QTL and chromosomal mapping for growth and egg performance in chickens: Applications and emphasis of results in Egypt

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Abstract

Quantitative trait loci (QTL) for growth and egg traits were identified in chickens. After parentage checking, data of F_2 chicks must be genotyped using genetic markers in the autosomal linkage groups and Z chromosome and the genotypes were used for QTL analysis. A mixed model included the fixed effects along with the additive and dominance effects of QTL as random effects were used for QTL analysis. In an Egyptian recent study, the total map length was 1901 cM for growth traits and 1949 cM for egg traits. A total of 34 QTL were detected for body weight traits (BW) where 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. In this study, a total of 19 significant genome QTL that affected body weights were located on seven macro-chromosomes (1, 2, 3, 4, 6, 8 and Z) and one micro-chromosome (11). The proportions of phenotypic variation explained by significant and suggestive QTL for body weight traits at 4, 8, 12 and 16 weeks were 21.1, 30.8, 29.3 and 25.4%, respectively. The additive effects of QTL on growth traits were positive, while the dominance effects were generally negative or not significant. A QTL for body weight at 12 weeks of age segregating on chromosome 4 had the largest additive effect and explained 13.8% of the phenotypic variation, while the largest dominance effect for QTL on chromosome 4 and accounted for 6.5% of the phenotypic variation. The QTL effects were found on chromosomes 2, 4, 8 and Z for weight at first egg (WFE), on chromosomes 3 and Z for age at first egg (AFE), on the chromosomes 4 and Z for egg weight, on the chromosomes 4 and Z for egg number (EN). The QTL effects expressed as the percentage of the phenotypic variance explained by each QTL were mostly of considerable importance ranging from 1 to 6.9 % of the phenotypic variation for WFE, 5 to 7.2 % for AFE, 5.6 to 13 % for EW and 3.6 to 5 % for EN. The whole genome scan for detection and localization of QTL affecting egg quality traits were described.

Keywords: Chickens, QTL, microsatellite markers, growth and egg traits, additive effects, dominance effects.

1. Introduction and objectives

In an earlier study by **van Kaam *et al.* (1998 and 1999)** was conducted to detect the whole genome scan for QTL affecting body weights and egg production in a 3-generation population generated from two broiler lines. In the last 15 years, several experiments in chicken populations (F_0, F_1, F_2 and F_3) have been constructed from different breeds for use in gene, chromosomal scanning chromosomal scanning and QTL mapping studies **(Jacobsson, 2005; Liu *et al.*, 2008; Bulut *et al.*, 2013)**. To exemplify, the chromosomal regions affecting phenotypic traits including body weight and egg traits 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 main objectives of this reviewed article are: (1) to localize QTL affecting egg and growth traits in the chickens using specific microsatellite markers, (2) to detect the chromosome group, number of informative microsatellite markers and the chromosome map length (cM), (3) to estimate QTL at chromosome-wise level along with the proportion of phenotypic variance explained by each QTL, and (4) to quantify the additive and dominance effects for QTL for egg and growth traits.

2. QTL applications in chickens

In QTL study, it is aimed to determine the most effective genes and chromosomal regions for the quantitative trait and to use this information in genomic 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 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. They can be used in marker-assisted selection programs (**MAS**) for improving egg and growth traits **(Liu *et al.*, 2007)**. 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.

The identification and utilization of QTL provide more rapid genetic improvement in selection programs, especially for traits that are difficult to improve with traditional selection programs **(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.

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.

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.

3. QTL markers to be used for genotyping growth and egg traits:

The markers to be selected based on the degree of polymorphism and the genome coverage recommended in the molecular genetic characterization of animal genetic resources are presented in Table 1 **(FAO, 2011)**. Detailed information about the selected microsatellites are available at the FAO website (www.dad.fao.org/en/refer/library/guidelin/marker.pdf). On most cases, the assessment of markers was based on their positions 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).

Some studies have reported associations between genetic markers and egg and growth traits in poultry **(Sasaki *et al.*, 2004; 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)**. 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)**. Based on chicken linkage maps and data from a variety of populations, several studies have reported many QTL for body weights and egg traits in chickens **(Tatsuda and Fujinaka, 2001; Sewalem *et al.*, 2002; Wardecka *et al.*, 2002, 2003; Tsuiskula-Haavisto *et al.*, 2002; Kerje *et al.*, 2003; 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)**.

