PRODUCTION, MODELING, AND EDUCATION

Growth performance, meat quality traits, and genetic mapping of quantitative trait loci in 3 generations of Japanese quail populations (*Coturnix japonica*)

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ABSTRACT The current research was conducted to compare growth, carcass traits, pH, intramuscular collagen (IMC) properties, and genetic bases of IMC and carcasses (breast-muscle weight) of different lines and generations of adult males and females of Japanese quail (*Coturnix japonica*). Forty-four quails (generation F_0), 22 Pharaoh (F-33) meat-type males and 22 Standard (S-22) laying-type females, were crossed to produce the F_1 hybrids generation. The F_2 generation was created by mating one F_1 male with one F_1 female, full siblings. The birds, randomly chosen from F_0 (22 males and 22 females), F_1 (22 males and 22 females), and F_2 (84 males and 152 females) were raised to 20 wk of age in collective cages. Quails were fed ad libitum commercial diets. At slaughter, all birds were individually weighed (after a fasting period of 12 h) and dressing yield (without giblets) was calculated. The carcasses were then dissected. Genomic DNA was extracted from all of the blood, and 30 microsatellite markers located on 2 quail chromosomes were genotyped. The F-33 quails had higher in vivo and postmortem performances and a higher abdominal fat percentage than those of the egg line. Meat from S-22 quails had a slower collagen maturation (hydroxylysylpyridinoline crosslink/collagen) and a higher ultimate pH. The F_1 and F_2 generations showed an evident sexual dimorphism, and an additional effect could be due to hybrid heterosis evident in F_2. Meat from quails of F_1 and F_2 generations had a lower IMC amount with a higher degree of collagen maturation compared with parental lines. Two statistically significant QTL have been detected on quail chromosome 2 (CJA02): a QTL with an additive effect (0.50) for IMC in the marker bracket GUJ0037 and GUJ0093; a second QTL with additive (1.32) and dominant (1.91) effects for breast-muscle weight in the marker bracket GUJ0084 and GUJ0073. To our knowledge, this is the first report of a QTL associated with breast-muscle weight and IMC in quail and poultry species, respectively.

Key words: quail, cross-breed, quantitative trait loci, productive trait, intramuscular collagen

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INTRODUCTION

The Japanese quail is the smallest avian species farmed for egg and meat production, and it has also assumed worldwide importance as a laboratory bird model for research. Females start laying at an average of 40 d, with high egg production. The Japanese quail has a short generation interval, from 3 to 4 generations per year (Kayang et al., 2004; Alkan et al., 2010). This bird is used among others for genetic, physiological, biomedical, behavioral, and embryological studies (Huss et al., 2008).

In the poultry world, quail-meat production is negligible when compared with that of broiler chickens, but nevertheless quail is a good source of meat and occupies a relevant place in poultry breeding and contributes to the global poultry industry (reviewed in Maiorano et al., 2009, 2011). The valuable taste and dietary properties of quail meat are pivotal in determining the growing interest of consumers to this product (Genchev et al., 2008). Therefore, quail meat could be an interesting niche business. Growth, carcass traits, and the quality and composition of meat are influenced by numerous factors, such as genotype of the birds, genetic selection, feeding mode, and slaughter age (Vali, 2008; reviewed in Maiorano et al., 2012). Generally, broiler quails are slaughtered at about 5 to 6 wk of age for economic reasons (Genchev et al., 2008). However, quails are also

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slaughtered as young–old broilers (8–13 wk; Boni et al., 2010; Lotfi et al., 2011) and spent birds (8 mo; Boni et al., 2010) and sold on the commercial market without any distinction being made of age (Shanaway, 1994; Minvielle, 2004).

Appearance (e.g., color of skin and meat) and tenderness are 2 extremely important traits in poultry meat quality (Fletcher, 2002). In particular, meat tenderness is the single most important sensory property affecting final quality assessment (Fletcher, 2002). Tenderness is affected by several factors, such as breed, sex, age, fiber resistance, sarcomere length, pH, and collagen morphology (Lepetit, 2007; Maiorano et al., 2009, 2012). Intramuscular collagen (**IMC**) is an important parameter to the meat industry; an increased amount of this component may affect toughness and meat quality (Karunaratne et al., 2005) of different domestic animals, including birds (Baeza et al., 1998). The contribution of collagen and its hydroxypyridinoline crosslinks (the main IMC mature crosslink) to meat toughness was recently reviewed by McCormick (2009). However, few studies are available on collagen crosslinks in quail intramuscular connective tissue (Maiorano et al., 2009, 2011).

In the available literature on Japanese quail, only few publications can be found reporting QTL responsible for laying traits, the quality of the egg and the shell (Minvielle et al., 2005), daily weight gains in certain weeks of life (Esmailizadeh et al., 2012; Sohrabi et al., 2012), the shape of the laying curve (Minvielle et al., 2006), or behavioral traits associated with fearfulness (tonic immobility; Beaumont et al., 2005). There is no information on the loci linked with carcass and meat quality traits in quails such as IMC properties.

The idea of QTL study is to identify linkage between the genotypic and phenotypic data. This can be done on the basis of interval mapping, which identifies QTL region located between 2 flanking molecular markers. In this QTL analysis method, it is assumed the existence of the reference population derived by crossing 2 inbred lines (meat-line males and laying-line females) that differ only with respect to the analyzed QTL. These inbred lines, by definition, are created by crossing male and female siblings over consecutive generations. The mapping of QTL is performed using regression analysis within F_2 generation. Cross of meat-type and laying-type Japanese quail, created for this experiment, fulfills all of these requirements. In reviewing the literature, no data were found on the effect of crossing 2 strains of Japanese quail on meat quality of the F_1 and F_2 generations, including QTL detection, whereas only few works (Esmailizadeh et al., 2012; Nejad et al., 2012) on QTL related to the in vivo performance were found. Additionally, very few studies have been conducted to compare meat quality of different lines or breeds of quail (reviewed in Maiorano et al., 2009, 2011). Therefore, this research was conducted to evaluate the effect of different lines (meat-type and egg-type quails), cross (meat-type × egg-type quails; $F_0 \times F_1$), and sex (males and females) on growth performance, carcass traits, and IMC properties, coupled with the genetic mapping of QTL in Japanese quails.

