Mapping of Quantitative Trait Loci for Growth and Carcass-Related Traits in Chickens Using a Restriction-Site Associated DNA Sequencing Method

Takashi Ono[1], Ken Ohara[1], Akira Ishikawa[2,3], Tomomi Kouguchi[4], Atsushi J. Nagano[5], Atsushi Takenouchi[1,3], Takeshi Igawa[3,6] and Masaoki Tsudzuki[1,3]

[1] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Hiroshima 739−8528, Japan
[2] Graduate School of Bioagricultural Science, Nagoya University, Nagoya, Aichi 464−8601, Japan
[3] Japanese Avian Bioresource Project Research Center, Higashi-Hiroshima, Hiroshima 739−8528, Japan
[4] NH Foods Ltd. R&D Center, Tsukuba, Ibaraki 300−2646, Japan
[5] Faculty of Agriculture, Ryukoku University, Otsu, Shiga 520−2194, Japan
[6] Graduate School of Science, Hiroshima University, Higashi-Hiroshima, Hiroshima 739−8526, Japan

In the present study, quantitative trait loci (QTLs) analysis was performed to identify the chromosomal positions of growth and carcass-related trait QTLs using 319 F_2 chickens obtained from intercrosses of an Oh-Shamo male and four White Plymouth Rock females. Body weight was measured weekly until the birds were 7 weeks old. Carcass-related traits were also measured at this timepoint. A genetic linkage map was constructed using 545 single nucleotide polymorphism (SNP) markers that were developed using a restriction-site associated DNA sequencing method. The linkage map included the 23 autosomes and the Z chromosome. Using simple interval QTL mapping, we were able to identify 10 significant and suggestive main-effect QTLs for growth and carcass-related traits present on chromosomes 1, 2, 3, 5, 8, 19, 24, and Z. These loci explained 5.60−16.52% of the phenotypic variances. The chromosomal positions of the 10 QTLs overlapped with those of previously reported QTLs, whereas the targeted traits varied. Our QTLs will aid future breeding programs in improving growth and meat yield of chickens (e.g., via marker-assisted selection), particularly in the Japanese brand chicken industry.

Key words: carcass-related traits, growth, QTL, RAD-seq, SNP marker

Introduction

In the last few decades, the body weight and meat yield of broiler chickens have increased significantly. Conversely, the age of chickens available for sale in the market has decreased (Zuidhof *et al*., 2014). However, selecting chickens solely for increased body weight may adversely affect meat quality (Nones *et al*., 2006; Wright *et al*., 2006; Nadaf *et al*., 2007). Currently, the method of intercrossing native Japanese chickens with either Plymouth Rock or Rhode Island Red chickens is being extensively used to produce brand chickens that produce high quality meat (Rikimaru and Takahashi, 2010; Japan Chicken Association, 2011). While Japanese brand chickens produce good quality meat, the growth and meat yield of these chickens do not match the levels of general broilers produced from the mating of male

White Cornish with female White Plymouth Rock chickens. This is due to the slow growth performance of Japanese brand chickens.

Marker-assisted selection (MAS) (Dekkers, 2004) is an efficient method used by chicken selection programs to improve the growth performance of Japanese chicken stocks. In general, economic traits show continuous values, which are controlled by quantitative trait loci (QTLs). Prior to using MAS, it is necessary to identify molecular markers flanking QTLs. Currently, several QTLs that affect growth and carcass-related traits have been mapped to a wide range of chromosomal positions (Chicken QTLdb; https://www.animalgenome.org/cgi-bin/QTLdb/GG/index). However, whether the QTL information can be used for the improvement of Japanese chicken stocks is not clear, as the majority of the resource families that were used in previous QTL analyses were derived from foreign chicken breeds/lines that were not directly related to the chicken stocks used in the Japanese brand chicken industry (Abasht *et al*., 2006). Reports on QTL mapping focusing on growth and carcass-related traits using chicken breeds/lines maintained in Japan

are limited (Tatsuda and Fujinaka, 2001; Tsudzuki *et al.*, 2007; Uemoto *et al.*, 2009; Rikimaru *et al.*, 2011). In addition, microsatellites were used as DNA markers in previous studies, resulting in large confidence intervals of QTL positions due to shortage of marker coverage for chicken chromosomes. Hence, MAS cannot be performed accurately and efficiently.

Recent improvements in next generation sequencing (NGS) techniques have enabled detection of large numbers of single nucleotide polymorphisms (SNPs) within DNA sequences (Zarger *et al.*, 2015). SNP markers allow generation of high-density genetic linkage maps due to their abundance and uniform distribution throughout genomes (Bai *et al.*, 2017). Among several NGS techniques, restriction site-associated DNA sequencing (RAD-seq) is an efficient method for developing SNP markers (Miller *et al.*, 2007; Baird *et al.*, 2008). RAD-seq has enabled efficient mapping of QTLs in several organisms (Zhou *et al.*, 2015; Larson *et al.*, 2016; Watanabe *et al.*, 2017).

