RESEARCH ARTICLE

Determination of chromosomal regions affecting body weight and egg production in Denizli X White Leghorn F2 populations

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Özet

Bulut Z, Kurar E, Ozsensoy Y, Nizamlioglu M, Garip M, Yilmaz A, Caglayan T, Dere S, Kurtoglu V, Dogan M. Denizli X Leghorn F2 popülasyonunda canlı ağırlık ve yumurta verimini etkileyen kromozom bölgelerinin tanımlanması. **Eurasian J Vet Sci, 2013, 29, 1, 30-38**

Amaç: Bu çalışmanın amacı; Denizli X Leghorn F2 populasyonunda yumurta verimi ve farklı dönemlerde canlı agırlığı kontrol eden kromozom bölgelerinin tanımlanmasıdır.

Gereç ve Yöntem: Denizli ve Leghorn ırkları kullanılarak F2 düzeyinde deneysel bir populasyon oluşturuldu ve verim kayıtları alındı. Kromozom tarama çalışmaları için kantitatif özellik lokusları (QTL) gen haritalama analizlerine uygun 113 mikrosatellit markörü F0, F1 ve F2 bireylerde Polimeraz Zincir Reaksiyonu (PZR) ile yükseltgendi.

Bulgular: Bu çalışmanın sonucunda farklı dönemlerde canlı ağırlık ile ilişkili QTL bölgeleri tavuk 1. kromozom çiftinde (GGA1), GGA2 ve GGA4 üzerinde tespit edildi. Yumurta verimi üzerine etkili iki farklı QTL bölgesinin varlığı, GGA8 ve cinsiyet kromozomu (GGAZ) üzerinde bulundu. GGA2, GGA4 ve GGAZ üzerinde bulunan üç farklı QTL ile yumurta ağırlığı arasında bir ilişki tespit edildi.

Öneri: QTL bölgelerinin yeni markörler ile daraltılması ve bölgesel klonlama çalışmaları ile bu verim özelliklerini kontrol eden genlerin tespit edilmesi gerekmektedir.

Anahtar kelimeler: Tavuk, et ve yumurta verimi, QTL gen haritalama, markör destekli ıslah

Abstract

Bulut Z, Kurar E, Ozsensoy Y, Nizamlioglu M, Garip M, Yilmaz A, Caglayan T, Dere S, Kurtoglu V, Dogan M. Determination of chromosomal regions affecting body weight and egg production in Denizli X White Leghorn F2 populations. **Eurasian J Vet Sci, 2013, 29, 1, 30-38**

Aim: The objective of the present study was identification of the chromosomal regions responsible for egg yield and body weight at different age periods in a Denizli and White Leghorn F2 population.

Materials and Methods: An experimental F2 population was constructed by crossing Denizli and White Leghorn breeds and the yields of the animals were recorded. In chromosomal scanning trials, a total of 113 microsatellite markers, suitable for use in quantitative trait locus (QTL) gene mapping, were amplified by the polymerase chain reaction (PCR) in F0, F1 and F2 animals.

Results: Data obtained in the present study demonstrated that QTL regions associated with body weight at different age periods were located on chromosome 1 (GGA1), GGA2 and GGA4. It was determined that, two different QTL regions affecting egg yield existed, on GGA8 and the sex chromosome (GGAZ). Three different QTL regions located on the chromosomes GGA2, GGA4 and GGAZ were associated with egg weight.

Conclusion: There is a need for narrowing these QTL regions by typing new markers in these intervals and for identifying genes that have affect on these economically important traits.

Keywords: Chicken, meat and egg yields, QTL gene mapping, marker-assisted selection

Introduction

Gene level dissection of diseases and economically important traits enables development of novel diagnostic, treatment and protection methods and serves for the more efficient and economic derivation of animal products. Economically important traits in animal production such as meat, milk and egg production, as well as fertility traits have quantitative character and are controlled by the additive effect of multiple genes. The chromosomal regions controlling quantitative traits are defined Quantitative Trait Loci (QTL). However, conventional quantitative-genetic theory and molecular genetic knowledge suggest that only a few of these genes control the majority of quantitative traits (Falconer 1960, Hill 2010).