MATERIALS AND METHODS

Experimental Population

The experiment was performed with 2 Japanese quail (*Coturnix japonica*) populations (meat type and egg type) reared at the Didactic Experimental Station of the University of Life Sciences in Lublin (Poland). Forty-four quails (generation F_0), 22 Pharaoh (**F-33**) meat-type males and 22 Standard (**S-22**) laying-type females, were crossed to produce the F_1 hybrids generation. The F_2 generation was created by mating one F_1 male with one F_1 female, full siblings. A total of 236 F_2 individuals were obtained (84 males, 152 females) in 2 hatches. The age of F_0 at the time of hatching offspring was 16 wk and that of F_1 was 16 wk (first hatch) and 18 wk (second hatch). The birds from F_2 were not parents of next generations.

The birds from F_0 (22 males and 22 females), F_1 (22 males and 22 females), and F_2 (84 males and 152 females) were raised to 20 wk of age in collective cages (F_0 and F_1: 6 birds in each of 6 cages and 4 birds in each of 2 cages; F_2 hatch 1: 6 birds in each of 16 cages; F_2 hatch 2: 6 birds in each of 22 cages and 4 birds in each of 2 cages) under continuous lighting (natural and artificial). The rearing temperature was gradually decreased, 38 to 34°C in the first week, 33 to 28°C in the second week, and 27 to 22°C in the third week. Afterward, it was maintained between 18 and 20°C. The quail were fed ad libitum commercial diets according to age. The diet containing 24% CP and 2,900 kcal of ME/kg was used for the first 28 d; the finisher ration had 20% CP and 2,800 kcal of ME/kg. Birds had free access to water during the experiment.

Slaughter Surveys

At slaughter (20 wk of age), all birds were individually weighed (after a fasting period of 12 h), stunned, and decapitated, and blood was collected for analyses of DNA from quails of F_0, F_1, and F_2 generations. Stunning was performed by a percussive blow to the back part of the head (occiput), and decapitation was performed with scissors between the cervical vertebrae and the base of the skull according to the EU regulations on the protection of animals at the time of killing (European Communities, 2009). After plucking and eviscerating, carcasses were weighted and dissected (leg, breast, giblets, abdominal fat; their percentages were calculated based on hot carcass weight) and, in addition, dressing percentage (without giblets) was calculated. After the refrigeration period (24 h at 4°C), the pH of the right pectoral muscle was recorded using a portable pH meter equipped with a glass electrode (R. Matthaüs, Pöttmes, Germany). The left pectoral

muscle was removed, vacuum packaged, and stored frozen (−40°C) for analyses of IMC.

Collagen Analysis

At analysis, muscle samples were thawed, at room temperature, trimmed of fat and epimysium, lyophilized for 48 h, weighed, and hydrolyzed in Duran tubes in 5 mL of 6-*N* HCl at 110°C for 18 to 20 h for determination of hydroxyproline (Woessner, 1961) and crosslinking. The analyses were carried out in duplicate. Intramuscular collagen concentration was calculated, assuming that collagen weighed 7.25 times the measured hydroxyproline weight (Eastoe and Leach, 1958) and expressed as micrograms of hydroxyproline per milligram of lyophilized tissue. Hydroxylysylpyridinoline (**HLP**) concentration (measured on 22 males and 22 females for each generation), the principal nonreducible crosslink of muscle collagen and highly correlated with the thermal stability of collagen (McCormick, 1999), was determined using the procedure described by Eyre et al. (1984). A Kontron HPLC (Kontron Instruments, Milan, Italy) model 535, equipped with a Luna C18 column (250 × 4.6 mm × 5 μm; Phenomenex, Torrance, CA), was used. The concentration of HLP residues in the samples was calculated based on the concentration of collagen in each hydrolyzate, assuming that the molecular weight of collagen was 300,000 and the molar fluorescence yield of pyridoxamine (internal standard) was 3.1 times that of HLP (Eyre et al., 1984). Crosslink concentration was expressed as moles of HLP per mole of collagen.

DNA Extraction and Microsatellite Genotyping

Genomic DNA was extracted from blood with the use of a QIAamp DNA Blood Mini Kit (Qiagen GmbH, Hilden, Germany) according to the protocol recommended by the manufacturer. The DNA quality was estimated by a spectrophotometer using BioPhotometer (Eppendorf AG, Hamburg, Germany). All together, 30 microsatellite markers located on 2 quail chromosomes (quail chromosome 1 and 2) were genotyped. The list of microsatellites used in this study, including primer sequence, position on the chromosome, and length of alleles, is presented in Table 1. The PCR reaction was performed in an MJ Research PTC-225 Tetrad thermocycler (MJ Research, San Diego, CA). Reverse primers were fluorescently labeled with 3 dyes: 6-FAM, VIC, NED (Applied Biosystems, Foster City, CA). The PCR mixture was as follows: 100 m*M* Tris-HCl (pH 8.9), 20 m*M* $MgCl_2$, 500 m*M* KCl, deoxynucleoside triphosphate, 20 ng of DNA, 0.25 U of AmpliTaq GOLD 360 DNA Polymerase (Applied Biosystems), primers (0.2–0.75 pmol). The PCR reaction profile was as follows: denature cycle at 95°C (600 s), then 30 cycles of the following: 95°C (30 s); optimized annealing temperature (as per locus: 48°C/52°C/55°C/60°C) for 30 s; elongation 72°C (30 s); followed by final extension at 72°C (1,200 s).

Microsatellite Scoring

The PCR products were subjected to electrophoresis on 4% polyacrylamide gel (POP4) using ABI Prism 3100-*Avant* Genetic Analyzer (Applied Biosystems). Markers scoring were performed with 2 types of software: 3100-*Avant* Abi Prism Data Collection and Gene Mapper v. 3.5. Allele length was analyzed based on internal size standard Gene-Scan-350 ROX with nucleotide sizes 35, 50, 75, 100, 139, 150, 160, 200, 250, 300, 340, and 350 bp.

Statistical Analyses

One-way ANOVA was performed for performance, carcass traits, and IMC properties (SPSS Inc., 2010). Scheffé's test was applied to compare the mean values among the 3 generations.

QTL Analysis

Regression interval mapping was used for QTL detection. Analyses were performed with web-based GRID QTL software (http://www.gridqtl.org.uk/index.htm; Seaton et al., 2006) and line-cross analysis model (F_2 inbred portlets). In the line-cross model, the power of QTL detection depends on the assumption of fixation of QTL alleles for the trait of interest in the founder lines. In this model the alternative alleles at the QTL are traced back to the founder line. In the line cross model, a simple regression analysis was used to calculate the test statistics (F) for the presence or absence of a single QTL at each centimorgan. Significance thresholds (5 and 1%) were calculated for each chromosome and each trait individually, by performing 500 chromosome-wide permutations. Confidence intervals of the QTL were calculated using bootstrap with resampling. The hatch and sex of birds were considered as fixed effects. The line cross model included additionally additive and dominant genetic effects.

