Identification of quantitative trait loci affecting production and biochemical traits in unique Japanese quail resource population

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ABSTRACT The objective of the current study was to identify QTL associated with body weight, growth rate, egg quality traits, concentration of selected blood plasma, and yolk lipids as well as concentration of selected macro- and microelements, color, pH, basic chemical composition, and drip loss of breast muscle of Japanese quail (*Coturnix japonica*). Twenty-two meat-type males (line F33) were crossed with twenty-two laying-type females (line S22) to produce a generation of F_1 hybrids. The F_2 generation was created by mating 44 randomly chosen F_1 hybrids, which were full siblings. The birds were individually weighed from the first to eighth week of age. At the age of 19 wk, 2 to 4 eggs were individually collected from each female and an analysis of the egg quality traits was performed. At slaughter, blood and breast muscles were collected from 324 individuals of the resource population. The basic chemical composition, concentration of chosen macro- and microelements, color, pH, and drip loss were determined in the muscle samples. The concentration of chosen lipids was determined in egg yolk and blood plasma. In total, 30 microsatellite markers located on chromosome 1 and 2 were genotyped. QTL mapping including additive and dominance genetic effects revealed 6 loci on chromosome 1 of the Japanese quail affecting the egg number, egg production rate, egg weight, specific gravity, egg shell weight, concentration of Na in breast muscle. In turn, there were 9 loci on chromosome 2 affecting the body weight in the first, fourth, and sixth week of age, growth rate in the second and seventh week of age, specific gravity, concentration of K and Cu in breast muscle, and the levels of triacylglycerols in blood plasma. In this study, QTL with a potential effect on the Na, K, and Cu content in breast muscles in poultry and on specific gravity in the Japanese quail were mapped for the first time.

Key words: Japanese quail, quantitative trait loci, production trait, microsatellite marker

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INTRODUCTION

The Japanese quail (*Coturnix japonica*) was domesticated and improved given its usability values as a producer of eggs and meat (Crawford, 1990). Due to their unique taste and nutritional value, these products are an important element of diet in many countries, whereas in other regions, they are regarded as a complementary "niche" food. The quail is characterized by rapid alternation of generations, small body size, high variability of some biological traits, high egg production (a great number of offspring), and lower susceptibility to diseases than that in the domestic chicken. Therefore, it has been recognized as an experimental animal and pilot species in genetic, physiological, biomedical, embryological, and behavioral research (Cheng and Kimura, 1990; Tsudzuki, 2008). However, in recent years, the domestic chicken, which exhibits close phylogenetic relatedness with the Japanese quail, has become a model species in genetic and molecular investigations of poultry (Burt, 2007; Cogburn et al., 2007). Both these species have a similar length of the genomes (1.2×10^9 base pairs) and an identical number of chromosomes ($2n = 78$). There are also similarities between these species in terms of the morphology of chromosomes. Fluorescence in situ hybridization studies have demonstrated high similarity in the gene order in the quail and domestic chicken (Shibusawa et al., 2001). This was confirmed by the results reported by Kayang et al. (2006), who showed a high similarity in the arrangement of microsatellite markers in analogous chromosomes of both species. The structural differences observed so far are small and limited to only a few chromosomes (Ryttman and Tegelström, 1981; Sasaki, 1981; Stock and Bunch, 1982; Shibusawa et al., 2001; Sasazaki

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et al., 2006; Recoquillay et al., 2015). Since the genome of the Japanese quail has been poorly explored, the species cannot compete with the domestic chicken as a model poultry species in molecular research; nevertheless, genetic analyses of the quail may provide valuable complementary data for investigations of chickens. This is possible due to the creation of special breeding or laboratory Japanese quail lines selected for specific traits, which have no counterparts in chickens. This can be illustrated by divergently selected lines for the duration of tonic immobility (Mills and Faure, 1991) and used for e.g. mapping of QTL that determine production traits and various forms of behavior (Beaumont et al., 2005; Minvielle et al., 2005; Frésard et al., 2012; Recoquillay et al., 2015). Another example is the quail line used in this study (line S22), which was selected for 18 generations towards a high concentration of total cholesterol in egg yolk (Baumgartner et al., 2008) as well as genetic lines bearing various mutations (Tsudzuki, 2008). These lines can be used, e.g., to complete the information about the localization of QTL, and further—genes, with a potential effect on traits that have not been analyzed either in the Japanese quail or in the domestic chickens. Currently, the ChickenQTLdb database comprises 7812 QTLs/associations from 273 publications and determining 380 different phenotypic traits in the domestic chicken. In the case of the Japanese quail, there are only 16 publications on identification of QTL for behavioral, production, and physiological traits (Beaumont et al., 2005; Minvielle et al., 2005, 2006; Esmailizadeh et al., 2012; Frésard et al., 2012; Sohrabi et al., 2012; Ahmadi et al., 2014; Charati et al., 2014; Moradian et al., 2014; Ori et al., 2014; Rezvannejad et al., 2014; Tavaniello et al., 2014; Recoquillay et al., 2015; Beck et al., 2016; Moradian et al., 2016; Nasirifar et al., 2016).

The objective of the current study was to identify QTL on Japanese quail chromosomes 1 and 2 based on the resource population formed by crossing quails from a non-selected meat-type line with a unique layer line, which has no counterpart in the domestic chicken (a high concentration of egg yolk cholesterol). Another aim was to compare and complement the findings of QTL identified in the domestic chicken.

