MAPPING OF QUANTITATIVE TRAIT LOCI AFFECTING PERFORMANCE OF SOME PRODUCTIVE TRAITS IN PUREBREDS AND CROSSBREDS OF CHICKENS

By

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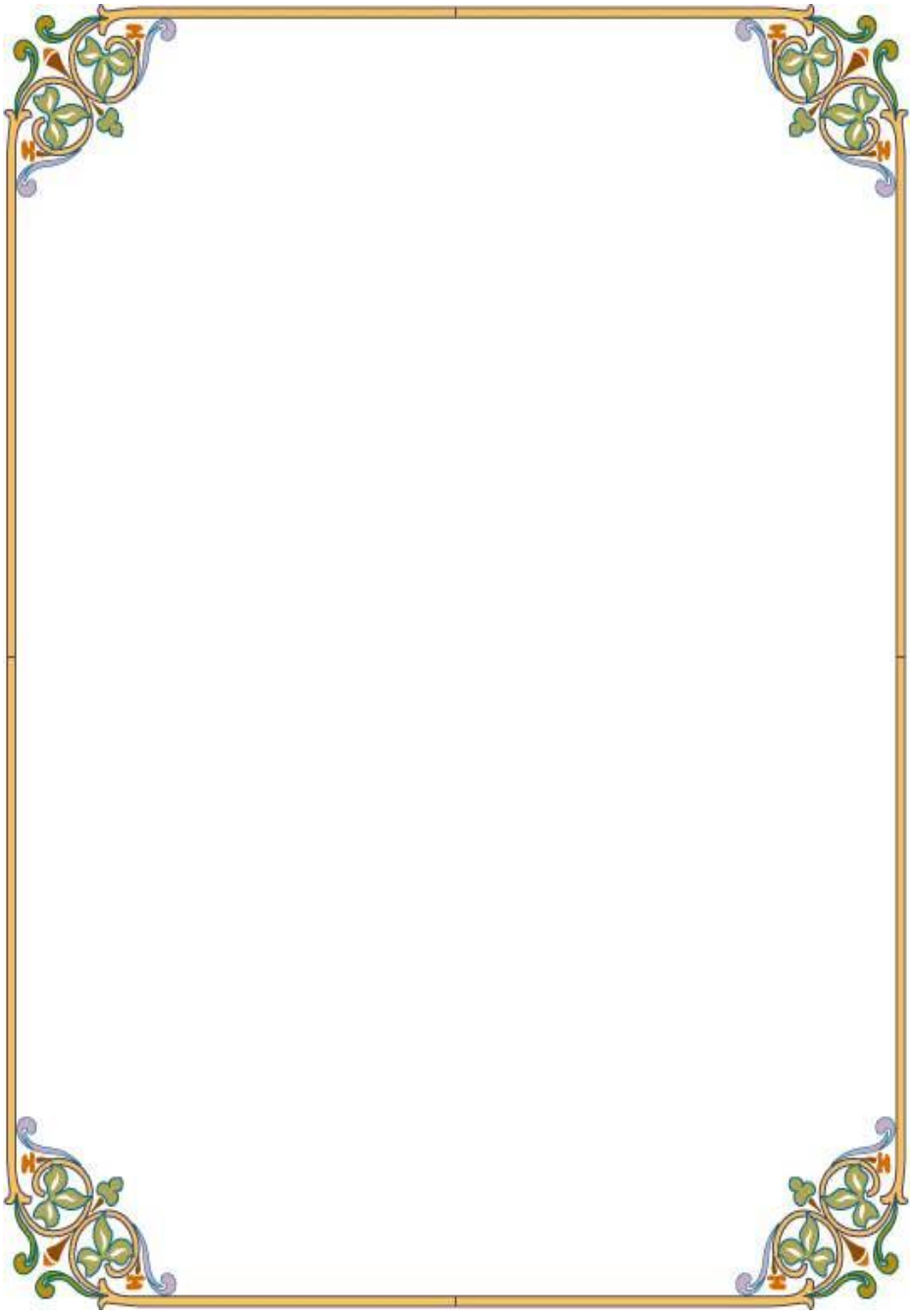


1. INTRODUCTION

Indigenous chickens appear to possess enormous genetic diversity, especially in adaptive traits, and the ability to survive in harsh conditions and under minimum feeding regimens **(Qu *et al.*, 2006; Kosba *et al.*, 2009; Eltanany 2011; Ramadan *et al.*, 2012)**. Comparing the local breeds of chickens with the improved exotic breeds, evidenced that the general performance of local chicken populations is generally low (**Hanafi *et al.*, 1991; Iraqi *et al.*, 2002)**. Nowadays, we need more work for crossing the Egyptian native breeds with the exotic ones to determine the superior breeds, gains in performance from complementary breed effects and heterosis and to develop the superior breeds through selecting the best combination of several breeds **(Iraqi *et al.*, 2013)**. Results of the most crossbreeding experiments that carried out in Egypt showed that crossing between the local breeds or strains of chickens with other local ones was generally associated with the existence of considerable heterotic effects on growth performance **(Ezzeldin and El-Labban, 1989; Khalil *et al.*, 1991; Nawar and Bahie El-Deen, 2000)**.

Body weight is a complex quantitative trait resulting from various developmental processes **(Brockmann *et al.*, 1998; Ankra-Badu *et al.*, 2010)**. Such quantitative trait is controlled by the additive effect of multiple genes. In QTL study, it is aimed to determine the most effective genes and chromosomal regions for such quantitative trait and to use these in molecular selection. Many molecular markers have became excellent

means for the study of genetic variation **(Chen *et al.*, 2003; Chang *et al.*, 2005)**, such as random amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLP), microsatellite DNA, and sequence-related amplified polymorphism (SRAP) **(Zietkiewicz *et al.*, 1994; Li and Quiros 2001)**. Microsatellites are tandem repeat loci with a core motif of 1 to 6 bp repeated several times. They are highly polymorphic and considered to be evenly distributed in the genome. The microsatellite markers may therefore be required to be used in improving the growth rate in genetic selection programs in poultry **(Liu *et al.*, 2007)**.

The identification and utilization of QTL provide the potential for more rapid genetic improvement in selection programs, especially for traits that are difficult to improve them using the traditional selection **(Ikeobi *et al.*, 2002)**. **van der Beek and van Arendonk (1996)** indicated additional selection responses of 6 to 13% using marker assisted selection (MAS) for growth traits by incorporating a marker-linked QTL in a simulation study after five generations of selection. Based on chicken linkage maps and data from a variety of populations, several studies have reported the discovery of QTL for body weight in chickens **(Tatsuda and Fujinaka, 2001; Sewalem *et al.*, 2002; Li *et al.*, 2003; Sasaki *et al.*, 2004; Schreiweis *et al.*, 2005; Gao *et al.*, 2006; McElroy *et al.*, 2006; Nones *et al.*, 2006; Zhou *et al.*, 2006; Liu *et al.*, 2007 & 2008; Ambo *et al.*, 2009; Ankra-Badu *et al.*, 2010; Wang *et al.*, 2012)**. A whole genome scan for QTL affecting body weight and growth in a 3-generation population generated from two broiler lines

genetically different was conducted by **van Kaam *et al.* (1998, 1999)**. The identification and use of QTL in selection programs, therefore, will offer the potential for more rapid genetic improvement.

In the last 15 years, several experimental chicken populations (F_0, F_1, F_2 and F_3) have been constructed from different breeds for use in gene and QTL mapping studies **(Jacobsson *et al.*, 2005; Liu *et al.*, 2008; Bulut *et al.*, 2013)**. Furthermore, chromosomal scanning studies have been conducted. To examplify, the chromosomal regions affecting phenotypic traits including body weight have been investigated in different chicken breeds **(van Kaam *et al.*, 1999; Tatsuda and Fujinaka 2001; Sewalem *et al.*, 2002; Carlborg *et al.*, 2003, Kerje *et al.*, 2003; Li *et al.*, 2003; Zhu *et al.*, 2003; Sasaki *et al.*, 2004; Siwek *et al.*, 2004; Gao *et al.*, 2006; Nones *et al.*, 2006)**. These studies are ongoing on the identification of the quantitative trait genes (QTGs) and quantitative trait nucleotide (QTNs) controlling these traits.

Egg production and quality traits in indigenous breeds of chickens in Egypt were usually not subjected to intensive selection program and consequently, high additive and non-additive genetic variations appeared to have meaningful effects (**Iraqi *et al.*, 2012**; **Khalil *et al.*, 2013**). Most of the crossbreeding experiments that had been carried out in Egypt showed that crossing between local breeds or strains of chickens with the other exotic ones was generally associated with the existence of considerable heterotic effects on egg traits **(El-Labban, 2000; El-Sisy, 2001; El-Soudany, 2003; Iraqi *et al.*,**

2012; Khalil *et al.*, 2013; Abou El-Ghar *et al.*, 2014). **Khalil *et al.* (2013)** concluded that crossing Golden Montazah with White Leghorn was associated with the existence of positive and high percentage of heterotic effects in terms of individual and maternal heterosis for most egg quality traits, i.e. egg components were improved when Golden Montazah was crossed with White Leghorn.

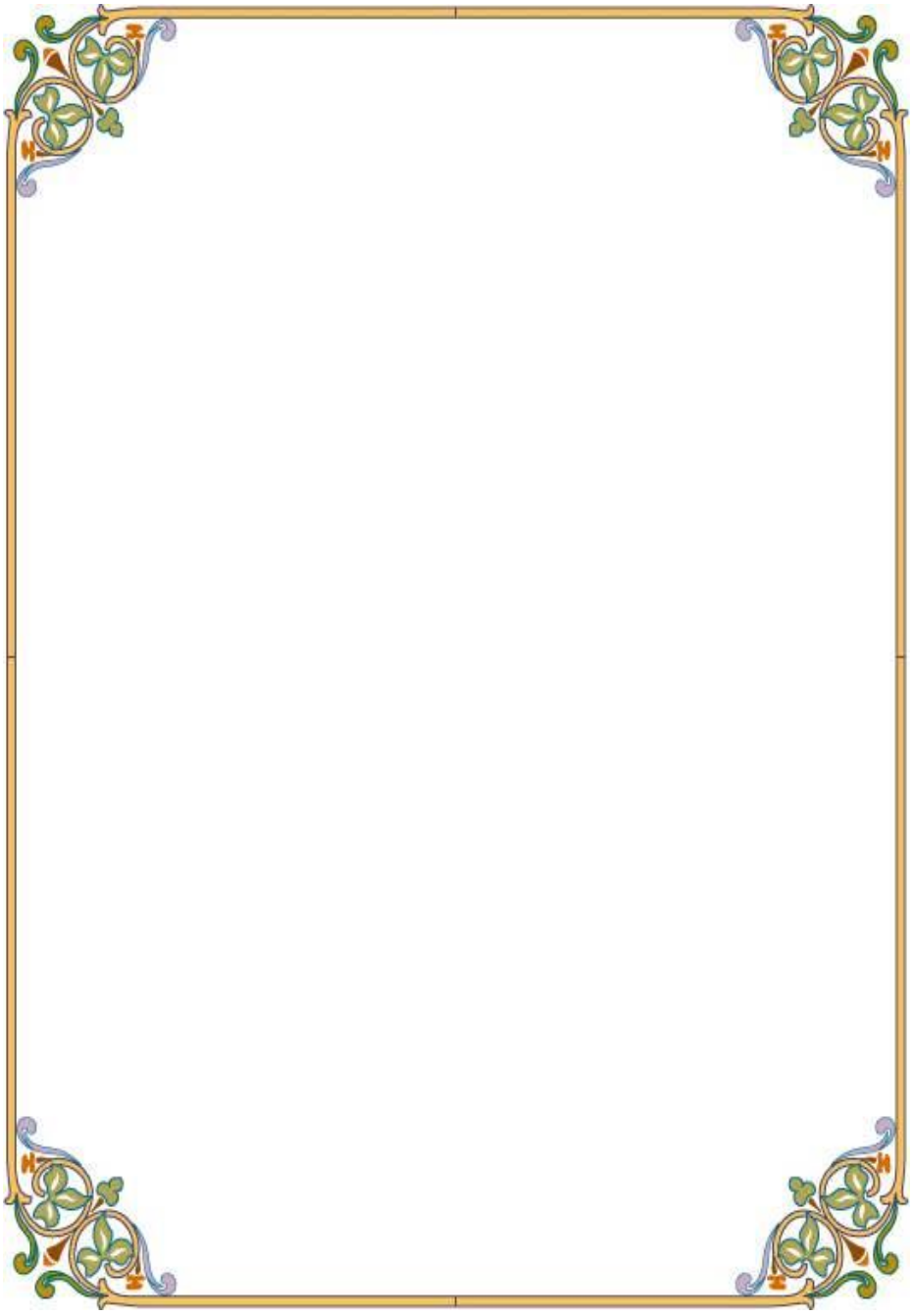
The chicken genome consists of 38 pairs of autosomes and sex chromosomes Z and W. The chromosomes can be classified into two size groups, nine macrochromosomes and 30 microchromosomes **(Bloom *et al.*, 1993)**. The classic genetic map of chicken consisted of 119 loci of morphological mutations, biochemical polymorphisms or chromosome breakpoints, 44 of which have map positions **(Bitgood and Somes, 1993)**.

The improvement of egg quality traits by traditional breeding methods is difficult because the phenotypic measurements are time consuming, and their use in breeding programs are complicated due to unfavorable negative correlations with other relevant traits. Therefore, direct selection of males based on their actual genotypes for important genes or markers linked to these genes (i.e. marker-assisted selection, MAS), rather than on their estimated breeding value, could greatly enhance the breeding program for egg quality traits **(van der Werf and de Boer, 1990)**.

Recent development of statistical methods and comprehensive linkage maps of the chicken genome has provided tools for mapping loci affecting quantitative traits **(Mackay *et al.*, 2009)**. However, only few genome-wide QTL

scans have been reported in poultry, and none of these has involved egg production and egg quality traits in layers. A better understanding of chicken QTL may facilitate the accurate selection of immature chickens. Therefore, MAS of immature females and males should greatly enhance genetic progress for egg character and production traits through accurate selection and accelerate genetic improvement at a young age. Some studies have reported associations between genetic markers and egg traits in poultry **(Sasaki *et al.*, 2004)**. In terms of egg production and eggshell quality, associations have been found for polymorphisms in the putative candidate genes IGF-1, GH, and GHR in the growth hormone endocrine pathway **(Feng *et al.*, 1997; Kuhnlein *et al.*, 1997; Nagaraja *et al.*, 2000)**.

The resource populations used in the present study were generated by crossing the males of Golden Montazah (GM) with the females of White Leghorn (WL). The main objectives were: (1) to phenotyping growth traits (body weights and daily gains), egg production and egg quality traits in the parental and F_2 generations in such crossbreeding program, (2) to localize QTL affecting growth, egg production and egg quality traits at different ages in the F_2 population using specific microsatellite markers, and (3) to detect the chromosome group, number of informative microsatellite markers, chromosome map length (cM) and average marker interval by the chromosome (cM), (4) to estimate QTL at chromosome-wise level along with the percentages of phenotypic variance explained by each QTL, (5) to explain the total variances attributable to QTL for each growth and egg trait, and (6) to quantify the additive and dominance effects attributable to QTL.



2. REVIEW OF LITERATURE

2.1 Growth traits:

Growth can be regarded as a direct fitness trait that increases productive efficiency and thereby decreases production costs. Crossing is a method that can improve growth performance in poultry, which have a main purpose that is to produce superior crosses for growth traits which are influenced by various genetic and non-genetic factors.

2.1.1 Crossbreeding and genetic groups favored for growth traits:

Crossing is one method that can improve growth performance in poultry. In Egypt, **Hanafi *et al.* (1991); Mohamed, 1997; Nawar and Abdou (1999); Sabri *et al.* (2000); Afifi *et al.* (2002) and Iraqi *et al.* (2002)** crossed native breeds or strains of chicken with exotic adapted ones under Egyptian conditions. Most of these reports evidenced that crossing local breeds with either local or exotic ones was associated with the existence of heterotic effects. Because native chicken breeds had high non-additive genetic variance **(Shebl *et al.*, 1990; Hanafi *et al.*, 1991; Sabri *et al.*, 2000)**. This would encourage the Egyptian breeders to improve local breeds through crossbreeding.

In Egypt, some authors crossed native breeds or strains of chicken with exotic adapted ones under Egyptian conditions **(Iraqi *et al.*, 2002 and Iraqi *et al.*, 2013)**. Exploitation of the genetic variation and the hybrid vigor by combination of

different important characteristics of each breed **(Hanafi and Iraqi 2001)** and for the exploitation of maternal genetic effects or sex-linked effects, associated to particular combinations between breeds or lines. The analysis of the combining aptitude and the difference between the productive performances of crossbreds help in identifying the best possible combinations in the exploitation of hybrid vigor according to the desired objectives **(Mekki *et al.*, 2005)**. The crossing between the adapted local chicken and exotic standard breeds would allow exploiting the rusticity of first and the productive performances of the later at a time in tropical environment to produce adapted and more productive genetic types. This crossing could consequently, allow higher genetic gains in shorter time and therefore reach the objectives of the crossing more quickly **(Mahmoud and El-Full, 2014)**.

Taha and Abd El-Ghany (2013) using Mandarah (MM), El-Salam (SS), crossbreds Mandarah x El-Salam (MS) and El-Salam x Mandarah (SM) as well as their crosses and reciprocal crosses showed non-significant increase for Mandarah strain in hatch weight followed by SM cross then their reciprocals (MS), while the lowest weight was recorded for El-Salam strain. On the other hand, SM cross showed higher significant BW than other lines at weeks 2, 4, 8, 12, 16 and 20 of age (120, 318, 674, 1072, 1458 and 1793 g; respectively). Mandarah strain recorded the lowest BW for the same periods. Simultaneous results were recorded by **Bekele *et al.* (2010)** who found that crossing between two chicken breeds resulted in improving body weight of one cross and reduced the weight of the reciprocal one. Also,

differences between reciprocal crossbred lines of chickens were recorded by **Razuki and ALShaheen (2011) and Ndegwa *et al.* (2012)**.

2.1.2 Heritabilities for growth traits:

The methods available for estimating the heritability for body weights in chickens were based either on the use of covariance between sibs or on the use of parent-offspring covariance. Most of the estimates cited in the literature have been obtained from covariance between sibs. The various estimates of heritability reported in literature differ widely in magnitude and this is due to that these estimates were made using widely varying breeds under varying environmental conditions. However, the apparent differences, among the h^2 estimates were probably due to (1) The genetic constitution of the breeds in the flock, (2) The method of analysis and estimation, (3) The available number of observations used, (4) The models applied on each set of data to correct for the non-genetic factors, and (5) The level of inbreeding and coefficient of relationship in the parent population (dams- or sires-related or sires related to dams) and (6) The selection if practiced. In general, more reliable estimate of h^2 were obtained from the animal models because these estimates might be more accurate (unbiased) than those estimated using other methods (i.e. Henderson's methods, ML, MIVIQUE and MINIQUE), because the relationship among animals are considered (**Quaas *et al.*, 1984; van der Werf and de Boer, 1990; Aggrey and Cheng, 1994).**

Heritability estimates for body weights (BW) in chickens were moderate to high, suggesting that body weight of chickens would respond favorably to selection **(Segura *et al.*, 1990; Nestor *et al.*, 1996; Iraqi *et al.*, 2002; Resende *et al.*, 2005)**. However, **Iraqi *et al.* (2002)** cited that high heritability for BW0 was 0.58 and low to moderate heritabilities were 0.21, 0.15, 0.20 and 0.14 for BW4, BW8, BW12 and BW16 respectively. **Prado Gonzalez *et al.* (2003)** reported low to moderate estimates of direct heritability in Creole chickens. The moderate to high heritabilities found in this study suggesting that selection at all stages of growth will result in genetic progress. For rapid genetic improvement in these chickens, it would be ideal to select at early ages. **Niknafs *et al.* (2012)** estimated that heritability for BW0 was 0.46 higher than the other body weights of BW8 and BW12 (0.24 and 0.29 respectively), while the lowest values in the range of heritability were reported in some previous studies **(Danbaro *et al.*, 1996; Ghazikhani Shad *et al.*, 2007; Kamali *et al.*, 2007; Lwelamira *et al.*, 2009). Dana *et al.* (2011)** stated that direct heritability of growth traits ranged from 0.15 for BW6 to 0.40 for BW0, while the values for body weight at 16 weeks of age were moderate (0.23). No systematic pattern (increasing or decreasing with age) was observed with these heritability values as found in some studies. **Faruque *et al.* (2013)** reported that the body weight at 12 weeks of age and 16 weeks of age for three native chickens in Ethiopia ranged from low (0.16) to high (0.73) heritabilities. **Hu *et al.* (1999)** and **Resende *et al.* (2005)** showed direct heritability estimates for body weights increasing with age in Japanese quails and Muscovy ducks, respectively, while **Saatei *et al.* (2002)** reported reduction in heritability

estimates as age increased, the reduction in estimates of direct heritability as age increased could have been due to confusion of maternal environment with direct genetic effects.

Iraqi *et al.* (2002) demonstrated that estimates of heritability using multi-trait animal model for body weight at hatch, 4, 8, 12 and 16 weeks of age were 0.58, 0.21, 0.15, 0.20 and 0.14, respectively. The magnitudes of estimates are very important in determining the type of selection and in practicing the genetic selection at early ages (0-4 weeks) to have rapid improvement in growth for local strains in Egypt. Some results **(Danbaro *et al.*, 1995; Iraqi *et al.*, 2000)** showed that heritability estimate for body weight at hatch was higher than that at 12 weeks which may be due to the small maternal effects at later age than at hatch, i.e. decreasing the non-additive genetic effects.

2.1.3 Genetic and phenotypic correlations among growth traits:

Zhou *et al.* (2006) stated that the phenotypic correlations between growth traits of BW and daily gains in the F_2 populations were highly positive. The phenotypic correlations between BW traits and neighbor BW traits or average daily gain traits were relatively higher than the other correlations, such as correlations among BW6 and BW4 (0.86), BW8 (0.95), ADG2-4 (0.84), and ADG4-6 (0.89). **Dana *et al.* (2011)** found that the correlations between hatch weight and most of the other growth traits were generally low; among other growth traits, the genetic correlations ranged from 0.51 for BW2 with BW16 to 0.99 for BW12 with BW16 and the phenotypic correlations ranged from

0.27 for BW2 with BW16 to 0.85 for BW6 with BW8. Therefore, body weights up to 16 weeks of age were used to characterize the growth performance of chickens and the selection for rapid early growth at a market age (40–50 days) has been the most common approach in broiler chicken breeding programs **(Emmerson, 2003)**. The body weight at 16 weeks of age has positive correlations with growth traits from 2 to 12 weeks of age and the correlations were particularly strong with certain growth traits (r_g=0.82 with BW8, and 0.99 with BW12). **Taha *et al.* (2012)** reported that there were highly positive correlations between body weights at 8 weeks, body weight at first 90 days, body weight at first 42 weeks of age and body weight at first 65 weeks of age. **Niknafs *et al.* (2012)** reported that the genetic correlations among body weight traits varied from relatively moderate to high (0.36–0.91), while they are mostly at the low end of the range existing in some previous reports with the exception of genetic correlation (0.91) between BW8 and BW12 **(Sang *et al.*, 2006; Lwelamira *et al.*, 2009).**

2.1.4 QTL markers:

van Kaam *et al.* (1999) indicated the region positioned between markers LEI166 and MCW166 as potential for identifying QTL for BW 48 days, since the authors found a significance level very near to the suggestive level. **Sewalem *et al.* (2002)** detected a QTL affecting BW at 3 and 6 weeks of age, and the markers related to this QTL were LEI0068, LEI0146, and MCW0018. **Nones *et al.* (2006)** reported a QTL affecting BW at 35 and 42 days and the flanking markers were LEI0068 and MCW0097. **Atzmon *et al.* (2006)** found a microsatellite

marker ADL0037 significantly associated with BW at 7 weeks. These studies suggested that different sets of genes may be involved at different life stages of chicken growth and development, and the QTL found may vary with the population used.

2.1.5 Chromosomal linkage analysis for growth traits:

Transmission of genes from parent to offspring occurs after meiosis where the pairs of chromosomes are duplicated and the pairs are separated to form the gametes. Recombination, or crossing over, between the chromosome pairs occurs during meiosis. This results in new combinations of alleles on the chromosome. The recombination frequency between two loci is a function of the distance between them. Therefore, it is possible to estimate the distance between two markers by measuring the recombination fraction between them. Markers on different chromosomes, or far apart on the same chromosome, have a recombination frequency of 0.5. If one could assume that only one recombination event occurs between two loci, the recombination fraction would be a direct measurement of genetic distance. But, this is not the case and several recombination events may occur between the two loci on the same chromosome. Map functions have been developed to compensate for such double recombinants and the most commonly used map functions are the Haldane **(Haldane, 1922)** and Kosambi **(Kosambi, 1944)**. A linkage map consists of marker loci in an order on the chromosome and the map distance between the markers. The distances are given in centiMorgan (cM, one cM is equal to one recombination event in 100 meioses) and are

calculated using one of the map functions. Linkage maps are constructed by linkage analysis in pedigrees where a number of markers have been genotyped **(Groenen *et al.,* 2000)**. In large pedigrees consisting of many individuals and where many markers are genotyped, computer programs are used to construct linkage maps **(White and Matise, 2001)**.

The growth traits are quantitative traits that controlled by many loci. A quantitative trait locus (QTL) is defined as a chromosomal region harbouring one or several genes that influence a quantitative trait. Analyses to identify QTL are based on co-segregation of markers and genes affecting the phenotypic trait variation **(Kerje *et al.,* 2003)**. In a classic single marker QTL analysis, the associations between marker genotypes were compared with the phenotypes in a single-locus test. In order to exploit the full potential of QTL analyses, **Lander & Botstein (1989)** proposed a QTL mapping method where the linkage map was utilized to estimate QTL effects between markers in crosses of inbred lines. **Haley *et al.* (1994)** extended the interval mapping method in order to apply it to intercrosses between outbred populations. Through the marker analysis, it is possible to trace recombination events and determine the founder origin for each F_2 individual at every position across the genome. The measured phenotypes are regressed onto the estimated genotype probabilities and the statistical analysis is performed to test how much of the phenotypic variation is explained by segregation at each position. Basically, the phenotype variation is compared to the inheritance pattern at marker loci. Matching inheritance patterns gives a signal of a QTL.

