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Published In:
Journal of Animal Science

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Quantitative trait locus detection in commercial broiler lines using candidate regions[1]

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ABSTRACT: A QTL that explained a large proportion of the phenotypic difference between broiler and layer chickens in an experimental cross was evaluated in a commercial broiler line. A three-generation design, consisting of 15 grandsires, 608 half-sib hens, and more than 50,000 third-generation offspring, was implemented within the existing breeding scheme of a broiler breeding company. Four markers from a candidate region on chicken chromosome 4 were selected for their informativeness in the grandsires and used to genotype the first two generations. Using half-sib analyses, linkage was studied between these markers and 13 growth and carcass traits. The QTL analyses confirmed the presence of significant QTL for body weight ($P < 0.01$) and residual feed intake ($P < 0.05$) on chicken chromosome 4. Furthermore, evidence was found for QTL affecting the relative weight of bone and muscle in the thigh. Four more markers were added to increase resolution of the QTL positions. This increased the significance of the QTL for body weight ($P < 0.001$) and residual feed intake ($P < 0.01$) and showed evidence ($P < 0.05$) for additional QTL affecting carcass weight and conformation score. This study showed for the first time that a QTL that explains differences between broilers and layers was segregating in lines that have been selected for body weight over 50 generations. A possible explanation could be a pleiotropic or closely linked effect on fitness-related traits that are not part of the present study. The results demonstrate the feasibility of QTL detection and the potential for marker-assisted selection within a commercial broiler line without altering the existing breeding scheme.

Key Words: Body Weight, Broilers, Genomes, Mapping, Poultry, Quantitative Trait Loci

Introduction

In poultry and pigs, most QTL mapping studies have been performed on crosses between genetically and phenotypically divergent lines (Andersson, 2001). In chicken, crosses that have been used to detect QTL range from broiler × layer (Sewalem et al., 2002) to crosses between two extreme broiler lines (Van Kaam et al., 1998). This approach has proved very successful in identifying QTL that explain differences between these lines, but they provide no insight into whether these QTL are segregating within current commercial lines that have been selected for at least 50 generations.

For successful implementation of marker-assisted selection, segregation of QTL needs to be verified within the selection lines. Confirmation of QTL within a commercial line is only realistic using the existing family structure and data recording of the breeding population and requires different statistical modeling compared to line-cross experiments. In this study, we assessed the feasibility and statistical power of a confirmation experiment. The first step was to find the optimal design for detecting QTL without hampering or altering the selection program. In the next step, we targeted a commercial broiler line for a published body weight QTL. We chose a region on chromosome 4 (GGA4) that has been shown to affect body weight (Van Kaam et al., 1998; Sewalem et al., 2002; Tuiskula-Haavisto et al., 2002) and feed intake (Van Kaam et al., 1999; Tuiskula-Haavisto et al., 2002).

Materials and Methods

Experimental Population and Data Collection

All the chickens used in this experiment were part of an active breeding population (The Cobb Breeding Co. Ltd., Chelmsford, U.K.). Therefore, the experiment used existing family structures arising from the mating structure of the commercial population. Following power calculations, 15 males of one broiler line were selected as grandsires in a three-generation half-sib design, based on the number of daughters available for these birds. Blood samples were collected on the grandsires (**G1**), their mates, and all the second-generation (**G2**) hens. From the offspring of these hens, the third generation (**G3**), only phenotypic information was gathered. Traits that are routinely measured on all birds included body weight at 40 d and conformation score. Prior to selection, a proportion of the birds was randomly selected for carcass dissection to allow sufficient numbers for QTL analysis. Following truncation selection on body weight, a proportion of the birds was subsequently tested for 2 wk for feed consumption and growth, whereas the remaining birds were culled after 40 d. This included all the selection candidates, so phenotypes that are derived from the test results are available for all animals in the first two generations and a proportion of animals in the third generation.

Genotyping and Map Construction

Markers in the QTL region on chicken chromosome 4 (GGA4) were selected from the consensus linkage map (Schmid et al., 2000) and tested for heterozygosity in the 15 grandsires. From a total of 14 reliable microsatellite markers, six were monomorphic across all grandsires and the remaining eight showed a heterozygosity between 50 and 85%. Initially, four markers covering 58 cM of GGA4 on the consensus linkage map were typed across the 15 grandsires, their mates (104 granddams), and a total of 604 G2 hens. Details on PCR amplification and gel electrophoresis can be found in Sewalem et al. (2002). Marker distances were estimated with the "build" option of Crimap (Green et al., 1990), and then subsequently with the "flips" option to evaluate alternative marker orders compared to the marker order of the consensus map. Following positive results of the initial QTL analyses, four more markers were typed across the population in an attempt to refine the QTL position and determine the number of QTL.