MATERIALS AND METHODS

Resource Population

Two divergent lines (meat-type and laying-type) bred and reared at the Didactic Experimental Station of the University of Life Sciences in Lublin (Poland) were used in the experiment. Forty-four quails (generation F0), 22 Pharaoh (line F-33) meat-type males and 22 Standard (line 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 in 2 hatches. The meat-type line was not selected. The egg-type line was selected previously over 18 generations for high yolk cholesterol content. The lines and experimental population has been described in detail elsewhere (Maiorano et al., 2011; Tavaniello et al., 2014). In terms of the number of the analyzed phenotypic traits, the resource quail population is unique on a world scale. In total, 236 quails (both sexes) of the F_2 generation were produced in 2 successive hatches and used for QTL detection analyses. More details on the housing conditions of the experimental birds are given by Tavaniello et al. (2014). The quails were fed ad libitum commercial diets according to the age. A 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 and was used until the seventh week of age. During the production period, the birds were fed a diet containing 21% CP and 2,800 kcal of ME/kg. The birds had free access to water during the experiment. The animal care and experimental procedures were in accordance with Polish and European regulations. All procedures were approved by the Local Ethical Commission for Animal Experiments in Lublin (permit number 50/2009).

Phenotypic Data

Body weight (**BW**) was measured weekly from the first up to eighth week of age. The growth rate (**GR**) was calculated between 2 consecutive BW measurements. The age of the first egg (**ASM**) and the number of eggs laid until 20 wk of age (**EN**) were individually recorded. The egg production rate (**EPR**) was calculated as well. At 19 wk of age, another 2 to 4 eggs were collected from each laying female and the egg weight (**EW**) in air and water was determined. This facilitated calculation of egg specific gravity (**SG**) using Archimedes' principle. The measurements were carried out using a WPS 1200/C electronic scale recording suspended materials (RadWag, Radom, Poland). Breaking strength (**BS**) was determined using the Instron Testing Machine Instrument Model Mini 55 (Instron Ltd, High Wycombe, UK). The measurements of yolk weight (**YW**), egg shell weight (**SW**), Haugh units (**HU**), and egg shell thickness (with internal shell membranes-**EST**) were performed with semi-automated egg quality assessment equipment (TSS-Technical Services and Supplies, York, UK). It was composed of a microprocessor (EQM+), two electronic scales (NavigatorXT model AV8101CM from Ohaus Corporation, Pine Brook, NJ, USA and KERN 440–49 from KERN & Sohn, GmBH, Balingen, Germany), a device for measurement of the thick albumen height (QCH), and a micrometer screw (QCT). Haugh units were automatically calculated by the EQM+ microprocessor. Albumen weight (**AW**) was calculated as the difference between the egg weight and the yolk and shell weight. Additionally, the shell (**S%**), yolk (**Y%**), and albumen (**A%**) percentages in the total egg weight were calculated. The quality analysis was carried out on the day the eggs were laid. All egg traits

analyzed represented the average measurement value of two to four eggs per female. The yolks collected during the egg quality analyses were determined for total cholesterol (**CHy**) and triacylglycerol (**TGy**) levels. Lipids were extracted from a 1-g yolk aliquot with the use of a chloroform: methanol mixture according to the method proposed by Washburn and Nix (1974). At 20 wk of age, the quails were individually weighted (after a fasting period of 12 h), stunned, and decapitated according to the EU regulations on the protection of animals at the time of killing (European Communities, 2009). At slaughter, peripheral blood was collected from the jugular vein for DNA extraction and biochemical analyses. Blood sampled for the biochemical analyses was centrifuged at 3,000 rpm for 5 min to separate the plasma from morphotic components. Plasma was transferred to separate tubes. Total cholesterol in blood plasma (**CHp**) and egg yolk was determined using a Liquick Cor–CHOL kit (Cormay, Lublin, Poland). The HDL fraction (**HDLp**) was quantified with a Cormay-HDL kit (Cormay, Lublin, Poland) and triacylglycerol levels in the plasma and egg yolks were assessed with a Liquick Cor-TG kit Cormay, Lublin, Poland) according to the manufacturer's instructions and with the use of a Genesys 10S Vis spectrophotometer (Thermo Fisher Scientific, Madison, WI, USA). The measurements of each sample were carried out in triplicate and the mean was calculated. At slaughter, breast muscles (pectoralis superficialis muscle) were excised and the CIE $L^*a^*b^*$ color indices of the inner surface of the muscle were determined using the Minolta CR-310 Chroma Meter (Minolta Co., Ramsey, NJ). Wide-angle illumination (wide-area illumination), 0° projection angle, and a 50-mm measuring area were used in the measuring head. The meter was calibrated using a white CR-A44 calibration plate. The results are expressed in the CIE color space, where $\mathbf{L}^*$—lightness; $\mathbf{a}^*$—red-green color; $\mathbf{b}^*$—yellow-blue color, **h°**—hue, and $\mathbf{C}^*$—chroma. Further determinations included analyses of the pH of the muscles (**pH1** and **pH4** after 1 and 4 h post slaughter, respectively) with the use of a portable CP-251 pH meter (Elmetron, Zabrze, Poland), drip loss 24 h post slaughter ($\mathbf{DL_{24}}$), total protein content (**PC**) with the Kjeldahl method, dry mass content (**DMC**), and ash content (**AC**). After incineration of the breast muscle samples, the contents of ash (0.25 mg), four macroelements (**Na**, **K**, **Mg**, and **Ca**), and two trace elements (**Fe** and **Zn**) were determined with the use of an atomic absorption spectrophotometer. The analyses of the basic chemical composition and macro- and microelements content of muscles were performed at the Central Laboratory of Agro-ecology of the University of Life Sciences in Lublin.

