Whole Genome Scan in Chickens for Quantitative Trait Loci Affecting Carcass Traits

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ABSTRACT An experiment was conducted to enable quantitative trait loci (QTL) mapping for carcass traits. The population consisted of 10 full-sib families originating from a cross between male and female founders chosen from two different outcross broiler lines. Founder animals, parents, offspring, and grandoffspring are denoted as generation (G) 0, 1, 2, and 3 animals, respectively. Microsatellite marker genotypes were collected on G_1 and G_2 animals. Phenotypic observations were collected on G_3 animals. Recorded traits were BW at 48 d, carcass weight, carcass percentage, breast meat color, and leg score.

Average adjusted progeny trait values were calculated for each G_2 animal and for each trait after adjusting phenotypic observations on G_3 animals for fixed effects, covariables, the additive genetic contribution of the other parent, and differences between sexes. The average adjusted progeny trait values were used as the dependent variable in the QTL analysis.

A QTL analysis was undertaken by modeling the segregation from G_1 to G_2, using a full-sib across family regression interval mapping approach. In total, 27 autosomal linkage groups covered with 420 markers were analyzed. Genomewise significance thresholds were derived using the permutation test and a Bonferroni correction. Two QTL, affecting two of the five analyzed traits, exceeded suggestive linkage. The most significant QTL was located on Chromosome 1 at 466 cM and showed an effect on carcass percentage. The other QTL, which affected meat color, was located on Chromosome 2 and gave a peak at 345 and 369 cM.

(*Key words*: chicken, quantitative trait loci, carcass traits, three generation design, regression)

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INTRODUCTION

Recently, much effort has been spent on obtaining knowledge about quantitative trait loci (QTL) in several species (e.g., Andersson *et al*., 1994; Georges *et al*., 1995). Such information on QTL would be useful for marker-assisted breeding as well as for improving the understanding of the biological background (i.e., which genes are involved and their effects) of traits. Usually, information from genetic markers is used for detecting QTL on chromosomes. Recently, a large number of genetic markers was generated in the chicken (Crooijmans *et al*., 1996, 1997), which enabled QTL detection. In order to detect QTL for broilers, an experimental broiler population was set up following recommendations of Van der Beek *et al*. (1995). Marker genotypes were collected in the first two generations of this population and used to construct a linkage map (Groenen *et al*., 1998). This technique facilitated a genomewide QTL analysis. Phenotypic observations were collected on third generation animals in different experiments. The first of these experiments was a feed efficiency experiment and the second was an experiment on carcass traits. Results of the feed efficiency experiment have been reported previously (Van Kaam *et al*., 1998, 1999). In total, four QTL were detected. One QTL was located on Chromosome 1 at 235 cM and had an influence on feed intake and growth between 23 and 48 d and on body weight at 48 d (BW48). A second QTL was located on linkage group WAU26 at 16 cM and showed an effect

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Abbreviation Key: ADL = Avian Disease and Oncology Laboratory, Michigan State University, East Lansing; BW48 = body weight at 48 d; CP = carcass percentage; CW = carcass weight; G_0 etc. = Generation 0 etc.; LEI = University of Leicester, Leicester; LS = leg score; LS1 = original leg score; LS2 = transformed leg score; LS3 = transformed leg score adjusted for BW48; MC = meat color; MC1 = meat color unadjusted for BW48; MC2 = meat color adjusted for BW48; MCW = Microsatellite chicken Wageningen; QTL = quantitative trait locus; UMA = University of Massachusetts, Amherst; WAU = Wageningen Agricultural University, Wageningen.

TABLE 1. Population structure with numbers of animals used in the analysis and types of observations collected[1]

Generation[2]	Males	Females	Total	Observations[3]
G_0[4]	14	14	28	. . .
G_1	10	10	20	Genotypes
G_2	175	274	449	Genotypes
G_3	969	984	1,953	Phenotypes on BW48
G_3	969	984	1,953	Phenotypes on CP
G_3	977	999	1,976	Phenotypes on CW
C_3	960	981	1,941	Phenotypes on MC
G_3	962	983	1,945	Phenotypes on LS

[1]Numbers exclude outliers and missing values.

[2]G_0 etc. = Generation 0, etc.

[3]BW48 - body weight at 48 d; CP = carcass percentage; CW = carcass weight; LS = leg score; MC = meat color.

[4]Male and female G_0 animals are from different lines.

for feed intake between 23 and 48 d. On Chromosome 4 at 147 cM, a third QTL affecting feed intake between 23 and 48 d and feed intake adjusted for BW, was located. Finally, a fourth QTL, which affected feed intake adjusted for BW, was located on Chromosome 2 at 41 cM.

