 with the objective of saving MNF from extinction in rural areas. The base generation of the MNFBC breeding scheme comprised hatched eggs laid by hens that are morphologically similar. The eggs were gathered from rural areas in the Mazandaran province. Growing birds were fed a diet containing 2900 kcal/kg metabolisable energy (ME) and 175g crude protein CP/kg. Laying birds were fed diets with 160g CP/kg and 2800 kcal/kg ME. For regeneration programs in MNFBC, one-day-old chicks were produced annually in 3 to 4 hatches. The chicks from each hatch were reared in different houses, under identical management conditions. Since this procedure was similar during 23 generations, the generation intervals did not change. In this study the hens were nested with the rooster with a hierarchical family structure. In the mating plan each rooster mated with 10 hens and each family unit was kept in a distinct pen. A total of 10 trapnests were used per each pen and only the trapnest records were considered.

Data and traits

The data analysed in the present study were collected over 23 generations. This dataset includes different records for production and reproduction traits such as body weights at day 1 of age, 8 weeks of age, 12 weeks of age and at sexual maturity, age at sexual maturity, the number of eggs during the first 12 weeks of the laying period, mean egg weight at weeks 28, 30 and 32 of age and egg weight at day 1 of laying. The traits of WSM and ASM were recorded when the hen laid the first egg. The detailed description of the data examined in this study is given in Table 1.

Table 1. Description of data used to estimate the (co)variance components for selected economic traits in Mazandaran native fowl

Item	Trait*							
	BW1(g)	BW8(g)	BW12(g)	WSM(g)	ASM(d)	EN	EW1(g)	AEW(g)
Number of records in data	50465	72547	63513	55662	56428	56039	47452	55170
Number of sires with progeny in the data	1340	2010	1637	1994	1996	1996	1711	1995
Number of dams with progeny in the data	9913	14475	12081	14026	13995	14010	11934	13968
Mean	36.33	577.09	1002.02	1708.22	160.44	39.05	41.22	48.45
Standard deviation	3.55	153.95	229.44	260.54	18.69	16.41	7.21	4.49
Minimum	20.10	300	500	1000	100	1	20	30.02
Maximum	65.10	1300	2000	2800	230	110	87	80.70

*BW1 – BW at day 1 of age; BW8 – BW at 8 weeks of age; BW12 – BW at 12 weeks of age; WSM – weight at sexual maturity; ASM – age at sexual maturity; EN – egg number in the first 12 weeks of the laying period; EW1 – egg weight at day 1 of laying; EW28-30-32 (AEW) – mean egg weight at 28, 30 and 32 weeks of age.

Statistical analyses

The dataset was first screened several times and faulty or outlier data points were excluded from final analyses. The descriptive statistics were calculated by the PROC GLM of the SAS software [Statistical Analysis System (SAS) 2004]. All birds were selected using an estimated breeding value (EBV) index for the direct genetic effect of four traits including BW12, EN, ASM and AEW. These traits were considered as the breeding objectives in the MNFBC throughout all the 23 generations. In this manner, genetic parameters were estimated by an animal model using the WOMBAT software [Meyer 2006]. In this study the generation, hatch and sex were considered as fixed effects.

Random effects that were included in the model were animal and residual. The following animal model was applied:

$$y_i = X_i b_i + Z_i a_i + e_i$$

where:

y_i – observations vector for the i^{th} trait;

X and Z – incidence matrices that relate observations to the fixed and random effects of model;

b_i – the fixed effects vector for the i^{th} trait;

a_i – the random additive genetic effect vector for the i^{th} trait;

e_i – the residual random effects vector for the i^{th} trait and $i = 1$ to 8 for eight traits including BW1, BW8, BW12, ASM, WSM, EW1, AEW and EN.

The genetic trends for the above-mentioned traits were assessed through the regression of average breeding values on the generation. The genetic trend for each trait over the generations was graphed by plotting the average breeding values over the generations. In order to avoid the mating of closely related birds resulting in increased inbreeding, we calculated the relationship coefficient between individuals using the CFC software package [Sargolzaei 2006].

