**Quantitative Trait Loci affecting growth performance in F2 of crossing Golden Montazah with White Leghorn chickens**

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**Abstract**

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 week were identified in F2 crossbred population produced by crossing males of Golden Montazah (GM) with females of White Leghorn (WL). Phenotypic data were analyzed using multi-traits animal model including the fixed effects of genetic group, sex and hatch and the additive genetic and common environmental effects as random effects. A linkage map was generated using Map Manager QTX version b20 software program. After parentage checking and F2 genotyping, data of 1011 chicks of F2 were genotyped using 43 genetic markers in nine autosomal linkage groups, Z chromosome and these genotypes were used for QTL analysis. A mixed model included the fixed effects of sex and hatch along with the additive and dominance effects of QTL as random effects were used for QTL analysis. The estimates of heritability for growth traits in genetic group were high heritable. The genotypic and phenotypic correlations between growth traits were high positive correlations between each two growth traits. The total map length was 1901 cM (ranging from 25 to 568 cM), with an average spacing of markers of 24.39 cM (ranging from 7.8 to 24.3 cM). A total of 34 QTL were detected for body weights of the birds evaluated in F2 cross. These QTL were distributed over five distinct regions on 10 chromosomes, and their effects ranged from 1.2 to 13.8% of the pheno­typic variation. A total of 19 significant genome QTL that affected body weight were located on seven macro-chromosomes (1, 2, 3, 4, 6, 8 and Z) and one micro-chromosome (11). A total of 14 significant QTL were detected for daily body gains, distributed over 7 distinct regions on 6 chromosomes, and their effects ranged from 2 to 8.9% of the pheno­typic variation. A total of 11 significant genome QTL that affected daily gain were located on five macro-chromosomes (1, 2, 3, 4 and 8) and there was statistical evidence for two QTL 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. The proportions of phenotypic variation explained by significant and suggestive QTL for daily gain at 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 8.9% for DG4-8 at 428 cM on chromosome 4. The additive effects of QTL on growth traits were positive values, while the dominance effects were generally negative or not significant. A QTL for body weight at 12 weeks of age segregating on chromosome 4 at 179 cM had the largest additive effect (205.7 ± 22.2 g) and explained 13.8% of the phenotypic variation. The largest dominance effect (−188.1 ± 55.0 g) was for QTL of body weight at 16 weeks of age segregation on chromosome 4 at 139 cM and the QTL effect accounted for 6.5% of the phenotypic variation. The total trait 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**.**

**Keywords:** Chickens, QTL, microsatellite markers, growth traits, genetic improvement, additive effects, dominance effects.

**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; Iraqi *et al.*, 2013)**. Nowadays, we need more workers for crossing Egyptian native breeds with exotic ones to determine the superior breeds, gains in performance from complementary breed effects and heterosis and to develop the superior new breeds through selecting the best combination of several breeds **(Iraqi *et al.,* 2013)**. Results of most crossbreeding experiments that carried out in Egypt showed that crossing between local breeds or strains of chickens with other local ones was generally associated with an 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 become excellent means for the study of genetic variation **(Chen *et al.,* 2003; Chang *et al.,* 2005)**, such as random amplified polymorphic DNAs (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. However, molecular microsatellite markers may be required to be used in improving the growth rate in genetic selection programs **(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 with 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) 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 (F0, F1, F2 and F3) have been constructed from different breeds for use in gene and QTL mapping studies **(Jacobsson, 2005; Liu *et al.,* 2008; Bulut *et al.,* 2013)**. Furthermore, chromosomal scanning studies have been conducted. To exemplify, 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.

The resource populations used in the present study were generated by crossing male Golden Montazah (GM) with female White Leghorn (WL). The main objectives were: (1) to phenotyping growth traits of body weights and daily body gains in the parental and F2 generations in such crossbreeding program, (2) to localize QTL affecting these growth traits in the F2 population using specific microsatellite markers, (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 proportion of phenotypic variance explained by each QTL, (5) to quantify the additive and dominance effects for QTL, (6) to explain the total variances attributable to QTL for each growth trait.