For the red jungle fowl (RJF) x White Leghorn (WL) intercross, 105 markers (100 microsatellites, 4 SNPs and 1 phenotypic trait) were genotyped in the pedigree and they formed 27 linkage groups including the Z chromosome. Twenty marker gaps were larger than 40 cM. The average information content at marker positions was 0.77 and the average marker distance was 24.3 cM. A test for differences in map length between the sexes showed some chromosomes where the female map was longer and some where the male map was longer. A linkage map comprising linkage groups for 25 autosomes and the Z chromosome was constructed by **Jacobsson *et al.* (2005)** for the intercross between the high (H) and low (L) weight selection lines and a total of 145 genetic markers were used, of which 14 had not been mapped to a chromosomal location before. Thy stated that the total map length was 2521.9 cM with 17 gaps greater than 40 cM and the average information content of 0.55 was increased to 0.72 when information from adjacent markers was included. **Ruy *et al.* (2005)** found that the greatest interval was 36 cM and the least 3 cM, with estimated coverage of 341 cM, supposing that the markers positioned at the extremes would cover up to 20 cM for each side. Selective genotyping on chromosome 5 was completed with eleven markers with the average spacing among them of 21.3 cM varying between 47 cM and 4 cM with estimated coverage of 222 cM the coverage obtained includes the entire extension of the chromosomes with lengths given in the consensus map of 317 and 198 cM for chromosomes 3 and 5, respectively. The greatest distance present among the markers was located at the end of chromosome 5 between markers ADL233 and ADL298. The only marker

available in this region, ADL166 would still maintain spacing greater than 30 cM **(Groenen *et al.*, 2000)**. Four regions on chromosome 3 were observed to concentrate eight markers indicating suggestive marker linkage with QTL for BW42. The first region is represented by LEI43 and MCW169 positioned at 9 and 31 cM, respectively (positions given on the consensus map). The region near marker MCW169 coincides with the position described by **McElroy *et al.* (2002)**, who identified QTL for body weight. The second region includes markers MCW222 and LEI161 positioned at 87 and 113 cM, respectively. **McElroy *et al.* (2002)** detected QTL significant for body weight, located at 154 cM on chromosome 3. In spite of two informative markers existing in this region, LEI115 at 143 cM and ADL371 at 163 cM, they were not significantly or suggestively linked to QTL and, at least in the present analysis of selective genotyping, these reported QTL were not confirmed. The fourth region was related to marker MCW116, located at 310 cM. In spite of not being previously described as a significant or suggestive QTL at this position, on chromosome 5, three regions were located where four markers with suggestive linkage with QTL for BW42 were found. The first region comprises markers MCW193 and MCW90 at 50 and 57 cM, respectively.

McElroy *et al.* (2002) found linkage between MCW193 and QTL, suggestive at 10%, for nine distinct characteristics including body weight at six week. However, these authors employed only this marker in chromosome 5, and detection of linkage between marker and QTL at significant levels depends,

among other factors, on distance and degree of marker information. Using a similar population based on a broiler x layer line, **Sewalen *et al.* (2002)** mapped QTL for body weight at three weeks at 58 cM, coinciding with the region associated in this study to QTL for BW42. **Tuiskula-Haavisto *et al.* (2002)** stated that the two regions suggestively linked to QTL for BW42 on chromosome 5 were located at 151 cM and 198 cM, where the markers ADL233 and ADL298 are located, respectively. **Zhou *et al.* (2006)** using 269 microsatellite markers genotyped in two F_2 crosses (broiler by Leghorn cross and broiler by Fayoumi cross) cover 23 autosomes, 3 linkage groups, the Z chromosome, and an unknown linkage group were detected. In the broiler-Leghorn cross, 19 autosomes, 1 linkage group, and the Z chromosome containing 195 microsatellite markers were used for linkage analysis. The total map length was 42.77 M, with average spacing of markers of 21.93 cM ranging from 8.71 to 31.33 cM. In the broiler-Fayoumi cross, nineteen autosomes, 2 linkage groups, and the Z chromosome containing 191 microsatellite markers were used for linkage analysis with total map length of 38.35 Morgan. The average marker interval ranged from 6.03 to 28.86 cM with average spacing of markers of 20.08 cM across the chromosomes. In this study, the map order of the markers in both F_2 crosses was similar to the chicken consensus map and map lengths for these chromosomes were considerably longer compared with the chicken consensus map.

2.1.6 QTL mapping:

McElroy *et al.* (2002) indicated that several regions were significantly associated with one or more growth traits.

Chromosome 2 showed three significant QTL for different traits at substantially different positions, indicating the presence of multiple 56 QTL. **Tatsuda and Fujinaka (2001)** found a QTL for body weight at 60 cM and **van Kaam *et al.* (1999)** detected a QTL for body weight at 41 cM on chromosome 2, chromosomes 3 and 13 were found to contain QTL for several traits at similar positions, which may represent single pleiotropic QTL. No QTL were found on chromosome 1, while several studies have been reported that chromosome 1 contain QTL for body weight **(Groenen *et al.*, 1997; Tatsuda *et al.*, 2000; Tatsuda and Fujinaka, 2001)**. However, **Tercic *et al.* (2009)** stated that QTL mapping analysis in the F_3 population revealed several QTL for various traits on chromosome 5 and chromosome 11 and the QTL for body weight at 21 and 42 days of age were localized on chromosome 5 at 172 and 163 cM, respectively. The peak locations for these two QTL were all flanked by the same pair of markers (MCW0029 and COM0184), suggesting that it is likely that a single QTL affects the two highly correlated traits. Also, two distinct QTL regions were identified on chromosome 2. At the proximal end of chromosome 2, a QTL was detected for BW55 at 15 cM in F_3 linkage map (between ADL0270 and ADL0190). In other studies, one QTL affecting 13 and 16 week weight that has been mapped at the same candidate interval **(Tatsuda & Fujinaka 2001)**. The second QTL region for BW55 was located at the distal end of chromosome 2 (flanking markers MCW0137 and LEI0147). Within this region, **Zhou *et al.* (2006)** also located a series of BW traits including BW at 8 weeks (similar to BW55), and another QTL affecting weight at hatch (BW1) at 81 cM on chromosome 5, peaking at a similar location

as an early growth QTL (body weight at 2 weeks) in a broiler-Leghorn cross, suggesting a possibility that these two QTL are allelic.

Nones *et al.* (2006) reported a QTL affecting BW at 35 and 42 days at 150 cM on the consensus map. The QTL affecting BW traits were detected in some reviewed studies that showed significant effect for QTL at 4 to 12 weeks of age **(van Kaam *et al.*, 1999; Sewalem *et al.*, 2002; Kerje *et al.*, 2003). Jacobsson *et al.* (2005)** located QTL for body weight at 70 days, indicating that this segment contains BW QTL segregating in several breeds and lines of chickens.

Liu *et al.* (2007) stated that body weight is under complex genetic control and uncovering the molecular mechanism of growth will contribute to more efficient selection for growth in broiler chickens. QTL affecting BW at 4 to 12 weeks of age were located in the region 523 to 555 cM on the linkage map of NEAURP; the markers associated with this region were LEI0079, ADL328, and ROS0025. On the other hand, **Liu *et al.* (2008)** suggested that very strong evidence pointing to QTL for BW12 was suggested between markers NEAU0006 and ADL0328, and the most likely position was at 590 cM or at marker ADL0328. Also, **Kerje *et al.* (2003)** indicated that when the 2 estimated QTL positions differed by a recombination distance of <30 cM in the chromosome region, a single QTL for the given trait was assumed to be on that chromosome. Because BW at 4 to 12 week of age were highly correlated and the QTL positions were close, it was reasonable to assume that the same QTL affected these traits. While, **Atzmon *et al.* (2006)** reported

that a microsatellite marker MCW0102 was significantly associated with BW at 7 weeks in a commercial broiler line.

van Kaam *et al.* (1999) performed a whole-genome scan for QTL affecting growth in chickens and detected four QTL on Gallus gallus autosomes (1, 2, 4, 23) that exceeded the thresholds of significance. **Tatsuda and Fujinaka (2001)** detected a QTL affecting body weight closely aligned with those reported using a reference population derived from a cross of a Satsumadori sire (slow-growing, lightweight Japanese native breed used for meat production) and a White Plymouth Rock dam (early maturing, heavy weight broiler). They reported that two QTL affecting body weight at 13 and 16 weeks were mapped at 220 cM on chromosome 1 and 60 cM on chromosome 2 and the closest QTL markers were LEI0071 on chromosome 1 and LMU0013 and MCW0184 on chromosome 2. QTL for body weight at 3, 6 and 9 weeks of age were investigated by **Sewalem *et al.* (2002)** using a broiler × layer crossbred and they stated that a QTL on chromosome 13 affected body weight at the three ages and QTL significant at the genome-wide level that affected body weight at two ages were found on chromosomes 1, 2, 4, 7 and 8.

Using genotypes for 52 microsatellite loci spanning regions of nine chicken chromosomes and half-sib analyses with a multiple QTL model, the linkage between these nine regions and growth traits was established. **Sasaki *et al.* (2004)** identified significant QTL for BW on chromosome 4. Significant QTL were also reported at similar positions on this chromosome for BW at 6 and 9 weeks from an intercross line between commercial broiler and WL **(Sewalem *et al.*, 2002)** and from an

intercross between WL and RIR **(Tsuiskula-Haavisto *et al.*, 2002)**. Another significant QTL for BW on chromosome 27 was reported by **(Sewalem *et al.* (2002) and Kerje *et al.* (2003)**. Numerous studies demonstrate that QTL displaying significant linkage with BW and located on chromosome 1 **(Groenen *et al.*, 1997; Tatsuda *et al.*, 2000; Tatsuda & Fujinaka 2001; Sewalem *et al.*, 2002; Kerje *et al.*, 2003)** and chromosome 2 **(Tatsuda & Fujinaka 2001; Sewalem *et al.*, 2002; Kerje *et al.*, 2003)**. However, no QTL on chromosomes 1 and 2 were identified by **Tsuiskula-Haavisto *et al.* (2002)**.

2.1.7 QTL confidence intervals for growth traits:

Tatsuda and Fujinaka (2001) identified two significant QTL for growth traits using a crossing population between a Satsumadori line and a White Plymouth Rock line and one QTL was identified on chromosome one and located at 220 cM. **Sewalem *et al.* (2002)** performed a genome scan for growth using a crossing between a White Leghorn line and a commercial broiler sire line and reported that two significant QTL of 145 and 481 cM for 3-week body weight were located on chromosome one, in which 95% confidence intervals were 113–217 and 441–526 cM, respectively. Another significant QTL for 9-week body weight was located on chromosome one at 414 cM with 34–419 cM of the 95% confidence interval. **Kerje *et al.* (2003)** identified two major QTL for growth, which were located on chromosome one using a crossing population between Red Jungle Fowl and White Leghorn; the two major QTL for growth traits were located around the positions of 68 and 416 cM.

Soller *et al.* (2006) reported that fine-mapping of QTL and the identification of causal gene and underlying genes still remains one of the major challenging tasks because the confidence interval (CI) of most reported QTL covers more than 20 cM. On the other hand, **Honkatukia *et al.* (2007)** reported that in F_2 population cross between two extreme egg layer lines Rhode Island Red and White Leghorn, the confidence interval for body weight at 16 weeks of age on chromosome 4 was 189-204 cM, while on chromosome 6 it was 15-56 cM. **Roa *et al.* (2007)** observed that in F_2 chicken population was established from a crossbreeding between Xinghua line and White Recessive Rock line there were two significant QTL for 3 week-BW and they were located on chromosome 1 at 145 cM and 481 cM, respectively, in which 95% of the confidence intervals were 113–217 cM and 441–526 cM, respectively. Another significant QTL for 9 week-BW was located on chromosome 1 at 414 cM with 34–419 cM of the 95% confidence interval. More markers and individuals were used to refine the confidence interval of these QTL to be a narrow region **(Liu *et al.*, 2008)**. However, there were still many genes in this narrow region, and it was difficult to identify the major genes for growth by positional cloning and the map position of the QTL for BW at 4–12 weeks of age was refined to a sub-centiMorgan level by haplotype analysis and the narrow region was possible for the positional cloning of the underlying candidate genes. However, **Demeure *et al.* (2013)** reported that in F_2 intercross between two meat-type lines of chickens the average confidence interval (CI) of growth traits was equal to 14 cM, with large differences depending on the region (from 2 cM to 36 cM), mainly due to differences in

marker density and informatively. In general, the information provided by the traditional microsatellite-based QTL analysis cannot be used in selection programs because of very large confidence intervals on QTL location.

2.1.8 Additive and dominance effects for QTL of growth traits:

Using 174 microsatellite markers, **Siwek *et al.* (2004)** found that the additive effects for QTL detected for body weight at 4, 6, 8, 12, and 18 week of age in F_2 cross were positive on chromosome 7, while the negative additive effects for QTL were detected on chromosome 3. **Zhou *et al.* (2006)** with broiler-Leghorn cross and broiler-Fayoumi cross found that most of the additive effects explained by QTL detected in the study showed positive values, in broiler-Leghorn cross, whereas the broiler-Fayoumi cross had a negative additive effect, which means that alleles of broiler-Leghorn cross and broiler-Fayoumi cross were generally superior in weight and growth relative to both purebred Leghorn and Fayoumi alleles. **Wang *et al.* (2012)** found that the positive additive effects indicating that increasing body weight allele was inherited from the broiler line in F_2 population cross of broiler sire with Chinese Bair layer dams. **Rosario *et al.* (2014)** in F_2 population obtained by crossing the males from a layer line (CC) and the females from a broiler line (TT) cited that most of the QTL showed negative additive effects, indicating that the alleles that increase body weights came from broiler line on chromosome 4, while most of the dominance effects were negative except body weight at 35 days of age it was positive

and indicating that the heterozygotes were heavier than the mid-parent.

2.1.9 Total variances explained by QTL for each growth trait:

Zhou *et al.* (2006) in F_2 population of broiler-Leghorn cross and broiler-Fayoumi cross found that a total of 52 and 38 QTL were detected at the 5% chromosome-wise level for the traits evaluated in the broiler-Leghorn cross and the broiler-Fayoumi cross respectively. Of the 52 suggestive QTL in the broiler-Leghorn cross, 17 QTL were significant at the 5% genome-wise level, while of the 38 suggestive QTL in the broiler-Fayoumi cross, 10 QTL were significant at the 5% genome-wise level**.** A total of 18 and 13 significant QTL were detected at a 1% chromosome-wise significance level for the 8 growth traits studied, of which 17 and 10 were significant at the 5% genome-wise level, respectively. Potential candidate genes within the QTL region for growth traits at 1% chromosome-wise significance level of considerable importance. **Wang *et al.* (2012)** in F_2 population cited that there are three QTL at 5 % chromosome-wise and 10 QTL at suggestive level on chromosome 3, 4 QTL identified on chromosome 5 at 5% genome-wide level, 8 QTL at 5% chromosome-wide level and one at suggestive level. On chromosome 7, there were 5 QTL identified at 5% genome-wide level, 4 QTL at the 5% chromosome-wide level and 4 QTL at suggestive level.

2.2 Egg production and egg quality traits:

There were wide variation in egg production between different breeds and strains of chickens. The effect of

crossbreeding is an increase in heterozygosity and attendant decrease in homozygosity **(Sheridan, 1981; Bourdon, 1997). Bourdon (1997)** Hybrid vigor is one of the most important reasons for crossbreeding, so any worthwhile crossbreeding system should provide an adequate amount of hybrid vigor. Breed complementarity refers to the production of a more desirable offspring by crossing breeds that are genetically different from each other, but have complementary attributes. However, the crossbreeding system should also produce a consistent product and it is much easier to market the uniform set of birds than the diverse ones.

The characteristics of the egg itself, for instance the character of weight, contents, shape and quality were very important for the fertility and hatchability which poor of them leads to a serious loss to the breeder. Egg quality is one of the most important economic characteristics for poultry breeders. Egg weight and its components have a role in determining hatchability percentage and marketing the eggs. Albumen is important for embryonic development at early stages, while yolk and shell are more important for the growing embryo than the albumen at later stages **(Iraqi *et al.*, 2012).**

2.2.1 Crossbreeding and genetic groups favored for egg traits:

Eggs of WL breed were better than eggs of Golden Montazah (GM) strain in most egg quality traits. But, GM strain was better in Haugh unit (HU), eggshell index (ESI) and eggshell thickness (STH) compared to WL breed. This may be due to genetic makeup of the two strains **(El-Labban 2000)**.

Eggs of crossbred hens were superior in most traits, probably due to the genetic and non-genetic additive effects of genes. Eggs of crossbreds were heavier in egg weight (EW), albumen weight (AW), yolk weight (YW) and shell weight (SW) than eggs of the purebred parents. Egg components were improved when GM was crossed with WL chickens as stated by **Kosba *et al.* (1981), El-Sisy (2001) and Iraqi *et al.* (2002)**.

2.2.2 Heritabilities for egg traits:

Many investigators estimated the heritability for egg production and related traits such as age and body weight at sexual maturity, as well as full and partial recording of egg performance, rate of laying and clutch size. The reviewed heretabilities for egg traits varied from one study to another and these differences were probably due to: (1) The genetic constitution of the breeds in the flock, (2) selection if practiced, (3) The available number of observations used, (4) Data set and its distribution, (5) The models applied on each set of data to correct for the non-genetic factors, (6) The level of inbreeding and coefficient of relationship in the parent population (dams- or sire related or sire related to dams), and (7) The method of analysis and estimation. However, more reliable estimates of heritability were obtained from the animal model procedure and this is because these estimates might be more accurate (unbiased) than those estimated using simple methods (i.e. Hendrson's methods, MIVIQUE, MINIQUE, REML), because the relationships among animals are considered (**Quaas *et al.*, 1984; van der Werf and de Boer, 1990; Aggrey and Cheng, 1994; Khalil *et al.*, 2002, 2004; Iraqi *et al.*, 2012).**

Number of eggs and age at first egg are two important production traits in layers, and producing hens with earlier sexual maturity and higher rate of lay has always been the goal of egg-type chicken breeding. As these reproductive traits are sex-limited and have low to moderate heritability, they would be of greatly benefit if the marker assisted selection was used, where the selection can be directed towards the actual genetic variation. Heritabilities of egg weight (EW) from many reports ranged from 0.52 **(Wei and van der Werf, 1995)** to 0.71 **(Besbes and Gibson, 1998),** while **Zhang *et al.* (2005)** reported heritability of 0.63.

2.2.3 Genetic and phenotypic correlations among egg traits:

The reviewed estimates of genetic and phenotypic correlation among egg production traits are mostly positive with high magnitudes. **Falconer and Mackay (1996)** notified that some of the genes may increase egg production characters, while the other genes increase one and reduce the other; the former tended to cause a positive correlation and sometimes a negative one**. Tuiskula-Haavisto *et al.* (2002)** reported that age at first egg (AFE) had positive phenotypic correlations of 0.29 and 0.22 with egg weight, while the correlation between AFE and egg number (EN) was negative (−0.52). **Zhang *et al.* (2005)** cited that both of the phenotypic and genetic correlations between EW and eggshell strength (ESS) were low, which in turn inferred that larger eggs were not weaker than smaller eggs. **El-Atrouny (2011)** stated that the average reviewed estimates of genetic correlation were 0.20 between age at sexual maturity (ASM) and body weight at sexual maturity (BWSM), 0.17 between ASM

and weight of first egg (WFE), 0.42 between BWSM and WFE and 0.27 between total egg number (TEN) and total egg mass (TEM).

2.2.4 QTL markers for egg traits:

Chatterjee *et al.* (2008) stated that egg weight and production traits showing significant correlations of the markers MCW0041, ADL0210, and MCW0110 with the egg production traits ($P<0.05$), while no significant correlations of MCW0014, MCW0049, ADL0158, and MCW0243 markers were found with any of the egg production traits. **Vilkki (2009)** reported that QTL affecting eggshell strength were identified within the markers ADL0236 and MCW0264 on the Z-chromosome. On the other hand, **Goto *et al.* (2014)** reported that significant QTLs were detected for egg weight around the marker MCW0095 on chromosome 8 and the marker MCW0240 on chromosome 4. For egg size, significant and suggestive QTLs were detected at around the marker MCW0154 on the Z chromosome. Additionally, a suggestive QTL affecting the egg size was found between the markers ADL0272 and ADL0106 on chromosome 10. For eggshell strength, significant QTLs were detected between the markers MCW0258 and ADL0273 and around the marker ADL0372 on chromosomes Z and 12, respectively. For eggshell thickness significant and suggestive QTLs were found around the markers MCW0305 and MCW0095 on chromosome 8. In addition, a suggestive QTL was found between the markers MCW0038 and MCW0214 on chromosome 5.

2.2.5 Chromosomal linkage analysis for egg traits:

Tuiskula-Haavisto *et al.* (2002) using 99 microsatellite markers spanning the nine largest linkage groups (chromosomes 1, 2, 3, 4, 5, 6, 7, and 8, and sex chromosome Z) and the five small linkage groups. The linkage groups covered 2311 cM, with an average spacing of 23.34 cM between markers. The estimates on the length of the complete genome ranged from 3064 to 3800 cM, based on the mapping function and the map distances covered 48 to 60% of the whole chicken genome. The markers MCW247 (on chromosome 2) and ADL345 (on chromosome 8) have been mapped only in the Wageningen reference population, while the marker MCW170 (on chromosome 4) and markers MCW133 and ADL315 (both on chromosome 7) and marker MCW129 (on chromosome 4) have been mapped only in the East Lansing population. **Sasaki *et al.* (2004)** reported that in F_2 population originated from a cross between WL males and RIR females, chromosome 1 was separated into four linkage groups, chromosome 2 into three linkage groups and chromosome 5 into two linkage groups and the linkage groups were encompassed at 800 cM of the autosomes based on the mapping function. Thirteen markers were mapped into a linkage group on the Z chromosome, encompassing 120 cM of the Z chromosome. The total linkage map spanned 920 cM, with an average marker spacing of 6.7 cM, while the remaining 13 markers could not be assigned to a linkage group and they were therefore excluded from the QTL analysis. **Honkatukia *et al.* (2005)** using 20 markers with reciprocal intercross of two parental lines, the White Leghorn (WL) and Rhode Island Red (RIR) showed a

significant QTL affecting HU40, with the position at 137 cM between marker MCW0206 (114 cM) and marker ADL0217 (152 cM).

Chatterjee *et al.* (2010) stated that egg weight and production showing microsatellite variability revealed a significant correlation of markers MCW0041, ADL0210 and MCW0110 with egg production traits ($P<0.05$); no significant correlations of MCW0014, MCW0049, ADL0158 and MCW0243 were found with any of the egg production traits. The ADL0210 genotypes revealed a significant correlation with egg production up to 52, 64 and 72 weeks of age ($P<0.05$). The MCW0041 genotypes showed a significant correlation with egg production up to 64 and 72 weeks of age ($P<0.05$). In addition, the marker MCW0110 showed a significant association with egg production up to 28 weeks of age. The marker MCW0041 had the highest egg production up to 64 and 72 weeks of age. The marker ADL0210 had the highest egg production up to 52, 64 and 72 weeks of age, while the marker MCW0110 produced the highest number of eggs up to 28 weeks of age, followed by 22, 13, and 23 weeks of age; with no significant association was observed between any microsatellites and egg weight at any age.

Vilkki (2009) reported that 23 QTL affecting eggshell strength were found in the genome scan. Genome-wide significant QTL were found on chromosomes 2, 6 and 14 and an additional chromosome-wise significant QTL seem to cluster on these chromosomes and on chromosome 3. At these regions with QTL for the same trait at several production ages, the results seem very convincing, for example, on chromosome 2, QTL

affecting shell breaking force (at 35 and 40 weeks of age) and QTL affecting shell deformation (at 35 and 40 weeks of age) were identified within the marker bracket ADL0236 - MCW0264. On the Z-chromosome, a cluster of QTL affecting both eggshell breaking strength and deformation was found within the marker interval ADL177-MCW0331. **Rosochacki *et al.* (2013)** cited that the reference population was based on two lines of chicken: Polish Green-Legged Partidgenous (GIP) and Rohde Island Red (RIR) are characterized by big genetic differences (specific allele for GlP 19 and 28 for RIR) and the phenotypic traits (laying and egg quality traits). Only four loci with the same alleles did not occur in RIR and GlP breeds (ADL244, LEI212, LEI075 and MCW157). Three alleles specific for GlP were observed in six loci (ADL180, ADL172, LEI074, LEI121, MCW0134 and MCW0256), but in RIR populations these were found only in three loci (MCW133, MCW256 and ADL326).

2.2.6 QTL mapping:

Goraga *et al.* (2012) stated that the most interesting result of multiple QTL region on chromosome 4 between 19.2 and 82.1 cM and at least two QTLs affected egg weight in this region at 37.6 and 76.4 cM. The distal QTL at 76.4 cM had pleiotropic effects on egg weight and body weight of the hens, suggesting that one gene or two closely linked genes affected both correlating traits. In addition, a QTL at 58 cM affected the number of eggs and QTLs for egg weight were repeatedly discovered in the region between 59.9 and 82.8 cM, with the alleles from the Rhode Island Red increasing the egg weight

(Tuiskula-Haavisto *et al.*, 2002; Sasaki *et al.*, 2004). **Schreiweis *et al.* (2005)** also reported a QTL for egg weight between 62.1 and 75.8 cM in a cross between Broiler and White Leghorn; the favourable allele for egg weight came from the broiler strain. In a cross between Red Junglefowl and White Leghorn, a QTL for egg weight was identified on the same chromosome between 51.6 and 67.1 cM **(Kerje *et al.*, 2003)**, with the allele for increasing the weight inherited from the White Leghorn. While, **Goto *et al.* (2011)** reported that QTL for age at first egg was found in the region around 130 cM on chromosome 1.

Linkage between 26 egg quality traits and 19 microsatellite loci were detected on chromosomes 6-8 and three linkage groups (**Tuiskula-Haavisto *et al.*, 2002).** The QTL relating to shell shape was mapped to chromosome 8 at position 42 cM, whilst, the QTL associated with egg numbers was linked to chromosome 8. The QTL accounted for Haugh units were found on chromosome 1 **(Hansen *et al.*, 2005)**. **Tuiskula-Haavisto *et al.* (2002)** confirmed the QTL for Haugh unit on chromosome 2 for Hugh units, while **Rosochacki *et al.* (2013)** mapped QTL on chromosome 8 and 9 linkage groups. **Sasaki *et al.* (2004)** identified several QTL for eggshell strength in chromosome 1. **Schreiweis *et al.* (2005)** showed two QTL regions on chromosome 2 and 9 QTL on chromosome 4. These QTL were: egg color, egg and albumen weight, percent of shell, body weight and egg production.

Previous work has suggested that chromosome 4 may be a critical region significantly associated with the variety of traits

across multiple resource populations **(Sewalem *et al.*, 2002; Tuiskula-Haavisto *et al.*, 2002; Sasaki *et al.*, 2004)**. **Rosochacki *et al.* (2013)** found that the QTL for shell strength was linked to chromosome 8 and the linkage group 26. There were several QTL areas found for all measured egg production traits. Most of the QTL are located on chromosomes 4 and Z. For production traits, the number of QTLs were distributed over chromosomes, such as the QTLs for AFE on chromosomes 3 and Z, for EW on chromosomes 2, 4 and Z **(Tuiskula-Haavisto, 2004)**. The QTL region on the Z chromosome was a large area including QTL for AFW, EW and EN as well as ESS. QTLs affecting egg number and egg weight were found in chromosomes 1, 2, 5, 6, 7, 8, 14 and Z **(Abasht *et al.*, 2006; Chatterjee *et al.*, 2008)**.