In the present paper, the results of a whole genome scan aimed at the detection and localization of QTL affecting carcass traits are presented. The traits analyzed were BW48, carcass weight (CW), carcass percentage (CP), meat color (MC), and leg score (LS). These traits are economically important for the broiler industry (Emmerson, 1997; Pollock, 1997). QTL for carcass traits are interesting for animal breeders, because most of these traits cannot be measured on living animals, which hampers selection. For these traits, utilization of QTL through marker-assisted selection could be beneficial.

MATERIALS AND METHODS

Experimental Population

A broiler population, consisting of three generations, was created for the purpose of QTL detection. The number of animals and the population structure are given in Table 1. Founder animals, parents, offspring, and grandoffspring are denoted as generation (G) 0, 1, 2, and 3 animals, respectively. Two genetically different outcross broiler dam lines (G_0) originating from the White Plymouth Rock breed, were chosen as the foundation of the experimental population. In one line, 14 males and in the other line 14 females were chosen and 14 G_0 couples were created. These 14 G_0 couples were mated in order to obtain 20 G_1 animals, 10 of each sex. From these 20 G_1 animals, 10 couples were created without known relationship, each couple being the basis of a family. The G_1 couples were mated to produce G_2 full sibs. G_2 animals were mated with G_2 animals from other families to produce G_3 animals. Each full-sib family consisted of two G_1 parents and on average 44.9 G_2 animals with marker genotypes and each G_2 animal had on average between 8.6 and 8.8 G_3 offspring with observations per trait. More details are given by Van Kaam *et al.* (1998, 1999).

In this population, G_1 and G_2 animals were typed for microsatellite markers and phenotypic observations were collected on G_3 animals. Phenotypic observations on G_3 animals were used for the calculation of average adjusted progeny trait values on G_2 animals. G_1 and G_2 animals were the same animals as in the previously reported feed efficiency experiment (Van Kaam *et al.*, 1998, 1999). However, in the experiment on carcass traits, different G_3 animals were used and housing was in floor pens instead of individual cages. Seven G_2 animals had no offspring with observations in this experiment.

G_3 animals were raised in six hatches and housed in a litter system for broilers until the age of 48 d. Animal density was around 20 animals per square meter. The animals were in the same pen starting from Day 0, where they received feed and water for *ad libitum* consumption and illumination was 23 h/d. A commercial broiler feed, consisting of crumbled concentrates containing 3,100 kcal/kg and 21% protein, was used. Around Day 47, the legs of these G_3 animals were scored (LS) on a scale from 1 to 9, by looking at the hock joints. Straight legs were considered as the optimum and received a score of 9. The lateral deviation of the legs from this optimum was judged. The further away from this optimum, the lower the score the animals received. Leg problems were considered to be an effect of weak hock ligaments or tendons, which could result in both varus (proximal hocks) as well as valgus (distal hocks) deformations. Therefore, both varus and valgus animals had a score below the optimum. In practice, the majority of the animals showed varus.

At 48 d, BW was measured and animals were slaughtered. After Day 48, CW was measured. For one hatch, CW was measured on two different days. The CW was measured on the chilled carcass after removal of feathers, head, lungs, liver, kidneys, gastrointestinal tract, abdominal body fat, subcutaneous leg fat, and lower legs and after loss of part of the animals blood due to bleeding. On the same day that CW was measured, measurements

of the MC were taken at three spots on the chilled breast fillet, using a fiber optic meat probe.[2] These three measurements were considered as repeated measurements of the same trait. The last hatch of animals was measured on a longer scale due to problems with the fiber optic meat probe. Linear transformation was applied to rescale these measurements to the same scale as measurements taken on other animals. Transformation was performed by multiplying the deviation of each observation from the mean with a constant and successively adding the mean. In total, 23 G_3 animals had missing data on BW48, 0 for CW, 23 for CP, 46 for MC, and 42 for LS.