Data analysis was conducted with the use of six different animal models, including or excluding maternal effects. The models were as follows:

$$y = Xb + Z_1 a + e \tag{1}$$

$$y = Xb + Z_1 a + Wc + e \tag{2}$$

$$y = Xb + Z_1 a + Z_2 m + e \quad \text{cov}(a, m) = 0 \tag{3}$$

$$y = Xb + Z_1 a + Z_2 m + e \quad \text{cov}(a, m) \neq 0 \tag{4}$$

$$y = Xb + Z_1 a + Z_2 m + Wc + e \quad \text{cov}(a, m) = 0 \tag{5}$$

$$y = Xb + Z_1 a + Z_2 m + Wc + e \quad \text{cov}(a, m) \neq 0 \tag{6}$$

y – the vector of observations;

$$V \begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_c\sigma_c^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

b – the vector of fixed generation-hatch (nested within generation) effects for all traits, and also sex effect for the BW1, BW8 and BW12 traits;

X – the incidence matrix for the fixed effects;

a – the vector with direct genetic effects with the associated matrix;

Z₁, c – the maternal common environmental effects vector with the associated matrix;

W, m – the maternal genetic effects vector with the associated matrix

Z₂, and e – the vector of residual effects.

The (co)variance structure is given below:

A – the additive numerator relationship matrix;

σ_a² – the direct additive genetic variance;

σ_m² – the maternal additive genetic variance;

σ_{am} – the direct-maternal additive genetic covariance;

σ_c² – the maternal common environmental variance;

σ_e² – the residual variance;

I_c, and I_n – identity matrices with orders equal to the numbers of dams and records, respectively.

Estimates of (co)variance components, as well as log likelihood values (log L) for each trait were obtained via fitting single-trait animal models. The models were analysed using the WOMBAT software with the average information restricted maximum likelihood (AI-REML) algorithm [Meyer 2006].

A likelihood ratio test (LRT) was run to select the most appropriate random effects. This test was applied to determine which model is statistically better for each trait by adding the random effects to the model. The LRT is based on the chi-square distribution with k degrees of freedom. In this way, degrees of freedom for the LR test (k) are equal to the number of additional parameters in the more complex model [Dobson 2002]. The following equation was used to describe LRT [Grosso *et al.* 2010]:

$$\chi_k^2 = 2 \log L (F) - 2 \log L (R)$$

L (F) – the likelihood for the full model;

L (R) – the likelihood for the residual model.

Results and discussion

Native fowls have played a significant role in rural societies of Iran. These birds are used for rural backyard production and to generate income. Therefore, there is an interest to genetically improve the meat and egg traits in native chickens for different rural conditions. At the Mazandaran native fowl breeding center (MNFBC) we have developed a breeding scheme in order to produce dual purpose birds for rural areas. In this way, fully pedigreed records were applied to estimate the variance components of some economic traits. In our program we evaluated the results of long term selection based on genetic merits of production and reproduction traits in a population of MNFs over 23 generations.

A multi-traits animal model was used to predict the breeding values in order to select the best birds as parents. The breeding value of each bird for selected traits based on the selection index was derived in such a way that the selected birds have a higher aggregate breeding value.

Finally, the parents were selected based on having the highest mean of each trait compared to the average of that trait in the population. Subsequently, an appropriate mating program based on the minimum relationship was designed to minimise the expected inbreeding in the next generation birds. In order to investigate the maternal effects, six different animal models were fitted to analyse the traits recorded over 23 generations. This fitting was performed to give the best model to analyse each trait in order to more accurately predict the breeding values in the breeding strategies for MNFBC.

The dataset analysed in this study was obtained from 1992 up to 2015 using 74351 birds. From the data highlighted in Table 1, it becomes evident that the traits including average BW1 (36.33 g), BW8 (577.09 g), BW12 (1002.02 g), EN (39.05), EW1 (41.22 g), AEW (48.45 g), ASM (160.44 d) and WSM (1708.22 g) in MNFs had lower values than those in the commercial layers reported by other authors [Olawumi and Ogunlade 2008, Zhang et al. 2005]. Since the MNF is considered a dual-purpose (meat-egg) breed, its eggs are smaller than those of commercial layers.

