Preliminary mapping of QTLs affecting egg quality on chromosomes 1–5 in chickens

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ABSTRACT: In order to detect QTLs affecting egg quality traits, an experimental population was developed from two breeds: Green-legged Partridgenous (GlP), a native Polish breed, and a highly productive Rhode Island Red (RIR) stock. These breeds differ considerably in egg laying performance – the mean egg weight for GlP hens is 48.9 g and for RIR 59.4 g; during the first 100 days of laying GlP hens lay about 40 eggs while the RIR flock, selected over several generations for high laying performance, 81 eggs. QTL analysis was conducted concerning egg quality traits, based on a population of 519 birds (F_2). 23 microsatellite loci on chromosomes 1, 2, 3, 4 and 5 were chosen from the Roslin Institute database on the basis of their utility and location. Within the mapped population a linkage analysis was performed of 23 microsatellite markers. Through a linkage analysis twelve QTLs were identified, affecting 9 egg quality traits: egg weight at week 53 of life, albumen weight at week 53, albumen weight at week 33, yolk weight at week 33, yolk weight at week 53, shell weight at week 53, shell thickness at week 33, shell thickness at week 53, shell colour at week 53.

Keywords: QTL mapping; egg quality traits; microsatellites; chicken

One of the major goals of agricultural research is the identification of genes controlling the expression of economically important traits. Most of these traits display a wide variation in the expression of genes at distinct loci, referred to as quantitative trait loci (QTLs) (Cheng *et al.*, 1995). The current availability of highly polymorphic DNA markers in many species renders possible the elaboration of well saturated genetic maps and consequently, genetic dissection of complex quantitative traits (Vallejo *et al.*, 1998). Among the genetic markers which are currently employed, microsatellites have been found to be abundant, evenly distributed and highly polymorphic in all resource populations (Cheng *et al.*, 1995).

Recently, a large number of genetic markers that facilitate QTL analysis has been generated and mapped in experimental populations. The genetic linkage maps of chicken contain over 1 900 loci, out of which nearly 800 are highly polymorphic microsatellite markers (Groenen *et al.*, 2000). The development of high resolution genetic maps and the necessary powerful statistical methods have initiated QTL mapping experiments for a variety of traits. Studies aimed at QTLs in chickens were reported by Khatib (1994), who studied juvenile growth rate and by Vallejo *et al.* (1998), who detected QTLs affecting susceptibility to tumours induced by Marek's disease virus. Moreover, Van Kaam *et al.* (1998, 1999a,b) reported QTLs affecting growth, feed efficiency and carcass traits while Yonash *et al.* (2001) identified QTLs affecting antibody response and survival rate in meat-type chickens. Recently, QTLs affecting body weight were reported on chromosomes 1 and 2 (Tatsuda and Fujinaka, 2001).

The results of the whole genome scan aimed at detection and localisation of QTL affecting egg quality traits were described by Tuiskula-Haavisto *et al.* (2001). At 1% genomewise significance level, 14 chromosomal areas affecting egg quality were found and at 5% only 6 suggestive QTLs. The effect of the RIR allele was associated with high egg weight, body weight, feed intake and with late sexual maturity and lower number of eggs.

In order to detect QTLs affecting egg quality traits, a F_2 cross between lines was developed, derived from two genetically different breeds. The search for QTLs was performed on progeny means of the second generation.

MATERIAL AND METHODS

Experimental population

The mapped population consisted of 10 full-sib families, originating from a cross between two chicken breeds: Green-legged Partridgenous (GlP), a native Polish breed maintained as a conservative flock, and a highly productive stock of Rhode Island Red (RIR). On the basis of DNA fingerprinting analysis, according to the lowest band sharing coefficient, 10 GlP cocks and 10 RIR hens were chosen as parental generation F_0. These 10 F_0 couples were mated in order to obtain 10 families for generation F_1 (130). 519 birds of full-sib F_2 generation were obtained by crossing one brother and one sister from each of the 10 F_1 families. These 669 birds were used as the experimental population.

The birds were maintained in batteries, in individual cages and an individual egg-laying control was performed. During the laying period 20 egg quality traits were recorded (Table 1). The albumen quality was evaluated in Haugh units (log of albumen height corrected for egg weight). Egg shell strength is a major trait affecting egg stability so shell quality was evaluated as a direct measurement of shell strength (SS). The evaluated shell traits included also shell weight, shell density, shell thickness and shell colour. Egg quality traits from F_2 individuals were measured at week 33 and 53 of life.

