Genome-Wide Linkage Analysis to Identify Chromosomal Regions Affecting Phenotypic Traits in the Chicken. II. Body Composition[1]

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ABSTRACT Two informative chicken F_2 populations based on crosses between a broiler breeder male line and dams from genetically distinct, highly inbred (>99%) chicken lines, the Leghorn G-B2 and Fayoumi M15.2, have been used for genome-wide linkage and QTL analysis. Phenotypic data on 12 body composition traits (breast muscle weight, breast muscle weight percentage, abdominal fat weight, abdominal fat weight percentage, heart weight, heart weight percentage, liver weight, liver weight percentage, spleen weight, spleen weight percentage, and drumstick weight, and drumstick weight percentage) were collected. Birds were genotyped for 269 microsatellite markers across the genome. The QTL Express program was used to detect QTL for body composition traits. Significant levels were obtained using the permutation test. For the twelve traits, a total of 61 (Gga 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, 18, 24, and Z) and 45 (Gga 1, 2, 3, 4, 6, 7, 8, 9, 10, 12, 15, 17, and E46) significant QTL were detected at the 5% chromosome-wise significance level, of which 19 and 11 were significant at the 5% genome-wise level for the broiler-Leghorn cross and broiler-Fayoumi cross, respectively. Phenotypic variation for each trait explained by all QTL across the genome ranged from 3.22 to 33.31% in the broiler-Leghorn cross and 4.83 to 47.12% in broiler-Fayoumi cross. Distinct QTL profiles between the 2 crosses were observed for most traits. Cryptic alleles were detected for each trait. Potential candidate genes within the QTL region for body composition traits at the 1% chromosome-wise significance level were identified from databases for future association study. The results of the current study will increase the knowledge of genetic markers associated with body composition traits and aid the process of identifying causative genes. Knowledge of beneficial genetic variation can be incorporated in breeding programs to enhance genetic improvement through marker-assisted selection in chickens.

Key words: genome scan, quantitative trait loci, body composition, broiler, inbred line

INTRODUCTION

Understanding the relative size of components that comprise the body of the chicken may yield information to improve fitness and increase feed efficiency. Breast muscle yield is the most economically valuable part in broilers. Excess fat in the poultry carcass is an important issue in the poultry industry. Fat can affect the animal industry in 4 aspects: consumer health concern, lower feed efficiency, undesired by-product, and labor expenses of trimming waste fat (Eisen, 1989). The internal organs are essential for supporting all physiological mechanisms of the large body mass of broilers. Due to the difficulty and expense of obtaining these phenotypic data, it is hard for traditional selection methods to make improvement in these body composition traits. The MAS method provides a promising way to make genetic improvement for these traits. There are general negative genetic correlations between growth and fitness traits; however, it is possible to select for genotypes with high body mass and high fitness using MAS when different linkage phases are detected between markers and QTL affecting growth and fitness.

A limited number of studies have mapped QTL for body composition traits in chickens. Jennen et al. (2004) conducted a genome scan analysis for QTL affecting fatness in a F_2 population generated by 2 broiler dam lines. Also, QTL for fatness traits were mapped in a F_2 population generated by crossing a broiler and layer line (Ikeobi et al., 2002). Lagarrigue et al. (2006) reported QTL affecting fatness and breast muscle weight (**BMW**) in meat-type chicken lines divergently selected for abdominal fatness. The QTL for body composition in an intercross between chicken lines divergently selected for growth were identified by Park et al. (2006). McElroy et al. (2006) identified

10 QTL affecting white meat in 7 F_2 half-sib families derived from crosses of 2 commercial broiler lines. Several studies have investigated QTL affecting carcass weight, fatness, and internal organ weights in swine (Malek et al., 2001; Geldermann et al., 2003) and in mice (Rocha et al., 2004). McElroy et al. (2002) reported QTL for breast meat yield in Gga 2 in a F_2 population generated from commercial broiler lines. Few investigations in the chicken have evaluated components of BW with a more holistic approach, including BMW and drumstick weight (**DS**), as well as fatness and weights of internal organs.

The Iowa Growth and Composition Resource Population, used in the present study, was produced by crossing sires from a broiler breeder male line with dams from genetically distinct, highly inbred (>99%) chicken lines, the Leghorn G-B2 and Fayoumi M15.2 (Zhou and Lamont, 1999; Deeb and Lamont, 2002). This resource population has been used to study associations of body composition traits with several candidate genes, such as insulin-like growth factor 1 and spot 14 (Wang et al. 2004; Zhou et al., 2005). Broilers used in the study have demonstrated considerable differences compared with the 2 diverse inbred lines in BMW, fatness, DS, and internal organs (Deeb and Lamont, 2002). This unique genetic resource, with novel experiment design, has provided an excellent opportunity to dissect genetic control of complex traits of body composition in chickens (Lamont, 2003). The objectives of the current study were aimed at detecting and localizing QTL affecting body composition traits in chickens with genome-wide scan analysis.

MATERIALS AND METHODS

Resource Populations

The 2 F_2 populations were generated from a broiler breeder male line crossed with dams from 2 genetically distinct, highly inbred (>99%) chicken lines, the Leghorn G-B2 and Fayoumi M15.2 (Zhou and Lamont, 1999; Deeb and Lamont, 2002). Details on the family structure are described in Zhou et al. (2006).

Phenotypic Measurements

The phenotypic measurements included BMW, DS, shank weight (**SHW**), shank length, tibia length, abdominal fat weight (**AFW**), spleen weight (**SW**), liver weight (**LW**), and heart weight (**HW**). All traits were also expressed and analyzed as a percentage of BW at 8 wk of age. Sex was determined by macroscopic inspection of the gonads. Details of means and variation are presented in Deeb and Lamont (2002). In brief, birds were euthanized at 8 wk of age. Chicken pectoralis major and pectoralis minor were measured as BMW. Drumstick weight included bone and muscle of the drum.

