doi: 10.17221/113/2014-CJAS

A chromosome-wide QTL mapping on chromosome 2 to identify loci affecting live weight and carcass traits in F_2 population of Japanese quail

E. Nasirifar[1], M. Talebi[1], A. Esmailizadeh[2,3], H. Moradian[3], S.S. Sohrabi[3], N. Askari[4]

[1]Department of Animal Science, Science and Research Branch, Islamic Azad University, Tehran, Iran
[2]State Key Laboratory of Genetic Resources and Evolution, Yunnan Laboratory of Molecular Biology of Domestic Animals, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, P.R. China
[3]Department of Animal Science, Faculty of Agriculture, Shahid Bahonar University of Kerman, Kerman, Iran
[4]National Institute for Genetic Engineering and Biotechnology, Tehran, Iran

ABSTRACT: The Japanese quail (*Coturnix japonica*) is a considerable species which is often used for animal modelling in breeding researches. This study aims to detect quantitative trait loci (QTL) underlying growth and carcass traits in Japanese quail. A three-generation resource population was developed using wild and white Japanese quail strains. The total mapping population consisted of 472 birds. Eight pairs of white and wild birds were mated reciprocally and 34 F_1 birds were generated. The F_1 birds were intercrossed to produce F_2 offspring (422 birds). All of the animals from three generations were genotyped for four microsatellite markers on chromosome 2 in quail. QTL analysis was performed with the Least Squares interval mapping method. The results indicated significant QTL for breast weight, carcass weight, pre-stomach weight, pancreas percentage, head weight, intestine weight, spleen weight, and heart weight. There was also evidence for dominance QTL affecting pre-stomach weight, percentage of pre-stomach weight, and percentage of breast on chromosome 2. The proportion of F_2 phenotypic variation explained by significant additive and dominance QTL effects ranged from 1.06 to 3.33% and 0.71 to 4.36%, respectively. There was no evidence for imprinting effect on the studied traits.

Keywords: DNA markers; growth traits; QTLs

INTRODUCTION

The Japanese quail (*Coturnix japonica*) inhabit parts of Russia and eastern Asia and are similar to chickens and turkeys in their sexual development and egg production. For the past 50 years, the Japanese quail have served as a popular animal model in numerous fields of research. There are many factors involved in the regulation of growth – some intrinsic and some environmental. Heredity is very important in determining the limit and the rate of growth. Narinc et al. (2010) showed the polygenetic nature of growth in the Japanese quail and determined body weight–age relationship by non-linear models in this bird.

Bonafe et al. (2011) reported the sixth order Legendre polynomial as the best fit for the growth rate curves of meat quail and body weight as an influential factor in processes of selection and genetic evaluation. Breeding programs in poultry are complicated, because it is necessary to consider many characteristics such as product quality, health, and reduction in production costs. On the other hand, the relationship between the

doi: 10.17221/113/2014-CJAS

traits is complicated and some traits are difficult to measure. In order to increase the yield per unit and achieve genetic progress, identifying quantitative trait loci (QTL) associated with traits and their use in selecting programs can be a useful strategy (Liu et al. 2007). Despite a large variation in traits that have been studied in Japanese quail, just a few studies have been focused on identifying the linkage groups and therefore the total number of identified genes in this species is still small (Tuiskula-Haavisto et al. 2002).

There are a few reports of identification of QTL using DNA markers in the Japanese quail. Roussot et al. (2003) constructed the amplified fragment length polymorphism (AFLP) linkage map of the Japanese quail and Beaumont et al. 2005 analyzed the QTL of body weight and tonic immobility in the Japanese quail using AFLP markers. A QTL analysis for some economic traits was done by Minvielle et al. 2005 using microsatellite markers detected by Kayang et al. 2004 in which significant and suggestive QTL affecting body weight in five weeks as well as feed consumption efficiency at close positions on chromosome 1 were identified. They also detected two significant QTL for egg number and age at first egg on the quail chromosome 6. On the other hand, Esmailizadeh et al. 2012 found a significant QTL for live weight at 3, 4, 5, and 6 weeks of age in a half-sib population of a commercial strain of the Japanese quail. Japanese quail and chicken have a similar karyotype and genome length (1.2×10^9 bp) (Shibusawa et al. 2001). However, only a small number of linkage groups have been reported for the quail (Ito et al. 1988). The purpose of this study is to map and characterize the mode of action for the QTL associated with growth and carcass related traits on chromosome 2 in the F_2 population of Japanese quail.