**MATERIALS AND METHODS**

**Breeding plan and experimental populations**

Chicks of F2 population were produced by crossing males of Golden Montazah (GM) with females of White Leghorn (WL). A total number of 18 and 8 cockerels and 64 and 51 pullets were chosen randomly from the WL and GM strains, respectively. Each cock was mated with 10 hens housed in separately breeding pen to produce F1 crossbred chicks (½GM½WL), then inter-se matings were practiced to produce F2 chicks with the genetic structure of (½GM½WL)2. Also, purebreds from the two strains were produced. The breeding plan permitted to produce four genetic groups as presented in Table 1. Pedigreed eggs from each individual breeding pen were collected from the four mating groups. On the hatching day, chicks produced from all genetic groups were wing banded, brooded on the floor and were grown in open houses up to 16 weeks of age.

All the chicks were medicated similarly and regularly and they were subject to the same managerial, hygienic and climatic conditions. During the growing and rearing periods, all the chicks were fed *ad libitum* using diet containing 23% and 21% crude protein and 3200 and 2900 metabolizable energy (kcal/kg) during the period from hatching to 6 weeks and from 6 to 16 weeks of age, respectively. Other details of breeding plan and management of the experimental populations were presented by **Khalil *et al.,* (2013) and Iraqi *et al.,* (2013).**

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

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Generation | Sire group | Dam group | 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 |
| F1 | GM | WL | (½GM½WL) | 18 | 103 | 1343 |
| F2 | F1 or ½GM½WL | F1 or ½GM½WL | (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.

**The phenotypic measurements**

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 period interval of 0-4 (DG4), 4-8 (DG8), 8-12 (DG12) and 12-16 (DG16) weeks of age.

**Statistical analysis of phenotypic data**

The phenotypic data collected were analyzed using multi-traits animal model of VCE6 program (**Groeneveld *et al.,* 2010**)**.** Firstly, data were 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 genetic groups were tested (P<0.05) using **Duncan (1955)** test. Secondly, the animal model used in matrix notation was as follows:

y = Xb + Zaua +Zcuc +e (Model 1)

Where: y= n×1 vector of observation of the bird, n = number of records; X= design matrix of order n×p, which related to the fixed effects of genetic group (four levels), year of birth (three levels), hatch (two levels) and sex; b= p×1 vector of the fixed effects of genetic group, year, hatch and sex; Za= the incidence matrix relating records to the additive genetic effect of the bird; ua= the vector of random additive genetic of the bird; Zc= the incidence matrix relating records to random common environmental effect of the bird; uc= the vector of random common environmental effect of the birds; and e= n×1 vector of random residual effects, NID (0, σ²e).

**Estimation of heritability:**

The heritability was computed based on the following equation:

Where: σa2,σc2 and σe2 are variances due to the effects of direct additive genetic, common environmental effect and random error, respectively.

**Estimation of correlations:**

The general formula used to calculate the additive genetic (rg) correlation between some traits were as follow **(Quaas *et al.,* 1984)**:

Where: Cov (X)ij = the additive genetic (a) and covariance between body weight and daily gain; Xii = the additive genetic (a) variance of body weight; Xij = the additive genetic (a) variance of daily gain.

**Genotyping**

**Blood sampling and DNA isolation:**

DNA samples (whole blood) were collected at 24 weeks of age from relevant mating birds of F0 parents, F1 and F2 to be included in the genotyping panel. Blood (10 ml) was collected from a wing vein of each bird into vacuum tubes containing EDTA and stored at -20 ˚C until extracting DNA by standard methods. Genomic DNA was isolated using the Maxwell® 16 blood DNA purification kit according to kit manual, designed specifically for the optimal automated extraction of DNA from whole blood samples on the Maxwell® 16 SEV Instrument. The quality and concentration of extracted DNA was checked spectrophotometrically.

**Markers selected:**

A total of 43 microsatellite markers covering nine autosomal linkage groups and the sex Z chromosome were considered in genotyping fifty F0 grandparents, twenty F1 and two hundreds F2 offspring (Table 2). These markers were selected based on the degree of polymorphism and the genome coverage recommended in the molecular genetic characterization of animal genetic resources **(FAO, 2011)**. Detailed information about microsatellites selected are available at the FAO website (www.dad.fao.org/en/ refer/library/guidelin/marker.pdf). Markers were selected to be tested basing on their position on the consensus map. A target for marker spacing of 10 cM was used to test markers across the genome (<http://www.ncbi.nlm.nih.gov>/mapview and <http://www.thearkdb.org>).