In the present study, we used an Oh-Shamo male and White Plymouth Rock females to develop an F_2 resource family for QTL mapping. Oh-Shamo is a well-known native Japanese chicken breed that was originally developed for cock fighting (Tsudzuki, 2003). In contrast, White Plymouth Rock originated in the United States and is often used as a broiler's dam breed (Bell, 2002). In the Japanese brand chicken industry, many F_1 hybrids are generated by mating Oh-Shamo males with White Plymouth Rock females (Japan Chicken Association, 2011). Therefore, the QTLs identified in this study will be directly related to the Japanese brand chicken industry.

The aim of this study was to identify QTLs that affect growth and carcass-related traits using SNP markers developed using the RAD-seq technique.

Materials and Methods

Animals

An F_2 resource family was created based on the mating of one Oh-Shamo male and four white Plymouth Rock females. In total, 319 F_2 chickens (164 males and 155 females) were produced from full-sib matings of five F_1 males and 16 F_1 females. In addition, the phenotypic traits of 66 Oh-Shamo, 94 White Plymouth Rock, and 85 F_1 birds were compared. All birds were kept in a battery brooder with continuous lighting and *ad libitum* access to food and water. Commercial diet for chicks (metabolic energy: 2,900 kcal/kg, crude protein: 22.0%) was fed to the chickens until they reached the slaughtering age of seven weeks. The chickens were treated according to the rules mentioned in the Guidelines for Proper Conduct of Animal Experiments (Science Council of Japan, 2006).

Determination of Phenotype

The body weights of the chickens were recorded weekly from the time of hatching until the birds were 7-week-old. Weekly body-weight gain was calculated as the difference between n and n + 1 weeks of age. At seven weeks of age, the birds were slaughtered, and carcass weight (CW), liver weight (LW), thigh muscle weight (TMW), pectoralis major weight (PMAW), pectoralis minor weight (PMIW), and abdominal fat weight (AFW) were measured. In addition, the CW to body weight ratio at seven weeks (CW%), LW to CW ratio (LW%), TMW to CW ratio (TMW%), PMAW to CW ratio (PMAW%), PMIW to CW ratio (PMIW%), AFW to CW ratio (AFW%), and TMW to PMAW ratio (TMW/ PMAW) were calculated.

Statistical Analysis Prior to QTL Analysis

Phenotypic data for Oh-Shamo, White Plymouth Rock, and their F_1 and F_2 birds were compared using one-way analysis of variance (ANOVA), followed by Tukey's HSD test using the JMP software version 11.20 (SAS Institute Japan, Tokyo). Pearson's correlation coefficients among all traits were determined using JMP.

Prior to QTL analysis, the statistical significance of three different environmental factors (sex, hatching date, and F_1 dams) was determined using the least squares method of JMP. When the factors were significant at $P<0.05$, raw data were adjusted for significant factors by including the factors as fixed effects in the linear model. The adjusted data was then tested for normality using the Shapiro-Wilk's W-test of JMP. The traits that did not meet normally at $P<0.05$ were subjected to Box-Cox transformation.

Marker Genotyping

Genomic DNA was extracted from whole blood samples collected from one Oh-Shamo male, four White Plymouth Rock females, five F_1 males, and 319 F_2 birds using the standard phenol-chloroform extraction method. The concentration of the DNA extracted was determined using a Qubit 3.0 fluorometer (Thermo Fisher Scientific, Waltham MD, USA). Forty nanograms of genomic DNA extracted from each sample were used to prepare a RAD-seq library. The detailed method for RAD-seq has been described previously (Sakaguchi *et al.*, 2015). A library constructed from DNA fragments of approximately 370-bp was used for single-end 50 bp sequencing using HiSeq 2500 (Illumina, CA, USA) at Macrogen (Seoul, Korea). The read data were preserved in the DDBJ Sequence Read Archive (accession no. DRA 006421). The reads were trimmed by following LEADING: 19 TRAILING:19 SLIDINGWINDOW:30:20 AVGQUAL: 20 MINLEN:51 parameters in Trimmomatic (Bolger *et al.*, 2014). The trimmed reads were then adapted to the reference positions of the domestic chicken genome (GCA_000002315.3 Gallus_gallus-5.0), and SNPs were called with stacks (Catchen *et al.*, 2013). Markers that did not fit the chi-squared goodness-of-fit test ($P<0.05$) or were genotyped in less than 80% of F_2 individuals, were excluded from this study. In total, 545 informative SNP markers covering 23 autosomes and the Z chromosome were used in this study.

A linkage map was created using the Map Manager QTX b20 software (Manly *et al.*, 2001). The total length of the constructed linkage map was 2384.2 cM in genetic distance and 861 Mb in physical distance, covering approximately 70% of the chicken genome (Warren *et al.*, 2017). The average marker interval was 4.38 cM in genetic distance and 1.58 Mb in physical distance.

QTL Analysis

Simple interval mapping (Haley and Knott, 1992) was performed using the R/qtl software (Broman *et al*., 2003). The identification of main and epistatic QTLs was conducted for three sex-groups (males, females, and combined sexes) separately using the scanone and scantwo functions of R/qtl. For autosomes, genome-wide significant (5%) and suggestive (10%) threshold levels for main-effect and epistatic QTLs, and sex-specific QTLs were calculated by performing 1,000 permutation tests (Broman and Sen 2009). For the Z chromosome, these thresholds were estimated using the method of Broman *et al*. (2006).