MATERIAL AND METHODS

Animals and phenotypic data. The experimental procedures of this study are in line with the regulations approved by the Animal Ethics Committee of the Shahid Bahonar University of Kerman, Iran. Two distinct Japanese quail strains, wild (W, meat type) and white (S, layer type), were developed in three-generation resource population. Eight pairs of W and S birds were crossed reciprocally and 25 females and 9 males were produced. White male × wild female and wild male × white female reciprocal crosses were used to generate F_1 birds including 17 SW and 17 WS reciprocal half of cross progeny respectively. In the F_1 generation, WS males were intercrossed to both WS and SW females generating 176 females and 246 males as F_2 offspring including 153 SWWS, 230 WSSW, and 39 WSWS birds respectively, whereas the SW males were just intercrossed to WS females.

The F_2 population was created in five consecutive hatches. The parents were kept in group cages and fed a layer diet *ad libitum*. The F_2 progeny were raised for 5 weeks on a floor covered with wood shavings in an environmentally controlled room with continuous artificial lighting and at a temperature which was decreased gradually from 37 to 25°C. The progeny received water and a mash starter diet (0–21 days) and a mash growing diet (22–35 days) *ad libitum*. F_2 birds were measured for hatching weight and live weight since week 1 till week 5 of age. The derived traits based on the live weights were growth rates (average daily increase in body weight between consecutive ages) and corresponding Kleiber ratio (KR) defined as $ADG/W^{0.75}$, an indirect criterion of feed efficiency (Kleiber 1947). At 38 days of age, the F_2 birds were slaughtered and carcass weight, internal organ weight, and carcass parts weight were recorded.

DNA extraction and genotyping. DNA was extracted from the whole blood using salting-out method. Microsatellite marker sequence amplifications (Table 1) were carried out by polymerase chain reaction (PCR) in total 25 ml reaction mixtures per individual sample. This mixture included 2.5 ml PCR buffer, 1 ml $MgCl_2$, 0.5 ml dNTP mix, 0.3 ml Taq DNA polymerase, 16.5 ml sterile water, and 2 ml of template DNA (SinaClon BioScience Co., Tehran, Iran). The reaction conditions were 95°C for 4 min, 30 cycles of 94°C for 30 s, annealing at the temperature set for each primer (43–55°C) for 1 min, 63°C for 2 min, and an extension at 72°C for 4 min. PCR products were run on 8% denaturing polyacrylamide gels using electrophoresis. 50 bp DNA ladder was used as a standard size for sizing the PCR products. In order to visualize the PCR products, gels were stained using silver staining (Bassam et al. 1991), the genotypes were scored by UVIdoc software after drying and scanning the gels.

Statistical analysis. The ASReml (Version 2.0, 2006) software was used for descriptive phenotypic data analysis. The model included: the mean of

doi: 10.17221/113/2014-CJAS

Table 1. General characteristics of microsatellite markers on Japanese quail chromosome 2 studied

Marker	Position[1] (cM)	Forward primer (5'-3')	Reverse primer (5'-3')	Size range (bp)	Annealing temperature (°C)
GUJ0073	0	GCTGCTATTCTGTTGATGTG	CAACTGCAAAGACAACATCC	144–160	54
GUJ0069	13	TTCAGGGTAGCAGTCATCTC	CACCAACCACCTTCATCTTC	201–211	52
GUJ0084	44	TCCCGTCTCCCGATGTGTTT	ACTCCTCCTCTTTCTCCCTC	159–165	55
GUJ0093	60	AGCCATAGAGGGCTATTAAG	CTCTTGTATTGTAACTGGGC	213–231	60

[1]marker position on chromosome based on Japanese quail sex averaged linkage map (Kayang et al. 2004)

the F_2 population for each trait, fixed effects of hatch (five levels) and sex (two levels), carcass weight as covariate and residual random term. QTL mapping was performed using the line-cross model developed by Haley et al. 1994. QTL effects (additive, dominance, and imprinting) were estimated using the following models:

Model 1

$$Y_{ijk} = \mu + H_i + S_j + \beta_k (X_k - \bar{X}) + aPak + e_{ijk}$$

Model 2

$$Y_{ijk} = \mu + H_i + S_j + \beta_k (X_k - \bar{X}) + aPak + dPdk + e_{ijk}$$

Model 3

$$Y_{ijk} = \mu + H_i + S_j + \beta_k (X_k - \bar{X}) + aPak + dPdk + iPik + e_{ijk}$$

where:

