

1 **QTL analysis for early growth in an intercross between native Japanese Nagoya and**  
2 **White Plymouth Rock chicken breeds using RAD sequencing-based SNP markers**

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11 **Running title:** Chicken early growth QTL

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## 1 **Summary**

2 An F<sub>2</sub> population of 239 chickens was obtained by an intercross between Nagoya (NAG), a  
3 native Japanese breed with low growth, and White Plymouth Rock (WPR), a Western breed  
4 with high growth. Using SNP markers obtained by restriction site-associated DNA  
5 sequencing, genome-wide QTL analysis was performed and it revealed three QTL for early  
6 postnatal growth in the F<sub>2</sub> population at genome-wide 5% significance levels. The most  
7 highly significant QTL affecting body weights at 2-4 weeks of age and weight gains at 2-3  
8 and 0-4 weeks was located on GGA4 between 34.0 and 65.6 Mb with LOD scores of 3.9-5.9  
9 and it explained 4.9-9.9% of the total variance of the traits. The analysis provided evidence  
10 for significant QTL on GGA2 between 105.6 and 125.2 Mb (LOD = 4.6) and on GGA1  
11 between 51.1 and 61.6 Mb (LOD = 4.0) which had effects on body weight at 3 weeks and  
12 body weight gain at 0-1 week, respectively. These two genomic regions explained 6.6% and  
13 6.9% of the phenotypic F<sub>2</sub> variance of the corresponding traits, respectively. The allele  
14 derived from WPR at all QTL increased the corresponding traits. Neither sex-specific nor  
15 epistatic QTL was detected. The results showed that the GGA4 QTL affecting multiple traits  
16 is a key locus responsible for early growth in our chicken cross, suggesting that this QTL  
17 may make a great contribution to genetic improvement of growth performance of the NAG  
18 breed with a low growth rate.

19 **Key words:** Body weight, Growth, Nagoya, QTL, RAD-seq, White Plymouth Rock.

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1 In Japan, approximately 50 native Japanese breeds have been developed for enjoyment of  
2 ornamental appearance, crowing and behavioral traits (Tsudzuki 2003). However, little  
3 attention has been paid to the use of the Japanese breeds as food resources. In the present  
4 study, we used Nagoya (NAG) and White Plymouth Rock (WPR) breeds. NAG is one of the  
5 most famous native breeds in Japan; it is commonly known as the Nagoya Cochin and yields  
6 high-quality meat and eggs; and it has more red meat than commercial broiler meat and has a  
7 good and chewy texture (Tsudzuki 2003). WPR is a Western breed with a high growth rate  
8 and a high level of abdominal fat deposition (Tatsuda & Fujinaka 2001) and it has been used  
9 as a parental breed of commercial broilers worldwide. Suzuki *et al.* (2019) reported marked  
10 differences in body weight, growth rate, organ weight, fat weight, breast muscle weight and  
11 feed intake between NAG and WPR breeds at 7 weeks after hatching, and they characterized  
12 NAG as a low growth breed. Ishikawa *et al.* (2019) confirmed approximately 1.5- or more  
13 fold differences in those traits between the two breeds at 4 weeks of age. NAG and WPR are  
14 reported to have distinct breed origins and genetic relationships (Osman *et al.* 2006), which  
15 makes the two breeds suitable for crossbreeding experiments to map QTL and identify genes  
16 responsible for the trait differences observed.

17 In this study, we performed QTL analysis for early growth traits until 4 weeks of age  
18 in an F<sub>2</sub> intercross population between NAG and WPR breeds of meat-type chickens, in order  
19 to obtain QTL information that is beneficial for genetic improvement of early growth in the  
20 NAG chickens characterized by a low growth rate. To the best of our knowledge, no QTL  
21 study on growth has been performed using the NAG breed.

22 An F<sub>2</sub> population of 119 males and 120 females was previously obtained by an initial  
23 cross between three NAG males and four WPR females. All trait data for NAG, WPR, F<sub>1</sub> and  
24 F<sub>2</sub> chickens were shown in Ishikawa *et al.* (2019). Body weight of the F<sub>2</sub> chickens was  
25 measured at hatching (BW0) and at 1 week (BW1), 2 weeks (BW2), 3 weeks (BW3) and 4

1 weeks (BW4) of age. Body weight gains from 0 to 1 week (Gain0-1), 1 to 2 weeks (Gain1-2),  
2 2 to 3 weeks (Gain2-3), 3 to 4 weeks (Gain3-4) and 0 to 4 weeks (Gain0-4) were calculated.  
3 Feed intake (FI) was measured from 3 to 4 weeks of age (FI3-4). A feed conversion ratio  
4 (FCR) for 3-4 weeks (FCR3-4) was obtained by dividing FI3-4 by Gain3-4. Details of  
5 chicken rearing and handling were described in Suzuki *et al.* (2019).

6 Genomic DNA was extracted from blood using a DNeasy blood & Tissue kit (Qiagen,  
7 Tokyo) and DNA concentration was measured with a Qubit fluorometer (Thermo Fisher  
8 Scientific, Tokyo). Restriction site-associated DNA sequencing (RAD-seq) analysis was  
9 performed as described by Sakaguchi *et al.* (2015). All read data sequenced by Illumina  
10 HiSeq2500 were deposited in the DDBJ Sequence Read Archive (accession no.  
11 DRA007023). The reads were aligned to the chicken reference genome, assembly GRCg5,  
12 and SNPs were called with Stacks software (Catchen *et al.* 2013). As SNP markers, we  
13 selected the rad-tags that had completely different alleles between NAG and WPR breeds and  
14 were genotyped in more than 75% of 239 F<sub>2</sub> birds. A linkage map of the SNP markers that  
15 statistically met the segregation ratio of 1:2:1 expected in the F<sub>2</sub> population at the nominal  
16 5% level (chi-squared test) was constructed with Map Manager QTX software with linkage  
17 criterion of  $P=0.001$  (Manly *et al.* 2001) (Tables S1 and S2).