The inbreeding coefficients were estimated in the Mazandaran native fowl population. As shown in Table 2, the level of inbreeding between the individuals is low. This may be related to our mating system. The total average inbreeding coefficient was 0.06. The estimate for average numerator relationships was 0.05.

Genetic trends for BW1, BW8, BW12, and WSM are shown in Figure 1 and for ASM, EN, EW1 and AEW are illustrated in Figure 2. The regression coefficients of average breeding values on generation number of the traits under direct selection were 9.99, -1.44, 1.32 and 0.06 for BW12, ASM, EN, and AEW, and for correlated ones they were 0.03, 6.30, -1.01 and -0.19 for BW1, BW8, WSM and EW1, respectively. In this study linear regression of the mean breeding values on generation was significant for all the traits except for WSM and AEW. The coefficient of regression for the average breeding value for BW12 on generation number was positive (9.99) and for BW1 and BW8 it was 0.03 and 6.30, respectively. The small magnitude of trends

Table 2. Estimated inbreeding coefficients in the Mazandaran native fowl population

Generation	Total number of animals	Minimum inbreeding coefficient	Maximum inbreeding coefficient	Mean inbreeding coefficient
1	1667	0.00	0.00	0.00
2	2469	0.00	0.00	0.00
3	2335	0.00	0.00	0.00
4	2323	0.00	0.00	0.00
5	3981	0.00	0.00	0.00
6	3391	0.00	0.13	0.001
7	3562	0.00	0.25	0.004
8	3737	0.00	0.07	0.003
9	3793	0.00	0.13	0.004
10	4088	0.00	0.25	0.008
11	3612	0.00	0.13	0.006
12	3865	0.00	0.08	0.03
13	3740	0.00	0.16	0.03
14	3310	0.00	0.10	0.05
15	2859	0.03	0.12	0.05
16	3445	0.04	0.17	0.05
17	3281	0.05	0.10	0.05
18	3024	0.05	0.29	0.08
19	2729	0.06	0.30	0.07
20	3167	0.07	0.15	0.08
21	2912	0.08	0.13	0.09
22	3279	0.03	0.17	0.10
23	2701	0.09	0.17	0.11

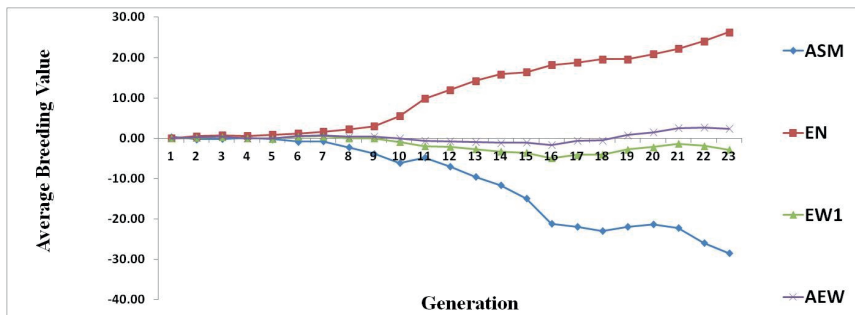


Fig. 1. Genetic trends of BW1, BW8, BW12 and WSM resulting from selection programmes across 23 generations.

observed could be a consequence of the absence of selection for the BW1, WSM, AEW and EW1 traits. The results revealed that selection has affected the selected traits and some of the correlated traits in MNF populations of MNFBC. Despite the negative correlations between BW12 with EN (-0.22) and EN with AEW (-0.30), the genetic gain was observed in three selected traits. In our program the intended purpose was to reduce the ASM and increasing the AEW levels, but they were significantly correlated. Despite the positive correlation between these traits, a genetic gain was obtained for both traits. For the other two studied traits (WSM and EW1), which are positively correlated with ASM, due to their lack of selection no genetic gain was observed.