**PCR amplification:**

The PCR amplification was performed in a 25-µl reaction mixture (Ready to use Master Mix Promega) containing 100–200 ng DNA template, 15 pM of each primer, 200 lM each dNTP, 1 U Taq DNA polymerase, and an optimized quantity of MgCl2. The reaction was carried out by initial denaturation at 94 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 the best amplification are presented in Table 2. Amplified products were electrophoresed at Metaphor gel **(Muhammad *et al.,* 2008)**. The gel was run with puc19 DNA marker at 120 V for 2 h in 1X TBE and stained with Ethidium Bromide. The gel was visualized and documented under a white light gel documentation system.

**Table 2. Microsatellite markers used in genotyping birds of F0, F1 and F2**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Microsatellite marker (Locus) | Forward primer sequence | Reverse primer sequence | SSR (bp)\* | Tm\*\* |
| ADL0114 | GGCTCATAACTACCTTTTTT | GCTCTACATTCCTTCAGTCA | 185 | 45 |
| ADL0142 | CAGCCAATAGGGATAAAAGC | CTGTAGATGCCAAGGAGTGC | 231 | 52 |
| ADL0166 | TGCCAGCCCGTAATCATAGG | AAGCACCACGACCCAATCTA | 135 | 47 |
| ADL0183 | TTGTGAAGTGGATAAGATGA | ACAGAAATGGAAAGCGAGAC | 102 | 47 |
| ADL0188 | CACTTCCAGTATTAACGTGA | GTGGACACAATGAGTTCCTC | 129 | 47 |
| ADL0225 | CCAAAAAGCTGTATCACCTT | GCCTGTTGTAAACCACCTGA | 149 | 48 |
| ADL0236 | CTGGTTGTCAGTTGAAGGAC | ATAAGGTGGTGAGCAGCACT | 132 | 51 |
| ADL0237 | GCTTGTGCCTAAGAATGAAC | TGTATGGAGTCTCAGCAAAT | 148 | 50 |
| ADL0238 | AAACCCAAACAAAAGCAGAC | GCTCCTCATAAGCAAAATGC | 160 | 53 |
| ADL0241 | AAAATAGCATGGCAAATCAT | CAGATGCATCAGCACAGAAA | 216 | 51 |
| ADL0255 | GGGTATTGGTCTTCAAAATG | GTAAAGGCCTTCCTCTTCTT | 110 | 47 |
| ADL0258 | TCATTTCAGCTCACATTTTA | TTTTCAGGTTGTCTGGTTGC | 168 | 48 |
| ADL0266 | GTGGCATTCAGGCAGAGCAG | AATGCATTGCAGGATGTATG | 113 | 50 |
| ADL0267 | AAACCTCGATCAGGAAGCAT | GTTATTCAAAGCCCCACCAC | 117 | 55 |
| ADL0280 | CCCCTATAGCACAGCAGTCC | GGAACCTCAGCCTTGACATT | 172 | 56 |
| ADL0317 | AGTTGGTTTCAGCCATCCAT | CCCAGAGCACACTGTCACTG | 199 | 51 |
| LEI0073 | TTGAGAGCAGTGAAGGCAAACG | TGGTGGGAACTGGAAGAAGAGG | 217 | 65 |
| LEI0075 | TTTCACATCCAGTGCGTGTCTG | GGGCAGAGAAAGACGAAATTGG | 188 | 65 |
| LEI0083 | AACCCTCACACACCCATTGCC | CACTCGCCTGTAATTTCTTGTGG | 259 | 65 |
| LEI0106 | TGTGGGTTGTAATCCCTTCACC | CTCCCAAAAAACCTTCAAATGG | 295 | 59 |
| LEI0110 | GGGACCCAAGGCACACACTA | ATCCTCTATGAGGAAGGGAAGTGA | 231 | 63 |
| LEI0111 | CCCACAAAAGAGACACCGTGG | CCTGTTTGCCGTACACTTGGC | 116 | 65 |
| LEI0161 | CAGCCTTTTCAAGCTTGCTGC | GTTCACTTTAGACATGAATCGG | 100 | 54 |
| LEI0166 | AAGCAAGTGCTGGCTGTGCTC | TCCTGCCCTTAGCTACGCAC | 267 | 54 |
| LEI0254 | AGACCACTGGATCCAACTC | GTCTGGAACTCATCCCTTCATC | 95 | 55 |
| MCW0010 | CTGTAGAATTACAGAAATACA | TAGTACAAGAATCTAGTGTTAAAA | 93 | 45 |
| MCW0040 | ACTCAAAAATGTGGTAGAATATAG | ACCGAAATTGAGCAGAAGTTA | 143 | 55 |
| MCW0080 | CCGTGCATTCTTAATTGACAG | GAAATGGTACAGTGCAGTTGG | 280 | 55 |
| MCW0083 | TACATTTCAGAAGGAATGTTGC | GCCTTTCACCCATCTTACTGT | 90 | 54 |
| MCW0097 | GGAGAGCATCTGCCTTCCTAG | TGGTCTTCCAGTCTATGGTAG | 309 | 56 |
| MCW0100 | GATCTAAACAAAAACAGACACA | TGTAGGCGATTAAACATACTTC | 90 | 55 |
| MCW0107 | GAACAGAACTCTGTTTACTG | TCTGCTTACCTCAACTGACA | 121 | 56 |
| MCW0135 | ATATGCTGCAGAGGGCAGTA | CATGTTCTGCATTATTGCTCC | 150 | 57 |
| MCW0169 | GATCCCACTTGTTAAGAAGTG | CCTGACCTTACTGAGCTTGGA | 96 | 58 |
| MCW0180 | GATCACATCACGTTAATTTT | GGTGGAGAAAAGTGAAAGAC | 88 | 55 |
| MCW0295 | ATCACTACAGAACACCCTCTC | TATGTATGCACGCAGATATCC | 99 | 55 |
| MCW0305 | TCAGAAACAAAGCAGGAGCTG | TGACATCTTTCAAACGAGACC | 259 | 55 |
| MCW0340 | ATTATCTGATGCATCAGCTGG | CACCGATTGTAGCGGAACATC | 174 | 55 |
| ROS0003 | GCAAAGTTATTCAGGAACTTGC | AAGTGGTCCCCTGATTTAACA | 250 | 56 |
| ROS0025 | AGATTGCTGGGGGAAAAAGT | ACTGAAAACCTGAACAGAAGGC | 210 | 58 |
| ROS0030 | CGGAGAGCATGGTTTCAAGT | CTCTGTGAGCTCCCCATCTC | 240 | 58 |
| ROS0074 | AGCACTTTTGGTGTTACCGG | CAGCTGATGCTTCCACAGAA | 320 | 58 |
| ROS0075 | CAGCTCCGTGCTCCTCTC | TTTTCAACCCGTTGTTCAGG | 216 | 58 |