DNA Extraction and Genotyping

DNA was isolated from blood cells with the use of a QIAamp DNA Blood Mini Kit (Qiagen GmbH, Hilden, Germany) in accordance with the manufacturer's instructions. The DNA quality was determined electrophoretically in 1% agarose gel with ethidium bromide (0.5 μg/mL). Electrophoresis was carried out in 1× TBE buffer at 70 V for 60 min. Gels were visualized in UV light and archived with ScionImage software (Syngen Biotech, Wroclaw, Poland). DNA purity and concentration were determined spectrophotometrically (absorbance at a wavelength of 260 nm and 280 nm) with the use of a BioPhotometer (Eppendorf, Hamburg, Germany). The resource population quails were genotyped using 30 microsatellite markers located on chromosomes 1 and 2. Full characterization of the analyzed microsatellite markers was presented in a previous study by Tavaniello et al. (2014). The PCR reaction was carried out in a MJ Research PTC-225 Tetrad thermocycler (MJ Research, San Diego, CA) with the use of fluorescent dye-labeled primers: 6-FAM, VIC, NED (Applied Biosystems, Foster City, CA). The PCR mixture was as follows: 100 mM Tris-HCl (pH 8.9), 20 mM MgCl2, 500 mM KCl, deoxynucleoside triphosphate, 20 ng of DNA, 0.25 U of AmpliTaq GOLD 360 DNA Polymerase (Applied Biosystems, Foster City, CA), and primers (0.2 to 0.75 pmol). The PCR reaction profile was as follows: denaturation 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). The PCR products were subjected to electrophoresis on 4% polyacrylamide gel (POP4) using an ABI Prism 3100-*Avant* Genetic Analyzer (Applied Biosystems, Foster City, CA). Marker scoring was performed with 2 types of software: 3100-*Avant* Abi Prism Data Collection and Gene Mapper v. 3.5 (Applied Biosystems, Foster City, CA). Allele length was analyzed based on internal size standard Gene-Scan-350 (Applied Biosystems, Foster City, CA) with nucleotide sizes 35, 50, 75, 100, 139, 150, 160, 200, 250, 300, 340, and 350 bp.

Statistical Analysis

Descriptive statistics (mean, standard deviation, coefficient of variation, minimum and maximum values) for the phenotypic data were calculated and one- or two-way ANOVA was performed using a statistical package SAS v. 9.3 (SAS Institute Inc., Cary, NC).

QTL Analysis

Regression interval mapping was used for QTL detection. Analyses were performed with web-based GRID QTL software (Seaton et al., 2006; Hernández-Sánchez and Knott, 2009) and a 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 (# Bootstrap sampling = 500). The hatch and sex of birds were considered as fixed effects. The line-cross model included additionally additive and dominance genetic effects. As far as the permutation and Bonferroni corrections are concerned, we followed the recommendations presented by van Kaam et al. (1998). These authors stated that permutation threshold might be considered to be an alternative to Bonferroni correction. In their publication, both tests (Bonferroni, permutations) were applied to the data. On average the significance thresholds obtained from both tests were similar.

RESULTS AND DISCUSSION

The assessment of 54 phenotypic traits involved 236 birds from the second hybrid generation—F_2. The values of the basic descriptive statistics of all analyzed phenotypic traits of individuals of the F_2 generation are presented in Table 1.

The results of the QTL mapping with additive effects on the chromosomes (CJA01, CJA02) of the Japanese quail are shown in Table 2. The profiles of the QTL detected for the analyzed traits are presented in Figures 1 and 2. In the model including additive effects, 12 QTL were identified: 6 on chromosome CJA01 and 6 on chromosome CJA02. The results of the QTL analysis including dominance and additive effects for chromosomes CJA01 and CJA02 are shown in Table 3. The profiles of QTL for the analyzed traits localized on these chromosomes are presented in Figures 3 and 4. The model employed allowed identification of 7 QTL with a potential effect on the analyzed traits. In the case of other traits, the values of test statistics did not exceed threshold values at the lowest possible significance level of 5%.

Significant QTL for BW1, BW4, BW6, GR2, and GR7 were detected on chromosome CJA02. Positive additive effects were noted for BW1, BW4, BW6, and GR2 and negative effects were found for GR7. In the case of QTL with a negative additive effect, it can be assumed that QTL alleles associated with the respective trait were inherited by the F_2 generation from a parent characterized by a low level of this trait, which resulted in its reduced value in the offspring as well. The presence of QTL for the body weight on chromosome 2 in the initial period of birds' life was demonstrated by Minvielle et al. (2005), who identified a significant ($P \leq 0.05$) QTL for body weight at the fifth week of age. The QTL was mapped at position 54 cM between markers GUJ0063 and GUJ0027. Similarly, Rezvannejad et al. (2014) indicated the presence of QTL for body weight on the hatching day and at 4 wk of age at position 60 cM on CJA02.

