

THE POTENTIAL OF NON-ADDITIVE GENE ACTION FOR IMPROVING EGG PRODUCTION IN FAYOUMI CHICKENS

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SUMMARY

Data from a complete 4 X 4 diallel crosses experiment with a total number of 1414 pullets representing sixteen different genotypes were used. The pure genotypes used were three lines of Fayoumi breed (a high egg production selected line, a heavier body weight at 8-wk of age selected line and a random bred control line) and a White Leghorn breed.

The objectives of this work were to examine the potential of the non-additive gene effects for improving egg production and egg weight of Fayoumi breed, through testing the significance and estimating the effects of: heterosis, maternal, general and specific combining abilities, and sex-linked effects. The potential of using different pure Fayoumi lines as sire or dam lines were also studied.

Sire effect proved to be more important for egg number (EN) measurements (egg number of 60, 90 and 120 days). Significant general combining ability, maternal and sex-linked effects were found for all studied traits. Heterosis was significant for all studied traits but sexual maturity weight. Specific combining ability was significant for sexual maturity age and egg weight (EW) measurements (average egg weight of 60, 90 and 120 days). Indication of incomplete dominance was found in EW measurements, while overdominance and epistasis associated with sex-linked and maternal effects were the major factors affected EN measurements.

The results proved the importance of non-additive gene effects for egg production traits (EN & EW). Results suggested that increasing egg production of Fayoumi could be achieved by crossing different Fayoumi lines (up to 15% increase) and strongly recommended crossing Fayoumi with White Leghorn breed (up to 36% increase). The improvement expected in one generation, from crossing Fayoumi with White Leghorn, is far more than what would be expected through conventional selection methods that use additive genetic variance. More improvement would be expected if crossing is accompanied with reciprocal recurrent selection.

Keywords: Diallel crossing, heterosis, maternal, general combining ability, specific combining ability, sex-linked

INTRODUCTION

Native breeds of chickens have been under different breeding programs for improving its performance. Most of these programs have been focussing on additive genetic effects. However, nonadditive genetic effects are very important for egg production in chickens (Sheridan and Randall, 1977; Sheridan, 1980; Bennett *et al.*, 1981; Fairfull *et al.*, 1983, 1987; Gowe and Fairfull, 1982). Studying the non-additive gene action requires crossing the genotypes of interest. Crossing a line to several others provides an additional measure of that line. The variance between crosses can be partitioned in a way that has great importance for understanding the use of crossbreeding for improvement (Falconer, 1991).

Historically, poultry breeders have used breed crosses and more recently strain crosses to take advantage of heterosis (Fairfull, 1990). Dominance was broadly believed to be the only caused of heterosis (Fairfull *et al.*, 1987). However, Dickerson (1965) and Sheridan (1980) stated that dominance model was not sufficient to explain heterosis that occurred in crosses between different breeds or between unrelated strains of the same breed. Epistasis was shown to be a major mechanism of heterosis in Leghorn strain crossing (Fairfull *et al.*, 1987).

There are some studies on local breeds crossing, however, most of these studies concentrated on the growing periods (Sabri, 1979; Stino, *et al.*, 1981; Sabra, 1990; Sheble *et al.*, 1990; Mandour *et al.*, 1996). More studies on the effect of non-additive gene action for egg production are needed for local breeds of chicken. Fayoumi is one of the most well characterized local breeds of chickens. It could be considered as an egg-type bird. Two lines of Fayoumi were established at Fayoum Poultry Research Station, one for heavier body weight at 8 wk of age, the other for high egg production number (Ragab and El-Hossari, 1970).

The objectives of this work were to examine the potential of the non-additive gene effects for improving egg production and egg weight of Fayoumi chickens, through testing the significance and estimating heterosis, maternal, general and specific combining abilities, and sex-linked effects. The potential of using different Fayoumi lines as sire or dam lines were also studied.

Three Fayoumi lines two of which were subjected to selection for several generations as well as, a White Leghorn breed were used to evaluate the effect of crossing.

MATERIALS AND METHODS

Birds and Measurements:

Data from 1414 pullets representing a complete 4 X 4 diallel cross were used in this study. The sixteen different genotypes were 4 pure genotypes, 6 two-way crosses and their 6 reciprocal crosses. The pure genotypes used were three lines of Fayoumi breed and a White Leghorn line (WW). The Fayoumi lines were two selected lines (PP: selected for high egg production; GG: selected for heavier body weight at 8 wk of age, Ragab and El-Hossari, 1970); and unselected random bred control line (RR). The data for this work were obtained from Fayoum Poultry Research Station records.

Birds were produced in two hatches. Sexual maturity age (SMAGE) and body weight (SMBW) were recorded as age and body weight at first egg for each pullet. Egg production was recorded individually for 120 days and was used for calculating egg production for 60 days (EN60), 90 days (EN90) and 120 days (EN120) for each hen. Eggs were weighed daily the next day of laying and average egg weight for 60 (EW60), 90 (EW90) and 120 days (EW120) were calculated for each hen.

Statistical analysis:

Raw data were corrected for hatch effect by Least Square Analysis of variance (Harvey, 1987), using genotype and hatch as fixed effects and error as a random effect. The corrected data were analyzed using the following two mathematical models:

Model 1:

$$Y_{ijk} = \mu + S_i + D_j + (SD)_{ij} + e_{ijk}$$

where:

Y_{ijk} = The k th observation on the hen from the i th line of sire mated to the j th line of dam

μ = The overall mean

S_i = The fixed effect of the i th sire line, $i=1, \dots, 4$

D_j = The fixed effect of the j th dam line, $j=1, \dots, 4$

$(SD)_{ij}$ = The fixed effect of the interaction between the i th line of sire and the j th line of dam

e_{ijk} = The random error effect associated with the ijk th individual

This model was applied to estimate the fixed effect of using any line as a sire or dam and the interaction between different combinations (Harvey, 1975).

