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Mapping of Quantitative Trait Loci Affecting Growth Traits in a Japanese Native Chicken Cross*

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ABSTRACT : The Hinai-dori is a breed of chicken native to Akita Prefecture, Japan. An F_2 resource population produced by crossing low- and high-growth lines of the Hinai-dori breed was analyzed to detect quantitative trait loci (QTL) for growth traits. Highly significant QTLs for body weight at 10 and 14 weeks of age and average daily gain between 4 and 10 weeks and between 10 and 14 weeks of age were accordingly mapped in a common region between *ADL0198* and *ABR0287* on chromosome 1 and between *MCW0240* and *ABR0622* on chromosome 4, respectively. A significant QTL for body weight at 4 weeks of age and a significant QTL for average daily gain between 0 and 4 weeks of age were mapped for the first time to the same region flanking *ABR0204* and *ABR0284* on chromosome 1. These QTLs are good candidates for application in the development of marker-assisted selection strategies for increasing growth efficiencies in the Hinai-dori breed and native breeds of chickens in Asia. (**Key Words :** Chicken, Hinai-dori Breed, Quantitative Trait Loci, Body Weight, Average Daily Gain)

INTRODUCTION

In poultry, many QTL mapping studies have been performed on breed crosses, e.g. broiler×layer (Sewalem et al., 2002), Red Junglefowl×White Leghorn (Kerje et al., 2003), White Leghorn×Rhode Island Red (Sasaki et al., 2004), and broiler×White Leghorn (Schreiweis et al., 2005). This approach has proved very successful in identifying QTLs that explain differences between these breeds; however, they provide no insight into whether these QTLs would be useful for breeds/lines other than the founder breeds used in the respective QTL studies. Therefore, studies using crosses between divergently selected lines within a breed are becoming popular for their potential contribution to the improvement of growth traits in broilers (Jacobsson et al., 2005; Ankra-Badu et al., 2009; Wahlberg et al., 2009) and eggshell traits in the White Leghorn (Takahashi et al., 2009, 2010; Yang et al., 2010). Moreover, there are few studies that described QTLs for growth traits within a native chicken breed.

The Hinai-dori is a slow-growing breed of chicken native to Akita Prefecture, in northern Honshu Island, Japan. Although Hinai-dori meat has a characteristic taste and the breed has been used for a long time, it has decreased in numbers in recent times owing to the introduction of exotic breeds, and for a while was at risk of extinction. The Hinai-dori breed has been conserved by hobbyists who belong to the Preservation Society (PS) of the Hinai-dori Breed and is now mainly used for exhibition purposes. For effective use of the breed, selection experiments have been performed at the Livestock Experiment Station (LES), Akita Prefectural Agriculture, Forestry, and Fisheries Research Center (since 1973 when fertilized eggs were introduced to LES from PS) with a view towards increasing growth performance. At present, the average body weight of LES males at 300 days of age is approximately 1 kg heavier than that of PS males. F_1 chickens produced by crossing the improved LES Hinai-dori sires with Rhode Island Red dams have been commercialized as the Hinai-jidori chicken, which is one of the most popular high-quality chickens on the Japanese market. The LES line was developed from PS chickens: hence, these individuals possessed genes that influence growth traits. In order to effectively detect QTLs affecting

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growth traits within the Hinai-dori breed, we developed an F_2 resource population by crossing PS sires with LES dams, and thereafter conducted QTL mapping.

MATERIALS AND METHODS

F_2 resource population

F_1 chickens were produced by crossing three PS males with nine LES females, with one to three females randomly selected to mate with each male. The mapping population consisted of 359 F_2 individuals comprising 173 males and 186 females. The F_2 individuals were produced by full-sib mating of 17 F_1 males and 60 F_1 females. The F_2 chickens were hatched on the same day, raised in the same chicken house, and fed the same diet *ad libitum* for the duration of the experiment. Body weight was measured at day 0 (BW-0), 4 weeks (BW-4 wk), 10 weeks (BW-10 wk), and 14 weeks (BW-14 wk) of age. Average daily gain between 0 and 4 weeks of age (ADG 0-4 wk), between 4 and 10 weeks of age (ADG 4-10 wk), and between 10 and 14 weeks of age (ADG 10-14 wk) was calculated from BW at each week of age.