The presence of QTL on chromosome 2, which may affect body weight in the first weeks of bird's life, was also confirmed by studies carried out on a species closely related evolutionally with the Japanese quail—the chicken (*Gallus gallus domesticus*). The chicken QTLdb database (Hu et al., 2016) comprises all available information about QTL/associations between the value of the trait identified in the domestic chicken. Currently, 42 of the 553 QTLs identified on chromosome GGA02 are known to be associated with BW measured at 1, 2, 3, 4, 5, 6, 7, and 8 wk of age (Carlborg et al., 2003; Zhou et al., 2006; Atzmon et al., 2007, 2008; Le Rouzic et al., 2008; Ambo et al., 2009; Ou et al., 2009; Terčič et al., 2009; Uemoto et al., 2009; Ankra-Badu et al., 2010; Liu et al., 2012; Podisi et al., 2013; Sheng et al., 2013; Goor et al., 2015; Jin et al., 2015; Nassar et al., 2015; Lien et al., 2017). The QTL identified previously have been found to form two major clusters: the first cluster comprises QTL mapped in the initial part of the chromosome between 0.0 and 120 cM and the other one contains QTL mapped at positions 226 to 395 cM. In the first cluster, 19 loci determining BW at 1, 2, 3, 4, 6, and 8 wk of age have been mapped, while 20 QTLs with a potential effect on BW between 2 and 8 wk of age have been mapped in the other cluster.

In the present study, the QTL associated with BW measured at 1, 4, and 6 wk of age were noted for the initial region of the chromosome between 0 and 15 cM. These results are in agreement with those reported by Atzmon et al. (2008), who identified a significant QTL at position 6 cM on chromosome GGA2 determining chicken body weight at 3 wk of age. In turn, Liu et al. (2012) mapped a locus of the GHRHR gene (Growth Hormone-releasing Hormone receptor) at position 1.7 cM. Analyses of the polymorphism of this gene revealed 3 SNPs in the promoter region, which had a significant effect on BW at 7, 9, 11, 13, and 17 wk of age (Liu et al., 2012).

To date, there have been no studies showing the presence of QTL for the growth rate during the rearing period (1 to 8 wk of life) on CJA02 of Japanese quail. However, their presence has been confirmed by studies conducted on chicken. So far, 11 QTLs for the growth rate between the 1st and 70th day of chicken's life has been mapped on GGA02 (Carlborg et al., 2003; Kerje et al., 2003; Carlborg et al., 2004; Zhou et al., 2006; Nassar et al., 2015).

In the present study, no significant QTL for body weight during the first weeks of life were found on chromosome CJA01. In turn, the investigations conducted by other authors show the presence of a significant genome-wide QTL on CJA01 determining BW at hatching and at the 3rd, 4th, 5th, 6th, 9th, and 70th week of bird's age (Minvielle et al., 2005; Esmailizadeh et al., 2012; Sohrabi et al., 2012; Recoquillay et al., 2015).

Table 1. Basic descriptive statistics of analyzed traits.

Trait type	Trait	Abbreviation	MV[1]	SD	CV	Min[2]	Max[3]
Growth	Body weight (wk/g)	BW1	28.7	4.2	14.5	16	40
		BW2	64.3	6.9	10.7	42	81
		BW3	96.1	9.0	9.4	72	120
		BW4	120.7	11.0	9.1	91	149
		BW5	141.6	15.4	10.9	108	178
		BW6	153.7	18.9	12.3	112	196
		BW7	160.7	20.1	12.5	119	215
		BW8	166.2	20.9	12.5	120	218
	Growth rate (wk/%)	GR2	76.4	7.4	9.7	55.9	97.7
		GR3	39.9	3.7	9.2	30.2	52.6
		GR4	22.6	3.5	15.4	10.4	33.5
		GR5	16.1	4.9	30.6	1.5	27.9
		GR6	7.8	5.1	64.8	−5.2	22.4
		GR7	4.3	4.4	101.9	−5	17.3
		GR8	3.4	2.7	78.3	−0.6	13.3
Egg production	Age at sexual maturity (d)	ASM	53.9	9.7	18.1	43.0	92.0
	Egg number (egg)	EN	40.7	15.2	37.4	0	66.0
	Egg production rate (%)	EPR	58.6	21.5	36.6	0	91.7
Egg quality traits	Breaking strength (N)	BS	9.6	3.3	34.5	1.7	16.7
	Egg weight (g)	EW	11.1	0.8	7.3	8.9	13.0
	Yolk weight (g)	YW	3.6	0.4	10.1	2.6	4.5
	Albumen weight (g)	AW	6.1	0.6	9.2	4.8	7.3
	Egg shell weight (g)	SW	1.47	0.19	13.25	1.0	2.0
	Specific gravity	SG	1.059	0.007	0.698	1.039	1.082
	Albumen height (mm)	AH	3.28	0.92	27.97	1.1	5.4
	Haugh units	HU	82.0	6.0	7.3	64.3	95.4
	Egg shell thickness (μm)	EST	162.3	16.8	10.4	117	203.7
	Yolk percentage (%)	Y%	32.2	2.2	6.7	26.2	38.2
	Albumen percentage (%)	A%	54.8	2.6	4.7	48.6	61.6
	Egg shell percentage (%)	S%	13.2	1.6	11.8	9.3	17.5
	pH 1 h after slaughter	pH1	6.1	0.3	4.6	5.3	6.9
	pH 4 h after slaughter	pH4	5.6	0.1	2.5	5.3	6.1
	Drip loss_{24} (%)	DL_{24}	0.6	0.2	24.2	0.3	1.4
Breast muscle macro- and microelement content	Cu (mg/kg fresh meat)	Cu	5.5	2.7	48.3	1.1	14.9
	Mn (mg/kg fresh meat)	Mn	3.3	2.2	68.0	0.2	8.9
	Fe (mg/kg fresh meat)	Fe	422.0	96.0	22.7	171.1	765.2
	Zn (mg/kg fresh meat)	Zn	18.7	16.0	85.5	5.3	84.8
	K (mg/kg fresh meat)	K	3,284	655.0	20.0	1,400	5,040
	Na (mg/kg fresh meat)	Na	476	75.0	16.0	275.0	714.0
	Ca (mg/kg fresh meat)	Ca	36.6	2.48	68.0	9.6	128.3
	Mg (mg/kg fresh meat)	Mg	305	79.0	26.0	54.0	447.0
Breast muscle basic chemical composition	Protein content (%)	PC	25.5	1.0	4.0	22.0	30.5
	Ash content (%)	AC	1.5	0.1	8.8	1.1	1.9
	Dry matter content (%)	DMC	32.3	2.0	6.2	28.6	41.4
Breast muscle color	L^*	L^*	36.5	2.1	5.7	31.6	42.0
	a^*	a^*	19.8	1.2	6.3	16.2	23.0
	b^*	b^*	1.8	1.0	56.9	−0.2	5.0
	C^*	C^*	19.9	1.3	6.5	16.2	23.4
	h°	h°	5.1	2.7	52.8	0.1	13.3
Plasma lipids content	Total cholesterol (mmol/dl)	CHp	6.7	2.7	40.6	1.4	16.1
	HDL (mmol/dl)	HDLp	2.5	1.4	54.2	0.2	6.2
	Triacylglycerols (mmol/dl)	TGp	9.5	8.0	84.3	0.7	27.2
Yolk lipid content	Total cholesterol (mmol/dl)	CHy	48.2	13.6	28.2	25.8	91.0
	Triacylglycerols (mmol/dl)	TGy	34.8	12.3	35.4	14.1	63.9