Table 1. Microsatellite markers used for genotyping growth and egg production traits

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
ADL0114	GGCTCATAACTACCTTTTTT	GCTCTACATTCCTTCAGTCA	2	185	45
ADL0142	CAGCCAATAGGGATAAAAGC	CTGTAGATGCCAAGGAGTGC	6	231	52
ADL0142	CAGCCAATAGGGATAAAAGC	CTGTAGATGCCAAGGAGTGC	6	231	52
ADL0143	CCTGTCTCTGGTCTTTATCC	AGTTTACTTCCTTTTCTTGC	4	170	51
ADL0155	GGTCCGACTGAAAGCATTAT	TTAAGACTGAAGCCAACCAG	3	107	49
ADL0166	TGCCAGCCCGTAATCATAGG	AAGCACCACGACCCAATCTA	6	135	47
ADL0183	TTGTGAAGTGGATAAGATGA	ACAGAAATGGAAAGCGAGAC	1	102	47
ADL0188	CACTTCCAGTATTAACGTGA	GTGGACACAATGAGTTCCTC	1	129	47
ADL0201	GCTGAGGATTCAGATAAGAC	AATGGCTGACGTTTCACAGC	Z	143	53
ADL0217	TCTACTTCGTTGGAGTGTCA	GGAAAACAGAGGAGAAATGG	2	161	52
ADL0225	CCAAAAAGCTGTATCACCTT	GCCTGTTGTAAACCACCTGA	13	149	48
ADL0236	CTGGTTGTCAGTTGAAGGAC	ATAAGGTGGTGAGCAGCACT	2	132	51
ADL0237	GCTTGTGCCTAAGAATGAAC	TGTATGGAGTCTCAGCAAAT	3	148	50
ADL0237	GCTTGTGCCTAAGAATGAAC	TGTATGGAGTCTCAGCAAAT	3	148	50
ADL0238	AAACCCAAACAAAAGCAGAC	GCTCCTCATAAGCAAAATGC	1	160	53
ADL0241	AAAATAGCATGGCAAATCAT	CAGATGCATCAGCACAGAAA	4	216	51
ADL0241	AAAATAGCATGGCAAATCAT	CAGATGCATCAGCACAGAAA	4	216	51
ADL0255	GGGTATTGGTCTTCAAAATG	GTAAAGGCCTTCCTCTTCTT	3	110	47
ADL0255	GGGTATTGGTCTTCAAAATG	GTAAAGGCCTTCCTCTTCTT	4	110	47
ADL0258	TCATTTCAGCTCACATTTTA	TTTTCAGGTTGTCTGGTTGC	8	168	48
ADL0266	GTGGCATTCAGGCAGAGCAG	AATGCATTGCAGGATGTATG	4	113	50
ADL0266	GTGGCATTCAGGCAGAGCAG	AATGCATTGCAGGATGTATG	4	113	50
ADL0267	AAACCTCGATCAGGAAGCAT	GTTATTCAAAGCCCCACCAC	2	117	55
ADL0280	CCCCTATAGCACAGCAGTCC	GGAACCTCAGCCTTGACATT	3	172	56
ADL0317	AGTTGGTTTCAGCCATCCAT	CCCAGAGCACACTGTCACTG	4	199	51

Table 1. Cont.