One-to-one correspondence, in the form of significance, between microsatellites and phenotypes like growth, egg production, and immune-competence traits may be the informative indicator for elucidating QTL and microsatellite relationships (**Sewalem *et al.*, 2002)**. The genetic principle of significant association of microsatellites and traits is possibly due to the phenomenon of linkage (linkage disequilibrium or LD marker). If the microsatellite is very closely linked (about 20 cM) with a certain phenotype, it will specifically be observed in terms of a significant association; the MCW0041, ADL0210, and MCW0110 microsatellites were significantly correlated with egg production up to a certain age ($P<0.05$). Sufficient polymorphic variation was not observed for MCW0014, MCW0049, LEI0089, and LEI0071, which could be one reason for the lack

of association with growth and egg production traits (**Chatterjee *et al.*, 2008)**. Another reason might be that these markers are not closely linked with the QTLs of the economic traits studied.

Differences in QTL mapping cited between different studies might be attributable to differences in: 1) crosses used in various studies; 2) ages of measurement of traits among the reviewed studies and 3) individuals would be at different physiological status caused at least in part by genetic differences **(Koerhuis and McKay 1996, Poggenpoel *et al.*, 1996, Chatterjee *et al.*, 2000, Tsuiskula-Haavisto *et al.*, 2002, Hocking *et al.*, 2003 and Wardecka *et al.*, 2003).**

2.2.7 QTL confidence intervals for egg traits:

Fine mapping can be performed for significant QTL to improve the precision of estimates of the QTL location **(Vilkki, 2009)**. A common method is to increase the marker density around the putative region. In fine mapping, the marker interval is generally located at 1-3 cM. To reduce the confidence intervals for a QTL and to define its location, the number of events of recombination becomes the limiting factor rather than the number of markers **(van Raden and Weller, 1994)**.

Tuiskula-Haavisto *et al.* (2002) stated that crossing two extreme lines of the Rhode Island Red (RIR) and WL was used to create the mapping population (F_2). The 90% confidence interval were 7.64 for Haugh unit at 40 weeks of age (HU40) and 7.17 for Haugh unit at 60 weeks of age (HU60), placing the most probable location for the QTL between 75 and 133 cM (HU40) or between 85 and 122 cM (HU60). For AFE, the 90%

confidence interval for QTL was 65 to 137 cM on chromosome 3, while, the 90% confidence interval for EN was 160 to 204 cM on chromosome 4. **Honkatukia *et al.* (2005)** reported that the 90% confidence interval for the QTL location was broadened from 58 cM to 64 cM despite the denser marker map and the auxiliary analyses fitting the two QTL simultaneously, indicated the existence of two distinct QTL areas affecting HU40 at 141 cM and at 54 cM. **Goraga *et al.* (2012)** using one male of the strain NHI was initially mated with two WL77 females and the F_1 chickens were intercrossed to generate F_2, cited that a genome-wide highly significant QTL for egg weight ($P < 0.01$) was identified on chromosome 4 at 154 cM. A search for multiple QTL in the chromosome 4 region provided evidence for two QTL affecting egg weight (one QTL at 154 cM and a second QTL at 93 cM). The position of the highest peak of QTL for the egg weight was shifted from 154 cM to 93 cM on chromosome 4 and the QTL at 93 cM was genome-wide significant ($P < 0.05$) for the egg weight during the laying, while the genome-wide suggestive QTL were mapped on chromosome 1 at 66–70 cM, chromosome 5 at 22–27 cM and chromosome 9 at 58–61 cM; the confidence interval overlapped with the QTL regions for egg weight.

2.2. 8 Additive and dominance effects for QTL of egg traits:

Tuiskula-Haavisto *et al.* (2002) found that the genome wide significant QTL affecting HU at 40 weeks was detected on chromosome 2, the RIR allele has an additive effect of −5.3 ± 1.2 HU and the QTL explains 7% of the total phenotypic variance of the F_2 population. For HU at 60 weeks, there is a

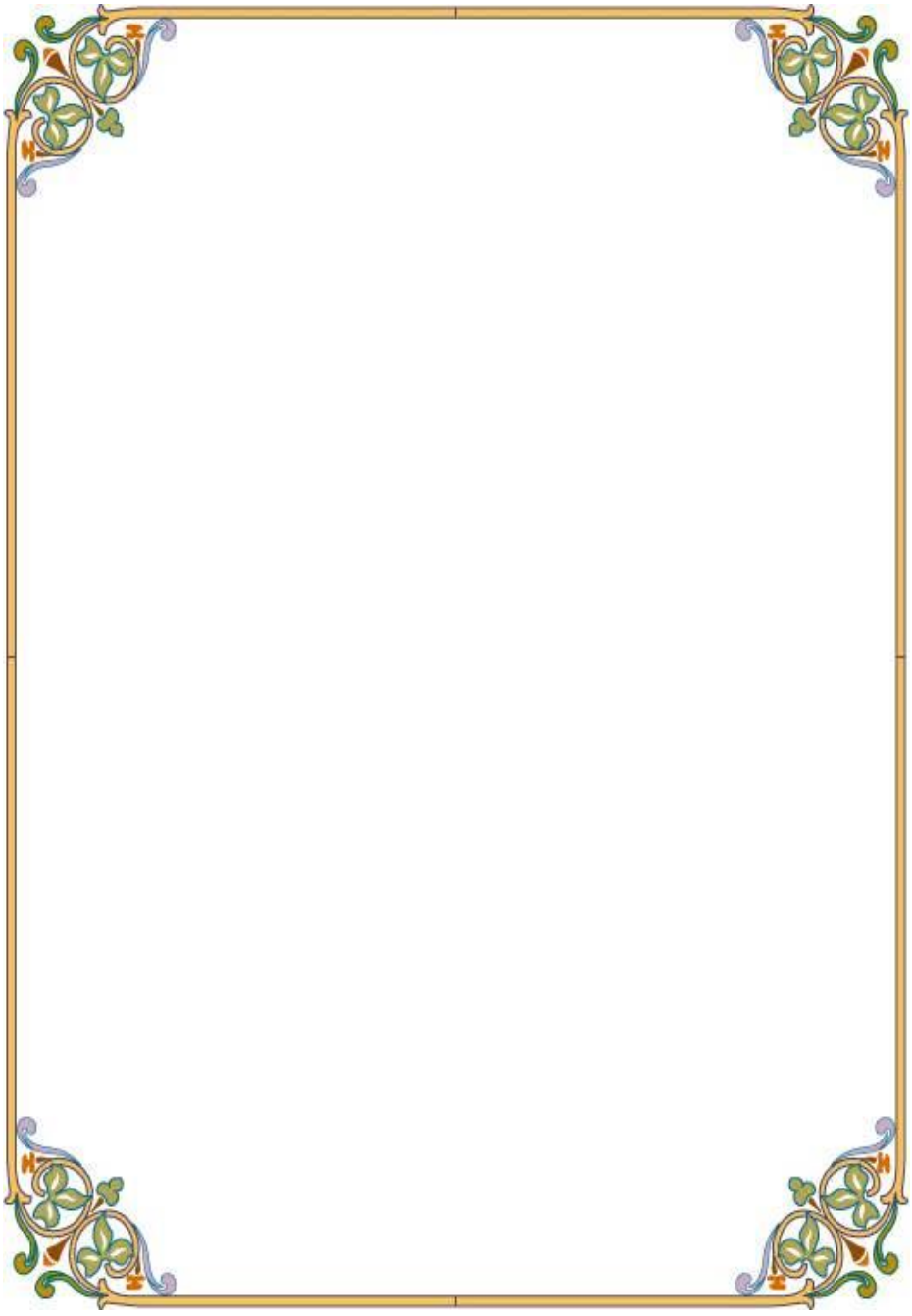
QTL in the same region with an additive effect of −8.6 ± 2.1 HU and the QTL explain 2 –5 % of the phenotypic variance. **Honkatukia *et al.* (2005)** found that the effect of the RIR allele was –3.73 HU (± 0.80), while the dominance effect was –1.74 HU (± 1.51) and the detectable QTL explained 6.7% of the phenotypic variance. **Goraga *et al.* (2012)** reported that the QTL at 93 cM had dominance effects from 1.51 to 1.99 g on egg weights, while the genetic effect of the QTL at 154 cM was additive from 1.93 to 2.40 g. The additive effect of QTL affecting number of eggs was detected on chromosome 7, while the dominance effects of QTL was detected on chromosomes 4 and 5.

2.2. 9 Total variances explained by QTL for each egg trait:

The results of the whole genome scan for detection and localization of QTL affecting egg quality traits were described by **Tuiskula-Haavisto *et al.* (2002)**. At 1% genome-wise significance level, 14 chromosomal areas affecting egg quality, while at 5% level only 6 suggestive QTL were found. Another whole genome scan (**Wardęcka *et al.*, 2002 & 2003)** was done in Green-legged Partridgenous (GLP) chickens, a native Polish breed maintained as a conservative flock, and in a highly productive stock of Rhode Island Red (RIR).

The significant effects of the genotypes (GLP-GLP, RIR-RIR, and GLP-RIR) were found for some egg traits: age at sexual maturity, Haugh units on week 53 and shell thickness on week 33 as stated by **Wardęcka *et al.* (2003)**. **Goraga *et al.* (2012)** found that the phenotypic F_2 variance for egg weights in the early and late production periods explained by the QTL at 93

and 154 cM ranged from 4.9 to 7.1% and 12.3 to 16.1%, respectively. These QTL explained 4.3–5.9% of the phenotypic variance of egg weight in F_2. The QTL allele contributing in the early age at first egg was explained by 6.5% of the phenotypic F_2 variance.



3. MATERIALS & METHODS

3.1 Location and experimental period:

The experimental work of this study was carried out in the Poultry Research Farm, Department of Animal Production, Faculty of Agriculture, Benha University, Egypt, and started in March 2008 and terminated in October 2010.

3.2 Strains of chickens used:

A local strain of chickens namely Golden Montazah and of White Leghorn were used in this study. Golden Montazah (GM) is a synthetic strain which has been developed in the Montazah Poultry Research Station, Alexandria Governorate, Egypt, from a cross between Rhode Island Red and Dokki-4 chickens, using systems of breeding coupled with selection, for five generations **(Mahmoud *et al.*, 1974)**.

The White Leghorn (WL) is one of the Mediterranean chicken breeds and grew up in the Italian city of Leghorn. This type of chicken is the most widespread breed in the world because of its importance in the trade and economic production of table eggs (www.cacklehatchery.com).

3.3 Breeding plan and management:

Number of 1500 egg from White Leghorn and 300 eggs from Golden Montazah were chosen randomly and came from El-Takamoly chicken project, Alazab, El-Fayoum Governorate, Egypt. These eggs were incubated and hatched in the laboratory of Poultry Research Farm, Benha University, Egypt. The base chicken population was developed by crossing a broiler male

strain Golden Montazah (GM) with the layer breed White Leghorn (WL). A total number of 18 cockerels and 180 pullets were chosen randomly from GM and WL strains, respectively. Each cock was mated to 10 hens housed in separate breeding pens to produce F_1 crossbred (½GM½WL), consequently inter-se matings were practiced for two generations to produce F_2 with genetic structure of $(½GM½WL)^2$. Also, purebreds from the two strains were produced. The pedigreed eggs from each individual breeding pen for the four mating groups, two foundations of GM and WL, two crossbreds of (½GM½WL) and $(½GM½WL)^2$ were collected daily for fifteen days and then incubated. The structures of data collected from all genetic groups are presented in Table1.

On hatching day, chicks produced from all genetic groups were wing banded and reared in floor brooded, then transferred to the rearing houses. All chicks were medicated similarly and regularly and they were subject to the same managerial, hygienic and climatic conditions. During growing, rearing period and laying period, all chicks were fed *ad libitum* using diet containing 23%, 21% and 18% crude protein and 3200, 2900, and 2700 metabolizable energy kcal/kg during the period from hatch to 8 weeks, from 8 to 20 weeks of age and more than 20 weeks of age, respectively. The feed requirements were supplied according to **NRC (1994)**.

Table 1. Number of sires, dams and chicks for genetic groups used in the experimental work

Generation	Group of sire	Group of dam	Genetic group[+]	No. of sires	No. of dams	No. of Hatched chicks
Parental	WL	WL	WL × WL	18	64	1002
Parental	GM	GM	GM × GM	8	51	775
F_1	GM	WL	(½GM½WL)	18	103	1343
F_2	F_1 or ½GM½ WL	F_1 or ½GM½ WL	$(½GM½WL)^2$	18	106	1011
			Total	62	324	4131

[+] WL and GM = White Leghorn and Golden Montazah strains, respectively; the first letter denoted to the sire group.

3.4 The phenotypic measurements:

3.4.1 Growth traits:

Individual body weight (BW) of 4131 chicks were recorded at hatch, 4, 8, 12 and 16 weeks of age, while the daily gains in weight for these chicks were calculated during the periods of 0-4 (DG4), 4-8 (DG8), 8-12 (DG12) and 12-16 (DG16) weeks of age.

Daily gains (DG) in weight (grams) were calculated between body weights in different weeks based on the following equation:

$$\text{Daily weight gain (gram/day)} = \frac{BWj - Bw\,i}{28}$$

Where BW_i = initial body weight at certain age, BW_j= final body weight at the certain age and 28= period of growth in days.

3.4.2 Egg traits:

Hen and egg traits were age at first egg (AFE), weight at first egg (WFE), 120-days of egg number (EN), egg weight (EW), yolk weight (YW), albumen weight (AW), shell weight (SW), Haugh unit, and eggshell thickness (EST). Three consecutive eggs per month were collected for each hen from all genetic groups during 120-days of egg production to study egg quality traits and included egg weight, albumen weight, yolk weight, shell weight, Haugh unit, and shell thickness. The collected eggs from all genetic groups were weighed using sensitive electronic scale to the nearest gram, then the length and width of each egg were measured using compass sensitive to 0.01 mm. After that, the eggs were broken within 24 hours on a glass table. Heights of yolk and albumen were measured with a micrometer sensitive to 0.01 mm. Yolk of each egg was separated from the albumen and their weights were obtained in grams and expressed as a percentage of egg weight. Shell of each egg was washed under slightly flowing water to remove the albumen remains, then they were left to air dry for 24 hours. The shell with its membranes was weighted together in grams for each egg and expressed as a percentage of egg weight. Egg, yolk, albumen, and shell weights were recorded individually to the nearest gram. Haugh unit (HU)

was calculated according to the formula of **Haugh (1937)** as follows:

$$HU = 100 \log (H+7.37-1.7\ EW^{0.37})$$

Where: H = Albumen height (mm), EW = Egg weight (g). Albumen height was measured by means of tripod micrometer reading to the nearest 0.01 cm. Diameter was measured by Vernier caliper nearest to mm **(Romanoff and Romanoff, 1949).** Egg shell thickness (EST) was measured using a micrometer to the nearest 0.01 mm at the broad and narrow ends, as well as at the middle of the egg. Average of eggshell thicknesses for the three regions was calculated.

3.5 Genotyping:

Blood samples (10 ml) were collected from the wing vein at 24 weeks of age from relevant mating birds of F_0 parents, F_1 and F_2 to be included in the genotyping panel. Blood samples were collected in vacuum tubes containing EDTA and stored at -20 ˚C until DNA extraction.

3.5.1 Isolation of genomic DNA:

The Maxwell® 16 Blood DNA Purification Kit was used according to kit manual, designed specifically for the optimal automated extraction of DNA from whole blood samples on the Maxwell® 16 SEV Instrument. The Maxwell® 16 Blood DNA Purification Kit is optimized to process a wide range of volumes of fresh or stored animal blood samples. Up to 400µl of whole blood can be processed to yield up to 15µg of.

3.5.2 DNA quantitation:

Nucleic acids in a solution absorb ultraviolet (UV) light in the range from 210 mm to 300 mm with absorption maximum at 260 mm and the extinction coefficients used were 50 for DNA. Absorbance readings were taken on NanoDrop spectrophotometer (NanoDrop 1000 spectrophotometer, Thermo Scientific, USA). DNA samples were diluted using DNase and RNase free water to give the required concentration (10-100 ng).

3.5.3 Markers selected:

A total of 68 microsatellites including 26 MCW (developed by Wageningen Agricultural University, Wageningen, The Netherlands), 22 ADL (Avian Disease and Oncology Laboratory, USDA-ARS, East Lansing, MI, USA), 14 LEI (University of Leicester, Leicester, UK) and six ROS (Roslin Institute, Roslin, UK) markers located on different chromosomes were considered for this study **(FAO, 2011)**. All primers are diluted with TE buffer Table (2) to give the relevant concentration 15 µM. Markers were selected based on their positions on the consensus map (Table 3 & 4).

Table 2 Preparation of reagents, buffers and diluents for PCR and agarose

Tris Borate EDTA (5X):	
Tris	54g
Boric acid	27.5g
EDTA	3.7g
DNase/RNase free Water	1000ml
To be used as 1X add one volume to 4 volumes of distilled water	
TE Buffer:	
Tris	0.0372g
EDTA	0.0012g
DNase/RNase free Water	100ml
Ethidium Bromide Working Solution:	
Ethidium Bromide (one tablet)	0.1g
Dnase/Rnase free Water	10ml
Agarose gel 3%:	
Metaphor Agarose	3g
Ethidium Bromide Working Solution	4 µl
DNase/RNase free Water	100ml
Boiled in microwave till obtaining a clear solution	

Table 3 Microsatellite markers used for genotyping of growth traits in birds of F_0, F_1 and F_2

Microsatellite marker (Locus)	Forward primer sequence	Reverse primer sequence	Chr. No. +	L++	A+++
ADL0114	GGCTCATAACTACCTTTTTT	GCTCTACATTCCTTCAGTCA	2	185	45
ADL0142	CAGCCAATAGGGATAAAAGC	CTGTAGATGCCAAGGAGTGC	6	231	52
ADL0166	TGCCAGCCCGTAATCATAGG	AAGCACCACGACCCAATCTA	6	135	47
ADL0183	TTGTGAAGTGGATAAGATGA	ACAGAAATGGAAAGCGAGAC	1	102	47
ADL0188	CACTTCCAGTATTAACGTGA	GTGGACACAATGAGTTCCTC	1	129	47
ADL0225	CCAAAAAGCTGTATCACCTT	GCCTGTTGTAAACCACCTGA	13	149	48
ADL0236	CTGGTTGTCAGTTGAAGGAC	ATAAGGTGGTGAGCAGCACT	2	132	51
ADL0237	GCTTGTGCCTAAGAATGAAC	TGTATGGAGTCTCAGCAAAT	3	148	50
ADL0238	AAACCCAAACAAAAGCAGAC	GCTCCTCATAAGCAAAATGC	1	160	53
ADL0241	AAAATAGCATGGCAAATCAT	CAGATGCATCAGCACAGAAA	4	216	51
ADL0255	GGGTATTGGTCTTCAAAATG	GTAAAGGCCTTCCTCTTCTT	3	110	47
ADL0258	TCATTTCAGCTCACATTTTA	TTTTCAGGTTGTCTGGTTGC	8	168	48
ADL0266	GTGGCATTCAGGCAGAGCAG	AATGCATTGCAGGATGTATG	4	113	50
ADL0267	AAACCTCGATCAGGAAGCAT	GTTATTCAAAGCCCCACCAC	2	117	55
ADL0280	CCCCTATAGCACAGCAGTCC	GGAACCTCAGCCTTGACATT	3	172	56
ADL0317	AGTTGGTTTCAGCCATCCAT	CCCAGAGCACACTGTCACTG	4	199	51
LEI0073	TTGAGAGCAGTGAAGGCAAACG	TGGTGGGAACTGGAAGAAGAGG	4	217	65
LEI0075	TTTCACATCCAGTGCGTGTCTG	GGGCAGAGAAAGACGAAATTGG	Z	188	65
LEI0083	AACCCTCACACACCCATTGCC	CACTCGCCTGTAATTTCTTGTGG	13	259	65
LEI0106	TGTGGGTTGTAATCCCTTCACC	CTCCCAAAAAACCTTCAAATGG	1	295	59
LEI0110	GGGACCCAAGGCACACACTA	ATCCTCTATGAGGAAGGGAAGTGA	11	231	63
LEI0111	CCCACAAAAGAGACACCGTGG	CCTGTTTGCCGTACACTTGGC	Z	116	65
LEI0161	CAGCCTTTTCAAGCTTGCTGC	GTTCACTTTAGACATGAATCGG	3	100	54
LEI0166	AAGCAAGTGCTGGCTGTGCTC	TCCTGCCCTTAGCTACGCAC	3	267	54
LEI0254	AGACCACTGGATCCAACTC	GTCTGGAACTCATCCCTTCATC	Z	95	55
MCW0010	CTGTAGAATTACAGAAATACA	TAGTACAAGAATCTAGTGTTAAAA	1	93	45
MCW0040	ACTCAAAAATGTGGTAGAATATAG	ACCGAAATTGAGCAGAAGTTA	3	143	55
MCW0080	CCGTGCATTCTTAATTGACAG	GAAATGGTACAGTGCAGTTGG	13	280	55
MCW0083	TACATTTCAGAAGGAATGTTGC	GCCTTTCACCCATCTTACTGT	3	90	54
MCW0097	GGAGAGCATCTGCCTTCCTAG	TGGTCTTCCAGTCTATGGTAG	11	309	56
MCW0100	GATCTAAACAAAAACAGACACA	TGTAGGCGATTAAACATACTTC	8	90	55
MCW0107	GAACAGAACTCTGTTTACTG	TCTGCTTACCTCAACTGACA	1	121	56
MCW0135	ATATGCTGCAGAGGGCAGTA	CATGTTCTGCATTATTGCTCC	9	150	57
MCW0169	GATCCCACTTGTTAAGAAGTG	CCTGACCTTACTGAGCTTGGA	3	96	58
MCW0180	GATCACATCACGTTAATTTT	GGTGGAGAAAAGTGAAAGAC	4	88	55
MCW0295	ATCACTACAGAACACCCTCTC	TATGTATGCACGCAGATATCC	4	99	55
MCW0305	TCAGAAACAAAGCAGGAGCTG	TGACATCTTTCAAACGAGACC	8	259	55
MCW0340	ATTATCTGATGCATCAGCTGG	CACCGATTGTAGCGGAACATC	13	174	55
ROS0003	GCAAAGTTATTCAGGAACTTGC	AAGTGGTCCCCTGATTTAACA	6	250	56
ROS0025	AGATTGCTGGGGGAAAAAGT	ACTGAAAACCTGAACAGAAGGC	1	210	58
ROS0030	CGGAGAGCATGGTTTCAAGT	CTCTGTGAGCTCCCCATCTC	9	240	58
ROS0074	AGCACTTTTGGTGTTACCGG	CAGCTGATGCTTCCACAGAA	2	320	58
ROS0075	CAGCTCCGTGCTCCTCTC	TTTTCAACCCGTTGTTCAGG	8	216	58

+ Chr. No. = chromosome number; ++ L = length (bp); +++ A = Annealing temperature

Table 4 Microsatellite markers used for genotyping of egg traits in birds of F_0, F_1 and F_2

Microsatellite marker (Locus)	Forward primer sequence	Reverse primer sequence	Chr. No.+	L++	A+++
ADL0022	GCATCAGAGGAAGAAGGAAA	GCATCAGAGGAAGAAGGAAA	Z	165	51
ADL0114	GGCTCATAACTACCTTTTTT	GCTCTACATTCCTTCAGTCA	2	185	45
ADL0142	CAGCCAATAGGGATAAAAGC	CTGTAGATGCCAAGGAGTGC	6	231	52
ADL0143	CCTGTCTCTGGTCTTTATCC	AGTTTACTTCCTTTTCTTGC	4	170	51
ADL0155	GGTCCGACTGAAAGCATTAT	TTAAGACTGAAGCCAACCAG	3	107	49
ADL0201	GCTGAGGATTCAGATAAGAC	AATGGCTGACGTTTCACAGC	Z	143	53
ADL0217	TCTACTTCGTTGGAGTGTCA	GGAAAACAGAGGAGAAATGG	2	161	52
ADL0237	GCTTGTGCCTAAGAATGAAC	TGTATGGAGTCTCAGCAAAT	3	148	50
ADL0241	AAAATAGCATGGCAAATCAT	CAGATGCATCAGCACAGAAA	4	216	51
ADL0255	GGGTATTGGTCTTCAAAATG	GTAAAGGCCTTCCTCTTCTT	4	110	47
ADL0266	GTGGCATTCAGGCAGAGCAG	AATGCATTGCAGGATGTATG	4	113	50
ADL0322	TGCGTTCTCCCCTTGGTTGC	GCAGCAGCTCCCACGACACA	8	140	55
LEI0065	TGAAACATGTATGGAGTCTCAGCA	GACAGCTAAATGCCAGTTCATGG	3	187	61
LEI0072	TAAGCTGACATTCACCACCAG	GACTCTTTCAGTACATACTGG	11	100	63
LEI0073	TTGAGAGCAGTGAAGGCAAACG	TGGTGGGAACTGGAAGAAGAGG	4	217	65
LEI0075	TTTCACATCCAGTGCGTGTCTG	GGGCAGAGAAAGACGAAATTGG	Z	188	65
LEI0081	ACTTACCTTTTCTTAGCTACTG	GATCCTTTCAATGCTCATGCT	4	260	61
LEI0111	CCCACAAAAGAGACACCGTGG	CCTGTTTGCCGTACACTTGGC	Z	116	65
LEI0163	ACTTGGGCATACTCTTGTTGC	CTGCAGGTACCGTGAGATGTG	2	207	64
LEI0214	TGCCTCGTCTTACTGAGTGA	GATCAAGCACTGTATTTTATTC	11	164	60
LEI0254	AGACCACTGGATCCAACTC	GTCTGGAACTCATCCCTTCATC	Z	95	55
MCW0004	GGATTACAGCACCTGAAGCCACTA	AAACCAGCCATGGGTGCAGATTGG	3	199	54
MCW0010	CTGTAGAATTACAGAAATACA	TAGTACAAGAATCTAGTGTTAAAA	1	93	45
MCW0045	CCAAAGGAAACAAATACTATACGA	GAAAGAAAAACTGACACTGTGACT	13	151	53
MCW0047	GGATTACGGCCGTTTGTGCACAAA	AATGGAACGCCGAACTCGCGTGCA	4	107	49
MCW0055	TTTGTAGTTACCTGGTACTGA	GTTTGCATTGTCTACAGCTCCTTG	Z	193	51
MCW0056	TGGTAACCTCTAACCTTGACG	AGTGAAGGAGACTCCACAGCCTCT	2	207	48
MCW0083	TACATTTCAGAAGGAATGTTGC	GCCTTTCACCCATCTTACTGT	3	90	54
MCW0100	GATCTAAACAAAAACAGACACA	TGTAGGCGATTAAACATACTTC	8	90	55
MCW0107	GAACAGAACTCTGTTTACTG	TCTGCTTACCTCAACTGACA	1	121	56
MCW0122	TCCTTTGGAGCACGGAGGAAC	AGATGCACAGGCAGAGCTCCA	4	270	56
MCW0129	ATTTGGTGAACACAAACCTGC	CCACTTGAATGAAGCACCTAC	4	118	52
MCW0135	ATATGCTGCAGAGGGCAGTA	CATGTTCTGCATTATTGCTCC	9	150	57
MCW0154	GATCTGTTTTATCACACACAC	CCATTTCCTTTGTTATCAGGC	Z	193	54
MCW0156	TCTGTAACATTTTTCCTTTTGTG	TTAATGTGGCAGACTCAAAGG	3	287	50
MCW0169	GATCCCACTTGTTAAGAAGTG	CCTGACCTTACTGAGCTTGGA	3	96	58
MCW0170	TTGTGAAACTCACAGCAGCTG	TTATAGCAGGCTGGCCTGAAG	3	177	52
MCW0180	GATCACATCACGTTAATTTT	GGTGGAGAAAAGTGAAAGAC	4	88	55
MCW0241	AACCAGTTTGTTAACATCAGC	ATTGGAGTTGGTACCATACTC	Z	276	51
MCW0246	TCATAAGGCAGAGAATTCATC	TTTCCATTCAGACAACAAGGC	Z	235	53
MCW0247	CTTCACATGCTCCACTTGATG	AGTGACTATACTTCTTCACGG	2	207	50
ROS0003	GCAAAGTTATTCAGGAACTTGC	AAGTGGTCCCCTGATTTAACA	6	250	56
ROS0026	GGCAAACACACAGTTTTCACA	ATGATCTCATGGAGTGCTGAGC	8	108	55
ROS0074	AGCACTTTTGGTGTTACCGG	CAGCTGATGCTTCCACAGAA	2	320	58
ROS0075	CAGCTCCGTGCTCCTCTC	TTTTCAACCCGTTGTTCAGG	8	216	58

+ Chr. No. = chromosome number; ++ L = length (bp); +++ A = Annealing temperature

3.5.4 PCR setup:

PCR was performed in thermal cycler (T100™ Thermal Cycler, Bio-Rad PCR systems) on a 25-µl reaction mixture (Ready to use Master Mix Promega) GoTaq® Green Master Mix is a premixed ready-to-use solution containing bacterially derived Taq DNA polymerase, dNTPs, MgCl2 and reaction buffers at optimal concentrations for efficient amplification of DNA templates by PCR. GoTaq® Green Master Mix contains two dyes (blue and yellow) that allow monitoring of progress during electrophoresis. Reactions assembled with GoTaq® Green Master Mix have sufficient density for direct loading onto agarose gels. (Green Master Mix: 12.5µl - Forward primer 15 µM: 2.5µl - Reverse primer 15 µM: 2.5µl - DNase / RNase free water: 1.5 µl - DNA template: 5µl). The reaction was carried out by initial denaturation at 95 ºC for 2 min, and then denaturing at 94 ºC for 30 s, annealing at the temperature optimized for each primer pair for 30 s and extending at 72 ºC for 30 s for 35 cycles, followed by an extra extension step at 72 ºC for 5 min. The optimum annealing temperatures for best amplification are presented in Tables 3 & 4.