Model 2:

$$Y_{hijk} = \mu + h_h + P_{ii} + g_i + g_j + m_j + c_{ij} + r_{ij} + e_{hijk}$$

where:

Y_{hijk} = The k th observation on the hen produced from mating a sire from the i th line with a dam from the j th line in the h th type of breeding (purebred or crossbred)

μ = The overall mean

h_h = An effect common to all progeny of the h th type of breeding (linebred or crossbred), $h=1,2$

P_{ii} = An effect common to all progeny of a mating between a dam of the i th line and a sire of the i th line, $i=1, \dots, 4$

g_{ij} = The effect of the general combining ability of the i th (j th) line

m_j = The effect of the maternal ability of the j th dam line, $j=1, \dots, 4$

c_{ij} = The effect of the specific combining ability of the ij th or ji th cross ($i?j$)

r_{ij} = The sex-linked or reciprocal effect of the ij th cross ($i?j$)

e_{hijk} = The random error

Model 2 was suggested by Kidwell *et al.* (1960). This model was used to test the significance and to estimate the effects of heterosis, pure, maternal, general combining ability (GCA), specific combining ability (SCA), and sex-linked, by applying the restrictions suggested by Harvey (1975). The restrictions were :

$$\sum h_h = \sum P_{ii} = \sum m_j = \sum g_i = \sum c_{ij} = \sum c_{ji} = \sum r_{ij} = \sum r_{ji} = 0.$$

Data from both pure and cross genotypes were used to estimate the heterosis effect, while pure genotype data were used to estimating the pure effect, however, cross genotype data were used to estimate general combining ability, specific combining ability, maternal and sex-linked effects.

General Linear Model procedure of SAS software (SAS Institute, 1985) was used for statistical analysis. Contrast statement available in SAS software was used for testing the significant of heterosis between each pair of pure genotypes, while the estimate statement was used for estimating the effects of different studied parameters. Least square means were ranked by Duncan's multiple range test (Duncan, 1955)

RESULTS AND DISCUSSION

Results showed common properties to all studied traits. Significant differences were found among the four pure genotypes (Table 1 & 2). Results from applying Model 1 indicated that the effect of, at least one pure genotype when used as a sire (dam) line depended upon the dam (sire) genotype. This was true for all studied traits, where sire by dam interaction was significant (Table 3). According to Kan *et al.* (1959) the variation between dams contains one-quarter of the additive genetic variance and all the maternal effects, while the interaction component in the diallel contains epistatic deviations. Using Model 2 showed that, except for both GCA and SCA, all other genetic parameters (heterosis, pure, maternal, sex-linked effects) were significant ($P < .0001$) for all studied traits. Least square constants estimated for GCA and maternal effects were, in most cases for all studied traits, opposite in signs (Table 5). This is in agreement with Kidwell *et al.* (1960) who reported a

negative correlation between the two effects and concluded that maternal and general combining ability effects were highly confounded.

Table 1. Number of birds and least square means \pm SE for sexual maturity traits

Genotype	Number	SMAGE	SMBW
Pure:			
PP	161	170.0 \pm 1.1 ^h	1215.8 \pm 8.8 ^{ef}
GG	174	179.3 \pm 1.1 ^{cdefg}	1284.5 \pm 8.5 ^d
RR	182	163.8 \pm 1.0 ⁱ	1262.8 \pm 8.3 ^d
WW	128	180.8 \pm 1.2 ^{cde}	1352.6 \pm 9.9 ^c
Crosses:			
PG	72	183.8 \pm 1.7 ^{b^{cd}}	1330.0 \pm 13.2 ^c
GP	47	163.3 \pm 2.0 ⁱ	1199.1 \pm 16.3 ^{fg}
PR	89	188.4 \pm 1.5 ^b	1283.9 \pm 11.9 ^d
RP	110	184.3 \pm 1.3 ^{b^c}	1245.5 \pm 10.7 ^{de}
PW	31	179.7 \pm 2.5 ^{cdef}	1202.9 \pm 20.1 ^{fg}
WP	71	184.2 \pm 1.7 ^{b^c}	1418.4 \pm 13.3 ^b
GR	72	186.4 \pm 1.7 ^b	1346.0 \pm 13.2 ^c
RG	48	175.7 \pm 2.0 ^{efg}	1201.5 \pm 16.2 ^{fg}
GW	59	197.7 \pm 1.8 ^a	1347.3 \pm 14.6 ^c
WG	47	178.7 \pm 2.0 ^{defg}	1262.2 \pm 16.3 ^d
RW	71	174.3 \pm 1.7 ^{gh}	1475.3 \pm 13.3 ^a
WR	52	174.6 \pm 1.9 ^{fgh}	1164.8 \pm 15.5 ^g

SMAGE : Sexual maturity age. SMBW : Sexual maturity body weight.

PP, GG, RR, WW : Fayoumi egg production, growth, and random bred lines; and White Leghorn breed, respectively.

Means within a column with no common letter are significantly different ($P < .05$).

Sexual maturity age:

GG and WW genotypes reached sexual maturity significantly at older age than PP and RR (Table 1). Significant differences were found between each of PG, GR and GW crosses and its reciprocal cross (GP, RG and WG, respectively). The difference between a cross and its reciprocal was associated with difference in sex-linked effects of both crosses, where PG, GR and GW showed positive sex-linked effects, while their reciprocal crosses (GP, RG, WG) showed negative sex-linked effects (Table 5). Hossari (1966) and Hossari *et al.* (1995) reported sex-linked effect in crossing PP and GG Fayoumi lines. Bordas *et al.* (1969) found marked differences between reciprocal crosses in SMAGE, when two lines of Rhode Island Red were crossed.