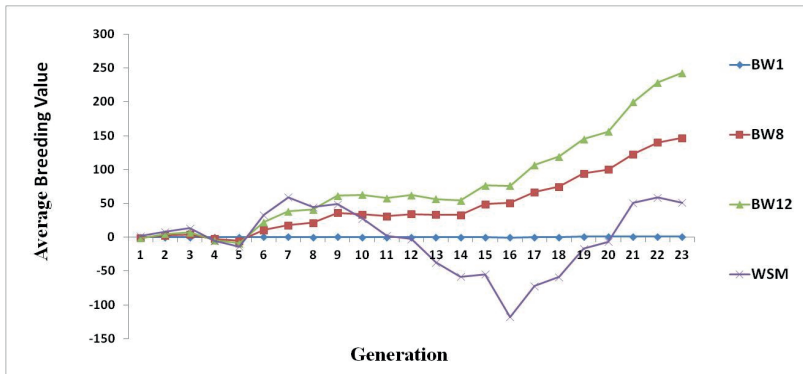


Fig. 2. Genetic trends of EN, EW1, AEW and ASM resulting from selection programmes across 23 generations.

This finding directs us to the importance of selection in the native flow populations. Table 3 presents the log L values obtained from analyses for each of the considered traits. The results indicated that model 5 was the most appropriate model for growth traits (BW1 and BW12), as fitting the maternal common environmental effects and maternal genetic effects for BW1 and BW12 had a significant effect on the log L value in comparison to the simple animal model. For the BW8, WSM, ASM, EW1, and AEW traits the direct-maternal genetic effect in addition to the maternal genetic and common environmental effects (model 6) resulted in a significant improvement in the log L values. Therefore, the full model (model 6) was selected as the most appropriate model based on the log L values. For the other studied traits (BW8, WSM, ASM, EW1 and AEW), model 6 provided a significant improvement in the log L values and thus it was selected as the most appropriate model. In this study EN was found to be influenced only by the maternal genetic effect (model 4).

Table 3. The log likelihood values for each trait (best model is bold)

Trait*	Model					
	1	2	3	4	5	6
BW1 (g)	-78972	-76188	-76229	-76220	-76000	-75999
BW8 (g)	-350132	-349967	-350042	-350039	-349964	-349958
Bw12 (g)	-334257	-334149	-334175	-334175	-334139	-334139
ASM (d)	-172276	-172163	-172199	-172152	-172154	-172097
WSM (g)	-321057	-321031	-321035	-321034	-321026	-321023
EN	-167801	-167982	-167791	-167768	-167973	-167972
EW1 (g)	-114541	-114534	-114539	-114532	-114534	-114526
AEW (g)	-95135	-95105	-95117	-95100	-95104	-95080

*BW1– BW at day 1 of age; BW8 – BW at 8 weeks of age; BW12 – BW at 12 weeks of age; WSM – weight at sexual maturity; ASM – age at sexual maturity; EN – egg number in the first 12 weeks of the laying period; EW1 – egg weight at day 1 of laying; EW28-30-32 (AEW) – average egg weight at 28, 30 and 32 weeks of age.

Table 4 summarises estimates of genetic parameters for the production and reproduction traits. Based on the most appropriate fitted models the estimates of direct heritability were 0.04, 0.22, 0.25, 0.49, 0.43, 0.20, 0.54 and 0.17 for BW1, BW8, BW12,

Table 4. Estimated genetic parameters for productive and reproductive traits

Trait	Model	$h^2 \pm SE$	$c^2 \pm SE$	$m^2 \pm SE$	r_{am}
BW1	5	0.04±0.01	0.21±0.01	0.16±0.01	-
BW8	6	0.22±0.01	0.05±0.01	0.01±0.01	-0.37
BW12	5	0.25±0.01	0.03±0.01	0.02±0.01	-
WSM	6	0.49±0.01	0.02±0.01	0.01±0.01	-0.23
ASM	6	0.43±0.01	0.05±0.01	0.04±0.01	-0.68
EN	4	0.17±0.02	-	0.03±0.02	-0.58
EW1	6	0.20±0.01	0.01±0.003	0.01±0.003	-0.56
AEW	6	0.54±0.01	0.02±0.004	0.01±0.004	-0.68

h^2 – direct heritability; m^2 – maternal heritability; c^2 – ratio of maternal common environmental variance to phenotypic variance; r_{am} – correlation between direct and maternal genetic effect.