The detection of the linkage between a QTL region and marker alleles (Sax 1923) or most ideally, the determination of the differences in the sequencing of the relevant genes would enable major advances in animal selection studies. The estimation of the phenotype based on genotype and its use in breeding programmes is referred to as marker-assisted selection (MAS). MAS provide potential for increasing the selection accuracy in animal breeding programmes.

Poultry production is an important sector in agriculture for obtaining economical animal originated foods. Apart from its economic value, the chicken is considered as an ideal and rather useful model organism for genetic research, owing to its small body size, the ease of its feeding and management, its short generation interval and the possibility of generating experimental populations from a single hen within a short time period at low costs (Burt 2005).

In the last 15 years, several experimental chicken populations (BC, F1, F2, F3) have been constructed from different breeds and pure lines for use in gene and QTL mapping studies. Furthermore, chromosomal scanning studies have been conducted. To exemplify, the chromosomal regions affecting phenotypic traits including growth (Carlborg et al 2003, Li et al 2003, Zhu et al 2003), body weight (Van Kaam et al 1999, Tatsuda and Fujinaka 2001, Sewalem et al 2002, Kerje et al 2003a, Sasaki et al 2004, Siwek et al 2004, Gao et al 2006, Nones et al 2006), body fat rate (Ikeobi et al 2002, Jennen et al 2005), feed conversion rate (Van Kaam et al 1999), egg yield (Tuiskula-Haavisto et al 2002, Kerje et al 2003b, Sasaki et al 2004), egg characteristics and egg quality (Wardecka et al 2003, Sasaki et al 2004), resistance to diseases (Hu et al 1997, Bumstead 1998, Forgetta 2001, Mariani et al 2001, Yonash et al 2001, Kaiser and Lamont 2002, Yunis et al 2002, Zhu et al 2003), plumage colour (Kerje et al 2003b) and behaviour (Schutz et al 2002, Buitenhuis et al 2003, Schutz et al 2003, Buitenhuis et al 2004, Keeling et al 2004) have been investigated in different chicken breeds. Studies are ongoing on the identification of the Quantitative Trait Genes (QTGs) and Quantitative Trait Nucleotide (QTNs) controlling these traits.

The aim of the present study was to detect the QTL regions for body weight at different age periods and egg yield using a F2 resource population produced by crossing Denizli and White Leghorn breeds.

Materials and Methods

The origin, production of the F2 resource population and husbandry of the birds were described elsewhere (Garip et al 2011). Briefly, 10 Denizli (D) roosters and 30 White Leghorn (WL) parental hens were chosed to construct a F0 breeder flock. For this purpose, 10 families were produced in total and 230 chicks (F1) were obtained. Small numbers of families with larger sizes were selected for generation of F2 population. In this respect, of the 10 families produced, 5 D males and 11 WL females were used to establish a F2 generation (n=441). The animals were raised in the same chicken house provided with *ad libitum* feed and drinking water throughout the trial. The hatching weights of the F2 chicks were measured using an assay balance sensitive to 0.01 g. F2 populations were weighted at an interval of 3 weeks during the growth period (at weeks 3, 6, 9 and 12) and at an interval of 4 weeks during the development and laying periods. Hens were placed in individual battery cages and the egg yields recorded on a daily basis at the same time of the day.

Blood and tissue samples were collected from the F0, F1 and F2 populations, and DNA was isolated using standard phenol/chloroform method. For chromosomal scanning, a total of 113 microsattelite markers (Table 1) at an interval of 30-40 cM were selected from previously published chicken consensus linkage map (Groenen et al 2000) and the ArkDB genome database (http://www.thearkdb.org). The forward primer of each locus was fluorescently labelled with WellRED dye (D4, D3 or D2) suitable for multiplex polymerase chain reaction (PCR) and fragment analysis. The multiplex PCRs were carried out in a total volume of 15 µL compromising 1x Mg^{++} free PCR buffer (Fermentas), 200 µMol dNTP (Fermentas), 1.5 mM $MgCl^{++}$, 0.375 U of *Taq* polymerase (Fermentas), 3-5 pMol of each primer pair (Table 1) and 50 ng template DNA.