Outlier detection was applied for BW48, CW, CP and separate fiber optic measurements. Because LS was classified from 1 to 9, outlier detection did not seem useful here, as it would lead to exclusion of the extreme animals (1) or the desired animals (9). Outliers for BW48, CW, CP, and fiber optic measurements were detected by applying the deviation of the observation from the mean divided by the standard deviation as test statistic for a single outlier. In order to be able to detect multiple outliers, the outlier test was applied iteratively, removing only a single outlier after each iteration, until no new outlier was detected. To account for different levels and variances between hatches and between males and females, the detection was applied per sex within each hatch separately. Critical values were those of Grubbs and Beck (1972) for a single outlier in normally distributed data of 0.5% per tail. These critical values depend on the sample size, i.e., with a larger sample size a larger deviation from the mean is still considered as normal. The number of outliers was, respectively, 8 for BW48, 7 for CW, 2 for CP and 4 for fiber optic scores. The outliers were randomly distributed across families, indicating that there probably was no genetic component involved. All outliers for BW48 and all except one outlier for CW were on the lower tail. All these animals with a low BW48 also had a low CW and vice versa. Because these traits are measured at different moments, the observations were probably correct and these animals were most likely suffering from illness. If either BW48, CW, or CP was considered as outlier, then all three traits were assigned as missing. In total, 11 animals obtained missing values for these traits.

An additional check was applied to the fiber optic scores. The availability of three fiber optic measurements for each animal provides a built-in control possibility. Fiber optic measurements that differed more than three standard deviations from their expectation based on the other two fiber optic measurements on the same animal were considered to be incorrect measurements and were assigned as missing. In total, one of the three measurements was assigned as missing for 45 animals, which were randomly distributed over hatches and families. These 45 animals had a standard deviation among their remaining two fiber optic measurements of 83% of the standard deviation, which the other animals had over all three measurements. Before removal of the extreme measurements, this was 318%. For all animals, the (remaining) fiber optic measurements were averaged to obtain a single value for MC.

Marker Data

The marker data and linkage map utilized in this study were identical to the information used in our previous study on other traits (Van Kaam *et al*., 1999). Genotypes for microsatellite markers were determined on 20 G_1 and 456 G_2 animals. In total 265 markers were determined on all 10 families and 155 markers were only typed on 4 families. These 420 informative markers were mapped on 27 autosomal linkage groups, which covered 3,363 cM. Map distances presented in this paper are always sex-averaged distances in centimorgans on the Haldane scale (Haldane, 1919). Because the segregation of the Z chromosome is different from autosomal chromosomes, the Z chromosome was not included in the present genome scan. Linkage groups WAU1 to WAU7 were assigned to Chromosome 1 to 7 and WAU11 to Chromosome 8 (Groenen *et al*., 1998). On the first 20 linkage groups, all 20 parents were informative. The number of informative parents was 8 for linkage group WAU21, 16 for WAU22, 19 for WAU23, 18 for WAU24, 7 for WAU25, 16 for WAU26, and 9 for WAU27. All markers on linkage group WAU21 were only typed on four families.

Analysis of the Phenotypic Data

A two-step procedure was applied for analysis of the data: first, average adjusted progeny trait values were calculated by adjusting phenotypic observations for systematic effects, and second, a QTL analysis was undertaken using the average adjusted progeny trait values as the dependent variable.

Five traits were analyzed: four measured traits and one inferred trait. Measured traits were BW48, CW, MC, and LS. The inferred trait was CP, which was defined as the ratio between CW and BW48 multiplied by 100%. For MC, the average of the fiber optic measurements per animal was taken. For MC, an analysis was done without and with adjustment for BW48. These analyses are labeled with MC1 and MC2, respectively, when necessary. The reason for adjustment for BW48 is the phenotypic correlation between BW48 and MC, which was 0.29 in males and 0.15 in females. This correlation could be caused by differences in muscle composition (water content) or postmortem transition to meat (pH change and drip loss) (Schreurs, 1999), and might have a genetic component. Because the distribution of LS had a skewness of –0.37, a second analysis was applied in which the scores were replaced with new values. With these new values, the distribution mimicked an underlying normal distribution with a mean of 5, a standard deviation of 2, and a skewness of 0. This transformation was applied because

[2]TBL Fiber Optics Ltd., Leeds, LS10 1AT, U.K.

normality is assumed in the estimation of variance components. A third analysis was applied in which the transformed values were used and an adjustment for BW48 was included. The analyses of LS are labeled with LS1, LS2, and LS3, respectively. The phenotypic correlation between BW48 and LS1 was –0.01 for males and –0.07 for females.

Two of the five traits showed a difference between standard deviation in males and females of more than 50%. These traits were BW48 and CW. In order to account for the heterogeneity of variance between sexes, these traits were analyzed with a bivariate approach, i.e., treating observations on male and female G_3 animals as different but correlated traits. Although CP had a small difference in standard deviation between the sexes, it was analyzed in the same manner as BW48 and CW, because it was derived from these traits. The following bivariate mixed model for male and female observations was applied:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & 0\\ 0 & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_1 & 0\\ 0 & \mathbf{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix} \qquad [1]$$

where $\mathbf{y}_i$ = vector of observations for i = 1 (male) or 2 (female); $\mathbf{b}_i$ = vector of fixed effects and covariables for trait i; $\mathbf{u}_i$ = vector of random direct additive genetic effects on trait i; $\mathbf{X}_i$ = incidence matrix relating observations for trait i to fixed effects and covariables; $\mathbf{Z_i}$ = incidence matrix relating observations for trait i to direct additive genetic effects; and $\mathbf{e_i}$ = vector of random residual effects for trait i.