Table 2. Least square means \pm SE for different egg number (EN) and egg weight (EW) measurements*

Genotype	Number	EN60	EW60	EN90	EW90	EN120	EW120
Pure:							
PP	161	31.8 \pm 0.3 h	35.8 \pm 0.1 l	49.0 \pm 0.4 i	36.6 \pm 0.1 l	67.2 \pm 0.5 i	37.6 \pm 0.1 k
GG	174	31.4 \pm 0.3 h	38.6 \pm 0.1 hi	47.4 \pm 0.4 j	39.5 \pm 0.1 ghi	64.5 \pm 0.5 j	40.3 \pm 0.1 g
RR	182	34.3 \pm 0.3 fg	36.9 \pm 0.1 k	51.9 \pm 0.4 h	37.7 \pm 0.1 k	69.8 \pm 0.4 h	38.4 \pm 0.1 j
WW	128	35.9 \pm 0.3 e	46.0 \pm 0.1 a	54.0 \pm 0.4 fg	46.9 \pm 0.1 a	71.3 \pm 0.5 gh	47.9 \pm 0.1 a
Crosses:							
PG	72	34.2 \pm 0.4 fg	39.3 \pm 0.2 ef	52.7 \pm 0.6 gh	39.6 \pm 0.1 gh	71.3 \pm 0.7 gh	40.0 \pm 0.1 gh
GP	47	35.8 \pm 0.5 e	38.9 \pm 0.2 fgh	56.2 \pm 0.7 e	39.5 \pm 0.2 ghi	74.6 \pm 0.9 e	40.0 \pm 0.2 gh
PR	89	34.9 \pm 0.4 efg	37.6 \pm 0.1 j	53.5 \pm 0.5 bgh	38.3 \pm 0.1 j	70.8 \pm 0.6 gh	38.9 \pm 0.1 i
RP	110	34.2 \pm 0.3 fg	38.3 \pm 0.1 l	54.7 \pm 0.5 cb	39.1 \pm 0.1 i	74.1 \pm 0.6 eb	39.7 \pm 0.1 h
PW	31	35.9 \pm 0.6 e	41.9 \pm 0.2 c	55.0 \pm 0.9 ef	42.6 \pm 0.2 cd	72.8 \pm 1.1 efg	42.9 \pm 0.2 d
WP	71	41.7 \pm 0.4 b	41.6 \pm 0.2 c	63.9 \pm 0.6 b	42.8 \pm 0.1 c	86.8 \pm 0.7 b	43.7 \pm 0.1 c
GR	72	35.2 \pm 0.4 ef	38.8 \pm 0.2 gh	53.7 \pm 0.6 fg	39.3 \pm 0.1 hi	72.3 \pm 0.7 fg	39.9 \pm 0.1 h
RG	48	38.7 \pm 0.5 d	39.3 \pm 0.2 efg	58.9 \pm 0.7 d	39.8 \pm 0.2 g	77.7 \pm 0.9 d	40.1 \pm 0.2 gh
GW	59	33.7 \pm 0.5 g	41.5 \pm 0.2 c	53.5 \pm 0.6 bgh	42.2 \pm 0.1 d	71.5 \pm 0.8 gh	42.7 \pm 0.1 d
WG	47	44.3 \pm 0.5 a	39.9 \pm 0.2 d	69.3 \pm 0.7 a	41.4 \pm 0.2 e	92.4 \pm 0.9 a	42.4 \pm 0.2 e
RW	71	40.0 \pm 0.4 c	42.9 \pm 0.2 b	60.2 \pm 0.6 cd	43.8 \pm 0.1 b	81.6 \pm 0.7 c	44.3 \pm 0.1 b
WR	52	39.9 \pm 0.5 cd	39.6 \pm 0.2 de	61.4 \pm 0.7 c	40.7 \pm 0.2 f	81.6 \pm 0.8 c	41.7 \pm 0.1 f

*Measurements for 60, 90 and 120 days from sexual maturity

PP, GG, RR, WW : Fayoumi egg production, growth, and random bred lines; and White Leghorn breed, respectively.

Means within a column with no common letter are significantly different ($P < .05$).