Marker Selection, Genotyping and Linkage Analysis, and QTL Mapping

All birds were genotyped for 269 markers, as described by Zhou et al. (2006). The marker linkage analysis and

Table 1. The 5 and 1% chromosome-wise significance levels, as determined by permutation test, for body composition traits by chromosome in the broiler-Leghorn cross and broiler-Fayoumi cross

Gga	Broiler-Leghorn cross		Broiler-Fayoumi cross	
	5%	1%	5%	1%
1	7.39	9.90	7.21	9.27
2	5.99	7.99	7.04	9.36
3	6.36	8.27	—	—
4	5.68	7.61	5.51	7.31
5	5.88	8.14	—	—
6	5.03	7.03	5.06	7.06
7	5.37	7.42	5.21	7.13
8	4.64	6.51	4.48	6.39
9	5.36	7.40	5.45	7.47
10	4.84	6.82	4.76	6.66
12	—	—	4.36	6.33
15	5.21	7.43	4.33	6.16
17	—	—	5.09	7.16
18	4.88	6.87	—	—
24	4.18	5.94	4.69	6.80
Z	4.84	6.71	—	—
E46	—	—	4.39	6.41

QTL mapping used were described in Zhou et al. (2006). Significance levels at the 5 and 1% chromosome-wise and the 5 and 1% genome-wise levels were determined by permutation, as described by Zhou et al. (2006).

Significance Thresholds

Individual chromosome significance levels at the 5 and 1% levels, as determined by the permutation test, differed slightly by trait (Table 1). Average 5% chromosome-wise thresholds ranged from 4.18 to 7.39 in the broiler-Leghorn cross and from 4.33 to 7.21 in the broiler-Fayoumi cross. Average 1% chromosome-wise thresholds ranged from 6.51 to 9.90 in the broiler-Leghorn cross and from 6.33 to 9.36 in the broiler-Fayoumi cross. Average 5 and 1% genome-wise thresholds were 9.60 and 11.81, respectively, in the broiler-Leghorn cross and were 9.45 and 12.28, respectively, in the broiler-Fayoumi cross.

RESULTS

Phenotypic Correlations Between Body Composition Traits

The partial correlations between body composition traits in the combined 2 F_2 populations are presented in Table 2. In general, there were high correlations between each 2 absolute traits (0.115 to 0.860), as expected, whereas there were low correlations between relative body composition traits (0.0006 to 0.700). The phenotypic correlations between each absolute trait and its relative trait were very high (0.34 to 0.82), whereas the correlation between BMW and BMW% was relatively low (0.34), compared with the others. Breast muscle weight had relative higher correlations with all absolute traits than with relative traits, whereas BMW% had low and negative correlations with all traits. There were negative correlations between AFW% and all traits, except AFW, LW, and LW%.

Table 2. Phenotypic correlations among body composition traits in the F$_2$ population ($P < 0.05$)[1]

Trait	BMW	AFW	AFW%	HW	HW%	LW	LW%	SW	SW%	DS	DS%
BMW	0.34	0.31	−0.21	0.68	0.04†	0.54	−0.17	0.57	−0.09	0.86	0.27
BMW%	—	−0.17	−0.13	−0.14	−0.13	−0.20	−0.17	−0.09	−0.04†	−0.06†	0.06†
AFW	—	—	0.82	0.18	−0.18	0.42	0.14	0.12	−0.23	0.22	−0.34
AFW%	—	—	—	−0.28	−0.26	0.04†	0.20	−0.26	−0.20	−0.32	−0.53
HW	—	—	—	—	0.69	0.59	0.01†	0.62	0.08	0.78	0.33
HW%	—	—	—	—	—	0.18	0.14	0.24	0.22	0.16	0.24
LW	—	—	—	—	—	—	0.66	0.41	−0.07†	0.58	0.06†
LW%	—	—	—	—	—	—	—	−0.08	−0.001†	−0.15	−0.17
SW	—	—	—	—	—	—	—	—	0.70	0.64	0.28
SW%	—	—	—	—	—	—	—	—	—	−0.03†	0.12
DS	—	—	—	—	—	—	—	—	—	—	0.58

[1]BMW = breast meat weight; AFW = abdominal fat weight; HW = heart weight; LW = liver weight; SW = spleen weight; DS = drumstick weight; and % = absolute measure/100 g of BW.

†$P > 0.05$.

General QTL Mapping Results

Estimates for QTL significant at the 5% chromosome-wise level are presented in Tables 3 and 4. For the QTL graphs, representing plots of the *F*-statistic across chromosomes, only QTL significant at the 1% chromosome-wise level are presented in Figures 1 and 2. The QTL for BMW, AFW, and HW traits are in Figure 1, and the QTL for LW, SW, and DS are in Figure 2. For comparison purposes, if one of the QTL in a group of traits in 1 cross was significant at the 1% chromosome-wise level, QTL for all traits in both F$_2$ crosses are presented. Although some graphs suggest evidence for multiple QTL in adjacent intervals for the same trait, only results for the most significant position are presented in Tables 3 and 4, because only single QTL models were tested.

For the 12 traits examined, 62 and 44 QTL in total were detected at the 5% chromosome-wise level in the broiler-Leghorn cross and the broiler-Fayoumi cross, respectively, not counting potential multiple QTL in adjacent intervals. Thirteen QTL would be expected to be significant at suggestive threshold by chance alone, given the 12 traits examined. Therefore, about 5 and 3 times as many QTL were detected at this level than were expected by chance in the broiler-Leghorn cross and the broiler-Fayoumi cross, respectively. Of the 62 suggestive QTL in the broiler-Leghorn cross, 19 QTL were significant at the 5% genome-wise level (Table 5). Of the 44 suggestive QTL in the broiler-Fayoumi cross, 11 QTL were significant at the 5% genome-wise level (Table 5). Over the 12 traits examined, 1 QTL would be expected to be significant at this level by chance alone. Thus, clearly, more QTL were identified at this level than were expected. The phenotypic trait variances explained by QTL ranged from 2.50 to 13.68% in the broiler-Leghorn cross and from 3.17 to 10.85% in the broiler-Fayoumi cross (Tables 3 and 4).