RESULTS

Performance, Carcass Traits, and Meat Quality

Growth, slaughter traits, pH, and IMC properties of meat line (F-33) and egg line (S-22) Japanese quail are presented in Table 2. Quails of meat line had higher ($P < 0.01$) final BW, carcass weight, and carcass yield (+8.3%) than those of the egg line. Breast muscle and legs yield did not differ significantly between the 2 lines; giblets percentage was higher ($P < 0.01$) in egg-type quails, whereas abdominal fat percentage was

Table 1. List of microsatellites, primer sequence, position on the chromosome and length of alleles, dye used for labeling reverse primers, and annealing temperature (T_A)

Locus	Primer[1]	Chromosome	Position (cM)	Range	Dye	T_A (°C)
GUJ0006	F–TGGGATGATAATGAGGTACGG	1	154	110–122	NED	55
	R–AGGATAGCATTTCAGTCACGG					
GUJ0013	F–ACCAAACCCGAGATCCGACA	1	126	127–145	VIC	55
	R–AGCGTTCGCGTTCCTCTTTC					
GUJ0017	F–AGAGAGATTAGAGGAGCTGC	1	39	145–163	6-FAM	48
	R–GGCACTAAAACCATCGAGAG					
GUJ0036	F–CTTTCACATTGCTTTTGCCT	1	55	150–156	6-FAM	55
	R–CACTAAAGATTGGCTAACAG					
GUJ0048	F–AACGCATACAACTGACTGGG	1	161	127–139	NED	55
	R–GGATAGCATTTCAGTCACGG					
GUJ0050	F–CTGCCATGTTACTAATCTAG	1	173	144–148	VIC	55
	R–TGGTTTCTTTACACTTGACA					
GUJ0051	F–CCTTAACCACTCCTACTGAC	1	193	183–189	VIC	55
	R–TTTTGTAAGTGGCCCCGTAC					
GUJ0052	F–AAACTACCGATGTAAGTAAG	1	232	99–105	6-FAM	55
	R–ATGAGATATATAAGGAACCC					
GUJ0055	F–GCATACTGCAATATACCTGA	1	244	155–179	NED	55
	R–TTGACATACTTGGATTAGAGA					
GUJ0056	F–GTTACATCCATCCTGCCTCA	1	96	178–190	NED	55
	R–CTCTTGAGCCTACCAGTCTG					
GUJ0062	F–TTATGTTTGATGGGCAGAGG	1	24	176–200	VIC	60
	R–CATGGCAAAAACTGAAGAGC					
GUJ0064	F–AAGCCTGATTCCCTGCCTTG	1	±275	218–222	VIC	55
	R–TTAAAGCTGGGAGGTGGAGG					
GUJ0068	F–TAGGAGAGGTCACGATTTGC	1	6	202–218	VIC	54
	R–ATCTTAACTCGCCCAGCCTT					
GUJ0077	F–TATAAGATGGGGAGTGGCAG	1	92	232–240	6-FAM	55
	R–ATTTTGCTGACCCCCTTCTG					
GUJ0078	F–TCTTTGATTGATGGCTTGCG	1	218	131–139	6-FAM	55
	R–GTTATCCTCTGAAGTGTAGC					
GUJ0090	F–GCCTTCAGAGTGGGAAAT	1	0	95–119	VIC	55
	R–TCTCACAGAAACAGCTCC					
GUJ0095	F–GCAACATTTTCAGTCAGATC	1	±126	120–126	VIC	55
	R–AATTCTCATCAGTCTCCAAC					
GUJ0098	F–GCATAACTGAACTACCACGC	1	32	199–211	6-FAM	55
	R–GCATCAGTTCCATCAGCTAG					
GUJ0037	F–CCATTCCTCCATCGTTCTGA	2	0	178–194	6-FAM	55
	R–GGGAAGGAGTGTAGGAAAGA					
GUJ0067	F–ACGTACGAGCTCAACATTTG	2	39	121–131	VIC	55
	R–GCGTGCATAAAGGCAACTTA					
GUJ0007	F–TGACTGCTTTCCACACACA	2	74	87–89	6-FAM	52
	R–CAGAAGGTAAAAGGACGGA					
GUJ0093	F–CTCTTGTATTGTAACTGGGC	2	91	213–231	NED	60
	R–AGCCATAGAGGGCTATTAAG					
GUJ0079	F–GAAAGATAAGCATGAGTGAC	2	99	121–135	VIC	55
	R–GTTTTGGCATTCACTTCAGA					
GUJ0027	F–TTCACAGATGACAATCTAGC	2	109	163–177	VIC	55
	R–CTGCAAGTAACAGAAGGTAA					
GUJ0084	F–ACTCCTCCTCTTTCTCCCTC	2	117	159–165	NED	55
	R–TCCCGTCTCCCGATGTGTTT					
GUJ0091	F–AAACCGCCATCCCCATTCC	2	156	172–188	NED	55
	R–AGCACGTGGGCAAAGGAAC					
GUJ0069	F–TTCAGGGTAGCAGTCATCTC	2	161	201–211	NED	55
	R–CACCAACCACCTTCATCTTC					
GUJ0073	F–GCTGCTATTCTGTTGATGTG	2	174	144–160	6-FAM	52
	R–CAACTGCAAAGACAACATCC					
GUJ0063	F–GCTCAGGTTCTCAGCTGATG	2	±110	242–250	6-FAM	55
	R–GGGAGAGATCAAGGGAACAG					
GUJ0066	F–GGGAAAACAATCACTGCCTC	2	±150	167–175	6-FAM	55
	R–TCTGCAAATCCCCCTTAGAG					

[1]F = forward; R = reverse.

higher ($P < 0.01$) in meat-type quails. Ultimate pH of meat-type quails was lower ($P < 0.05$) than that of the egg-type quails. The IMC amount was similar ($P > 0.05$) between the 2 quail lines. Compared with the quails of meat line, those of the egg line had a slower ($P < 0.01$) collagen maturation (HLP/collagen).

