

## **Linkage analysis of microsatellite markers on chromosome 5 in an F2 population of Japanese quail to identify quantitative trait loci affecting carcass traits**

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**Abstract** An F2 Japanese quail population was developed by crossing two strains (wild and white) to map quantitative trait loci (QTL) for performance and carcass traits. A total of 472 F2 birds were reared and slaughtered at 42 days of age. Performance and carcass traits were measured on all of the F2 individuals. Parental (P0), F1 and F2 individuals were genotyped with 3 microsatellites from quail chromosome 5. Based on five quantitative genetic models analyzed, QTL affecting carcass efficiency, breast percentage, femur percentage, back weight and back percentage, head weight, gizzard weight, uropygial weight, liver weight and liver percentage and neck percentage were mapped. The results provided an important framework for further genetic mapping and the identification of quantitative trait loci controlling performance carcass traits in the Japanese quail

**Keywords:** carcass trait, microsatellite markers, quantitative trait loci

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### **Introduction**

The recent developments in molecular biology and statistics have increased the possibility of identifying and using genomic variation and major genes for the genetic improvement of livestock. The characteristics for which the application of marker assisted selection can be more effective are those that are expressed late in the life of the animal, or controlled by a few pairs of genes. The first example corresponds to the longevity and carcass characteristics in meat producing animals, the second, to the resistance to certain diseases or defects of simple inheritance. During the last five decades, the application of methods based on population genetics and statistics has allowed the development of animals with high productive efficiency. Their efficiency decreases when traits are difficult to measure or have a low heritability. Additionally, selection has been generally limited to those characteristics that can more accurately be measured in a large number of animals. Several characteristics such as the rate of survival that are expressed very late in the life may serve as useful criteria of selection. Also, the traditional selection within populations is not very efficient when selection objectives involve several characteristics with unfavorable genetic correlation (Carlborg et al., 2001). The impetus to reveal the underlying mechanisms of complex traits has led to detection

of major genes and quantitative trait loci (QTL) for many traits in various species. The traditional approach for detecting the major genes and QTL is by looking for marginal (additive and dominance) effects of the individual loci (Chase et al., 1997). Researchers have developed a variety of strategies to attain greater precision when mapping QTL (Darvasi and Soller, 1997). Advanced statistical approaches are necessary for unbiased genome-wide QTL mapping to be successful in ultimately identifying which gene(s) underlies the observed phenotype. Several experiments have been conducted to map QTL on the marker map (Anderson et al., 1994, Georges et al., 1994). More QTL mapping experiments will probably follow and the approximate position and effect of the largest QTL will be assessed. It will be difficult to distinguish whether an effect is due to one or several closely linked QTL, but regions where the QTL for the economically most important traits resided can be located. The goal of a genetic mapping experiment is to detect and localize the genetic elements responsible for the variation in a phenotype of interest. In the last few years, microsatellites became one of the most popular molecular markers used in different fields. The simple sequence repeats (SSRs), also known as microsatellites, are stretches of DNA sequence consisting of short

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tandem repeats of mono-, di-, tri-, tetra-, penta- and hexa-nucleotides (Tautz et al., 1994). SSRs are widely distributed throughout genomes and have been found in all prokaryotic and eukaryotic genomes analyzed to date (Katti et al., 2001, Toth et al., 2000). Microsatellite markers are powerful genetic markers, due to their genetic co-dominance, abundance, dispersal throughout the genome, multi-allelic variation, high reproducibility, and high level of polymorphism. This high level of polymorphism is due to mutations affecting the number of repeat units (Chris et al., 2009).

In recent years, genetic linkage maps based on microsatellite markers have been constructed for a number of livestock including the Japanese quail (*Coturnix japonica*) (Kayang et al., 2002). This bird belongs to the Phasianidae family (Crawford, 1990). The Japanese quail is now a well established animal model in biology and genetics (Minvielle, 2004). Japanese quail is phylogenetically closely related to the chicken (Stock and Bunch., 1982). Until recently, marker information in quail was very scanty and only three classical linkage groups based on plumage color and blood protein markers (Ito et al., 1988a, Ito et al., 1988b, Shibata and Abe., 1996, Minvielle et al., 2000) were available. But the situation began to change with the development of original microsatellite markers for quail (Kayang et al., 2000, Kayang et al., 2002) and the recent publication of the first ever quail genetic map was based completely on DNA markers (Haley et al., 1994). Taking advantage of the available genetic map of the SSR markers in Japanese quail, this study aimed at mapping QTL for performance and carcass traits.