The percentage of phenotypic variance explained by each QTL detected for each trait was estimated using the scanone and scantwo functions. In addition, the multiple QTL model was used with R/qtl to estimate the total phenotypic variance explained by all QTLs detected for the trait. To estimate the confidence interval (CI) of physical distance (Mb), we defined the CI (Mb) by extending the distance of the CI (cM) to the position of the nearest flanking markers that were located outside the boundaries as the R/qtl software only calculates the genetic distance (cM).

Results

Phenotypic Values

The phenotypic values for growth and carcass-related traits in Oh-Shamo, White Plymouth Rock, and their F_1 and F_2 birds are shown in Table 1. The values obtained for White Plymouth Rock birds were significantly higher than those of Oh-Shamo birds, whereas their F_1 and F_2 birds yielded intermediate values at all ages in terms of body weight, weekly body-weight gain, and weights for all carcass-related traits. Among Oh-Shamo, White Plymouth Rock, and their F_1 and F_2 generations, no significant difference was observed in CW% and LW% across all generations. White Plymouth Rock birds showed significantly higher TMW% than Oh-Shamo birds, whereas their F_1 and F_2 birds showed values that were similar to those of their parents. Oh-Shamo birds showed significantly lower PMAW% values than other groups. PMIW% derived for F_2 was significantly higher than that for Oh-Shamo birds, whereas the values for White Plymouth Rock and F_1 birds were similar. Significantly higher AFW% was observed for White Plymouth Rock birds than for Oh-Shamo birds, whereas intermediate values were determined for their F_1 and F_2 birds. TMW/PMAW for Oh-Shamo birds was significantly higher than in other populations.

Phenotypic correlations between growth (body weight and weekly body-weight gain) and carcass-related traits are shown in Table 2. For growth traits, positive correlations were observed between the majority of the traits with the exception of WG2-3 and BW2, and WG2-3 and WG1-2, where negative correlations with relatively high values were observed. No correlation was observed between BW0 and any weekly body-weight gains. We observed the following trend for body-weight gains: weights recorded when the birds were over four weeks of age showed no correlation with those recorded before the birds had reached three weeks of age, i.e., WG4−5 to WG1−2 and WG2−3; WG5−6 to WG0−1 and WG1−2; and WG6−7 to WG0−1, WG1−2, and WG2−3. Furthermore, body-weight gains in birds after they had reached five weeks of age (WG5−6 and WG6−7) generally showed no correlation with body weight at or before three weeks of age (BW0−3). Most of the carcass-related weight traits (CW, LW, TMW, PMAW, and PMIW) showed positive correlations with all growth traits except for the correlation with BW0. However, AFW showed no correlation with any growth traits except for BW0. Contrary to CW−PMIW, percentage traits generally showed no correlation with any trait, including growth and carcass-related traits. LW% and AFW% showed negative correlations with all corresponding traits.

QTL Analysis

In this study, no epistatic QTLs were observed for any growth and carcass-related traits. Main-effect QTLs for the growth and carcass-related traits were identified on chromosomes 1, 2, 3, 5, 8, 19, 24, and Z, as shown in Table 3. Seven significant QTLs and two suggestive QTLs for growth traits were detected on chromosomes 1, 3, 8, and Z. Among the nine QTLs, six were expressed as male-specific QTLs. Male-specific significant QTLs for body weight at the earlier stage (BW1, BW2, and BW3) were identified between 102.21 Mb and 105.44 Mb SNPs on chromosome 1. For BW4 and BW5, suggestive QTLs were detected in close proximity to the 6.85 Mb SNP on chromosome 8. QTLs affecting BW6, BW7, and WG4−5, which are expressed only in males, were identified on chromosome Z. The positions of these QTLs were between 33.79 Mb and 35.06 Mb SNPs for BW6 and BW7, and at approximately 35.06 Mb SNP for WG4−5. A significant QTL for WG6−7 was detected in close proximity to the 8.30 Mb SNP on chromosome 3. These QTLs accounted for 5.64−16.52% of the phenotypic variance.

For carcass-related traits, five significant QTLs and four suggestive QTLs were identified on chromosomes 1, 2, 3, 5, 19, 24, and Z. Among these nine QTLs, two are expressed only in males and three are expressed only in females. A male-specific suggestive QTL for CW and a female-specific significant QTL for PMIW were positioned between the 33.79 Mb and 35.06 Mb SNPs and was in close proximity to the 35.06 Mb SNP on chromosome Z. The positions of these QTLs was coincident with those of BW6, BW7, and WG4−5. A suggestive QTL was detected for PMAW between 26.51 Mb and 30.75 Mb SNPs on chromosome 3. For AFW, a female-specific suggestive QTL was detected in close proximity to the 27.55 Mb SNP on chromosome 2. A suggestive QTL for LW% specific to males was identified close to the 100.92 Mb SNP on chromosome 1. A significant QTL for PMIW% was detected close to the 0.57 Mb SNP on chromosome 24. A female-specific significant QTL for TMW% and a significant QTL for TMW/PMAW, which was expressed in both sexes, were detected between 9.13 Mb and 12.00 Mb SNPs on chromosome 5. Furthermore, a second significant QTL for TMW/PMAW was also identified

Table 1. **Means and standard deviations for body weight and carcass-related traits in Oh-Shamo, White Plymouth Rock, and their F$_1$ and F$_2$ birds**