A touchdown PCR profile was employed as previously described (Ozsensoy et al 2010) using a MJ Research PTC-200 Thermal cycler. PCR products were separated using capillary electrophoresis on a Beckman Coulter CEQ-8000 Genetic Analysis System, and marker genotypes were determined after fragment analysis.

The genetic distances between the markers and linkage groups were determined by using the TWOPOINT, BUILD, CROMPIC and ALL options of the CRI-MAP software (Green et al 1990) on a MS-DOS system. Comprehensive linkage gene maps were constructed as described in elsewhere (Kurar et al 2002).

Table 1. Microsatellite loci used in genotyping.

Locus	Chromosome	Primer Sequence		Labeling
		Forward	Reverse	
MCW0168	1	gatcagatttatttcccctca	ctgatttctagagctgactga	D4
HUJ0001	1	ctttgttaacacctactgca	tccggcttatacagagcaca	D4
GCT0006	1	atttcctattcccctctc	ccagaaaacatcaccaac	D3
MCW0106	1	ggcaactaagttgtggactg	gcagcattcagtgggataat	D3
ADL0019	1	tgctgcctagaccagttcaa	tctgctgggattatgtgtca	D2
ADL0234	1	ctggacgcgtgaaaaagttc	ccctggggctccctcagcac	D2
UMA1.125	1	ccagcatgtgattcccaagt	agtgtttccaggggcaagga	D4
ADL0150	1	atgccaagcattacagaagc	cctgcagcacctttatctct	D3
MCW0101	1	gtttgtttgcatctgtagtctg	ccatattctgttagaaagtagag	D4
ADL0251	1	tttggcttagggtgatgctg	cgtgctccacacaggaatgt	D4
LEI0217	1	gatgactgagagaaataacttg	aaattactgaggcacaggag	D4
UMA1.117	1	ttagaatgcactggacacag	tgttcttttgagggatgatt	D3
ADL0037	1	atgccccaaatctcaactct	tctctaaaatccagccctaa	D3
UMA1.019	1	acactggcaggcgtgcttag	gcttgaggacaggggtcagg	D2
LAMP1	1	gcgttgagtgagaggagcga	caacccgcggagagcgctat	D2
MCW0145	1	actttattctccaaatttggct	aaacacaatggcaacggaaac	D4
ABR0328	1	cacccatagctgtgactttg	aaaaccggaatgtgtaactg	D4
ADL0101	1	ccccaaggagaactgattac	gaaaagtgaaaacgcaaaca	D3
ADL0238	1	aaacccaaacaaaagcagac	gctcctcataagcaaaatgc	D2
MCW0082	2	gatctttaaggggaaagatat	cttttgatgcctctccatttc	D3
ADL0152	2	agattagtgcagatcatcca	tgttttgccatttcagaagc	D4
ADL0185	2	catggcagctgactccagat	agcgttacctgttcgtttgc	D3