18 The effects of five environmental factors (seven dams, two sexes, two rearing  
19 persons, two dissection persons and 48 hatching dates) on phenotypic traits were tested using  
20 a linear model of the JMP software version 13.2.0 (SAS Institute Japan Ltd., Tokyo). After  
21 removal of the environmental effects that were significant at nominal 5% levels from the raw  
22 trait data, the residuals were used for QTL analysis using the Haley-Knott regression method  
23 of the R/qtl package version 3.5.1 (Broman & Sen 2009). To find QTL with main effects on  
24 traits, a single-QTL genome scan with a single QTL model was performed using sex-  
25 combined data. A two-dimensional genome scan with a two-QTL model was performed to

1 find QTL with epistatic interaction effects on the traits. Logarithms of the odds (LOD) scores  
2 were calculated at a 2-cM interval across the linkage map constructed. Genome-wide  
3 significance thresholds at 5% (significant) and 10% (suggestive) levels were calculated by  
4 10,000 permutations for main effect QTL and 500 permutations for epistatic QTL. The 1.8-  
5 LOD drop (comparable to 95%) confidence interval (CI), percentage of phenotypic variance  
6 explained, and additive and dominant effects of the QTL detected were computed by R/qtl. In  
7 addition, to detect QTL with sex-specific effects on traits, a single-QTL genome scan was  
8 performed using a single QTL model with or without sex as an interactive covariate in the  
9 model and permutation tests were performed according to the methods of Broman & Sen  
10 (2009).

11 As shown in Table 1 and Figs. S1 to S4, genome-wide QTL analysis revealed three  
12 QTL for several BW and Gain traits at different ages on GGA1b, 2, and 4b, either at genome-  
13 wide 5% or 10% levels. The most significant QTL in a confidence interval of 34.0-65.6 Mb  
14 on GGA4 affected BW2, BW3 and BW4 with LOD scores of 4.8, 5.3 and 5.9, respectively,  
15 and it explained 7.2, 7.8 and 9.9% of body weight variances, respectively. This QTL also  
16 affected Gain2-3 and Gain0-4 with LOD scores of 3.9-5.7, and it explained 4.9-9.6% of  
17 weight gain variances. The QTL in an interval of 37.4-143.8 Mb on GGA2 affected BW2,  
18 BW3 and Gain2-3 with LOD scores of 3.5, 4.6 and 3.5, and it explained 3.9, 6.6% and 4.9%  
19 of variances in body weight and weight gain, respectively. The QTL in an interval of 51.1-  
20 61.9 Mb on GGA1b affected BW1 and Gain0-1 with LOD scores of 3.6 and 4.0 and  
21 explained 6.1% and 6.9% of the trait variations, respectively. The allele derived from WPR at  
22 all QTL detected increased body weights and weight gains (Fig. 1 and Table 1). No main-  
23 effect QTL for the remaining traits was revealed at genome-wide 10% or less levels (Fig. S5).  
24 In addition, neither sex-specific nor epistatic QTL were identified for any traits at genome-  
25 wide 10% or less levels.

1           Our results suggested that a single QTL with a pleiotropic effect on body weight and  
2 weight gain may be located on each of the three chromosomal regions. However, we cannot  
3 rule out the possibility that multiple loci for those traits are closely linked on the small  
4 chromosomal region because Mollah & Ishikawa (2011) revealed two very closely linked  
5 QTL with opposite effects on body weight by fine mapping using subcongenic strains of  
6 mice.

7           Many QTL for body weight and growth at various ages have been reported on GGA1,  
8 2 and 4 (chickenQTLdb; Hu et al. 2019), supporting the presence of our QTL on those  
9 chromosomes. However, most of the QTL previously reported have broad confidence  
10 intervals due to the QTL mapping method using linkage analysis in crossbred populations.  
11 Furthermore, the map positions of those QTL are not well defined physically. It is hence  
12 difficult to precisely determine whether our QTL coincide with the previous QTL. We  
13 however compared our QTL to the previous QTL with known physical map positions. QTL  
14 for body weight at 46 days of age found in a broiler population (Mebratie *et al.* 2019) was  
15 located at the distal end of our GGA1 QTL interval between 51.1 and 61.6 Mb. That interval  
16 contains the insulin-like growth factor- I (*IGF-I*) gene. *IGF-I* is a strong functional candidate  
17 gene for our QTL because Abdalhag *et al.* (2016) reported an association between a SNP in  
18 *IGF-I* and body weight at 8-16 weeks of age in Jinghai yellow chickens. Our GGA2 QTL  
19 interval between 105.6 and 125.2 Mb overlapped with that of growth QTL found in an  
20 advanced intercross line (AIL) established from an F<sub>2</sub> population between two Virginia lines  
21 divergently selected for juvenile body weight (Brandt et al. 2017). In an AIL between New  
22 Hampshire and White Leghorn lines, Lyu *et al.* (2017) fine-mapped GGA4 QTL for body  
23 weight at 4-20 weeks of age to a region of 74.5-78.0 Mb (based on GRCg5 assembly  
24 obtained from chickenQTLdb). Around that region, several other loci for body weight and  
25 carcass weight have been reported in different chicken populations (Sasaki *et al.* 2004; Gu *et*

1 *al.*, 2011; Liu *et al.*, 2013). Interestingly, Rikimaru *et al.* (2013) reported associations of body  
2 weight and growth with a SNP on the cholecystokinin type A receptor (*CCKAR*) gene at 73.7  
3 Mb in Hinai-dori chickens. Guo *et al.* (2020) reported associations of length and weight of  
4 tibia with two SNPs in the ligand dependent nuclear receptor corepressor like (*LCORL*) gene  
5 at 76.3 Mb and the non-SMC condensin I complex subunit G (*NCAPG*) gene at 76.4 Mb.  
6 However, the regions of the above previous QTL/SNPs did not overlap with a confidence  
7 interval (34.0-65.6 Mb) of our GGA4 QTL. In an AIL between broiler and Fayoumi  
8 chickens, van Goor *et al.* (2015) reported body weight QTL at 35.8-36.8 Mb, which is the  
9 proximal end of our QTL interval but is distant far from the peak QTL position at  
10 approximately 66 Mb.

11       Taken together, at least, our GGA4 QTL, a key locus responsible for multiple early  
12 growth traits, may be a new locus, though we cannot rule out the possibility that previous  
13 QTL with physically undefined map positions are coincident with our locus. Since hundreds  
14 of genes can still be involved in the confidence intervals of our three QTL, it is premature to  
15 search for positional candidate genes with known or unknown functions for our QTL, except  
16 for *IGF-I* described above, without further fine mapping of the QTL. Furthermore, as the  
17 native Japanese NAG breed with a genetically distinct breed origin (Osman *et al.* 2006) was  
18 used for the first time in the present QTL study, the NAG alleles at our three QTL may have  
19 novel genetic variants. The findings provide information that is beneficial for genetic  
20 improvement in early growth of NAG chickens with a lower growth rate than that of WPR.

21       In conclusion, this study revealed that the GGA4 QTL makes an important  
22 contribution to early growth performance in the intercross between NAG and WPR breeds,  
23 suggesting that this QTL may be effective in genetic improvement of NAG with a low  
24 growth. In addition, the study was the initial step for identification of causal quantitative trait  
25 genes and causal variants for differences in early growth between NAG and WPR chickens.

1 The identification of a causal gene and variant(s) for the QTL will provide deep insights into  
2 the genetic basis of chicken growth.