BMW and BMW%. For the broiler-Leghorn cross, 6 QTL for BMW were detected on Gga 2, 3, 4, 7, 8, and 9, and 5 QTL for BMW% were detected on Gga 2, 8, 9, 12, and Z (Table 3). The additive effect suggested that broiler alleles were superior to the Leghorn alleles, except for the QTL for BMW% on Gga 12 and Z. Three of the 6 QTL for BMW showed overdominance, and heterozygotes, concerning QTL breed origin, had greater BMW than either of the homozygotes, except for the QTL on Gga 8 (Table 3). For the broiler-Fayoumi cross, QTL for BMW were identified on Gga 1, 2, 4, 7, 8, and 9, and QTL for BMW% were identified on Gga 2, 7, 8, and 9 (Table 4). Broiler alleles tended to be associated with greater BMW or BMW% than the Fayoumi alleles for 7 out of 10 QTL (Table 4). Six of the 10 QTL showed overdominance. Heterozygotes had greater BMW or BMW% than either of the homozygotes, except for the QTL on Gga 1 for BMW and the QTL on Gga 7 for BMW% (Table 4). The total trait variances explained by QTL for BMW and BMW% were 30.59 and 16.92% in the broiler-Leghorn cross and 28.43 and 16.46% in the broiler-Fayoumi cross, respectively (Table 5).

AFW and AFW%. For the broiler-Leghorn cross, 6 QTL for AFW were identified on Gga 5, 7, 8, 15, 24, and Z, and 6 QTL for AFW% were identified on Gga 1, 5, 7, 8, 24, and Z (Table 3). Broiler alleles tended to be associated with greater AFW or AFW% than the Leghorn alleles, except for AFW on Gga 8 and AFW% on Gga 1 and 8 (Table 3). Two of the 12 QTL showed overdominance (Gga 24 for both AFW and AFW%). Heterozygotes had greater AFW and AFW% than either of the homozygotes (Table 3). For the broiler-Fayoumi cross, 3 QTL for AFW were identified on Gga 4, 6, and 9, 5 QTL for AFW% were identified on Gga 4, 6, 9, 10, and 17 (Table 4). The additive effect suggested that broiler alleles were superior to the Fayoumi alleles, except for the QTL on Gga 9 for AFW. One of 3 QTL for AFW had a high degree of overdominance, and heterozygotes had greater AFW than either of the homozygotes (Table 4). The total trait variances explained by QTL for AFW and AFW% were 26.62 and 30.11% in the broiler-Leghorn cross and 19.35 and 23.51% in the broiler-Fayoumi cross, respectively (Table 5).

HW and HW%. For the broiler-Leghorn cross, QTL effects on HW were detected on Gga 1, 2, 4, 6, 7, 18, and 24, and 6 QTL for HW% were detected on Gga 9 (Table 3). Broiler alleles were superior to the Leghorn alleles for 5 out of 7 QTL for HW. Only 1 QTL on Gga 1 had an overdominance effect. For the broiler-Fayoumi cross, 3 QTL for HW were identified on Gga 1, 9, and 12, and 4 QTL for HW% were identified on Gga 1, 9, 10, and 12 (Table 4). Fayoumi alleles were superior to the broiler

Table 3. The QTL significant at the 5% chromosome-wise level for body composition in the broiler-Leghorn cross. Estimated significance levels (*F*-value), location, gene effects, and percentage of F$_2$ variance explained by each QTL

