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Identification of quantitative trait loci affecting shank length, body weight and carcass weight from the Japanese cockfighting chicken breed, Oh-Shamo (Japanese Large Game)

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Abstract. We performed a quantitative trait locus (QTL) analysis to map QTLs controlling shank length, body weight, and carcass weight in a resource family of 245 F_2 birds developed from a cross of the large-sized, native, Japanese cockfighting breed, Oh-Shamo (Japanese Large Game), and the White Leghorn breed of chickens. Interval mapping revealed three significant QTLs for shank length on chromosomes 1, 4 and 24 at the experiment-wise 5% level, and a suggestive shank length QTL on chromosome 27 at the experiment-wise 10% level. For body weight two QTLs, one significant and the other suggestive, were identified on chromosomes 4 and 24, respectively. As expected, QTLs for carcass weight, which was highly correlated with body weight (r = 0.95), were detected at the same chromosomal locations as the detected body weight QTLs. Interestingly, the chromosomal locations containing these body weight and carcass weight QTLs coincided with those of two of the four shank length QTLs detected. No QTL with an epistatic interaction effect was discovered for any trait. The total contribution of all detected QTLs to genetic variance was 98.4%, 27.0% and 25.9% for shank length, body weight and carcass weight, respectively, indicating that most shank length QTLs have been identified but many body weight and carcass weight QTLs have been overlooked by the present analysis because of a low coverage rate of the 88 microsatellite markers used here (approximately 46% of the whole genome).

The majority of economic traits in domestic animals exhibit quantitative variation that is controlled by many quantitative trait loci (QTLs) with relatively small effects and is modified by environment. Mapping QTLs can lead to marker-assisted selection (Lande and Thompson, 1990; van der Beek and van Arendonk, 1996), and the results might contribute to increases in the products or improvements in health. Although QTL mapping had been impossible for a long time, development of DNA markers such as microsatellites and computer technology have made it possible to map QTLs since the first half of the 1990s (Haley and Knott, 1992; Knott and Haley, 1992; Andersson et al., 1994). In chickens, the earliest QTL reports were made in 1998 (Vallejo et al., 1998; van Kaam et al., 1998). Information on QTLs affecting body weight, growth, and carcass composition traits, egg quality and egg production traits, and disease susceptibility (resistance) or immune response trait had been accumulated by 2004 (summarized by Hocking, 2005).

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Since then a growing body of literature related to chicken QTL analysis has been published on body composition and production-related traits (for example, Navarro et al., 2005; Schreiweis et al., 2005; McElroy et al., 2006), disease-related traits (McElroy et al., 2005; Rabie et al., 2005; Tilquin et al., 2005; Siwek et al., 2006), and behaviour traits (Schutz et al., 2004; Jensen et al., 2005). Finding of QTLs for egg-related traits and body/carcass-related traits will contribute to layer and broiler industries, respectively, through future marker-assisted selection. Detection of QTLs for feed efficiency and disease resistance will contribute to both layer and broiler industries. The utility of already found QTLs begins to be verified by performing actual marker-assisted selection (Pakdel et al., 2005).

In almost all studies for QTL mapping, F_2 or backcross resource populations were constructed using common commercial layer and/or broiler lines (McElroy et al., 2006). In the present study, we used Oh-Shamo (Japanese Large Game) and White Leghorn breeds as parental breeds to create an F_2 resource population because the use of genetically different parental breeds is thought to result in efficient finding of distinguished QTLs. The characteristics of the two breeds are greatly different from each other in many points (Roberts, 1997; Tsudzuki, 2003). First, the origins of Oh-Shamo and White Leghorn are greatly different. Oh-Shamo is a native Japanese breed, the ancestors of which are thought to have been introduced from Thailand around the end of the 16th century or the beginning of the 17th century. In contrast, White Leghorn has its origin in Italy. Second, Oh-Shamo is originally a game bird for cockfighting with large body size (adult male, 4–7 kg; adult female, 3–5 kg). Besides the high body weight, this breed is characterized by erect body shape with large height (about 70–80 cm in adult males) and long legs. Accordingly, body weight and body shape are quite different between Oh-Shamo and White Leghorn. Furthermore, it is well known in Japan that the meat of Oh-Shamo is very delicious. Contrary to the benefit in meat volume and quality, egg production rate in this breed is very low as compared with the White Leghorn breed. The phenotypic differences mentioned above strongly hold out hope that gene constitution and microsatellite marker genotypes are greatly different between the two breeds.