3

4 **Acknowledgements** BHE was supported by the scholarship of the Joint Supervision  
5 Program of the Mission Sector, Ministry of Higher Education of Egypt. This work was in part  
6 supported by Kieikai Research Foundation (No. 2016C010) to AI.

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8 **Data availability**

9 All read data for the RAD-seq analysis were deposited in the DDBJ Sequence Read Archive  
10 (accession no. DRA007023). All QTL results generated during the current study were shown  
11 in supporting information. The other datasets analyzed during the current study are available  
12 from the corresponding author on reasonable request.

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14 **Conflict of interest**

15 The authors declare that they have no conflict of interest.

16



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1 **Figure legend**

2 **Figure 1** Genotype effect plots of the SNP markers nearest to the peaks of three QTL on  
3 GGA4b, 2 and 1b affecting (a) body weight at 4 weeks of age (BW4), (b) body weight at 3  
4 weeks of age (BW3) and (c) body weight gain at 0-1 weeks of age (Gain0-1), respectively.  
5 Each dot with vertical bars shows mean  $\pm$  SE. *P* values were obtained from one-way  
6 ANOVA. \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001 refer to statistical differences between two  
7 genotypes (Tukey's honestly significant difference test). A: NAG allele, B: WPR allele.

**Table 1** QTL mapped for early growth traits in the F<sub>2</sub> cross between NAG and WPR breeds

Trait <sup>1</sup>	GGA	Position <sup>2</sup>	LOD	Nearest marker	CI <sup>3</sup>	Additive effect <sup>4</sup>	Dominant effect <sup>4</sup>	% Var <sup>5</sup>
BW1	1b	26 (59.7)	3.6	<i>SNP59</i>	8-57 (52.0-61.9)	2.9±1.1	1.8±1.7	6.1
BW2	2	86 (117.3)	3.5	<i>SNP79</i>	68-287 (37.4-120.9)	6.0±2.1	-0.3±3.2	3.9
	4b	118 (65.1)	4.8*	<i>SNP189</i>	103-137 (55.8-64.9)	8.3 ±2.1	4.2±2.8	7.2
BW3	2	86 (117.3)	4.6*	<i>SNP79</i>	48-105 (105.6-125.2)	16.8±4.2	-1.9±7.0	6.6
BW3	4b	132 (66.3)	5.3*	<i>SNP192</i>	109-137 (57.4-64.9)	18.2±4.0	-0.6±6.4	7.8
BW4	4b	130 (65.7)	5.9*	<i>SNP199</i>	111-131 (59.0-65.6)	37.8±7.8	0.9±11.2	9.9
Gain0-1	1b	28 (59.5)	4.0*	<i>SNP39</i>	9-59 (51.1-61.6)	3.5±0.9	1.9±1.4	6.9
Gain2-3	2	84 (117.9)	3.5	<i>SNP79</i>	16-107 (104.9-143.8)	0.3±0.09	-0.1±0.1	4.9
	4b	130 (65.7)	3.9*	<i>SNP199</i>	7-137 (34.0-65.2)	0.3±0.09	-0.1±0.1	4.9
Gain0-4	4b	130 (65.73)	5.7*	<i>SNP199</i>	111-137 (57.2-58.4)	36.2±7.2	-1.6±12.1	9.6

<sup>1</sup>For an explanation of the trait abbreviations, see Materials and methods.

<sup>2</sup>Position in cM is based on our linkage map position (see Tables S1 and S2); Physical position in Mb (GRCg5 assembly) is given in parenthesis.

<sup>3</sup>Confidence interval in cM, which is a 1.8-LOD drop of the peak LOD score; The physical interval in Mb is given in parenthesis.

<sup>4</sup>The additive and dominant effects with positive signs indicate that the WPR-derived allele increased the trait value.

<sup>5</sup>Percentage of the trait variance explained by the QTL.

\* Significant at genome-wide 5% levels; no star, suggestive at genome-wide 10% levels (see Table S3).

1 **Legends for Supporting information**

2 **Fig. S1** Genome-wide LOD score plots obtained by main-effect QTL analysis for BW0 to  
3 BW2. See Table S3 for details of the 5% and 10% threshold levels.

4 **Fig. S2** Genome-wide LOD score plots obtained by main-effect QTL analysis for BW3 and  
5 BW4.

6 **Fig. S3** Genome-wide LOD score plots obtained by main-effect QTL analysis for Gain0-1 to  
7 Gain2-3.

8 **Fig. S4** Genome-wide LOD score plots obtained by main-effect QTL analysis for Gain3-4  
9 and Gain0-4.

10 **Fig. S5** Genome-wide LOD score plots obtained by main-effect QTL analysis for FI3-4 and  
11 feed FCR3-4.

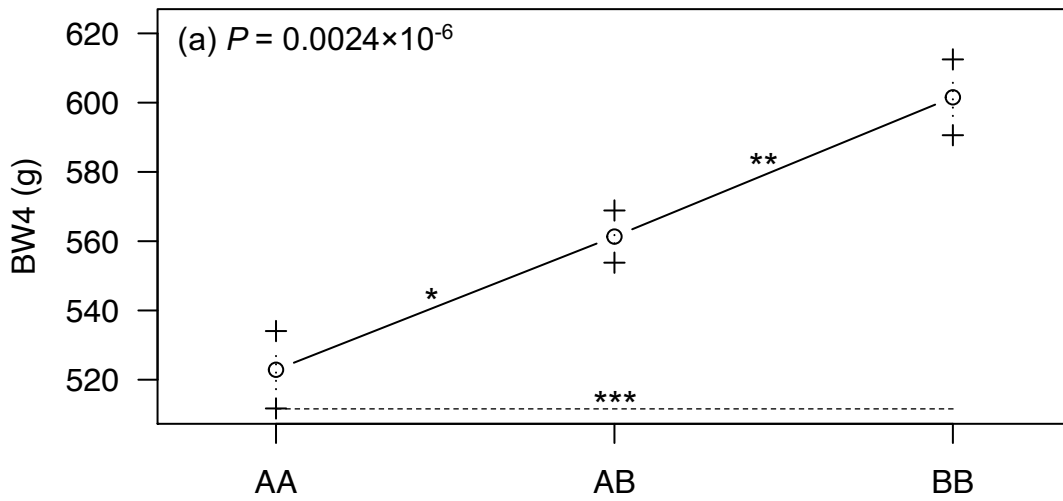
12 **Table S1** SNP markers developed by RAD-seq analysis.

13 **Table S2** The genetic linkage map for RAD-seq based SNP markers.