Traits[1]	Oh-Shamo	White Plymouth Rock	F$_1$	F$_2$
Growth traits	$n=62$	$n=94$	$n=85$	$n=319$
Body weight (g)				
BW0	36.24±2.97^c	44.48±4.81^a	42.67±4.32^b	42.32±3.69^b
BW1	61.72±9.23^c	102.37±17.33^a	83.86±13.84^b	82.61±13.94^b
BW2	126.40±24.79^c	248.34±52.18^a	181.02±42.98^b	179.10±38.61^b
BW3	219.45±49.47^c	475.79±92.05^a	341.53±76.23^b	330.77±68.31^b
BW4	358.74±67.74^c	831.63±136.55^a	577.15±114.61^b	559.50±103.41^b
BW5	516.20±85.91^c	1229.16±180.53^a	866.76±139.74^b	843.90±128.29^b
BW6	708.89±98.82^c	1630.19±203.28^a	1156.08±171.77^b	1151.28±153.86^b
BW7	865.35±116.35^c	1949.54±266.59^a	1413.63±209.26^b	1396.50±174.60^b
Weekly gain (g)				
WG0-1	25.48±9.13^c	57.89±14.96^a	41.19±14.30^b	40.31±13.14^b
WG1-2	64.68±19.84^c	145.97±38.34^a	97.16±34.84^b	96.48±29.47^b
WG2-3	93.05±28.47^c	227.45±51.75^a	160.51±41.13^b	151.91±36.83^b
WG3-4	133.51±48.96^c	355.85±73.21^a	235.62±49.82^b	228.56±47.21^b
WG4-5	163.24±52.10^c	397.53±88.60^a	289.61±42.23^b	284.40±51.02^b
WG5-6	192.69±39.66^c	401.03±101.90^a	289.32±56.76^b	307.38±51.76^b
WG6-7	156.46±33.95^c	319.35±103.46^a	257.55±65.08^b	245.21±63.30^b

Table 1. **(continued)**

Traits[1]	Oh-Shamo	White Plymouth Rock	F$_1$	F$_2$
Carcass-related traits	$n=53$	$n=66$	$n=63$	$n=302$
Weight (g)				
CW	559.92±78.74^c	1267.55±203.09^a	908.19±153.70^b	928.04±124.27^b
LW	20.05±3.46^c	47.68±7.56^a	34.49±7.21^b	34.20±5.60^b
TMW	128.42±22.47^c	301.11±51.46^a	212.78±36.96^b	215.89±33.65^b
PMAW	62.62±12.06^c	167.37±36.68^a	114.54±29.10^b	117.62±20.11^b
PMIW	20.89±3.75^c	47.83±9.03^a	34.68±7.48^b	35.93±5.53^b
AFW	5.43±2.69^c	33.30±11.90^a	14.59±6.56^b	12.76±6.10^b
Percentage (%)				
CW%	65.88±1.71^a	66.50±4.38^a	66.43±2.27^a	66.61±3.35^a
LW%	3.64±0.84^a	3.84±0.80^a	3.89±0.93^a	3.71±0.54^a
TMW%	22.86±1.57^b	23.74±1.33^a	23.39±1.46^{ab}	23.22±1.63^{ab}
PMAW%	11.22±1.81^b	13.22±2.06^a	12.57±2.19^a	12.67±1.35^a
PMIW%	3.73±0.40^b	3.77±0.33^{ab}	3.79±0.33^{ab}	3.87±0.31^a
AFW%	0.97±0.48^c	2.61±0.86^a	1.61±0.69^b	1.39±0.69^b
TMW/PMAW	208.22±31.93^a	184.37±33.53^b	192.40±37.77^b	185.29±23.30^b

[1] BWn＝body weight at n weeks of age; WGn-(n＋1)＝weekly gains from n to n＋1 weeks of age; CW＝carcass weight; LW＝liver weight; TMW＝thigh muscle weight; PMAW＝pectoralis major weight; PMIW＝pectoralis minor weight; AFW＝abdominal fat weight; CW%＝CW/BW7; LW%＝LW/CW; TMW%＝TMW/CW; PMAW%＝PMAW/CW; PMIW%＝PMIW/CW; AFW%＝AFW/CW; TMW/PMAW＝TMW percentage to PMAW.

[a–c] Means with different superscript are significantly different at $P<0.05$ (Tukey's HSD test).

between 4.90 Mb and 5.10 Mb SNPs on chromosome 19. These single QTLs explained 5.60–12.91% of the phenotypic variance. QTLs for TMW/PMAW accounted for 13.46% of the phenotypic variance.

In summary, we identified 10 independent QTL regions for growth and carcass-related traits (Table 4). These regions include two QTLs that are present on chromosome 1 (around 100.92 Mb and between 102.21 Mb and 105.44 Mb SNPs), one QTL on chromosome 2 (around 27.55 Mb SNP), two QTLs on chromosome 3 (approximately 8.30 Mb and between 26.51 Mb and 30.75 Mb SNPs), one QTL on chro-

mosome 5 (between 9.13 Mb and 12.00 Mb SNPs), one QTL on chromosome 8 (approximately 6.85 Mb SNP), one QTL on chromosome 19 (between 4.90 Mb and 5.10 Mb SNPs), one QTL on chromosome 24 (around 0.57 Mb SNP), and one QTL on the Z chromosome (between 33.79 Mb and 35.06 Mb). Known and unknown genes of 4–78 existed between two flanking markers or around a single flanking marker at each coincident QTL.