Table 3. The ANOVA Table for Model 1 & 2 for the different studied traits

Source	df	SAGE		SABW		EN60		EW60		EN90		EW90		EN120		EW120	
		MS	Pr <F	MS	Pr <F	MS	Pr <F	MS	Pr <F	MS	Pr <F	MS	Pr <F	MS	Pr <F	MS	Pr <F
Model 1:																	
SIRE	3	3012.7	.0001	96919.3	.0001	2326.4	.0001	467.8	.0001	5215.2	.0001	665.2	.0001	8975.2	.0001	835.6	.0001
DAM	3	2621.4	.0001	355028.6	.0001	89.5	.0001	1199.2	.0001	189.6	.0001	1196.6	.0001	473.8	.0001	1107.6	.0001
S X D	9	9006.9	.0001	588935.4	.0001	815.7	.0001	118.3	.0001	2268.8	.0001	91.3	.0001	3864.7	.0001	73.8	.0001
Model 2:																	
Heterosis	1	18384.2	.0001	38561.5	.0795	5359.6	.0001	143.2	.0001	17086.6	.0001	108.6	.0001	27329.7	.0001	30.2	.0001
Pure	3	10524.4	.0001	459133.8	.0001	679.7	.0001	2888.9	.0001	1296.1	.0001	2954.4	.0001	1407.2	.0001	3015.6	.0001
G.C.A.	3	609.4	.0257	31291.7	.0581	1806.9	.0001	105.3	.0001	4168.7	.0001	221.6	.0001	7830.8	.0001	314.2	.0001
Maternal	3	2298.9	.0001	150749.1	.0001	1022.4	.0001	117.2	.0001	2574.7	.0001	89.2	.0001	4919.2	.0001	56.9	.0001
S.C.A.	2	11092.0	.0001	4720.4	.6860	73.5	.0026	75.7	.0001	3.2	.8668	47.5	.0001	2.5	.9331	36.9	.0001
Sex-Linked	3	6243.3	.0001	1541816.6	.0001	446.1	.0001	23.2	.0001	747.8	.0001	25.5	.0001	1227.1	.0001	31.8	.0001
Heterosis																	
Contrast:																	
PP & GG	1	99.8	.4760	17598.8	.2360	991.6	.0001	317.1	.0001	3322.2	.0001	183.3	.0001	4266.5	.0001	96.0	.0001
PP & RR	1	47290.7	.0001	80594.3	.0113	277.3	.0001	324.6	.0001	1661.4	.0001	301.7	.0001	1977.7	.0001	211.9	.0001
PP & WW	1	2855.8	.0001	46329.4	.0546	1621.1	.0001	44.8	.0001	4158.7	.0001	54.3	.0001	7395.9	.0001	21.7	.0001
GG & RR	1	7904.1	.0001	0.2	.9971	1473.8	.0001	154.3	.0001	3925.0	.0001	79.0	.0001	5372.1	.0001	32.0	.0001
GG & WW	1	5101.4	.0001	14747.5	.2780	2226.1	.0001	187.2	.0001	8841.3	.0001	151.1	.0001	15200.2	.0001	193.0	.0001
RR & WW	1	393.0	.1573	13025.0	.3079	1991.5	.0001	3.2	.1822	5341.1	.0001	0.2	.7077	10434.9	.0001	1.9	.1944
Error	1398	196.3		12521.4		12.3		1.8		22.7		1.2		36.6		1.1	

SMBW : Body weight at sexual maturity.
 SMAGE : Age at sexual maturity.
 Egg number (EN) and egg weight (EW) measurements for 60, 90 and 120 days from sexual maturity.
 PP, GG, RR, WW : Fayoumi egg production, growth and random bred lines; and White leghorn breed, respectively.

Table 4. Least square estimated effects from Model 1 for different studied traits

Classification	SMAEG	Pr<F	SMBW	Pr<F	EN60	Pr<F	EW60	Pr<F	EN90	Pr<F	EW90	Pr<F	EN120	Pr<F	EW120	Pr<F
Sire Effect:																
PP	1.4 ± 8	.06	-28.9 ± 6.0	.01	-2.2 ± 2	.01	-1.1 ± 1	.01	-3.4 ± 3	.01	-1.3 ± 1	.01	-4.5 ± 3	.01	-1.4 ± 1	.01
GG	2.6 ± 7	.01	7.2 ± 5.8	.22	-2.3 ± 2	.01	-3.1 ± 1	.01	-3.3 ± 2	.01	-5.1 ± 1	.01	-4.3 ± 3	.01	-5.1 ± 1	.01
RR	-4.5 ± 7	.01	9.2 ± 5.5	.01	4 ± 2	.02	-5.1 ± 1	.01	5 ± 2	.05	-5.1 ± 1	.01	.8 ± 3	.01	-6.1 ± 1	.01
WW	.5 ± 7	.50	12.5 ± 6.0	.04	4.1 ± 2	.01	1.9 ± 1	.01	6.2 ± 3	.01	2.3 ± 1	.01	8.0 ± 3	.01	2.6 ± 1	.01
Dam Effect:																
PP	-3.6 ± 7	.01	-17.3 ± 5.6	.01	-5 ± 2	.01	-1.1 ± 1	.01	0 ± 2	.96	-1.1 ± 1	.01	7 ± 3	.03	-1.0 ± 1	.01
GG	3 ± 7	.69	-17.5 ± 6.0	.01	8 ± 2	.01	-5 ± 1	.01	1.1 ± 3	.01	-5 ± 1	.01	1.5 ± 3	.01	-6 ± 1	.01
RR	-8 ± 7	.26	-22.7 ± 5.6	.01	-3 ± 2	.10	-1.6 ± 1	.01	-8 ± 2	.01	-1.6 ± 1	.01	-1.4 ± 3	.01	-1.5 ± 1	.01
WW	4.1 ± 8	.01	57.5 ± 6.3	.01	0 ± 2	.98	3.3 ± 1	.01	-3 ± 3	.26	3.2 ± 1	.01	-7 ± 3	.04	3.1 ± 1	.01
Interaction:																
PP X PP	-6.9 ± 1.1	.01	-25.0 ± 8.7	.01	-1.9 ± 3	.01	-1.7 ± 1	.01	-3.5 ± 4	.01	-1.5 ± 1	.01	-4.0 ± 5	.01	-1.2 ± 1	.01
PP X GG	3.0 ± 1.3	.02	89.3 ± 1.2	.00	-8 ± 3	.02	1.2 ± 1	.01	-1.0 ± 4	.03	9 ± 1	.01	-7 ± 6	.22	8 ± 1	.01
PP X RR	8.7 ± 1.2	.01	48.4 ± 9.5	.01	1.0 ± 3	.01	5 ± 1	.01	1.8 ± 4	.01	6 ± 1	.01	1.7 ± 5	.01	6 ± 1	.01
PP X WW	-4.8 ± 1.6	.01	-112.7 ± 12.8	.01	1.7 ± 4	.01	-1 ± 2	.71	2.7 ± 5	.01	0 ± 1	.77	3.0 ± 7	.01	-1 ± 1	.32
GG X PP	-14.7 ± 1.4	.01	-77.8 ± 11.0	.01	2.3 ± 3	.01	6 ± 1	.01	3.5 ± 5	.01	4 ± 1	.01	3.2 ± 6	.01	3 ± 1	.01
GG X GG	-2.7 ± 1.1	.02	7.8 ± 8.7	.37	-3.4 ± 3	.01	-4 ± 1	.01	-6.4 ± 4	.01	-1.1 ± 1	.35	-7.7 ± 5	.01	2 ± 1	.03
GG X RR	5.5 ± 1.2	.01	74.4 ± 9.9	.01	1.5 ± 3	.01	9 ± 1	.01	1.9 ± 4	.01	8 ± 1	.01	3.0 ± 5	.01	7 ± 1	.01
GG X WW	11.9 ± 1.3	.01	-4.4 ± 1.7	.68	-3 ± 3	.34	-1.2 ± 1	.01	1.1 ± 5	.02	-1.2 ± 1	.01	1.5 ± 6	.01	-1.2 ± 1	.01
RR X PP	13.4 ± 1.1	.01	-33.4 ± 8.9	.01	-2.1 ± 3	.01	1 ± 1	.31	-1.7 ± 4	.01	2 ± 1	.09	-2.3 ± 5	.01	1 ± 1	.22
RR X GG	9 ± 1.4	.52	-77.3 ± 11.0	.01	1.1 ± 3	.01	5 ± 1	.01	1.4 ± 5	.01	2 ± 1	.06	4 ± 6	.46	0 ± 1	.90
RR X RR	-1.0 ± 1.0	.01	-1.8 ± 8.2	.19	-2.2 ± 3	.01	-9 ± 1	.01	3.7 ± 4	.01	-8 ± 1	.01	-4.6 ± 4	.01	-7 ± 1	.01
RR X WW	-4.3 ± 1.3	.07	121.5 ± 1.1	.01	3.2 ± 3	.01	3 ± 1	.02	4.1 ± 4	.01	4 ± 1	.01	6.5 ± 5	.01	5 ± 1	.01
WW X PP	8.2 ± 1.3	.01	136.2 ± 1.0	.01	1.7 ± 3	.01	1.0 ± 1	.01	1.7 ± 4	.01	9 ± 1	.01	3.1 ± 5	.01	8 ± 1	.01
WW X GG	-1.2 ± 1.4	.40	-19.8 ± 11.3	.08	3.1 ± 4	.01	-1.3 ± 1	.01	6.0 ± 5	.01	-1.0 ± 1	.01	7.9 ± 6	.01	-1.0 ± 1	.01
WW X RR	-4.2 ± 1.3	.01	-112.1 ± 1.7	.01	-3 ± 3	.42	-6 ± 1	.01	1 ± 5	.83	-6 ± 1	.01	-1 ± 6	.92	-7 ± 1	.01
WW X WW	-2.8 ± 1.2	.02	-4.4 ± 9.4	.64	-4.5 ± 3	.01	1.0 ± 1	.01	-7.9 ± 4	.01	7 ± 1	.01	-11.0 ± 5	.01	8 ± 1	.01