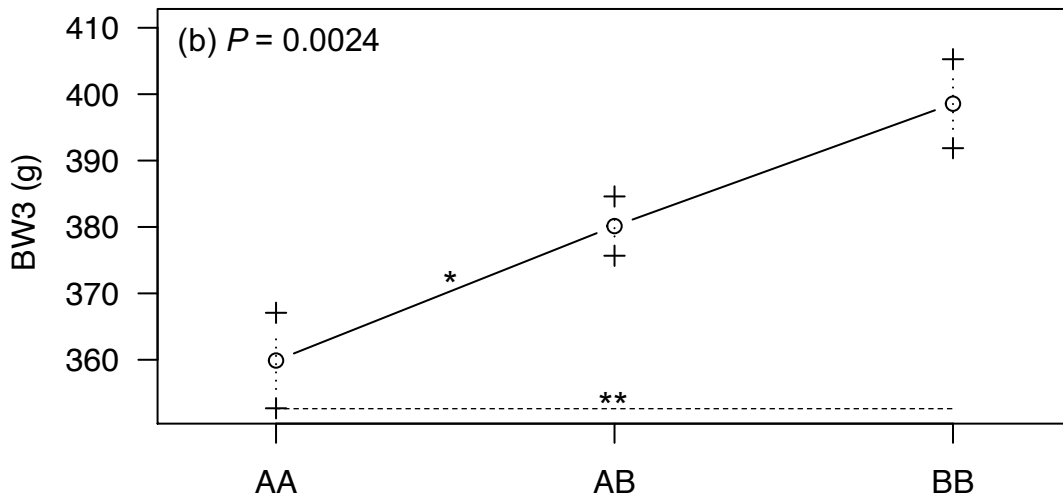
14 **Table S3** Genome-wide significance threshold levels used for main-effect QTL analyses.

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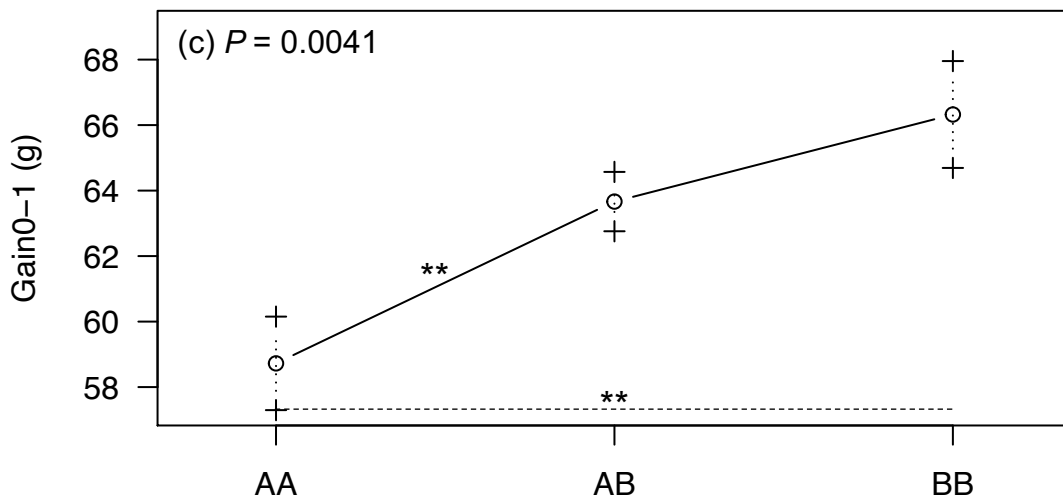
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SNP79



SNP39

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### Supporting information

**Title:** QTL analysis for early growth in an intercross between native Japanese Nagoya and White Plymouth Rock chicken breeds using RAD sequencing-based SNP markers