Y_{ijk} = observed phenotype of individual k

μ = mean of the population

H_i = fixed effect of hatch

S_j = fixed effect of sex

β_k = regression coefficient of the observed phenotype on carcass weight

X_k = carcass weight of individual k

$\bar{X}$ = mean of carcass weight

a = estimated additive effect of QTL

d = estimated dominance effect of QTL

P_{ak} = conditional probability of animal k to carry the allele of wild strain

P_{dk} = conditional probability of animal k to be heterozygous

P_{ik} = conditional probability of animal k to be heterozygous and inheriting the wild strain allele from its sire

e_{ijk} = random residual error

To examine whether the putative QTL was different in female in comparison to male F_2 offspring, QTL by sex interaction effect was also included in model 4. Additive QTL effect by hatch interaction was also analyzed in model 5.

The QTL analysis was performed using GridQTL portal (available at http://www.gridqtl.org.uk/). Applying the above mentioned models, the *F*-statistic profiles were generated at 1 cM intervals along the chromosome to identify the most likely QTL position. Significance thresholds were determined empirically by permutation testing (Churchil and Doerge 1994). Data permutation with 10 000 replicates was used to determine the empirical distribution of the test statistics under the null hypothesis of no QTL.

Percentage of the trait variance among the F_2 birds cited by the detected QTL (V_{QTL}) was calculated as:

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

RMS = residual mean squares from the reduced model (eliminating the desired effect of QTL)

FMS = residual mean squares from the full model (containing the desired effect of QTL)

RESULTS AND DISCUSSION

Descriptive analysis. The descriptive analysis of all the traits under study, including number of observations, minimum values, maximum values, means, residual standard deviation, and coefficient of variation is summarized in Table 2. The effect of hatch was significant for all the traits except for the uropygial gland weight. The effect of sex was significant for weight at 3–5 weeks of age, pre-slaughter weight, carcass weight, gizzard weight, pre-stomach weight, head weight, bursa of fabricius weight, back weight, and wing weight.

QTL mapping analysis. In this study, the polymorphism information content (PIC) of the markers was calculated according to the frequency of individual alleles for the surveyed microsatellite DNA sites. The PIC value indicates the useful information created by a marker on the genome. The

doi: 10.17221/113/2014-CJAS

Table 2. Descriptive statistics, including the estimates for significant fixed effects (sex and hatch) for the Japanese quail F_2 birds data

Trait	*n*	Mean	Minimum	Maximum	r.s.d.	CV (%)	LS Means	
							hatch[1]	sex[2]
BW0	422	6.8	4.8	9.50	0.69	10.10	0.97***	0.10
BW1	419	23.1	11.3	41.4	4.76	20.60	6.55***	0.29
BW2	420	47.6	21.0	74.8	9.30	19.80	12.35***	1.26
BW3	420	83.0	15.9	124.1	13.55	16.60	23.89***	4.12**
BW4	417	120.9	63.1	168.3	17.96	15.10	22.04***	12.83***
BW5	353	153.1	82.5	202.7	18.15	12.00	20.07***	9.14***
Pre-slaughter weight	418	152.4	83.7	199.2	17.58	11.60	11.33***	8.80***
Carcass weight	421	104.5	46.3	141.0	13.22	12.65	5.30***	6.00***
Intestine weight	422	7.0	3.46	15.14	1.14	16.23	2.70***	0.20
Pancreas weight	422	0.5	0.05	0.94	0.10	21.33	0.50***	0.00
Liver weight	422	3.4	1.85	9.64	0.55	15.84	0.80***	0.10
Spleen weight	416	0.1	0.02	0.23	0.03	32.42	0.00***	0.00**
Heart weight	422	1.3	0.59	2.01	0.16	13.18	0.40***	0.10
Gizzard weight	422	4.0	1.86	6.05	0.45	11.35	0.90***	–0.20***
Pre-stomach weight	421	0.6	0.05	0.92	0.10	15.54	0.10***	0.00*
Head weight	422	5.9	4.06	7.53	0.29	5.00	1.00***	–0.20***
Carcass fat weight	422	0.7	0.05	5.54	0.71	100.01	0.40***	0.00
Uropygial gland weight	400	0.3	0.03	0.65	0.07	25.97	0.00	0.00
Bursa of fabricius weight	410	0.1	0.03	0.33	0.04	32.70	0.10***	0.00**
Femur weight	422	21.4	9.91	30.08	1.64	7.67	0.90**	0.20
Neck weight	422	4.2	2.12	6.91	0.46	11.10	0.30***	0.1
Breast weight	422	36.9	14.39	54.80	3.10	8.39	1.70**	1.70
Back weight	422	17.3	8.54	30.95	1.83	10.58	1.50***	0.50*
Wing weight	422	9.8	4.69	13.52	1.09	11.15	0.80***	0.30**