WSM, ASM, EW1, AEW and EN, receptively. The h^2 estimates for BW1, BW8 and BW12 showed an increase from 0.04 (BW1) to 0.25 (BW12). The h^2 estimates for the other traits showed different values between the models with the presence of maternal effects; although a negligible difference was found between them. The estimates for maternal heritability (m^2) ranged from 0.01 to 0.16 and for the maternal common environmental variance (c^2) they ranged from 0.01 to 0.21 for all the studied traits according to the most suitable model. The results indicated a negative correlation between direct and maternal additive genetic effects (r_{am}) for all the considered traits. In poultry maternal effects are the most important part of variation in early life, particularly in the case of body weights. Exclusion of both genetic and environmental maternal effects from the model leads to an overestimation of h^2 [Aslam *et al.* 2011]. According to some studies, these effects gradually disappear with the age of chicks [Aslam *et al.* 2011, Chambers 1990, Le Bihan-Duval *et al.* 1998]. By considering the role of maternal effects (both genetic and environmental) in growth traits, it is of significant importance to include these effects in the estimation of genetics parameters.

The h^2 estimates from BW1 to WSM gradually increased from 0.04 to 0.49. When both maternal genetic and common environmental effect were taken into consideration, the direct heritability estimate for BW1 (0.04, model 5) in Mazandaran native fowls was similar to the results found in other studies, e.g. in turkey (0) [Aslam *et al.* 2011]. Estimates of c^2 and m^2 from BW8 to WSM were low and remained relatively constant, except for BW1, which parameters were moderate ($c^2=0.20$ and $m^2=0.16$). As shown in Table 3, surprisingly c^2 created a significant variation for the BW1 trait.

The first traits which are recorded in Mazandaran native hens after laying the first egg are age and weight at sexual maturity. Since these traits are generally recorded at 22 to 23 weeks of age, the WSM data is collected for a long time after hatching. The results from this study are in agreement with the previous reports on chickens [Koerhuis and Thompson 1997, Norris and Ngambi 2006] and turkeys [Chapuis *et al.* 1996] documenting that maternal effects contribute to body weight variation at older ages, while accounting for its small part, they are non-negligible. Previous findings from a study on growth traits in Horro chickens demonstrated that the h^2 estimate for body weight at the first day of life was 0.40. Then h^2 estimates for this trait decreased until 6 weeks of age (0.15) followed by an increase at 16 weeks of

age (0.23). Although an unusual trend for the estimated h^2 values was observed in their study, the c^2 estimates were as expected and gradually decreased with age (0.01, 0.03, 0.11 and 0.39 for BW8, BW6, BW2 and BW0, respectively). Our estimate of c^2 for BW8 (0.05) was to some extent similar to the estimate of their study (0.01). Contrary to the findings of our study, they reported that the maternal common environment effect for BW12 was not found to be statistically significant in Horro chicken [Dana *et al.* 2011]. As shown in Table 4, surprisingly, c^2 created a significant variation for the BW1 trait. BW12 is a very important production trait in the MNFBC selection programme and is considered as the selection objective. In our study a negative correlation was found between direct and maternal genetic effects for body weight traits. It has been demonstrated that once the covariance between direct and maternal genetic components becomes non-negligible, the genetic effects estimated via an animal model tend to be overestimated due to the action of an inflated negative correlation between direct and maternal effects [Meyer 1997].

It has been demonstrated that once there is a minor (non-negligible) covariance between direct and maternal genetic components, the estimates for genetic effects obtained via an animal model have a tendency towards overestimation. This is due to the action of an inflated negative correlation between both effects [Meyer 1997]. According to some literature sources, in poultry species the impact of maternal effects on reproduction traits is typically non-significant [Kranis *et al.* 2006, Saatici *et al.* 2006]. A clear example is provided by a previous report by Kranis *et al.* [2006] on the estimates of genetic parameters for egg production via six models containing maternal genetic and maternal common environmental effects in two turkey populations. Their report showed that the maternal effects had no impact on egg production [Kranis *et al.* 2006].