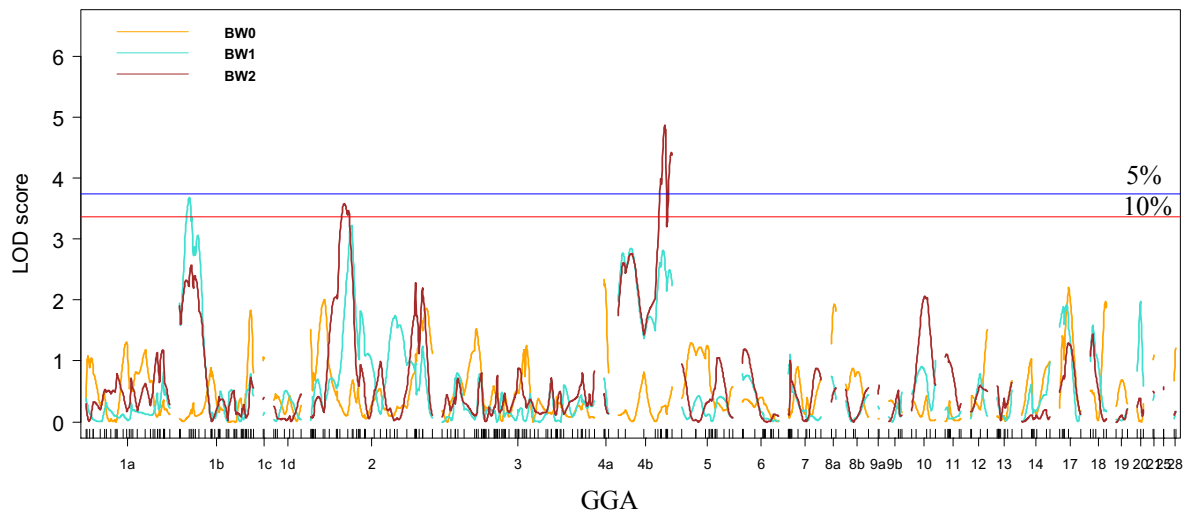
**Journal name:** Animal Genetics

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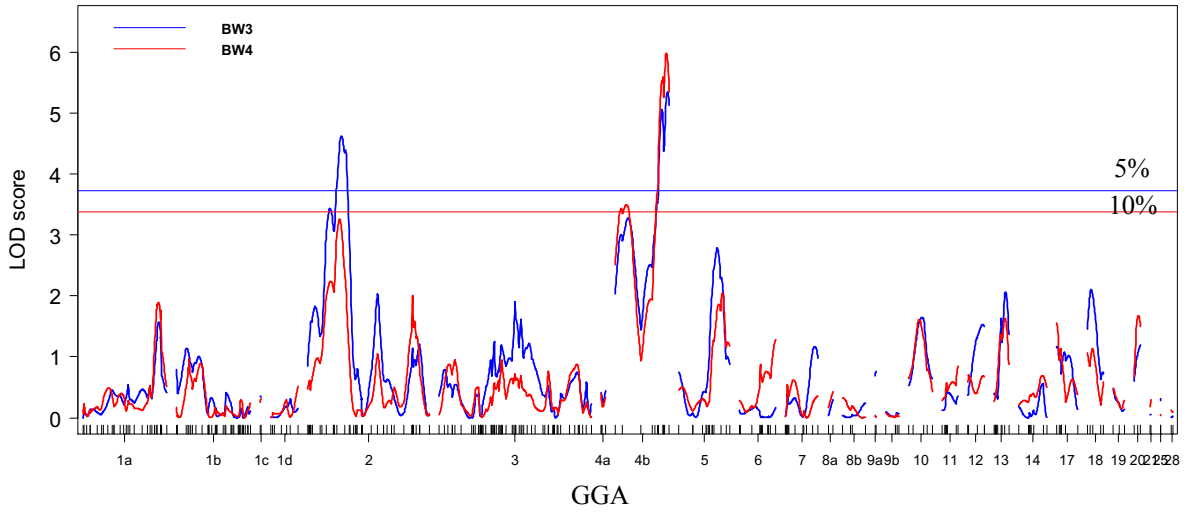
<sup>§</sup> Department of Animal Husbandry and Animal Wealth Development, Faculty of Veterinary Medicine, Damanhour University, Damanhour 22511, Egypt



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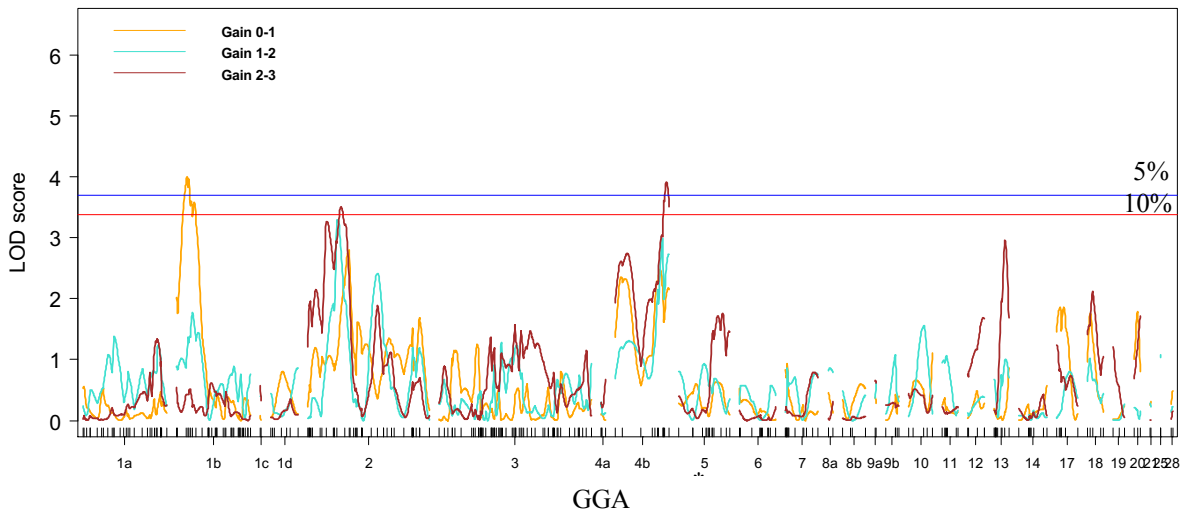
**Figure S1** Genome-wide LOD score plots obtained by main-effect QTL analysis for BW0 to BW2. See Table S3 for details of the 5% and 10% threshold levels. See Table S3 for details of the 5% and 10% threshold levels.

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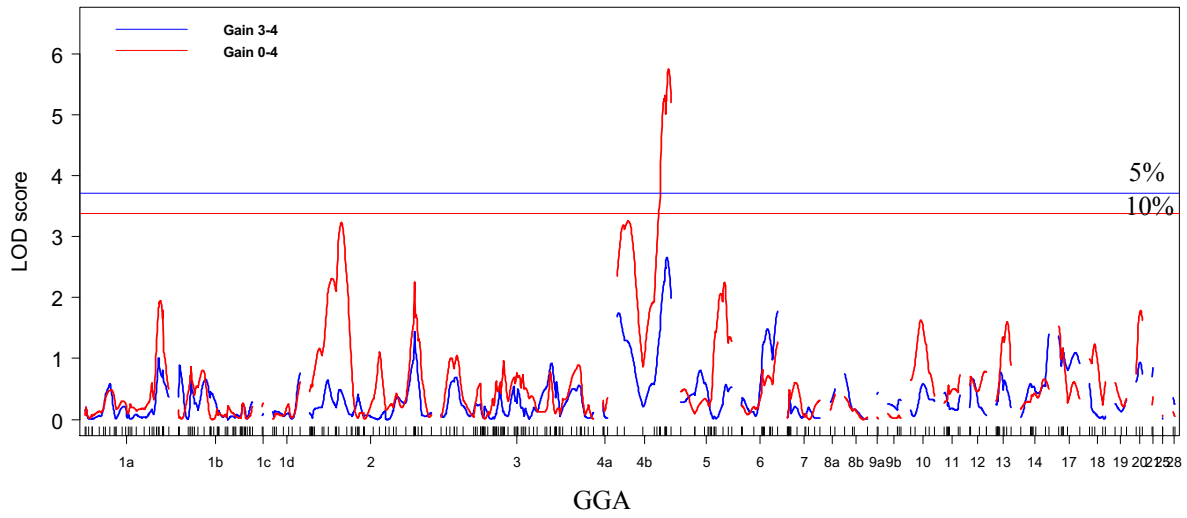
**Figure S2** Genome-wide LOD score plots obtained by main-effect QTL analysis for BW3 and BW4.