[1]MV—mean value.
[2]Min—minimum value.
[3]Max—maximum value.

In this study, a significant chromosome-wide QTL for EN and EPR were detected at position 36 to 42 cM on chromosome CJA01. EPR is calculated based on the EN value, which probably explains the convergence of the QTL locations for these traits and the similar F value. The additive effects contributed to a decline or increase in the value of the EN and EP depending on the model used. The dominance effects of the detected QTL exerted a positive impact on the level of the analyzed traits. In turn, Minvielle et al. (2005) identified a significant QTL on chromosome CJA06 for the number of eggs laid by females up to 69 wk of age. The differences between the investigation results may be related to the different duration of control of the egg production. The results of these investigations are consistent with those obtained by Hansen et al. (2005) and Atzmon et al. (2008), who mapped a significant QTL determining this trait in the domestic chicken (GGA01).

Table 2. Summary of quantitative trait loci obtained from modelling additive QTL effects.

Trait[1]	Chromosome	Position (cM)	CI (cM)	F-value[2]	A[3]	Closest marker
EN	CJA01	41	29 to 59	26.02**	−8.07	GUJ0017
EPR		41	19 to 48	25.35**	−11.22	GUJ0017
EW		4	0 to 243	9.75*	0.03	GUJ0068
SG		7	0 to 160	9.37*	33.67	GUJ0068
SW		114	0 to 165	9.93*	0.11	GUJ0095
Na		113	6 to 295	10.0*	34.91	GUJ0095
BW1	CJA02	9	0 to 174	7.24*	1.31	GUJ0066
BW4		0	0 to 149	9.81*	3.41	GUJ0037
BW6		0	0 to 156	9.18*	5.64	GUJ0037
GR7		44	19 to 174	7.74*	−1.56	GUJ0067
K		157	39 to 159	13.37*	−258.10	GUJ0091
TGp		64	21 to 151	8.93*	−298.0	GUJ0007

[1]EN = egg number; EPR = egg production rate; EW = egg weight; SG = specific gravity; SW = egg shell weight; Na = Na content in breast muscle; BW1 = BW in 1st week of age; BW4 = BW in 4th week of age; BW6 = BW in 6th week of age, GR7 = growth rate in 7th week of age; K = K content in breast muscle; TGp = blood plasma triacylglycerols content.
[2]*F*-value—value of *F* statistics; $^{**}P \leq 0.01$; $^{*}P \leq 0.05$ for chromosome-wide significant QTL.
[3]A—additive QTL effect.

Table 3. Summary of quantitative trait loci obtained from joint modelling of additive and dominance QTL effects.

Trait[1]	Chromosome	Position (cM)	CI (cM)	*F*-value[2]	A[3]	D[4]	Closest marker
EN	CJA01	36	15 to 203	13.42**	7.9	2.85	GUJ0017
EPR		42	28 to 160	12.8**	11.23	2.53	GUJ0017
SG	CJA02	156	0 to 161	5.83*	0.49	55.32	GUJ0091
BW1		15	0 to 174	6.86*	1.27	3.14	GUJ0037
GR2		3	0 to 174	5.68*	0.96	4.72	GUJ0037
Cu		129	0 to 154	7.82*	0.50	3.21	GUJ0084
K		157	0 to 169	7.83*	−259.4	114.3	GUJ0091

[1]EN = egg number; EPR = egg production rate; SG = specific gravity; BW1 = BW in 1st week of age; GR2 = growth rate in 2nd week of age; Cu = Cu content in breast muscle; K = K content in breast muscle.
[2]*F*-value—value of *F* statistics, $^{**}P \leq 0.01$; $^{*}P \leq 0.05$ for chromosome-wide significant QTL.
[3]A—additive QTL effect.
[4]D—dominance QTL effect.