DNA samples

Blood samples were collected into vacuum tubes containing EDTA and stored at –20°C. The DNA was extracted by standard methods. DNA concentration was determined spectrophotometrically and DNA was diluted to a final concentration of 0.1 µg/µl.

Microsatellite markers

Microsatellite loci were chosen from *MCW* (Crooijmans *et al.*, 1996; Groenen *et al.*, 1997), *LEI* (Gibbs *et al.*, 1997) and *ADL* markers (Cheng *et al.*, 1995). In total 23 informative markers were mapped. The microsatellite markers are available from the Roslin Institute database (http://www.thearkdb.org.).

Microsatellite repeat *MCW0041* is situated in the chicken *GGVAY Y*-gene of the chicken ovalbumin family, *MCW0051* in *GGCALBO4* chicken vitamin D-induced calbinding *D28K* gene, and *MCW0047* in high-mobility group protein 14 *A1* gene.

PCR conditions

The PCR was carried out in a volume of 7.5 µl comprising 100 ng of template DNA, 2.5 pmol

Table 1. List of recorded egg quality traits

Trait	Symbol	Trait	Symbol
Egg specific gravity at week 33 (g)	SG33	Egg specific gravity at week 53 (g)	SG53
Shell strength at week 33 (kg/cm2)	SS33	Shell strength at week 53 (kg/cm2)	SS53
Shell colour at week 33	SC33	Shell colour at week 53	SC53
Egg weight at week 33 (g)	EW33	Egg weight at week 53 (g)	EW53
Haugh units at week 33	HU33	Haugh units at week 53	HU53
Shell weight at week 33 (g)	SW33	Shell weight at week 53 (g)	SW53
Shell density at week 33	SD33	Shell density at week 53	SD53
Shell thickness at week 33 (µm)	ST33	Shell thickness at week 53 (µm)	ST53
Yolk weight at week 33 (g)	YW33	Yolk weight at week 53 (g)	YW53
Albumen weight at week 33 (g)	AW33	Albumen weight at week 53 (g)	AW53

of each primer, 100 µM of each dNTP, 0.5 unit of DNA polymerase, 10 mM tris- HCl, pH 8.8, 1.5 mM $MgCl_2$, 50 mM KCl, 0.1% Triton X-100.

One primer for each locus was labelled with fluorescein. The following amplification conditions were adopted: 5 min denaturation at 94°C followed by 25–37 cycles of denaturation at 94°C for 45 s, annealing at 48–68°C and extension at 72°C for 60 s. The PCR was performed using a PTC-200 Programmable Thermal Controller.

DNA genotyping

The fluorescent PCR products were separated on 6% denaturing polyacrylamide gels, using an Automated Laser Fluorescent (ALFexpress) DNA Sequencer. The PCR products were analysed after 5 min denaturation in a 50% formamide solution containing blue dextran. The results were visualised and the genotyping completed with Allele Links 1.01. After automated allele calling and binning within the Allele Links 1.01 software, individual genotypes were checked by a manual inspection before exporting the genotype database to Excel. Moreover, (potential) typing errors detected with the CRI-MAP program were re-checked and corrected. The data was extracted from Excel worksheets and put into a correct format for the CRI-MAP linkage analysis program. Linkage analysis was performed using CRI-MAP version 2.4 program (Green *et al.*, 1990).

Variance and covariance components were estimated using EM-REML with multitrait animal model (Misztal, 1999).

QTL analysis and significance thresholds

The mapping of QTLs was performed using the program QTL Cartographer vers. 1.13 (Basten *et al.*, 1999). The program uses linear regression, composite interval mapping (Zeng, 1993, 1994) methods to dissect the underlying genetics of the quantitative traits. Composite interval mapping combines interval mapping with multiple regression.

Significance thresholds were calculated using the permutation test (Churchill and Doerge, 1994). It is an empirical method that accounts for the structure of marker data and distribution of phenotypic data. Through the random shuffling of phenotypic observations and the corresponding weighting factors for these observations, any relation between QTL and marker genotypes is broken. The distribution under the null hypothesis of no QTL is constructed in this way. For each shuffle a test statistic was calculated and stored. The stored test statistics were sorted in a descending order – the threshold for each required significance level can be derived in this way. Genomewise thresholds were derived for each trait by permutating all markers simultaneously. It was repeated 500 times in order to construct the distribution under a null hypothesis (Table 2). Three levels of significance thresholds were derived: 1% genomewise significance thresholds, 5% genomewise significance thresholds and 10% genomewise significance thresholds.