\* SSR = Simple Sequence Repeats; \*\* Tm = annealing temperature

**Linkage analysis and QTL mapping**

A linkage map was generated using Map Manager QTX version b20 software program **(Manly *et al.,* 2001)**. After parentage checking, data of 1011 chicks from F2 individuals were genotyped using 43 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 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 the markers. The maps were then used for QTL detection on the autosomes, linkage groups, and the Z chromosome. Data of F2 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 F2 cross was analyzed using the following mixed model including the fixed effect of sex along with the additive and dominance effects of QTL as random effects **(Haley *et al.,* 1994; Manly *et al.,* 2001**):

**yij= Xijb + Zaa + Zdd + ei (Model 2)**

Where: yij is the phenotype of F2 birds, Xij is the designed 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, Za 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, Zd is the probability of being heterozygous at the putative QTL locus given marker genotypes for the bird i, and ei is the random error, typically assumed to be normally distributed as N(0, σ2) **(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 = α/n, where α = 0.05, n was the total number of tests (traits x chromosome).

Percentage of F2 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:

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).

**RESULTS AND DISCUSSION**

**Phenotypic means of genetic groups:**

Means presented in Table (3) showed that the GM strain was significantly better (P<0.05) in most of the body weight and daily gain traits compared to WL breed. But, WL strain was better than GM strain in BW0 and DG8-12. This superiority may be due to genetic makeup of GM strain **(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 foundations. In general, 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 **(Galal *et al.,* 2007; Iraqi *et al.,* 2013)**.