Yuan et al. (2015) identified SNPs associated with the number of eggs laid between 37 and 72 wk of age, which were located between 56.34 and 65.16 Mb on chromosome 1 (GGA01) of the domestic chicken and explained 4.56% of phenotypic variance. One of them was identified in intron 18 of gene KIAA, which has been found to be fused to the BRAF oncogene in many cases of pilocytic astrocytoma in humans. Furthermore, the SNP in GGA01 influenced the number of eggs laid between 21 and 72 wk of age. The presence of QTL determining the laying performance percentage was confirmed in the investigations of the domestic chicken conducted by Sasaki et al. (2004). The researchers identified a QTL at position 205 cM. In turn, at positions 128, 283, and 386 cM of the same chromosome, Atzmon et al. (2007) identified significant QTL for this trait.

In the present investigations, a significant QTL for EW was identified at position 4 cM on CJA01. The additive effects were positive and had values of 0.03. At position 193 cM on the same chromosome, Recoquillay et al. (2015) mapped QTL with a potential effect on the mean egg weight in quails analyzed at 13 to 14 wk of age ($P \leq 0.01$). The differences in the positions of QTL determining EW between the investigation results may be related to the different dates of weighing the eggs and suggest that other genes exert an effect during the laying period than at a later stage. The presence of QTLs associated with egg weight on GGA01 was also indicated in other investigations of the domestic chicken (Kerje et al., 2003; Wright et al., 2008; Liu et al., 2011; Goraga et al., 2012).

A significant chromosome-wide QTL for the SG was identified at position 7 cM on CJA01 and at position 156 cM on CJA02. In both cases, the additive and dominance effects were positive. The SG was calculated from Archimedes' principle based on EW and egg weight in water, which probably explains the convergence of the QTL locations for these traits. Both QTL were separated by a distance of 4 cM and exhibited a similar value of the *F* statistics. To date, there have been no investigations of the identification of QTL regions determining SG in the Japanese quail. Nevertheless, there are available results of mapping quantitative trait loci for this trait in the domestic chicken. In investigations of an experimental population composed of two breeds, Greenlegged Partridge-like and Rhode Island Red hens, Wardęcka et al. (2002) identified a highly significant QTL for egg SG on chromosome GGA01. In turn, using a resource population created by crossing White Leghorn and Cornish, Hansen et al. (2005) identified

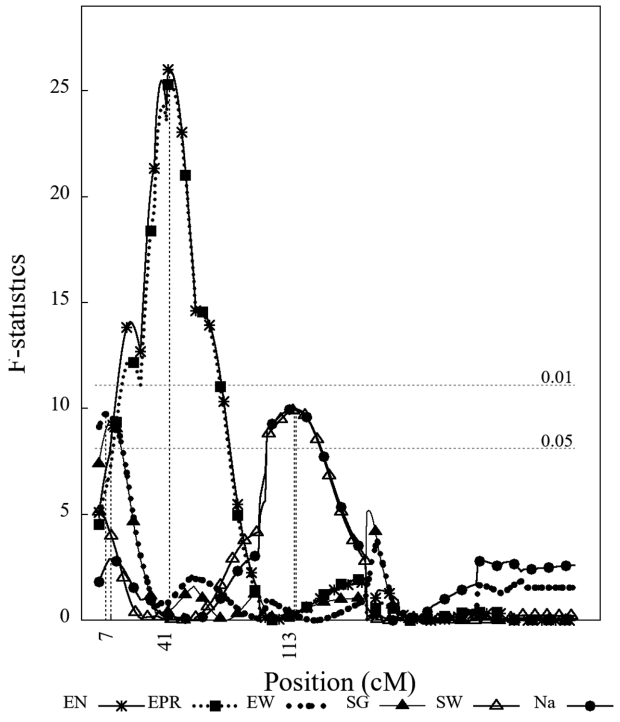

Figure 1. Regression analysis in the line-cross model including additive effects on chromosome CJA01. EN = egg number (solid line with stars); EPR = egg production rate (dotted line with filled squares); EW = egg weight (dotted line); SG = specific gravity (solid line with filled triangles); SW = shell weight (solid line with open triangles); Na = Na content in breast muscle (solid line with filled circle); horizontal dotted lines indicate threshold: 0.05 = 5% chromosome-wide threshold; 0.01 = 1% chromosome-wide threshold; vertical dotted lines indicate the chromosomal positions of maximum values of *F*-statistics.