3.5.5 DNA separation by electrophoresis:

Ten microliters from the amplified products were electrophoresed on Metaphor Agarose gel 3% **(Muhammad *et al.*, 2008)**. The gel was run at 120 V for 2 h in 1X TBE and stained with ethidium bromide using pUC19 ladder (Table 2). The gel was visualized and documented under a white light gel documentation system (Alpha Innotech – AlphaImager).

3.6 Statistical analysis:

3.6.1 Statistical analysis of growth traits:

3.6.1.1 Statistical analysis of phenotypic data:

The phenotypic data set was firstly analyzed using SAS program **(SAS, 2004)** to estimate the starting values of additive and residual variances to be used as prior values in the animal model analysis. The significant differences ($P \leq 0.05$) between means of the genetic groups were assessed ($P<0.05$) using **Duncan (1955)**. The data set was then analyzed using multi-traits animal model of VCE6 program (**Groeneveld *et al.*, 2010**). The animal model used in the matrix notation was as follows:

$$\mathbf{y = Xb + Z_a u_a + Z_c u_c + e} \quad \textbf{(Model 1)}$$

Where: y= n×1 vector of observation of the bird, n = number of records; X= design matrix of order n×p, which is related to the fixed effects of genetic group (four levels), year (three levels), hatch (two levels) and sex (two levels); b= p×1 vector of the fixed effects of genetic group, year, hatch and sex; Z_a= the incidence matrix relating records to the additive genetic effect of the bird; u_a= the vector of random additive genetic of the bird; Z_c= the incidence matrix relating records to random common environmental effect of the bird; u_c= the vector of random common environmental effect of the birds; and e= n×1 vector of random residual effects, NID $(0, \sigma^2 e)$.

3.6.1.2 Estimation of heritability:

The heritability was estimated using the following equation:

$$h_a^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma^2 c + \sigma_e^2}$$

Where: σ_a^2, σ_c^2 and σ_e^2 are variances due to the effects of direct additive genetic, common environmental effect and random error, respectively.

3.6.1.3 Estimation of genetic and phenotypic correlations:

The additive genetic (r_g) correlation between the traits were estimated according to the formula of **Quaas *et al.* (1984)**:

$$r_g = \frac{\text{Cov } (X)_{ij}}{\sqrt{[\![\text{Var}(X)]\!]_{ii}.\text{Var}\left(X_{ij}\right)}}$$

Where: Cov $(X)_{ij}$ = the covariance between additive genetic effects on body weight and daily gain; X_{ii} = the additive genetic (a) variance of body weight; X_{ij} = the additive genetic (a) variance of daily gain.

The phenotypic (r_p) correlation between the traits were estimated according to the formula of:

$$r_p = \frac{Cov_e + Cov_a}{\sqrt{\left[\sigma^2 e_{(X1)} + \sigma^2 a_{(X1)}\right] + \left[\sigma^2 e_{(X2)} + \sigma^2 a_{(X2)}\right]}}$$

Where: Cov_e = covariance of error between body weight and daily gain; Cov_a = covariance between body weight and daily gain for animal; $\sigma^2 e_{(X1)}$ = the variance of error for body weight; $\sigma^2 a_{(X1)}$ = the variance of animal for body weight; $\sigma^2 e_{(X2)}$ = the

variance of error for daily gain; $\sigma^2a_{(X2)}$ = the variance of animal for daily gain.

3.6.1.4 Statistical analysis of molecular data (QTL analysis)

A linkage map was generated using Map Manager QTX version b20 software program **(Manly *et al.*, 2001)**. After parentage checking and genotyping edits, data from 1011 F_2 individuals with genotypes on 43 microsatellite markers in nine autosomal linkage groups and Z chromosome were available for QTL analysis. Markers that did not meet the criteria of polymorphism were deleted from the analysis. The linkage map analysis was used to get the best order of the markers, and to detect the map distance among markers. The maps were then used for QTL detection on the autosomes, linkage groups, and the Z chromosome. Data of F_2 was used for analyzing the additive (a) and dominance effects (d) of a QTL at a given position for each trait where the additive effect was defined as half the difference between the two homozygotes and the dominance effect as the difference between the means of the heterozygotes and homozygotes. The following mixed model included the fixed effect of sex along with the additive and dominance effects of QTL as random effects were used **(Haley *et al.*, 1994; Manly *et al.*, 2001**):

$$\mathbf{y_{ij} = X_{ij}b + Z_a a + Z_d d + e_i, \text{ (Model 2)}}$$

Where: y_{ij} is the phenotype of F_2 individual, X_{ij} is the design matrix, and b is the vector of coefficients for sex and hatch as fixed effects, *a* is the vector of additive effect of the QTL, *d* is the vector of dominance effect of the QTL, Z_a is the probability

of one homozygous type at the putative QTL locus given the marker information minus the probability of the other homozygous type at the locus given the marker information for animal i, Z_d is the probability of being heterozygous at the putative QTL locus given marker genotypes for animal i, and e_i is the random error, typically assumed to be normally distributed as $N(0, \sigma^2)$ **(Haley and Knott, 1992)**. Detection of QTL was based on an F-statistic test that was computed from sums of squares explained by the additive and dominance coefficients for QTL. Additive and dominance effects were estimated for each putative QTL. The informativeness of the markers was assessed at each location as described by **Knott *et al.* (1998)**.

Significance thresholds at 1% and 5% levels, and confidence intervals were determined by Map Manager QTX software. Significant and suggestive QTL were defined by test statistics exceeding the 5% significance thresholds. The 5% chromosome-wise level threshold was used as suggestive QTL, and the 5% genome-wise level threshold was used as significant QTL, namely, $P_{genome} = \alpha/n$, where $\alpha = 0.05$ and n was the total number of tests (traits x chromosome).

Percentage of F_2 phenotypic variance explained by the model was calculated as:

Phenotypic variance percentage = 100 x (RMS − FMS)/RMS

Where: RMS = the residual mean square from the reduced model, omitting QTL but including all fixed effects, and FMS = the residual mean square from the full model, including QTL and all fixed effects.

The Likelihood ratio test was performed as:

$$n \log\left(\frac{\text{residual sum of squares reduced model}}{\text{residual sum of squares full model}}\right)$$

Where: n is the number of observations. This test statistics distributed approximately as a chi-square with degrees of freedom equal to the number of parameters included in the full model (i.e., estimating the QTL effects) but omitted from the reduced model (i .e., omitting QTL).

3.6.2 Statistical analysis of egg traits

3.6.2.1 Statistical analysis of phenotypic data

The phenotypic data set of AFE, WFE, EN, EW, AW, YW, SW, HU and ESS were firstly analyzed using SAS program **(SAS, 2004)** to estimate the starting values of additive and residual variances to be used as prior values in the animal model analysis. The differences between means of the genetic groups were tested ($P<0.05$) and then, the data set was analyzed using multi-traits animal model of VCE6 program (**Groeneveld *et al.*, 2010**). The animal model used in matrix notation was as follows:

$$\mathbf{y = Xb + Z_a u_a + Z_p u_p + e} \quad \textbf{(Model 3)}$$

Where: y= n×1 vector of observation of the hen, n = number of records; X= design matrix of order n×p, which is related to the fixed effects of genetic group (four levels), year (three levels) and hatch (two levels); b= p×1 vector of the fixed effects of genetic group, year and hatch; Z_a= the incidence matrix relating records to the additive genetic effect of the hen; u_a= the vector of random additive genetic of the hen; Z_p= the incidence matrix

relating records to random permanent environmental effect of the hen; u_p= the vector of random permanent environmental effect of the hen; and e= n×1 vector of random residual effects, NID (0, $\sigma^2 e$).

3.6.2.2 Estimation of heritability:

The heritability was estimated using the following equation:

$$h_a^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma^2 p + \sigma_e^2}$$

Where: σ_a^2, σ_p^2 and σ_e^2 are variances due to the effects of direct additive genetic, permanent environmental effect and random error, respectively.

3.6.2.3 Estimation of correlations:

The additive genetic (r_g) and phenotypic (r_p) correlations between the traits were estimated according to the formula of **Quaas *et al.* (1984)**:

$$r = \frac{\mathrm{Cov}\,(X)_{ij}}{\sqrt{[\mathrm{Var}(X]_{ii}).\,\mathrm{Var}\left(X_{jj}\right)}}$$

Where: Cov $(X)_{ij}$ = the covariance between additive genetic effects for egg traits; X_{ii} and X_{jj} = the additive genetic (a) variances of ith and j^{th} egg traits.

The phenotypic (r_p) correlation between the traits were estimated according to the formula of:

$$r_p = \frac{Cov_e + Cov_h}{\sqrt{\left[\sigma^2 e_{(X1)} + \sigma^2 h_{(X1)}\right] + \left[\sigma^2 e_{(X2)} + \sigma^2 h_{(X2)}\right]}}$$

Where: Cov_e = covariance of error between egg traits; Cov_h = covariance between egg traits for hen; $\sigma^2 e_{(X1)}$ = the variance of error for trait 1; $\sigma^2 a_{(X1)}$ = the variance of hen for trait 1; $\sigma^2 e_{(X2)}$ = the variance of error for trait 2; $\sigma^2 a_{(X2)}$ = the variance of hen for trait 2.

3.6.2.4 Statistical analysis of molecular data (QTL analysis)

A linkage map was generated using Map Manager QTX version b20 software program **(Manly *et al.*, 2001)**. After parentage checking, data of 1011 pullets from F_2 individuals were genotyped using 45 microsatellite markers in nine autosomal linkage groups and Z chromosome and these genotypes were available for QTL analysis. Markers that did not meet the criteria of polymorphism were avoided from the analysis. The linkage map analysis was used to get the best order of the markers, and to detect the map distance among the markers. The maps were then used for QTL detection on the autosomes, linkage groups, and the Z chromosome. Data of F_2 was used for analyzing the additive (a) and dominance effects (d) of QTL at a given position for each trait where the additive effect was defined as half the difference between the two homozygotes and the dominance effect as the difference between the means of the heterozygotes and homozygotes. Data of F_2 cross was analyzed using the following mixed model including the fixed effects of hatch along with the additive and dominance effects of QTL as random effects **(Haley *et al.*, 1994; Manly *et al.*, 2001**):

$$\mathbf{y_{ij} = X_{ij}b + Z_a a + Z_d d + e_i \text{ (Model 4)}}$$

Where: y_{ij} is the phenotype of F_2 birds, X_{ij} is the designed matrix, and b is the vector of coefficients for hatch as fixed effects, *a* is the vector of additive effect of the QTL, *d* is the vector of dominance effect of the QTL, Z_a the probability of one homozygous type at the putative QTL locus given the marker information minus the probability of the other homozygous type at the locus given the marker information for the bird i, Z_d is the probability of being heterozygous at the putative QTL locus given marker genotypes for the bird i, and e_i is the random error, typically assumed to be normally distributed as $N(0, \sigma^2)$ **(Haley and Knott, 1992)**. Detection of QTL was based on an F-statistic that was computed from sums of squares explained by the additive and dominance coefficients for the QTL. Additive and dominance effects were estimated for each putative QTL. The informativeness of the markers was assessed at each location as described by **Knott *et al.* (1998)**. Significance thresholds at 1% and 5% levels, and confidence intervals were determined by Map Manager QTX software. Significant and suggestive QTL were defined by test statistics exceeding the 5% significance thresholds. The 5% chromosome-wise level threshold was used as suggestive QTL, and the 5% genome-wise level threshold was used as significant QTL, namely, $P_{genome} = \alpha/n$, where $\alpha = 0.05$, n was the total number of tests (traits x chromosome).

Percentage of F_2 phenotypic variance explained by the model was calculated as:

Phenotypic variance percentage = 100 x (RMS − FMS)/RMS

Where: RMS = the residual mean square from the reduced model, omitting QTL but including all fixed effects, and FMS = the residual mean square from the full model, including QTL and all fixed effects.

The Likelihood ratio test was performed as:

$$n \log\left(\frac{\text{residual sum of squares reduced model}}{\text{residual sum of squares full model}}\right)$$

Where: n is the number of observations. This test statistics distributed approximately as a chi-square with degrees of freedom equal to the number of parameters included in the full model (i.e., estimating the QTL effects) but omitted from the reduced model (i .e., omitting QTL).

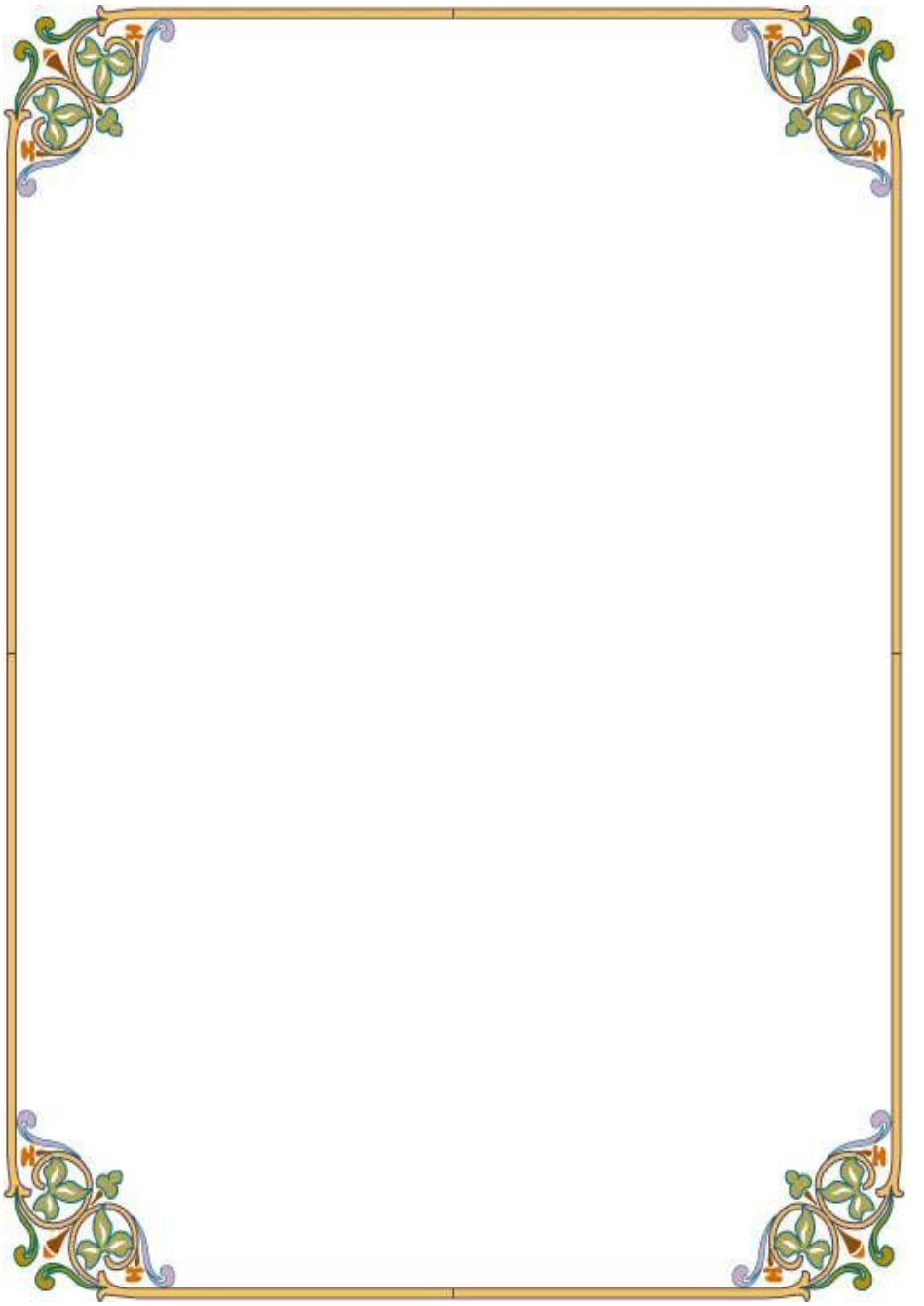
3.7 Identification of main effect QTL under an additive-dominance model :

The first element involved the standard processes of conducting QTL searching, testing, permutation and bootstrapping for a single-QTL F_2 analysis by fitting an additive-dominance model following **Haley *et al.*, (1994)**. Whole genome scans were conducted iteratively using forward selection of significant QTL for each trait **(Carlborg *et al.*, 2004)**. The probabilities of the parent of origin of each gamete based on the marker genotypes were calculated at 1 cM intervals throughout the genome. Under the assumption that QTL were fixed for alternate alleles in the local strain and layer breed, coefficients of additive and dominance components for putative QTL at each position were

calculated from the conditional probabilities given the marker genotypes. The trait data were then regressed against the coefficients and an F-test to determine association was conducted at 1 cM intervals **(Haley *et al.*, 1994 and Jacobsson *et al.*, 2005)**. Exhaustive QTL searches performed at 1 cM intervals with an updated model were implemented by fitting the suggestive and significant QTL as co-factors **(Jansen, 1994; Zeng 1994)** until no additional significant QTL were detected.

3.8 Determination of significance thresholds under the additive – dominance model :

Significance thresholds for detection of single QTL with significant marginal effects were used to generate 95% confidence intervals for the QTL positions **(Visscher *et al.*, 1996)**. An F value greater than the $P \leq 0.05$ and $P \leq 0.01$ experiment wide threshold values respectively were used to identify a significant and highly significant QTL **(Kruglyak and Lander 1995)**. Alternatively QTL that achieved an F ratio exceeding the $P \leq 0.05$ chromosome-wide threshold were considered to be suggestive. The genome-wide level thresholds of highly significant, significant and suggestive mean that there is a probability to make 0.01, 0.05 and 1 false positive(s) respectively per genome scan **(Kruglyak and Lander 1995)**.



4. RESULTS AND DISCUSSION

4.1 Growth traits:

4.1.1 Phenotypic means of genetic groups:

Means presented in Table (5) showed that GM strain was significantly heavier (P<0.05) in most of the body weight and daily gain traits compared to WL breed. But, WL strain was higher than GM strain in BW0 and DG8-12. This superiority may be due to the genetic makeup of GM strain and the genotype-environment interaction that favours GM strain over WL breed **(El-Labban, 2000)**.

Crossbred chicks were superior (P<0.05) for most growth traits, probably due to genetic and non-genetic additive effects of genes. **Afifi *et al.* (2002), Iraqi *et al.* (2002), Khalil and Al-Homiadan (2003), Iraqi *et al.* (2013) and Mahmoud and El-Full (2014)** found that crossbreeds were significantly (P<0.01) superior in growth traits compared to the parental populations. In general, the overall performances of the crossbred chickens of (1/2GM1/2WL) and $(1/2GM1/2WL)^2$ were found to be faster than those for local chickens of GM **(Galal *et al.*, 2007; Iraqi *et al.*, 2013)**.

4.1.2 Heritability :

Estimates of heritability (h^2) for growth traits in genetic group of $(½GM½WL)^2$ are presented in Table 6. The estimates showed that these growth traits are highly heritable; the estimates ranging from 0.43 to 0.52. Thus, we would recommend the selection for growth in these strains at early ages, so time and

efforts can be saved. Estimates of h^2 in the present study were generally within the range of those estimates obtained for the same strains by **Khalil *et al.* (1991) and Iraqi *et al.* (2000)**.

Table 5. Means and standard errors (SE) for growth traits in Golden Montazah (GM), White Leghorn (WL) and their crosses of chickens

Trait	Symbol	Genetic group			
		GM	WL	½GM½WL	(½GM½WL)^2
		Mean ±S.E (N= 775)	Mean ±S.E (N= 1002)	Mean ±S.E (N= 1343)	Mean ±S.E (N= 1011)
Body weight traits (g):					
0 week	**BW0**	33.3±0.13^b	34.1±0.12^a	29.6±0.10^d	32.3±0.12^c
4 weeks	**BW4**	221.4±1.92^c	216.7±1.67^c	250.8±1.47^a	234.9±1.68^b
8 weeks	**BW8**	601.6±4.90^b	515.2±4.23^d	640.9±3.74^a	554.2±4.32^c
12 weeks	**BW12**	977.3±8.25^c	914.4±7.13^d	1121±6.25^a	992.4±7.29^b
16 weeks	**BW16**	1347±11.90^c	1279±10.27^d	1517±8.98^a	1490±10.46^b
Daily gain traits (g):					
0-4 weeks	**DG04**	6.71±0.06^c	5.51±0.05^d	7.90±0.05^a	7.23±0.06^b
4-8 weeks	**DG48**	13.52±0.14^b	10.65±0.12^d	13.92±0.10^a	11.34±0.12^c
8-12 weeks	**DG812**	13.26±0.17^c	14.14±0.15^d	17.06±0.13^a	15.43±0.15^b
12-16 weeks	**DG1216**	13.26±0.21^c	13.11±0.18^c	14.23±0.16^b	17.78±0.19^a

$^{a-d}$ Means with the same letters within each row of the trait are non-significantly different (P≤0.05).

4.1.3 The genetic and phenotypic correlations:

The genotypic and phenotypic correlations among growth traits in the F_2 population are presented in Table 6. As expected,

there were moderate to high positive correlations between the growth traits studied.

Table 6. Heritabilities of growth traits (diagonals), genetic (above diagonals), and phenotypic (below diagonals) correlations of investigated traits

Trait+	BW4	BW8	BW12	BW16	DG04	DG48	DG812	DG1216
BW4	**0.51****	0.25**	0.22**	0.11**	0.20**	0.18**	0.11**	0.10**
BW8	0.25**	**0.45****	0.64**	0.58**	0.20**	1.00**	0.29**	0.29**
BW12	0.19**	0.59**	**0.52****	0.75**	0.54**	0.63**	0.92**	0.23**
BW16	0.17**	0.62**	0.75**	**0.43****	0.50**	0.58**	0.63**	0.73**
DG04	0.20**	0.25**	0.53**	0.53**	**0.46****	0.19**	0.59**	0.31**
DG48	0.18**	1.00**	0.58**	0.62**	0.24**	**0.45****	0.29**	0.29**
DG812	0.12**	0.19**	0.90**	0.57**	0.48**	0.18**	**0.51****	0.11**
DG1216	0.09**	0.33**	0.24**	0.76**	0.38**	0.33**	0.08*	**0.47****

+ Traits as defined in Table 5.

*** P < 0.05; ** P < 0.01.**

4.1.4 Chromosomal linkage analysis:

The chromosome group, number of informative microsatellite markers, chromosome map length (cM), average marker interval by the chromosome (cM) and the first marker on each chromosome that was used for a whole genome scan in F_2 cross are presented in Table (7). Ultimately, nine autosomal linkage groups, and the Z chromosome containing 43 microsatellite markers in the F_2 cross were used for linkage analysis.

The total chromosomal map length was 1901 cM ranging from 25 cM on chromosome 11 to 568 cM on chromosome 1,

with an average marker spacing of 44.21 cM and ranging from 7.8 cM on chromosome 8 to 24.3 cM on chromosome 1. Map lengths for these chromosomes were considerably similar to those cited in the chicken consensus map reported by **Zhou *et al.* (2006)**. **Ikeobi *et al.* (2002)** stated that the total map length was 2923 cM or about 75% of the consensus linkage map and the average marker interval was 40 cM. **Zhou *et al.* (2006)** in F_2 population of broiler-Leghorn cross and broiler-Fayoumi cross reported that the QTL covered a 20 to 30 cM chromosome region and this size region may contain many candidate genes. The same authors concluded that chromosome 1 had potential positional candidate genes like growth hormone 1, lysosomal associated membrane protein 1, and uncoupling protein 2. The potential candidate genes mapped in the region on chromosome 2 are transforming growth factor-β (TGFB) type I receptor and pituitary adenylate cyclase-activating polypeptide 1. The TGFB type II receptor is mapped on chromosome 4 nearby QTL affecting growth traits. A potential candidate gene on Chromosome 10 is insulin-like growth factor type 1 receptor. Growth hormone gene has been associated with growth in chickens **(Kuhn *et al.*, 2002)**. The insulin-like growth factor and TGFB family genes have previously shown associations with growth-related traits in chickens **(Amills *et al.*, 2003; Li *et al.*, 2003; Zhou *et al.*, 2005)**. So far, no association has been found for the genes above with growth-related traits in chickens. **Nassar *et al.* (2012)** found that the most genomic region affecting body weight was mapped on chromosome 4 at 155 cM.