**Table 3. 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±0.13b | 34.1±0.12a | 29.6±0.10d | 32.3±0.12c |
| 4 weeks | BW4 | 221.4±1.92c | 216.7±1.67c | 250.8±1.47a | 234.9±1.68b |
| 8 weeks | BW8 | 601.6±4.90b | 515.2±4.23d | 640.9±3.74a | 554.2±4.32c |
| 12 weeks | BW12 | 977.3±8.25bc | 914.4±7.13d | 1121±6.25a | 992.4±7.29b |
| 16 weeks | BW16 | 1347±11.90d | 1279±10.27e | 1517±8.98a | 1490±10.46b |
| **Daily gain traits (g):** | | | | | |
| 0-4 weeks | DG04 | 6.71±0.06d | 5.51±0.05e | 7.90±0.05a | 7.23±0.06b |
| 4-8 weeks | DG48 | 13.52±0.14b | 10.65±0.12d | 13.92±0.10a | 11.34±0.12c |
| 8-12 weeks | DG812 | 13.26±0.17c | 14.14±0.15d | 17.06±0.13a | 15.43±0.15b |
| 12-16 weeks | DG1216 | 13.26±0.21d | 13.11±0.18d | 14.23±0.16c | 17.78±0.19a |

a-e Means with the same letters within each row of the trait are non-significantly different (P≤0.05).

**Heritability**

Estimates of heritability (*h*a2) for growth traits in genetic group of (½GM½WL)2F2 in presented in Table 4. The estimates showed that these growth traits are high heritable traits. The estimate 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. Thus, we would recommend the Egyptian poultry breeder to select these strains at early ages without waiting to later ages to save time and efforts. Estimates of *h*a2 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)**.

**The genetic and phenotypic correlations**

The genotypic and phenotypic correlations between growth traits in the F2 population in the QTL analysis are presented in Table 4. As expected, there were high positive correlations between each two growth traits.

**Table 4. Heritabilities (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 3.

**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 F2 cross are presented in Table (5). Ultimately, nine autosomal linkage groups, and the Z chromosome containing 47 microsatellite markers in the F2 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 24.39 cM and that 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 F2 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 will contain many candidate genes. The same authors concluded that chromosome 1 had potential positional candidate genes like they are 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 5. 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 F2 cross**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Chromosome | Number of microsatellite markers | Chromosome map length (cM) | Average marker spacing by the chromosome (cM) | First marker on each chromosome |
| 1 | 10 | 568 | 24.3 | ROS0003 |
| 2 | 8 | 298 | 18.7 | LEI0073 |
| 3 | 2 | 273 | 11.6 | MCW0169 |
| 4 | 7 | 198 | 17.6 | ADL0317 |
| 6 | 4 | 111 | 10.4 | ADL0280 |
| 8 | 3 | 97 | 7.8 | MCW0080 |
| 9 | 1 | 123 | 20.1 | ROS0074 |
| 11 | 5 | 25 | 8.3 | LEI0110 |
| 13 | 2 | 71 | 14.5 | MCW0340 |
| Z | 5 | 137 | 11.5 | LEI0075 |
| Total | 47 | 1901 | 24.39 |  |

**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 6 and 7. 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 F2 reciprocal populations (TCTC and CTCT) to map QTL. Several QTL have been mapped in the TCTC population **(Nones *et al.,* 2006; Ambo *et al.,* 2009; Campos *et al.,* 2009; Baron *et al.,* 2011; Nones *et al.,* 2012; Boschiero *et al.,* 2013)**.

**Table 6. 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 F2 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) | Proportion of phenotypic variance explained by each QTL |
| 4-weeks 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-weeks 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 |
| 12-weeks 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-weeks 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.

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

**Table 7. 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 F2 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) | Proportion 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.