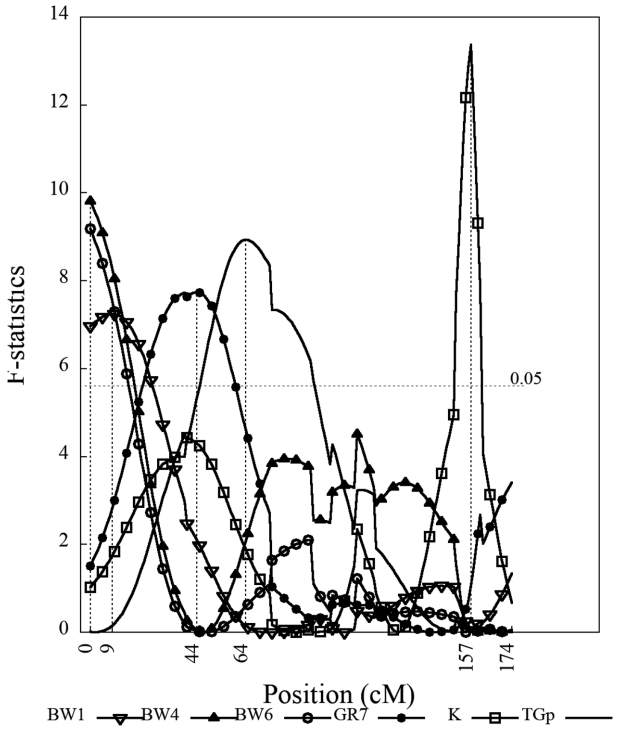

Figure 2. Regression analysis in the line-cross model including additive effects on chromosome CJA02. BW1 = body weight in 1st week of age (solid line with open triangles); BW4 = body weight in 4th week of age (solid line with filled triangles); BW6 = body weight in 6th week of age (solid line with open circles); GR7 = growth rate in 7th week of age (solid line with filled circles); K = K content in breast muscle (solid line with open squares); TGp = triacylglycerols content in blood plasma (solid line); horizontal dotted lines indicate threshold: 0.05 = 5% chromosome-wide threshold; 0.01 = 1% chromosome-wide threshold; vertical dotted lines indicate the chromosomal positions of maximum values of *F*-statistics.

QTL for SG on GGA02 of the chicken at position 23 cM.

In this study, a significant QTL region determining SW was mapped at position 114 cM on chromosome 1 of Japanese quail. The additive effect was positive and increased egg SW by 0.11 g. Minvielle et al. (2005) mapped a significant QTL for this trait on the same chromosome but at position 191 cM (between GUJ0062 and GUJ0068). In the case of the domestic chicken, QTL that may exert an effect on SW were identified on chromosomes 1, 2, 3, 4, 5, 9, 11, 12, 17, 24, and Z (Wardęcka et al., 2002; Sasaki et al., 2004; Liu et al., 2011; Tuiskula-Haavisto et al., 2011; Goto et al., 2014; Sun et al., 2015). In a resource population obtained by crossing Leghorn and Rhode Island Red chicken breeds, Sasaki et al. (2004) identified QTL on chromosome GGA1, which suggested association with the egg SW. Similarly, Sun et al. (2015) demonstrated the presence of significant QTL at positions 173 to 192 cM on chromosome GGA1 that may have an effect on this trait.

In the present investigations, a significant chromosome-wide QTL for the blood plasma triacylglycerols content (**TGp**) was identified at position 64 cM on CJA02 and its additive effect was negative. To date, there have been no investigations of the identification of QTL regions determining TGp in the Japanese quail. Nevertheless, there are available results of mapping QTL for this trait in the domestic chicken. Park et al. (2006) searched QTL on 26 different chromosomes of the chicken that are associated with, e.g., the concentration of selected biochemical components in birds' blood. They demonstrated the presence of a significant QTL on chromosome 2 that may exert an effect on serum triacylglycerol concentrations. The QTL was located at position 217 cM between markers UMA2.080 and MCW0234 and explained merely 2% of phenotypic variation. LPIN1 was the candidate gene. A negative correlation was noted between its expression and the concentration of HDL and total cholesterol in chicken serum (Wang et al., 2012). In our studies, a significant QTL affecting plasma triacylglycerol concentration was found to be located at positon 64 cM of CJA02. In turn, Sasazaki et al. (2006) mapped gene PON2 (paraoxonase 2) at position 58.4 cM of CJA02. Paraoxonase 2 is involved in protection of low-density lipoproteins (LDL) from oxidation leading to formation of fatty streaks in the arterial tunica intima in children and adolescents, which are the first step towards development of atherosclerosis (Ng et al., 2001). It has been found that Japanese quails are susceptible to atherosclerosis, both spontaneous

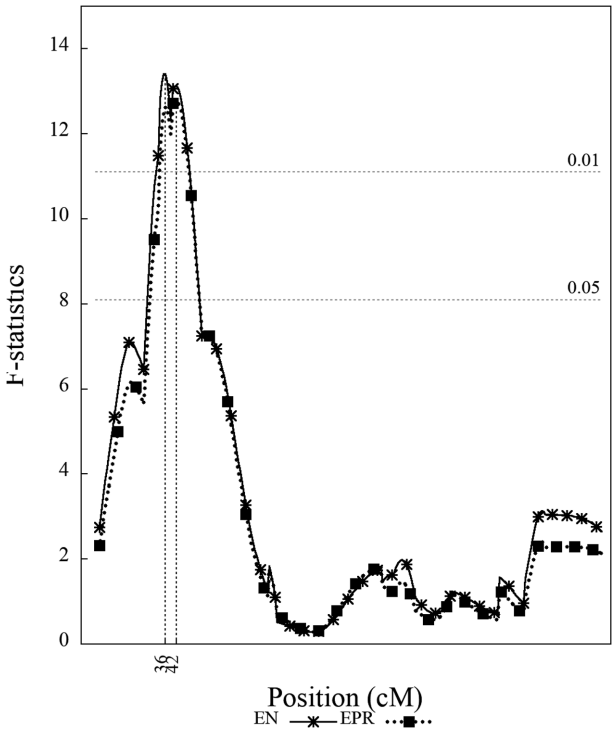

Figure 3. Regression analysis in the line-cross model including additive and dominance effects on chromosome CJA01. EN = egg number (solid line with stars); EPR = egg production rate (dotted line with filled squares); horizontal dotted lines indicate threshold: 0.05 = 5% chromosome-wide threshold; 0.01 = 1% chromosome-wide threshold; vertical dotted lines indicate the chromosomal positions of maximum values of *F*-statistics.