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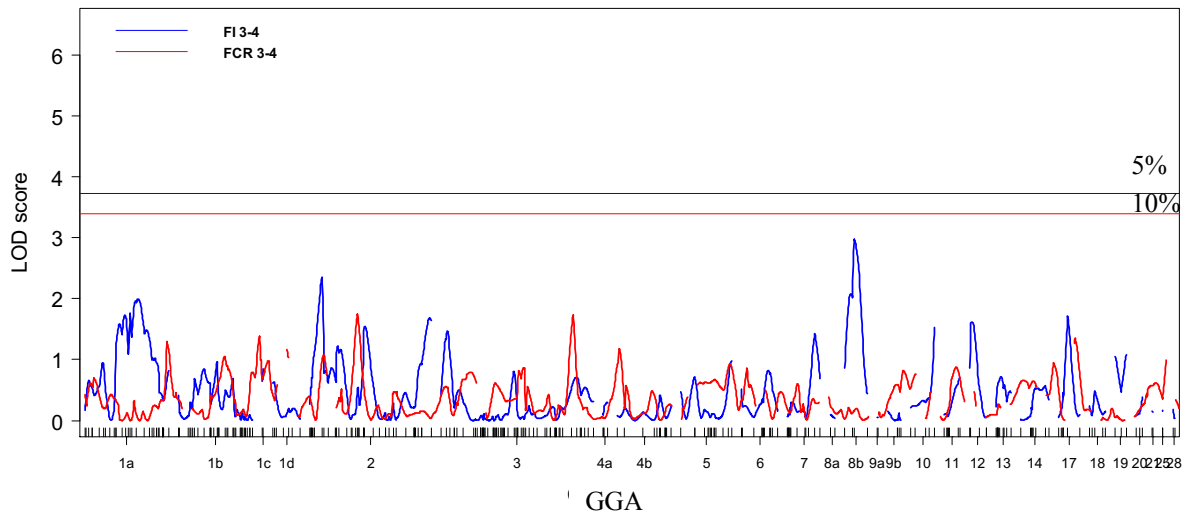
**Figure S3** Genome-wide LOD score plots obtained by main-effect QTL analysis for Gain0-1 to Gain2-3.

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**Figure S4** Genome-wide LOD score plots obtained by main-effect QTL analysis for Gain3-4 and Gain0-4.



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**Figure S5** Genome-wide LOD score plots obtained by main-effect QTL analysis for FI3-4 and feed FCR3-4.

1 **Table S1** SNP markers developed by RAD-seq analysis.

SNP marker	GGA	Map position <sup>1</sup>	
		cM	bp
<i>SNP24</i>	1a	0	188529007
<i>SNP50</i>	1a	4	188217366
<i>SNP26</i>	1a	11.6	184822994
<i>SNP66</i>	1a	20.3	184047694
<i>SNP31</i>	1a	21.9	182401284
<i>SNP4</i>	1a	43.2	180623288
<i>SNP27</i>	1a	53.7	177537693
<i>SNP29</i>	1a	58.1	176358715
<i>SNP51</i>	1a	72.5	174644104
<i>SNP19</i>	1a	84.7	172187165
<i>SNP40</i>	1a	89.1	170395012
<i>SNP30</i>	1a	90.4	170233092
<i>SNP67</i>	1a	108	166612632
<i>SNP21</i>	1a	118.8	160002151
<i>SNP1</i>	1a	125.1	154698065
<i>SNP62</i>	1a	130.5	150333378
<i>SNP74</i>	1a	133.9	145701371
<i>SNP55</i>	1a	147.7	142911362
<i>SNP6</i>	1a	172	141849171
<i>SNP69</i>	1a	186.6	141412938
<i>SNP15</i>	1a	194.3	138247899
<i>SNP75</i>	1a	201.9	137421398
<i>SNP36</i>	1a	209.2	134051928
<i>SNP71</i>	1a	216.6	132587138
<i>SNP48</i>	1a	219.1	132379492
<i>SNP18</i>	1a	228.9	128107746
<i>SNP43</i>	1a	229.8	126742928
<i>SNP22</i>	1a	230.7	126699171
<i>SNP65</i>	1a	231.3	126667668
<i>SNP17</i>	1a	233.3	126633885
<i>SNP10</i>	1a	235.7	125220291
<i>SNP33</i>	1a	248.2	125107921
<i>SNP11</i>	1b	0	64926066
<i>SNP56</i>	1b	4.5	62635352
<i>SNP59</i>	1b	25.5	59752251
<i>SNP39</i>	1b	33.5	59156584
<i>SNP60</i>	1b	35.5	58547607
<i>SNP2</i>	1b	40.5	57179637
<i>SNP34</i>	1b	48.4	54514843
<i>SNP5</i>	1b	57.5	51944967
<i>SNP63</i>	1b	73.1	48146326

<i>SNP70</i>	1b	87.1	40577508
<i>SNP61</i>	1b	88	40277266
<i>SNP42</i>	1b	89.3	39516492
<i>SNP77</i>	1b	90.9	38744188
<i>SNP28</i>	1b	99	35672939
<i>SNP9</i>	1b	107.6	33563594
<i>SNP8</i>	1b	109.2	33387711
<i>SNP53</i>	1b	111.1	32398147
<i>SNP38</i>	1b	112.6	31240649
<i>SNP68</i>	1b	130.4	24346857
<i>SNP57</i>	1b	136.3	24022782
<i>SNP23</i>	1b	139.1	23105198
<i>SNP16</i>	1b	151	15767568
<i>SNP7</i>	1b	152.4	15627141
<i>SNP49</i>	1b	159.8	15396650
<i>SNP73</i>	1b	162.6	14650697
<i>SNP14</i>	1b	171.5	12576498
<i>SNP46</i>	1b	174.4	12533265
<i>SNP76</i>	1b	175.1	11467670
<i>SNP45</i>	1b	179.7	7251124
<i>SNP12</i>	1b	184.3	7183185
<i>SNP32</i>	1b	192.5	7137113
<i>SNP37</i>	1b	195.4	4728608
<i>SNP58</i>	1b	201.7	3652955
<i>SNP13</i>	1b	209.5	2781210
<i>SNP52</i>	1b	209.8	2599796
<i>SNP25</i>	1b	216.3	1881844
<i>SNP47</i>	1c	0	191978687
<i>SNP72</i>	1c	3.3	189144934
<i>SNP3</i>	1d	0	85162684
<i>SNP44</i>	1d	5.2	86152831
<i>SNP54</i>	1d	9	89911362
<i>SNP20</i>	1d	29.5	100180504
<i>SNP64</i>	1d	42.4	105447559
<i>SNP41</i>	1d	53.5	109858283
<i>SNP35</i>	1d	73.1	126890319
<i>SNP84</i>	2	0	147691949
<i>SNP93</i>	2	5.9	147151247
<i>SNP105</i>	2	8.8	147104297
<i>SNP117</i>	2	10.4	146506923
<i>SNP114</i>	2	12.2	145434985
<i>SNP82</i>	2	16.3	139176582
<i>SNP99</i>	2	16.3	139167127
<i>SNP92</i>	2	37	128153753