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

For daily body gains (DG), a total of 14 QTL were detected (Table 7). 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. The same 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 (6) 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 (7) 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. **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 F2 cross, a total of 34 QTL were detected and these QTL were distributed over five distinct regions on 10 chromosomes (Table 6). 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 F2 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 4th week of age on chromosomes 2, 3, and 9; three QTL for body weight at the 6th week of age on chromosomes 2, 3, and 6; one QTL for body weight at the 8th 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 F2 population in the present study are similar to those QTLs obtained by **Sewalem *et al.,* (2002)**, in which a F2 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, 3 out of 4 QTL on chromosome 3 were suggestive QTL (Tables 6 & 7). **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 F3 population generated from crossing two White Plymouth Rock broilers **(Jennen *et al.,* 2004)** and in F2 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 F2 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 6 for different body weights showing that 19 QTL 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 these QTL chromosomes 4 and 27 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)** stated that there were 10 QTL were identified at the 1% chromosome wide level, 2 QTL were identified at the 5% chromosome wide level, and 5 QTL were identified at the suggestive level for body weight, **Wang *et al.,* (2012)** found that on chromosome 3, three QTL and 10 QTL were identified at the 5% chromosome wide level and suggestive level, respectively.

**Confidence intervals**

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. **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.

**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 (RJF) and White Leghorn. The two major QTL for growth were located around positions of 68 and 416 cM.

The QTL effects expressed as the percentage of phenotypic variance is 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 8.9 % for daily gains in weight (Tables 6 & 7). 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 6). 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 (Table 7). 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.,* 2011; Bulut *et al.,* 2013).** Differences cited between different studies might be attributable to differences in: 1) crosses used in various studies; 2) ages of measurement of growth among studies and 3) individuals would be at different physiological status caused at least in part by genetic differences.

**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 8. 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 (Table 6). 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 8).

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%.

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 F2 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, as expected 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 Leghorn and Fayoumi alleles. **Wang *et al.,* (2012)** found that positive additive effects, indicating that increasing body weight allele was inherited from the broiler line in F2 population cross of broiler sire with Bair layer dams (Chinese local breed). **Rosario *et al.,* (2014)** in F2 population obtained by crossing males from a layer line (CC) and females from a broiler line (TT) cited that most QTL presented 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 was positive, indicating that heterozygotes were heavier than mid-parent.

**Table 8. 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 F2 population of chickens**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait / Chromosome | Additive effect, g | SE | VPa (%) + | Dominance effect, g | SE | VPd (%) ++ |
| 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 |

+VPa (%) = Percentage of additive variance explained by each QTL.

++VPd (%) = Percentage of dominance variance explained by each QTL.

The estimates of the additive effects attributable to QTL were of considerable importance ranging from 11.1 to 25.8 g, 18.5 to 94.5 g, 25.8 to 205.7 g and 63.2 to 369.2 g for body weights 4, 8, 12 and 16 weeks of age, respectively (Table 8). 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 8).

As for body weights, all the additive effects detected in daily gains in weight were also of positive values, while most of the dominance effects are negative values (Table 9). 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 (Table 9). 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).

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 percentage of dominance variance ranged from -14.8 % to 12.7%.

**Table 9. 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 F2 population of chickens**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait / Chromosome | Additive effect, g | SE | VPa (%) + | Dominance effect, g | SE | VPd (%) ++ |
| 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 |

+VPa (%) = Percentage of additive variance explained by each QTL.

++VPd (%) = Percentage of dominance variance explained by each QTL.

**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 10). 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 (Table 10). **Zhou *et al.,* (2006)** in F2 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 the5% 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.

**Table 10. Number of significant QTL at the 5 and 1% chromosome-wise levels and genome-wise level for each trait F2 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.

Potential candidate genes within the QTL region for growth traits at 1% chromosome-wise significance level of considerable importance. **Wang *et al.,* (2012)** in F2 population of broiler sire with Bair layer dams (Chinese local breed) cross cited that three QTL at 5 % chromosome-wise and 10 QTL at suggestive level on chromosome 3, on chromosome 5 there were 4 QTL identified 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.

**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. The present genome wide QTL mapping in F2 populations lays the foundation for identifying the DNA variants causally 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 be detected or segregation of QTL within commercial population needs be verified before further efforts are made.
3. A single-QTL model was used to detect QTL for growth traits in chickens. Different QTL locations in the same chromosome were observed on several chromosomes. Further analysis with multi-trait QTL model might confirm these multiple QTL. The dissection of the underlying mechanism of quantitative traits is very complicated. Further studies with this approach might be able to obtain more understanding of the complex genetic architecture underlying quantitative trait variation for growth in chickens.
4. 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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