Shank length is an important trait for the meat-type chicken industry. Moderately short shanks are desirable, as too long legs give rise to leg problems in high body weight chickens (Deeb and Lamont, 2002). Furthermore, shank length relates to working efficiency in processing plants (Yamamoto A, personal communication). Finding QTLs for shank length will contribute to improvement of health control for broilers in hen houses and efficient management in processing plants. Of course, it is apparent that the detection of QTLs for body weight and carcass weight is useful to efficiently improve meat-type chickens. In addition to these industrial demands, the detection of such QTLs would contribute to basic scientific fields in which the molecular mechanisms of bone and/or body growth regulation are being studied.

In this article, we describe the chromosomal regions harboring QTLs for shank length, body weight, and carcass weight that are found in the unique F_2 resource population constructed from the Oh-Shamo and White Leghorn breeds of chickens. To our knowledge, this is the first report dealing with shank length QTLs.

Materials and methods

Animals

We mated an Oh-Shamo male to three White Leghorn females. Subsequently, we mated an F_1 male to six F_1 females in full-sib matings. A total of 245 F_2 birds were produced. Feed and water were supplied for ad libitum consumption. Birds were fed a starter diet (crude protein (CP) 20%, metabolic energy (ME) 2900 kcal/kg) up to 6 weeks of age under 24 h illumination. From 7 to 10 weeks of age, and from 11 to 16 weeks of age, a grower diet (CP 17%, ME 2850 kcal/kg) and a developer diet (CP 15%, ME 2800 kcal/kg) were given, respectively. After 16 weeks of age, layer diet (CP 17%, ME 2800 kcal/kg) was supplied. After 6 weeks of age, birds were kept in the condition of a 14 h light: 10 h dark photoperiod.

Trait measurements

At 20 weeks of age, shank length, body weight, and carcass weight were measured. For shank length, the distance from the hind corner of the hock joint to the first scale of the third (middle) toe was measured with a vernier caliper. Birds used in the present study were treated according to the rules described in Standards Relating to the Care and Management of Experimental Animals (Prime Minister's Office, Japan, 1980) and Guide for the Use of Experimental Animals in Universities (The Ministry of Educations, Science, Sports, and Culture, Japan, 1987).

Marker genotyping and linkage map construction

Eighty-eight microsatellite markers spanning 24 autosomes and the Z chromosome were employed, which are listed in Table 1. These markers were selected from Comprehensive Mapping Kits #1, #2, and #3 supplied by the Poultry Genome Coordinators (http://poultry.mph.msu.edu) and were fully informative between Oh-Shamo and White Leghorn breeds. Genomic DNA extraction and polymerase chain reaction procedures were performed as described previously (Osman et al., 2005). Marker genotyping was completed using an ABI 310 DNA sequencer and Genescan (version 2.1) and Genotyper (version 2.5) softwares (Applied Biosystems, Foster City, CA, USA).

A marker linkage map was constructed with the computer software, Map Manager QTXb20 (Manly et al., 2001). Recombination frequencies (%) were converted into genetic distances in cM using the Kosambi map function.

QTL analyses

Prior to QTL analyses, exploratory statistical analysis was performed with the statistical discovery software JMP version 6.0 (SAS Institute Inc., Cary, NC, USA) to reduce the effects of four environmental factors (sex, birthday, sire, and dam) on shank length and two weight traits. These factors were treated as fixed effects in a linear model. The interaction of sex and dam was additionally included in the model. The fixed effects significant at the nominal 5% level were used for data adjustment. That is, the effects of sex, birthday and dam were significant for shank length, and those of sex and dam for both body weight and carcass weight. Next, the data adjusted were subjected to the Shapiro-Wilk's W-test of JMP to test the trait distributions for normality. The data for shank length fitted to a normal distribution ($P = 0.68$). But those for body weight and carcass weight did not fit, so they were subjected to the Box-Cox scale transformation, resulting in a distribution close to the normal ($P = 0.052$ and 0.0012 for body and carcass weights, respectively). All data were finally standardized for QTL analyses to facilitate the comparison of parameter estimates of detected