Genotyping and QTL mapping

Chicken genomic DNA was extracted from blood using a DNA isolation kit (SepaGene, Sanko Junyaku, Tokyo, Japan). PCR amplifications were performed in a 6 μl reaction volume, which included 2.5 pmols of each primer, 200 μM each dNTP, 1.2 mM MgSO4, 0.125 units of KOD plus polymerase (KOD-201, Toyobo, Tokyo, Japan), 1× reaction buffer provided by the supplier and 30 ng genomic DNA in a 384-well plate on an iCycler Thermal Cycler (Bio-Rad Laboratories, Hercules, CA, USA). PCR was performed as follows: hot start 75 s at 94°C followed by 10 cycles of 15 s at 94°C, 30 s at 60°C, and 60 s at 68°C, followed by 10 cycles with the same conditions except that the annealing temperature was 55°C, and then 30 cycles with an annealing temperature of 50°C, and finally with an elongation time of 9 min at 68°C. PCR products were electrophoresed on an ABI PRISMTM 3100 DNA Sequencer (Perkin-Elmer, Foster City, CA, USA) and analyzed using GeneScan (Ver. 3.7) and GeneMapper (Ver. 2.0) programs (Perkin-Elmer). One hundred and twenty-two microsatellite markers, which are informative in the F_2 resource population, were used (Table 1). Linkage analysis was performed using the program Map Manager QTX b18 (Manly et al., 2001) and linkage groups were compared with our linkage map (Takahashi et al., 2005). QTL analysis was performed using the QTL EXPRESS program (Seaton et al., 2002). A least-squares regression model was used for single-QTL analysis, including the fixed effects of sex, along with additive and dominance coefficients for the putative QTL. Detection of QTLs was based on an *F*-statistic that was computed from the sums of squares explained by the additive and dominance coefficients for the QTL. Significance thresholds of the *F*-statistic were derived at the experimental level on a single-trait basis using a permutation test, with 1,000 repetitions for each trait. The threshold levels of 5% and 1% at the experimental

Table 1. Information for chicken microsatellite markers used in this study

No.	Chromosome	Marker[1]	Map position in the draft sequence (May 2006 assembly, Mb)
1	chr1	*ABR0352*	9.2
2		*ABR0328*	18.5
3		*ABR0528*	29.1
4		*ABR0007*	40.1
5		*ABR0379*	48.4
6		*LEI0146*	55.3
7		*ABR0594*	59.0
8		*ABR0280*	63.1
9		*ABR0521*	69.7
10		*ABR0373*	88.9
11		*ABR0504*	92.2
12		*ABR0204*	124.2
13		*ABR0284*	133.5
14		*LEI0106*	148.1
15		*ABR0424*	166.0
16		*ADL0198*	171.7
17		*ABR0287*	173.4
18		*ABR0641*	176.7
19		*ABR0631*	182.9
20		*ABR0692*	190.2
21		*ABR0140*	190.2
22	chr2	*LEI0124*	2.4
23		*ABR0359*	5.6
24		*ABR0004*	7.1
25		*ABR0153*	22.0
26		*ABR0188*	27.4
27		*ABR0107*	31.7
28		*ABR0008*	Unknown
29		*ABR0599*	61.4
30		*ABR0189*	70.0
31		*ABR0539*	71.5
32		*ABR0537*	81.5
33		*ABR0655*	87.3
34		*ABR0579*	99.3
35		*ABR0067*	103.4
36		*ABR0433*	113.2
37		*ABR0493*	132.4
38		*ABR0249*	136.2
39		*ABR0659*	149.7
40		*MCW0311*	153.7

Table 1. Information for chicken microsatellite markers used in this study (Continued)