SMAEG : Age at sexual maturity. SMBW : Body weight at sexual maturity. Egg number (EN) and egg weight (EW) measurements for 60, 90 and 120 days from sexual maturity.

PP, GG, RR, WW : Fayoumi egg production, growth, and random bred lines; and White leghorn breed, respectively.

Table 5. Least square effects for sexual maturity and egg production measurements estimated using Model 2

Classification	SMAGE	P<F SMBW	P<F EN60	P<F EW60	P<F EN90	P<F EW90	P<F EN120	P<F EW120	P<F
Pure Effect :									
PP	-3.4±.01	-63.1±7.01	-1.6±2.01	-3.5±1.01	-1.5±3.01	-3.5±1.01	-1.0±.02	-3.5±.01	.01
GG	5.8±.01	5.6±7.545	-1.9±2.01	-7±1.01	-3.2±3.01	-7±1.01	-3.7±.01	-7±.01	.01
RR	-9.7±.01	-16.1±7.403	1.0±2.01	-2.4±1.01	1.3±3.01	-2.5±1.01	1.6±.01	-2.6±.01	.01
WW	7.3±1.01	73.7±8.301	2.5±3.01	6.6±1.01	3.4±4.01	6.7±1.01	3.1±.01	6.8±.01	.01
GCA Effect :									
PP	2.1±1.04	-2.4±8.102	-2.7±3.01	-5±1.01	-4.3±3.01	-8±1.01	-5.9±.01	-9±.01	.01
GG	1.2±1.23	-8±7.892	-2.1±2.01	-4±1.01	-2.7±3.01	-7±1.01	-3.9±.01	-7±.01	.01
RR	-2.3±1.02	1.6±7.617	.0±2.92	-3±1.01	-3±3.29	-3±1.01	-3±.42	-4±.01	.01
WW	-9±1.37	1.6±7.817	4.8±2.01	1.2±1.01	7.4±3.01	1.8±1.01	1.1±.01	2.1±.01	.01
Maternal :									
PP	-5.0±1.01	11.6±8.919	1.7±3.01	-0±1.97	3.4±4.01	2±1.01	5.2±.01	4±.01	.01
GG	-2.3±1.05	-24.7±9.201	3.1±3.01	-2±1.10	4.4±4.01	-0±1.63	5.7±.01	-0±.59	.01
RR	3.8±1.01	-31.9±8.301	-7±3.01	-1.1±1.01	-1.3±4.02	-1.1±1.01	-2.2±.01	-9±.01	.01
WW	3.6±1.01	45.0±9.601	-4.1±3.01	1.3±1.01	-6.5±4.01	.9±1.01	-8.8±.01	5±.01	.01
SCA Effect :									
PP & GG	-4.8±.01	-1.1±4.302	.0±1.85	-3±1.01	.2±2.32	-3±0.01	.4±.13	-4±.01	.01
PP & RR	2.7±.01	-12.6±3.801	-9±1.01	-1.0±0.01	-9±2.01	-9±0.01	-1.1±.01	-8±.01	.01
PP & WW	.2±.72	16.8±4.701	2±1.29	.9±1.01	.1±2.73	.9±0.01	.3±.30	8±.01	.01
GG & RR	.4±.47	-14.4±4.201	.3±1.01	-4±0.01	.1±2.73	-5±0.01	-1±.52	-6±.01	.01
GG & WW	3.7±.01	7.6±4.409	.3±1.04	.3±1.01	.9±2.01	4±0.01	1.0±.01	4±.01	.01
RR & WW	-2.1±.01	12.7±4.201	.1±1.61	.5±0.01	-3±2.09	.5±0.01	-4±.08	5±.01	.01