Table 1. The microsatellite markers genotyped in the Oh-Shamo × White Leghorn F_2 population

Marker	Chromosome or linkage group	Position (cM)[a]	Reference position (cM)[b]	Marker	Chromosome or linkage group	Position (cM)[a]	Reference position (cM)[b]
MCW0248	1	0	19	LEI0196	6	40	110
LEI0209	1	31.64	56	MCW0183	7	0	86
ADL0188	1	92.29	133	LEI0158	7	24.25	122
LEI0146	1	116.02	169	ADL0315	7	32.2	140
MCW0112	1	153.86	205	ADL0169	7	54.2	165
MCW0058	1	175.31	241	ADL0258	8	0	23
LEI0101	1	188.94	259	ADL0154	8	14	46
MCW0313	1	242.83	295	ADL0191	9	*	44
LEI0088	1	260.15	316	MCW0134	9	*	132
LEI0198	1	290.62	364	MCW0067	10	0	59
MCW0036	1	316.14	386	ADL0106	10	23.72	88
MCW0283	1	339.28	414	LEI0112	10	45.72	107
LEI0106	1	353.8	426	ADL0123	11	0	22
MCW0145	1	380.71	455	ADL0210	11	30	54
MCW0115	1	444.57	518	ADL0372	12	0	0
MCW0107	1	482.57	565	LEI0099	12	80	63
ADL0190	2	0	62	ADL0147	13	0	32
ADL0176	2	48.49	116	ADL0310	13	18.54	51
ADL0257	2	88.12	153	MCW0322	13	38.54	67
MCW0062	2	101.85	172	MCW0031	15	0	7
LEI0096	2	171.58	233	MCW0080	15	44	49
MCW0027	2	186.77	255	ADL0293	17	0	26
LEI0237	2	218.72	320	MCW0330	17	12	41
LEI0070	2	272.14	379	MCW0217	18	0	24
LEI0104	2	290.14	403	MCW0094	19	0	9
MCW0169	3	0	31	ADL0193	20	0	16
MCW0222	3	62.9	85	MCW0022	20	8	20
ADL0229	3	86.33	111	LEI0102	23	0	0
ADL0280	3	128.18	170	ADL0262	23	10.78	0
MCW0252	3	155.82	201	MCW0165	23	19.55	1
MCW0016	3	194.37	247	ADL0289	23	29.55	7
MCW0156	3	208.37	276	MCW0301	24	0	48
ADL0143	4	0	0	MCW0262	26	0	26
ADL0317	4	14.74	12	MCW0069	26	14	47
MCW0295	4	118.32	75	MCW0233	27	0	19
MCW0005	4	129.58	101	MCW0328	27	30.1	47
ADL0266	4	174.64	138	ADL0376	27	38.1	59
LEI0094	4	196.48	153	LEI0135	28	0	0
MCW0240	4	224.48	201	ADL0284	28	24	25
MCW0193	5	0	50	GCT0004	E50C23	0	40
MCW0214	5	30.3	88	ADL0022	Z	0	0
MCW0029	5	52.02	128	ADL0273	Z	37.91	73
ADL0166	5	78.02	162	MCW0154	Z	68.5	95
LEI0092	6	0	59	LEI0121	Z	84.5	131

[a] Position on a sex averaged map. Distances are in Kosambi cM relative to the position of the first marker on each chromosome or linkage group. * No linkage resulted after calculation by Map Manager QTXb20 software (Manly et al., 2001).
[b] From Animal Sciences Group AceBrowser (Public ChicAce) of Wageningen UR (https://acedb.asg.wur.nl/).

QTLs between individual traits. Correlation analyses between each pair of the three traits, adjusted for sex, and the other general statistical analyses were performed with JMP.