ADL0322	TGCGTTCTCCCCTTGGTTGC	GCAGCAGCTCCCACGACACA	8	140	55
LEI0065	TGAAACATGTATGGAGTCTCAGCA	GACAGCTAAATGCCAGTTCATGG	3	187	61
LEI0072	TAAGCTGACATTCACCACCAG	GACTCTTTCAGTACATACTGG	11	100	63
LEI0073	TTGAGAGCAGTGAAGGCAAACG	TGGTGGGAACTGGAAGAAGAGG	4	217	65
LEI0073	TTGAGAGCAGTGAAGGCAAACG	TGGTGGGAACTGGAAGAAGAGG	4	217	65
LEI0075	TTTCACATCCAGTGCGTGTCTG	GGGCAGAGAAAGACGAAATTGG	Z	188	65
LEI0075	TTTCACATCCAGTGCGTGTCTG	GGGCAGAGAAAGACGAAATTGG	Z	188	65
LEI0081	ACTTACCTTTTCTTAGCTACTG	GATCCTTTCAATGCTCATGCT	4	260	61
LEI0083	AACCCTCACACACCCATTGCC	CACTCGCCTGTAATTTCTTGTGG	13	259	65
LEI0106	TGTGGGTTGTAATCCCTTCACC	CTCCCAAAAAACCTTCAAATGG	1	295	59
LEI0110	GGGACCCAAGGCACACACTA	ATCCTCTATGAGGAAGGGAAGTGA	11	231	63
LEI0111	CCCACAAAAGAGACACCGTGG	CCTGTTTGCCGTACACTTGGC	Z	116	65
LEI0111	CCCACAAAAGAGACACCGTGG	CCTGTTTGCCGTACACTTGGC	Z	116	65
LEI0161	CAGCCTTTTCAAGCTTGCTGC	GTTCACTTTAGACATGAATCGG	3	100	54
LEI0163	ACTTGGGCATACTCTTGTTGC	CTGCAGGTACCGTGAGATGTG	2	207	64
LEI0166	AAGCAAGTGCTGGCTGTGCTC	TCCTGCCCTTAGCTACGCAC	3	267	54
LEI0214	TGCCTCGTCTTACTGAGTGA	GATCAAGCACTGTATTTTATTC	11	164	60
LEI0254	AGACCACTGGATCCAACTC	GTCTGGAACTCATCCCTTCATC	Z	95	55
LEI0254	AGACCACTGGATCCAACTC	GTCTGGAACTCATCCCTTCATC	Z	95	55
MCW0004	GGATTACAGCACCTGAAGCCACTA	AAACCAGCCATGGGTGCAGATTGG	3	199	54
MCW0010	CTGTAGAATTACAGAAATACA	TAGTACAAGAATCTAGTGTTAAAA	1	93	45
MCW0010	CTGTAGAATTACAGAAATACA	TAGTACAAGAATCTAGTGTTAAAA	1	93	45
MCW0040	ACTCAAAAATGTGGTAGAATATAG	ACCGAAATTGAGCAGAAGTTA	3	143	55
MCW0045	CCAAAGGAAACAAATACTATACGA	GAAAGAAAAACTGACACTGTGACT	13	151	53
MCW0047	GGATTACGGCCGTTTGTGCACAAA	AATGGAACGCCGAACTCGCGTGCA	4	107	49
MCW0055	TTTGTAGTTACCTGGTACTGA	GTTTGCATTGTCTACAGCTCCTTG	Z	193	51
MCW0056	TGGTAACCTCTAACCTTGACG	AGTGAAGGAGACTCCACAGCCTCT	2	207	48
MCW0080	CCGTGCATTCTTAATTGACAG	GAAATGGTACAGTGCAGTTGG	13	280	55
MCW0083	TACATTTCAGAAGGAATGTTGC	GCCTTTCACCCATCTTACTGT	3	90	54
MCW0083	TACATTTCAGAAGGAATGTTGC	GCCTTTCACCCATCTTACTGT	3	90	54