To be continued

Table 5. (Continued)

Classification	SMAGE	P<F	SMBW	P<F	EN60	P<F	EW60	P<F	EN90	P<F	EW90	P<F	EN120	P<F	EW120	P<F
Sex-Linked :																
PG	1.6±1.0	.10	46.2±7.8	.01	-2.1±2.0	.01	-2.1±2.0	.01	-3.2±3.0	.01	-4.4±1.0	.01	-3.6±4.0	.01	-5.1±1.0	.01
PR	3.6±9.0	.01	11.5±7.1	.11	-7.7±2.0	.01	-1.1±1.0	.01	-1.1±3.0	.01	-1.1±1.0	.01	-1.9±4.0	.01	-1.1±1.0	.01
PW	-3.1±1.3	.02	-78.1±1.6	.01	1.3±.78	.8±1.0	.01	-0.5±.99	.8±1.0	.01	-5.6±.38	.7±1.0	.01	-5.6±.38	.7±1.0	.01
GP	-12.4±1.1	.01	-7.1±8.8	.01	-2.3±.47	.6±1.0	.01	-1.4±.75	.7±1.0	.01	-8.5±.09	.7±1.0	.01	-8.5±.09	.7±1.0	.01
GR	2.7±9.0	.01	48.6±7.5	.01	-4.2±.08	.3±1.0	.01	-3.3±1.0	.4±1.0	.01	-4.4±1.0	.01	-1.1±4.0	.01	-4.4±1.0	.01
GW	1.9±1.0	.01	2.7±8.3	.02	-1.5±3.0	.1±1.0	.01	-1.4±4.0	.1±1.0	.01	5.1±1.0	.01	-1.9±4.0	.01	4.1±1.0	.01
RP	5.0±8.0	.01	-39.0±6.5	.01	-2.4±2.0	.1±1.0	.01	-2.5±3.0	.1±1.0	.01	-1.2±1.0	.01	-3.0±4.0	.01	-1.2±1.0	.01
RG	-2.3±1.1	.04	-63.4±8.8	.01	3.3±.32	.4±1.0	.01	-1.4±.70	.6±1.0	.01	-1.1±5.0	.02	-8.1±1.0	.01	-1.1±5.0	.02
RW	-5.0±1.0	.01	113.0±7.7	.01	2.2±2.0	.1±1.0	.01	2.3±3.0	.1±1.0	.01	1.4±1.0	.01	3.8±4.0	.01	1.5±1.0	.01
WP	4.5±1.0	.01	1.3±7.6	.01	1.6±2.0	.1±1.0	.01	1.7±3.0	.1±1.0	.01	3.1±1.0	.01	3.1±4.0	.01	1.4±1.0	.01
WG	-4.1±1.1	.69	-8.2±8.9	.36	2.8±3.0	.1±1.0	.01	-0.1±.86	5.0±4.0	.01	3.1±1.0	.01	6.5±5.0	.01	5.1±1.0	.01
WR	-4.9±1.1	.01	-81.4±8.5	.01	4.3±.11	.0±1.0	.67	.6±4.0	.07	1.1±1.0	.14	5.5±5.0	.27	2.1±1.0	.01	
Heterosis :																
PP & GG	-1.1±1.5	.48	14.4±12.1	.23	3.4±4.0	.01	1.9±1.0	.01	6.3±5.0	.01	1.5±1.0	.01	7.1±7.0	.01	1.1±1.0	.01
PP & RR	19.5±1.3	.01	25.4±1.0	.01	1.5±3.0	.01	1.6±1.0	.01	3.6±4.0	.01	1.6±1.0	.01	4.0±5.0	.01	1.3±1.0	.01
PP & WW	6.6±1.7	.01	26.4±13.7	.06	4.9±4.0	.01	8.2±.01	.7±9.6	.01	9.9±1.0	.01	1.6±7.0	.01	6.1±1.0	.01	
GG & RR	9.5±1.5	.01	0±12.0	.99	4.1±4.0	.01	1.3±1.0	.01	6.7±5.0	.01	1.0±1.0	.01	7.9±6.0	.01	6.1±1.0	.01
GG & WW	8.1±1.6	.01	-13.8±12.7	.28	5.4±4.0	.01	-1.6±2.0	.1±1.0	1.7±5.0	.01	-1.4±1.0	.01	14.0±7.0	.01	-1.6±1.0	.01
RR & WW	2.1±1.5	.16	12.3±12.1	.31	4.8±4.0	.01	-2.1±.18	7.9±5.0	.01	-0.1±.71	11.0±7.0	.01	-2.1±.19	.19		

SMAGE : Age at sexual maturity.