A segregation pattern for marker genotypes was clearly different between autosomes and the Z chromosome in the F_2 mapping population used for QTL analysis. That is, two parental types of homozygotes and a heterozygote were segregating for autosomes, whereas for Z one parental type of homozygote and a heterozygote appeared in males and two types of hemizygotes in females. Hence the QTL analysis described below was performed for the autosomes and Z chromosome separately. Also it was conducted under the assumption that the two parental breeds are fixed for alternative QTL alleles.

To identify QTLs with main effects on the three traits, two methods of simple interval mappings based on the maximum-likelihood method (Lander and Botstein, 1989) and multiple regression analysis (Haley and Knott, 1992) were implemented with two computer softwares, QTL Cartographer Version 1.17j (Basten et al., 2003) and Map Manager QTX, respectively. Subsequently, composite interval mapping that allows better resolution and precision of QTL location and effect (Zeng, 1993, 1994) was performed with QTL Cartographer. A forward/backward selection with an acceptance/rejection significance threshold of 1% was used to select background cofactors for composite interval mapping, and a window size of 10 cM was adopted. The above interval mappings were performed with 2 cM steps within each interval.

Experiment-wise significance thresholds for both simple and composite interval mappings were established with 1000 permutations of QTL Cartographer, and evaluated as LOD scores by dividing the likelihood ratio statistics by 4.605. The parameter estimates of detected QTLs, such as map position, additive effect (half the difference between two homozygotes) and dominance effect (deviation of a heterozygote from the mean of the two homozygotes), were estimated with QTL Cartographer. For the Z chromosome of females, the expected additive effect was half the computed value due to its hemizygous state. The 95% confidence intervals of QTL locations were calculated according to Darvasi and Soller (1997).

The mode of inheritance of alleles at the QTL detected was determined by two statistical tests. First, one of additive, dominance and recessive regression models was contrasted with a no QTL model using the software Map Manager QTX. The likelihood ratio statistic obtained was tested for significance using the approximate experiment-wise 5% threshold that was converted from that threshold for simple interval mapping as described by Knott et al. (1998). Second, if significant, that model was compared with a free model. When the difference in likelihood ratio statistic between the two models exceeded the above approximate threshold, that model was rejected. In contrast, when the difference was within the threshold, that model was accepted.

Using one-way ANOVA of the JMP software, a single point analysis was performed for six microsatellite markers that consisted of only one marker on chromosomes/linkage groups 18, 19, 24, and E50C23 and two markers on chromosome 9 not linked with each other due to a very long map distance between them (see Table 1 for details). The significance thresholds determined for simple interval mapping were adopted for significance tests after converting *P* values to LOD scores using a chi-square distribution.

To identify QTLs with epistatic interaction effects, all possible pairwise comparisons between the 84 marker loci on autosomes were performed with Map Manager QTX. The significance tests to declare significant epistatic QTLs were carried out following the method of Ishikawa et al. (2005).

The total contribution of all detected QTLs to the phenotypic variance for each trait was estimated by JMP multiple regression analysis. Furthermore, that contribution to genetic variance was calculated. The genetic variance was obtained at the time of calculation of broadsense heritability according to the method of Fishman et al. (2002).

Results

Table 2 shows sex-adjusted mean values for shank length, body weight, and carcass weight at 20 weeks after hatching in two parental breeds, Oh-Shamo and White Leghorn, and their F_1 and F_2 progeny. Oh-Shamo and White Leghorn had the longest and shortest shank lengths, respectively. The F_1 and F_2 showed nearly a mid-parental value for that trait. A similar tendency was observed for carcass weight. On the other hand, the mean body weight of Oh-Shamo was not significantly different from that of F_1 and their values were highest. White Leghorn had the lowest body weight. The frequency distributions of values for the three traits in the F_2 were all unimodal (data not shown), implying that those traits are under polygenic controls. In the F_2 a very high phenotypic correlation was observed between body weight and carcass weight ($r = 0.95$, $P = 1.5 \times 10^{-127}$), as expected. Shank length significantly correlated with body weight ($r = 0.67$, $P = 1.2 \times 10^{-31}$) and carcass weight ($r = 0.70$, $P = 1.2 \times 10^{-35}$).

The total length of the marker linkage map used for QTL analysis was 1840 cM, and average marker spacing was 29 cM (Table 1). A marker coverage rate in this study was approximately 46% of the whole genome (relative to 4000 cM, Groenen and Crooijmans, 2003).