### **Material and Methods**

#### *Japanese quail resource population and phenotypic data*

An F2 population was derived from a cross between two strains of Japanese quail (meat and layer types). The parental generation (P0) consisted of 8 dams and 8 sires originating from the wild (W) and white (S) strains which were reciprocally crossed to produce the F1 offspring. F1 birds were generated from S ♂ × W ♀ and W ♂ × S ♀ mating. All of the F1 individuals including 34 birds (9 males and 25 females) were intercrossed to produce 422 F2 offspring (246 males and 176 females) in five consecutive hatches. Thus, 472 quails (16 F0, 34 F1 and 422 F2) constituted the mapping population. All birds were slaughtered at 42 days of age and carcass components, and hot and cold carcasses were evaluated.

#### *DNA extraction and genotyping*

Blood samples were collected at slaughter in tubes containing

EDTA and stored at -20°C. Genomic DNA was purified from each sample (100 µL) using the salting-out extraction method. Microsatellite markers (GuJ0059, GuJ0049 and GuJ0100) on Japanese quail chromosome 5 (CJA05) were chosen from the genetic consensus map based on their location on this chromosome (0, 12 and 21 cM) according to the literature (Kayang et al., 2002).

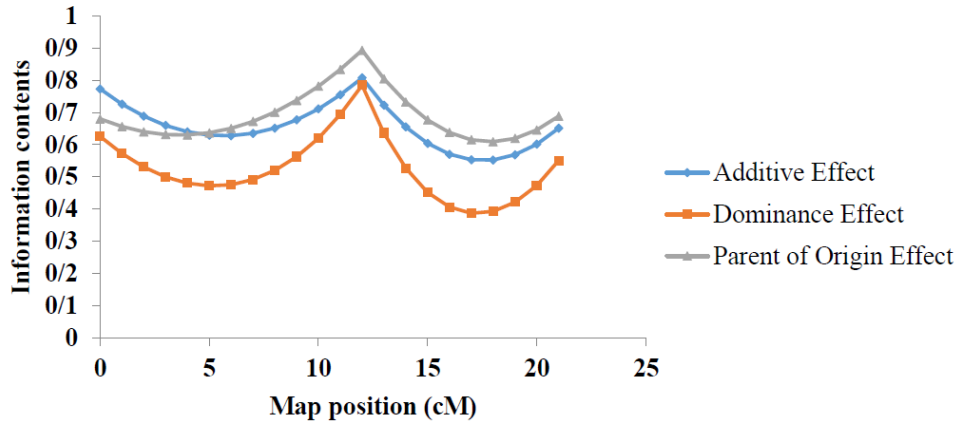
#### *Analyses of microsatellite markers*

Polymerase chain reaction (PCR) amplifications of each marker for 472 birds were carried out on a Thermal Cycler (Eppendorf, UK) in 25 µL reaction mixtures containing 2 µL of the DNA template, 1 µL of forward and reverse primers, 0.5 µL of dNTP mix, 1 µL MgCl<sub>2</sub>, 2.5 µL PCR buffer and 0.5 µL AmpliTaq and 16.5 µL sterile water. The PCR conditions were as follow: 94°C for 4 min, followed by 30 cycles of 94°C for 30 s, annealing for 45 s at 50–55°C depending on the optimized annealing temperature of the primer used, and a final extension at 72°C for 4 min. The PCR products were electrophoresed at 200 V on an 8.0% polyacrylamide gel and visualized by staining with silver nitrate method. All birds were genotyped for the markers by diversity size of the amplified fragments.