Gga	Trait[1]	*F*-value	Location	Additive effect[2]	SE	Dominance effect[3]	SE	Percentage of variance
1	AFW%	7.79	683	−0.22	0.06	−0.11	0.09	4.09
1	HW	12.17**	536	0.37	0.76	−0.66	0.78	6.25
1	SW	14.65***	725	0.45	0.09	−0.03	0.10	7.43
1	SW%	10.9**	522	0.52	0.01	−0.07	0.02	5.63
1	DS	10.01**	95	6.45	1.46	−1.88	3.43	5.20
1	DS%	8.6	89	0.14	0.03	−0.09	0.07	4.50
2	BMW	15.04***	238	4.49	2.68	−7.25	4.89	7.59
2	BMW%	6.45	219	0.27	0.07	0.04	0.12	3.41
2	HW	8.67*	272	0.41	0.10	−0.08	0.17	4.52
2	DS	11.41**	241	4.52	0.96	−1.38	1.77	5.77
2	DS%	6.31	96	−0.07	0.02	0.09	0.05	3.33
3	BMW	6.43	140	15.47	5.46	−12.53	7.56	3.39
4	BMW	18.45***	435	17.44	3.37	12.33	5.50	9.13
4	HW	13.44***	445	0.61	0.12	−0.03	0.23	6.86
4	LW%	6.97	428	−0.12	0.04	−0.08	0.06	3.68
4	SW	10.27**	236	0.24	0.05	−0.006	0.07	5.32
4	DS	28.93***	431	7.71	1.07	1.88	1.63	13.68
4	DS%	11.74**	428	0.13	0.03	−0.0001	0.04	6.05
5	AFW	7.79	165	5.34	1.36	0.03	2.24	4.09
5	AFW%	6.88	166	0.29	0.08	−0.05	0.13	3.64
5	LW%	7.31	155	−0.08	0.03	−0.13	0.05	3.85
5	DS%	11.2***	185	−0.12	0.03	0.05	0.03	5.78
6	HW	6.51	88	−0.47	0.13	−0.22	0.17	3.44
6	LW	7.95*	87	5.71	1.45	4.78	1.77	4.16
6	LW%	8.51*	46	0.26	0.06	0.18	0.08	4.46
6	DS	5.15	83	−4.01	1.38	−0.34	1.71	2.75
6	DS%	5.51	81	−0.10	0.03	−0.02	0.04	2.93
7	BMW	7.29	33	11.00	3.30	−14.07	5.17	3.84
7	AFW	16.94***	211	16.83	3.71	−2.06	4.27	8.50
7	AFW%	16.03***	237	0.78	0.17	0.21	0.20	8.12
7	HW	7.29	73	0.40	0.12	0.11	0.17	3.84
7	LW	15.47***	52	4.04	0.81	0.51	1.18	7.82
7	LW%	7.75*	53	0.11	0.04	0.10	0.06	4.07
7	SW	7.37	28	0.13	0.05	−0.25	0.07	3.88
7	DS	6.45	34	3.47	1.17	−5.17	1.81	3.41
7	DS%	7.39	208	−0.58	0.18	−0.40	0.19	3.89
8	BMW	5.33	61	7.68	3.11	8.97	4.64	2.84
8	BMW%	7.95*	60	0.27	0.08	0.24	0.12	4.18
8	AFW	6.67*	41	−7.44	3.02	−1.69	3.74	3.53
8	AFW%	11.43**	48	−0.42	0.09	0.03	0.14	5.89
8	DS	4.68	63	3.00	1.13	2.16	1.69	2.50
8	DS%	8.16*	67	0.12	0.03	0.005	0.04	4.28
9	BMW	7.2	151	21.40	6.66	−6.48	11.05	3.80
9	BMW%	6.85	230	0.48	0.14	0.17	0.17	3.62
9	HW%	6.1	180	−0.02	0.03	−0.015	0.03	3.22
9	LW%	5.66	112	−0.62	0.19	−0.60	0.19	3.01
10	LW	5.4	113	0.68	0.87	−5.92	1.89	2.87
10	LW%	7.37*	47	0.79	0.22	−0.54	0.22	3.88
10	SW%	10.01**	0	−0.01	0.002	−0.003	0.003	5.19
12	BMW%	5.14	0	−0.25	0.08	0.05	0.11	2.74
15	AFW	6.84	0	4.98	1.52	−1.08	1.96	3.61
18	HW	5.18	32	−0.55	0.22	−0.06	0.26	2.76
18	LW	4.92	21	−4.75	1.52	3.50	1.85	2.62
18	SW%	5.72	23	0.007	0.005	0.02	0.007	3.04
24	AFW	5.32	11	3.36	1.64	4.69	2.16	2.83
24	AFW%	4.63	5	0.03	0.08	0.32	0.11	2.47
24	HW	5.91	0	0.30	0.09	−0.14	0.11	3.41
Z	BMW%	5.58	36	−0.21	0.09	−0.21	0.09	2.97
Z	AFW	7.73**	36	6.00	1.56	0.87	1.54	4.06
Z	AFW%	11.43**	37	0.38	0.09	0.16	0.09	5.90
Z	LW%	5.72	109	−0.02	0.04	−0.14	0.04	3.03
Z	SW%	5.52	0	0.01	0.003	−0.002	0.003	2.94

[1]AFW = abdominal fat weight; HW = heart weight; SW = spleen weight; DS = drumstick weight; BMW = breast meat weight; LW = liver weight; and % = absolute measure/100 g of BW.

[2]Additive (a) and dominance (d) QTL effects correspond to genotype values of +a, d, and −a, respectively, for individuals having inherited 2 broiler alleles, heterozygotes, and individuals with 2 inbred alleles. Positive additive effects indicate that broiler alleles were associated with high trait values; negative additive effects indicate that broiler alleles were associated with low trait values.

[3]Dominance effects are relative to the mean of the 2 homozygotes.

*Significant at 1% chromosome-wise level; **significant at 5% genome-wise level (*F* > 9.60), and ***significant at 1% genome-wise level (*F* > 11.81).

Table 4. The QTL significant at the 5% chromosome-wise level for body composition traits in the broiler-Fayoumi cross. Estimated significance levels (*F*-value), location, gene effects, and percentage of F_2 variance explained by each QTL

Gga	Trait[1]	*F*-value	Location	Additive effect[2]	SE	Dominance[3] effect	SE	Percentage of variance
1	BMW	11.7**	627	12.54	3.85	−19.00	5.31	6.90
1	HW%	14.04***	67	−0.028	0.005	−0.013	0.009	8.16
1	LW%	10.23**	238	−0.13	0.03	−0.09	0.05	6.08
2	BMW	8.7	435	13.84	3.32	2.11	4.58	5.26
2	BMW%	7.94	422	0.36	0.09	0.04	0.13	4.83
2	HW	8.86	501	1.17	0.28	−1.26	0.56	5.36
2	SW	7.04	100	0.20	0.05	0.10	0.10	4.31
2	SW%	19.03***	90	−0.02	0.003	0.006	0.006	10.85
3	SW%	9.40*	75	−0.02	0.005	−0.002	0.009	5.67
4	BMW	6.04	232	−7.87	5.94	52.48	15.33	3.71
4	AFW	11.29**	21	14.45	3.05	−10.07	3.79	6.73
4	AFW%	9.3*	20	0.77	0.18	−0.62	0.22	5.61
4	SW	9.27*	150	−0.36	0.09	−0.15	0.01	5.59
4	SW%	18.27***	149	−0.03	0.005	−0.015	0.006	10.47
6	AFW	14.23***	43	8.07	1.54	−0.19	2.34	8.34
6	AFW%	12.93***	42	0.43	0.09	−0.006	0.13	7.63
6	LW	7.95*	44	3.26	0.83	0.10	1.27	4.83
6	LW%	7.22*	17	0.35	0.09	0.29	0.11	4.41
6	DS%	5.16	3	0.79	0.26	0.71	0.26	3.19
7	BMW	6.29	31	15.75	4.69	−3.67	9.77	3.87
7	BMW%	6.21	0	0.26	0.12	−1.28	0.44	3.81
7	SW%	6.87	146	−0.02	0.008	−0.001	0.01	4.22
8	BMW	8.57*	51	6.63	2.35	10.45	3.58	5.19
8	BMW%	5.69	54	0.24	0.08	0.17	0.02	3.51
8	SW%	5.13	87	−0.013	0.004	0.007	0.005	3.17
8	DS	8.56*	63	2.21	0.76	3.26	1.17	5.01
8	DS%	6.32	59	0.08	0.02	0.03	0.03	3.87
9	BMW	5.68	36	−43.38	24.43	57.48	25.11	3.50
9	BMW%	6.88	40	−2.40	0.69	2.56	0.70	4.21
9	AFW	7.0	22	−0.92	12.73	16.17	13.32	4.28
9	AFW%	5.52	19	0.13	0.76	0.91	0.79	3.40
9	HW	6.35	41	−2.74	0.76	2.74	0.78	3.90
9	HW%	10.13**	41	−0.16	0.04	0.15	0.04	6.07
9	SW%	11.09**	54	−0.01	0.003	0.008	0.004	6.63
10	AFW%	5.84	17	1.61	0.47	−0.21	0.58	3.60
10	HW%	5.23	115	−0.008	0.008	0.04	0.01	3.23
10	LW%	6.62	41	0.45	0.13	−0.48	0.13	4.06
12	HW	5.84	17	−1.82	0.57	1.83	0.69	3.27
12	HW%	5.23	115	−0.08	0.02	0.09	0.03	3.88
12	DS%	5.2	11	−0.60	0.19	0.61	0.19	3.21
15	SW	8.93*	0	−0.23	0.06	−0.02	0.07	5.40
15	SW%	10.18**	0	−0.001	0.003	−0.001	0.004	6.11
17	AFW%	5.3	0	0.22	0.09	0.33	0.16	3.27
17	DS	5.27	75	−0.84	1.04	−3.86	1.27	3.26
E46	LW%	6.04	68	−0.22	0.11	−0.54	0.17	3.72