Table 2. Means ± standard deviations (SD) (averaged across sex) for shank length, body weight, and carcass weight at 20 weeks of age in Oh-Shamo and White Leghorn breeds and their F_1 and F_2 birds

Trait	Group	No. of birds	Mean ± SD
Shank length (mm)	Oh-Shamo	39	121.7 ± 6.8^a
	White Leghorn	49	94.2 ± 5.4^b
	F_1	53	111.7 ± 2.7^c
	F_2	232	107.7 ± 6.0^d
Body weight (g)	Oh-Shamo	39	1937.9 ± 188.7^a
	White Leghorn	49	1171.8 ± 150.6^b
	F_1	53	1860.9 ± 137.1^a
	F_2	245	1680.7 ± 212.2^c
Carcass weight (g)	Oh-Shamo	39	1372.2 ± 140.8^a
	White Leghorn	49	737.6 ± 93.0^b
	F_1	53	1276.4 ± 103.4^c
	F_2	244	1137.1 ± 157.8^d

[a–d] Means with the same superscript letter are not significantly different among the groups at $P > 0.05$ in each trait (one way ANOVA followed by Tukey's HDS test).

To detect QTLs with main effects, simple interval mapping was performed on the three traits, using QTL Cartographer and Map Manager QTX which have different statistical algorithms. Furthermore, composite interval mapping was carried out with QTL Cartographer. Because the two simple interval mappings and also the composite interval mapping provided nearly the same results, only the result for the simple interval mapping using QTL Cartographer is described below. In addition, a single point analysis was performed on six markers which were not linked or only a marker on chromosomes 9, 18, 19, 24 and E50C23, using one-way ANOVA.

The experiment-wise 10%, 5% and 1% significance threshold levels, determined by 1000 permutations and expressed as LOD scores, were not greatly different among the three traits and were estimated to be 3.0–3.1, 3.3–3.5 and 3.9–4.3, respectively.

The LOD score plots are shown in Figs. 1 and 2. The parameter estimates such as map positions and maximum LOD scores, are shown in Table 3. Highly significant or significant QTLs controlling shank length were detected on chromosomes 1, 4, and 24. Also, a suggestive QTL was identified on chromosome 27. The QTLs on chromosomes 1, 4, and 24 were found just at the positions of markers ADL0188, MCW0240, and MCW0301, respectively. The QTL on chromosome 27 mapped 2 cM proximal to ADL0376. For body weight, significant and suggestive QTLs were discovered on chromosomes 4 and 24, respectively. At the same chromosomal positions as those of the body weight QTLs, significant and suggestive QTLs affecting carcass weight were identified. The QTLs for both body weight and carcass weight had nearly the same additive and dominance effects.