SMBW : Body weight at sexual maturity.

GCA : General combining ability.

SCA : Specific combining ability.

Egg number (EN) and egg weight (EW) measurements for 60, 90 and 120 days from sexual maturity.

PP, GG, RR, WW : Fayoumi egg production, growth, and random bred lines; and White leghorn breed, respectively.

Although the overall heterosis effect was significant ($P < .0001$), testing the heterosis effect for each pair of pure genotypes showed insignificant heterosis between PP and GG; and between RR and WW (Table 3). The crosses RW and WR showed intermediate SMAGE compared to their parent values (Table 1), which was an indication of additive gene effect. The cross GP was significantly younger while its reciprocal (PG) was older than their parents (PP and GG). Insignificant heterosis between PP and GG pure genotypes (Table 3) was a result of the way heterosis was calculated. Heterosis was calculated as the difference between the mean of each pair of crosses and the mean value of their parents. However a positive sex-linked (Table 5) effect was found for PG cross and a negative sex-linked effect was found for GP cross. Heterosis in SMAGE was reported in crossing two lines of Rhode Island Red divergently selected for residual feed consumption by Bordas *et al.* (1996).

Additive gene effects were observed in progeny of crossing RR with WW, where RW and WR crosses were intermediate in SMAGE between their parent values (Table 1), as well as, heterosis between RR and WW was not significant (Tables 3 & 8). However, other crosses (PG, GP, GR, RG, GW, WG) showed different degree of maternal and sex-linked effects. Dominance gene action was observed in crossing PP with WW, while overdominance effects were observed in crossing PP with RR, where PR and RP crosses reached SM older than their parents.

Sexual Maturity Body Weight:

Significant differences were found between each cross and its reciprocal except for PR and RP crosses (Table 1). PG, WP, GR, GW and RW crosses recorded significantly heavier SMBW than their reciprocal crosses GP, PW, RG, WG and WR, respectively. The difference between any cross and its reciprocal was associated with a differences in sex-linked effect, where all heavier crosses showed positive sex-linked effects while their reciprocal crosses showed negative effects. Fairfull, 1990 stated that some reciprocal differences could result from sex-linked and maternal effects. Dominance gene effect was noticed when crossing RR with PP lines, where their crosses were not significantly different than the heavier RR parent. However, all other crosses showed significant differences with their reciprocal crosses as a result of maternal and sex-linked effects. Although the heaviest genotype was RW cross, the lightest was its reciprocal cross WR. This indicated the magnitude of maternal and sex-linked effects associated with overdominance and epistatic gene action in these crosses.

Results indicated that dam effect is more important than sire effect for SMBW trait, where only PP and WW lines showed significant sire effect while all lines showed significant dam effect (Table 4). Dam effect contains one-quarter of the additive genetic variance and all the maternal effects (Kan *et al.*, 1959). The relative effects for PP when used as a sire or a dam line were

negative. The PP was subjected to selection for high egg number for several generations, which resulted in lighter SMBW than GG and RR Fayoumi lines.

Insignificant heterosis, GCA and SCA effects were found for SMBW (Table 3). Several investigators reported significant heterotic and SCA effects for body weight of growing period when applied crossing within local lines or breeds (Sabri, 1979 & Sabra, 1990) or when crossing local with exotic breeds (Sabra, 1990; Sheble *et al.*, 1990; Mandour *et al.*, 1996). Bordas reported heterosis for SMBW, however, Ramappa and Goward (1973) reported insignificant SCA for growing period and concluded that non-additive gene effects might not be important for body weight during this period.

Egg Numbers Measurements:

Comparing the significance of the least square constants estimated for sire effect with those of dam effect for EN60, EN90 and EN120 showed that sire effects were more substantial than dam effects for these egg number measurements (Table 4). Significant differences between each two reciprocal crosses were found except for RW and WR reciprocal crosses. Superiority of one of the two reciprocal crosses could result from sex-linked and maternal effects (Fairfull, 1990). Except for PW, GP and WR crosses, all crosses showed significant sex-linked effects at EN120 measurements. Reciprocal effects are more of a consideration in layers than in meat birds. Gowe and Fairfull (1982) and Fairfull *et al.* (1983) have reported important reciprocal effects for most traits of commercial significance in White Leghorn chickens.

Heterosis was positive and significant for all egg number measurements (Table 5). Although heterosis could be due to different degrees of dominance or epistasis, the significant differences between reciprocal crosses in this experiment would suggest that some genes responsible for dominance and epistasis effects are presented on sex-chromosomes, and accountable for maternal and sex-linked effects expression. Significant GCA, maternal and sex-linked effects were found in EN measurements, however, SCA was significant only at EN60 (Table 3). Poggenpoel *et al.* (1996) found indication for maternal or dominance effects for egg number traits in a flock of White Leghorn selected for egg production. Significant heterosis, maternal, sex-linked and SCA found in our study, indicated the importance of non-additive gene effects for egg production. This is in agreement with Fairfull *et al.* (1987) who concluded that egg production is a trait that is heavily influenced by non-additive gene action.

Crosses of Fayoumi with WW showed higher heterotic effects than crosses among Fayoumi genotypes. This is in agreement with Gowe and Fairfull (1982), where they reported substantial heterosis with unrelated scrosses. Crossing GG with WW resulted in the highest heterotic value of all other crosses for all EN measurements, while crossing GG with RR showed the highest heterotic effect of all crosses among Fayoumi genotypes (Table 4).