Elements in the vectors of fixed effects included for each trait the overall mean of the trait. Furthermore, for BW48 an interaction term between the hatch of the recorded animal and the hatch of the dam was included and for CW and CP an interaction term between the hatch of the recorded animal, the hatch of the dam and the day of measuring CW was included. The interaction term between the hatch of the recorded animal and the hatch of the dam represented the period of the year and the age of the dam at reproduction. G_3 animals were born in six different hatches, their dams were born in eight hatches. Because CW was measured on 2 d in one hatch, dehydration can have an influence on the measurement within batch, and, therefore, the day of measuring CW was included in the interaction term.

The difference in standard deviation between males and females for MC was smaller than 1% and for LS1 and LS2/LS3 it was 9 and 2%, respectively. Therefore, for LS and MC, no adjustment for heterogeneity of variance between the sexes was necessary. A univariate approach, with an equivalent model was applied. For MC, the overall mean of the trait, the sex, and an interaction term between the hatch of the recorded animal, the hatch of the dam, and the day of measuring MC were included as fixed effects. BW48 was included as linear covariable for MC2 only. For LS, the overall mean of the trait, the sex and an interaction term between the hatch of the recorded animal and the hatch of the dam were included as fixed effects. For LS3, BW48 was included as a linear covariable. Variance components, fixed effects, covariables, and breeding values were estimated using MTDFREML (Boldman *et al.*, 1995).

After adjusting the phenotypic observations for fixed effects and covariables, adjustment was for the additive genetic contribution of the male or the female parent, which resulted in two adjusted trait values for each G_3 animal. In the bivariate approach, all adjusted trait values were standardized to a mean of 0 and to the variance of the male G_3 adjusted trait values. Subsequently, adjusted trait values were combined to average adjusted progeny trait values for G_2 animals by averaging over all their G_3 progeny.

Quantitative Trait Locus Analysis

The multimarker regression method for outbred populations with a half-sib structure (Knott *et al.*, 1994) was extended to enable analysis of the full-sib design (Van Kaam *et al.*, 1998, 1999). The analysis is an across-family weighted full-sib regression analysis, which is nested within families in order to account for differences in marker-QTL linkage phase. Average adjusted progeny trait values of G_2 animals were regressed on the probabilities of inheriting the first allele of each G_1 parent. In order to account for polygenic differences between families, the family mean was included in the model. Differences in number of G_3 animals contributing to G_2 average adjusted progeny trait values were taken into account by applying a weighting factor, which is based on the variance of the average adjusted progeny trait values. At each centimorgan, test statistics were calculated to test for the presence of QTL effects vs the absence of QTL effects. The test statistic was the ratio of the explained mean square of the QTL effects in the numerator and the residual mean square of the full model in the denominator. A constant number of degrees of freedom was applied across all linkage groups.

Significance Thresholds

For each trait, significance thresholds were calculated empirically using the chromosomewise permutation method (Churchill and Doerge, 1994). To obtain genomewise significance thresholds, chromosomewise significance thresholds were adjusted for multiple testing along the genome using the Bonferroni correction. Using the genomewise significance thresholds, two types of significance thresholds were derived: significant and suggestive linkage (Lander and Kruglyak, 1995). Significant linkage is defined as a 5% genomewise significance threshold and suggestive linkage is equivalent to one expected false positive result per trait in a whole genome scan. Because all parents were informative on the first 20 linkage groups, the test statistics on these linkage groups were comparable (Van Kaam *et al.*, 1998). Therefore, these linkage groups were permuted together and common thresholds were applied. For each trait, 10,000 permutations were performed. For the other linkage groups, some parents were uninformative. Hence, no QTL effect could be fitted for these parents and test statistics on these

TABLE 2. Heritabilities, genetic correlations, and phenotypic variances

Trait[1]	h^2_m[2]	h^2_f	r_g	$\sigma^2_{p,m}$[3]	$\sigma^2_{p,f}$
BW48	0.36	0.48	0.92	60,725	38,351
CW	0.36	0.47	0.93	30,055	19,628
CP	0.43	0.52	1.00	2.07	2.62

	h^2	σ^2_p
MC1	0.37	16.53
MC2	0.38	16.30
LS1	0.13	3.49
LS2	0.13	3.57
LS3	0.13	3.51

[1]BW48 = body weight at 48 d; CP = carcass percentage; CW = carcass weight; LS1 = original leg score; LS2 = transformed leg score; LS3 = transformed leg score adjusted for BW48; MC1 = meat color unadjusted for BW48; MC2 = meat color adjusted for BW48.