MCW0097	GGAGAGCATCTGCCTTCCTAG	TGGTCTTCCAGTCTATGGTAG	11	309	56
MCW0100	GATCTAAACAAAAACAGACACA	TGTAGGCGATTAAACATACTTC	8	90	55
MCW0100	GATCTAAACAAAAACAGACACA	TGTAGGCGATTAAACATACTTC	8	90	55
MCW0107	GAACAGAACTCTGTTTACTG	TCTGCTTACCTCAACTGACA	1	121	56
MCW0107	GAACAGAACTCTGTTTACTG	TCTGCTTACCTCAACTGACA	1	121	56
MCW0122	TCCTTTGGAGCACGGAGGAAC	AGATGCACAGGCAGAGCTCCA	4	270	56
MCW0129	ATTTGGTGAACACAAACCTGC	CCACTTGAATGAAGCACCTAC	4	118	52
MCW0135	ATATGCTGCAGAGGGCAGTA	CATGTTCTGCATTATTGCTCC	9	150	57
MCW0135	ATATGCTGCAGAGGGCAGTA	CATGTTCTGCATTATTGCTCC	9	150	57
MCW0154	GATCTGTTTTATCACACACAC	CCATTTCCTTTGTTATCAGGC	Z	193	54
MCW0156	TCTGTAACATTTTTCCTTTTGTG	TTAATGTGGCAGACTCAAAGG	3	287	50
MCW0169	GATCCCACTTGTTAAGAAGTG	CCTGACCTTACTGAGCTTGGA	3	96	58
MCW0169	GATCCCACTTGTTAAGAAGTG	CCTGACCTTACTGAGCTTGGA	3	96	58
MCW0170	TTGTGAAACTCACAGCAGCTG	TTATAGCAGGCTGGCCTGAAG	3	177	52
MCW0180	GATCACATCACGTTAATTTT	GGTGGAGAAAAGTGAAAGAC	4	88	55
MCW0180	GATCACATCACGTTAATTTT	GGTGGAGAAAAGTGAAAGAC	4	88	55
MCW0241	AACCAGTTTGTTAACATCAGC	ATTGGAGTTGGTACCATACTC	Z	276	51
MCW0246	TCATAAGGCAGAGAATTCATC	TTTCCATTCAGACAACAAGGC	Z	235	53
MCW0247	CTTCACATGCTCCACTTGATG	AGTGACTATACTTCTTCACGG	2	207	50
MCW0295	ATCACTACAGAACACCCTCTC	TATGTATGCACGCAGATATCC	4	99	55
MCW0305	TCAGAAACAAAGCAGGAGCTG	TGACATCTTTCAAACGAGACC	8	259	55
MCW0340	ATTATCTGATGCATCAGCTGG	CACCGATTGTAGCGGAACATC	13	174	55
ROS0003	GCAAAGTTATTCAGGAACTTGC	AAGTGGTCCCCTGATTTAACA	6	250	56
ROS0003	GCAAAGTTATTCAGGAACTTGC	AAGTGGTCCCCTGATTTAACA	6	250	56
ROS0025	AGATTGCTGGGGGAAAAAGT	ACTGAAAACCTGAACAGAAGGC	1	210	58
ROS0026	GGCAAACACACAGTTTTCACA	ATGATCTCATGGAGTGCTGAGC	8	108	55
ROS0030	CGGAGAGCATGGTTTCAAGT	CTCTGTGAGCTCCCCATCTC	9	240	58
ROS0074	AGCACTTTTGGTGTTACCGG	CAGCTGATGCTTCCACAGAA	2	320	58
ROS0074	AGCACTTTTGGTGTTACCGG	CAGCTGATGCTTCCACAGAA	2	320	58
ROS0075	CAGCTCCGTGCTCCTCTC	TTTTCAACCCGTTGTTCAGG	8	216	58
ROS0075	CAGCTCCGTGCTCCTCTC	TTTTCAACCCGTTGTTCAGG	8	216	58