RESULTS

Heterozygosity

The average number of different alleles for the markers in this population was 4.12 per locus. In total, over 65% of markers in the tested F_2 showed a high heterozygosity exceeding 60% (Jaszczak *et al.*, 2001).

Linkage analysis

A linkage analysis was performed for 23 microsatellite markers within the mapped population. Map distances between adjacent loci are given using the Kosambi scale in centimorgans (cM) (Table 3).

Heritabilities and genetic correlations

Table 4 shows correlations between the mean adjusted progeny trait values obtained for all birds. Shell strength (SS) proved to be highly correlated with shell density (SD) and shell thickness (ST). The correlation between albumen weight (AW) and egg weight (EW) was close to 1. High correlations were also observed between EW, SW and YW as well as between shell weight (SW) and SD, ST and AW.

The heritabilities estimated for these traits vary on average between 0.4 (egg weight, shell colour) and 0.2 for the remaining analysed traits.

Table 2. Threshold *P*-values for genomewise QTL analysis

Significance level	Traits	*P*-values	Traits	*P*-values	Traits	*P*-values	Traits	*P*-values
0.1		12.3851		12.4713		12.9502		13.2319
0.05	SG33	14.0008	SW33	14.6013	SG53	14.2942	SW53	14.6185
0.01		16.8038		19.6956		18.5063		18.2477
0.1		12.7509		12.9955		13.3255		13.2216
0.05	SS33	14.1597	SD33	15.0747	SS53	14.8999	SD53	15.3849
0.01		19.1018		19.9337		17.7742		18.3651
0.1		13.5141		12.5342		13.6760		12.6794
0.05	SC33	14.5763	ST33	13.8237	SC53	15.3230	ST53	14.3963
0.01		19.8742		16.8468		20.0591		16.7848
0.1		12.5833		12.0423		12.9066		13.1109
0.05	EW33	14.3098	YW33	13.2971	EW53	14.7752	YW53	15.3215
0.01		17.6079		17.2604		18.9988		21.7459
0.1		13.1197		12.6586		13.1153		13.3460
0.05	HU33	15.0394	AW33	13.9797	HU53	15.0501	AW53	14.8469
0.01		19.1495		18.0169		18.5606		17.8389

Significance thresholds

Genomewise significance thresholds are presented in Table 2. These 1%, 5%, and 10% thresholds were calculated by means of permutation over all linkage groups simultaneously in one analysis.

QTL analysis

A linkage analysis between genotypes and 20 egg quality traits, recorded for generation F_2, led to the identification of twelve QTLs. The effect of the found QTLs' area explained approximately from

Table 3. Linkage analysis of 23 microsatellite markers on chromosomes 1–5

Position	Chromosome 1	Chromosome 2	Chromosome 3	Chromosome 4	Chromosome 5
Locus 1	*MCW0018*	*MCW0063*	*MCW0127*	*MCW0167*	*MCW0081*
(cM)	0	0	0	0	0
Locus 2	*MCW0200*	*MCW0131*	*MCW0126*	*MCW0170*	*ADL0187*
(cM)	100	27.5	45.2	100	21.9
Locus 3	*MCW0068*	*MCW0051*	*LEI113*	*MCW0114*	*MCW0029*
(cM)	142.2	95.1	91.5	182	38.8
Locus 4	*MCW0283*	*MCW0056*	*MCW0040*	*MCW0047*	*MCW0032*
(cM)	185.8	132.6	134.2	241.5	57.7
Locus 5	*MCW0145*	*MCW0041*	*MCW0139*		
(cM)	267.7	188.3	223.8		