BW0 = hatching weight, BW1–BW5 = live weight at 1–5 weeks of age, *n* = number of observations, Mean = trait mean adjusted for fixed effects included in the model, r.s.d. = residual standard deviation, CV = coefficient of variation

[1]difference between maximum and minimum LS Means of traits in different hatches

[2]difference between sexes (female/male) in LS Means of traits

*$P < 0.05$, **$P < 0.01$; ***$P < 0.001$

PIC > 0.50 is extremely informative, 0.50 > PIC > 0.25 is appropriately informative, and PIC < 0.25 is negligibly informative (Botstein et al. 1980). The PIC values of the markers used in this study in various parts of the chromosome 2 are shown in Table 3 and Figure 1.

In this study, we used 5 different statistical models to identify significant QTL. In model 1, only the additive effect of QTL was fitted. The results from this model indicated significant QTL affecting bursa of fabricius weight ($P < 0.05$), head weight ($P < 0.01$), and bursa of fabricius percentage ($P < 0.05$) at 60, 44, and 60 cM of the linkage map respectively. The closest marker locus to QTL affecting bursa of fabricius weight and bursa of fabricius percentage was GUJ0093 and the closest marker locus to QTL affecting head weight was GUJ0084. The results of this analysis are summarized in Table 4.

In model 2, in addition to the additive effect, the dominance effects were also fitted. According to the results of this analysis, 12 chromosome-wide significant QTL were found for intestine weight ($P < 0.01$), breast weight ($P < 0.01$), spleen weight ($P < 0.05$), heart weight ($P < 0.01$), pre-stomach weight ($P < 0.05$), intestine percentage ($P < 0.01$), heart percentage ($P < 0.01$), pre-stomach percentage (P

doi: 10.17221/113/2014-CJAS

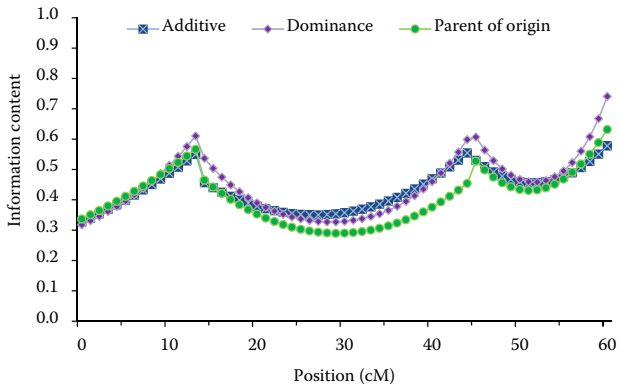

Figure 1. Useful information content (PIC values) across chromosome 2 of Japanese quail for the additive, dominance, and parent of origin effects

< 0.05), breast percentage ($P < 0.01$), pre-slaughter weight ($P < 0.05$), Kleiber ratio 1–2 ($P < 0.05$), and Kleiber ratio 0–5 ($P < 0.05$). The mode of action of the detected QTL for all the traits was only dominance. The closest marker locus to QTL affecting intestine weight, intestine percentage, pre-stomach percentage, pre-slaughter weight, Kleiber ratio 1–2, and Kleiber ratio 0–5 was GUJ0073 and the closest marker locus to QTL affecting breast weight, spleen weight, heart weight, pre-stomach weight, heart percentage, and breast percentage was GUJ0084. The results from the joint modelling of additive and dominance QTL effects are summarized in Table 5.

In the third analysis the additive, dominance, and imprinting (parent-of-origin) effects of QTL were jointly modelled to identify imprinting QTL. There was no evidence for the imprinting effect for the studied traits.

Inclusion of the interaction between the additive effect of QTL and hatch in the additive QTL model revealed a number of significant effects (Table 6). There was also a significant interaction between the additive effect of QTL and sex (Table 7).