[2]h^2, h^2_m, h^2_f = heritability of all observations respectively only male or female observations; r_g = correlation between additive genetic effects on male and female observations; σ^2_p, $\sigma^2_{p,m}$, $\sigma^2_{p,f}$ = phenotypic variances based on all, male, or female observations.

[3]Weights are measured in grams.

linkage groups are not comparable with other linkage groups. For each of these linkage groups, 100,000 permutations were executed, because a larger Bonferroni correction was necessary to obtain reliable genomewise significance thresholds.

Permutation was also applied to determine which parents were segregating for a QTL on those locations where a QTL was detected in the across family analysis. Per parent, a test comparing a model with a QTL vs a model without a QTL was applied, accounting for the presence or absence of QTL effects in the mate. A 10% comparisonwise threshold was obtained from 10,000 permutations. Parents with a test statistic above this threshold were assumed to be segregating for the QTL.

RESULTS

Variance Components

In Table 2, estimated heritabilities, genetic correlations, and phenotypic variances are presented. Three traits, BW48, CW, and CP, have separate variance estimates per sex, because these traits were analyzed using a bivariate approach. Estimated heritabilities based on males and females differed at most 0.12. The genetic correlation between male and female observations was close to unity for all three traits. Estimated heritabilities for BW48 and CW were similar to those mentioned by Bernon and Chambers (1988) and Wang *et al.* (1991). Leg scores (LS1, LS2, and LS3) had a low heritability of 0.13, which might in part be due to the subjective scoring.

Table 3 shows the correlations between the average adjusted progeny trait values of the G_2 animals for all traits. BW48 and CW showed a very high correlation of 0.97 and, therefore, similar results were expected in the QTL analysis. This high correlation can be expected because CW is a large part of BW48. MC1 and MC2 showed a correlation close to unity. The same holds for LS1, LS2, and LS3. These high correlations indicate that the effect of the differences in the analyses were small. A moderate correlation was found between CW and CP. All

TABLE 3. Correlations between the average adjusted progeny trait values of Generation 2 animals

Trait[1]	BW48	CW	CP	MC1	MC2	LS1	LS2	LS3
BW48								
CW	0.97							
CP	0.16	0.37						
MC1[1]	0.19	0.17	–0.07					
MC2[2]	0.14	0.11	–0.08	1.00				
LS1	0.14	0.13	0.00	0.05	0.04			
LS2	0.14	0.13	–0.00	0.05	0.04	0.99		
LS3	0.06	0.05	–0.02	0.03	0.03	0.99	1.00	

[1]BW48 = body weight at 48 d; CP = carcass percentage; CW = carcass weight; LS1 = original leg score; LS2 = transformed leg score; LS3 = transformed leg score adjusted for BW48; MC1 = meat color unadjusted for BW48; MC2 = meat color adjusted for BW48.

[2]Higher values represent darker meat.

TABLE 4. Summary of interesting regions per trait. Indicated per trait are the number assigned to the quantitative trait locus (QTL), the linkage group, the most likely location in centimorgans, the markers bracketing this location and the genomewise significance level of the QTL at this location

Trait[1]	QTL	Chromosome	Location	Markers[2]	Significance[3]
					(%)
BW48	. . .	3	366	LEI166 – MCW148/MCW116	86
CW	. . .	3	365	LEI166 – MCW148/MCW116	72
CP	1	1	466	ADL183 – LEI79	17*
MC1	2	2	345	MCW185 – MCW234	38*
MC2	2	2	344	MCW185 – MCW234	42*
MC1	2	2	369	MCW264 – ADL164	41*
MC2	2	2	369	MCW264 – ADL164	48*
LS1	. . .	2	269	MCW65 – ADL212	93
LS2	. . .	2	268	MCW65 – ADL212	80
LS3	. . .	1	565	ADL238 – UMA350	64

[1]BW48 = body weight at 48 d; CP = carcass percentage; CW = carcass weight; LS1 = original leg score; LS2 = transformed leg score; LS3 = transformed leg score adjusted for BW48; MC1 = meat color unadjusted for BW48; MC2 = meat color adjusted for BW48.