[1]BMW = breast meat weight; HW = heart weight; LW = liver weight; SW = spleen weight; AFW = abdominal fat weight; DS = drumstick weight; % = absolute measure/100 g of BW.

[2]Additive (a) and dominance (d) QTL effects correspond to genotype values of +a, d, and −a, respectively, for individuals having inherited 2 broiler alleles, heterozygotes, and individuals with 2 inbred alleles. Positive additive effects indicate that broiler alleles were associated with high trait values; negative additive effects indicate that broiler alleles were associated with low trait values.

[3]Dominance effects are relative to the mean of the 2 homozygotes.

*Significant at 1% chromosome-wise level; **significant at 5% genome-wise level (*F* > 9.45); and ***significant at 1% genome-wise level (*F* > 12.28).

alleles, except for the QTL affecting HW on Gga 2. One of the 7 QTL showed strong overdominance, and heterozygotes showed greater HW% than either of the homozygotes at the QTL on Gga 10 (Table 4). The total trait variances explained by QTL were 31.08 and 3.22% for HW and HW% in the broiler-Leghorn cross and 12.53 and 21.34% in the broiler-Fayoumi cross, respectively (Table 5).

LW and LW%. For the broiler-Leghorn cross, QTL affecting LW were found on Gga 6, 7, 8, 10, and 18, and QTL for LW% were found on Gga 4, 5, 6, 7, 9, 10, and Z (Table