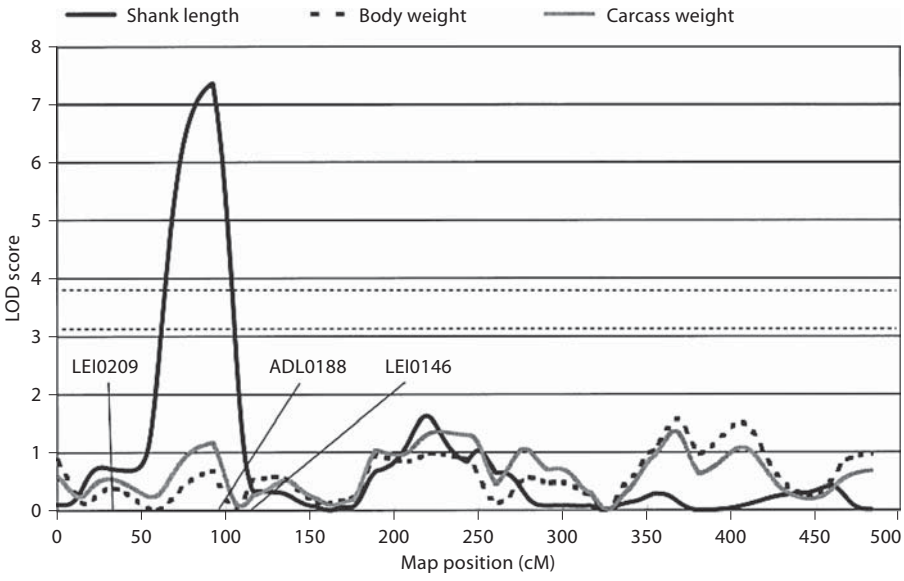

Fig. 1. LOD score plots of QTLs affecting shank length, body weight, and carcass weight traits on chicken chromosome 1. Simple interval mapping was carried out with the software QTL Cartographer (Basten et al., 2003). The horizontal dotted lines show the experiment-wise 5% (upper) and 10% (lower) levels estimated by the permutation test of QTL Cartographer. The markers near the peak LOD score are shown.

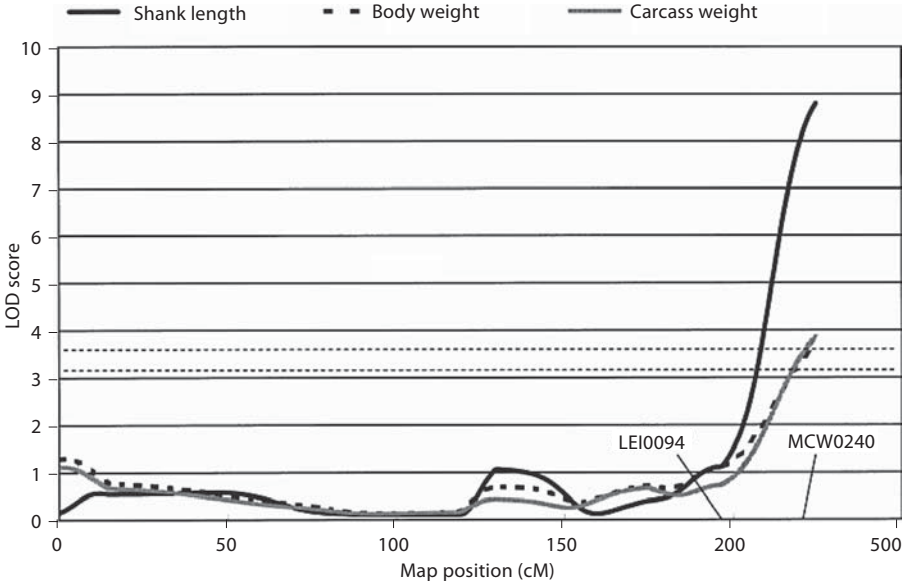

Fig. 2. LOD score plots of QTLs affecting shank length, body weight, and carcass weight traits on chicken chromosome 4. Simple interval mapping was carried out with the software QTL Cartographer (Basten et al., 2003). The horizontal dotted lines show the experiment-wise 5% (upper) and 10% (lower) levels estimated by permutation test of QTL Cartographer. The markers near the peak LOD score are shown.

Furthermore, the map positions of these two QTLs were the same as those of the two shank length QTLs detected on chromosomes 4 and 24.

As shown in Table 3, individual QTLs detected accounted for 6.6–17.5% of the phenotypic variance. At the QTLs affecting any trait on chromosomes 1 and 4, the allele derived from Oh-Shamo increased trait values, whereas it decreased them at the QTLs on chromosome 24. The Oh-Shamo allele showed the additive, dominance, or recessive mode of inheritance depending on the QTL detected. No QTL with an epistatic effect on any trait was detected in this study.

Table 4 shows the total contributions of all detected QTLs for the three traits to the phenotypic and genetic variances. The total contribution of all detected QTLs for shank length to the phenotypic variance was 36.6%, whereas those of body weight and carcass weight were 12.6–12.9%. However, all QTLs detected for shank length accounted for most of the genetic variance, i.e. 98.4%, contrasting to 25.9–27.0% for the body weight and carcass weight QTLs.