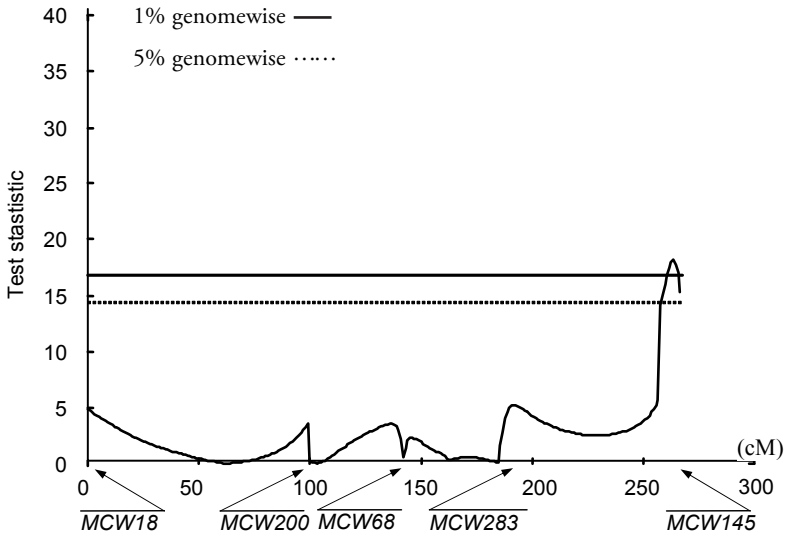

Figure 1. Test statistic values from the analysis of shell thickness at week 53 of life (ST53) for quantitative trait loci on chromosome 1. The 1% and 5% genomewise significance thresholds of ST53 are included

1.7% to 31.1% of the variance within the analysed traits (Table 5).

Two QTL regions were found on chromosome 1 for shell weight at week 53 (142 cM and 256 cM; SW53), and one region around 263 cM for shell thickness at week 53 (ST53, Figure 1). SW and ST proved to be highly correlated (Table 4).

Three QTLs were found on chromosome 3 linked with marker *MCW00139*: egg weight (EW53, Figure 2), yolk (YW53) and albumen weight at week 52 (AW53). A high correlation was observed between these traits.

QTL for shell thickness at week 53 (ST53) was mapped on chromosome 4 (around 182 cM, Figure 3) and for albumen weight at week 33 – on the same chromosome (around 99 cM, Figure 4).

Shell colour at week 53 (SC53) showed a linkage at significance level $P = 0.05$ on chromosome 5.

Two suggestive linkages were identified at significance level $\alpha = 0.1$: yolk weight at week 33 (chromosome 1) and shell thickness at week 33 (chromosome 5).

Table 4. Correlations between mean adjusted progeny trait values of all animals

Trait	h^2	EW	SG	SS	SC	HU	SW	SD	ST	YW
EW	0.395									
SG	0.190	–0.172								
SS	0.175	–0.147	0.389							
SC	0.463	–0.053	–0.101	–0.017						
HU	0.267	0.245	0.307	0.155	–0.010					
SW	0.244	0.532	0.486	0.293	–0.359	0.256				
SD	0.200	0.065	0.730	0.491	–0.394	0.135	0.836			
ST	0.226	0.318	0.299	0.520	–0.104	0.355	0.553	0.673		
YW	0.138	0.651	–0.459	–0.292	–0.149	0.049	0.224	–0.162	–0.099	
AW	0.298	0.952	–0.083	–0.169	0.043	0.275	0.510	–0.017	0.300	0.423

EW = egg weight; SG = egg specific gravity; SS = shell strength; SC = shell colour; HU = haugh units; SW = shell weight; SD = shell density ST = shell thickness; YW = yolk weight; AW = albumen weight

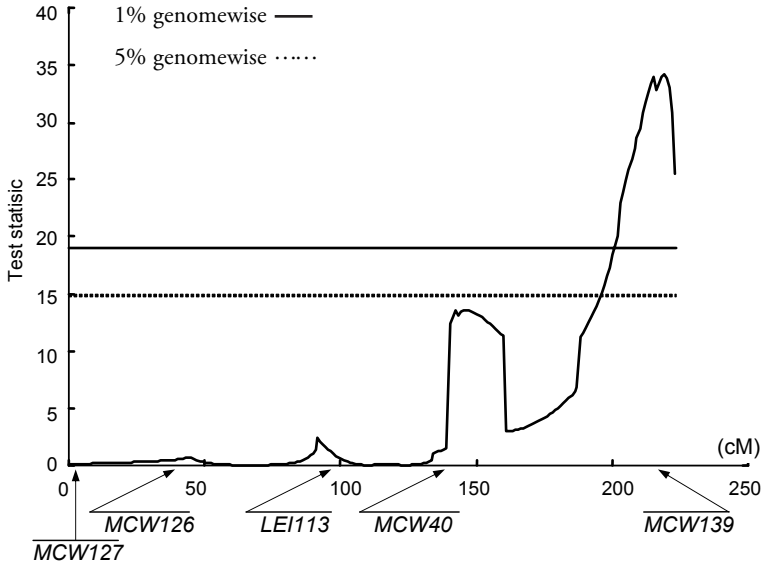

Figure 2. Test statistic values from the analysis of egg weight at week 53 of life (EW53) for quantitative trait loci on chromosome 3. The 1% and 5% genomewise significance thresholds of EW53 are included