Hossari (1970), Dourgham (1980) and Hossari, *et al.* (1995) reported a heterosis in egg production from crossing PP and GG Fayoumi lines. The cross RG recorded the highest egg production at EN120 among all Fayoumi crosses, where its production (77.7 eggs) represented about 15.7% increase over its mid-parent value $((64.5+69.8)/2)=67.15$ eggs). Crosses WP and WG showed higher egg production than their reciprocal crosses (PW and GW respectively), as well as, higher egg production than all other genotypes. These indicated the presence of genes linked to Z chromosome in WW breed, which affected positively egg production. The cross WP recorded EN120 of 86.8 eggs, while mid-parent value for that cross $((71.3+67.2)/2)$ was 69.25 eggs. The WP value represented about $(86.8/69.25)$ 25% increase over its mid-parent value and about 29% over its PP Fayoumi parent. For WG cross the EN120 was 92.4 eggs, which represented about 36% increase over its mid-parent value $((71.3+64.5)/2)=67.9$ eggs) and about 43% over its GG Fayoumi parent.

Egg Weight Measurements:

Egg weight of WW was significantly the heaviest and that of PP was significantly the lightest of all genotypes studied at all EW measurements (Table 2). Examining the difference between each cross and its reciprocal showed that in most cases it was narrower than the difference between the two parents. Comparing crosses with their mid-parent indicated an incomplete dominance in EW traits, where values for each pair of reciprocal crosses were, generally, between their mid-parent value and the higher value of the two parents (Table 2).

Significant sire, dam, and interaction were found for egg weight measurements (Table 3). Relative WW sire and dam effects were positive, while other lines showed negative values, which reflected the magnitude of the differences in EW values between WW and Fayoumi lines (Table 2).

Significant differences were observed in heterosis, maternal, GCA, SCA and sex-linked effects (Table 3). Poggenpoel *et al.* (1996) reported sex-linked effect for egg weight. Abplanalp *et al.* (1984), Fairfull *et al.* (1983, 1987) and Bordas *et al.* (1996) reported a heterotic effect in egg weight. The difference between each pair of reciprocal crosses was less demonstrated in EW measurements compared to the other studied traits in this study. Bordas *et al.* (1996) reported a reciprocal difference in egg weight.

Although the three Fayoumi lines had the same genetic base, significant heterosis was obtained, which indicates that selection in PP and GG lines may have modified their genome, which was revealed through heterosis when crossing these Fayoumi lines. Dam effects were more substantial than sire effects for SMBW, however, sire effects proved to be more important for egg production measurements. Significant heterosis, maternal and sex-linked effects for egg number and egg weight measurements proved the importance

of non-additive gene effects for these traits. Indication of incomplete dominance was found in egg weight. Results suggested that improving egg production of Fayoumi could be achieved by crossing different Fayoumi lines and strongly recommended crossing Fayoumi with White Leghorn breed. The improvement expected in one generation, from crossing Fayoumi with White Leghorn, which can be up to 43% increase, is far more than that would be expected from conventional selection methods which focusing on additive genetic effects. More improvement would be expected if crossing is accompanied with reciprocal recurrent selection.

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قدرة التأثير غير التجمعي للجينات على تحسين إنتاج البيض في الدجاج الفيومي

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استخدمت بيانات من تجربة خلط متبادل ٤ X ٤ كاملة بعدد ١٤١٤ دجاجة بياضة تمثل ١٦ تركيباً وراثياً مختلفاً. التركيب الوراثية الأصلية المستخدمة كانت ثلاث خطوط من الفيومي (خط منتخب لإنتاج البيض و خط منتخب لثقل وزن الجسم عند عمر ٨ أسابيع و خط المقارنة عشوائى التربية) وسلالة دجاج اللجهورن الأبيض.

لهدف من هذه الدراسة هو معرفة إمكانية استخدام التأثير غير التجمعي للجينات لتحسين عدد ووزن البيض في الدجاج الفيومي، وذلك باختبار معنوية و تقدير تأثير قوة الهجين، التأثير الأمي، قدرة التوافق العامة و الخاصة، و التأثير المرتبط بالجنس. إمكانية استخدام خطوط الدجاج الفيومي كخطوط آباء أو كخطوط أمهات تم أيضا دراستها.

أثبتت النتائج أن تأثير الأب أكثر أهمية بالنسبة لمقاييس عدد البيض (عدد البيض ل-٦٠، ٩٠ و ١٢٠ يوم). كانت قدرة التوافق العامة، و تأثير الأم، و التأثير المرتبط بالجنس معنويا لكل الصفات التي درست. قوة الهجين كانت معنوية لكل الصفات عدا وزن الجسم عند النضج الجنسي. كانت قدرة التوافق الخاصة معنوية للعمر عند النضج الجنسي و صفات وزن البيض (متوسط وزن بيض ٦٠، ٩٠ و ١٢٠ يوم). ظهرت دلائل على وجود سيادة غير كاملة في صفات وزن البيض، بينما كانت السيادة الفائقة و التفوق مصاحبا للعوامل المرتبطة بالجنس و التأثير الأمي هم العامل الرئيسي لمقاييس عدد البيض.

أظهرت النتائج أهمية التأثير غير التجمعي للجينات لصفات إنتاج البيض (عدد و وزن). أظهرت النتائج أن زيادة إنتاج البيض (حتى ١٥ ٪ زيادة) يمكن تحقيقها بالخلط بيض خطوط الدجاج الفيومي وأيدت بقوة خلط الفيومي مع سلالة اللجهورن الأبيض (أدى إلى زيادة حتى ٣٦٪). التحسن المتوقع في جيل واحد من خلط الفيومي مع اللجهورن الأبيض يفوق بكثير المتوقع من خلال الطرق التقليدية للانتخاب و التي تعتمد على التباين الوراثي التجمعي. ويمكن توقع الحصول على تحسن كبير إذا صاحب الخلط الانتخاب العكسي المتكرر.