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

van Kaam *et al.* (1999) indicated the region positioned between markers LEI166 and MCW166 as potential for identifying QTL for BW at 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 these 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 of 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.

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.

4. The chromosomal and QTL linkage mapping and their positions in chicken genome:

The chromosomal map to be used for detecting growth and egg traits in F_2 population are presented in Figure 1 as cited by **Abd Alal (2016)**. The 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 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)**. 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.

The 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; Wardecka *et al.*, 2003; Abd Alal, 2016).**

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)** in F_2 population originated from a cross between White Leghorn males and Rhode Island Red females reported that: (1) the chromosome number 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, (2) thirteen markers were mapped into a linkage group on the Z chromosome, encompassing 120 cM of the Z chromosome, and (3) 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.

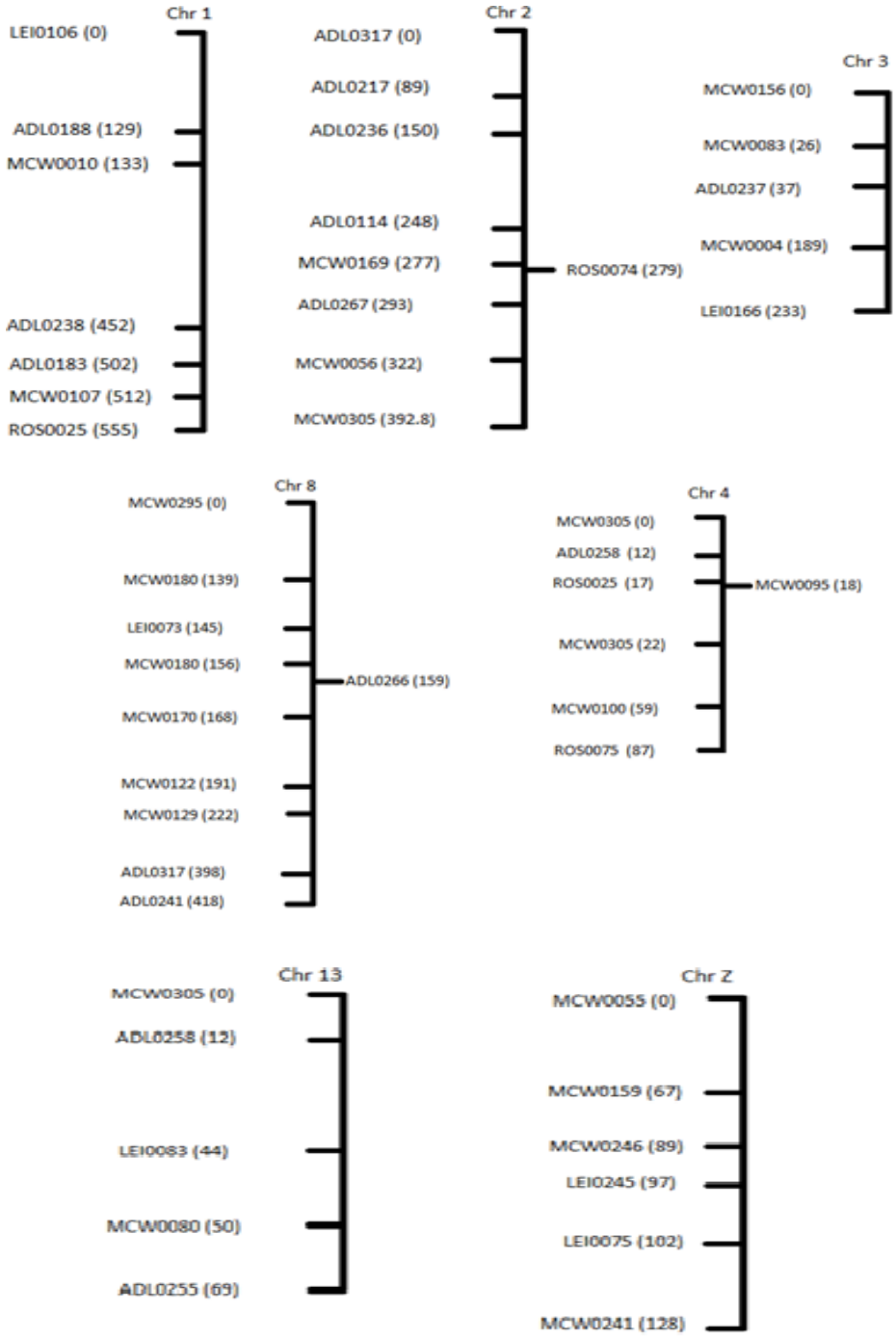

Figure 1. Linkage map for QTL analysis in chickens, including positions and names of the markers as cited by the Egyptian study of **Abdel Alal (2016)**.

4.1 QTL linkage mapping and their positions detected for growth traits:

As illustrated by **Abdel Alal et al (2016)**, the chromosome group, number of informative microsatellite markers, chromosome map length (*cM*), that was used for a whole genome scan of growth traits in F_2 cross are presented in Table 2. He reported that 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. 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.

Table 2. Chromosome (linkage) group, number of microsatellite markers and map length (cM), that was used for a whole genome scan of growth and egg traits in F_2 cross

Chromosome	Number of microsatellite markers		Chromosome map length (cM)		Average marker spacing by the chromosome (cM)	
	Growth	Egg	Growth	Egg	Growth	Egg
1	10	9	568	542	24.3	60.2
2	8	8	298	401	18.7	50.1
3	2	6	273	144	11.6	24
4	7	4	198	286	17.6	15.3
6	4	3	111	123	10.4	71.5
8	3	2	97	88	7.8	44
9	1	2	123	112	20.1	56
11	5	3	25	52	8.3	17.3
13	2	2	71	69	14.5	34.5
Z	5	6	137	132	11.5	22
Total	47	45	1901	1949	14.48	43.3

Source: Abdel Alal et al (2016)

He also cited that the total chromosomal map length for egg production and egg quality traits 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.