MCW0065	2	tcagcaacagaagtgaagggcaat	caggcattacttcaataacgaggc	D2
LEI0089	2	gatccaggtggctctaacacg	ttagctcctgcttgtcactgc	D2
MCW0039	2	cattggactgagatgtcactgcag	acatttgtctaatggtactgttac	D2
BCL2	2	tcgcaccgttaagttacacc	agcatcaaagcgtcgcgttc	D4
ADL0267	2	aaacctcgatcaggaagcat	gttattcaaagccccaccac	D3
LEI0147	2	tcaggcctcttgaactcagg	gctattaagatacctcagctc	D4
ADL0114	2	ggctcataactacctttttt	gctctacattccttcagtca	D4
MCW0166	2	gatcagaaagaactggaactg	aggagttagttgaaccagaac	D3
LEI0070	2	tgcggagagcaattagtctgc	ggaaaacaatcactgcctcg	D2
ADL0146	2	tgcttcctacccattctcct	gacctgcattgtcagtgacc	D4
MCW0157	2	gtgtgatgtaggccagatgtc	gtgctgcattctgccaatagg	D3
MCW0169	3	gatcccacttgttaagaagtg	cctgaccttactgagcttgga	D4
MCW0083	3	gcctttcacccatcttactgt	tacatttcagaaggaatgttgc	D3
ADL0370	3	acagatatcaaacttccaag	aatatctatgctgaaatgtg	D4
ADL0155	3	ggtccgactgaaagcattat	ttaagactgaagccaaccag	D4
ADL0127	3	gaaccagcaattatattaaata	ttaacacaaaagaaccaggcag	D4
ADL0115	3	ggatgagaagaagaaaggca	caatggtggttcaggtaatc	D3
ADL0306	3	gttactgtatcttggctcat	tcagtttgactttccttcat	D2
GCT0053	3	catcagcatcagcgttgttt	atgtgcaccctctcatcaca	D4
ROS0305	3	aatagatcccttggctacac	tgtgcagcaacctcagatgt	D3
ADL0203	4	acccctccccatctcactgc	gctccaccactgctcgtgtg	D4
ADL0145	4	cgtggtgttgtgtatcattt	ctcttttgcagtcctcctac	D4
MCW0005	4	acctcctgctggcaaataaattgc	tcactttagctccatcaggattca	D3
ADL0266	4	aatgcattgcaggatgtatg	gtggcattcaggcagagcag	D3
LEI0094	4	gatctcaccagtatgagctgc	tctcacactgtaacacagtgc	D3
LEI0081	4	acttacctttttcttagctactg	gatcctttcaatgctcatgct	D2
UMA4.034	4	ggtgatttggggagaatgag	agggaggaggggctttactc	D2
LEI0073	4	ccatatcatttgtcaagcacc	aattcctgacctccatgatac	D2
ADL0247	5	ctcttgttgtctgtcttgtg	tgcatgttgtcagttttcag	D4
MCW0090	5	gatccttcttcctctctcctg	ccttcaacttaaaacattatagag	D4
ADL0292	5	ccaaatcaggcaaaacttct	aaatggcctaaggatgagga	D3
ADL0239	5	gaaaaagcagagcagtgtct	gtgatgggaaaatcttcagg	D3
ADL0233	5	gccctttaaacccaagactc	gggggaaaaggatgcttagc	D2
ADL0298	5	caaggctgggattgatgaaa	tggcgtgtgggtttacaaaa	D2