Discussion

In this study, we identified 10 main-effect QTLs for

Table 2.   **Phenotypic correlations between growth and carcass-related traits in F$_2$ birds[1]**

Traits[2]	BW0	BW1	BW2	BW3	BW4	BW5	BW6	BW7	WG0-1	WG1-2	WG2-3	WG3-4	WG4-5	WG5-6	WG6-7
BW0	1.00														
BW1	0.33	1.00													
BW2	NS	0.45	1.00												
BW3	0.19	0.57	0.51	1.00											
BW4	0.14	0.43	0.46	0.91	1.00										
BW5	0.15	0.41	0.42	0.81	0.89	1.00									
BW6	0.14	0.36	0.37	0.74	0.82	0.95	1.00								
BW7	0.13	0.29	0.31	0.65	0.75	0.88	0.96	1.00							
WG0-1	NS	0.97	0.45	0.55	0.42	0.39	0.34	0.27	1.00						
WG1-2	NS	0.24	0.97	0.41	0.39	0.35	0.32	0.27	0.24	1.00					
WG2-3	NS	0.19	-0.39	0.58	0.54	0.46	0.43	0.39	0.17	-0.48	1.00				
WG3-4	NS	0.17	0.28	0.58	0.86	0.77	0.73	0.68	0.16	0.26	0.36	1.00			
WG4-5	NS	0.14	0.12	0.18	0.21	0.63	0.64	0.63	0.13	NS	NS	0.19	1.00		
WG5-6	NS	NS	NS	0.26	0.32	0.43	0.69	0.72	NS	NS	0.17	0.32	0.37	1.00	
WG6-7	NS	NS	NS	NS	0.17	0.27	0.37	0.62	NS	NS	NS	0.22	0.30	0.43	1.00

Table 2.   **(continued)[1]**

	BW0	BW1	BW2	BW3	BW4	BW5	BW6	BW7	WG0-1	WG1-2	WG2-3	WG3-4	WG4-5	WG5-6	WG6-7
CW	NS	0.22	0.29	0.63	0.75	0.79	0.85	0.88	0.21	0.26	0.38	0.72	0.42	0.64	0.53
LW	NS	0.18	0.19	0.39	0.50	0.52	0.59	0.63	0.16	0.16	0.24	0.50	0.28	0.50	0.43
TMW	NS	0.25	0.30	0.61	0.68	0.72	0.78	0.81	0.24	0.27	0.35	0.60	0.40	0.59	0.51
PMAW	NS	0.23	0.27	0.56	0.60	0.63	0.67	0.67	0.23	0.23	0.32	0.50	0.34	0.47	0.37
PMIW	NS	0.20	0.28	0.54	0.60	0.64	0.66	0.66	0.19	0.26	0.29	0.52	0.35	0.44	0.36
AFW	0.12	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
CW%	NS	NS	NS	0.18	0.27	NS	0.12	0.12	NS	NS	NS	0.32	-0.23	NS	NS
LW%	NS	NS	NS	-0.19	-0.20	-0.21	-0.19	-0.18	NS	NS	NS	-0.16	NS	NS	NS
TMW%	NS	NS	NS	0.16	NS	0.13	0.14	0.16	NS	NS	NS	NS	0.12	0.12	0.13
PAW%	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
PIW%	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
AFW%	NS	NS	NS	NS	NS	NS	-0.13	-0.13	NS	NS	NS	NS	NS	-0.15	NS
TMW/PMAW	NS	NS	NS	NS	NS	NS	NS	0.14	NS	NS	NS	NS	NS	0.12	0.15

Table 2.   **(continued)[1]**

	CW	LW	TMW	PMAW	PMIW	AFW	CW%	LW%	TMW%	PAW%	PIW%	AFW%	TMW/PMAW
CW	1.00												
LW	0.62	1.00											
TMW	0.85	0.53	1.00										
PMAW	0.73	0.48	0.71	1.00									
PMIW	0.73	0.41	0.73	0.66	1.00								
AFW	NS	NS	NS	NS	NS	1.00							
CW%	0.56	0.22	0.38	0.38	0.37	NS	1.00						
LW%	-0.31	0.55	-0.27	-0.21	-0.28	NS	-0.34	1.00					
TMW%	NS	NS	0.57	0.20	0.26	NS	-0.17	NS	1.00				
PAW%	NS	NS	NS	0.64	0.15	NS	NS	NS	0.25	1.00			
PIW%	NS	NS	0.12	0.13	0.64	NS	NS	NS	0.32	0.26	1.00		
AFW%	-0.17	NS	-0.12	-0.12	-0.12	0.97	-0.12	NS	NS	NS	NS	1.00	
TMW/PMAW	NS	NS	0.32	-0.43	NS	NS	NS	NS	0.45	-0.74	NS	NS	1.00

[1] Trait abbreviations are explained in Table 1.
[2] NS=not significant at $P<0.05$ estimated using Pearson's correlation coefficients.