Sex effect on BW, slaughter traits, and meat quality (pH and IMC properties) of the F_1 generation is shown in Table 3. Females were heavier than males ($P < 0.01$) and had a higher ($P < 0.01$) giblets percentage, whereas males showed a higher ($P < 0.01$) carcass yield (+6.2%) and abdominal fat percentage. Breast and legs

Table 2. Least squares means and SE for BW, slaughter traits, pH, and intramuscular collagen properties of pectoral muscle from Japanese quails of F_0 generation

Item[1]	Group[2]		*P*-value
	F-33 (male)	S-22 (female)	
n	22	22	
Final BW (g)	166.21 ± 2.62	149.00 ± 3.82	0.001
Carcass weight (g)	115.65 ± 2.41	91.26 ± 2.58	0.001
Carcass yield (%)	69.52 ± 0.71	61.24 ± 0.67	0.001
Breast yield (%)	33.45 ± 0.50	33.04 ± 0.44	0.538
Legs yield (%)	24.67 ± 0.61	25.52 ± 0.69	0.358
Giblets (%)	5.35 ± 0.11	7.52 ± 0.16	0.001
Abdominal fat (%)	7.53 ± 0.86	2.56 ± 0.40	0.001
pH_{24}	5.67 ± 0.02	5.79 ± 0.05	0.033
IMC (μg/mg of lyophilized muscular tissue)	14.14 ± 0.61	13.22 ± 0.42	0.221
HLP (mol/mol of collagen)	0.121 ± 0.005	0.098 ± 0.003	0.001

[1]pH_{24} = pH after refrigeration period (24 h at 4°C); IMC = intramuscular collagen; HLP = hydroxylysylpyridinoline.

[2]F-33 = meat-line males; S-22 = egg-line females.

yields, ultimate pH, and IMC amount were not significantly influenced by sex. The meat from females had a slower ($P < 0.01$) collagen maturation (HLP/collagen).

Sex effect on BW, slaughter traits, and meat quality (pH and IMC properties) of the F_2 generation is shown in Table 4. Except for IMC properties, which were not significantly affected by sex, and the ultimate pH, which was higher for males in comparison with females ($P < 0.01$), the same trend as in the F_1 generation was found for the BW and slaughter traits (carcass weight; carcass, breast, and legs yields; giblets and abdominal fat percentages). Considering the hatch effect, it influenced significantly only the IMC amount (8.51 versus 10.15 μg/mg for hatch 1 and hatch 2, respectively; $P < 0.01$), and data regarding slaughter performance and pH are not shown.

The comparison of performance traits and pH among the 3 generations, according to the sex, are shown in Figure 1 (males and females). The BW of F_1 and F_2 males compared with F-33 males (F_0 generation) was not affected ($P > 0.05$) by the crosses. However, the carcass weight of F_0 males was higher than that of F_1 ($P < 0.01$) and F_2 ($P < 0.05$) males. On the contrary, the F_1 and F_2 females were heavier ($P < 0.01$) than parental line (S-22). The F_1 quails (males and females) showed the lowest carcass yield ($P < 0.01$), and F_2 quails had an intermediate value ($P < 0.01$ and $P < 0.05$). Abdominal fat was lower in F_2 males compared with F_0 and F_1 males ($P < 0.05$); on the contrary, it slightly increased ($P = 0.067$) in F_1 females and markedly ($P < 0.01$) in F_2 females compared with F_0 ones. Legs yield was lower ($P < 0.01$) in both F_1 and F_2 males and in F_2 females compared with parental lines. Differently, the giblets percentage of males and females was higher for F_2 in comparison with F_0 quails ($P < 0.01$ and $P < 0.05$), and moreover, the giblets percentage from F_2 males was higher ($P < 0.05$) than that of the F_1 birds. Breast yield did not differ ($P > 0.05$) among the 3 bird groups (males and females). In general, pH was significantly ($P < 0.01$ and $P < 0.05$) affected by crosses.

The comparison of IMC properties among the 3 generations, according to the sex and hatch, are shown in Figure 2. Collagen amount, in both males and females, decreased ($P < 0.01$) from F_0 to F_1 and from F_1 to F_2 (this decrease was evident only in females of hatch 1

Table 3. Least squares means and SE for BW, slaughter traits, pH, and intramuscular collagen properties of pectoral muscle from Japanese quails of F_1 generation

Item[1]	Group		*P*-value
	Male	Female	
n	22	22	
Final BW (g)	163.00 ± 2.78	184.58 ± 3.52	0.001
Carcass weight (g)	101.98 ± 1.59	104.30 ± 2.15	0.391
Carcass yield (%)	62.71 ± 0.75	56.54 ± 0.58	0.001
Breast yield (%)	33.12 ± 0.52	33.50 ± 0.66	0.652
Legs yield (%)	22.90 ± 0.34	23.30 ± 0.27	0.363
Giblets (%)	5.74 ± 0.18	7.90 ± 0.16	0.001
Abdominal fat (%)	7.35 ± 0.42	4.13 ± 0.32	0.001
pH_{24}	5.78 ± 0.02	5.74 ± 0.05	0.535
IMC (μg/mg of lyophilized muscular tissue)	10.99 ± 0.23	11.58 ± 0.37	0.185
HLP (mol/mol of collagen)	0.144 ± 0.008	0.119 ± 0.005	0.008

[1]pH_{24} = pH after refrigeration period (24 h at 4°C); IMC = intramuscular collagen; HLP = hydroxylysylpyridinoline.

Table 4. Least squares means and SE for BW, slaughter traits, pH, and intramuscular collagen properties of pectoral muscle from Japanese quails of F_2 generation

	Group		
Item[1]	Male	Female	*P*-value
n	84	152	
Final BW (g)	164.0 ± 2.60	195.8 ± 1.80	0.001
Carcass weight (g)	108.86 ± 1.64	114.4 ± 1.12	0.003
Carcass yield (%)	66.77 ± 0.37	58.49 ± 0.25	0.001
Breast yield (%)	32.37 ± 0.50	32.35 ± 0.34	0.610
Legs yield (%)	22.48 ± 0.37	22.15 ± 0.25	0.195
Giblets (%)	6.38 ± 0.16	8.43 ± 0.11	0.001
Abdominal fat (%)	5.73 ± 0.30	4.30 ± 0.21	0.001
pH_{24}	5.69 ± 0.01	5.62 ± 0.01	0.001
IMC (μg/mg of lyophilized muscular tissue)	9.69 ± 0.18	9.37 ± 0.12	0.799
HLP (mol/mol of collagen)	0.219 ± 0.012	0.221 ± 0.012	0.907

[1]pH_{24} = pH after refrigeration period (24 h at 4°C); IMC = intramuscular collagen; HLP = hydroxylysylpyridinoline (n = 22 males and 22 females).

and hatch 2), whereas an increase of collagen maturation (HLP/collagen) with $F_0 < F_1 < F_2$, in both males and females, was apparent; however, the HLP values significantly ($P < 0.01$) differed only between F_2 and the other 2 generations.