A genetic analysis of the F_2 intercross between two strains of the Japanese quail was carried out and there was convincing evidence for quantitative trait loci underlying carcass characteristics and growth traits on chromosome 2.

Three main QTL regions can be identified on chromosome 2. The first is located at 0 cM relative to the centromeric region of the chromosome (in position marker GUJ0069), which contains QTLs associated with intestine weight, intestine percentage, pre-stomach percentage, pre-slaughter weight, Kleiber ratio 1–2, and Kleiber ratio 0–5. It can be concluded that the same gene or a group of linked genes are involved in the phenotypic variation of those traits. The second region is located between 37 and 48 cM (adjacent marker GUJ0084), which contains QTLs associated with head weight (at 37 cM), breast weight (at 43 cM), spleen weight (at 45 cM), pre-stomach weight (at 45 cM), and breast percentage (at 48 cM). The third region is located at the end of the chromosome between 50 and 57 cM (adjacent marker GUJ0093) containing QTL for heart weight (at 50 cM), heart percentage (at 51 cM), bursa of fabricius weight (at 57 cM), and bursa of fabricius percentage (at 57 cM).

Table 3. Useful information content of each marker

Marker	Position (cM)	Alleles	Information			Genotyped individuals (%)		
			additive	dominance	imprinting	P (%)	F_1 (%)	F_2 (%)
GUJ0073	0	3	0.43	0.54	0.51	16 (100%)	32 (94%)	375 (88%)
GUJ0069	13	2	0.01	0.00	0.01	16 (100%)	34 (100%)	376 (89%)
GUJ0084	44	2	0.42	0.48	0.48	16 (100%)	34 (100%)	357 (84%)
GUJ0093	60	3	0.52	0.62	0.57	16 (100%)	34 (100%)	316 (74%)

P = parents

Table 4. Summary of quantitative trail loci (QTL) obtained from modelling additive QTL effects (A)

Trait	Position (cM)	*F*-value	A	SE	$\%V_{QTL}$	Closest marker
Bursa of fabricius weight	57	6.94*	–0.01	0.004	1.61	GUJ0093
Head weight	37	11.52**	–0.09	0.026	2.66	GUJ0084
Bursa of fabricius percentage	57	7.29*	–0.01	0.004	1.69	GUJ0093

SE = standard error, V_{QTL} = QTL variance percentage

*$P < 0.05$, **$P < 0.01$ for chromosome-wide significant QTL

doi: 10.17221/113/2014-CJAS

Table 5. Summary of quantitative trail loci (QTL) obtained from joint modelling additive (A) and dominance (D) QTL effects

Trait	Position (cM)	*F*-value	A	SE	D	SE	%V_{QTL}		Closest marker
							A	D	
Intestine weight	0	10.42**	0.20	(0.135)	0.87	(0.198)	0.43	3.93	GUJ0073
Breast weight	43	8.76**	–0.03	(0.236)	–1.37	(0.327)	3.62	3.83	GUJ0084
Spleen weight	45	4.51*	0.00	(0.003)	0.01	(0.004)	0.99	0.71	GUJ0084
Heart weight	50	10.32**	–0.01	(0.016)	0.10	(0.022)	0.09	4.21	GUJ0084
Pre-stomach weight	45	6.29*	–0.01	(0.009)	–0.04	(0.012)	0.00	2.71	GUJ0084
Intestine percentage	0	11.10**	0.17	(0.137)	0.92	(0.199)	0.38	4.28	GUJ0073
Heart percentage	51	10.52**	0.00	(0.015)	0.09	(0.020)	0.03	4.36	GUJ0084
Pre-stomach percentage	0	4.98*	0.00	(0.012)	0.05	(0.017)	0.00	2.11	GUJ0073
Breast percentage	48	6.79**	–0.08	(0.299)	–1.52	(0.413)	0.00	2.93	GUJ0084
Pre-slaughter weight	0	5.09*	–2.74	(2.410)	–10.17	(3.331)	0.01	1.52	GUJ0073
Kleiber ratio 1–2	0	5.19*	0.00	(0.003)	–0.01	(0.004)	2.00	2.11	GUJ0073
Kleiber ratio 0–5	0	5.50*	0.00	(0.001)	0.00	(0.001)	0.91	2.13	GUJ0073

SE = standard error, V_{QTL} = QTL variance percentage
*$P < 0.05$, **$P < 0.01$ for chromosome-wide significant QTL