LEI0212	6	tttgccaatccctattgagc	ttttcatatttgtggcgtgc	D4
ADL0040	6	tttccccagatttacaactt	gccagtgatactccagcagc	D4
ADL0377	6	atattctggggacatctgtg	gtagggatccgtagtttttg	D2
ADL0142	6	cagccaatagggataaaagc	ctgtagatgccaaggagtgc	D2
ABR0326	7	gctcacaagaaggggtcaca	ccacctctggtttcctcacc	D4
ADL0107	7	attatccatccacttgagaa	tatttttgaacattaccag	D3
MCW0178	7	actggaattttagggcaacag	aactgttagctaatatgacctg	D4
ADL0279	7	catggctgttgctttacata	catggctgttgctttacata	D3
ADL0109	7	atctccataacttctgctgc	atctccataacttctgctgc	D4
ADL0315	7	tccttgggcagtagtttcaa	tccttgggcagtagtttcaa	D3
ADL0169	7	ccacaccaaactgcttcata	ccacaccaaactgcttcata	D2
MCW0095	8	gatcaaaacatgagagacgaag	gatcaaaacatgagagacgaag	D2
ABR0345	8	tttcacacgcagcctttctc	tttcacacgcagcctttctc	D2
ADL0301	8	tcctccctgaagtccttaca	tcctccctgaagtccttaca	D3
ADL0191	9	aaaggaaagcctatgtgaat	aaaggaaagcctatgtgaat	D4
MCW0190	9	gtgatcatttctacatgcag	gtgatcatttctacatgcag	D3
ADL0136	9	tgtcaagcccatcgtatcac	tgtcaagcccatcgtatcac	D3
MCW0134	9	ggagacttcattgtgtagcac	ggagacttcattgtgtagcac	D3
ADL0209	10	ggttagctccctccttccag	ggttagctccctccttccag	D2
ADL0231	10	aaggaaacaaagagaaatcc	aaggaaacaaagagaaatcc	D4
ADL0102	10	ttccacctttctttttatt	gctccactcccttctaaccc	D3
ADL0112	10	atctcaaatgtaatgcgtgc	ggcttaagctgacccattat	D2
ADL0123	11	gctgtgtcaagattagaatcac	aacaatgaaaaacactacctga	D4
ADL0210	11	acaggaggatagtcacacat	gccaaaaagatgaatgagta	D3
MCW0230	11	tgcacagagccaagctgcttc	gatcctctgatggctgccg	D4
ADL0372	12	cgccccgtttactgatttg	ggcgccgttcaaggaagcac	D4
ADL0044	12	aagtggtttattgaagtaga	ctgtggtgttgcgttagttg	D3
GCT0055	12	gaacatgggcaatgctcttt	tgtgttcctctccatgcgta	D2
MCW0332	12	tgggtttgcaacgggacatag	gaacaatggtgagagcactgc	D4
ADL0147	13	ctggtgaatgagaagcgatg	gctgcggcaataaactccct	D3
LEI0251	13	gggttactcttatgtttaatgatgtc	gatctagaaatggctgactgac	D2
MCW0104	13	tagcacaactcaagctgtgag	agacttgcacagctgtgacc	D4
LEI0098	14	cagttagcagagattttcctac	tgccactgatgctgtcactg	D3
ADL0263	14	agagtcagaaagtgggaagg	ctgttcggttggttgttgg	D2
MCW0080	15	gaaatggtacagtgcagttgg	ccgtgcattcttaattgacag	D2
LEI0258	16	caggcagcagaacttggtaagg	agctgtgctcagtcctcagtcg	D3
HUJ0002	17	gaatcctggatgtcaaagcc	atctcacagagccagcagtg	D2
ADL0202	17	ctgcttgttcttccccttca	ctctgctctctgtgcctcaa	D4
MCW0217	18	gatctttctggaacagatttc	ctgcacttggttcaggttctg	D4
MCW0094	19	ggagctggtatttgtcctaag	gcacagccttttgacatgtac	D2
LEI0090	23	tagtgcagccctatggagcg	ggtgagtgtgcgttacacgc	D3
ROS0302	24	cacagacaccccgtacag	acacagcgttggttatgcc	D2
ROS0314	26	cagctcacattttagcagtc	tttattgatttctccaacaa	D3
LEI0074	26	aaacgtctgccttcatgcgag	catcaattagagcgaagcctc	D4
COL1A1	27	cggaccatgaatttggcatt	ttactctctcctgtcacgcg	D3
ADL0376	27	gccccacggagatggaacac	cctgccctgctgctggaact	D2
MCW0188	E22	gtgacagcggcagagatgga	cgcacagccccactcgcaca	D4
GCT0037	E26	agccacacagcacacagttc	attggttttctgatggcctg	D3
GCT0042	E38	gggtttgtcacctcctggt	tagaggcacgggaaggtatg	D2
ADL0034	E47	aacctaaaaactcctgctgc	gggaacctgtgggctgaaag	D3
GCT0004	E50	gtgatgcacacacaactg	cttcttcatctacgctgtc	D4
ROS0309	Z	gtgccaccaattaacagagg	gatcaggaaaggctgtgaag	D3
ADL0273	Z	gccatacatgacaatagagg	tggtagatgctgagaggtgt	D2
MCW0246	Z	tcataaggcagagaattcatc	tttccattcagacaacaaggc	D4
LEI0121	Z	ttgacgtcctggatagattac	attatccagaactaacatcaac	D3
LEI0075	Z	ctatgctatcattgaaacacagc	atccagtgcgtgtctggtcag	D2