Discussion

In the present study, we detected four QTLs for shank length on chromosomes 1, 4, 24 and 27. These QTLs explained 98.4% of the genetic variance. This high value

Table 3. Summary of QTLs affecting shank length, body weight, and carcass weight detected in the Oh-Shamo × White Leghorn F_2 population

Trait	Chromosome	Map position[a]	CI[b]	LOD[c]	Var[d]	Additive[e]	Dominance[f]	Inheritance[g]	Difference[h]
Shank length	1	ADL0188 + 0	16.7	7.4***	13.7	0.51	–0.32	Rec, Add	S > H ≥ W
	4	MCW0240 + 0	13.1	8.8***	17.5	0.57	0.03	Add, Dom	S > H > W
	24	MCW0301 + 0	27.5	3.7**	8.3	–0.38	–0.18	ND	W > H ≥ S
	27	ADL0376 – 2	30.0	3.3*	7.6	0.29	0.37	ND	H ≥ S > W
Body weight	4	MCW0240 + 0	31.4	3.6**	6.9	0.34	0.14	Add, Dom	S ≥ H > W
	24	MCW0301 + 0	33.3	3.2*	6.5	–0.35	–0.08	ND	W > H ≥ S
Carcass weight	4	MCW0240 + 0	29.8	3.9**	7.3	0.34	0.16	Dom, Add	S ≥ H > W
	24	MCW0301 + 0	32.9	3.2*	6.6	–0.35	–0.11	ND	W > H ≥ S

[a] The positive and negative signs indicate that the QTL maps that distance (cM) distal and proximal, respectively, to the nearest marker.
[b] The 95% confidence interval (cM) calculated from the formula of Darvasi and Soller (1997).
[c] The maximum LOD score significant at the genome-wide 10% (*), 5% (**) and 1% (***) levels, respectively.
[d] The phenotypic variance (%) explained by the QTL.
[e] The additive effect of the QTL shown in standard deviation unit. The positive value shows that the QTL allele derived from the Oh-Shamo breed increases the trait value.
[f] The dominance effect of the QTL shown in standard deviation unit.
[g] The mode of inheritance of the QTL determined by two statistical tests (see text for the detailed methods). The most likely mode is shown on the left. Rec, recessive; Add, additive; Dom, dominance; ND, could not be determined by the tests.
[h] The phenotypic difference among three possible genotypes at the nearest marker locus, two homozygotes for either the Oh-Shamo (S) or White Leghorn (W) allele and heterozygote (H), estimated by one-way ANOVA (followed by Tukey's HDS test).

Table 4. Total contributions of all detected QTLs affecting shank length, body weight and carcass weight to the phenotypic and genetic variances

Trait	Total number of QTLs detected	Phenotypic variance[a]	Genetic variance[b]	Broadsense heritability
Shank length	4	36.6	98.4	37.2
Body weight	2	12.6	27.0	46.7
Carcass weight	2	12.9	25.9	49.9

[a] The phenotypic variance (%) explained by all detected QTLs, which was estimated by a multiple regression analysis.
[b] The genetic variance (%) explained by all detected QTLs, i.e., estimated by dividing the phenotypic variance by the broadsense heritability (%).

strongly indicates that, irrespective of a low marker coverage rate of the whole genome, almost all QTLs with a main effect on shank length have been identified in our study although QTLs with small main and epistatic-interaction effects will be overlooked. On the other hand, for body weight and carcass weight, we detected only two main effect QTLs accounting for one fourth of the genetic variance. This means that many QTLs with main and/or interaction effects remain undiscovered. Those QTLs are probably located on chromosomal regions we did not scan here.

Shank length

It is known that shank length and body weight show high positive correlation (Chambers, 1990). In the present study also, the two traits were positively correlated with each other, meaning that heavier birds tend to have longer shanks. In such a case, if a traditional phenotypic selection method applied, it would be considerably difficult to make birds possess both high body weight and short shanks at the same time. In this QTL experiment, two out of four shank length QTLs were found at the same locations as those for body weight QTLs. However, the great difference in the genetic variance observed for shank length QTLs (98.4%) and body weight QTLs (27.0%) suggests that there are other body weight QTLs which are not linked with the shank length QTLs. That is, it seems to be possible to create birds that have short shank length and high body weight at the same time, especially with marker-assisted selection.