Genotypic Data

The effective number of alleles in the parental generation ranged from 1.0 in monomorphic loci GUJ0063 and GUJ0095 to 4.57 in the most polymorphic locus GUJ0077. All of the analyzed marker loci were characterized by a lower effective number of alleles compared with the total number of alleles. According to Botsein's scale (1980), classifying the level of informativeness of the markers based on polymorphic information content (**PIC**) values, 13 microsatellite markers were characterized by a high level of variation (PIC >0.5) and 11 markers by a moderate level of variation (0.25 < PIC < 0.5). Markers GUJ0063 and GUJ0095 (monomorphic loci) and GUJ0064, GUJ0084, and GUJ0073 are classified as low informative (PIC < 0.25).

QTL Results

Two statistically significant ($P < 0.05$) QTL were detected on quail chromosome 2. First, QTL with additive effect (0.50) for intramuscular collagen was detected at 39 cM in the marker bracket GUJ0037 and GUJ0093. Figure 3 presents test statistic and additive effect plot of this QTL. Second, QTL with additive (1.32) and dominant (1.91) effects for breast-muscle weight was detected at 163 cM in the marker bracket GUJ0084 and GUJ0073. Figure 4 presents test statistic and both effects (additive and dominant) of this QTL.

DISCUSSION

Performance and Carcass Traits

The results of growth and slaughter traits observed in the present study, comparing meat line and egg line (F_0 generation), agree with the findings of Boon et al. (2000) and Maiorano et al. (2009), who reported significant differences in BW gain, carcass weight, and carcass yield between fast growing Japanese quails bred for meat production (broilers) and normal growing ones bred for egg production (layers): broilers grew faster than layers. The carcass yield values found in the present study are higher (+7.72% and +2.54% for meat and egg type, respectively) than those found in quails of 35 d old (Maiorano et al., 2009) and in quails of 45 d old (Caron et al., 1990); these latter authors reported a lighter increase in carcass yield with an increase in mean BW of Japanese quails. A comparable carcass yield was reported by Attia et al. (2013) for 84-d-old quails (males and females) of the same breed, as well as for giblets percentage. The breast-muscle yields, not affected by genotype, were similar to those found by Al Daraji et al. (2011) for 20-wk-old Japanese quail fed with different dietary fat.

The significantly higher abdominal fat percentage measured in meat type (+5%) was also reported by Genchev et al. (2005), who observed that the content of abdominal fat is significantly higher in the Pharaoh breed (specialized for meat production) than in the White English breed (good for meat and egg production). Abdominal fat is being regarded as the main source of waste in poultry and it is highly correlated (0.6 to 0.9) with the total carcass fat; it is used as the main criterion reflecting excessive fat deposition in birds (Chambers, 1990).

Ultimate pH values, lower in meat type than that of egg type, are close to the normal values for breast muscles in broiler chickens (Maiorano et al., 2012). It is well known that the ultimate pH of the muscle is an important contributing factor to meat quality expressed as tenderness, color, and storage live (Van Laack et al., 2000). Differences in pH could be due to the variation in muscle glycogen content (Berri et al., 2005). However, ultimate pH value is also dependent on the antemortem stress, type of breed, and the genetic variation within breeds (Terlouw, 2005).