No.	Chromosome	Marker[1]	Map position in the draft sequence (May 2006 assembly, Mb)
41	chr3	*ABR0547*	7.0
42		*ABR0141*	9.8
43		*ABR0339*	17.5
44		*ABR0509*	24.1
45		*ABR0472*	34.5
46		*ABR0303*	40.0
47		*ABR0353*	46.8
48		*ABR0025*	50
49		*ABR0161*	53.1
50		*ABR0388*	63.2
51		*ABR0587*	68.7
52		*ADL0306*	84.8
53		*MCW0002*	92.8
54		*ABR0232*	100.2
55	chr4	*GCT0026*	21.5
56		*ABR0423*	29.6
57		*ABR0346*	47.7
58		*ABR0382*	49.5
59		*ABR0315*	55.5
60		*MCW0240*	69.9
61		*ABR0622*	86.3
62		*ABR0357*	89.7
63	chr5	*ABR0392*	0.6
64		*ABR0046*	Unknown
65		*ABR0391*	8.9
66		*ADL0253*	10.8
67		*ABR0390*	25.2
68		*ABR0209*	30.8
69		*ABR0399*	36.6
70		*ABR0541*	51.7
71		*ABR0262*	53.0
72	chr6	*ABR0028*	9.5
73		*ABR0281*	17.5
74		*ABR0605*	23.3
75		*ABR0543*	27.4
76	chr7	*ABR0041*	5.1
77		*ABR0419*	22.2
78		*ABR0636*	26.3
79		*ABR1326*	27.4
80		*ABR0274*	36.2

Table 1. Information for chicken microsatellite markers used in this study (Continued)

No.	Chromosome	Marker[1]	Map position in the draft sequence (May 2006 assembly, Mb)
81		*ABR0300*	92.8
82	chr8	*ABR0228*	Unknown
83		*ABR0647*	12.2
84		*ADL0154*	19.9
85		*ABR0060*	21.3
86		*ABR0604*	29.5
87	chr9	*ABR0148*	3.5
88		*ADL0191*	5.3
89		*ABR0299*	13.7
90		*LEI0130*	15.4
91		*ABR0526*	19.3
92		*MCW0134*	24.8
93	chr11	*ABR0478*	6.6
94		*ABR0389*	12.5
95		*ADL0308*	17.4
96		*ABR0037*	20.6
97	chr13	*ABR0506*	5.1
98		*ADL0147*	8.1
99		*LEI0251*	11.9
100		*ADL0225*	17.2
101	chr14	*ABR0365*	15.5
102		*ADL0263*	14.7
103		*ABR0517*	20.4
104	chr18	*ABR0374*	1.6
105		*MCW0217*	3.2
106		*ABR0650*	7.0
107	chr19	*ABR0133*	3.9
108		*ABR0180*	6.4
109		*MCW0304*	8.2
110	chr20	*ABR0364*	4.0
111		*ABR0001*	9.4
112		*ABR0026*	13.3
113	chr23	*LEI0102*	0.7
114		*ADL0262*	5.7
115	chr24	*MCW0301*	4.6
116		*ROS0302*	Unknown
117	chr26	*MCW0262*	1.4
118		*ABR0006*	4.0
119	chr27	*ABR0015*	3.9
120		*ABR0076*	3.9
121	chr28	*ABR0378*	2.5
122		*ABR0066*	3.6

[1] Markers were as detailed in Takahashi et al. (2005).

level were used to define a significant and a highly significant QTL, respectively. The percentage of F_2 variance explained by the model was calculated as

$$\text{Variance percentage} = 100\times(\text{RMS}-\text{FMS})/\text{RMS},$$

where RMS is the residual MS from the reduced model, omitting the QTL but including all fixed effects, and FMS is the residual MS from the full model, including the QTL and

all fixed effects. A draft sequence of the chicken genome (May 2006 assembly), available on the University of California, Santa Cruz (UCSC) Genome Browser (2004) and the Ensembl Genome Browser (2004), was used in the present study.