Table 3. **Summary of the QTLs identified in this study**

Traits[1]	Sex[2]	Chr	Position (cM)[3]	CI (cM)[4]	Flanking markers (Mb)[5]	LOD[6]	% var.[7]	Add.[8]	Dom.[9]	Differences[10]
Growth traits										
BW1	M	1	216.5	22	102.21–105.44	5.80*	16.52	6.21	8.32	A<B≤H
BW2	M	1	220.5	20	102.21–105.44	5.60*	16.01	12.94	30.00	A<B<H
BW3	M	1	221.5	22	102.21–105.44	3.87*	11.36	14.66	12.18	A<B<H
BW4		8	69.8	39	6.85	3.73†	5.64	16.23	−22.33	H≤A<B
BW5		8	69.8	43	6.85	3.73†	5.64	23.94	−28.27	H≤A<B
BW6	M	Z	79	55	33.79–35.06	2.92*	8.68	35.88	—	A<B
BW7	M	Z	80	55	33.79–35.06	3.13*	9.28	44.46	—	A<B
BW4-5	M	Z	84.1	91	35.06	2.87*	10.78	8.54	—	A<B
BW6-7		3	0	95	8.30	4.29*	6.46	10.28	13.46	A<B≤H
Carcass-related traits										
CW	M	Z	83	96	33.79–35.06	2.61†	8.07	29.64	—	A<B
PMAW		3	48	39	26.51–30.75	3.63†	5.60	4.99	−3.26	A≤H<B
PMIW	F	Z	84.1	47	35.06	2.66†	7.98	1.45	—	A<B
AFW	F	2	84.3	17	27.55	3.55†	10.53	0.56	3.39	A≤B<H
LW%	M	1	214.5	41	100.92	3.52†	10.70	−0.12	−0.06	B≤H<A
TMW%	F	5	130	19	9.13–12.00	4.41*	12.91	−0.13	0.66	B≤A<H
PMIW%		24	0	12	0.57	4.59*	7.03	−0.06	0.00	B<H<A
TMW/PMAW		5	131	20	9.13–12.00	4.28*	6.57	−2.32	9.21	B<A<H
TMW/PMAW		19	1	9	4.90–5.10	4.67*	7.15	−5.60	−4.53	B≤H<A

[1] Trait abbreviations are explained in Table 1.
[2] M＝expressed only in males, F＝expressed only in females, none＝expressed in both sexes.
[3] Peak position.
[4] Confidence interval at 1.8-LOD drop.
[5] Physical position of the markers.
[6] Genome-wide significant and suggestive QTL detected (* significant at 5% level, † suggestive at 10% level).
[7] Percentage of the phenotypic variance explained by the QTL.
[8] Additive effect of the QTL shown in standard deviation unit.
[9] Dominance effect of the QTL shown in standard deviation unit.
[10] Phenotypic differences between three possible genotypes at the nearest marker locus in autosomes, two homozygote for either the Oh-Shamo (A) or White Plymouth Rock (B) alleles and heterozygote (H), estimated using Tukey's HSD test. For the Z chromosome, two possible geno-types in each sex, a homozygote for the Oh-Shamo allele (A) and heterozygote (H) in males, and two hemizygotes for the Oh-Shamo (A) or White Plymouth Rock (B) allele in females using the Student's t-test.

growth and carcass-related traits on chromosomes 1, 2, 3, 5, 8, 19, 24, and Z (QTL1 to QTL10 in Table 4). According to the Chicken QTLdb (https://www.animalgenome.org/cgi-bin/QTLdb/GG/index), all QTLs detected in this study over-lapped with previously reported QTLs that affect body weight and/or carcass traits. A QTL for liver percentage was in close proximity to QTL1 (Zhou et al., 2006a). QTLs for body weight at various age and abdominal fat weight were identified in close proximity to QTL2 on chromosome 1 (Sewalem et al., 2002; Liu et al., 2007; Rao et al., 2007; Uemoto et al., 2009; Nassar et al., 2012). QTLs for body weight (Tatsuda and Fujinaka 2001; Siwek et al., 2004; Uemoto et al., 2009), muscle weight (Ikeobi et al., 2004), and fat weight (Nassar et al., 2013) were detected in close proximity to QTL3 on chromosome 2. QTLs that affect growth (Carlborg et al., 2003, 2004; Zhou et al., 2006a; Le Rouzic et al., 2008; Wahlberg et al., 2009) were identified in close proximity to QTL4 on chromosome 3. Several QTLs identified for breast muscle weight, breast muscle percent-age, abdominal fat weight, and chest width (Park et al., 2006; Sharman et al., 2007; Nadaf et al., 2009; Baron et al., 2011)

were in close proximity to QTL5 on chromosome 3, which affected PMAW. McElroy et al. (2006), Gao et al. (2009), and Baron et al. (2011) identified QTLs for breast and thigh muscle weight, which were in close proximity to QTL6 on chromosome 5. The position of QTL7 at approximately 6.85 Mb on chromosome 8 overlapped with the position of pre-viously reported QTLs for growth traits (Sewalem et al., 2002; Carlborg et al., 2004; Podisi et al., 2013). A QTL for chest width was identified in close proximity to QTL8 on chromosome 19 (Gao et al., 2011). QTL9, which affected PMIW% on chromosome 24, was detected in close proximity to the QTLs for liver weight, eggshell weight, and meat color (Navarro et al., 2005; Tuiskula-Haavisto et al., 2011; Yoshida et al., 2013). The position of QTL10 on the Z chromosome and those of BW6, BW7, WG4-5, CW, and PMIW QTLs were identical to those of QTLs for body weight and carcass traits reported previously (Sewalem et al., 2002; Kerje et al., 2003; Siwek et al., 2004; Sasaki et al., 2004; Navvaro et al., 2005; Zhou et al., 2006b; Hocking et al., 2012; Podisi et al., 2013). Although the positions of the QTLs identified in the present study overlapped with those of previously reported