3). The additive effect suggested that broiler alleles were superior to Leghorn alleles for LW and LW% in half of the QTL (Table 3). Two of the 12 QTL showed strong overdominance, and heterozygotes showed the lowest LW at QTL on Gga 10 and Z. For the broiler-Fayoumi cross, QTL were identified for LW only on Gga 6 and for LW% on Gga 1, 6, 10, and E46 in the broiler-Fayoumi cross (Table 4). Broiler alleles were superior to the Fayoumi alleles for 3 of the 5 QTL. One of the 5 QTL showed overdominance, and heterozygotes showed lower LW% than either of the
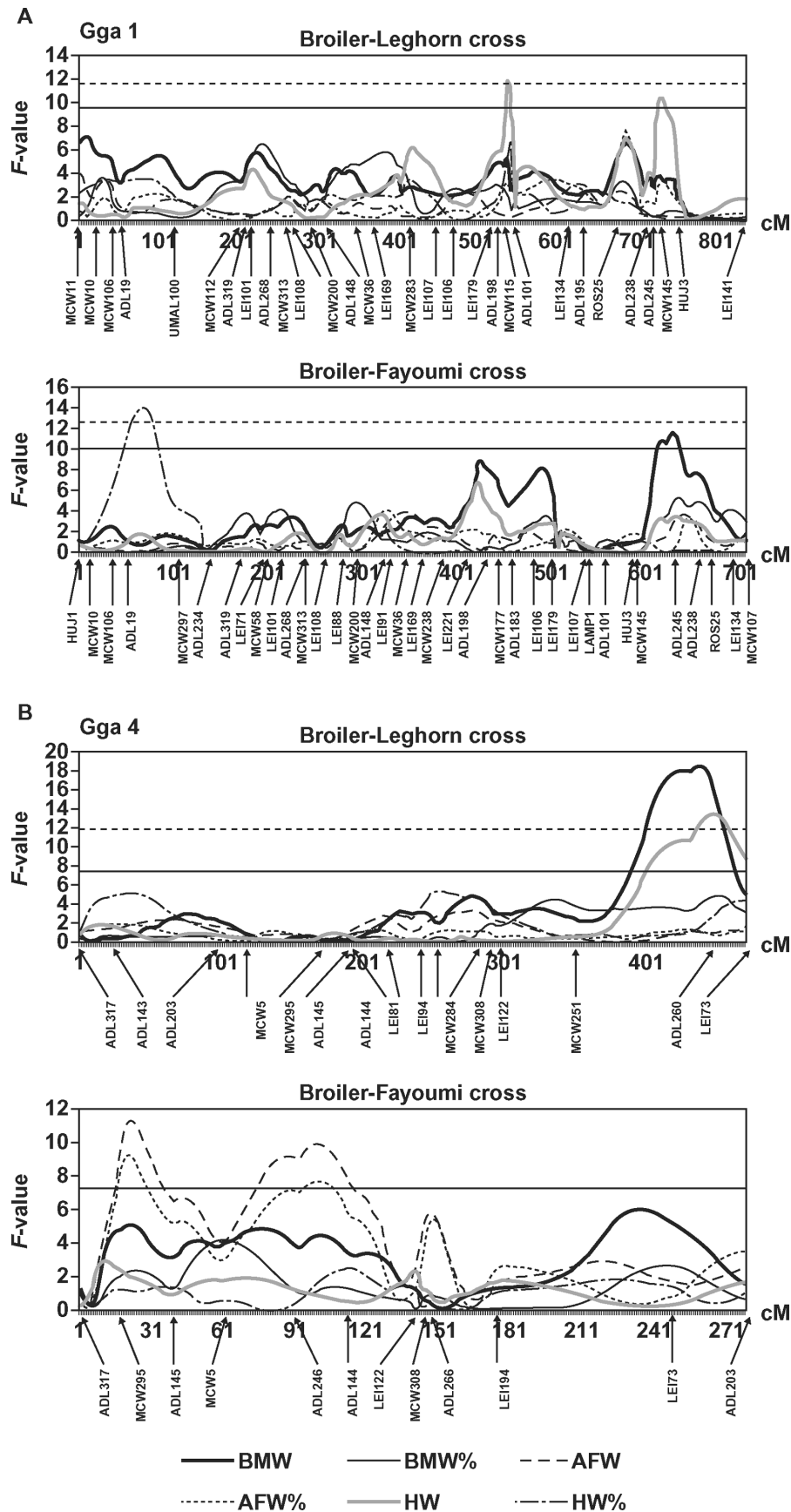
Figure 1. The *F*-value curves for evidence of QTL for breast muscle weight (BMW), BMW%, abdominal fat weight (AFW), AFW%, heart weight (HW), and HW% traits. The x-axis indicates the relative position on the linkage group. The y-axis represents the *F*-value. Arrows on the x-axis indicate the positions in which a marker was present. Two lines are provided for 1% chromosome-wise (----) and 1% genome-wise (——) significance.
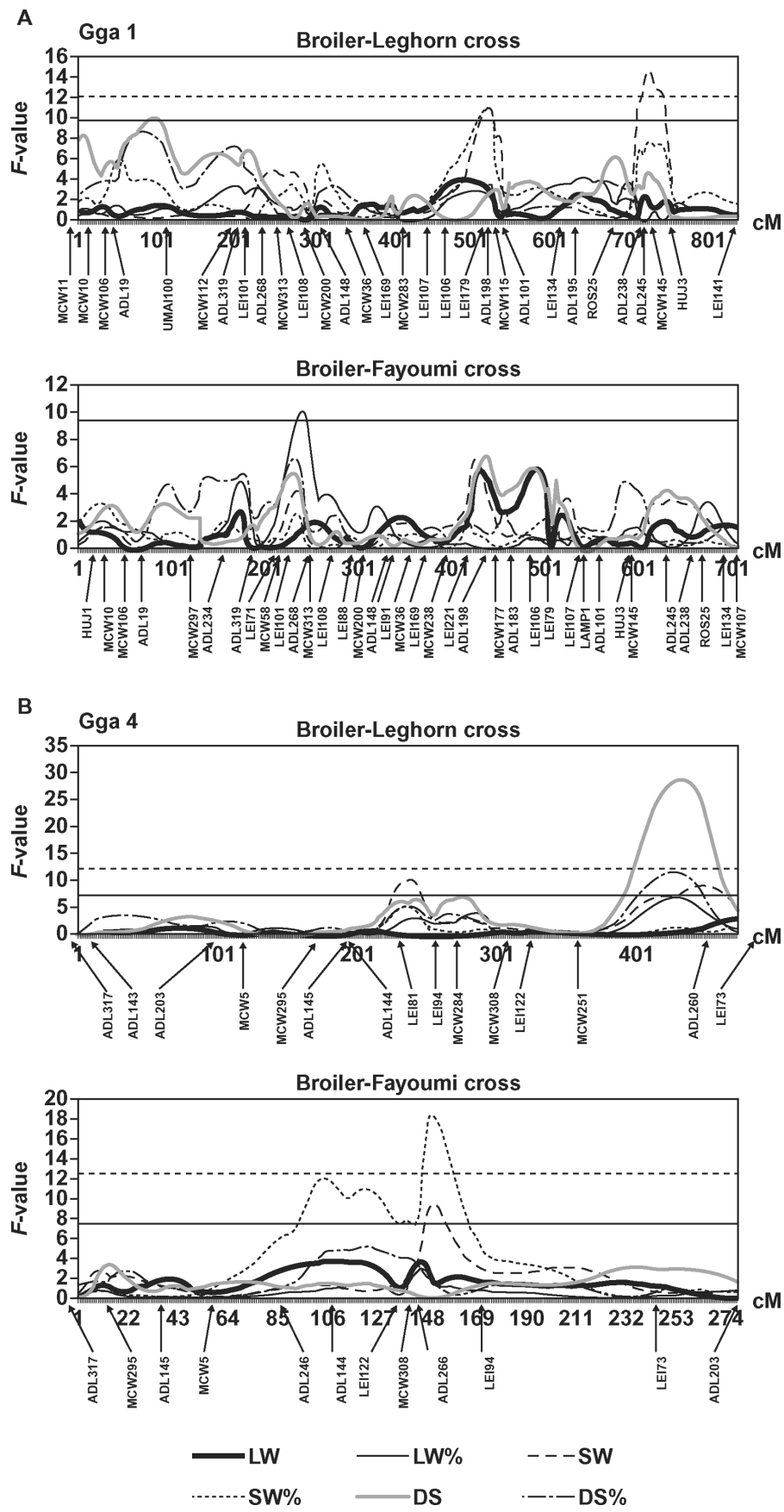
Figure 2. The *F*-value curves for evidence of QTL for liver weight (LW), LW%, spleen weight (SW), SW%, drumstick weight (DS), and DS% traits. The x-axis indicates the relative position on the linkage group. The y-axis represents the *F*-value. Arrows on the x-axis indicate the positions in which a marker was present. Two lines are provided for 1% chromosome-wise (----) and 1% genome-wise (—) significance.