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)**. **McElroy *et al.* (2002)** found the linkage between MCW193 and QTL was suggestive at 10%, for nine distinct characteristics including body weight at six week in chromosome 5. Using the population of 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.

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. 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). **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 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. **Atzmon *et al.* (2006)** reported that a microsatellite marker MCW0102 was significantly associated with BW at 7 weeks in a commercial broiler line. **Tatsuda and Fujinaka (2001)** detected a QTL affecting body weight and 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, **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** and **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)**.

4.2 QTL linkage mapping and their positions detected for egg traits:

There were several QTL areas found for all measured egg production traits. Previous work has suggested that chromosome 4 may be a critical region significantly associated with the variety of egg traits across multiple resource populations **(Sewalem *et al.*, 2002; Tuiskula-Haavisto *et al.*, 2002; Sasaki *et al.*, 2004)**.

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. **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).

Goraga *et al.* (2012) stated that the most interesting result of multiple QTL regions 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. **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. **Rosochacki *et al.* (2013)** found that the QTL for shell strength was linked to chromosome 8 and the linkage group 26.

Most of the QTL are located on chromosomes 4 and Z. For production traits, the number of QTLs was distributed over chromosomes, such as the QTLs for AFE on chromosomes 3 and Z, for EW on chromosomes 2, 4 and Z **(Tuiskula-Haavisto, 2002)**. The QTL region on the Z chromosome was a large area including QTL for age at first egg, egg weight and egg numbers. QTLs affecting egg number and egg weight were found in chromosomes 1, 2, 5, 6, 7, 8, 14 and Z **(Chatterjee *et al.*, 2008)**.

5. The phenotypic variance explained by QTL:

In Egypt, the markers and significance for each QTL at chromosome-wise level along with the proportion of phenotypic variance explained by each QTL for body weights are presented in Table 3 by **Abdel Alal (2016)**. 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.

The total variances explained by QTL for growth traits are reported by **Abdel Alal et al (2016)** who reported that 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. For egg traits, **Abdel Alal (2016)** stated that the total variances explained by QTL were 10.7, 12.2, 18.6, 12.2, 15.3 and 5 % in WFE, AFE, EW, EN, Hugh unit and eggshell thickness, respectively. 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. **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. **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.

6. Additive and dominance effects for QTL:

As cited by **Abdel Alal (2016)** and **Abdel Alal et al (2016), t**he details of the additive and dominance effects of the 19 significant QTL for body weights are presented in Table 4. The additive effects were positive, while the dominance effects were generally negative or not significant. 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.

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.

Table 3. The markers, significance of QTL at chromosome-wise level, and the percentage phenotypic variance (PV) explained by QTL for body weights and egg traits of F_2 population

Chr. No	Markers	PV explained by QTL (%)	Chr. No	Markers	PV explained by QTL (%)
4-weeks weight:			**Weight at first egg (WFE):**		
1	ADL0183-ROS0025	2.4	2	ADL0114 - MCW0056	1.4**
2	ADL0236-ROS0074	5.8**	4	ADL0241 - MCW0180	6.9**
4	ADL0266-LEI0073	3.1*	8	MCW0100 - ROS0075	1.4**
6	ROS0003 - ADL0142	2.6*	Z	LEI0111 – LEI0075	1.0*
8	MCW0100- ROS0075	2.1			
11	LEI0110 - MCW0097	1.2**	**Age at first egg (AFE):**		
13	LEI0083 - MCW0080	1.6	3	ADL0155 – MCW0004	5.0**
Z	LEI0111 - LEI0075	2.3	Z	ADL0201-MCW0241	7.2**
8-weeks weight:					
1	MCW0010-ADL0188	4.9**	**Egg number (EN):**		
2	ADL0236-ROS0074	1.3	4	MCW0047 – ADL0266	3.6**
3	LEI0161-ADL0280	3.0*	4	ADL0266 – MCW0170	3.6**
3	MCW0040-LEI0166	1.5	Z	MCW0241 – MCW0246	5.0**
4	ADL0317 - MCW0295	2.5*			
4	ADL0266-LEI0073	7.0**	**Egg weight (EW):**		
8	MCW0100-ROS0075	2.5	4	LEI0081-MCW0122	13**
11	LEI0110-MCW0097	3.5**	Z	ADL0022 – MCW0154	5.6**
13	MCW0340-ADL0225	1.6			
Z	LEI0111-LEI0075	3.0**			
12-weeks weight:			**Haugh unit (HU):**		
1	MCW0010-ADL0188	3.3**	2	MCW0247 – ADL0217	6.5**
3	ADL0237-ADL0166	3.0*	4	MCW0180 - MCW0129	4.3*
4	ADL0317-MCW0295	2.4*	8	ADL0322 - MCW0095	4.5*
4	ADL0266-LEI0073	13.8**			
8	MCW0100- ROS0075	1.4**	**Egg shell strength (ESS):**		
9	MCW0135- ROS0030	1.3	Z	MCW0154-LEI0254	5.0**
13	MCW0340-ADL0225	1.4			
Z	LEI0111-LEI0075	2.7*			
16-weeks weight:					
1	MCW0010-ADL0188	2.5			
1	ADL0183-ROS0025	1.6			
2	ADL0236-ROS0074	1.9			
4	ADL0241-MCW0180	6.5**			
8	MCW0305-ADL0258	4.2**			
8	MCW0100-ROS0075	2.3			
13	MCW0340-ADL0255	2.8			
Z	LEI0111-LEI0075	3.6**			