Table 7. Chromosome (linkage) group, number of microsatellite markers, map length (cM), marker intervals and the first marker on each chromosome that was used for a whole genome scan of F_2 cross

Chromosome	Number of microsatellite markers	Chromosome map length (cM)	Average marker spacing by the chromosome (cM)	First marker on each chromosome
1	7	568	24.3	ROS0003
2	4	298	18.7	LEI0073
3	8	273	11.6	MCW0169
4	6	198	17.6	ADL0317
6	3	111	10.4	ADL0280
8	4	97	7.8	MCW0080
9	2	123	20.1	ROS0074
11	2	25	8.3	LEI0110
13	4	71	14.5	MCW0340
Z	3	137	11.5	LEI0075
Total	43	1901	-	-
Mean+	-	-	44.21	-

+ Mean = chromosome map length / number of microsatellite marker

4.1.5 Estimates of QTL mapping:

The flanking markers, position of QTL relative to the first marker (cM), F-ratio and significant for each QTL at chromosome-wise level along with the proportion of phenotypic

variance explained by each QTL for body weights and daily gains in weight are presented in Tables 8 and 9. The results in the current study lay the foundations for fine mapping of the traits in the advanced intercross lines and provide a start point for identifying the causative genes responsible for growth traits in chickens. In Brazil, a layer (CC) and a broiler (TT) lines were crossbred to generate two F_2 reciprocal populations (TCTC and CTCT) to map QTL **(Nones *et al.*, 2006; Ambo *et al.*, 2009; Campos *et al.*, 2009; Baron *et al.*, 2011; Nones *et al.*, 2012; Boschiero *et al.*, 2013)**.

For daily body gains (DG), a total of 14 QTL were detected (Table 9). These QTL were distributed over 7 distinct regions on 6 chromosomes. A total of 11 genome significant QTL that affected daily gain were located on five macro-chromosomes (1, 2, 3, 4 and 8). There was statistical evidence for two QTL on chromosome 4 for daily gains at 0-4, 4-8 and 8-12 weeks of age. A further three suggestive QTL were identified for daily gain at DG4-8 and DG0-4 on chromosomes 1, 8 and 13. Similar results were obtained by **Carlborg *et al.* (2003), Jennen *et al.* (2004), McElroy *et al.* (2006)** and **Rosario *et al.* (2014)**.

The position of QTL relative to the first marker (cM) given in Table (8) indicated that QTL were located in the region of 0 to 502 cM, 0 to 233 cM, 0 to 179 cM and 12 to 555 cM for body weights at 4, 8, 12 and 16 weeks of age, respectively. For daily gains, the position of QTL relative to the first marker (cM) given in Table (9) indicated that QTL were located in the region of 67 to 452 cM, 0 to 436 cM, 26 to 512 cM and 17 cM for daily gain intervals at 0-4, 4-8, 8-12 and 12-16 weeks, respectively.

Table 8. Flanking markers, position of QTL relative to the first marker (cM), F-ratios and significance of QTL at chromosome-wise level confidence interval at 95% (cM) for body weights at 4, 8, 12 and 16 weeks of age in phenotypic population of chickens along with the percentage of F_2 variance explained by each QTL

Trait / Chromosome	Flanking markers	Position of QTL relative to the first marker (cM)	F-ratio for each QTL at chromosomal wise level	Confidence interval at 95% (cM)	Percentage of phenotypic variance explained by each QTL
4-week weight					
1	ADL0183-ROS0025	502	4.6†	74-615	2.4
2	ADL0236-ROS0074	292	16.1**	43-367	5.8
4	ADL0266-LEI0073	145	8.8*	12-183	3.1
6	ROS0003 - ADL0142	29	9.6*	0-42	2.6
8	MCW0100-ROS0075	62	7.6†	1-87	2.1
11	LEI0110 - MCW0097	0	12.5**	0-10	1.2
13	LEI0083 - MCW0080	50	5.6†	9-71	1.6
Z	LEI0111 - LEI0075	125	6.9†	0-125	2.3
8-week weight					
1	MCW0010-ADL0188	128	17.0**	76-219	4.9
2	ADL0236-ROS0074	150	5.1†	34-370	1.3
3	LEI0161-ADL0280	49	11.4*	14-219	3.0
3	MCW0040-LEI0166	233	5.4†	12-266	1.5
4	ADL0317 - MCW0295	0	8.2*	0-69	2.5
4	ADL0266-LEI0073	159	23.5**	140-183	7.0
8	MCW0100-ROS0075	67	7.5†	0-87	2.5
11	LEI0110-MCW0097	0	12.1**	0-57	3.5
13	MCW0340-ADL0225	44	5.6†	12-71	1.6
Z	LEI0111-LEI0075	117	9.6**	14-127	3.0

Continue Table 8.

Trait / Chromosome	Flanking markers	Position of QTL relative to the first marker (cM)	F-ratio for each QTL at chromosomal wise level	Confidence interval at 95% (cM)	Percentage of phenotypic variance explained by each QTL
12-week weight					
1	MCW0010-ADL0188	133	11.9**	67-227	3.3
3	ADL0237-ADL0166	37	10.0*	155-183	3.0
4	ADL0317-MCW0295	0	8.4*	0-177	2.4
4	ADL0266-LEI0073	179	44.5**	155-183	13.8
8	MCW0100-ROS0075	59	13.2**	12	1.4
9	MCW0135-ROS0030	90	5.0†	0	1.3
13	MCW0340-ADL0225	8	5.1†	0-71	1.4
Z	LEI0111-LEI0075	120	8.9*	8-127	2.7
16-week weight					
1	MCW0010-ADL0188	129	6.4†	109-543	2.5
1	ADL0183-ROS0025	555	5.3†	96-598	1.6
2	ADL0236-ROS0074	277	5.7†	0-297	1.9
4	ADL0241-MCW0180	139	16.9**	19-169	6.5
8	MCW0305-ADL0258	12	11.5**	0-86	4.2
8	MCW0100-ROS0075	87	6.2†	14-87	2.3
13	MCW0340-ADL0255	69	7.0†	2.0-71.0	2.8
Z	LEI0111-LEI0075	125	9.3**	0-125	3.6

Total QTL detected = 34.
***significant linkage at $P \leq 0.05$; ** significant linkage at $P \leq 0.01$ and † Suggestive linkage.**

Table 9. Flanking markers, position of QTL relative to the first marker (cM), F-ratios and significance of QTL at chromosome-wise level confidence interval at 95% (cM) for daily gain at 0-4, 4-8, 8-12 and 12-16 weeks of age in F_2 population of chickens along with the percentage of phenotypic variance explained by each QTL

Trait / Chromosome	Flanking markers	Position of QTL relative to the first marker (cM)	F-ratio for each QTL at chromosomal wise level	Confidence interval at 95% (cM)	Percentage of phenotypic variance explained by each QTL
Daily gain 0-4 week					
1	ROS0025-ADL0238	452	9.15*	69-437	4.99
2	ADL0267-ADL0236	239	12.88**	80-504	6.89
4	ADL0317-MCW0295	398	10.87**	104-310	5.95
4	ADL0241-MCW0180	418	11.66**	154-208	6.03
13	MCW0340-ADL0225	67	5.82†	32-165	2.04
Daily gain 4-8 week					
1	ADL0183-LEI0106	0	7.61†	0-37	4.19
2	ROS0074-ADL0114	248	9.80**	15-384	4.81
4	ADL0317-MCW0295	428	16.88**	65-540	8.88
4	ADL0241-MCW0180	436	15.46**	98-506	7.68
8	ROS0026-MCW0305	22	5.56†	0-32	3.54
Daily gain 8-12 week					
1	ADL0183-MCW0107	512	9.83**	106-584	3.05
3	MCW0169-MCW0083	26	10.02**	0-186	4.12
4	ADL0241-MCW0180	168	18.99**	138-198	2.18
Daily gain 12-16 week					
8	ROS0025-MCW0305	17	9.76**	0-158	3.9

Total QTL detected = 14.

***significant linkage at $P \leq 0.05$; ** significant linkage at $P \leq 0.01$. and † Suggestive linkage;**

Wang *et al.* (2012) stated that the QTL for body weight at 2 to 5 and 8 to 10 week of age were located in the region of 89 to 104 cM and the QTL for body weight at 6, 7, 10 to 12 week of age located in the region of 246 to 248 cM.

For body weights evaluated in F_2 cross, a total of 34 QTL were detected and these QTL were distributed over five distinct regions on 10 chromosomes (Table 8). A total of 19 genome significant QTL that affecting body weight were located on seven macro-chromosomes (chromosomes 1, 2, 3, 4, 6, 8 and Z) and one micro-chromosome (chromosome 11). There was statistical evidence for two QTL on chromosome 4 for body weight at 8 and 12 weeks of age. A further 15 suggestive QTL were identified for body weight at different ages on chromosomes 2, 6, 9 and 13.

Previous QTL mapping indicated that chromosome 3 harboured QTL regions are responsible for body weight at different ages (**Ikeobi *et al.*, 2002; Wardecka *et al.*, 2002; Kerje *et al.*, 2003; Siwek *et al.*, 2004; Tuiskula-Haavisto *et al.*, 2004; Zhou *et al.*, 2006)**. **Siwek *et al.* (2004)** using 174 microsatellite markers detected QTL for body weights at 4, 6, 8, 12, and 18 week of age in an experimental F_2 cross of layers applying two genetic models in the QTL analysis: a half-sib model and a line-cross model. In the half-sib model, three QTL were detected for body weight at the 4^{th} week of age on chromosomes 2, 3, and 9; three QTL for body weight at the 6^{th} week of age on chromosomes 2, 3, and 6; one QTL for body weight at the 8^{th} week of age on chromosome 7, and one QTL for body weights at 12 and 18 weeks of age on chromosome Z.

With the line-cross analysis model, one QTL was detected on chromosome 7 for body weight at the 4th week of age, two QTL on chromosomes 3 and 7 for body weight at the 6th week of age, and one QTL on chromosome 3 for body weights at 8 and 12 weeks of age, and there was no QTL for body weight at 18 week of age. **Rosario *et al.* (2014)** detected five QTL on chromosomes 1, 3 and 4 for body weight at 35 days of age, five QTL for body weight at 41 days of age on chromosomes 1, 3 and 4. Three QTL for body weight at 35 days and two QTL for body weight at 41 days of age were identified on chromosome 4. **De Koning *et al.* (2003; 2004)** validated the presence of QTL for body weight in a commercial broiler line. **Zhu *et al.* (2003)** detected potential QTL for growth to be located on chromosomes 1, 6, and 8.

The QTLs detected in F_2 population in the present study are similar to those obtained by **Sewalem *et al.* (2002)**, in which a F_2 population was generated from a commercial broiler line and White Leghorn line. More QTL were detected by **Sewalem *et al.* (2002)** for body weights at 3, 6, and 9 weeks of age on chromosomes 4, 8, and 13. In this study, one out of 4 QTL on chromosome 3 was suggestive (Tables 8 & 9). **Carlborg *et al.* (2003); Jennen *et al.* (2004) and McElroy *et al.* (2006)** reported that QTL for growth was detected on chromosome 3. The QTL detected for growth on chromosomes 1, 2, 3, 4, 6, 8, 11 and Z in the present study were also found in F_3 population generated from crossing two White Plymouth Rock broilers **(Jennen *et al.*, 2004)** and in F_2 population generated by Red Jungle Fowl and White Leghorn line **(Carlborg *et al.*, 2003)**. Several QTL for growth traits on chromosomes 11, 12, and 15 were reported in

other studies **(Carlborg *et al.*, 2003; Kerje *et al.*, 2003)**. **Carlborg *et al.* (2003)** and **McElroy *et al.* (2006)** detected QTL for growth on chromosomes 20 and 26. **Zhou *et al.* (2006)** reported that most of the QTL for growth traits were detected in chromosomes 1, 2, 4, 7, and 14 for the broiler-Leghorn cross and chromosomes 1, 2, 4, 5, 8, and 13 for the broiler-Fayoumi cross, i.e. majority of the QTL detected for growth traits were similar between the two line crosses. Moreover, they mentioned that there were no QTL affecting growth-related traits detected on chromosomes 11, 12, 13, 15, 17, 27, and Z in the broiler-Leghorn cross, and there were no QTL detected on chromosomes 10, 11, 12, 15, 17, 18, 24, 27, E46, E47, and Z in the broiler-Fayoumi cross. **Bulut *et al.* (2013)** using Denizli X White Leghorn F_2 populations and a total of 113 microsatellite markers, demonstrated that QTL regions associated with body weight at different age periods were located on chromosomes 1, 2, 4, 8 and Z and the distances between the QTL regions were wide (>30 cM). Therefore, the relevant QTL intervals should be narrowed by the use of new markers.

The F-ratios for each QTL at chromosome-wise level illustrated in Table 8 for different body weights showed that 19 out of 34 QTL were significant ($P < 0.05$ or $P < 0.01$). **Schreiweis *et al.* (2005)** reported that five QTL influencing body weight at 35 or 55 week of age were identified on chromosomes 4, 12, and 27, and four of them were located on chromosomes 4 and 27 and surpassed a 1% genome-wise significance threshold. Each of the significant QTL is associated with an increase in body weight from the broiler allele, while the suggestive QTL is

primarily associated with dominant gene action. While, **Liu *et al.* (2007)** reported 10 QTL identified at the 1% chromosome wide level, two QTL identified at the 5% chromosome wide level, and five QTL identified at the suggestive level for body weight. **Wang *et al.* (2012)** found on chromosome 3 that three QTL were identified at the 5% chromosome-wide level and 10 QTL were suggestive.

4.1.6 Confidence intervals:

For 4-week body weight, four significant QTL were located on chromosomes 2, 4, 6 and 11 at positions of 292, 145, 29 and 0 cM, respectively, with 95% confidence intervals of 43–367, 12–183, 0-42 and 0-10 cM, respectively. For 8-week body weight, a significant QTL was located on chromosomes 1, 3, 4, 11 and Z sex chromosome at positions of 128 , 48, 0, 159, 0 and 117 cM respectively, with 95% confidence intervals of 76-219, 14-219, 0-69, 140-183, 0-57 and 14-127 cM.. For 12-week body weight, six significant QTL were located on chromosomes 1, 3, 4, 8 and Z at positions of 133, 37, 0, 179, 59 and 120 cM respectively, with 95% confidence intervals of 67-227, 155-183, 0-177, 155-183, 12 and 8-127 cM, respectively. For 16-week body weight, a significant QTL was located on chromosomes 4, 8 and Z at positions of 139, 12, and 125 cM, respectively, with 95% confidence intervals of 19-169, 0-86 and 0-125 cM. **Soller *et al.* (2006)** reported that fine-mapping of QTL and the identification of causal gene and underlying genes still remains one of the major challenging tasks because the confidence interval of most reported QTL covers more than 20 cM.

van Kaam *et al.* (1999) performed a genome scan for growth and carcass composition using a crossing population between two broiler lines. Only one QTL was up to a genome-wide significant level. This growth QTL was located on chromosome one at 235 cM. **Tatsuda and Fujinaka (2001)** identified two significant QTL for growth using a crossing population between a Satsumadori line and a White Plymouth Rock line. One QTL identified on chromosome one was located at 220 cM. **Sewalem *et al.* (2002)** performed a genome scan for growth using a crossing between a White Leghorn line and a commercial broiler sire line. Two significant QTL of 145 and 481 cM for 3-week body weight were located on chromosome one, in which 95% confidence intervals were 113–217, and 441–526 cM. Another significant QTL for 9-week body weight was located on chromosome one at 414 cM with 34–419 cM of the 95% confidence interval. Also, **Kerje *et al.* (2003)** identified two major QTL for growth, which were located on chromosome one using a crossing population between Red Jungle Fowl and White Leghorn. The two major QTL for growth were located around positions of 68 and 416 cM.

The effects of QTL expressed as the percentage of phenotypic variance explained by each QTL were mostly of considerable importance ranging from 1.2 to 13.8 % of the phenotypic variation for body weights and from 2.04 to 8.88 % for daily weight gains (Tables 8 & 9). The largest proportion of the phenotypic variation explained by a QTL was 13.8% for 12-week body weight at 179 cM on chromosome 4 (Table 8). The total proportions of phenotypic variation explained by all

significant and suggestive QTL for body weight at 4, 8, 12 and 16 weeks were 21.1, 30.8, 29.3 and 25.4%, respectively. The proportions explained by significant and suggestive QTL for daily gain 0-4, 4-8, 8-12 and 12-16 weeks were 25.9, 29.1, 9.35 and 3.9%, respectively (Table 8). The largest proportion of the phenotypic variation explained by a QTL was 8.88% for DG 4-8 week at 428 cM on chromosome 4. **Zhou *et al.* (2006)** found that the phenotypic trait variances explained by QTL ranged from 2.24 to 10.12% in the broiler-Leghorn cross and from 2.94 to 9.14% in the broiler-Fayoumi cross. **Rosario *et al.* (2014)** reported that the phenotypic variance attributable by each QTL for body weight at 35 and 41 days of age were 10.76 and 10.75 %, respectively.

In general, results of QTL mapping of the present study are in agreement with the previous studies that have identified numerous QTL affecting body weights at different ages in chickens **(Tatsuda and Fujinaka 2001; Deeb and Lamont 2002; Sewalem *et al.*, 2002; Kerje *et al.*, 2003; Siwek *et al.*, 2004; Jacobsson *et al.*, 2005; Zhou *et al.*, 2006; Atzmon *et al.*, 2007, 2008; Ambo *et al.*, 2009; Wahlberg *et al.*, 2009; Goraga *et al.*, 2012; Bulut *et al.*, 2013).**

4.1.7 Additive and dominance effects for QTL:

Details of the additive and dominance effects of the 19 significant QTL for body weights are presented in Table 10. The additive effects were positive, while the dominance effects were generally negative or not significant with the exception of body weights at 4, 8, 12 and 16 weeks of age (QTL on chromosomes 2, 3, 4, 8, 11 and Z). **Wang *et al.* (2012)** found that positive

additive effects, indicating that increasing body weight allele was inherited from the broiler line in F_2 population cross of broiler sire with Bair layer dams (Chinese local breed). Using 174 microsatellite markers, **Siwek *et al.* (2004)** found that additive effects for QTL detected for body weight at 4, 6, 8, 12, and 18 week of age in F_2 cross were positive on chromosome 7, while the negative additive effects for QTL were detected on chromosome 3. **Zhou *et al.* (2006)** with a broiler-Leghorn cross and a broiler-Fayoumi cross found that most of the additive effects explained by QTL detected in the study were positive in the broiler-Leghorn cross, and negative in the broiler-Fayoumi cross, which means that alleles of broiler-Leghorn cross and broiler-Fayoumi cross were generally superior in weight and growth relative to both Leghorn and Fayoumi alleles. In F_2 population obtained by crossing males from a layer line (CC) and females from a broiler line (TT), **Rosario *et al.* (2014)** cited that most QTL presented negative additive effects. These results indicated that the alleles that increase body weights came from broiler line on chromosome 4, while most of the dominance effects were negative except for body weight at 35 days of age, indicating that heterozygotes were heavier than mid-parents.

The estimates of the additive effects attributable to QTL were of considerable importance and ranged from 11.1 to 25.8 g, 18.5 to 94.5 g, 25.8 to 205.7 g and 63.2 to 369.6 g for body weights at 4, 8, 12 and 16 weeks of age, respectively (Table 10). Also, the dominance effects attributable magnitude ranging from -18.6 to 16.4 g, -34.9 to 33.0 g, 127.2 to 155.7 g and -188.1 to

110.1 g for body weights at 4, 8, 12 and 16 weeks of age, respectively (Table 10).

The largest additive effect (369.6 ± 64.6 g) was for QTL of body weight at 16 weeks of age on chromosome 4 at 179 cM (Table 8). The largest dominance effect (−188.1 ± 55.0 g) was for a QTL of body weight at 16 weeks on chromosome 4 at 139 cM (Table 10).

The percentage of additive variance explained by each QTL for body weights were mostly moderate and ranged from 2.6% to 24.8%, and the percentage of dominance variance ranged from 0.3 % to 15.7%.

As for body weights, all the additive effects detected in daily gains were also positive, and most of the dominance effects were negative (Table 11). The estimates of the additive effects explained by QTL were positive and of moderate magnitude ranging from 1.20 g on chromosome 2 to 1.77 g on chromosome 4 for DG 0-4 weeks, from 1.39 g on chromosome 1 to 3.89 g on chromosome 4 for DG 4-8 weeks, from 1.38 g on chromosome 2 to 3.84 g on chromosome 4 for DG 8-12 weeks and 1.21 g on chromosome 8 for DG 12-16 weeks. On the other hand, the estimates of dominance effects attributable to QTL were mostly negative, i.e. nine estimates out of 14 QTL were negative. The smallest dominance effect was recorded on chromosome 3 for DG 8-12 week (-2.09 g), while the largest dominance effect was recorded on chromosome 4 for DG 4-8 week (1.44 g).

Table 10. Estimates of additive and dominance effects (g) attributable to QTL and their standard errors for body weights at 4, 8, 12 and 16 weeks of age in F_2 population of chickens

Trait / Chromosome	Additive effect, g	SE	VP_a (%) [+]	Dominance effect, g	SE	VP_d (%) [++]
4-weeks weight (overall mean ± SE = 234.9 ± 1.68)						
1	11.6	4.8	4.9	13.4	12.8	5.7
2	13.9	3.2	5.9	16.4	5.5	7.0
4	25.8	6.7	11.0	-6.5	23.8	2.8
6	11.1	3.1	4.7	-11.1	4.9	4.7
8	13.6	4.1	5.8	15.4	8.5	6.6
11	13.2	2.7	5.6	7.3	3.9	3.1
13	13.9	4.8	5.9	-18.6	11.8	7.9
Z	12.8	4.0	5.4	3.3	4.0	1.4
8-weeks weight (overall mean ± SE = 554.2 ± 4.3)						
1	43.4	7.5	7.8	-2.8	11.9	0.5
2	42.1	14.7	7.6	-34.9	43.4	6.3
3	48.7	10.2	8.8	11.8	17.4	2.1
3	18.5	8.2	3.3	33.0	12.0	6.0
4	33.1	7.4	6.0	-1.5	10.9	0.3
4	94.5	14.6	17.1	6.0	40.7	1.1
8	43.2	11.5	7.8	25.3	23.0	4.6
11	32.3	7.4	5.8	13.4	10.6	2.4
13	47.2	14.0	8.5	-6.8	37.7	1.2
Z	52.8	12.2	9.5	19.8	13.2	3.6
12-weeks weight (overall mean ± SE = 992.4 ± 10.5)						
1	85.5	16.9	8.6	-5.5	26.3	0.6
3	90.1	20.1	9.1	-5.7	35.1	0.6
4	63.0	15.2	6.3	-4.0	22.6	0.4
4	205.7	22.2	20.7	15.6	44.4	1.6
8	72.0	23.1	7.3	155.7	46.0	15.7
9	25.8	21.9	2.6	-127.2	43.9	12.8
13	48.6	18.4	4.9	54.0	32.5	5.4
Z	112.0	25.5	11.3	32.2	27.9	3.2
16-weeks weight (overall mean ± SE = 1490 ± 10)						
1	90.9	26.1	6.1	26.2	36.9	1.8
1	93.1	34.2	6.2	91.0	66.8	6.1
2	93.9	27.3	6.3	-6.0	44.4	0.4
4	369.6	64.6	24.8	-188.1	55.0	12.6
8	107.3	25.4	7.2	105.3	39.1	7.1
8	108.2	32.0	7.3	-72.6	48.8	4.9
13	63.2	31.1	4.2	-155.5	47.7	10.4
Z	137.7	35.5	9.2	110.1	38.1	7.4

[+]VP_a (%) = Percentage of additive variance explained by each QTL.

[++]VP_d (%) = Percentage of dominance variance explained by each QTL.

The percentage of additive variance explained by each QTL for daily gains were moderate and ranged at different intervals from 6.8% to 34.3%, while, the percentages of dominance variance ranged from 0.5 % to 12.7%.

Table 11. Estimates of additive and dominance effects (g) attributable to QTL and their standard errors for daily gains at 0-4, 4-8, 8-12 and 12-16 weeks of age in F_2 population of chickens

Trait / Chromosome	Additive effect, g	SE	VP_a (%) [+]	Dominance effect, g	SE	VP_d (%) [++]
Daily gain 0-4 week (overall mean ± SE = 7.23 ± 0.06)						
1	1.30	0.30	18.0	-0.20	0.43	2.8
2	1.20	0.24	16.6	-0.57	0.44	7.9
4	1.27	0.25	17.6	-0.29	0.32	4.0
4	1.77	0.39	24.5	0.62	0.74	8.6
13	1.42	0.42	19.6	-0.52	0.88	7.2
Daily gain 4-8 week (overall mean ± SE = 11.34 ± 0.12)						
1	1.39	0.58	12.3	-1.68	0.73	14.8
2	1.86	0.48	16.4	0.45	0.80	4.0
4	3.18	0.59	28.0	1.44	0.73	12.7
4	3.89	0.81	34.3	0.87	1.02	7.7
8	3.22	1.25	28.4	-0.33	1.15	2.9
Daily gain 8-12 week (overall mean ± SE = 15.4 ± 0.15)						
1	1.65	0.57	10.7	-1.99	0.98	12.9
3	1.38	0.31	9.0	-2.09	0.88	13.6
4	3.84	0.44	24.9	0.08	0.66	0.5
Daily gain 12-16 week (overall mean ± SE = 17.8 ± 0.2)						
8	1.21	0.32	6.8	-1.18	0.36	6.6

[+] VP_a (%) = Percentage of additive variance explained by each QTL.

[++] VP_d (%) = Percentage of dominance variance explained by each QTL.

4.1.8 Total variances explained by QTL for each growth trait:

The total variances explained by QTL for each growth trait were 21.1, 30.8, 31.7, 25.4, 25.9, 29.1, 9.35 and 3.9 % in BW4, BW8, BW12, BW16, DG04, DG48, DG812 and DG1216, respectively (Table 12). Across the traits studied, a total of 18 significant QTL were detected at a 5 % chromosome-wise significance level, while a total of 8 and 22 significant QTL were detected at a 5 % and 1 % genomic-wise significance level, respectively. In F_2 population of a broiler-Leghorn cross and a broiler-Fayoumi cross, **Zhou *et al.* (2006)** found that a total of 52 and 38 QTL were detected at the 5% chromosome-wise level for the traits evaluated in the broiler-Leghorn cross and the broiler-Fayoumi cross, respectively. Of the 52 suggestive QTL in the broiler-Leghorn cross, 17 QTL were significant at the 5% genome-wise level, while of the 38 suggestive QTL in the broiler-Fayoumi cross, 10 QTL were significant at the 5% genome-wise level**.** A total of 18 and 13 significant QTL were detected at a 1% chromosome-wise significance level for the 8 growth traits studied, of which 17 and 10 were significant at the 5% genome-wise level, respectively.

Potential candidate genes within the QTL region for growth traits at 1% chromosome-wise significance level were of considerable importance. In F_2 population of broiler sire with Bair layer dams (Chinese local breed) cross, **Wang *et al.* (2012)** cited that three QTL at 5 % chromosome-wise and 10 QTL at suggestive level on chromosome 3; on chromosome 5, there were four QTL identified at 5% genome-wide level, eight QTL

at 5% chromosome-wide level and one at suggestive level. On chromosome 7, there were five QTL identified at 5% genome-wide level, four QTL at the 5% chromosome-wide level and four QTL at suggestive level.

Table 12. Number of significant QTL at the 5 and 1% chromosome-wise levels and genome-wise level for each trait F_2 cross

Trait	Chromosome-wise level		Genome-wise level		Variance (%) [+]
	5%	1%	5%	1%	
BW4	4	-	2	2	21.1
BW8	4	-	2	4	30.8
BW12	2	-	3	3	31.7
BW16	5	-	-	3	25.4
DG04	1	-	1	3	25.9
DG48	2	-	-	3	29.1
DG812	-	-	-	3	9.35
DG1216	-	-	-	1	3.9
Total	18	-	8	22	-

[+] The sum of the total variances explained by the each QTL.