[2]ADL = Avian Disease and Oncology Laboratory, Michigan State University, East Lansing; LEI = University of Leicester, Leicester; MCW = Microsatellite chicken Wageningen; UMA = University of Massachusetts, Amherst; WAU = Wageningen Agricultural University, Wageningen.

[3]*Suggestive linkage.

other combinations of traits showed a correlation close to zero.

Quantitative Trait Locus Analysis

Two QTL were detected: both QTL showed suggestive linkage. However, no QTL showed significant linkage. Two of the five analyzed traits showed QTL reaching suggestive linkage. CP showed suggestive linkage once and MC showed suggestive linkage twice in both analyses. In Table 4, the most interesting regions are presented for each trait. For BW48, CW, LS1, LS2, and LS3 the test statistic did not reach the suggestive linkage threshold on any linkage group, although LS3 came very close to it.

QTL1 (Figure 1) was located on Chromosome 1 and showed suggestive linkage for CP. The peak of the test statistic was located at 466 cM. Five sires and three dams showed significant QTL effects. The average allele substitution effect (α; Falconer, 1989) in these parents was 0.7 σ_a.

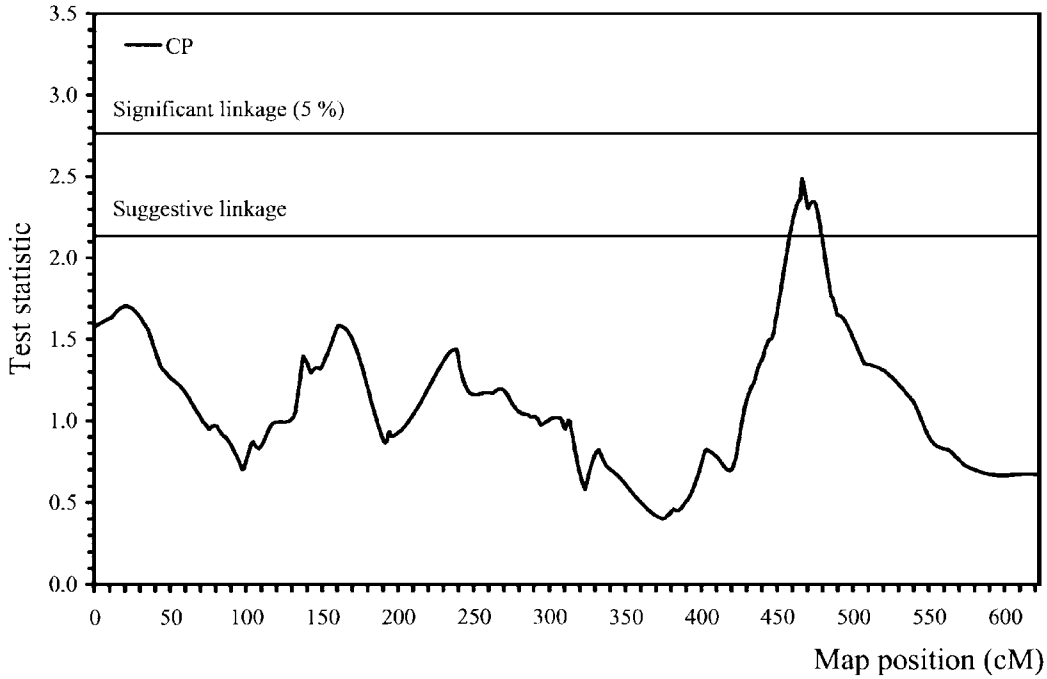

FIGURE 1. Test statistic values from the analysis of carcass percentage (CP) for quantitative trait loci on chromosome 1. Significant and suggestive linkage thresholds of CP are included. Map positions are given using the Haldane scale.