Schreiweis et al. (2005) identified significant QTLs affecting tibia and humerus lengths at 35 and 55 weeks of age on chromosomes 4 and 27 in the resource family based on common layer and broiler lines. Moreover, they also detected a suggestive QTL for 35-week humerus length on chromosome 1. The positions of their QTLs on chromosomes 4 and 27 are similar to those of ours. Also, the position of their QTL on chromosome 1 is relatively close to that of ours. Thus, there is a possibility that the QTLs on chromosomes 1, 4, and 27 detected by us and Schreiweis et al. (2005) are loci that are not only particular about the length of tibia, humerus and metatarsus (shank), but also influence the length of all long bones in fore and hind limbs of chickens.

Differing somewhat from the result of Schreiweis et al. (2005), we detected a highly significant QTL for shank length on chromosome 1 and another significant one on chromosome 24. This discrepancy may reflect the difference between the grandparental breeds used for construction of the F_2 resource families.

Body weight and carcass weight

QTLs affecting body weight at various bird ages have been found on many chromosomes, i.e. 1 to 9, 11 to 15, 17, 21, 23, 27, 28 and Z (for example, Sewalem et al., 2002; Kerje et al., 2003; Siwek et al., 2004; Jacobsson et al., 2005; Jennen et al., 2005; McElroy et al., 2006). Of these, major QTLs are commonly identified on chromosomes 1 and/or 4. For chromosome 1, there seem to be two major QTL regions where they are separately located from 70 cM to 250 cM and from 400 cM to 530 cM in the consensus map distance (Schmid et al., 2000; Groenen and Crooijmans, 2003). In contrast, on chromosome 4, almost all body weight QTLs have been discovered at one region from 200 cM to 230 cM, with an exceptional case for de Koning et al. (2004) reporting a body weight QTL around 100–120 cM.

In addition, there seem to be age-specific QTLs controlling body weight on chromosomes 1 and 4. Almost all QTLs for body weight at 20 weeks or later ages are uncovered on chromosome 4, with a few exceptional cases of Wardecka et al. (2002) and Kerje et al. (2003). QTLs influencing body weight up till 16 weeks of age seem to be located both on chromosomes 1 and 4. In the present study, we discovered a significant QTL for 20-week body weight on chromosome 4 and a suggestive QTL on chromosome 24. Caution should be exercised in the age-specificity of the QTLs because these results have been obtained from different resource families under different environmental conditions. Thus, QTL studies on body weight at every week from hatching to adult age in the same resource family will be necessary for identification of the age-specific QTLs.

So far, QTLs influencing carcass weight at 6–9 weeks of age have been identified on chromosomes 1, 2, 3, 4, 5, 6, 8, 13 and 27 (van Kaam et al., 1999; de Koning et al., 2004; Navarro et al., 2005; McElroy et al., 2006). We detected a significant QTL for carcass weight at 20 weeks of age on chromosome 4. A carcass weight QTL on chromosome 4 was also reported by de Koning et al. (2004) and Navarro et al. (2005). We and Navarro et al. (2005) found the QTL at the region around 200 cM, whereas de Koning et al. (2004) identified the QTL around the 100 cM region.

In the present study, the positions of carcass weight QTLs were the same as those of body weight QTLs. Similar results have been observed in other research (van Kaam et al., 1999; de Konning et al., 2004; McElroy et al., 2006). If these QTLs had a pleiotropic effect, body weight QTLs would be effectively used in marker-assisted selection for carcass weight. In QTL analysis prior to the marker-assisted selection, the measurement of body weight is further easier than that for carcass weight. However, there remains doubt concerning the significance of the body weight and carcass weight QTLs on chromosome 4, because their LOD scores just exceeded the 5% significant level under the condition of low marker coverage on the chromosome. Further studies are necessary to confirm whether they are really significant QTLs and their locations are really the same, using a dense marker map. Similarly, further studies are necessary for the shank length QTL on chromosome 24, because this chromosome had only one marker in the present study.

In conclusion, using the unique Japanese cockfighting breed, Oh-Shamo, we have mapped several QTLs with main effects on shank length, body weight and carcass weight. Especially, our study is the first one for QTLs affecting shank length. This study is the first step forward to finding candidate genes for the shank length QTLs identified.

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