<i>SNP98</i>	2	43.1	126890319
<i>SNP116</i>	2	53.9	126310459
<i>SNP81</i>	2	75.4	118199177
<i>SNP78</i>	2	77.5	118016447
<i>SNP108</i>	2	79.8	117917805
<i>SNP101</i>	2	87.6	115169393
<i>SNP79</i>	2	107	104974103
<i>SNP104</i>	2	119	98570448
<i>SNP88</i>	2	123	98166312
<i>SNP111</i>	2	131.9	91321288
<i>SNP96</i>	2	137.6	89566973
<i>SNP112</i>	2	139.1	89124513
<i>SNP91</i>	2	143.7	85975429
<i>SNP107</i>	2	153	77435448
<i>SNP90</i>	2	153.2	77152879
<i>SNP118</i>	2	155.4	75885815
<i>SNP85</i>	2	180	65602878
<i>SNP102</i>	2	196.4	62576523
<i>SNP109</i>	2	211.1	56553363
<i>SNP106</i>	2	212.6	54862890
<i>SNP113</i>	2	239.8	46791949
<i>SNP100</i>	2	251.5	45385043
<i>SNP110</i>	2	260.5	42579119
<i>SNP94</i>	2	283.3	36167156
<i>SNP80</i>	2	304.3	30415070
<i>SNP97</i>	2	307	26956392
<i>SNP83</i>	2	307	26846902
<i>SNP115</i>	2	307.3	26839062
<i>SNP87</i>	2	308.5	25032485
<i>SNP95</i>	2	319.4	23632314
<i>SNP86</i>	2	331	21490257
<i>SNP119</i>	2	331.4	21237010
<i>SNP103</i>	2	355.6	7457342
<i>SNP153</i>	3	0	6310854
<i>SNP143</i>	3	2.8	7250634
<i>SNP134</i>	3	12.5	9136024
<i>SNP139</i>	3	24.6	12392569
<i>SNP164</i>	3	26.2	12412446
<i>SNP152</i>	3	33.1	12592496
<i>SNP131</i>	3	49.9	17231980
<i>SNP124</i>	3	78.9	17356889
<i>SNP170</i>	3	83.9	17432803
<i>SNP182</i>	3	90.2	18166326
<i>SNP140</i>	3	97.4	19189813

<i>SNP147</i>	3	97.4	19259875
<i>SNP158</i>	3	98.6	20790598
<i>SNP155</i>	3	101.5	22951608
<i>SNP129</i>	3	101.5	22952143
<i>SNP163</i>	3	102.4	23091810
<i>SNP166</i>	3	103.3	23300980
<i>SNP150</i>	3	105.8	23736395
<i>SNP156</i>	3	108.2	24179162
<i>SNP162</i>	3	122.6	24520699
<i>SNP126</i>	3	146.3	25373630
<i>SNP171</i>	3	153.1	25469780
<i>SNP128</i>	3	154	25557452
<i>SNP145</i>	3	154.3	25756876
<i>SNP172</i>	3	158.4	27271535
<i>SNP178</i>	3	158.7	27378314
<i>SNP136</i>	3	160.3	27395405
<i>SNP177</i>	3	166.2	29139253
<i>SNP141</i>	3	172.5	31663229
<i>SNP142</i>	3	174.5	31843285
<i>SNP138</i>	3	181.4	34568798
<i>SNP146</i>	3	184.9	35133008
<i>SNP122</i>	3	187.3	36317764
<i>SNP149</i>	3	199.9	37608247
<i>SNP176</i>	3	222.4	38991459
<i>SNP130</i>	3	228.9	39400202
<i>SNP174</i>	3	234.3	40887363
<i>SNP148</i>	3	236.4	41275478
<i>SNP169</i>	3	236.4	41288048
<i>SNP135</i>	3	247.8	44229889
<i>SNP161</i>	3	257.6	44532769
<i>SNP137</i>	3	261.1	45660592
<i>SNP175</i>	3	266.3	46829204
<i>SNP154</i>	3	276.4	53760550
<i>SNP133</i>	3	288.5	60378396
<i>SNP173</i>	3	296.4	66338586
<i>SNP183</i>	3	317.5	71945934
<i>SNP179</i>	3	325.3	72858233
<i>SNP167</i>	3	336.8	74233093
<i>SNP157</i>	3	338.2	74988013
<i>SNP160</i>	3	350.6	77215270
<i>SNP120</i>	3	353.7	78557281
<i>SNP132</i>	3	354.1	78557288
<i>SNP184</i>	3	356.1	79053114
<i>SNP121</i>	3	364.6	82710869

<i>SNP159</i>	3	367.2	83984876
<i>SNP123</i>	3	376.5	84007977
<i>SNP185</i>	3	405.8	96323267
<i>SNP144</i>	3	421.2	97325055
<i>SNP168</i>	3	433.5	102548378
<i>SNP180</i>	3	435.8	103281659
<i>SNP125</i>	3	438	104264153
<i>SNP181</i>	3	448.7	105138379
<i>SNP127</i>	3	459.8	105598672
<i>SNP165</i>	3	473.5	107141932
<i>SNP195</i>	4a	0	15712900
<i>SNP198</i>	4a	2.5	25811709
<i>SNP196</i>	4a	6.7	28079214
<i>SNP201</i>	4a	15.2	29460902
<i>SNP197</i>	4b	0	32416143
<i>SNP190</i>	4b	19.5	48047145
<i>SNP188</i>	4b	68.1	52950094
<i>SNP187</i>	4b	96.1	53969904
<i>SNP191</i>	4b	104.6	56995168
<i>SNP200</i>	4b	111.7	58550718
<i>SNP194</i>	4b	114.9	65109360
<i>SNP189</i>	4b	126.1	65360693
<i>SNP193</i>	4b	131.6	65890271
<i>SNP186</i>	4b	132.8	67179811
<i>SNP199</i>	4b	133.7	67642813
<i>SNP192</i>	4b	148.3	67958652
<i>SNP212</i>	5	0	9024864
<i>SNP209</i>	5	34.2	17743789
<i>SNP206</i>	5	35.1	18079274
<i>SNP210</i>	5	60.7	28723038
<i>SNP202</i>	5	71.8	34150822
<i>SNP207</i>	5	76.4	35498039
<i>SNP213</i>	5	80.3	37542089
<i>SNP205</i>	5	83.6	38100452
<i>SNP204</i>	5	90.4	41988375
<i>SNP208</i>	5	91	42355761
<i>SNP214</i>	5	96.9	44620396
<i>SNP203</i>	5	112.5	51197747
<i>SNP211</i>	5	126.6	54260266
<i>SNP215</i>	5	136.6	55962744
<i>SNP221</i>	6	0	758313
<i>SNP222</i>	6	3.1	1191556
<i>SNP216</i>	6	31.8	4608358
<i>SNP220</i>	6	48.9	11101144