Table 5. Numbers of QTL significant at the 5 and 1% chromosome-wise (CHR) levels and genome-wise (GEN) level, respectively, by trait in F_2 broiler by Leghorn and broiler by Fayoumi crosses

Trait[1]	Broiler-Leghorn cross					Broiler-Fayoumi cross				
	5% CHR	1% CHR	5% GEN	1% GEN	Percentage of variance[2]	5% CHR	1% CHR	5% GEN	1% GEN	Percentage of variance[2]
BMW	4	—	—	2	30.59	4	1	1	—	28.43
BMW%	4	1	—	—	16.92	4	—	—	—	16.36
AFW	2	2	—	1	26.62	1	—	1	1	19.35
AFW%	3	—	2	1	30.11	3	1	—	1	23.51
HW	4	—	2	1	31.08	3	—	—	—	12.53
HW%	1	—	—	—	3.22	2	—	1	1	21.34
LW	2	1	—	1	17.47	—	1	—	—	4.83
LW%	4	3	—	—	22.97	2	1	1	—	18.27
SW	1	—	1	1	16.63	1	2	—	—	15.30
SW%	2	—	2	—	16.80	2	1	2	2	47.12
DS	3	—	2	1	33.31	1	1	—	—	8.27
DS%	4	1	2	—	30.76	3	—	—	—	10.27

[1]BMW = breast meat weight; AFW = abdominal fat weight; HW = heart weight; LW = liver weight; SW = spleen weight; DS = drumstick weight; and % = absolute measure/100 g of BW.

[2]The sum of the total variances explained by the individual QTL.

homozygotes. The total trait variances explained by QTL for LW and LW% were 17.47 and 22.97% in the broiler-Leghorn cross and 4.83 and 18.27% in the broiler-Fayoumi cross, respectively (Table 5).

SW and SW%. The QTL effects on SW were detected on Gga 1, 4, and 7, and the QTL effects on SW% were detected on Gga 1, 10, 18, and Z in the broiler-Leghorn cross (Table 3). Broiler alleles showed associations with higher SW and SW% than the Leghorn alleles, except for the QTL on Gga 10. Four QTL were identified on Gga 2, 4, and 15 for SW and for SW% on Gga 2, 3, 4, 7, 8, 9, and 15 in the broiler-Fayoumi cross (Table 4). Broiler alleles showed lower SW and SW% than the Fayoumi alleles, except for the QTL affecting SW on Gga 2. The total trait variances explained by QTL for SW and SW% were 16.63 and 16.80% in the broiler-Leghorn cross and 15.30 and 41.45% in the broiler-Fayoumi cross, respectively (Table 5).

DS and DS%. Five QTL affecting DS were found on Gga 1, 2, 4, 6, 7, and 8 and DS% on Gga 1, 2, 4, 5, 6, 7, and 8 in the broiler-Leghorn cross (Table 4). The additive effect indicated that broiler alleles were superior to the Leghorn alleles, except for the QTL on Gga 6 for DS. The opposite effect was observed for DS%, except for the QTL on Gga 1, 4, and 8. One of the 13 QTL showed overdominance, and heterozygotes had lower DS than either of the homozygotes. Two QTL for DS were identified on Gga 8 and 17 and for DS% on Gga 6, 8, and 12 in the broiler-Fayoumi cross (Table 4). Broiler alleles were superior to the Fayoumi alleles for 3 of the 5 QTL. Two of the 5 QTL showed overdominance, and heterozygotes had lower DS than either of the homozygotes on Gga 17, and the opposite was found on Gga 8. The total trait variances explained by QTL for DS and DS% were 33.31 and 30.76% in the broiler-Leghorn cross and 8.27 and 10.27% in the broiler-Fayoumi cross, respectively (Table 5).

DISCUSSION

The results from the present study showed relatively low phenotypic correlations between all body composition traits compared with correlations between growth and daily average gain traits (Zhou et al., 2006). However, 3 clusters of relatively high correlation traits, in general, could be observed (breast meat weight) and DS, breast meat and AFW, and breast meat and internal organ weight). The QTL positions within each cluster frequently overlapped, as expected. For QTL affecting BMW, DS, and HW (relatively high phenotypic correlations among them), it is clear that QTL on Gga 2 (252 to 290 cM) and Gga 4 (232 cM) have large influences on these 3 traits. These broadly acting QTL may result from pleiotropic effects of distinct alleles of 1 locus or by linkage disequilibria of alleles at different loci. The advanced intercross lines generated from same parental lines would provide good opportunity to fine-map chromosomal regions and pinpoint potential causative positional candidate genes for these traits.

For the fatness trait, a suggestive QTL for AFW% at 8 wk on Gga 1 (527 cM on consensus map) in the current study confirmed QTL that has been detected for AFW% at 9 wk in a F_3 population generated from 2 White Plymouth Rock dam lines (Jennen et al., 2004).

The QTL affecting AFW or AFW% on Gga 1, 4, 5, 6, 7, 9, 15, and 24, detected either in the broiler-Leghorn cross or the broiler-Fayoumi cross in the present study, were supported by 3 studies with similar traits (Ikeobi et al., 2002; Jennen et al., 2004; Lagarrigue et al., 2006). Several QTL affecting AFW or AFW% (Gga 8, 10, 17, and Z) identified in the current study have not been reported in other studies, although some QTL were found in the same chromosomes in other studies, but not in similar positions. Several QTL affecting fatness traits reported in other studies have not been detected in the present study (Tatsuda and Fujinaka 2001; McElroy et al., 2002; Jennen et al., 2004). Several reasons might cause the differences for QTL affecting fatness in different studies. Different breeds, measurements, and generations were used for the other studies. For example, fatness traits were measured at 7 wk in F_3 and F_9 crosses from White Plymouth Rock dam lines (Jen-

nen, 2004; Jennen et al., 2004), and fatness traits were measured at 6, 9, or 10 wk in other studies (Tatsuda and Fujinaka, 2001; McElroy et al., 2002).