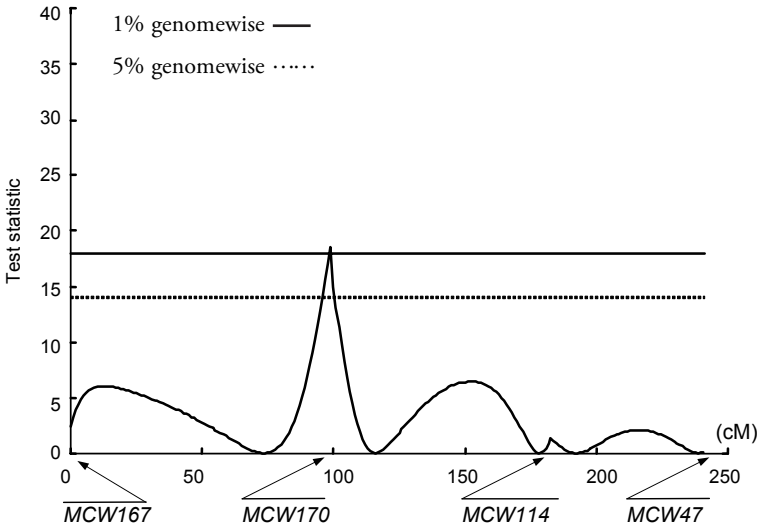

Figure 3. Test statistic values from the analysis of albumen weight at week 33 of life (AW33) for quantitative trait loci on chromosome 4. The 1% and 5% genomewise significance thresholds of AW33 are included

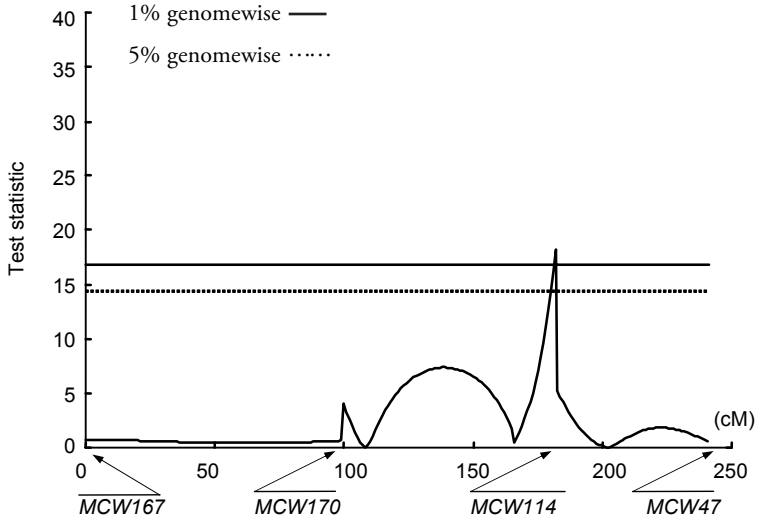

Figure 4. Test statistic values from the analysis of shell thickness at week 53 of life (ST53) for quantitative trait loci on chromosome 4. The 1% and 5% genomewise significance thresholds of ST53 are included

Table 5. The most likely positions of QTLs in centimorgans on chromosomes per traits. Genomewise significance level of QTLs at these positions, the closest markers to the QTL and this location and the explained variance of QTLs

Traits	Chromosome	QTL position (cM)	Significance level	*P*-values	Marker	Marker position	Explained variance (%)
YW33	1	142.0	0.1	12.28	*MCW0068*	142.2	1.7
SW53		256.8	0.01	30.18	*MCW0145*	267.7	31.1
ST53		263.8	0.01	18.13	*MCW0145*	267.7	21.9
YW53	3	213.2	0.01	21.57	*MCW0139*	223.8	26.2
AW53		214.2	0.01	53.57	*MCW0139*	223.8	25.3
EW53		219.2	0.01	34.20	*MCW0139*	223.8	20.1
AW33	4	099.0	0.01	18.55	*MCW0170*	100.0	3.3
ST53		182.0	0.01	18.21	*MCW0114*	182.0	7.5
ST33	5	0.0	0.1	12.89	*MCW0081*	0.0	2.2
SC53		56.8	0.05	16.57	*MCW0032*	57.7	7.4

YW33 = yolk weight at week 33; SW53 = shell weight at week 53; ST53 = shell thickness at week 53; YW53 = yolk weight at week 53; AW53 = albumen weight at week 53; EW53 = egg weight at week 53; AW33 = albumen weight at week 33; ST33 = shell thickness at week 33; SC53 = shell colour at week 53; *MCW* = microsatellite chicken wageningen

DISCUSSION

Egg quality traits

There are several factors affecting the detection power for QTL mapping. Traits-associated factors, such as the number and genome locations of genes affecting the traits, the distribution of the gene effects and interactions and trait heritability, are not controllable. Some factors including population size and type can be artificially manipulated to enhance the detection for QTL mapping. Theoretically, a large full-sib family that is fully informative, with all distinguishable parental alleles at all loci, is sufficient for QTL mapping (Zhu *et al.*, 2001).