Table 6. Summary of quantitative trait loci (QTL) results obtained from modelling QTL by hatch interaction

Trait	Position[1] (cM)	*F*-value	QTL additive effect by hatch interaction		Hatch	%V_{QTL}	Closest marker
			A	SE			
Heart weight	44	12.34**	–0.14	–0.07	2	2.66	GUJ0084
Pancreas percentage	44	3.13*	–0.08	–0.02	3	2.50	GUJ0084
Spleen percentage	18	3.84**	–0.03	–0.01	2	3.33	GUJ0069
Carcass percentage	10	2.97*	0.36 0.51	–0.14 –0.20	2 3	2.32	GUJ0069
ADG (g)	50	2.90*	–0.67	–0.22	5	1.82	GUJ0084

[1]marker position on chromosome based on Japanese quail sex averaged linkage map (Kayang et al. 2004)
A = additive QTL effect, SE = standard error, V_{QTL} = QTL variance percentages, ADG = average daily gain at 3–4 weeks of age
*$P < 0.05$, **$P < 0.01$ for chromosome-wide significant QTL

Table 7. Summary of quantitative trait loci (QTL) results obtained from modelling QTL by sex interaction

	Position (cM)	*F*-value	QTL additive effect by sex interaction				%V_{QTL}	Closest marker
			male		female			
			A	SE	A	SE		
Bursa of fabricius weight	60	4.26*	–0.01	(0.01)	–0.01	(0.00)	1.61	GUJ0093
Head weight	44	6.18**	–0.10	(0.04)	–0.09	(0.03)	2.43	GUJ0084
Bursa of fabricius percentage	60	4.55*	–0.01	(0.01)	–0.01	(0.00)	1.74	GUJ0093
Kleiber ratio 3–4	47	4.14*	0.00	(0.00)	–0.01	(0.00)	1.06	GUJ0084

A = additive QTL effect, SE = standard error, V_{QTL} = QTL variance percentage
*$P < 0.05$, **$P < 0.01$ for chromosome-wide significant QTL

In this study, we also detected QTL for heart weight, pancreas percentage, spleen percentage, carcass percentage, average daily gain, and Kleiber ratio (Table 6) that significantly interacted with hatch. The QTL additive effect of these traits interacted significantly with hatch indicating the

doi: 10.17221/113/2014-CJAS

environmental factors associated with the hatch influenced the expression of the loci controlling these traits. In addition, the QTL additive effect of bursa of fabricius weight, head weight, bursa of fabricius percentage, and Kleiber ratio 3–4 (Table 7) interacted significantly with sex. The QTL by sex can be measured as a genotype by environment interaction, deliberating sex as an environment for the genotype expression; therefore the same phenotypic measurement could then be measured as different traits in the sexes (Abasht et al. 2006). More generally, based on the biological attitude, Hamoen et al. 2001 suggested that the QTL by sex interactions might be described by genes with different effects in sexually different environments.

The QTL variance shows the contribution of specific trait loci to the total phenotypic variance of the trait. At each position, mapping QTL using desirable model determines whether a significant amount of the variance in a quantitative trait can be associated with a QTL at that position. QTL variance determined as the reduction of the residual variance acquired by fitting a QTL at the corresponding location was relatively small for the detected loci (Sohrabi et al. 2012). The proportion of the F_2 phenotypic variation explained by the significant additive and dominance QTL effects ranged from 1.06 to 3.33% and 0.71 to 4.36%, respectively.

In this study, chromosome-wide significant QTL for growth and carcass traits were found on chromosome 2. QTL significant for growth traits were found also on chromosome 1 in this population (Sohrabi et al. 2012).

There are also a large number of QTL studies that identified QTL for growth and carcass traits on chicken chromosome 2. As the chicken and quail are two species of animals belonging to the same family with identical karyotype (2n = 78), QTL for the traits identified in this study on chromosome 2 may be comparable with the same trait, or a very similar trait obtained from chicken. Zhou et al. (2006) reported two chromosome-wide significant QTL for heart weight positioned at 242 and 286 cM and one QTL affecting spleen weight positioned at 103 cM on chicken chromosome 2. Ikeobi et al. (2004) mapped significant QTL for breast muscle using carcass weight as a covariate on chromosome 2 in the F_2 population chicken. For this trait, a significant QTL at 77 cM and 266 cM was also reported on chicken chromosome 2 (Zhou et al. 2006; Atzmon et al. 2008). Baron et al. (2010) identified two significant QTL for breast percentage located at 172–226 and 302–320 cM and also two significant QTL at 172–226 and 282–302 cM for the percentage of head in chicken chromosome 2.