Table 4.   **Summary of the previously identified QTLs that overlapped with our QTLs in the position**

QTL no.	Position			Traits[3]	Previously identified QTLs that overlapped with our QTLs in the position	
	Chr	Peak (Mb)[1]	CI (Mb)[2]		Traits	References
QTL1	1	100.92	91.4–114.2	LW%[M]	Liver percentage	Zhou *et al.* (2006b)
QTL2	1	102.21–105.44	91.4–108.6	BW1[M] BW2[M] BW3[M]	Body weight (3 weeks) Body weight (1, 4, 8, 9, 11 and 12 weeks) Body Weight (5 weeks) Abdominal fat weight Body weight (20 weeks)	Sewalem *et al.* (2002) Liu *et al.* (2007) Rao *et al.* (2007) Uemoto *et al.* (2009) Nassar *et al.* 2012
QTL3	2	27.55	23.1–31.5	AFW[F]	Body weight (13 and 16 weeks) Body weight (4 and 6 weeks) Drumstick and thigh muscle weight Body weight (6 weeks) Visceral fat weight Total white fat weight Subcutaneous fat weight	Tatsuda and Fujinaka (2001) Siwek *et al.* (2004) Ikeobi *et al.* (2004) Uemoto *et al.* (2009) Nassar *et al.* (2013)
QTL4	3	8.30	8.3–49.3	WG6–7	Growth (8–46, 46–112 days) Growth (6–9 weeks) Growth (4–6 weeks) Growth (1–8 days) Growth (0–2 weeks)	Carlborg *et al.* (2003) Carlborg *et al.* (2004) Zhou *et al.* (2006a) Le Rouzic *et al.* (2008) Wahlberg *et al.* (2009)
QTL5	3	26.51–30.75	17.8–31.7	PMAW	Pectoralis major weight Abdominal fat weight Chest width Breast muscle percentage Breast percentage	Park *et al.* (2006) Sharman *et al.* (2007) Nadaf *et al.* (2009) Baron *et al.* (2011)
QTL6	5	9.13–12.00	1.4–12.0	TMW%[F] TMW/ PMAW	Breast muscle weight Thigh muscle weight Breast percentage	McElroy *et al.* (2006) Gao *et al.* (2009) Baron *et al.* (2011)
QTL7	8	6.85	3.7–23.5	BW4 BW5	Body weight (3, 6, and 9 weeks) Body weight (9 weeks) Body weight (3, 6, 12, 24, 48, and 72 weeks) Average daily gain	Sewalem *et al.* (2002) Carlborg *et al.* (2004) Podisi *et al.* (2013)
QTL8	19	4.90–5.10	4.9–8.9	TMW/ PMAW	Chest width	Gao *et al.* (2011)
QTL9	24	0.57	0.6–2.6	PMIW%	Liver weight Eggshell Weight Meat color	Navarro *et al.* (2005) Tuiskula-Haavisto *et al.* (2011) Yoshida *et al.* (2013)
QTL10	Z	33.79–35.06	21.0–48.0	BW6[M] BW7[M]	Body weight (200 days) Growth (112–200 days) Body weight (12 and 18 weeks)	Kerje *et al.* (2003) Siwek *et al.* (2004)
		35.06	21.0–40.2	PMIW[F]	Liver weight Breast muscle percentage Abdominal fat weight	Navarro *et al.* (2005) Zhou *et al.* (2006b)
		33.79–35.06 35.06	21.0–68.7	CW[M] WG4–5[M]	Body weight (3 and 6 weeks) Body weight (239 days) Body weight (3 weeks) Body weight (3, 6, 12, and 24 weeks)	Sewalem *et al.* (2002) Sasaki *et al.* (2004) Hocking *et al.* (2012) Podisi *et al.* (2013)

[1] Physical position of the markers flanking the QTLs.
[2] Physical distance of the confidence interval predicted by extending the distance to the position of the nearest flanking markers that were located outside the confidence interval of centi morgan.
[3] Trait abbreviations are explained in Table 1. M＝expressed only in males, F＝expressed only in females, none＝expressed in both sexes.

QTLs, our targeted traits were different from those reported in previous studies, except for QTL5, which affects breast muscle (pectoralis major) weight. Furthermore, it is highly likely that the precise positions of the QTLs identified in this study are different from the positions of previously identified QTLs, as the positions of previously identified QTLs were

only rough estimations based on microsatellite markers.