In order to increase the probability of parents being heterozygous for the given QTLs, and thus enhance the detection power of QTL mapping, the population was produced by crossing two genetically different breeds (GlP and RIR). As proposed by Hillel (1997), DNA fingerprinting was used to select distantly related individuals for mating and thus to obtain highly informative offspring. Seventeen alleles were identified as specific for the GlP, and forty-two for the RIR chickens from the parental generation. The reference family was characterised by a high level of polymorphism at the examined microsatellite loci and high heterozygosity. Highly heterozygous individuals not only enhance the probability of QTL detection but also improve the accuracy of linkage maps and determination of linkage phases (Zhu *et al.*, 2001).

In our study the critical values for test statistics were determined for each trait on significance levels of $\alpha = 0.01$, $\alpha = 0.05$ and $\alpha = 0.1$ (Lander and Kruglyak, 1995). Twenty egg quality traits have been analysed. At the genomewise significance level of 1% nine sites were found while at 5% one chromosomal area.

The QTL for shell weight was found on chromosome 1 around 256 cM (SW53), and in a near position a significance linkage was found (around 263 cM) for shell thickness (ST53) (Figure 1). These results could be expected as the mentioned traits (SW and ST) are highly correlated. Similarly,

for three highly correlated traits (egg weight, yolk and albumin weight) a significance linkage with marker *MCW00139* was estimated on chromosome 3.

The presented results lead to a conclusion that chromosomes 1, 3, 4, 5 could contain genes affecting chicken egg quality traits.

In our study the effect of the RIR alleles was associated with high yolk weight at week 33, shell weight at week 53, shell thickness at week 53, albumen weight at week 33, shell colour at week 53 and GlP alleles were favourable for yolk weight at week 53, albumen weight at week 53, egg weight at week 53, shell thickness at week 33.

Further analyses should include a larger number of markers in the examined chromosome regions so as to reach a final distance of around 20 cM between bracketing markers. Moreover, a comparison with the human genome map should be performed as it is essential for finding candidate genes, their sequence and mutations affecting egg quality traits.

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ABSTRAKT

Předběžné mapování QTL ovlivňujících kvalitu vajec na chromozomech 1–5 u slepic

K detekci QTL, které ovlivňují znaky kvality vajec, jsme vytvořili pokusnou populaci složenou ze dvou plemen: zelenonohé koroptví vlašky (GlP), domácího polského plemene, a vysoce produktivní červené rodajlendky (RIR). Tato plemena se značně odlišují svou užitkovostí – průměrná hmotnost vejce u GlP je 48,9 g a u RIR 59,4 g; během prvních 100 dní snášky nosnice GlP snesou kolem 40 vajec, zatímco nosnice RIR, které byly po několik generací šlechtěny na vysokou užitkovost, snesou 81 vajec. Analýzu QTL zaměřenou na znaky kvality vajec jsme provedli v rámci populace 519 jedinců (F_2). Z databáze Roslinova ústavu jsme na základě vhodnosti a polohy vybrali 23 lokusů mikrosatelitů na chromozomech 1, 2, 3, 4 a 5. V rámci mapované populace jsme provedli analýzu genetických vazeb u 23 mikrosatelitních markerů. Pomocí analýzy genetických vazeb bylo identifikováno 12 QTL, které ovlivňují těchto devět znaků kvality vajec: hmotnost vejce v 53. týdnu života, hmotnost bílku v 53. týdnu, hmotnost bílku ve 33. týdnu, hmotnost žloutku ve 33. týdnu, hmotnost žloutku v 53. týdnu, hmotnost skořápky v 53. týdnu, tloušťku skořápky ve 33. týdnu, tloušťku skořápky v 53. týdnu, barvu skořápky v 53. týdnu.

Klíčová slova: mapování QTL; znaky kvality vajec; mikrosatelity; slepice

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