Source: Abdel Alal (2016) and Abdel Alal et al (2016).
*significant linkage at $P \leq 0.05$ and ** significant linkage at $P \leq 0.01$.

Table 4. Estimates of additive and dominance effects (g) attributable to QTL for body weights and egg traits in F_2 population of chickens

	Body weights			**Egg production and egg quality traits**	
Chr. No	Additive effect explained by each QTL (%)	Dominance effect explained by each QTL (%)	Chr. No	Additive effect explained by each QTL (%)	Dominance effect explained by each QTL (%)
4-weeks weight			Weight at first egg:		
1	4.9	5.7	2	5.4	0.3
2	5.9	7.0	4	53.0	10.5
4	11.0	-2.8	8	7.0	2.3
6	4.7	-4.7	Z	6.1	1
8	5.8	6.6			
11	5.6	3.1	Age at first egg:		
13	5.9	-7.9	3	1.6	4.0
Z	5.4	1.4	Z	1.7	-
8-weeks weight					
1	7.8	-0.5	Egg Number:		
2	7.6	-6.3	4	8.2	1.1
3	8.8	2.1	4	4.4	18.0
3	3.3	6.0	Z	5.4	-
4	6.0	-0.3			
4	17.1	1.1	Egg weight:		
8	7.8	4.6	4	6.5	1.6
11	5.8	2.4	Z	3.0	-
13	8.5	-1.2			
Z	9.5	3.6			
12-weeks weight			Haugh unit:		
1	8.6	-0.6	2	6.2	4.5
3	9.1	-0.6	4	2.4	3.9
4	6.3	-0.4	8	0.6	5.3
4	20.7	1.6			
8	7.3	15.7	Egg shell strength:		
9	2.6	-12.8	Z	55.6	
13	4.9	5.4			
Z	11.3	3.2			
16-weeks weight					
1	6.1	1.8			
1	6.2	6.1			
2	6.3	-0.4			
4	24.8	-12.6			
8	7.2	7.1			
8	7.3	-4.9			
13	4.2	-10.4			
Z	9.2	7.4			

Conclusions:

1) QTL detected for body weight on chromosomes 1, 2, 3, 4, 6, 8, 11 and Z and those detected on chromosomes 2, 3, 4, 8 and Z for egg production and egg quality traits were significant and concluded that there are different sets of genes affecting early and late body weights and egg production and egg quality traits.
2) The genome wide QTL mapping in F_2 populations lays the foundation for identifying the DNA variants causally responsible for variation in growth and egg production traits in chickens. To utilize these results for further identifying causative functional genes or using marker assisted selection (MAS) in poultry improvement program, the detection of fine-mapping QTL is required or the segregation of QTL within commercial population is being to be verified before further efforts are made.
3) A single-QTL model could be used to detect QTL for growth and egg production 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. Further studies with this approach might be able to obtain more understanding of the complex genetic architecture underlying quantitative trait variation for body weight and egg production 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.

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