#### *QTL analysis*

A genetic model, line-cross (Roussot et al., 2003), was applied for QTL interval mapping analyses using the regression method in the QTL Express software (Seaton et al., 2006). The probability of an F2 offspring being each of the four QTL genotypes (QQ, Qq, qQ, and qq) was calculated conditionally upon the marker genotype at each position in the genome at 1cM intervals. In the line-cross analysis, the fixed effects of hatch and sex were included in the model for QTL mapping. The line-cross analysis was initiated with an additive genetic model followed by the models including joint effects of additive, dominance and imprinting. The QTL by sex interaction was assessed to determine whether the effect did differ between the two sexes. The additive QTL effect by hatch interaction was also analyzed.

Chromosome-wide significant thresholds for the presence of a QTL were determined empirically by permuting marker data, as described by Churchill and Doerge (1994). Thresholds were obtained from 10,000 permutations and are presented as  $F_{0.05}$  and  $F_{0.01}$  for significance at  $\alpha = 0.05$  and  $\alpha = 0.01$  levels, respectively. Confidence intervals for QTL location were calculated from 10,000 bootstrap samples (Lander and Kruglyak, 1995). Percentage of the trait variance among the F<sub>2</sub> birds explained by the detected QTL ( $V_{QTL}$ ) was calculated as:



**Fig. 1.** The useful information content (the PIC values) across chromosome 3 of Japanese quail for the additive, dominance, and imprinting effects

$$V_{QTL} = 100 \times (RMS - FMS) / RMS$$

where RMS is the residual mean squares from the reduced model, omitting desired effect of QTL and FMS is the residual mean squares from the full model, including desired effect of QTL.

### Results and discussion

The information content (IC) shows the useful information provided by a marker on the genome. In this study, the three markers tested on chromosome 5, were polymorphic. The IC values vary among the markers, where some markers are fully informative and others have an IC < 0.5. The useful information contents of the markers used in this study in different parts of the chromosome 5 of Japanese quail are presented in Fig. 1.

The QTL, with suggestive and significant linkages obtained from each model, are summarized in Tables 1-5. The QTL regions were identified for eleven carcass traits on chromosome 5; the QTL effects ranged from

0.2 to 5% of the phenotypic variation. The first QTL was located at 0 cM and associated with the uropygial weight. This QTL interacted with the sex of the birds. The second region was located at 9 cM containing QTL associated with the carcass efficiency. Close to this region, significant QTL were found that were related to percentage of gizzard.

The QTL for liver percentage, back weight and percentage of back were identified at 12 cM on chromosome 5. Additional QTL were mapped at 13 cM for head weight, at 14 cM for liver weight, at 17 cM for back weight, at 18 cM for percentage of neck and back weight, at 20 cM for breast percentage. At the end of chromosome (21 cM) significant QTL were located for percentage of femur and breast.

One of the most important traits in poultry industry is carcass efficiency. For this trait, a significant ( $p < 0.05$ ) QTL was located at 9 cM of the centromere on 5 chromosome with additive effect (Table 1). This QTL explained 1.15% of the phenotypic variance. Interaction of

**Table 1.** Summary of quantitative trait loci (QTL) obtained from modeling additive QTL effects

Trait	Position (cM)	F-value	QTL Effect <sup>1</sup> (S.E.)	V <sub>QTL</sub> <sup>2</sup>	Closest marker
Carcass efficiency	9	5.64*	0.21 (0.08)	1.15	GUJ0049
breast percentage	21	7.56*	-0.24 (0.08)	1.55	GUJ0100

<sup>1</sup>The additive QTL effect, <sup>2</sup> QTL variance (the reduction in residual variance of the F<sub>2</sub> population obtained by inclusion of a QTL at the given position), \* P < 0.05.

**Table 2.** Summary of quantitative trait loci (QTL) obtained from joint modeling of the additive and dominance QTL effects

Trait	Position (cM)	F-value	QTL Effect <sup>1</sup>		V <sub>QTL</sub> <sup>2</sup>		Closest Marker
			a (S.E.)	d (S.E.)	a	D	
Back weight	18	4.43*	-0.20(0.13)	-0.61(0.22)	0.33	1.28	GUJ0100
Breast percentage	20	5.23*	-0.47(0.26)	-0.49(0.15)	1.53	0.44	GUJ0100

<sup>1</sup>a, d: The additive and dominance QTL effects, respectively; <sup>2</sup> QTL variance (the reduction in residual variance of the F<sub>2</sub> population obtained by inclusion of a QTL at the given position), \* P < 0.05.