Potentially pleiotropic effects of QTL were observed on chromosome 2 at 0 cM relative to the centromeric region of the chromosome. In this region of the chromosome, significant QTL were detected for six different traits with dominance effects which could probably be explained by a pleiotropic effect of this QTL.

Our study described several important QTL with additive and dominance effects for growth and carcass traits in an F_2 population of the Japanese quail. This study adds new important information from a chromosome-wide search for QTL in Japanese quail, and is the first to report the detection and positioning of the loci affecting important traits on chromosome 2 in the Japanese quail. These results might be anticipated as the mentioned traits are highly correlated. However, characterizing a single gene in contrast to the cluster of genes with individual QTL analyzed seems to be difficult, given the current marker density in the first generation linkage map of the Japanese quail. Therefore, further studies with more markers are needed to recognize the full spectrum of genetic changes that cause growth differences and to narrow down the location of a gene or genes within each chromosome interval with contribution to growth divergence. For the construction of a high resolution linkage map for fine mapping of the detected QTL in this study and determining the new potential genes of interest, it is necessary to isolate additional microsatellites, single nucleotide polymorphisms (SNPs), and microsatellites in expressed sequence tags and genes.

REFERENCES

Abasht B., Pitel F., Lagarrigue S., Le Bihan-Duval E., Le Roy P., Demeure O., Vignoles F., Simon J., Cogburn L., Aggrey S., Vignal A., Douaire M. (2006): Fatness QTL on chicken chromosome 5 and interaction with sex. Genetics Selection Evolution, 38, 297–311.

Atzmon G., Blum S., Feldman M., Cahaner A., Lavi U., Hillel J. (2008): QTLs detected in a multigenerational resource chicken population. Journal of Heredity, 99, 528–538.

Baron E.E., Moura A.S., Ledur M.C., Pinto L.F., Boschiero C., Ruy D.C., Nones K., Zanella E.L., Rosario M.F., Burt D.W., Coutinho L.L. (2010): QTL for percentage of carcass and

doi: 10.17221/113/2014-CJAS

carcass parts in a broiler × layer cross. Animal Genetics, 42, 117–124.

Bassam B.J., Caetano-Anolles G., Gresshoff P.M. (1991): Fast and sensitive silver staining of DNA in polyacrylamide gels. Analytical Biochemistry, 196, 80–83.

Beaumont C., Roussot O., Feve K., Plisson-Petit F., Leroux S., Pitel F., Faure J.M., Mills A.D., Guemene D., Leterrier C., Sellier N., Mignon-Grasteau S., Sellier N., LeRoy P., Perez-Enciso M., Vignal A. (2005): A genome scan with AFLP™ markers to detect fearfulness-related QTLs in Japanese quail. Animal Genetics, 36, 401–407.

Bonafe C.M., Torres R.A., Teixeira R.B., Silva F.G., Sousa M.F., Leite C.D.S. (2011): Heterogeneity of residual variance in random regression models in the description of meat quail growth. Brazilian Journal of Animal Science, 40, 2129–2134.

Botstein D., White R.L., Skolnick M., Davis R.W. (1980): Construction of a genetic linkage map in man using restriction fragment length polymorphisms. American Journal of Human Genetics, 32, 314–331.

Churchill G.A., Doerge R.W. (1994): Empirical threshold values for quantitative trait mapping. Genetics, 138, 963–971.

Esmailizadeh A.K., Baghizadeh A., Ahmadizadeh M. (2012): Genetic mapping of quantitative trait loci affecting bodyweight on chromosome 1 in a commercial strain of Japanese quail. Animal Production Science, 52, 64–66.

Haley C., Knott S., Elsen J. (1994): Mapping quantitative trait loci in crosses between outbred lines using Least Squares. Genetics, 136, 1195–1207.

Hamoen F.F., Van Kaam J.B., Groenen M.A., Vereijken A.L., Bovenhuis H. (2001): Detection of genes on the Z-chromosome affecting growth and feathering in broilers. Poultry Science, 80, 527–534.

Ikeobi C.O.N., Woolliams J.A., Morrice D.R., Law A., Windsor D., Burt D.W., Hocking P.M. (2004): Quantitative trait loci for meat yield and muscle distribution in a broiler layer cross. Livestock Production Science, 87, 143–151.