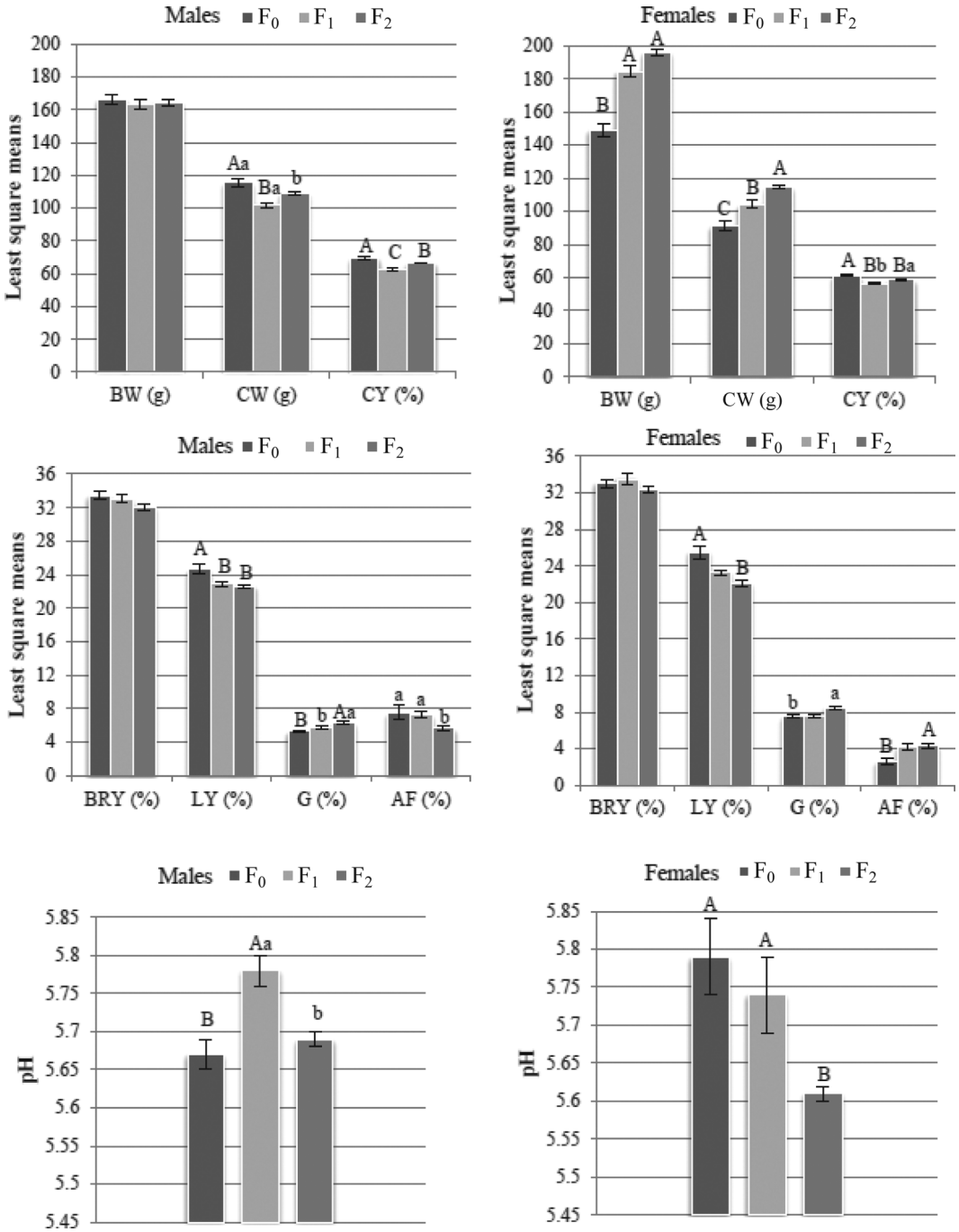

Figure 1. Least squares means and SE for BW, slaughter traits, and pH of Japanese quail males and females of F_0, F_1, and F_2 generations. CW = carcass weight; CY = carcass yield; BRY = breast yield; LY = legs yield; G = giblets; AF = abdominal fat. A, B, C: $P < 0.01$; a, b: $P < 0.05$.

The analyzed data from the F_1 cross-breed between the 2 genetic lines (meat and egg) show an evident sexual dimorphism, and an additional effect could be due to hybrid heterosis. In fact, the females had greater final live weight (+13.2%) and giblets percentage (+2.16%), whereas the males had higher carcass yield and abdominal fat percentage. However, the effect of sex on slaughter and carcass characteristics is well known in quail (reviewed in Alkan et al., 2013). Large reproductive organs in females, such as ovary and oviduct, and heavier liver are the main reason behind lower carcass yield in females (Lotfi et al., 2011; Sari et al., 2011). The lower abdominal fat shown from females, which is consistent with other studies (Banerjee, 2010, quails of 50 d old; Alkan et al., 2013, quails of 5 wk old), may be attributed to the fact that the abdominal fat occupies space that would otherwise be available for the development of the yolk needed for egg production (Banerjee, 2010). Furthermore, Le Bihan-Duval et al. (1998) reported that the differences in fatness between sexes are due to the greater competition between males, different nutritional requirements, and greater effects of hormones on fatness. The abdominal fat values, found in the present study, are higher than those obtained

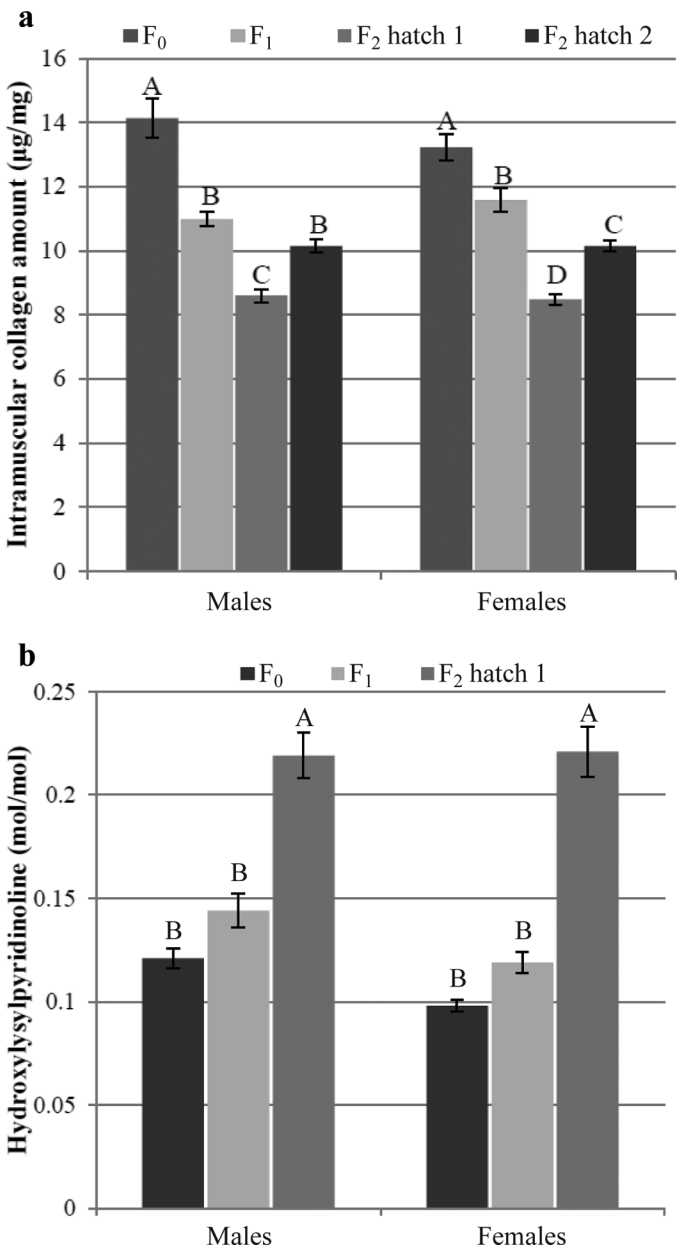

Figure 2. Least squares means and SE for intramuscular collagen amount (a) and hydroxylysylpyridinoline concentration (b) of pectoral muscle from Japanese quail males and females of F_0, F_1, and F_2 generations; A, B, C, D: $P < 0.01$.

by Banerjee (2010) in Japanese quails slaughtered at 50 d of age (4.04 and 0.75% for males and females, respectively); the same can be attributed to the genetic makeup of the strain and also due to different age or better nutritional regimen (reviewed in Crespo and Esteve-Garcia, 2002). That fact is of great importance for the modern quality and dietary assessment of quail meat. Consumers' preferences are an important argument in developing the strategies of modern poultry breeding, influencing the choice of breeds and hybrid combinations for fattening, as well as the methods and duration of the fattening period (Genchev et al., 2005).