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**Table 3.** Summary of quantitative trait loci (QTL) results obtained from modeling of additive, dominance and imprinting QTL effects

Trait	Position (cM)	F-value	QTL Effect <sup>1</sup>			VQTL <sup>2</sup>			Closest Marker
			a (S.E.)	d (S.E.)	I(S.E.)	a	d	i	
Back weight	17	3.58*	-0.21(0.13)	0.66(0.22)	-0.18(-0.12)	0.33	1.28	0.20	GUJ0100

<sup>1</sup> a, d, i: The additive, dominance and imprinting QTL effects, respectively; <sup>2</sup> QTL variance (the reduction in residual variance of the F<sub>2</sub> population obtained by inclusion of a QTL at the given position), \* P < 0.05.

QTL by hatch for carcass efficiency was significant (p<0.01) in two hatches (Table 4).

Breast muscle is the most economically valuable part in poultry. Two suggestive linkages were found for percentage of breast (20, 21 cM). The additive effects of this QTL were negative (Table 1). A QTL by sex interaction was detected for breast percentage at this region that was significant only in female quails (Table 5). More generally, a QTL by sex interaction can be considered as a genotype by environment interaction, considering sex as an organismal environment for gene expression. The same phenotypic measurement could then be considered as different traits in the sexes. Significant QTL by sex interactions were also found for back weight and percentage of back weight, uropygial weight and head weight (Table 5).

When analyzing a three-generation QTL design, using a cross between divergent lines (same as the meat type wild and layer type white strains studied herein), the line-cross model can provide the best fit to the data. Such a design fitted well into our current objective of QTL coarse mapping. A genome scan involves fitting a statistical model at multiple locations in the genomic grid with the objective of finding the location(s) in the genome with significant statistical support for a QTL or multiple QTL. We used a genetic-map-based grid with a genetic distance of 1 cM between the nodes. We used five different genetic models and successfully identified the QTL evaluated among all the possible combinations of QTL that exist.

In chicken, there are several QTL studies carried out for a number of growth (Li et al., 2003, Zhu et al., 2003),

body weight (Van Kaam et al., 1999, Tatsuda and Fujinaka., 2001, Sewalem et al., 2002, De Koning et al., 2003) and fat (Ikeobi et al., 2002) traits. The first genetic map for quail was produced exclusively with AFLP markers and was used for mapping QTL responsible for behavioral traits (Roussot et al., 2003). However, in the context of the QTL localization in Japanese quail, Minvielle et al. (2005), using the first microsatellite linkage map, reported QTL for growth traits, feed intake, weight and total number of eggs, tonic immobility and rectal temperature. In addition, Esmailzadeh et al. (2012) and Sohrabi et al. (2012) reported QTL for growth traits on chromosome 1 while Moradian et al. (2014) found QTL for carcass trait on chromosome 1. Jabbari et al. (2013) identified QTL for growth traits on chromosome 3 in Japanese quail. Our finding is the first report of QTL on chromosome 5 affecting carcass traits in Japanese quail.

In this study, QTL affecting different traits were mapped to similar chromosomal regions. These represent evidence for the basis of genetic correlations among traits, and for correlated response to selection, if they are indeed controlled by the same pleiotropic QTL or by closely linked QTL that are in linkage disequilibrium (LD). However, higher resolution analysis is required to distinguish LD from pleiotropy.