The size of the CI depends on the number of birds and markers used (Wang *et al*., 2011). Shortening of the CI is important for the accuracy of MAS and future candidate gene selection at QTLs. In general, larger population size and more marker density can shorten the intervals (Visscher *et al*., 1996; Da *et al*., 2000; Bennewitz *et al*., 2002). In the present study, the average CI of our QTLs was 41.2 cM in terms of genetic distance when 319 F_2 birds and 545 markers were used. Compared to our study, Sewalem *et al*. (2002) detected QTLs for body weight and bone traits showing 61.9 cM CI in average from 546 F_2 birds and 169 markers. Nadaf *et al*. (2009) identified QTLs for growth and shank traits based on 698 F_2 individuals and 129 markers with average interval of 81.0 cM. Podisi *et al*. (2013) identified QTLs for growth traits with average 169.8 cM CI using 500 F_2 birds and 106 markers. Based on the results of this study and those of previous studies, we suggested that high marker density provides good mapping resolution than a larger population.

In the present study, alleles derived from White Plymouth Rock increased the phenotypic values of QTLs for body weight, weekly gain, and weights of carcass-related traits. In contrast, alleles derived from Oh-Shamo increased the phenotypic values of QTLs for percentage of carcass-related traits, which suggests that the meat yield of Oh-Shamo may be as good as that of White Plymouth Rock. According to these facts, introgressing of only White Plymouth Rock alleles cannot always efficiently improve growth performance. Therefore, we recommend introgressing of Oh-Shamo alleles at QTL1, QTL6, QTL8, and QTL9, and White Plymouth Rock alleles at the other six QTLs into the Oh-Shamo breed in the future MAS program.

Positive phenotypic correlations were observed between majority of growth traits. However, certain trait combinations showed either negative correlations (*e.g*., between BW2 and WG2-3) or no correlations (*e.g*., between BW0 and WG0-1). We speculated that this is due to the age-specific expression of QTLs. QTLs for growth traits were identified on chromosomes 1, 3, 8, and Z, which are expressed at different timepoints. Age-specific QTLs for growth traits have also been identified in previous QTL mapping studies (Sewalem *et al*., 2002; Carlborg *et al*., 2003; Gao *et al*., 2006; Wahlberg *et al*., 2009; Ankra-Badu *et al*., 2010a; Podisi *et al*., 2013). In our study, six QTLs showed a male-specific effect. This suggests that the sex-specific QTLs may induce phenotypic differences between males and females. Therefore, QTLs that affect growth traits in sex- and age-specific manner may be common in chickens.

QTLs for carcass-related traits were detected on chromosomes 1, 2, 3, 5, 19, 24, and Z. Of these QTLs, QTL10 affected both growth and carcass-related traits with a male-specific or female-specific effect, suggesting that this QTL either has a pleiotropic effect or that it may consist of multiple QTLs linked closely around the position. This may also be the case for other QTLs that were found to overlap with previously reported QTLs as shown in Table 4. Therefore, accumulation of QTL information focusing on a range of traits from several resource families will be important to gain better understanding of the genetic basis of growth in chickens.

Currently, QTLs have been mapped for various carcass-related traits, including carcass weight, muscle weight, bone weight, viscera weight, and its ratio to carcass weight or body weight at slaughtering age (Sharman *et al*., 2007; Ankra-badu *et al*., 2010b; Nassar *et al*., 2012; Moura *et al*., 2016). In the present study, we focused on the TMW to PMAW ratio, which is possibly the first trial in QTL mapping for carcass-related traits. Two of the QTLs were mapped to chromosomes 5 and 19. Although the positions of these two QTLs overlapped with those of loci reported by previous studies (as shown in Table 4), we hypothesize that the QTLs identified in this study may regulate breast or thigh meat yield.

The parental breeds in the present study were the same as those used in a study by Uemoto *et al*. (2009) in which QTLs for growth and carcass traits were identified on chromosomes 1, 2, 3, 5, 6, and 10. However, according to chicken QTLdb, only three QTLs (QTL1, QTL2, and QTL3) identified in our study overlapped with the QTLs identified by Uemoto *et al*. (2009) with respect to chromosomal positions. This discrepancy is possibly because of differences between the two studies in terms of animal feed, slaughtering age, and the DNA markers and statistical methods used. Although the experimental conditions used in our study were different from those used by Uemoto *et al.* (2009), we suggest that the QTLs identified in our study are novel QTLs for growth and carcass-related traits in an F_2 resource family of Oh-Shamo and White Plymouth Rock breeds.

Although several previous studies have reported the presence of epistatic QTLs in chickens for growth and carcass-related traits (Carlborg *et al*., 2003, 2004, 2006; Wahlberg *et al*., 2009; Ankra-Badu *et al*., 2010b; Sheng *et al*., 2013), we were unable to identify any epistatic QTL in this study. The identification of epistatic QTLs is important for our understanding of the complex genetic control of traits described by Carlborg and Haley (2006). We cannot rule out the possibility that epistatic QTLs remained undetected in our F_2 resource family, which warrants further investigations.

In conclusion, we identified 10 main-effect QTLs that affect growth and carcass-related traits using an F_2 resource population, which is a cross between Oh-Shamo and White Plymouth Rock breeds. These breeds are commonly used as parental breeds for the production of Japanese brand chickens. The QTLs identified will improve our understanding of the genetic basis of growth and carcass-related traits and assist in selecting birds for the Japanese brand chicken industry in future.

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