Estimates of direct heritability for production and reproduction traits under the simple animal model (Model 1) ranged from 0.16 (EN) to 0.49 (AEW). The values were high for BW1, WSM, and AEW (0.42, 0.48 and 0.49, respectively), while they remained moderate for the other traits (the values for BW8, BW12, ASM, EN and EW1 were 0.27, 0.31, 0.37, 0.16 and 0.20, respectively). The findings of previous studies by Lwelamira *et al.* [2009] and Wolc *et al.* [2011] for the h^2 estimate of ASM are consistent with our results. It should be noted that our estimate is obtained based on the most suitable model (0.43), but their estimates were obtained via only a simple animal model without maternal effects. Our results for the ASM trait indicated that it is more influenced by the direct additive effect of the birds than maternal effects. According to the earlier study by Hartmann *et al.* [2003], the h^2 and c^2 estimates for ASM were 0.34 and 0.09, respectively, which is in agreement with our results. In addition, in another study by Fathi *et al.* [2005] the direct and maternal effects for some traits of a commercial broiler line were investigated. Their findings revealed that ASM was maternally affected. Different reports for these estimates could be due to some important factors such as differences in the breed's genetic background, data structure and breeding objectives. In poultry breeding schemes, ASM has been considered to be one of the important reproduction traits [Arthur and Albers 2003].

In the MNFBC one of the selection objectives is to reduce the ASM. In this way, based on the findings of the current study and reviewed literature, maternal genetic and common environmental effects should be considered for a reduced ASM in MNFs. Improving the egg weight traits in poultry is of significant importance for poultry productivity. The h^2 estimates for EW1 and AEW were 0.20 and 0.54, respectively. The h^2 estimate of AEW (0.54) in the present study was similar to the h^2 estimates in other studies [Hartmann 2003, Lwelamira *et al.* 2009, Zhang *et al.* 2005]. In our analyses the maternal effects estimated for EW1 and AEW traits were low and the maternal effects had a statistically significant effect on egg production traits. In contrast, a previous study reported that both direct genetic and common environment effects affected AEW [Saatci *et al.* 2006]. Egg number is another breeding objective for breeders in MNFBC. Based on the analysis it was found that egg number was only influenced by the maternal genetic effect; therefore, the h^2 estimate for this trait was 0.17. This estimate was within the range reported by other previous studies [Lwelamira *et al.* 2009, Nurgiantiningsih *et al.* 2004, Sabri *et al.* 1999]. Perhaps the cytoplasmic effect (mitochondrial DNA) had little influence on our findings. Szwaczkowski *et al.* (1999) estimated the cytoplasmic variance for egg production traits in laying hens. They found a very small contribution of variance from both maternal and cytoplasmic effects to the phenotypic variance for all analysed traits. It was concluded that cytoplasmic effects may be omitted in the genetic evaluation of laying hens. In order to understand the biological foundation of how the maternal effects affect the egg production traits in their progeny further work is needed.

Correlations between traits were estimated by multivariate analyses and the results are given in Table 5. Genetic correlations between the studied traits ranged between -0.46 (EW1 with EN) and 0.92 (BW8 with BW12), whilst phenotypic correlations ranged from -0.19 (ASM with EN) to 0.62 (BW8 with BW12). The genetic correlations between traits under selection were low to moderate including ASM with AEW (0.26) and BW12 with AEW (0.45), respectively. However, there were negative correlations between BW12 and EN (-0.22), BW12 and ASM (-0.01), ASM and EN (-0.38) and EN and AEW (-0.30). The selection strategy in our study was to improve the BW12, ASM, EN and AEW. Although there was no desirable correlation between the selected traits (Tab. 5), we designed a strategy for selecting the birds and a genetic gain was observed for all these traits.