In conclusion, the current study identified informative QTL regions that would form a useful resource as a part of our initiative to develop DNA tests for carcass quality in Japanese quail. However, it should be emphasized that to identify candidate genes and informative markers that are in linkage disequilibrium with QTL affecting

**Table 4.** Summary of quantitative trait loci (QTL) results obtained from modeling QTL by hatch interaction

Trait	Position (cM)	F-value	QTL additive effect					VQTL <sup>1</sup>	Closest marker
			H1 (S.E.)	H2 (S.E.)	H3 (S.E.)	H4 (S.E.)	H5 (S.E.)		
Carcass efficiency	9	5.33**	0.79(.23)	0.87(0.22)	0.00(0.18)	0.07(0.15)	0.06(0.18)	5.00	GUJ0049
Liver weight	14	3.14*	-0.30(0.20)	-0.10(0.23)	0.09(0.20)	0.01(0.14)	-0.14(0.09)	2.50	GUJ0049
Neck percentage	18	2.85*	0.45(0.16)	-0.02(0.25)	-0.51(0.23)	0.09(0.18)	0.04(0.19)	2.16	GUJ0100
Breast percentage	20	3.91**	-0.20(0.18)	-0.66(0.23)	-0.71(0.21)	0.02(0.18)	0.04(0.19)	3.38	GUJ0100
Femur percentage	21	2.67*	0.43(0.16)	-0.53(0.22)	-0.12(0.20)	-0.06(0.16)	0.20(0.17)	1.97	GUJ0100
Gizzard percentage	10	3.81*	-0.58(0.21)	-0.67(0.21)	-0.08(0.17)	0.21(0.13)	0.02(0.17)	3.30	GUJ0049
Liver percentage	12	3.31*	-0.20(0.18)	-0.32(0.20)	-0.18(0.16)	0.07(0.12)	0.56(0.16)	2.70	GUJ0049

<sup>1</sup> QTL variance (the reduction in residual variance of the F<sub>2</sub> population obtained by inclusion of a QTL at the given position), \* P < 0.05 and \*\* P < 0.01.

**Table 5.** Summary of quantitative trait loci (QTL) results obtained from modeling QTL by sex interaction

Trait	Position (cM)	F value	QTL additive effect		VQTL <sup>1</sup>	Closest marker
			Male (.S.E.)	Female (.S.E.)		
uropygial weight	0	4.57**	0.14(0.00)	0.28(0.00)	1.92	GUJ0059
Back weight	12	6.58*	-0.60(0.16)	0.14(0.14)	2.73	GUJ0049
Head weight	13	4.79*	-0.58(0.20)	0.13(0.17)	1.76	GUJ0049
Breast percentage	20	4.91*	-0.08(0.14)	-0.37(0.12)	1.85	GUJ0100
Back percentage	12	3.83*	-0.31(0.11)	-0.03(0.10)	1.34	GUJ0049

<sup>1</sup> QTL variance (the reduction in residual variance of the F<sub>2</sub> population obtained by inclusion of a QTL at the given position).

carcass traits, association studies using SNPs markers might be needed for the significant QTL regions detected in this study.

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## آنالیز لینکاژی مارگرهای میکروساتلایت بر روی کروموزوم شماره ۵ در یک جمعیت F2 از بلدرچین ژاپنی برای شناسایی جایگاه صفات کمی موثر بر صفات لاشه

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**چکیده** یک جمعیت F2 از بلدرچین ژاپنی با تلاقی دو سویه ( وحشی و سفید) برای نقشه یابی جایگاه صفات کمی (QTL) برای صفات لاشه و عملکرد آنها ایجاد شده بود. مجموع ۴۷۲ پرنده F2 پرورش داده و در سن ۴۲ روزگی کشتار شدند. صفات لاشه و عملکرد آنها روی همه افراد F2 اندازه گیری شد. والدین (P0)، F1 و پرندگان نسل F2 با استفاده از ۳ مارکر میکروساتلایت از کروموزوم ۵ بلدرچین ژنوتیپ یابی شده بودند. آنالیز بر اساس ۵ مدل ژنتیک کمی انجام شد که QTL موثر بر کارایی لاشه، درصد سینه، درصد ران، وزن و درصد پشت، وزن سر، وزن چینه دان، وزن یورویپجیال، وزن و درصد کبد و درصد گردن نقشه یابی شد. نتایج یک چهارچوب مهم برای نقشه یابی ژنتیکی موثر و شناسایی جایگاههای صفات کمی کنترل کننده عملکرد صفات لاشه را در بلدرچین ژاپنی ارائه دادند.