<i>SNP223</i>	6	50.9	12273931
<i>SNP224</i>	6	54.4	16744103
<i>SNP218</i>	6	57.5	17833005
<i>SNP219</i>	6	71.2	24350804
<i>SNP226</i>	6	73.1	25503926
<i>SNP225</i>	6	81.5	26057885
<i>SNP217</i>	6	101.6	27986171
<i>SNP230</i>	7	0	13186679
<i>SNP227</i>	7	2	14415673
<i>SNP233</i>	7	2.9	14861208
<i>SNP235</i>	7	4.1	15928304
<i>SNP228</i>	7	7.3	16732641
<i>SNP240</i>	7	10.2	18070929
<i>SNP231</i>	7	11.2	18091122
<i>SNP238</i>	7	13.8	20438423
<i>SNP236</i>	7	27.9	24753436
<i>SNP241</i>	7	50.7	30968142
<i>SNP239</i>	7	54.4	31505509
<i>SNP234</i>	7	61.7	32176504
<i>SNP232</i>	7	79.7	34360383
<i>SNP229</i>	7	95	36535345
<i>SNP242</i>	8a	0	23503923
<i>SNP246</i>	8a	0.7	23567289
<i>SNP244</i>	8a	12.6	24729017
<i>SNP248</i>	8b	0	9556381
<i>SNP245</i>	8b	22.2	6912802
<i>SNP243</i>	8b	27.5	6105295
<i>SNP247</i>	8b	61.4	3516252
<i>SNP252</i>	9a	0	23803751
<i>SNP253</i>	9a	4.3	21673903
<i>SNP250</i>	9b	0	13999328
<i>SNP249</i>	9b	25.1	12969358
<i>SNP251</i>	9b	27.5	12044546
<i>SNP255</i>	9b	31.3	9640230
<i>SNP254</i>	9b	38	9374051
<i>SNP257</i>	10	0	19769452
<i>SNP260</i>	10	12.2	16991424
<i>SNP256</i>	10	37.7	12804450
<i>SNP259</i>	10	47	10315551
<i>SNP258</i>	10	65.2	3463658
<i>SNP265</i>	11	0	12598781
<i>SNP261</i>	11	8.8	11999569
<i>SNP262</i>	11	11.5	10555547
<i>SNP264</i>	11	15.5	9929887

<i>SNP267</i>	11	19	9818042
<i>SNP266</i>	11	41.3	5084253
<i>SNP263</i>	11	47.7	1302548
<i>SNP272</i>	12	0	17906753
<i>SNP268</i>	12	3.2	17392924
<i>SNP270</i>	12	24.1	10866961
<i>SNP269</i>	12	42.3	7131468
<i>SNP271</i>	12	43	7037075
<i>SNP279</i>	13	0	6167860
<i>SNP283</i>	13	3.8	6216050
<i>SNP274</i>	13	5.7	6271305
<i>SNP280</i>	13	6.4	6515882
<i>SNP273</i>	13	7	6529782
<i>SNP275</i>	13	7.6	6685366
<i>SNP284</i>	13	8.2	6824887
<i>SNP282</i>	13	14.8	8672979
<i>SNP278</i>	13	26.3	10592711
<i>SNP281</i>	13	29.5	11230051
<i>SNP277</i>	13	40.5	11415848
<i>SNP276</i>	13	60.3	14198790
<i>SNP287</i>	14	0	13913008
<i>SNP290</i>	14	25.7	12093590
<i>SNP285</i>	14	30.5	9893128
<i>SNP286</i>	14	31.4	9631686
<i>SNP289</i>	14	34.5	9122075
<i>SNP292</i>	14	46.4	7991276
<i>SNP288</i>	14	70.7	2337145
<i>SNP291</i>	14	79.7	1042148
<i>SNP298</i>	17	0	6702510
<i>SNP299</i>	17	8.3	5172158
<i>SNP294</i>	17	12.7	4521421
<i>SNP296</i>	17	13	4520878
<i>SNP300</i>	17	13.7	4461256
<i>SNP295</i>	17	26.7	3145495
<i>SNP297</i>	17	58.8	2534867
<i>SNP302</i>	18	0	199806
<i>SNP301</i>	18	7.8	1833174
<i>SNP303</i>	18	15.5	2670691
<i>SNP304</i>	18	39.8	5561978
<i>SNP305</i>	18	47.2	7501508
<i>SNP306</i>	19	0	6349765
<i>SNP307</i>	19	16.7	4584070
<i>SNP308</i>	19	30.4	3796447
<i>SNP310</i>	20	0	10589473

<i>SNP309</i>	20	9.9	8667919
<i>SNP311</i>	20	18.9	8611136
<i>SNP312</i>	21	0	1166041
<i>SNP313</i>	21	2.1	1373782
<i>SNP316</i>	25	0	1107730
<i>SNP317</i>	25	1.3	1973033
<i>SNP319</i>	28	0	1791874
<i>SNP320</i>	28	5.1	2293698

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1 <sup>1</sup> Map positions are based on the chicken RefSeq GRCg5.  
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**Table S2** The genetic linkage map for RAD-seq based SNP markers

Chr	No. of markers	Length (cM)	Marker spacing (cM)			3
			Average	Maximum	Minimum	4
1a	32	212.8	6.9	20.7	0.2	6
1b	36	188.7	5.4	20.8	0.1	7
1c	2	2.6	2.6			8
1d	7	68.5	11.4	19.2	1.6	9
2	41	309.6	7.7	24.1	0.1	10
3	65	387.5	6.1	27.0	0.1	11
4a	4	11.2	3.7	7.9	0.3	12
4b	12	137.2	12.5	47.1	1.3	13
5	14	129.2	9.9	34.9	0.2	14
6	11	92.7	9.3	28.6	0.9	15
7	14	83.2	6.4	20.5	0.3	16
8a	3	12.0	6.0	11.8	0.7	17
8b	4	57.1	19.0	32.7	2.7	
9a	5	31.7	7.9	23.2	1.2	
9b	2	3.6	3.6			
10	5	62.0	15.5	26.2	5.9	
11	7	39.4	6.6	21.3	1.4	
12	5	42.0	10.5	21.1	0.2	
13	12	37.8	3.4	10.8	0.2	
14	8	71.0	10.1	24.9	0.3	
17	7	53.8	9.0	29.6	0.1	
18	5	41.1	10.3	21.5	4.4	
19	3	27.8	13.9	14.9	9.4	
20	3	17.0	8.5	8.7	5.7	
21	2	1.4	1.4			
25	2	0.5	0.5			
28	2	4.4	4.4			
Overall	313	2125.8	7.4	47.1	0.1	

1 **Table S3** Genome-wide significance threshold levels used for main-effect QTL analyses.

Trait	5%	10%
BW0	3.7	3.4
BW1	3.7	3.3
BW2	3.7	3.3
BW3	3.7	3.3
BW4	3.7	3.3
Gain0-1	3.7	3.3
Gain1-2	3.7	3.4
Gain2-3	3.7	3.3
Gain3-4	3.7	3.2
Gain0-4	3.7	3.3
FI3-4	3.7	3.4
FCR3-4	3.7	3.3

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