QTL mapping was conducted using the QTL Express Programme (Seaton et al 2002) that enables the calculation of F2 population data based on the regression model (Haley et al 1994). Marker genotypic probabilities were calculated in 1 cM interval covering the genome. Chromosome- and genome-wide critical thresholds were also calculated by the QTL Express Programme. Chromosome-wide thresholds ($p<0.05$) were calculated by 1,000 permutation tests (Churchill and Doerge 1994). Furthermore, genome-wide statistical threshold values were derived using the Bonferroni correction (de Koning et al 1999).

Results

Multiplex PCR and genotyping were performed for microsatellite analyses. Owing to its flexible annealing property, the touchdown PCR protocol enabled the amplification of different primers under the same conditions. Using the F0 DNA samples, the multiplex PCR and capillary electrophoresis analyses of the 113 microsatellite loci were optimized. Eleven loci were excluded from the analyses due to various problems encountered in fragment analysis, including unsuitability for multiplex analyses, the presence of non-specific allele peaks and interference between the allele peaks of other loci. It was observed that ADL247, MCW0217 and ROS0309 loci were homozygous for the same alleles in the Denizli and Leghorn parent populations. Since these markers did not bear any informative value for the detection of chromosomal heredity, they were not used in the genotypic analyses of the F1 and F2 populations.

Table 2. The QTL regions determined to be responsible for hatching weight and body weight at different age periods.

Chromosome	Phenotype	Marker Interval	QTL Region (cM)
GGA1a	Hatching Weight	MCW0106-ADL0019	75
GGA1a	3	MCW0106-ADL0019	72
GGA1a	6	MCW0106-ADL0019	77
GGA1a	9	MCW0106-ADL0234	71
GGA1a	12	MCW0106-ADL0019	78
GGA1a	16	MCW0106-ADL0234	99
GGA1a	20	MCW0106-ADL0234	82
GGA1a	24	MCW0106-ADL0019	71
GGA1a	28	ADL0150-ADL0251	203
GGA1a	32	ADL0150-ADL0251	209
GGA1b	6	LAMP1-MCW0145	84
GGA1b	9	LAMP1-MCW0145	75
GGA1b	12	LAMP1-MCW0145	77
GGA2	6	MCW082-ADL185	33
GGA2	12	MCW082-ADL185	38
GGA4	28	LEI0094-UMA4.034	195
GGA4	32	ADL0266-UMA4.034	130

A total 28 linkage groups, including 3 for the chromosome 1 (GGA1) and 2 groups for GGA3 and GGA9, were established. After excluding monomorphic and problematic loci from the linkage analyses, GGA16, GGA18 and GGA19 were remained uncovered and no markers represented these chromosomes.

The chromosomal regions associated with different body weights were shown in Table 2. The QTL regions responsible for hatching weight and body weight at weeks 3, 6, 9, 12, 16, 20, 24, 28 and 32 were determined on GGA1, GGA2 and GGA4. Three potential QTL regions were determined on GGA1.

Chromosomes GGA8 and GGAZ harboured two different QTL regions which were responsible for the controlling egg yield (Table 3). GGA2, GGA4 and GGAZ harboured 3 different QTL regions affecting egg weight (Table 3). A QTL region found on chromosome GGAZ was associated with both egg yield (number of eggs produced) and egg weight. Similarly, evidence for a location affecting both body weight at the 32nd week and egg weight on GGAZ was obtained

Discussion

In general, the conventional methods applied in livestock and poultry breeding and the genetic improvement are based on principles of Mendelian inheritance and the theory of quantitative genetics. The most of animal traits bear quantitative character and are controlled by the additive effect of multiple genes (Falconer 1960). Therefore, marker genotypes linked to highly effective gene(s) can be used in order to improve a trait with high heritability.

Natural populations are generally preferred in QTL analyses of animal species such as cattle, sheep and equine. In QTL analyses of mice, rats and poultry however, experimental populations are used owing to multiple reasons including their shorter generation interval and ease in feeding and management compared to other animals species. Backcross (BC) and F2 hybrids are mostly used for development of experimental populations. Generation and analysis of BC populations are generally easier however distributions of the traits and recombination levels are often remained limited. Construction and statistitical methods used in F2 population may be sophisticated however distribution of the trait of the interest and relatively higher recombination rates makes F2 populations preferable population structure in QTL and gene mapping studies (Alfonso and Haley 1998). The analysis of a F2 population composed of 400-600 individuals enables the identification of QTL regions (Burt and Hokking 2002).