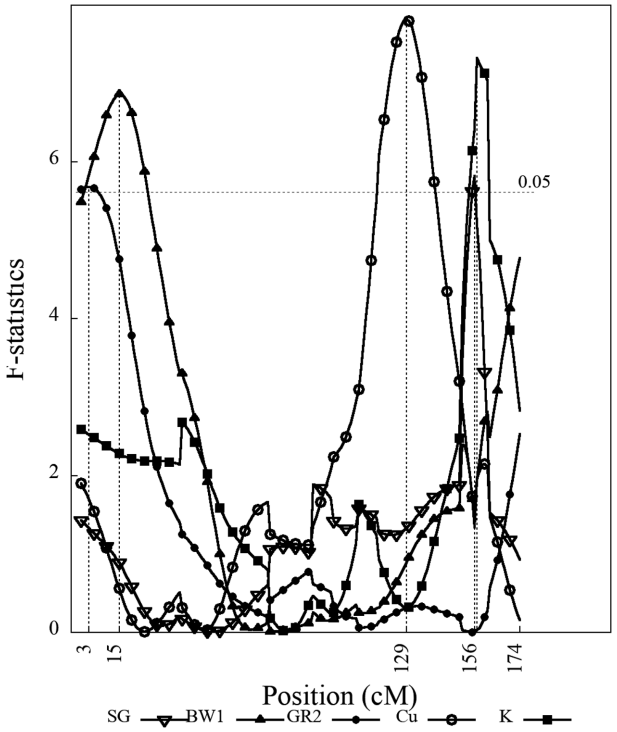

Figure 4. Regression analysis in the line-cross model including additive and dominance effects on chromosome CJA02. SG = specific gravity (solid line with open triangles); BW1 = body weight in 1st week of age (solid line with filled triangles); GR2 = growth rate in 2nd week of age (solid line with filled circle); Cu = Cu content in breast muscle (solid line with open circles); K = K content in breast muscle (solid line with filled squares); horizontal dotted lines indicate threshold: 0.05 = 5% chromosome-wide threshold; 0.01 = 1% chromosome-wide threshold; vertical dotted lines indicate the chromosomal positions of maximum values of *F*-statistics.

and induced by high-cholesterol diet (Shih, 1983). Boright et al. (1998) showed a correlation between polymorphism in the PON2 gene and the concentration of total cholesterol and apolipoprotein B in human serum.

A significant chromosome-wide QTL for the Na content was identified at position 113 cM on CJA01. The additive effect was positive. The QTL for K and Cu were mapped on CJA02. In the case of K, the additive effect was negative while the dominance effect was positive. The QTL for a given trait with higher values of dominance than the additive effect indicate a higher value of that trait in a heterozygous than in a homozygous individual. In both models used (including the additive as well as the additive and dominance effect), the QTL for K was mapped at the same location (position 157 cM) on chromosome 2. For Cu, the additive and dominance effect were positive. To date, there have been no investigations of the identification of QTL regions determining the content of chosen macro- and microelements in poultry breast muscle. The results of this study indicate the presence of 12 significant QTL on chromosomes CJA01 and CJA02 for growth, egg production, egg quality, biochemical parameters of blood plasma, and the content of selected macro- and microelements in the breast muscle of the Japanese quail. The analyses included additive and dominance effects of the individual QTL. For the first time, QTL regions with a potential effect on the K, Na, and Cu content in the breast muscle were identified in poultry in these investigations. However, the low resolution of the linkage maps of chromosomes CJA01 and CJA02 does not allow typing candidate genes that can significantly influence the analyzed traits. We also need to bear in mind that a linkage analysis can be well regarded as a preliminary tool, but not as an indicator of final results. Similar conclusion was drawn from a series of QTL linkage analysis, meta QTL analysis, combined QTL analysis (Siwek et al., 2010; Slawinska et al., 2011; Slawinska and Siwek, 2013). Only final association analysis (Siwek et al., 2015) allowed for more detailed characteristic of the genetic structure of phenotypic variation. Therefore, the current results might be seen as preliminary in the process of explaining genetic bases for phenotypic variation in quail.

To expand the research and include the other chromosomes of the Japanese quail, it is necessary to develop a high-resolution SNP-based linkage map. The first attempt to construct an SNP-based linkage map of the Japanese quail was presented in the investigations conducted by Frésard et al. (2012). Sequencing resulted in identification of 17,433 SNPs, some of which were used for QTL mapping. In 2015, Recoquillay et al. developed a panel of 2,145 SNP markers and used it for creation

of a linkage map with a length of 3,057 cM and an average distance between neighboring markers of 2.1 cM. Unfortunately, no commercial SNP microarrays for investigating the species are currently available. Their development could greatly reduce the cost of genotyping. The results of this study indicate that investigations of the Japanese quail can complement the analyses of the domestic chicken, especially when genetic lines that have no counterparts in other poultry species are used.

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