The analyzed data from F_2 cross-breed, obtained from males and females of the F_1 generation, had the

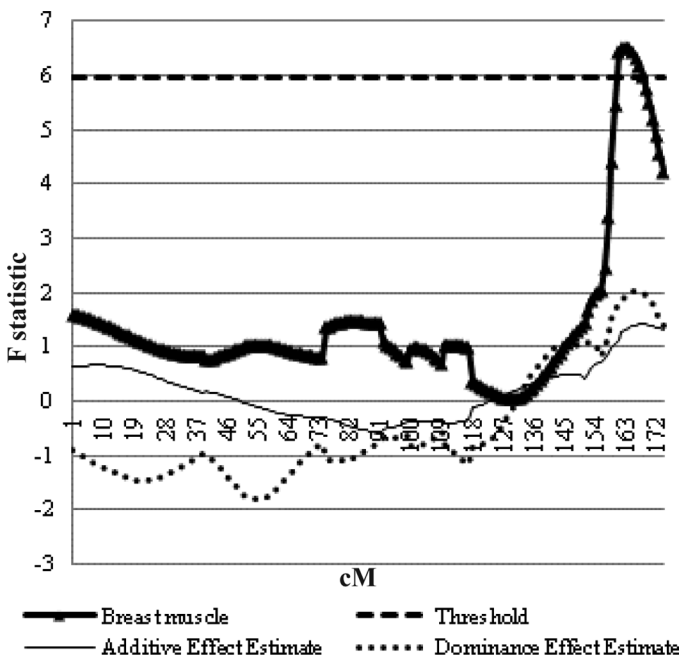

Figure 3. Test statistic for CJA02 with regard to breast muscle under line cross analysis model F_2 cross between Pharaoh (F-33) meat-type males and Standard (S-22) laying-type females population. The solid curve with triangles describes the test statistic, and the dashed flat line indicates threshold. The dotted curve indicates QTL dominant effect; the solid curve shows QTL additive effect.

same trend as in the F_1 generation, with a more marked sexual dimorphism. In the present study, we did not observe any effect of the hatch on growth, carcass traits, and pH. These results disagree with those reported in literature (Vali et al., 2005; Lotfi et al., 2011). Vali et al. (2005) observed that quails of fourth hatch at 35,

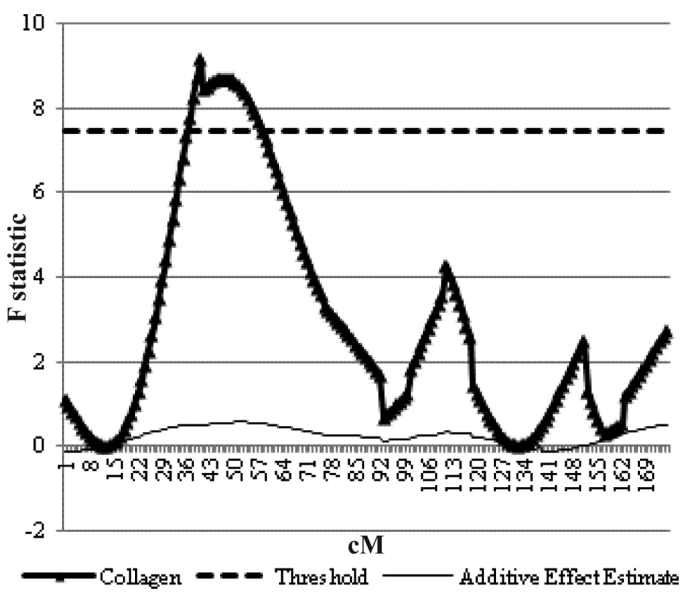

Figure 4. Test statistic for CJA02 with regard to intramuscular collagen under line cross analysis model F_2 cross between Pharaoh (F-33) meat-type males and Standard (S-22) laying-type females population. The solid curve with triangles describes the test statistic, and the dashed flat line indicates threshold. The solid curve shows QTL additive effect.

42 and 49 d of age were heavier than those of previous hatches. Lotfi et al. (2011) reported that hatch has a significant effect on growth and carcass traits in Japanese quail at 42 and 91 d of age. The authors observed that the mean values of studied traits were higher in birds with older mothers than in those with younger mothers. Older hens compared with younger ones lay larger eggs that hatch into larger chickens, and egg weight and hatching weight of chickens is correlated to final BW and carcass traits (Peebles et al., 1999). Our inconsistent results with the literature may be due to the short period between the 2 hatches (14 d) and to the age of the mothers that was almost similar.

The comparison of performance traits among the 3 generations (Figure 1) showed an evident phenotypic variation. The cross between 2 genetically distant lines as well as the cross between full siblings hybrids did not influence the BW of hybrid males but had a negative effect on their carcass weight. Instead, hybrid females were heavier than females of parental line (S-22): F_1 hybrids had an increase of BW of 23.9%, whereas F_2 showed an increase of 31.4%. Also the carcass yield was negatively affected by first- and second-generation crosses. Legs and giblets percentage were also affected by crosses, but no significant influence was observed on the breast yield. However, the breast weight (data not showed) was lower in both F_1 and F_2 males than in males of parental line (33.78 ± 0.73 g and 34.74 ± 0.38 g vs. 38.53 ± 0.64 g, respectively; $P < 0.01$). Conversely, the breast weight of F_1 and F_2 females was heavier compared with S-22 females (34.88 ± 0.91 g and 36.87 ± 0.52 g vs. 30.06 ± 0.79 g, respectively; $P < 0.01$). Hybrid combinations increased the abdominal fat percentage in F_2 females (+1.7%), whereas it decreased in F_2 males (−1.83%). Excessive fat has been recognized as an undesirable correlate of selection for rapid growth and high live BW (Deeb and Lamont, 2002). These results therefore provide evidence of a markedly positive heterosis in the F_2. The present findings are partially consistent with Deeb and Lamont (2002), who found a high level of heterosis only for the abdominal fat percentage in the F_2 chicken population. As suggested by Sohrabi et al. (2012), a possible explanation for the higher level of heterosis in the F_2 generation might be related to the genetic structure of the F_2 birds as regards the sex chromosomes.

Ultimate pH of breast muscle was different among the 3 experimental groups, ranged from 5.61 to 5.79. However, contradictory data regarding pH exist. Narinc et al. (2013) and Genchev et al. (2008) reported higher pH values (5.94 and 6.17, respectively). Genchev et al. (2008) suggest that the main reason behind the high pH values found in quail breast muscle were due to the morphology of muscle, which is mostly composed by aerobic-red muscle fibers. On the contrary, other studies (Remignon et al., 1998; Ribarski and Genchev, 2013), according to our findings, reported low ultimate pH value. Nevertheless, poultry meats with ultimate pH between 5.7 and 6.1 are called normal and do not reveal any quality problems (Zhang and Barbut, 2005; Zhang et al., 2005).