Numerous F2 populations have been constructed for linkage and QTL gene mapping and research using pure lines of the Red Jungle Fowl (RJF), Rhode Island Red (RIR) and

White Leghorn (WL) breeds. For example, F2 populations of RJF X WL (Kerje et al 2003b, Keeling et al 2004), RIR X WL (Tuiskula-Haavisto et al 2002, Sasaki et al 2004), WL X WL (Yonash et al 2001, Buitenhuis et al 2003, Siwek et al 2003) intercrosses have been generated. Size of the F2 populastions were ranged from 238 (Gao et al 2006) to 2063 (Nones et al 2006) hens. In the present study, a F2 level Denizli X White Leghorn population was constructed including 211 male and 230 female F2 animals. Therefore, population size of this study met the minimum level set for QTL analyses by Burt and Hokking (2002). No potential problem was encountered for QTL analysis of traits including hatching weight and body weight gain. However, in the QTL analyses of sex-specific traits, such as the egg yield of female animals, the size of the population seems to be inadequate. Related to this issue, a number of QTL research are available, which were conducted in relatively smaller (238-265) F2 chicken populations (Sasaki et al 2004, Gao et al 2006).

Table 3. The QTL regions identified for egg production traits.

Chromosome	Phenotype	Marker Interval	QTL Region (cM)
GGA8	Number of eggs	MCW0095-ARB0345	19
GGAZ	Number of eggs	ADL0273-MCW0246	22
GGA2	Egg weight	ADL185-MCW0065	93
GGA4	Egg weight	ADL0266-UMA.4034	125
GGAZ	Egg weight	ADL0273-MCW0246	19

It was determined that the linkage map were generallly in agree with the previously published chicken consensus linkage map (Groenen et al 2000). However, the marker intervals were generally longer than expected. Based on a simulation study, Buetow (1991) reported that an error rate of 1% in genotyping data could increase the map length 2 cM for every interval. A similar situation was also encountered in the chromosome linkage maps of other species (Kurar 2001).

In the present study, the QTL Express Programme (Seaton et al 2002) was used for the analysis of QTL regions using the regression model (Haley et al 1994). QTL regions were determined on GGA1, GGA2 and GGA4 responsible for the body weights at weeks 3, 6, 9, 12, 16, 20, 24, 28 and 32 (Table 2). These QTL regions were similar to those previously identified in different populations using different statistical methods. The marker set used in the present study was different than the other QTL studies, however findings were compared based on the use of the chicken consensus linkage map (Groenen 2000) as a standard.

Two different regions of the GGA1 harboured three different QTL regions, which affected body weights at different age periods (Table 2). The first QTL region, which was found on the first linkage group (GGA1a) within a range of 71-99 cM, controlled the body weight up to the week 24. Previous studies indicated that this region was associated with body weights at different ages including hatching (Kerje et al 2003a) and body weights at weeks 5 (Nones et al 2006), 6 (Nones et al 2006, Zhou et al 2006), 7 (Kerje et al 2003a), 8 (Zhou et al 2006), 13 (Tatsuda et al 2000) 16 and 29 (Kerje et al 2003a).

Nones et al (2006) investigated QTL regions for body weight, carcass weight, organ and various carcass parameters using a F2 population composed of 2063 laying hens and broilers. By performing selective genotyping approach, GGA1 was detaily investigated in detail using 80 microsatellite markers and it was determined that the GGA1 harboured two different QTL regions affecting body weight at the 5th and 6th weeks. One of these regions displayed a similar localization to that of a QTL region determined in the present study.

A second QTL region exists within a range of 203-209 cM at the first linkage group of chromosome 1 (GGA1a). This QTL region was associated with adult body weight at weeks 28 and 32. This QTL region was also determined for body weight at different age periods and body weight gain in previous studies (Van Kaam et al 1999, Tatsuda and Fujinika 2001, Jennen et al 2004, Tuiskula-Haavisto et al 2004). Another QTL located in the GGA1b was determined within a range of 75-84 cM that was responsible for body weight between weeks 6 to 12 (Table 2). The same region was also reported to associate with body weight at weeks 4, 6, 7, 8 and 9 and growth performance traits in different populations (Van Kaam et al 1999, Sewalem et al 2002, Wardecka et al 2002, Kerje et al 2003a, Zhou et al 2006). GGA2 harbours another QTL (33-38 cM) associated with body weight between weeks 6 and 12. It was reported (Tatsuda and Fujinika 2001, Siwek et al 2004) that the same region of GGA2 had an effect on body weight at weeks 4-16.