RESULTS AND DISCUSSION

We accordingly mapped a significant QTL for BW-4 wk to a region flanking *ABR0204* (chr1:124.1 Mb) and *ABR0284* (chr1: 133.5 Mb) (Table 2). Highly significant QTLs for BW-10 wk and BW-14 wk were mapped in a common region between *ADL0198* (chr1: 171.7 Mb) and *ABR0287* (chr1: 173.4 Mb), and *MCW0240* (chr4: 69.9 Mb) and *ABR0622* (chr4: 86.3 Mb), respectively. A significant QTL for ADG 0-4 wk and highly significant QTLs for ADG 4-10 wk and ADG 10-14 wk were mapped to the same QTL regions for BW. We hereafter refer to the two QTLs on chromosome 1 (*ABR0204–ABR0284* and *ADL0198-ABR0287*) and the one QTL on chromosome 4 (*MCW0240-ABR0622*) as HG1, HG2, and HG3 (*H*inai-dori *G*rowth), respectively.

Several previous studies have suggested the presence of two major QTLs for growth traits on chromosome 1, one in the proximal (52-79.5 Mb) and the other in the distal (164.9-191.8 Mb) region. For example, QTLs associated with BW assigned to regions flanking *LEI0174* (chr1: 64.9 Mb) to *LEI0071* (chr1: 79.5 Mb) (Tatsuda and Fujinaka, 2001), *LEI0068* (chr1: 52.0 Mb) to *MCW0018* (chr1: 65.7 Mb) and *ADL0359* (chr1: 57.6 Mb) to *MCW 0018* (65.7 Mb) (Jennen et al., 2004), *ADL0245* (chr1: 171.7 Mb) to *LEI0134* (chr1: 191.8 Mb) (Jacobsson et al., 2005; Wahlberg et al., 2009), and *LEI0168* (chr1: 164.9 Mb) to *ABR0044* (chr1: 173.4 Mb) (Uemoto et al., 2009). HG2 flanking *ADL0198* (chr1: 171.7 Mb) and *ABR0287* (chr1: 173.4 Mb) is suggested to be included in the QTL in the distal region of chromosome 1; however, QTLs affecting growth traits have not been previously reported around HG1. HG1 was detected only during the early phase of growth until 4 weeks of age, whereas HG2 and HG3 were detected during the late phases of growth. The data thus provide evidence for different QTL regions specific to developmental stages affecting growth.

Some studies have also reported various growth QTLs on chromosome 4. For example, QTLs for BW were assigned to regions flanking *ADL0317* (chr4: 3.5 Mb) to *MCW0251* (chr4: 19.2 Mb) (Jacobsson et al., 2005), *ABR0354* (chr4: 22.9 Mb) to *MCW0005* (chr4: 31.1 Mb) (Yang et al., 2010), *LEI0125* (chr4: 42.0 Mb) to *LEI0076* (chr4: 62.1 Mb) (Jacobsson et al., 2005), *ADL0266* (chr4: 46.7 Mb) to *LEI0094* (chr4: 51.6 Mb) (Kerje et al., 2004),

Table 2. Phenotypic values of quantitative traits and quantitative traits loci affectiing body weight and average daily gain

Trait (unit)[1]	Phenotypic values			Position	*F*-value	Flanking markers	Additive effect		Dominance effect		Variance (%)
	n	Mean	SD	chromosome: cM			Mean	SE	Mean	SE	
BW-0 (g)	359	34.5	2.4	-							
BW-4wk (g)	359	235.1	36.1	chr1 : 285	6.4*	*ABR0204-ABR0284*	-27.7	8.5	-63.9	37.3	2.9
BW-10wk (g)	359	972.6	161.8	chr1 : 371	10.2**	*ADL0198-ABR0287*	-60.4	13.6	20.9	24.7	4.9
				chr4 : 211	11.2**	*MCW0240-ABR0622*	-60.0	13.2	-31.7	25.7	5.4
BW-14wk (g)	359	1,478.9	261.2	chr1 : 371	19.2**	*ADL0198-ABR0287*	-107.8	17.6	31.9	32.1	9.2
				chr4 : 208	16.3**	*MCW0240-ABR0622*	-99.3	17.5	-13.8	34.3	7.9
ADG 0-4wk (g/d)	359	7.2	1.3	chr1 : 286	6.8*	*ABR0204-ABR0284*	-1.0	0.3	-2.2	1.3	3.1
ADG 4-10wk (g/d)	359	17.6	3.3	chr1 : 371	9.9**	*ADL0198-ABR0287*	-1.2	0.3	0.5	0.5	4.7
				chr4 : 210	13.1**	*MCW0240-ABR0622*	-1.3	0.3	-0.5	0.5	6.4
ADG 10-14wk (g/d)	359	18.1	4.4	chr1 : 368	20.7**	*ADL0198-ABR0287*	-1.7	0.3	0.4	0.5	10.0
				chr4 : 201	14.6**	*MCW0240-ABR0622*	-1.4	0.3	0.7	0.5	7.1