IMC Properties

Meat is a complex, composite substance. It consists of myofibers, connective tissue, and lipids. It has been established that collagen, the major component of the intramuscular connective tissue, plays a key role in determining the background toughness of meat from different domestic animals, including birds (reviewed in Maiorano et al., 2012). Furthermore, a marked difference in collagen maturity could affect meat tenderness (McCormick, 2009; Maiorano et al., 2011, 2012) and technological yield (Boutten et al., 2000). The results of IMC properties showed a similar collagen content (μg/mg) of the breast muscle between the 2 lines (F-33 and S-22), whereas a higher degree of collagen maturation (mol of HLP/mol of collagen) was found in the meat-type quails. These findings are in contrast with the results of Maiorano et al. (2009, 2011), who reported no effect of genetic lines on intramuscular collagen properties in the breast muscle of young quails.

The comparison among the 3 generations showed evident differences in the IMC properties of the breast muscle in both males and females (Figure 2). No information is available from current literature on the effect of sex or hatch on IMC properties in quails. Differences in collagen content and maturity between the sex of animals, attributed to hormonal effect, has been reported in findings on pork, beef, lamb, and deer (reviewed in Maiorano et al., 2013). However, the question of sex differences in terms of IMC seems to vary with species. Differently, it is not easy to explain the higher amount of IMC found in quails of hatch 2 (+18.85%) compared with those of hatch 1. Although, according to Laurent et al. (1978), this trend could reflect the relationship between the synthesis of total muscle protein and intramuscular collagen synthesis; in fact, we found a positive correlation between muscle total protein (data not published) and IMC amount ($r = 0.193$; $P < 0.01$).

In general, HLP values were inversely proportional to the amount of collagen (Maiorano et al., 2009). The steady increase in mature collagen crosslinking is due to progressive and ongoing crosslinking reactions that occur within fibrillar collagen with the slowing of collagen synthesis rates as animals reach maturity. Less collagen synthesis and turnover provide existing fibrillar collagen time to progressively crosslink or mature (McCormick, 1994).

The quality of collagen gives toughness to the meat (Corò et al., 2003). Lepetit (2007) analyzed various studies in which collagen crosslinks in muscle tissue were measured. He suggested that measurement of crosslinks (pyridinoline) is a reasonable predictor of tenderness. According to HLP crosslinks values, the meat produced from F_0, F_1, and F_2 could be different in background toughness. In other words, results of HLP crosslink indicate that meat from F_0 quails could be more tender

than that from the F_1 and F_2 groups and that from F_2 quails could be tougher than that from F_1 quails. The comparison between the IMC properties of the present study and those reported by Maiorano et al. (2011) for pectoral muscle of Japanese quail (meat line and egg line) and for other quail breeds, slaughtered at 35 d old, revealed that the collagen content in the muscle of quails used in this study is lower (maybe because of a slower collagen synthesis), and on the contrary, the average of collagen maturation (0.146 and 0.161 HLP/collagen for females and males, respectively) is comparable to the degree of collagen stability observed in the above-mentioned birds.

Moreover, values for collagen content (ranging from 8.48 to 14.14 μg/mg) and HLP crosslinks (ranging from 0.098 to 0.221 mol of HLP/mol of collagen) are lower and higher, respectively, to the values reported in pectoral muscle of 6-wk-old control broiler chicken (Ross 308; Maiorano et al., 2012). It is known that collagen synthesis and maturation differ between species, muscles, bird age, growth rate, and management practices (McCormick, 1994; Purslow, 2005).

QTL Results

The QTL for intramuscular collagen is the very first report of a QTL in quail and other poultry species for this trait. Intramuscular collagen is composed mainly of different proportions of type I and type III collagen. When proportions of types I and III collagen from different muscles have been compared, increased proportions of type III collagen have been associated with, in some cases, diminished tenderness or in others with increased tenderness (McCormick, 2009; reviewed in Maiorano et al., 2011). A single report of QTL for collagen content concerns limousine cattle. This QTL has been detected on BTA2 and is attributed to myostatin gene (Lines at al., 2009). Quail linkage maps contain mostly microsatellite (Kayang et al., 2004) and amplified fragment length polymorphism markers (Roussot et al., 2003). Therefore, to look for biological and positional candidate genes we have used alignments of Japanese quail microsatellite and amplified fragment length polymorphism maps linked to assembled chicken sequence (Kayang et al., 2006). A QTL region linked with intramuscular collagen in the quail experimental population shows synteny with chicken chromosome 2 (GGA2, region: 14.8–46.4 Mbp). The most probable candidate gene in this region is *COL1A2* (LOC396243), collagen type I α 2, chain precursor. According to Gene Cards (www.genecards.org), this gene encodes the pro-alpha2 chain of type I collagen whose triple helix comprises 2 alpha1 chains and one alpha2 chain. Type I is a fibril-forming collagen found in most connective tissues. The *COL1A2* gene has been reported in other studies in chicken (Sun et al., 2013) and pig (Lobjois et al., 2008; Li et al., 2010). Sun et al. (2013) proposed *COL1A2* as a candidate gene for meat color lightness based on the association study of a single SNP located 58.0 Kb away from the collagen type I α 2 gene. However, in the study by Sun and coauthors, intramuscular collagen was not included on the list of meat quality traits. Lobjois et al. (2008) proposed *COL1A2* as a positional and biological candidate gene for meat tenderness in the study of complex traits in pig. A QTL for intramuscular collagen is in agreement with differences in phenotypic values between 2 parental lines (Table 2). A positive value for the additive effect implies that the Pharaoh (F-33) meat-type male parent allele results in an increase in phenotype. Lack of QTL for other traits (final BW, carcass yield, giblets, abdominal fat) under the study in current experimental cross might be explained by the limited number of chromosomes genotyped.

To our knowledge, QTL for breast weight is the very first report of such a QTL in Japanese quail. There are 3 QTL for breast-muscle weight reported on chicken chromosome 2 (Chicken QTL database); however, their location does not agree with comparative region between quail and chicken genomes. The higher dominant compared with additive effect for this QTL suggests that heterozygous individuals have bigger breast-muscle weight.

In conclusion, the present study describes new data regarding 3 generation cross of 2 types (meat line and egg line) of Japanese quail with respect to analysis of carcass and meat quality traits, and QTL study for IMC and breast-muscle weight. Our results provide evidence of a marked positive heterosis in the F_2. Observed effect might be a parent of origin sex chromosome effect, which cannot be fully investigated due to experimental design and which did not account for a reciprocal cross. According to HLP crosslinks values, the meat produced from F_0, F_1, and F_2 could be different in background toughness. Further research is warranted to increase knowledge regarding the effect of different lines (meat-type and egg-type quails), cross (meat-type × egg-type quails; $F_0 \times F_1$), and sex (males and females) on growth performance, carcass traits, and IMC properties in adult Japanese quails.

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