Genetic correlations between pairs of body weight levels were positive and moderate to high, ranging from 0.32 to 0.93. Therefore, selection for a higher BW1 would result in a greater body weight at 8, 12 weeks of age and also weight at sexual maturity. It seems that body weight traits (BW1, BW8, BW12 and WSM) are genetically associated with egg weight traits (EW1 and AEW), because the genetic correlation between these traits was estimated at 0.37 to 0.65. This finding may suggest that the direct selection for body weight traits results in indirect genetic gains for egg weight traits. In this study a low correlation between body weight traits and ASM was found. This is in agreement with previous studies and is favourable

Table 5. Genetic (below the diagonal) and phenotypic (above the diagonal) correlations between traits*

	BW1	BW8	BW12	ASM	WSM	EN	EW1	AEW
BW1	*	0.12±0.01	0.11±0.01	0.03±0.01	0.15±0.01	0.04±0.01	0.09±0.01	0.17±0.01
BW8	0.38±0.02	*	0.62±0.03	-0.14±0.01	0.30±0.01	-0.002±0.01	0.06±0.01	0.19±0.01
BW12	0.37±0.02	0.92±0.01	*	-0.16±0.01	0.39±0.01	-0.01±0.01	0.08±0.01	0.22±0.01
ASM	0.10±0.02	-0.03±0.02	-0.01±0.02	*	0.30±0.01	-0.20±0.01	0.30±0.01	0.14±0.01
WSM	0.43±0.02	0.59±0.02	0.73±0.01	0.45±0.02	*	-0.11±0.01	0.29±0.01	0.33±0.01
EN	-0.21±0.03	-0.20±0.03	-0.22±0.03	-0.38±0.03	-0.38±0.03	*		
EW1	0.48±0.02	0.38±0.02	0.41±0.02	0.54±0.02	0.65±0.02	-0.46±0.03	*	
AEW	0.63±0.02	0.41±0.02	0.45±0.02	0.26±0.02	0.54±0.01	-0.30±0.03	0.84±0.01	*

*BW1 – BW at day 1 of age; BW8 – BW at 8 weeks of age; BW12 – BW at 12 weeks of age; WSM – weight at sexual maturity; ASM – age at sexual maturity; EN – egg number in the first 12 weeks of the laying period; EW1 – egg weight at day 1 of laying; AEW – mean egg weight at 28, 30 and 32 weeks of age.

in breeding programmes [Kamali *et al.* 2007, Sabri *et al.* 1999]. The correlations between egg number and other traits ranged from -0.20 (EN with BW8) to -0.46 (EN with EW1). The finding of an earlier study showed that there is a strong negative genetic correlation between body weight and total egg production. Its magnitude demonstrated that the concurrent selection for both traits may not be effective [Kranis *et al.* 2006]. The correlation analysis revealed a positive and high correlation between egg weight related traits with other traits, except for the number of eggs produced. This evidence shows that genetic improvement for EW will lead to a decrease in egg production. However, some authors reported a positive correlation between EN and EW in unselected control lines of white leghorns [Fairfull and Gowe 1990].

A negative genetic correlation was found for egg production with age at sexual maturity and the mean egg weights (-0.38 and -0.30, respectively). Early maturity leads to an early start of egg production, bringing about more produced eggs. On the other hand, increasing the number of produced eggs would decrease the mean egg weights. Similar results have been reported in other studies for the genetic correlations between these traits [Kamali *et al.* 2007, Lubritz and Smith 1996, Poggenpoel *et al.* 1996], while we also need to stress contradictory results obtained by other authors for these traits [Liu *et al.* 1995].

In conclusion, considering the results of the current study a mix of effects (direct and maternal genetic and environmental effects) influenced all the studied traits. It was found that maternal genetic and common environmental effects provide important potential sources for phenotypic variation in the studied traits. Thus, maternal effects need to be considered in order to avoid overestimation of the heritability. Hence, it is recommended to include the maternal effects in animal models to estimate the genetic parameters of the studied traits in MNF. Our study revealed that model choice is an important factor in the accurate estimation of production and reproduction traits. Regarding the program of MNFBC in producing dual purpose chickens, despite the negative correlations between some of the selected traits, the genetic gain was observed in all the selected traits of MNFs during the 23 generations. The outcomes and findings of our study have provided considerable insight resulting in more accurate planning of selection programmes and improving the selection efficiency of production and reproduction traits in MNF.

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