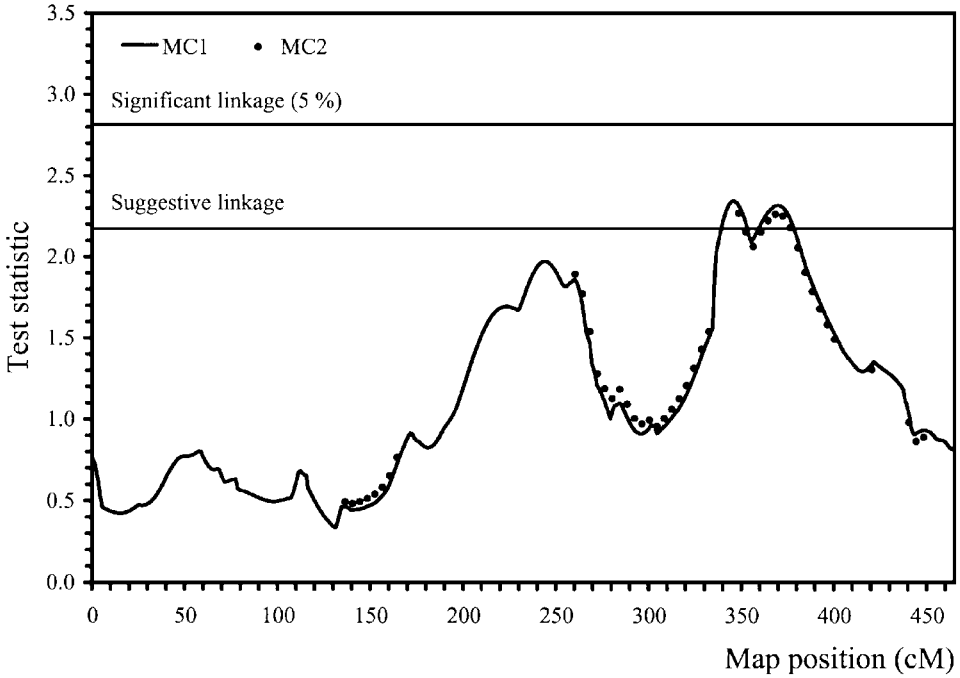

FIGURE 2. Test statistic values from the analysis of meat color unadjusted for BW at 48 d (MC1) for quantitative trait loci on chromosome 2. Significant and suggestive linkage thresholds of MC1 are included. Locations were meat color adjusted for BW at 48 d (MC2) differed from MC1 are indicated with dots. Map positions are given using the Haldane scale.

QTL2 (Figure 2) was detected on Chromosome 2. Two peaks for this QTL showed suggestive linkage for MC1 and MC2. The highest test statistic for QTL2 was found at 345 cM for MC1 and at 344 cM for MC2. In both analyses, a slightly lower test statistic was found at 369 cM between markers MCW264 and ADL164. Although the possibility of presence of more than one QTL cannot be excluded, the present data set does not provide enough evidence to conclude that more than one QTL is segregating and, therefore, one QTL is assumed. One sire and two dams showed significant QTL effects for a QTL at the first peak. In both analyses, the estimated average allele substitution effect was 1.0 σ_a in these parents. For MC1, an additional sire and two additional dams gave significance for the segregation of a QTL at the second peak. For MC2, one of these additional dams was not significant. The estimated average allele substitution effect was 1.2 σ_a in these five respectively six parents. Because the same parents tend to show the largest effect, it seems most likely that only one QTL is segregating in this region.

On Chromosome 1, at 565 cM suggestive linkage was almost reached for LS3 (Figure 3). Two sires and three dams showed significant QTL effects. The average allele substitution effect in these parents was 1.4 σ_a. The two most likely locations of LS1 and LS2 swapped in order of likelihood for LS3.

DISCUSSION

Carcass Traits

Five carcass traits have been analyzed. The traits BW48 and CW are related to the growth rate. A higher growth rate is important for farmers, because it enables them to increase the production per pen. For processors, CW is a more useful measure than BW48; however, in practice, BW48 is easier to measure. In order to increase the efficiency of growth, CP could be increased.

Meat color is important as a quality trait for processors, retailers, and consumers. Relationships between MC and several other quality traits have been reported. Lighter meat is associated with a lower pH, lower water binding capacity, lower total pigment, myoglobin, and iron concentrations, and higher cooking loss (Barbut, 1993, 1997; Boulianne and King, 1995; Allen *et al*., 1997). Darker meat is related to a higher pH, a higher susceptibility to bacterial spoilage, loss of a fresh odor, and a shorter shelf life (Fletcher, 1995; Allen *et al*., 1997). A protein that might be related to MC is myosin. The light polypeptide of the myosin gene (MYLL1) is located about 25 cM left of QTL2 at 320 cM.

Leg problems are of increasing importance for the poultry industry and can affect growth performance, efficiency, and mortality (Emmerson *et al*., 1991). Kestin *et al*. (1992) report up to 90% gait abnormalities in broilers. Furthermore, they signal an increase in gait abnormalities with increasing BW. Given the differences in prevalence of gait abnormalities between the breeds in their study, a genetic basis is assumed. With increasing BW there is a tendency towards an increase of the proportion breast muscle and a decrease of the proportion leg muscle (Emmerson *et al*., 1991; Pollock, 1997), which might increase leg problems. Leg score was measured by looking at the lateral deviation of the legs. Lateral deviation was previously scored in turkeys by Nestor (1984).