4.2 Egg production and egg quality traits:

4.2.1 Phenotypic means of genetic groups:

Results obtained in Table (13) showed that the superiority of WL for AFE and EN than GM, while GM had the superiority in WFE. The crossbreds were superior in egg production traits relative to the purebreds. The first cross of ½GM½WL had the

superiority of egg production traits then the intercross of $(½GM½WL)^2$. In general, results of the present study indicated that egg traits of local chickens in Egypt could be improved by crossbreeding. These results are in agreement with **El-Sisy (2001), El-Soudany (2003), Iraqi (2008), El-Atrouny (2011) and Abou El-Ghar *et al.* (2014)**.

Table 13. Means and standard errors (SE) for egg production and egg quality traits in Golden Montazah (M), White Leghorn (L) and their crosses of chickens

Trait+	Genetic group			
	GM	WL	½GM½WL	$(½GM½WL)^2$
	Mean ±S.E	Mean ±S.E	Mean ±S.E	Mean ±S.E
AFE (days)	168.9±0.52^{a}	162.09±0.40^{bc}	158.31±0.49^{d}	161.07±0.49^{c}
WFE (g)	1566.3±20.9^{b}	1465.2±16.23^{c}	1825.4±19.7^{a}	1567.0±19.8^{b}
EN (egg)	61.67±0.57^{d}	74.01±0.44^{c}	83.44±0.54^{a}	79.27±0.54^{b}
EW (g)	44.04±0.14^{d}	45.67±0.10^{c}	47.70±0.14^{b}	49.44±0.19^{a}
AW (g)	24.19±0.10^{d}	25.62±0.07^{c}	27.22±0.09^{b}	28.10±0.13^{a}
YW (g)	14.38±0.06^{c}	14.51±0.04^{bc}	14.66±0.06^{b}	15.35±0.08^{a}
SW (g)	5.45±0.02^{d}	5.53±0.01^{c}	5.82±0.02^{b}	5.97±0.03^{a}
HU	94.10±0.80^{a}	90.19±0.59^{b}	88.87±0.78^{b}	78.60±1.05^{c}
EST (mm)	78.10±0.004^{a}	76.19±0.003^{b}	76.41±0.004^{b}	76.78±0.006^{ab}

+ traits = AFE (age at first egg), WFE (weight at first egg), EN (egg number), EW (egg weight), AW (albumen weight), YW (yolk weight), SW (shell weight), HU (haugh unit) and EST (eggshell thickness).

$^{a-d}$ Means with the same letters within each row of the trait are non-significantly different (P≤0.05).

Least-squares means presented in Table (13) showed that most of egg-quality traits of WL breed were higher than egg-quality of GM strain. But, GM strain was better in HU and EST compared to WL breed. This may be due to differences in genetic makeup of the two strains **(El-Labban, 2000)**. Eggs of crossbred hens were superior in most of the traits, probably due to genetic and non-genetic additive effects of genes. Eggs of the F_2 cross had the heaviest egg weight, albumen weight, yolk weight and shell weight compared to F_1 cross.

4.2.2 Heritability:

Heritability estimates were 0.11, 0.11, 0.34, 0.14, 0.18 and 0.22 for AFE, WFE, EN, EW, EST and HU traits, respectively; these results agreed with **Iraqi (2008)**. Using the sire and/or animal model analysis, these estimates are fall within the ranges reported by some investigators for age at sexual maturity and for egg number (**Wei** and **van der Werf, 1995; El-Labban, 2000; Anang *et al.*, 2000; Reddy *et al.*, 2004; Nurgiartiningsih *et al.*, 2004, Kosba *et al.*, 2006; El-Atrouny, 2011)**.

As AFE, WFE and EW are sex-limited traits and they are lowly to moderate heritable (Table 14), they would greatly beneficial marker assisted selection, where the selection can be directed towards breeding value. The heritabilities of EW in many reports ranged from 0.52 **(Wei and van der Werf, 1995)** to 0.71 **(Besbes and Gibson, 1998; Zhang *et al.*, 2005)**.

Table 14. Heritabilities (diagonals), genetic (above diagonals), and phenotypic (below diagonals) correlations of investigated traits

Traits+	AFE	WFE	EN	EW	ES	HU
AFE	**0.11****	0.01^{ns}	-0.39**	-0.04^{ns}	0.12**	-0.10**
WFE	0.04^{ns}	**0.11****	-0.28**	0.13**	0.00^{ns}	-0.01 ^{ns}
EN	-0.09**	-0.26**	**0.34****	0.15**	-0.03^{ns}	0.11**
EW	0.01^{ns}	-0.09**	0.15**	**0.14****	0.02^{ns}	-0.94**
EST	-0.02^{ns}	0.00^{ns}	0.03^{ns}	0.01^{ns}	**0.18****	-0.06 ^{ns}
HU	0.03^{ns}	0.03^{ns}	0.07*	-0.84**	-0.04^{ns}	**0.22****

+ Traits as defined in Table 13.

*** P < 0.05; ** P < 0.01.**

4.2.3 Phenotypic (r_p) and genetic (r_g) correlations:

The estimates of r_g among the egg traits studied are presented in Table 14. The estimates of genetic correlation were almost positive and low (Table 14). These correlations were lower than those obtained by **El-Labban (2000),** who found that the estimates of r_g ranged from 0.50 to 0.81 between the egg traits in different local strains of chickens. These results are in agreement with report of **Kosba *et al.* (2006)**, who found that estimate of r_g was 0.05 among the egg traits**.** On the contrary, **Jeyaruban** and **Gibson (1996)** found that estimates of r_g were moderate and ranged from 0.32 to 0.492 among the egg traits.

Tuiskula-Haavisto *et al.* (2002) reported that AFE had a phenotypic correlation of 0.29 with EW and of -0.52 with EW. **Zhang *et al.* (2005)** cited that both of the phenotypic and the genetic correlations between EW and EST were low, which in

turn inferred that the larger eggs were not weaker than the smaller eggs.

4.2.4 Chromosomal linkage analysis:

The chromosome group, number of informative microsatellite markers, chromosome map length (cM), average marker interval by the chromosome (cM) and the first marker on each chromosome that was used for the whole genome scan in F_2 cross are presented in Table (15). Ultimately, the nine autosomal chromosome groups and the Z chromosome that containing 45 microsatellite markers in the F^2 cross were used for chromosomal linkage analysis.

The total chromosomal map length was 1949 cM ranging from 52 cM on chromosome 11 to 542 cM on chromosome 1, with an average marker spacing of 43.3 cM and that ranging from 15.3 cM on chromosome 4 to 71.5 cM on chromosome 6 (Table 15). Map lengths for these chromosomes were considerably similar to those cited in the chicken consensus map reported by **Tuiskula-Haavisto *et al.* (2002)** for egg production and quality traits using 99 microsatellite markers spanning the nine largest linkage groups (chromosomes 1, 2, 3, 4, 5, 6, 7, and 8, and Z) and the five small linkage groups. They added that the linkage groups covered 2311 cM, with an average spacing of 23.34 cM between markers and the estimates on the length of the complete genome ranged from 3064 to 3800 cM, based on the mapping function. The map distances in this study covered 48 to 60% of the whole chicken genome and the marker MCW247 assigned for chromosome 2 and the marker ADL345 assigned for chromosome 8 have been mapped only in the Wageningen

Table 15. Chromosome (linkage) group, number of microsatellite markers, map length (cM), marker intervals and the first marker on each chromosome that was used for a whole genome scan of F_2 cross

Chromosome	Number of microsatellite markers	Chromosome map length (cM)	Average marker spacing by the chromosome (cM)	First marker on each chromosome
1	2	542	60.2	MCW0107
2	6	401	50.1	LEI0163
3	8	144	24	MCW0169
4	10	286	15.3	ADL0143
6	2	123	71.5	ADL0322
8	4	88	44	ROS0075
9	1	112	56	MCW0135
11	2	52	17.3	ROS0003
13	1	69	34.5	ADL0255
Z	9	132	22	ROS0074
Total	45	1949	-	-
Mean+	-	-	43.3	-

+ Mean = chromosome map length / number of microsatellite marker

reference population. The marker MCW170 assigned for chromosome 4 and both MCW133 and ADL315 assigned for chromosome 7 have been mapped only in the East Lansing population, and the marker MCW129 assigned for chromosome 4. **Sasaki *et al.* (2004)** using F_2 population originated from a cross between WL males and RIR females, reported that: (1) chromosome 1 was separated into four linkage groups, chromosome 2 was separated into three linkage groups and

chromosome 5 was separated into two linkage groups, (2) the linkage groups encompassed 800 cM of the autosomes based on the mapping function, (3) thirteen markers were mapped into a linkage group on the Z chromosome, encompassing 120 cM of the Z chromosome, (4) the total linkage map spanned 920 cM, with an average marker spacing for 6.7 cM, and (5) the remaining 13 markers could not be assigned to a linkage group and were therefore excluded from the QTL analysis. **Honkatukia *et al.* (2005)** using 20 markers with the reciprocal intercross of two parental lines, the White Leghorn (WL) and Rhode Island Red (RIR) showed a significant QTL affecting HU, with a position at 137 cM between the marker MCW0206 (114 cM) and the marker ADL0217 (152 cM).

Chatterjee *et al.* (2008) stated that the correlations of markers MCW0041, ADL0210, and MCW0110 with egg production traits were significant ($P<0.05$), while the correlations of MCW0014, MCW0049, ADL0158, and MCW0243 with any of the egg production traits were not significant. The ADL0210 genotypes revealed a significant correlation with egg production up to 52, 64, and 72 weeks of age ($P<0.05$). The MCW0041 genotypes showed a significant correlation with egg production up to 64 and 72 weeks of age ($P<0.05$). In addition, MCW0110 showed a significant association with egg production up to 28 weeks of age. No significant association was observed between any microsatellites and egg weight at any age. **Vilkki (2009)** reported that 23 QTL affecting eggshell thickness were found in the genome scan. Genome-wide significant QTL were found on chromosomes 2, 6

and 14, and additional chromosome-wise significant QTL seem to cluster on these chromosomes and on chromosome 3. On chromosome 2, QTL affecting shell breaking force (at 35 and 40 weeks of age) and QTL affecting shell deformation (average and at 35 and 40 weeks of age) were identified within the marker bracket ADL0236 - MCW0264. On the Z-chromosome, a cluster of QTL affecting both eggshell breaking thickness and deformation was found within the marker interval ADL177-MCW0331. **Rosochacki *et al.* (2013)** cited that the reference population was based on two lines of chicken: Polish Green-Legged Partidgenous and Rohde Island Red characterized by big genetic differences (specific allele for GlP 19 and 28 for RIR) and phenotypic traits (laying and egg quality traits). Only four loci with the same alleles did not occur in RIR and GlP breeds (ADL244, LEI212, LEI075 and MCW157). Three alleles specific for GlP were observed in six loci (ADL180, ADL172, LEI074 and LEI121, MCW0134 and MCW0256), but in RIR populations these were found only in three loci (MCW133, MCW256 and ADL326).

4.2.5 QTL estimates and confidence intervals:

The flanking markers, position of QTL relative to the first marker (cM), F-ratio and significant for each QTL at chromosome-wise level along with the percentage of phenotypic variance explained by each QTL for egg traits are presented in Table 16. The position of QTL relative to the first marker indicated that QTL were located in the region of 61 to 322 cM, 128 to 189 cM, 76 to191 cM, 55 to 168 cM, 18 to 222 cM and 97 cM, for WFE, AFE, EW, EN, HU and EST, respectively. The

egg production and egg quality traits were evaluated in F_2 cross and the F-ratio for each QTL at chromosomal wise level indicated that a total of 15 significant QTL were detected and these QTL were distributed over four distinct regions on 5 chromosomes (Table 16), i.e. 15 significant QTL that affecting egg production and egg quality traits were located on five macro-chromosomes (chromosomes 2, 3, 4, 8 and Z). **Goraga *et al.* (2012)** cited that a genome-wide highly significant QTL for egg weight ($P < 0.01$) was identified on chromosome 4 at 154 cM and the search for multiple QTL in chromosome 4 region provided evidence for two QTL affecting egg weight (one QTL at 154 cM and a second QTL at 93 cM and the position of the highest peak of the egg weight QTL shifted from 154 cM to 93 cM). The genome-wide suggestive QTL for egg weight were mapped on chromosome 1 at 66–70 cM, chromosome 5 at 22–27 cM and chromosome 9 at 58–61 cM.

Goraga *et al.* (2012) stated that the most interesting result of multiple QTL region on chromosome 4 was between 19.2 and 82.1 cM. At least two QTLs in this region at 37.6 and 76.4 cM affected egg weight and a QTL at 58 cM affected the number of eggs. QTLs for egg weight were repeatedly discovered in a region between 59.9 and 82.8 cM **(Tuiskula-Haavisto *et al.*, 2002; Sasaki *et al.*, 2004)**. **Schreiweis *et al.* (2005)** also reported a QTL for egg weight between 62.1 and 75.8 cM in a cross between Broiler and White Leghorn; the favourable allele for egg weight came from the broiler strain. In a cross between Red Junglefowl and White Leghorn, a QTL for egg weight was identified on the same chromosome between 51.6 and 67.1 cM

Table 16. Flanking markers, position of QTL relative to the first marker (cM), F-ratios and significance of QTL at chromosome-wise level confidence interval at 95% (cM) for egg production and egg quality traits in phenotypic population of chickens along with the percentage of F_2 variance explained by each QTL

Trait / Chromosome	Flanking markers	Position of QTL relative to the first marker (cM)	F-ratio for each QTL at chromosomal wise level	Percentage of phenotypic variance explained by each QTL	Confidence interval at 95% (cM)
Weight at first egg (WFE):					
2	ADL0114 - MCW0056	322	11.6**	1.4	244-422
4	ADL0241 - MCW0180	156	38.9**	6.9	144-185
8	MCW0100 - ROS0075	61	11.1**	1.4	0-75
Z	LEI0111 – LEI0075	102	8.9*	1	60-127
Age at first egg (AFE):					
3	ADL0155 – MCW0004	189	7.55**	5	155-200
Z	ADL0201- MCW0241	128	21.9**	7.2	65-135
Egg number (EN):					
4	MCW0047 – ADL0266	55	7.5**	3.6	30-178
4	ADL0266 – MCW0170	168	7.4**	3.6	30-178
Z	MCW0241 – MCW0246	89	14.22*	5	15-95
Egg weight (EW):					
4	LEI0081- MCW0122	191	27.18**	13	185-198
Z	ADL0022 – MCW0154	76	20.11**	5.6	35-96
Haugh unit (HU):					
2	MCW0247 – ADL0217	89	10.33**	6.5	75-131
4	MCW0180 - MCW0129	222	6.48*	4.3	211-224
8	ADL0322 - MCW0095	18	5.99*	4.5	0-21
Eggshell thickness (EST):					
Z	MCW0154- LEI0254	97	13.33**	5	77-134

Total QTL detected = 15.

***significant linkage at $P \leq 0.05$ and ** significant linkage at $P \leq 0.01$.**

(Kerje *et al.*, 2003), with the allele for increasing weight inherited from the White Leghorn. While, **Goto *et al.* (2011)** reported that QTL for AFE was found in the region around 130 cM on chromosome one.

Tuiskula-Haavisto *et al.* (2002) reported linkage between 26 egg quality traits and 19 microsatellite loci on chromosomes 6-8 and three linkage groups, the QTL relating to shell shape was mapped to chromosome 8 at position 42 cM. Whilst, the QTL associated with egg numbers was linked to chromosome 8. The QTL accounted for Hugh units were found on chromosome 1 **(Hansen *et al.*, 2005)**. **Tuiskula-Haavisto *et al.* (2002)** confirmed the QTL on chromosome 2 for Hugh units, while **Rosochacki *et al.* (2013)** mapped Hugh unit QTL on chromosome 8 and 9 linkage groups. **Sasaki *et al.* (2004)** identified several QTL for eggshell thickness in chromosome 1. **Schreiweis *et al.* (2005)** showed two QTL regions on chromosomes 2 and nine QTL on chromosome 4 and these QTL were: egg color, egg and albumen weight, percent of shell, body weight and egg production, while earlier works had suggested that chromosome 4 may be a critical region significantly associated with the variety of traits across multiple resource populations **(Sewalem *et al.*, 2002; Tuiskula-Haavisto *et al.*, 2002; Sasaki *et al.*, 2004)**. **Rosochacki *et al.* (2013)** found QTL for shell thickness linked to chromosome 8 and linkage group 26 and there were several QTL found for all the measured egg production traits and most of the QTL are located on chromosomes 4 and Z. For egg production traits, a number of QTLs were distributed over chromosomes, such as the QTLs for

AFE on chromosomes 3 and Z, and for EW on chromosomes 2, 4 and Z **(Tuiskula-Haavisto *et al.*, 2004)**.

The QTL region on the Z chromosome was a large area including QTL for AFW, EW and EN as well as eggshell thickness. QTLs affecting egg number and egg weight were found in chromosomes 1, 2, 5, 6, 7, 8, 14, and Z **(Abasht *et al.*, 2006; Chatterjee *et al.*, 2008)**. If the microsatellite is very closely linked (about 20 cM) with a certain phenotype, it will specifically be observed in terms of a significant association, MCW0041, ADL0210, and MCW0110 microsatellites were significantly correlated with egg production up to a certain age ($P<0.05$). Sufficient polymorphic variation was not observed for MCW0014, MCW0049, LEI0089, and LEI0071, which could be one reason for the lack of association with growth and egg production traits.

The QTL effects were expressed as the percentages of phenotypic variance that are explained by each QTL and they were mostly of considerable importance ranging from 1 to 6.9 % of the phenotypic variation for WFE, from 5 to 7.2 % for AFE, from 5.6 to 13 % for EW, from 3.6 to 5 % for EN, from 4.3 to 6.5 % for HU and 5 % for EST (Table 16). The largest percentage of the phenotypic variation explained by a QTL was 13% for EW at 191 cM on chromosome 4.

Fine mapping can be performed for significant QTL to improve the precision of estimates of the QTL location. A common method is to increase marker density around the putative region. In fine mapping the marker interval is generally 1-3 cM. To reduce confidence intervals for a QTL and define its

location, the number of events of recombination becomes the limiting factor rather than the number of markers **(VanRaden and Weller, 1994)**.

For WFE, four significant QTL were located on chromosomes 2, 4, 8 and Z at position of 322, 156, 61 and 102 cM, respectively with 95% confidence intervals of 244-422, 144-185, 0-75 and 60-127 cM, respectively (Table 16). For AFE, two significant QTL were located on chromosomes 3 and Z at position of 189 and 128 cM, respectively with 155-200 and 65-135 cM of the 95% confidence interval. For EW, two significant QTL were located on chromosomes 4 and Z at positions of 191 and 76 cM, respectively with 95% confidence intervals of 185-198 and positions of 35-96 cM, respectively. For EN, three significant QTL were located on chromosomes 4 and Z (two QTL on chromosome 4 and one on Z sex chromosome) at positions of 55, 168 and 89 cM, respectively with 95% confidence intervals at 30-178 and 15-95 cM, respectively. Moreover, HU has three significant QTL was located on chromosomes 2, 4 and 8 at positions of 89, 222, and 18 cM, respectively, with 75-131, 211-224 and 0-21 cM of the 95% confidence intervals. For EST, one significant QTL was located on Z chromosome at positions of 97 cM, with 77-134 cM at 95% confidence interval. **Tuiskula-Haavisto *et al.* (2002)** stated that the 90% confidence interval for AFE was 65 to 137 cM on chromosome 3, while, it was 160 to 204 cM for EN on chromosome 4. **Honkatukia *et al.* (2005)** reported that the 90% confidence interval for the QTL location was broadened from the previous 58 cM to 64 cM despite the denser marker map.

4.2.6 Additive and dominance effects for QTL:

The estimates of additive and dominance effects (g) attributable to QTL for egg production and quality traits are given in Table 17. The QTL affecting WFE was found on chromosome 2, 4, 8 and Z. The additive effects attributable to QTL were 85 ±17.6, 830 ±44.8, 109 ±22.9 and 95 ±30.5 grams, QTL explained 1.4%, 6.9, 1.4% and 1% of the total phenotypic variance of the F_2 population, respectively. The dominance effects were 5 ±28.8, 164± 169.5, 36 ±46.9 and 15.4±8.5, respectively.

The QTL effects on AFE were found on chromosome 3 and Z, explaining 5% and 7.2% of the phenotypic variance, respectively (Table 16). The additive effects attributable to QTL were -2.5 ±1.1 and 2.77 ±0.6 day, while the dominance effect was 6.5 ±2.2 day for chromosome 3 and with no dominance effect for chromosome Z.

There are two QTL on chromosome 4 and chromosome Z influencing egg number and explained 7.2% and 5% of the phenotypic variance, respectively. The additive effect accounted for -6.5 ±1.9, -3.5±2.2 and -4.3± 1.3, while the dominance effects accounted for -0.9 ±2.3 and 14.3 ±4.5 for chromosome 4 and with no dominance effect for chromosome Z.

The QTL effects on egg weight detected on chromosomes 4 and Z, and explained 13% and 5.6% of the phenotypic variance, respectively. The additive effects of both QTL were 3.2 ± 0.5 and 1.5 ± 0.3 g, while the effects were -0.8±0.6 g of chromosome 4 with no dominance effect for chromosome Z.

Table 17. Estimates of additive and dominance effects (g) attributable to QTL and their standard errors (SE) for egg production and egg quality traits in F_2 population of chickens

Trait / Chromosome	Additive effect, g	SE	VP_a (%) [+]	Dominance effect, g	SE	VP_d (%) [++]
Weight at first egg (WFE), overall mean = 1567.0 ± 19.8						
2	85	17.6	5.4	5	28.8	0.3
4	830	44.8	53.0	164	169.5	10.5
8	109	22.9	7.0	36	46.9	2.3
Z	95	30.5	6.1	15.4	8.5	1
Age at first egg (AFE), overall mean =161.07 ± 0.49						
3	-2.5	1.1	1.6	6.5	2.2	4.0
Z	2.77	0.6	1.7	-	-	-
Egg Number (EN), overall mean = 79.27 ± 0.54						
4	-6.5	1.9	8.2	-0.9	2.3	1.1
4	-3.5	2.2	4.4	14.3	4.5	18.0
Z	-4.3	1.3	5.4	-	-	-
Egg weight (EW), overall mean = 49.44 ± 0.19						
4	3.2	0.5	6.5	-0.8	0.6	1.6
Z	1.5	0.3	3.0	-	-	-
Haugh unit (HU), overall mean = 78.6 ± 1.05						
2	-4.9	1.8	6.2	-3.5	3.3	4.5
4	1.9	0.6	2.4	-3.1	1	3.9
8	-0.5	0.6	0.6	4.2	1.1	5.3
Egg shell thickness (EST), overall mean = 0.27 ± 0.01						
Z	-0.15	0.04	55.6	-	-	-

[+]VP_a (%) = Percentage of additive variance explained by each QTL.

[++]VP_d (%) = Percentage of dominance variance explained by each QTL.

The QTL was detected at the end of chromosome Z for EST and explained 5 % of total phenotypic variance. The additive effect was −0.15 ± 0.04, with no dominance effect (Table 17).

The QTL for Hu was detected on chromosomes 2, 4 and 8 and explained 6.5%, 4.3% and 4.5% of the total phenotypic variance of the F_2 population. The additive effects were −4.9 ± 1.8, 1.9 ± 0.6 and -0.5 ± 0.6,, while the dominance effects were -3.5 ± 3.3, -3.1 ± 1 and 4.2 ± 1.1, respectively.

Tuiskula-Haavisto *et al.* (2002) found that a genome wide significant QTL affecting HU at 40 and 60 weeks was detected on chromosome 2, the RIR allele has an additive effect of −5.3 ± 1.2 and -8.6±2.1 that QTL explains 7% and 5% of the total phenotypic variance of the F_2 population, respectively. **Honkatukia *et al.* (2005)** reported that the additive effect of the Rhode Island Red (RIR) allele was –3.73 for HU (± 0.80), while the dominance effect was –1.74 HU (± 1.51) and the detected QTL explained 6.7% of the phenotypic variance. **Goraga *et al.* (2012)** reported that the QTL at 93 cM had dominance effects from 1.51 to 1.99 on egg weights, while the additive effect of the QTL at 154 cM was from 1.93 to 2.40. The QTL affecting number of eggs on chromosome 7 had additive effect, while the QTL had dominance effects on chromosomes 4 and 5.

In general, QTL mapping of the present study for egg production and egg quality traits are in agreement with the previous studies that have identified numerous QTL affecting these traits **(Koerhuis and McKay 1996; Poggenpoel *et al.*,**

1996; Chatterjee *et al.*, 2000; Tsuiskula-Haavisto *et al.*, 2002; Hocking *et al.*, 2003 and Wardecka *et al.*, 2003).

4.2.7 Total variances explained by QTL in egg trait:

The total variances explained by QTL for each egg trait were 10.7, 12.2, 18.6, 12.2, 15.3 and 5 % in WFE, AFE, EW, EN, HU and EST, respectively (Table 18). Across the traits studied, a total of four significant QTL were detected at a 5 % chromosome-wise significance level, while a total of 11 significant QTL were detected at 1 % genomic-wise significance level (Table 18). The whole genome scan for detection and localization of QTL affecting egg quality traits were described by **Tuiskula-Haavisto *et al.* (2002),** who found 14 chromosomal areas affecting egg quality at 1% genome-wise significance level, while at 5% level only 6 suggestive QTL were found. Another whole genome scan for age at sexual maturity, Haugh units and shell thickness was done by **Wardęcka *et al.* (2002; 2003),** in Green-legged Partridgenous Polish chickens (GLP), and in a highly productive stock of RIR. **Goraga *et al.* (2012)** found that the phenotypic F_2 variance for egg weights in the early and late production periods explained by the QTL at 93 cM and 154 cM ranged from 4.9 to 7.1% and 12.3 to 16.1%, respectively. These QTL explained 4.3–5.9% of the phenotypic F_2 variance of egg weight and the QTL allele contributed to early age at first egg explained 6.5% of the phenotypic F_2 variance.