Ito S., Kimura M., Isogai I. (1988): A sex difference in recombination values between extended brown and phosphoglucose isomerase loci in Japanese quail. Japanese Journal of Zootechnical Science, 59, 801–805.

Kayang B.B., Vignal A., Inoue-Murayama M., Miwa M., Monvoisin J.L., Ito S., Minvielle F. (2004): A first-generation microsatellite linkage map of the Japanese quail. Animal Genetics, 35, 195–200.

Kleiber M. (1947): Body size and metabolic rate. Physiology Reviews, 27, 511–541.

Liu X., Li H., Wang S., Hu X., Gao Y., Wang Q., Li N., Wang Y., Zhang H. (2007): Mapping quantitative trait loci affecting body weight and abdominal fat weight on chicken chromosome one. Poultry Science, 86, 1084–1089.

Minvielle F., Kayang B., Inoue-Murayama M., Miwa M., Vignal A., Gourichon D., Neau A., Monvoisin J., Ito S. (2005): Microsatellite mapping of QTL affecting growth, feed consumption, egg production, tonic immobility and body temperature of Japanese quail. BMC Genomics, 6, 87.

Narinc D., Aksoy T., Karaman E. (2010): Genetic parameters of growth curve parameters and weekly body weights in Japanese quails (Coturnix coturnix japonica). Journal of Animal and Veterinary Advances, 9, 501–507.

Roussot O., Feve K., Plisson-Petit F., Pitel F., Faure J.M., Beaumont C., Vignal A. (2003): AFLP linkage map of the Japanese quail Coturnix japonica. Genetics Selection Evolution, 35, 559–572.

Shibusawa M., Minai S., Nishida-Umehara C., Suzuki T., Mano T., Yamada K., Namikawa T., Matsuda Y. (2001): A comparative cytogenetic study of chromosome homology between chicken and Japanese quail. Cytogenetics and Cell Genetics, 95, 103–109.

Sohrabi S.S., Esmailizadeh A.K., Baghizadeh A., Moradian H., Mohammadabadi M.R., Askari N., Nasirifar E. (2012): Quantitative trait loci underlying hatching weight and growth traits in an F2 intercross between two strains of Japanese quail. Animal Production Science, 52, 1012–1018.

Tuiskula-Haavisto M., Honkatukia M., Vilkki J., de Koning D.J., Schulman N.F., Maki-Tanila A. (2002): Mapping of quantitative trait loci affecting quality and production traits in egg layers. Poultry Science, 81, 919–927.

Zhou H., Deeb N., Evock-Clover C.M., Ashwell C.M., Lamont S.J. (2006): Genome-wide linkage analysis to identify chromosomal regions affecting phenotypic traits in the chicken. II. Body composition. Poultry Science, 85, 1712–1721.

Received: 2014–10–31
Accepted after corrections: 2016–03–08

Corresponding Author

Ehsan Nasirifar, Ph.D., Islamic Azad University, Science and Research Branch, Hesarak, Tehran 1477893855, Iran
Phone: +989 131 974 456, e-mail: Ehsan.nasirifar@gmail.com

CZECH ACADEMY OF AGRICULTURAL SCIENCES

Těšnov 65/17, 110 00 Prague 1, Czech Republic
workplace: Slezská 7, 120 00 Prague 2, Czech Republic
e-mail: redakce@cazv.cz
Tel.: + 420 227 010 427, Fax: + 420 227 010 116

Bank account No. 107-9595250287/0100
IBAN: CZ25 0100 0001 0795 9525 0287; BIC (SWIFT code): KOMBCZPPXXX

The Czech Academy of Agricultural Sciences published scientific journals dealing with the problems of agriculture, forestry and food sciences and technology. The periodicals are published in English.

Journal	Number of issues per year	Yearly subscription in USD
Plant, Soil and Environment	12	850
Czech Journal of Animal Science	12	850
Agricultural Economics (Zemědělská ekonomika)	12	850
Journal of Forest Science	12	700
Veterinární medicína (Veterinary Medicine – Czech)	12	950
Czech Journal of Food Sciences	6	740
Plant Protection Science	4	200
Czech Journal of Genetics and Plant Breeding	4	200
Horticultural Science	4	230
Research in Agricultural Engineering	4	180
Soil and Water Research	4	230

Prices include VAT (15%)

Subscription to these journals be sent to the above-mentioned address.