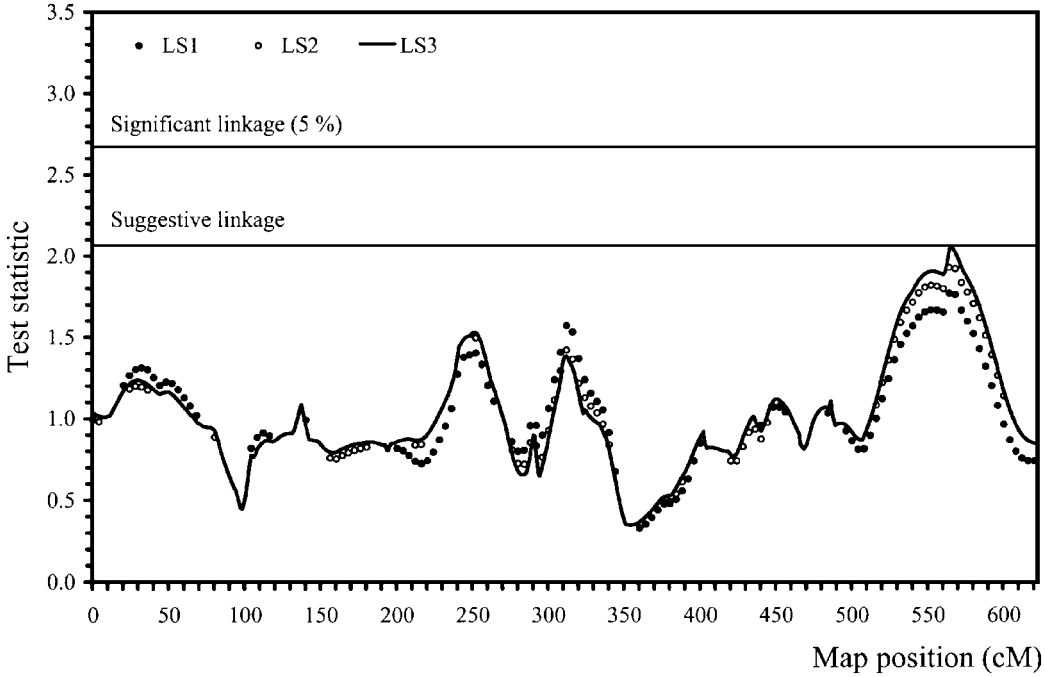

FIGURE 3. Test statistic values from the analysis of transformed leg score adjusted for BW at 48 d (LS3) for quantitative trait loci on chromosome 1. Significant and suggestive linkage thresholds of LS3 are included. Locations were original leg score (LS1) and transformed leg score (LS2) differed from LS3 are indicated with dots and circles respectively. Map positions are given using the Haldane scale.

Comparison with Previous Results

Because BW48 was also analyzed in the feed efficiency experiment (Van Kaam *et al*., 1998, 1999), it is interesting to compare the results. In the feed efficiency experiment, a QTL was located at 240 cM on Chromosome 1. Furthermore, high test statistic values were found on linkage group WAU26, although not significant for BW48. In the experiment on carcass traits, however, no evidence for the presence of QTL at these locations was found. The test statistic was below one on both locations. These differing results can be explained by the low correlation between the average adjusted progeny trait values of the G_2 animals (0.25) for BW48 in both experiments. The genetic correlation between BW48 in both experiments was 0.60. Apparently, the performance of chickens is quite different under different housing conditions, free housing vs individual housing, despite the same genetic background, availability of feed and water, and use of commercial broiler feed and a 23 h / d light scheme. The mortality rate from 22 until 48 d was 4% for both husbandry systems. It is possible that the QTL has an effect on BW48 under certain conditions and hardly any effect under other conditions, i.e., a genotype by environment interaction. Stress can be a factor causing differences between free and individual housing. In free housing there could be more competition between chickens. On the other hand, chickens housed individually can be stressed due to their limited freedom and due to change in housing at 22 d, when they were switched to individual housing. Some chickens might show temporary cessation of growth when switched to individual housing whereas other chickens seem unaffected. The low correlation between the average adjusted progeny trait values of the G_2 animals affects the power for detecting the same QTL. Tolon and Yalcin (1997) concluded that husbandry system by sex interaction significantly affected 7-wk BW in broilers. Other reasons for different results can be that the previously reported result is a false positive result or that a QTL was segregating, but was not detected.

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