Table 18. Number of significant QTL at the 5 and 1% chromosome-wise levels and genome-wise level for each trait in F_2 cross

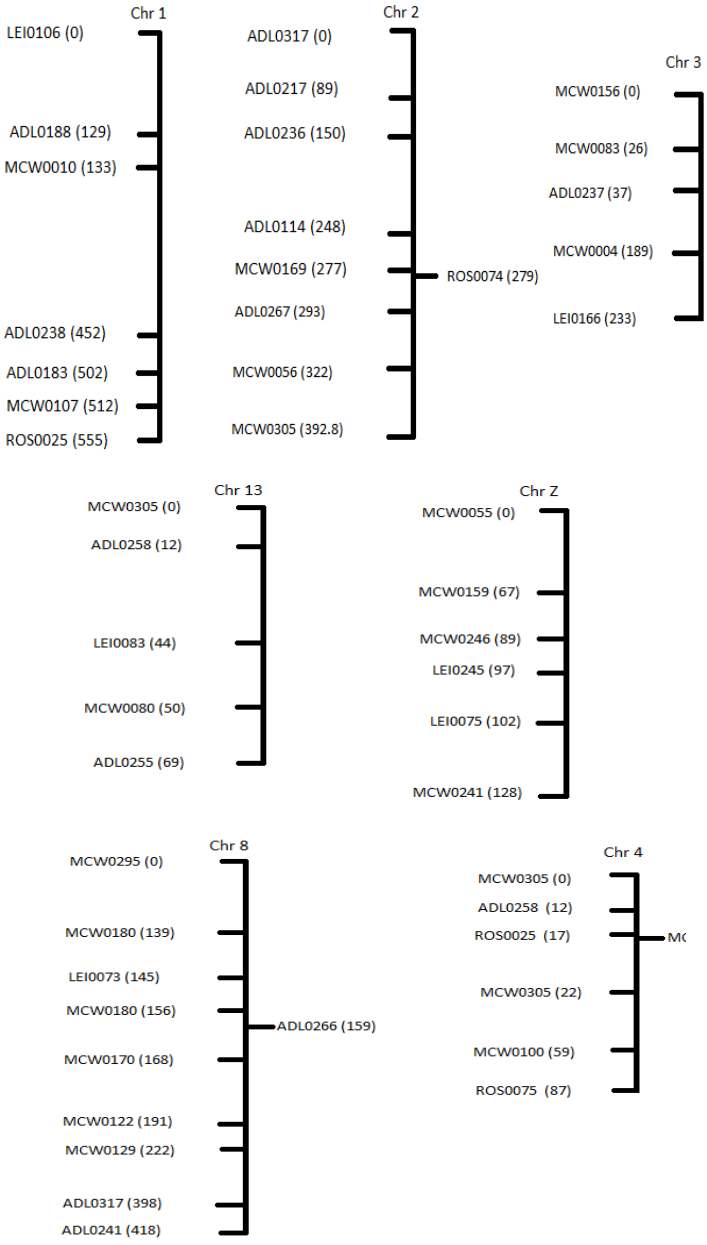
Trait	Chromosome-wise level		Genome-wise level		Variance (%) [+]
	5%	1%	5%	1%	
WFE	1	-	-	3	10.7
AFE	-	-	-	2	12.2
EN	1	-	-	2	12.2
EW	-	-	-	2	18.6
HU	2	-	-	1	15.3
ES	-	-	-	1	5
Total	4	-	-	11	-

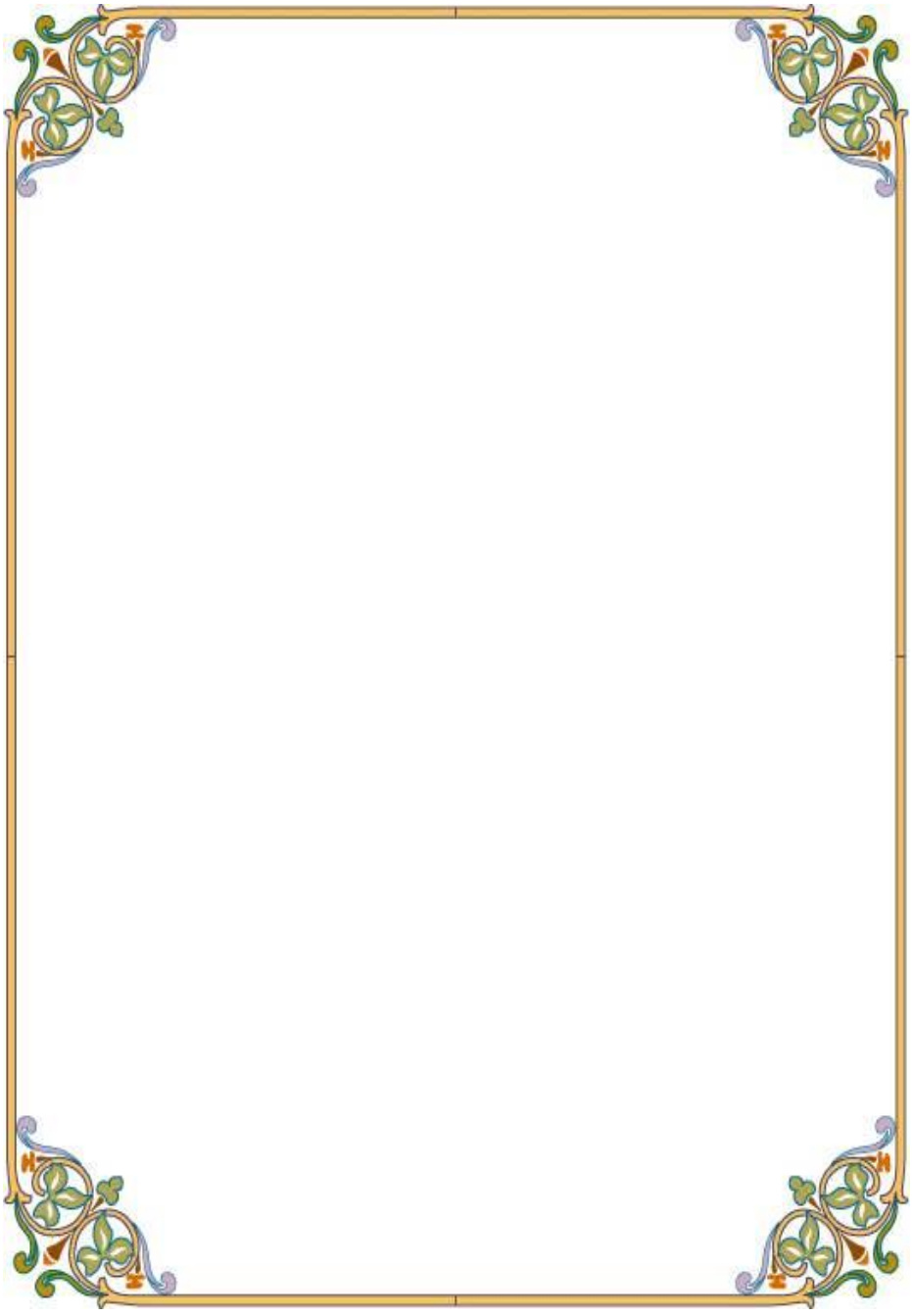
[+] The sum of the total variances explained by the QTL in each trait.

4.3 Linkage map of growth and egg traits:

The chromosomal map for detecting growth and egg traits in F_2 population was presented in Figure 1. In Figure 1, the linkage map for quantitative trait loci analysis was illustrating the positions and names of the markers.

Figure 1. Chromosomal map used for detection growth and egg traits.





5. SUMMARY

The experimental work of this study was carried out at the Poultry Research Farm, Department of Animal Production, Faculty of Agriculture, Benha University, Egypt, started in March 2008 and terminated in October 2010. Number of 1500 eggs from White Leghorn and 300 eggs from Golden Montazah were chosen randomly and came from El-Takamoly chicken project, Alazab, El-Fayoum Governorate, Egypt. These eggs were incubated and hatched in the laboratory of Poultry Research Farm, Benha University, Egypt. The F_2 chicken population was developed by crossing a broiler males of strain Golden Montazah (GM) with a layer females of White Leghorn breed (WL). A total number of 18 cockerels and 180 pullets were chosen randomly from the GM strain and WL breed, respectively. Each cock was mated with 10 hens housed in separately breeding pen to produce F_1 crossbred (½GM½WL), consequently inter-se matings were practiced for two generations to produce F_2 with the genetic structure of $(½GM½WL)^2$. Also, purebreds from the two populations were produced. The pedigreed eggs from each individual breeding pen for the four mating groups, two foundations of GM and WL, two crossbreds of (½GM½WL) and $(½GM½WL)^2$ were collected daily for fifteen days and then incubated. The studied traits were the phenotyping of growth, egg production and egg quality traits in the parental and F_2 generations in such crossbreeding program. The F_2 population was used to detect and localize QTL affecting

growth and egg production and egg quality traits at different ages using specific microsatellite markers.

First: Growth traits:

Quantitative trait loci (QTL) for body weights (BW) at 4, 8, 12, 16 weeks of age and daily gains (DG) at intervals of 0-4, 4-8, 8-12 and 12-16 weeks were identified in F_2 crossbred population. Phenotypic data were analyzed using multi-traits animal model including the genetic group, sex and hatch as fixed effects and the additive genetic and common environmental effects as random effects. After parentage checking and F_2 genotyping, data of F_2 were genotyped using 43 genetic markers in nine autosomal linkage groups, Z chromosome and the genotypes were used for QTL analysis. A mixed model included the sex and hatch as fixed effects along with the additive and dominance effects of QTL as random effects were used for QTL analysis.

Results obtained in this study could be summarized as follows:

1) The overall performance of the crossbred chickens of (1/2GM1/2WL) and $(1/2GM1/2WL)^2$ was found to be better than local chickens of GM.
2) The estimate of heritability in $(½GM½WL)^2$ for BW at hatch was higher than that at later ages except (at 12 weeks). The estimates are 0.51 for BW0, 0.52 for BW12 and 0.43 for BW16. The largest estimate for DG is 0.51 for DG812, 0.46 for DG04, 0.45 for DG48 and 0.47 for DG1216.

3) The genotypic and phenotypic correlations between growth traits in the F_2 population in the QTL analysis were high positive correlations between each two growth traits.
4) The total chromosomal map length was 1901 cM ranging from 25 cM on chromosome 11 to 568 cM on chromosome 1, with an average marker spacing of 24.39 cM and that ranging from 7.8 cM on chromosome 8 to 24.3 cM on chromosome 1.
5) The flanking markers, position of QTL relative to the first marker (cM), F-ratio and significant for each QTL at chromosome-wise level along with the proportion of phenotypic variance explained by each QTL for body weights and daily gains in weight.
6) The position of QTL relative to the first marker (cM) indicated that QTL were located in the region of 0 to 502 cM, 0 to 233 cM, 0 to 179 cM and 12 to 555 cM for body weights at 4, 8, 12 and 16 weeks of age, respectively. For daily gains, the position of QTL relative to the first marker (cM) indicated that QTL were located in the region of 67 to 452 cM, 0 to 436 cM, 26 to 512 cM and 17 cM for daily gain intervals at 0-4, 4-8, 8-12 and 12-16 weeks, respectively.
7) For body weights evaluated in F_2 cross, a total of 34 QTL were detected and these QTL were distributed over five distinct regions on 10 chromosomes. A total of 19 genome significant QTL that affecting body weight were located on seven macro-chromosomes (chromosomes 1,

2, 3, 4, 6, 8 and Z) and one micro-chromosome (chromosome 11). There was statistical evidence for two QTL on chromosome 4 for body weight at 8 and 12 weeks of age. A further 15 suggestive QTL were identified for body weight at different ages on chromosomes 2, 6, 9 and 13.

8) For daily body gains (DG), a total of 14 QTL were detected. These QTL were distributed over 7 distinct regions on 6 chromosomes. A total of 11 genome significant QTL that affected daily gain were located on five macro-chromosomes (1, 2, 3, 4 and 8). There was statistical evidence for two QTL on chromosome 4 for daily gains at 0-4, 4-8 and 8-12 weeks of age. A further three suggestive QTL were identified for daily gain at DG4-8 and DG0-4 on chromosomes 1, 8 and 13.

9) For confidence intervals of 4-week body weight, four significant QTL were located on chromosomes 2, 4, 6 and 11 at position of 292, 145, 29 and 0 cM, respectively, in which 95% confidence intervals were 43–367, 12–183, 0-42 and 0-10 cM, respectively. For 8-week body weight, another significant QTL was located on chromosomes 1, 3, 4, 11 and Z sex chromosome at position of 128 , 48, 0, 159, 0 and 117 cM, respectively with 76-219, 14-219, 0-69, 140-183, 0-57 and 14-127 cM of the 95% confidence interval. For 12-week body weight, six significant QTL were located on chromosomes 1, 3, 4, 8 and Z sex chromosome at position of 133, 37, 0, 179, 59 and 120 cM respectively, in which 95% confidence intervals were

67-227, 155-183, 0-177, 155-183, 12 and 8-127 cM, respectively. Moreover, at 16-week body weight significant QTL for was located on chromosomes 4, 8 and Z sex chromosome at position of 139, 12, and 125 cM, respectively, with 19-169, 0-86 and 0-125 cM of the 95% confidence intervals.

10) The largest proportion of the phenotypic variation explained by a QTL was 13.8% for 12-week body weight at 179 cM on chromosome 4. The proportions of phenotypic variation explained by significant and suggestive QTL for body weight at 4, 8, 12 and 16 weeks were 21.1, 30.8, 29.3 and 25.4%, respectively, while the proportions explained by significant and suggestive QTL for daily gain 0-4, 4-8, 8-12 and 12-16 weeks were 25.9, 29.1, 9.35 and 3.9%, respectively. The largest proportion of the phenotypic variation explained by a QTL was 8.88% for DG 4-8 week at 428 cM on chromosome 4.
11) The additive effects detected in the study showed positive values, as expected, while the dominance effects were generally negative or not significant with the exception of body weight at 4, 8, 12 and 16 weeks of age (QTL on chromosomes 2, 3, 4, 8, 11 and Z). The largest additive effect (369.6 ± 64.6 g) was for QTL of body weight at 16 weeks of age on chromosome 4 at 179 cM. The largest dominance effect (−188.1 ± 55.0 g) was for a QTL of body weight at 16 weeks on chromosome 4 at 139 cM.
12) The percentage of additive variance explained by each QTL for body weights ranged from 2.6% to 24.8%.

While, the percentage of dominance variance ranged from -12.8 % to 15.7%.

13) The estimates of the additive effects explained by QTL were positive and of moderate magnitude ranging from 1.20 g on chromosome 2 to 1.77 g on chromosome 4 for DG 0-4 weeks, from 1.39 g on chromosome 1 to 3.89 g on chromosome 4 for DG 4-8 weeks, from 1.38 g on chromosome 2 to 3.84 g on chromosome 4 for DG 8-12 weeks and 1.21 g on chromosome 8 for DG 12-16 weeks. On the other hand, the estimates of dominance effects attributable to QTL were mostly negative, i.e. nine estimates out of 14 QTL were negative. The smallest dominant effect was recorded on chromosome 3 for DG 8-12 week (-2.09 g), while the largest dominant effect was recorded on chromosome 4 for DG 4-8 week (1.44 g).
14) The percentage of additive variance explained by each QTL for daily gains ranged at different intervals from 6.8% to 34.3%. While, the percentage of dominance variance ranged from -14.8 % to 12.7%.

Second: Egg traits:

Quantitative trait loci (QTL) affecting age at first egg (AFE), weight at first egg (WFE), 120-days of egg number (EN), egg weight (EW), Hugh unit (HU) and eggshell strength (ESS) were identified in F_2 crossbred population. Phenotypic data of egg traits were analyzed using multi-traits animal model including the effects of genetic group, year-month of laying and hatch as fixed effects and the additive genetic and permanent

environmental effects as random effects. After parentage checking and F_2 genotyping, data of F_2 were genotyped using 45 genetic markers in nine autosomal linkage groups and Z chromosome and these genotypes were used for QTL analysis. For QTL analysis a mixed model included the fixed effects of hatch along with the additive and dominance effects of QTL as random effects were used.

Results obtained in this study could be summarized as follows:

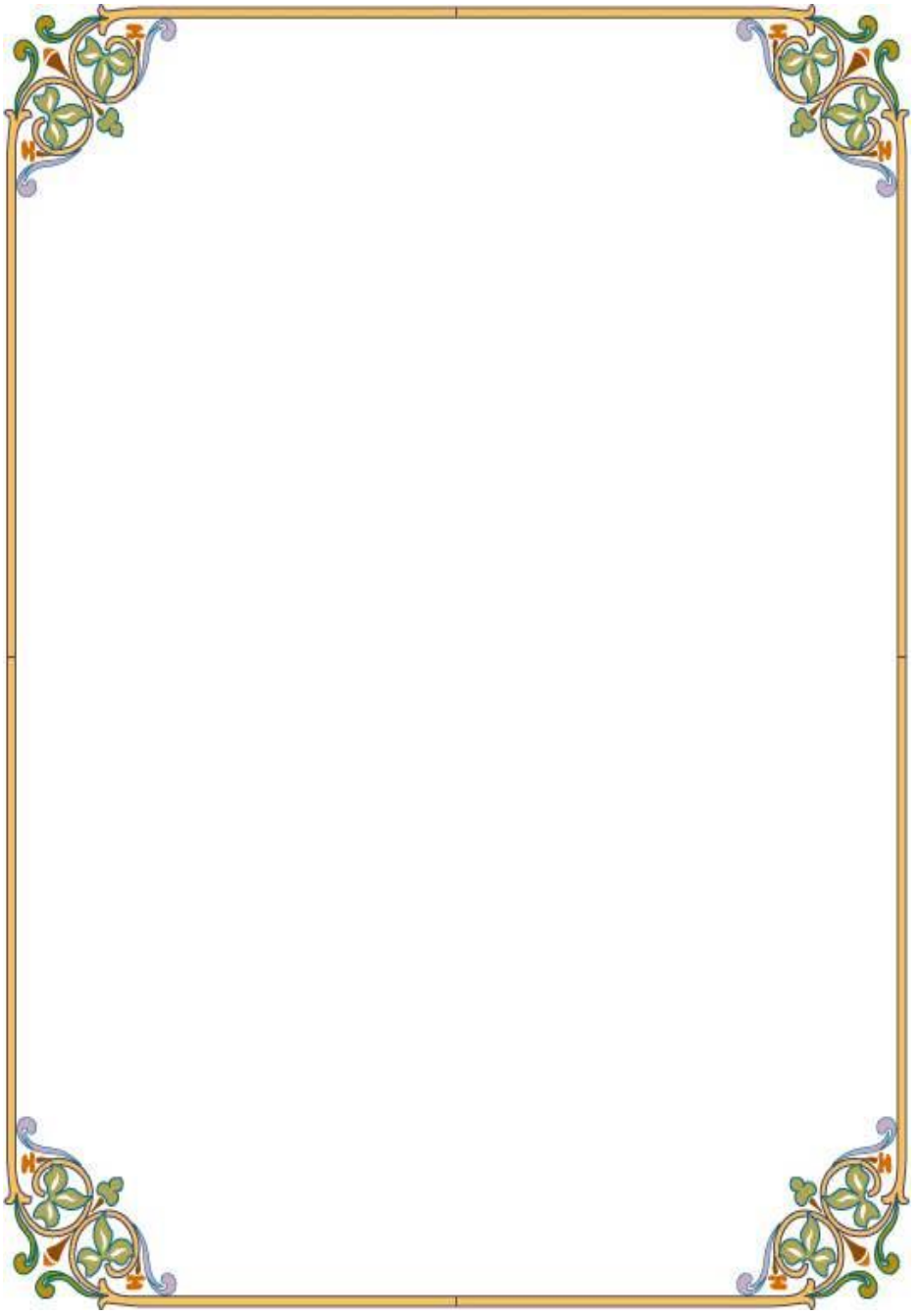
1) The crossbreds were superior for egg production traits than purebreds. In general, results in the present study indicated that growth and egg production traits in local chickens in Egypt could be improved by crossbreeding.
2) For egg production and egg quality traits total chromosomal map length was 1949 cM ranging from 52 cM on chromosome 11 to 542 cM on chromosome 1, with an average marker spacing of 43.3 cM and that ranging from 15.3 cM on chromosome 4 to 71.5 cM on chromosome 6.
3) For confidence intervals of WFE, four significant QTL were located on chromosomes 2, 4, 8 and Z sex chromosome at position of 322, 156, 61 and 102 cM, respectively, in which 95% confidence intervals were 244-422, 144-185, 0-75 and 60-127 cM, respectively.
4) For AFE, two significant QTL was located on chromosomes 3 and Z sex chromosome at position of 189 and 128 cM, respectively with 155-200 and 65-135 cM of the 95% confidence interval.

5) The additive effect is −4.9 ± 1.8, 1.9 ± 0.6 and -0.5 ± 0.6 HU on chromosome 2, 4 and 8, QTL explains 6.5%, 4.3% and 4.5% respectively of the total phenotypic variance of the F_2 population. For dominance effect is -3.5 ± 3.3, -3.1 ± 1 and 4.2± 1.1 HU.
6) The ES a QTL at the end of the chromosome Z was detected. The additive effect was −0.15 ± 0.04 that explains 5% of the total phenotypic variance. The confidence interval ranged from 77 to 134 cM with no dominance effect.
7) A QTL affecting WFE was found on chromosome 2, 4, 8 and Z. The additive effect is 85±17.6g, 830±44.8g, 109±22.9g and 95±30.5g, QTL explains 1.4%, 6.9%, 1.4% and 1% respectively of the total phenotypic variance of the F_2 population. For dominance effect is 5±28.8, 146±169.5, 36±46.9 and 15.4±8.5 respectively.
8) QTL effects on egg weight were found on the chromosome 4 and Z, explaining 13% and 5.6%, of the phenotypic variance, respectively. The additive effect is 3.2±0.5 g and 1.5±0.3 g. For dominance effect is -0.8 ±0.6 g of chromosome 4 and with no dominance effect for chromosome Z.
9) QTL affecting egg number were found in the chromosome 4 and Z. There are two QTL on chromosome 4 explaining 7.2% of the phenotypic variance and 5% for chromosome Z. The additive effect is -6.5 ±1.9, -3.5±2.2 and -4.3± 1.3. For dominance effect is -0.9 ±2.3 and 14.3

±4.5 of chromosome 4 and with no dominance effect for chromosome Z.

10) QTL effects on AFE were found on the chromosome 3 and Z, explaining 5% and 7.2%, of the phenotypic variance, respectively. The additive effect is -2.5 ±1.1 and 2.77 ±0.6 day. For dominance effect is 6.5±2.2 day of chromosome 3 and with no dominance effect for chromosome Z.

11) The QTL effects expressed as the percentage of phenotypic variance is explained by each QTL were mostly of considerable importance ranging from 1 to 6.9 % of the phenotypic variation for WFE, from 5 to 7.2 % for AFE from 5.6 to 13 % for EW, from 3.6 to 5 % for EN, from 4.3 to 6.5 % for HU and 5 % for ES. The largest proportion of the phenotypic variation explained by a QTL was 13% for EW at 191 cM on chromosome 4. The proportions of phenotypic variation explained by significant and suggestive QTL for WFE, AFE, EW, EN, HU and ES were 10.7, 12.2, 18.6, 12.2, 15.3 and 5%, respectively.



6. CONCLUSIONS

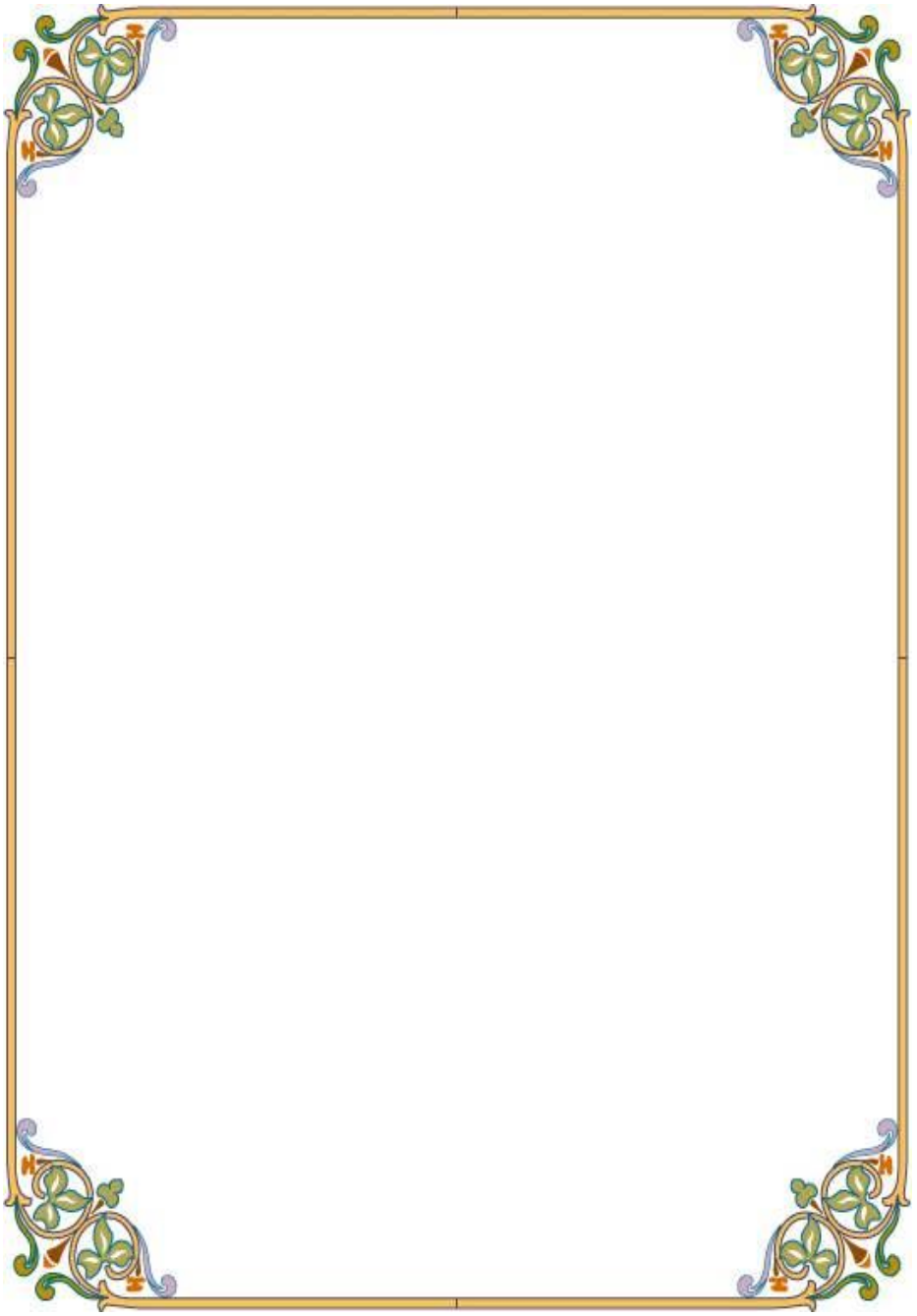
1) Significant QTL for body weight detected on chromosomes 1, 2, 3, 4, 6, 8, 11 and Z concluded that there are different sets of genes affecting early and late body weight.

2) Significant QTL for egg production and egg quality traits detected on chromosomes 2, 3, 4, 8 and Z concluded that there are different sets of genes affecting egg production and egg quality traits.

3) A single-QTL model used was of considerable importance to detect QTL for egg traits in chickens. Different QTL locations in the same chromosome were observed on several chromosomes. Further analysis using multi-trait QTL model might confirm these approaches of QTL.

4) The present genome wide QTL mapping in F_2 populations lays the foundation for identifying the DNA variants that are responsible for variation in growth traits in chickens. To utilize these results for further identifying causative functional genes or using Marker Assisted Selection (MAS) for animal improvement, fine-mapping QTL needs to be detected before further efforts are made.