[1] BW-4wk = Body weight at 4-weeks; BW-10 wk = Body weight at 10-weeks; BW-14 wk = Body weight at 14-weeks; ADG 0-4 wk = Average daily gain between 0 and 4 weeks; ADG 4-10 wk = Average daily gain between 4 and 10 weeks; ADG 10-14 wk = Average daily gain between 10 and 14 weeks.
* Experimental-wide significance of 5%; ** Experimental-wide significance of 1%.

MCW0122 (chr4: 76.4 Mb) to *LEI0062* (chr4: 85.9 Mb) (Sasaki et al., 2005), and *MCW0240* (chr4: 69.9 Mb) to *LEI0073* (chr4: 88.4 Mb) (Ankra-Badu et al., 2010). Our data suggest that HG3 flanking *MCW0240* (chr4: 69.9 Mb) to *ABR0622* (chr4: 86.3 Mb) may correspond to the QTLs reported by Sasaki et al. (2005) and Ankra-Badu et al. (2010).

It has been reported that there are many QTLs with minor additive effects in a broiler×broiler cross (Jacobsson et al., 2005; Wahlberg et al., 2009). These studies failed to detect any highly significant ($p<0.01$) QTLs at the experimental level, and each QTL accounted for a small proportion of the phenotypic variance, ranging from 1.5% to 4.4%; however, these authors used a resource population produced by crossing two broiler lines with significantly different body weights. Ankra-Badu et al. (2010) analyzed a similar broiler cross and detected a highly significant QTL on chromosome 4 flanking *MCW0240* to *LEI0073*, which accounted for 4.92% of the phenotypic variance in body weight at 7 weeks, whereas the other QTLs accounted for small proportions of the phenotypic variance, ranging from 1.97% to 3.49%. We successfully detected two highly significant QTLs (HG2 and HG3) and one significant QTL (HG1), which accounted for a relatively large proportion of the phenotypic variance, ranging from 2.9% to 10.0%. In particular, HG2 plus HG3 accounted for 10.3% (HG2: 4.9% +HG3: 5.4%) and 18.1% (HG2: 9.2%+HG3: 7.9%) of the phenotypic variance of BW-10 wk and BW-14 wk, respectively. Moreover, HG1, HG2, and HG3 appear to act independently on each growth trait, since we could detect no QTL when we performed analysis using the F2 epistasis module in GridQTL software (Hernández-Sánchez et al., 2009). These data suggest that marker-assisted selection on the three QTLs could be effective in improving growth performance within the Hinai-dori breed without considering the epistatic interaction effects among the QTLs.

In conclusion, three QTL regions affecting growth traits were successfully detected in a resource population of the Hinai-dori breed. Of the three, a QTL in the middle of chromosome 1 affecting early development was detected for the first time. Since the resource population was developed from the same founder population, we believe that these QTLs contain key genes affecting growth traits. We plan to use the experience we gained in identifying a gene associated with eggshell traits from QTL analyses in the White Leghorn breed (Takahashi et al., 2009, 2010) to approach to the candidate genes for the QTLs on chromosome 1 and 4 in future studies.

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