The investigation of GGA4 revealed the presence of a QTL region within a range of 130-195 cM, which was associated with adult body weight (at weeks 28 and 32). Similarly, the same QTL region was reported to be linked to body weight at different periods and growth performance in previous literature (Van Kaam et al 1999, Sewalem et al 2002, Wardecka et al 2002, Kerje et al 2003a, Sasaki et al 2004, Tuiskula-Haavisto et al 2004). The QTL interval determined in the present study is quite wide (~45 cM) and was associated body weight at different age periods. Therefore, these finding suggest that there may have more than one QTL exist in this region.

Previous QTL mapping efforts indicated that GGA3 harboured QTL regions responsible for body weight at different age periods and growth (Ikeobi et al 2002, Wardecka et al 2002, Kerje et al 2003a, Siwek et al 2004, Tuiskula-Haavisto et al 2004, Zhou et al 2006). However, in the present study, no QTL region was

identified on chromosome 3. Three microsatellite markers of GGA3 were excluded from linkage analyses due to genotyping problems and two different linkage groups were established for GGA3. It was considered that the absence of body weight-associated QTLs on GGA3 was due to either inadequate recombination events in this genomic region or the nature of the population used in the study.

It is known that quantitative traits such as body weight are controlled by the additive effect of multiple genes. In QTL research, it is aimed to determine the most effective gene and chromosomal regions on quantitative traits and to use these in molecular selection studies. The results of the present study have demonstrated the presence of at least five QTL regions on chromosomes GGA1, GGA2 and GGA4 in a Denizli X Leghorn population. Naturally, there may be the effect of multiple genes in a particular QTL region. However, the results of the present study and the QTL regions determined in the literature discussed above suggested that different QTL regions and genes may be effective in the control of body weight at different age periods in the chicken. For example, the QTL region determined on the chromosome GGA4 controls body weight in the adult period. Therefore, genes may control body weights in different periods of the lifespan through different mechanisms such as development of the digestive system, muscular development, fat deposition etc.

Egg yield (number of eggs produced) analyses performed in the Denizli X Leghorn F2 population revealed the presence of two different QTL regions on the chromosome GGA8 and the sex chromosome (GGAZ). Tuiskula-Haavisto et al (2004) have reported the presence of QTLs affecting egg yield, in similar regions of the chromosomes GGA8 and GGAZ. Three different QTL regions associated with egg weight were determined on GGA2, GGA4 and GGAZ. In previous studies, QTL regions associated with egg weight and egg quality traits (egg yolk, egg shell and albumen weight) were determined in the similar regions (Tuiskula-Haavisto et al 2002, Kerje et al 2003b, Sasaki et al 2004). The QTL associated with egg yield and egg weight were located in the same region of the GGAZ demonstrated that these traits could be under control of the same gene(s). A pleitropic effect therefore may exist. This situation may be explained by the proximity of the genes controlling these traits to each other, and thus the existence of a linkage. Similarly, both the QTLs associated with egg weight and body weight at week 32 were found to be located in the same region of GGA4. Therefore, it is considered that a QTL with pleitropic effect on body weight and egg yield may be present in this region. In fact, body weight and egg weight are positively correlated with each other.

In the present study, only a limited number of QTL regions affecting egg yield could be identified. This may have arisen from the feature of the Denizli X Leghorn F2 population in which a sufficient distribution was occurred for this particular phenotypic trait. This may have resulted from the marker set used in this QTL mapping effort as well.

Conclusions

In the present study, a F2 level population was generated using the Denizli, a local genetic resource, and the Leghorn breeds. It was determined that QTL regions, affecting body weight at different age periods and egg yield, were located on the chromosomes GGA1, GGA2, GGA4, GGA8 and GGAZ. In general, the distances between the QTL regions were wide (>30 cM). Therefore, the relevant QTL intervals should be narrowed by the use of new markers and there is need for positonal cloning studies to detect the genes as well as nucleotide variations controlling these traits.

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