5) It is not very easy at this moment to look for candidate genes in the regions with QTL. The most important reason is that the QTL regions are still too large. The confidence intervals for all of the significant QTL have to be reduced by fine mapping in the further generations with larger numbers of DNA markers than used so far.



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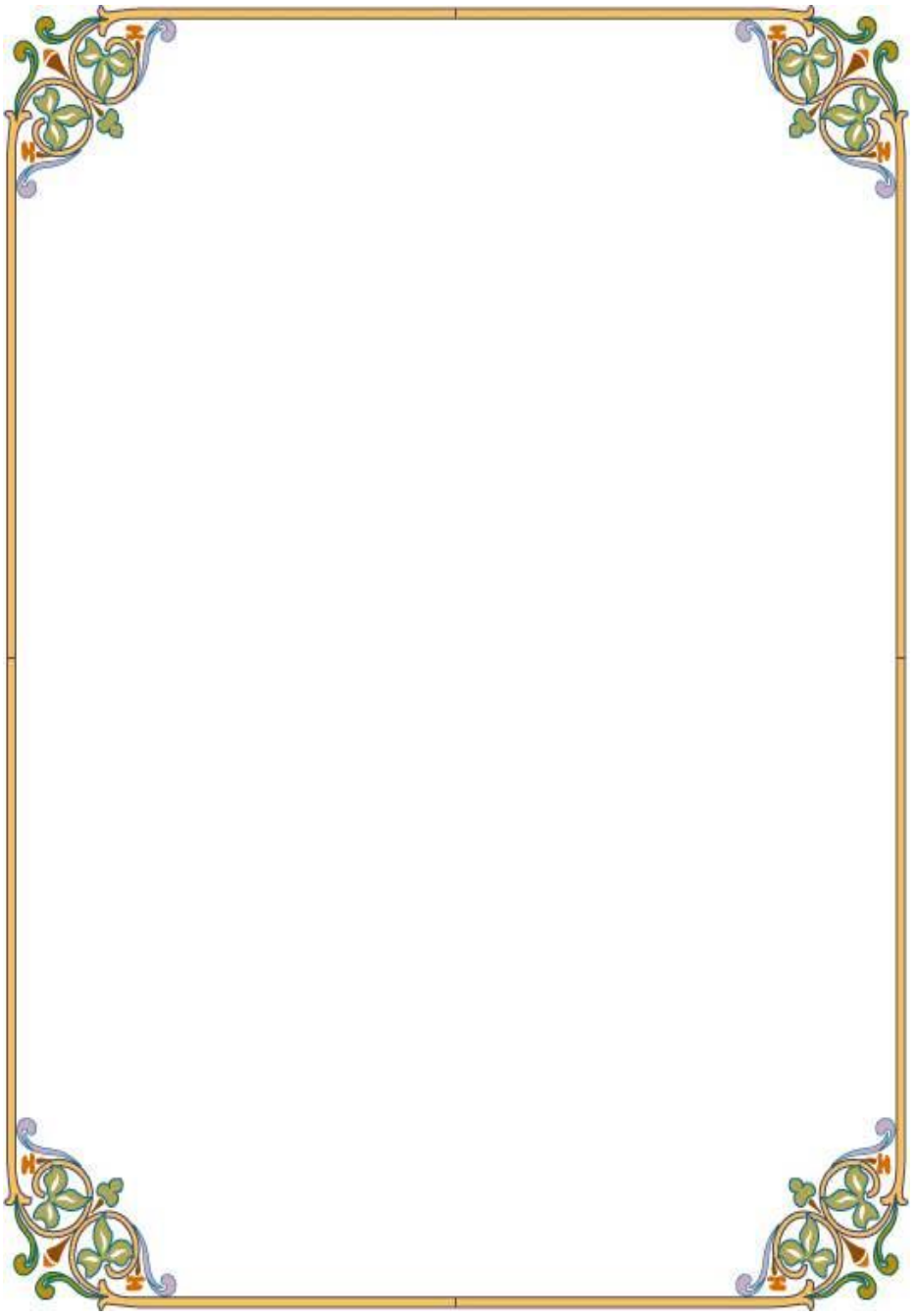


الملخص العربي

أجريت التجربة محل الدراسة بمزرعة بحوث الدواجن- قسم الإنتاج الحيواني – كلية الزراعة – جامعة بنها ، خلال الفترة من مارس 2008 حتي أكتوبر 2010حيث تم تجميع 1500 بيضة من سلالة اللجهورن الأبيض ، 300 بيضة من سلالة المنتزه الذهبي عشوائياً من مشروع الدجاج التكاملي – العزب – محافظة الفيوم – مصر. تم تحضين وتفريخ البيض بمعمل مزرعة بحوث الدواجن- قسم الإنتاج الحيواني – كلية الزراعة – جامعة بنها – مصر. أنتج قطيع الجيل الثاني F_2 عن طرق خلط ذكور سلالة المنتزه الذهبي (GM) مع إناث سلالة اللجهورن الأبيض (WL). تم إختيار 18 ديك ، 180 دجاجة عشوائياً من سلالة GM ، WL علي التوالي حيث تم تخصيص ديك لكل 10 دجاجات في عش منفصل لإنتاج قطيع الجيل الأول (½GM½WL) ثم تزاوج ذكور وإناث الجيل الأول مع بعضهما لإنتاج الجيل الثاني $(½GM½WL)^2$ وكذلك تم إنتاج الأفراد النقية لكلا من السلالتين. تم تجميع البيض المنسب من كل عش تزاوج للاربعة مجموعات الوراثية (GM، WL، (½GM½WL) ، $(½GM½WL)^2$) يومياً ولمدة خمسة عشر يوماً ثم تفريخه بعد ذلك. تم دراسة الصفات المظهرية لصفات النمو وإنتاج البيض وصفات جودة البيض في قطعان الآباء والجيل الثاني. كشف وتحديد مواقع الصفات الكمية المؤثرة علي صفات النمو وإنتاج وجودة البيض في الأعمار المختلفة في قطيع الجيل الثاني بإستخدام الواسمات الوراثية المتخصصة.

أولاً.. صفات النمو:

تم تحديد مواقع الصفات الكمية Quantitative trait loci (QTL) المؤثرة علي وزن الجسم عند عمر 4، 8، 12، 16 أسبوع وكذلك الزيادة اليومية خلال الفترات صفر-4، 4-8، 8-12، 12-16 أسبوع في قطيع الجيل الثاني. وتم تحليل البيانات المظهرية بإستخدام نموذج الحيوان متعدد الصفات (Multi-traits animal model) المشتمل على تأثير المجاميع الوراثية، الجنس، تاريخ الفقس كتأثيرات ثابتة والتأثيرات الوراثية التجمعية والتأثيرات البيئية المشتركة كتأثيرات عشوائية. إستخدمت 43 من الواسمات الوراثية لتوصيف التركيب الوراثي لقطيع الجيل الثاني في تسعة من مجاميع الارتباط علي الكروموسومات الجسمية والكروموسوم الجنسي Z . إستخدم التركيب الوراثي في تحليل مواقع الصفات الكمية بإستخدام النماذج المختلطة Mixed Model المشتمل على تأثير الجنس وتاريخ الفقس كتأثيرات ثابتة والتأثيرات التجمعية والسيادية لمواقع الصفات الكمية Additive and dominance effects of QTL كتأثيرات عشوائية. **ويمكن تلخيص النتائج في النقاط التالية:**

1- كان الأداء الكلي للدجاج الخليط (½GM½WL) ، $(½GM½WL)^2$ أفضل من أداء سلالة المنتزة الذهبي (المحلي).
2- كان تقدير المكافئ الوراثي لصفة وزن الجسم عند الفقس في خليط $(½GM½WL)^2$ أعلي من التقديرات عند الأعمار المختلفة ماعدا عند عمر 12 أسبوع حيث كانت قيم المكافئ الوراثي لأوزان الجسم هي 0.51 عند الفقس، 0.52 عند 12 أسبوع ، 0.43 عند 16

أسبوع من العمر. بينما كانت اعلي التقديرات للمكافئ الوراثي لمعدل الزيادة اليومية هي 0.51 للفترة من 8 إلي 16 أسبوع من العمر، 0.46 للفترة من الفقس حتي أربعة اسابيع من العمر، 0.45 للفترة من 4 إلي 8 أسابيع من العمر ، 0.47 للفترة من 12 حتي 16 أسبوع من عمر الطائر.

3- كان الإرتباط الوراثي والمظهري في قطيع الجيل الثاني إرتباطا ايجابيا عاليا بين كل صفة من صفات النمو(وزن الجسم ومعدل الزيادة اليومية).

4- كان المجموع الطولي للخريطة الكرومسومية 1901 سنتي مورجان (cM) حيث تراوحت من 25 cM علي الكروموسوم رقم 11 إلي 568 cM علي الكروموسوم رقم 1 بمتوسط مسافة بين الواسمات 24.39 cM بتراوح مقداره 7.8 cM علي الكروموسوم رقم 8 إلي 24.3 cM علي الكروموسوم رقم 1 .

5- أوضحت مواقع الصفات الكمية نسبة إلي الواسمة الوراثية الأولى أنها تقع في المناطق من صفر إلي 502 cM ، صفر إلي 233 cM ، صفر إلي 179 cM ، 12 إلي 555 cM لوزن الجسم عند أعمار 4، 8، 12 ، 16 أسبوع علي التوالي. بينما كانت 67 إلي 452 cM ، صفر إلي 436 cM ، 26 إلي 512 cM ، 17 cM لمعدل الزيادة اليومية عند فترات 0-4 ، 4-8 ، 8-12 ، 12-16 أسبوع من العمر علي التوالي.

6- تم تحديد مواقع الصفات الكمية المؤثرة علي صفة وزن الجسم في خليط الجيل الثاني حيث وجد أن مجموع المواقع الكمية المؤثرة علي

هذة الصفة 34 موقعا موزعة علي خمس مناطق مختلفة علي عشرة من الكروموسومات. تسعة عشر موقعا منها ذات تأثير معنوي Significant QTL علي وزن الجسم تقع علي سبع من الكروموسومات الكبرى أرقام 1 ، 2 ، 3 ، 4 ، 6 ، 8 ، Z وواحد علي الكروموسوم الصغرى رقم 11 مع التأكيد على أن هناك موقعان للكرموسوم رقم 4 مؤثران علي صفة وزن الجسم عند عمر 8 ، 12 أسبوع. كما تم التعرف علي 15 موقعا محتملا Suggestive QTL لصفة وزن الجسم للأعمار المختلفة علي الكروموسومات أرقام 2 ، 6 ، 9 ، 13 .

7- تم تحديد 14 موقعا للصفات الكمية المؤثرة علي معدل الزيادة اليومية موزعة علي 7 مناطق مختلفة علي تسعة من الكروموسومات. أحدي عشر موقعا منها ذات تأثير معنوي علي معدل الزيادة اليومية تقع علي 5خمس من الكروموسومات الكبرى أرقام 1 ، 2 ، 3 ، 4 ، 8. كما والكرموسوم رقم 4 به موقعان مؤثران علي معدل الزيادة اليومية في الفترات صفر -4، 4-8 ، 8-12 أسبوع من العمر. كما تم التعرف علي ثلاثة من المواقع المحتملة لمعدل الزيادة اليومية في الفترات من صفر -4 ، 4-8 علي الكروموسومات أرقام 1 ، 8 ، 13 .

8- وجد اربعة مواقع كمية معنوية لوزن الجسم عند عمر 4 أسابيع تقع علي الكروموسومات 2 ، 4 ، 6 ، 11 تقع على المناطق 292 ، 145 ، 29 ، 0 cM علي التوالي وعند حدود ثقة 95 % وكانت على مسافات كرموسومية هي 43-367 ، 12-183 ، 0-42 ، 0-10 cM علي التوالي. بينما كانت المواقع الكمية المعنوية الأخري

لوزن الجسم عند 8 أسابيع من العمر علي الكروموسومات 1 ، 3 ، 4 ، 11 والكروموسوم الجنسي Z والتي وقعت المناطق 128 ، 48 ، 0 ، 59 ، 0 ، 117 cM علي التوالي وعند حدود ثقة 95 % على المسافات الكرموسومية 219-76 ، 219-14 ، 69-0 ،183-140 ، 57-0 ، 127-14 cM. ووجد هناك 6 مواقع كمية معنوية لوزن الجسم عند عمر 12 أسبوع تقع علي الكروموسومات 1 ،3 ، 4 ، 8 ، Z وعلي المناطق 133 ، 37 ، 0 ، 179 ، 59 ، 120 cM علي التوالي وعند حدود ثقة 95 % كانت 227-67 ، 183-155 ، 177-0 ، 183-155 ، 12 ، 127-8 cM علي التوالي. وعند عمر 16 أسبوع وجد أن المواقع الكمية المعنوية علي الكروموسومات 4 ، 8 والكروموسوم الجنسي Z علي المناطق 139 ، 12 ، 125 cM و عند حدود ثقة 95 % كانت 169-19 ، 86-0 ، 125-0 cM.

9- كانت أعلي نسبة للتباين المظهري للمواقع الكمية هي 13.8 % لوزن الجسم عند 12 أسبوع عند 179 cM علي الكروموسوم 4 . و كانت نسب التباين المظهري للمواقع الكمية المعنوية المحتملة لوزن الجسم عند عمر 4 ، 8 ، 12 ، 16 أسبوع هي 21.1 ، 30.8 ، 29.3 ، 25.4 % علي التوالي. بينما كانت لمعدل الزيادة اليومية عند فترات صفر-4 ، 4-8 ، 8-12 ، 12-16 أسبوع هي 25.9 ، 29.1 ، 9.35 ، 3.9 علي التوالي حيث كانت أعلي نسبة للتباين المظهري للمواقع الكمية المؤثرة علي معدل الزيادة اليومية هي 8.88

% لمعدل الزيادة اليومية من 4-8 أسابيع عند المنطقة 428 cM علي الكروموسوم 4 .

10- كانت تقديرات الأثر التجمعي موجبة كما هو متوقع بينما كانت أغلب تقديرات الأثر السيادي سالبة وغير معنوية عدا وزن الجسم عند عمر 4 ، 8 ، 12 ، 16 أسبوع للمواقع الكمية علي الكروموسومات 2 ، 3 ، 4 ، 8 ، 11 ، Z . كان أعلي تقدير للأثر التجمعي (369.6 ± 64.6 جم) لوزن الجسم عند 16 أسبوع علي الكروموسوم رقم 4 عند 179 cM ، وكان أعلي تقدير للأثر السيادي (-188.1 ± 55 جم) لوزن الجسم عند عمر 16 أسبوع علي الكروموسوم 4 عند 139 cM.

11- كانت نسبة تباين الأثر التجمعي لكل موقع كمي لوزن الجسم تتراوح من 2.6 % إلي 24.8 % ، بينما كانت نسبة تباين الأثر السيادي تتراوح من -12.8 إلي 15.7 %.

12- كانت تقديرات الأثر التجمعي للمواقع الكمية موجبة ومتوسطة وتتراوح من 1.2 جم علي الكروموسوم رقم 2 إلى 1.77 جم علي الكروموسوم رقم 4 لمعدل الزيادة اليومية 0-4 أسابيع، ومن 1.39 جم علي الكروموسوم رقم 1 إلي 3.89 جم علي الكروموسوم رقم 4 لمعدل الزيادة اليومية 4-8 أسابيع، ومن 1.38 جم علي الكروموسوم رقم 2 إلي 3.84 جم علي الكروموسوم رقم 4 لمعدل الزيادة اليومية 8-12 أسبوع ومن 1.21 جم علي الكروموسوم رقم 8 لمعدل الزيادة اليومية 12-16 أسبوع. من ناحية أخري كانت معظم التقديرات للأثر السيادي سالبة حيث كان هناك 14 موقعا ذات أثر سياديا سالبا.

وكانت أصغر قيمة سجلت للأثر السيادي علي الكروموسوم رقم 4 لمعدل الزيادة اليومية 4-8 أسابيع (1.44 جم).

13- كانت نسبة تباين الأثر التجمعي لكل موقع كمي لصفات معدل الزيادة اليومية تتراوح من 6.8 % إلي 34.3 % ، بينما كانت نسبة تباين الأثر السيادي تتراوح من -14.8 إلي 12.7 %.

ثانياً: صفات البيض:

تم تحديد مواقع الصفات الكمية المؤثرة علي صفات العمر عند أول بيضة، الوزن عند أول بيضة، عدد البيض خلال 120 يوم من الانتاج، وزن البيضة، وحدات هو، قوة قشرة البيضة في قطيع الجيل الثاني. تم تحليل البيانات المظهرية بإستخدام نموذج الحيوان متعدد الصفات (Multi-traits Animal Model) ليشمل المجموعة الوراثية، تأثير الشهر/السنة، تاريخ الفقس كتأثيرات ثابتة والأثر الوراثي التجمعي والأثر البيئي الدائم كتأثيرات عشوائية. إستخدمت 45 من الواسمات الوراثية لتوصيف التركيب الوراثي لقطيع الجيل الثاني في تسعة مجاميع ارتباط أتوسومية للكروموسومات الجسمية وللكروموسوم الجنسي Z وإستخدمت هذه التراكيب الوراثية في تحليل مواقع الصفات الكمية بإستخدام النماذج المختلطة ليشمل تاريخ الفقس كتأثير ثابت بالإضافة إلى التأثير التجمعي والسيادي لمواقع الصفات الكمية كتأثيرات عشوائية. و**يمكن تلخيص النتائج فى النقاط التالية:**

1- تفوقت الخلطان علي القطعان النقية في صفة إنتاج البيض ومن ثم يمكن تحسين السلالات المحلية في مصر لصفات النمو وإنتاج البيض عن طريق الخلط بين السلالات.

2- كان مجموع طول الخريطة الكرومسومية 1949 cM حيث تراوحت من 52 cM علي الكروموسوم رقم 11 إلي 542 cM علي الكروموسوم رقم 1 بمتوسط مسافة بين الواسمات مقداره 43.3 cM ويتراوح من 15.3 cM علي الكروموسوم رقم 4 إلي 71.5 cM علي الكروموسوم 6 .

3- وجد اربعة مواقع كمية معنوية لصفة وزن الجسم عند أول بيضة والتي تقع علي الكروموسومات 2 ، 4 ، 8 ، Z وعلي المناطق 322 ، 156 ، 61 ، 102 cM علي التوالي وعند حدود ثقة 95 % كانت علي المناطق 244-422 ، 144-185 ، 0-75 ، 60-127 cM علي التوالي.

4- وجد موقعان معنويان لصفة العمر عند أول بيضة علي الكروموسوم 3 و الكروموسوم الجنسي Z علي المناطق 189 ، 128 cM علي التوالي وعند حدود ثقة 95 % كانت علي المناطق 155-200 ، 65-135 cM.

5- كانت تقديرات الأثر التجمعي هي -4.9 ± 1.8 ، 1.9 ± 0.6 ، 0.5 ± 0.6 لوحدة هو علي الكروموسومات 2 ، 4 ، 8 لتفسر 6.5 % ، 4.3 % ، 4.5 % من التباين المظهري الكلي لقطيع الجيل الثاني علي التوالي. وكانت تقديرات الأثر السيادي هي -3.5 ± 3.3 ، -3.1 ± 1 ، 4.2 ± 0.04 .

6- كان الموقع الكمي لصفة قوة قشرة البيضة يقع علي نهاية الكروموسوم الجنسي Z ، و كان الأثر التجمعي مقداره -0.15 ± 0.04 ليفسر

5 % من التباين المظهري الكلي وكانت حدود الثقة على المناطق التي تتراوح من 77 إلي 134 cM وعدم وجود أثر سيادي.

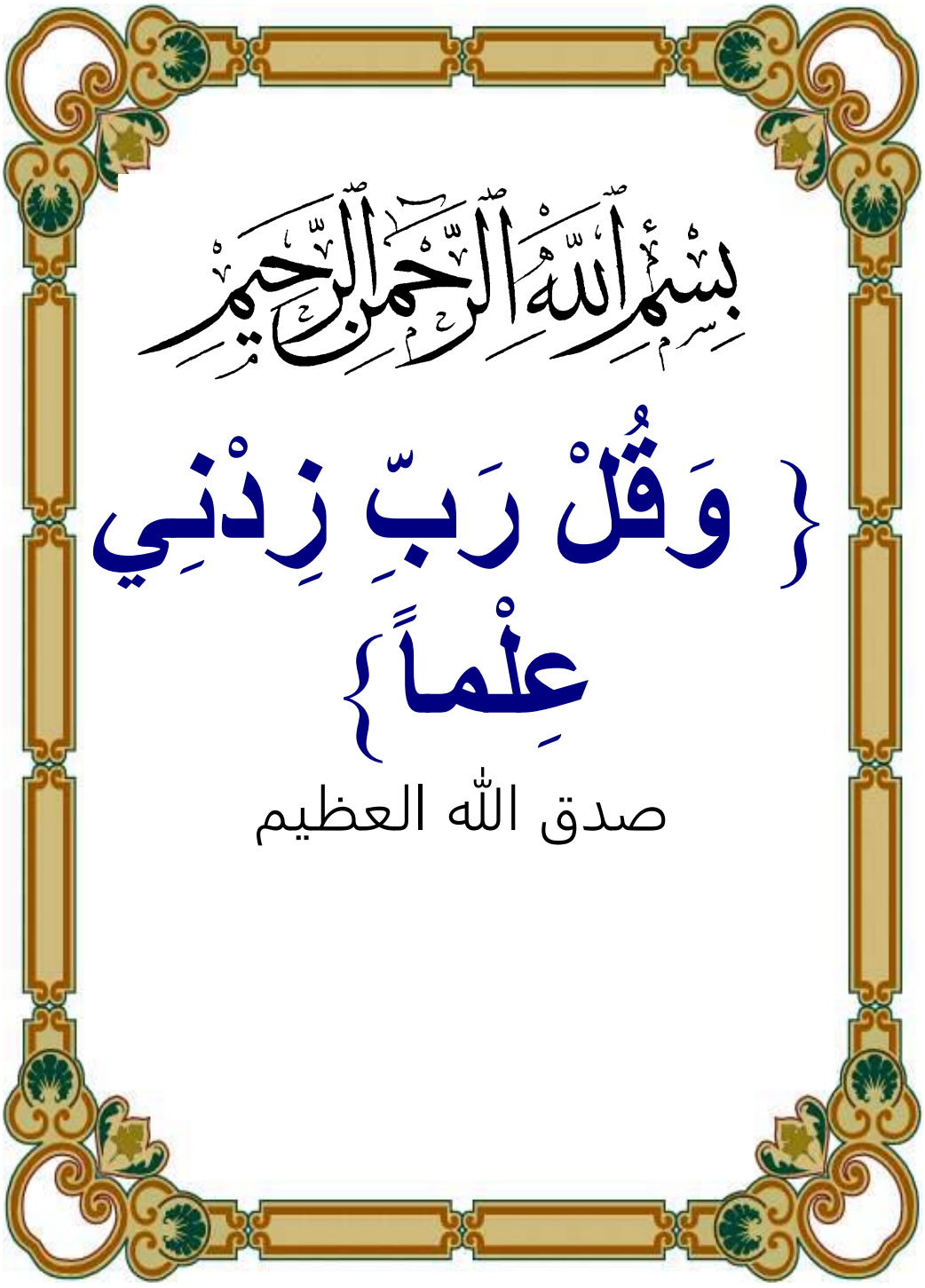
7- كان الموقع الكمي لصفة الوزن عند أول بيضة يقع علي الكروموسومات 2 ، 4 ، 8 ، Z ، وكان الأثر التجمعي مقداره 17.6 ± 85 جم، 830 ± 44.8 جم، 109 ± 22.9 جم، 95 ± 30.5 جم ليفسر 1.4 % ، 6.9 % ، 1.4 % ، 1% من التباين المظهري الكلي لقطيع الجيل الثاني علي التوالي. وكانت تقديرات الأثر السيادي هي 5 ± 8.8 جم، 146 ± 169.5 جم، 36 ± 46.9 جم، 15.4 ± 8.5 جم علي التوالي.

8- كان الموقع الكمي لصفة وزن البيضة يقع علي الكروموسوم رقم 4 وعلى الكروموسوم الجنسي Z، وكان الأثر التجمعي مقداره 3.2 ± 0.5 جم ، 1.5 ± 3 جم ليفسر 13 % ، 5.6 % من التباين المظهري الكلي لقطيع الجيل الثاني علي التوالي. و كانت تقديرات الأثر السيادي هي -0.8 ± 0.6 جم ولا يوجد أثر سيادي للكروموسوم Z.

9- كان الموقع الكمي لصفة عدد البيض يقع علي الكروموسوم رقم 4 وعلى الكروموسوم الجنسي Z ، ويوجد موقعان علي الكرموسوم رقم 4 يفسران 7.2 % من التباين المظهري الكلي ، 5 % للكرموسوم Z . وكان الأثر التجمعي مقداره -6.5 ± 1.9، -3.5 ± 2.2 ، -4.3 ± 1.3 بيضة. وكانت تقديرات الأثر السيادي هي -0.9 ± 2.3 ، 14.3 ± 4.5 بيضة للكرموسوم 4 ولا يوجد أثر سيادي للكروموسوم Z.

10- كان الموقع الكمي لصفة العمر عند وضع أول بيضة يقع علي الكروموسوم رقم 3 وعلى الكروموسوم الجنسي Z ، ليفسران 5 % ، 7.2 % من التباين المظهري الكلي علي التوالي. وكان الأثر التجمعي مقداره -2.5 ± 1.1يوم ، 2.77 ± 0.6 يوم. وكانت تقديرات الأثر السيادي هي 6.5 ± 2.2 يوم للكروموسوم رقم 3 ولا يوجد أثر سيادي للكروموسوم Z.

11- تراوحت نسبة تباين الأثر التجمعي لكل موقع كمي إلى التباين المظهري الكلي لمواقع صفات الوزن عند أول بيضة من 1 % إلي 6.9 % ومن 5 % إلي 7.2 % لصفة العمر عند أول بيضة ومن 5.6 % إلي 13 % لصفة وزن البيضة ومن 3.6 % إلي 5 % لصفة عدد البيض ومن 4.3 % إلي 6.5 % لوحدات هو ، 5 % لصفة قوة قشرة البيضة. وكان أعلي تباين مظهري لمواقع الصفات الكمية المؤثرة علي صفة وزن البيضة 13 % علي الكروموسوم رقم 4 عند المنطقة 191 cM. وكانت نسب التباين المظهري لمواقع الصفات الكمية المعنوية والمحتملة لصفات الوزن عند أول بيضة ، العمر عند أول بيضة ، وزن البيض ، عدد البيض ، وحدات هو ، قوة قشرة البيضة هي 10.7 %، 12.2 %، 18.6 %، 12.2 %، 15.3 %، 5 % علي التوالي.


بسم الله الرحمن الرحيم
{ وَقُلْ رَبِّ زِدْنِي عِلْماً }
صدق الله العظيم

رسم الخرائط الجينية لمواقع الصفات الكمية المؤثرة علي أداء بعض الصفات الإنتاجية في سلالات الدواجن الأصيلة و المهجنة

رسالة مقدمة من

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للحصول على

درجة الدكتوراة فى العلوم الزراعية

إنتاج حيواني (تربية و وراثة الدواجن)

من

قسم الإنتاج الحيوانى

كلية الزراعة بمشتهر

جامعة بنها

2016