Ikeobi et al. (2004) found QTL on Gga 1, 2, 7, 8, 13, and 18 for breast muscle using carcass weight as a covariate in a F_2 population obtained from White Leghorn and commercial broiler lines. These QTL on Gga 2, 7, and 8 were confirmed by the current study, either in the broiler-Leghorn cross or the broiler-Fayoumi cross. The current study detected additional QTL for BMW on Gga 1 in the broiler-Fayoumi cross, which was also shown in the study by Park et al. (2006). The QTL affecting white meat in a F_2 population generated from reciprocal crosses of 2 commercial broiler lines and an intercross divergently selected for growth were identified in Gga 3 by McElroy et al. (2002) and in Gga 3 and 4 by Park et al. (2006), which were also detected for BMW in the present broiler-Leghorn cross.

Compared with the QTL study of Ikeobi et al. (2004) for drumstick traits, the QTL on Gga 1 and 4 were confirmed in the current study. Different QTL were found for DS or DS% on Gga 5 and 7 from the Ikeobi et al. (2004) study. The QTL on Gga 13 and Z were not detected in the current study, whereas the present study found QTL on Gga 2, 6, 8, 12, and 17 in both F_2 crosses.

No QTL has previously been reported for internal organ weights, such as the spleen, liver, and heart in chickens. Rocha et al. (2004) reported many QTL affecting internal organ weights in the mouse. The QTL for the spleen, liver, and HW on chromosome 7 in the mouse is the synteny region of Gga 7 in chickens, in which QTL for these internal organ weights were detected.

Both positive and negative additive effects for fatness traits originating from the broiler line were found. A cryptic allele on Gga 1 in the present study was reported in another study (Ikeobi et al., 2002). Several cryptic alleles (broiler alleles associated with lower fat) were detected in the current study. These cryptic alleles of broiler origin can be used to decrease fatness in the future breeding program. For both AFW and AFW%, high degrees of over-dominance effects were observed on Gga 24 and 9 in the broiler-Leghorn cross and the broiler-Fayoumi cross, respectively. The heterozygotes have higher fat deposition than both homozygotes, which is an important issue for further application of the QTL in breeding programs.

Because of the negative association between fitness and growth, it is difficult to improve both growth traits and fitness traits using traditional selection methods. The linkage disequilibrium detected between microsatellite markers and QTL affecting breast muscle yield, fatness, and the relative weight of internal organs might be applied to improve these traits simultaneously. For example, on Gga Z in the broiler-Leghorn cross, the opposite additive effects of QTL affecting BMW% and those affecting AFW and AFW% could be used to increase BMW% and decrease AFW and AFW%.

The unique F_2 cross design in the current study provides an opportunity to investigate how genetic background differences affect QTL profiles in the 2 F_2 crosses. For the QTL affecting breast muscle, drumstick, and fatness traits

at the 1% significance level, there was no overlap in QTL position within 20 cM found between the 2 F_2 crosses, even though similar phenotypic values for these traits exist between these 2 crosses (Deeb and Lamont, 2002). There were similar QTL detected for internal organ weight on Gga 3 and 6 for both crosses. Significant differences of QTL for the body composition traits in the present study detected between the 2 crosses may reflect different allele effects of the 2 inbred lines on these traits. Different QTL detected from the 2 inbred crosses provide more resource QTL for future study and possible MAS.

For the QTL affecting body composition traits at the 1% significance chromosome-wise level, either in the broiler-Leghorn cross or the broiler-Fayoumi cross, potential positional candidate genes from database analysis of detected QTL regions are found. For the fatness traits, these candidate genes are involved in the synthesis, transport, and storage of fat, as well as hormones and transcription factors influencing these processes. Some of these candidate genes have previously been associated with fatness or obesity in chickens, other livestock, humans, or mice (Fuhrmann and Sallmann, 1995; Zhao et al., 2002; Miyazaki et al., 2003; Pearce et al., 2003; Shang and Waters, 2003). Within the QTL region for AFW and AFW% on Gga 24, although this QTL was only suggestively significant, 3 members of the apolipoprotein (**APO**) gene family (APOA1, APOA4, and APOA5) in this region warranted more attention to this QTL (Jennen et al., 2002). The APOA1 mRNA levels showed associations with fatness in chickens (Douaire et al., 1992; Lagarrigue et al., 2000).

For BMW and DS, positional candidate genes within QTL regions on each chromosome are found. Three genes of transforming growth factor beta (**TGFB**) families (TGFB3, TGFBR1, and TGFBR2) and insulin-like growth factor 1 have previously been associated with muscle growth, cell proliferation, and cell growth in chickens and other species (Burt and Law, 1994; Li et al., 2003; Zhou et al., 2005). Potential candidate genes on Gga 8 and 10 are protein tyrosine phosphate receptor C and macrophage migration inhibitory factor. The protein tyrosine phosphate receptor C protein encoded by this gene is a member of the protein tyrosine phosphatase family. Protein tyrosine phosphatases are known to be signaling molecules that regulate a variety of cellular processes, including cell growth and differentiation. There is no association reported between these genes and muscle growth.

In summary, the current study identified QTL regions for well-studied traits of body composition (such as BMW), as well as traits (such as internal organ weights) for which no previous studies are reported. Several QTL in the current study confirmed those found in other studies on unrelated populations. Additionally, many QTL were detected that have not previously been reported.

Besides composition traits measured in this resource population, other meat quality traits, such as meat moisture, color, pH, and shear force, have been studied in inbred lines, broilers, and advanced intercrosses among these 3 lines (Lonergan et al., 2003). The considerable differences of these meat quality traits in the genetic resource

lines will lay exceptional foundation for future QTL detection of these traits in chickens.

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