Analysis of Phenotypic Data

Prior to QTL analysis, trait scores for the G2 hens needed to be derived from the trait data that was gathered on the hens themselves and/or on the G3 birds. Although the emphasis was on the confirmation of QTL for body weight and feed intake, we used infor-mation on all recorded traits for the QTL analysis. Trait definitions were chosen according to those used by the breeding company, although some additional traits were derived. For the thigh and the drum, the weight of the muscle divided by that of the corresponding bone was used as the meat:bone ratio. To get optimal estimation of fixed effects and covariates, all available pedigree and phenotypic information from the generations involved in this experiment were used. The fixed effects of sex and hatch within flock were used for all traits, except those recorded during the 2-wk test, which had separate contemporary groups. For body weight-related traits, age of dam was included as an additional fixed effect. Residual feed intake (**RFI**) was defined as feed intake during test adjusted for average body weight (to account for maintenance) and growth during test (to account for "production"). Conformation score was subjectively scored from 1 to 6 with increasing breast muscle mass. Because the distribution of the conformation scores mimicked a normal distribution, it was analyzed as if the scores were normally distributed. All carcass measures were evaluated with dissection weight as a covariate, except for the meat:bone ratios. An overview of traits and their phenotypic means is presented in Table 1. Following exploratory analyses with GENSTAT (Lawes Agricultural Trust, Harpenden, U.K.), variance components were estimated with ASREML (Gilmour et al., 2000). The initial model included all the fixed effects and covariates, as well as a random polygenic component. Subsequently, a direct maternal effect was added to the model and tested against a polygenic model with a likelihood ratio test. When the direct maternal effect was significant, the model was extended with a genetic maternal component. It was then tested whether there was a significant correlation between the maternal genetic and polygenic component.

Derivation of Trait Scores

For the QTL analyses, trait scores for the G2 dams were derived in two ways. The first way was with offspring yield deviations (**OYD**), where the trait scores are an average of the G3 trait scores adjusted for systematic effects and any maternal effects. The initial trait score for every offspring was the EBV plus the residual after the ASREML analyses. To account for sex differences, the male trait scores were scaled to have the same mean and variance as the female trait scores. Subsequently, half the offspring's sire genotype was deducted from the trait score because we were only interested in genes coming from the G2 hens. This procedure was similar to that employed by Van Kaam et al. (1998). For traits where the G2 hens also had observations, these were combined with the G3 observations using a selection index formula:

$$Index = b_1 X_1 + b_2 X_2 \qquad [1]$$

Table 1. Characteristics for 13 traits that were derived from the commercial broiler breeding population

Trait	Mean[a]	SD	$h^2 \pm$ SE	Maternal effect[b]	N	Average G2/G1[c]	Average G3/G2[d]
Body weight at 40 d, g	2,415	276	0.11 ± 0.01	0.02/0.01	50,398	35	28
Feed conversion during test	1.82	0.31	0.07 ± 0.01	—	11,060	29	5
Residual feed intake during test, g	1,042	223	0.11 ± 0.02	0.02	11,060	29	5
Conformation score	3.35	0.88	0.23 ± 0.02	0.01	50,676	35	29
Dissection weight at 41 d, g	2,291	268	0.10 ± 0.03	0.04	6,432	31	11
Abdominal fat weight, g	28	10	0	—	6,095	31	10
Breast muscle weight, g	450	67	0.43 ± 0.04	—	6,095	31	10
Thighbone weight, g	20	4.5	0.06 ± 0.02	—	4,078	30	10
Thigh muscle weight, g	92	13	0.10 ± 0.03	0.02	4,078	30	10
Thigh meat:bone ratio	4.8	1.1	0.10 ± 0.02	—	4,078	30	10
Drumbone weight, g	33	7.3	0.07 ± 0.02	—	4,084	30	9
Drum muscle weight, g	76	13	0.16 ± 0.03	—	4,084	30	9
Drum meat:bone ratio	2.4	0.7	0.04 ± 0.02	—	4,084	30	9

[a]Raw phenotypic means.
[b]Proportion of total variance explained by the direct maternal effect. The second value is for the maternal genetic effect.
[c]Average number of second generation hens/grandsire with at least one informative offspring.
[d]Average number of third generation offspring per second generation hen.

where X_1 is the adjusted trait score of a second-generation hen and X_2 is the mean adjusted trait score of n full-sib offspring of this hen. The weighting factors b_1 and b_2 were derived using:

$$\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = \begin{bmatrix} 1 & 0.5h^2 \\ 0.5h^2 & \dfrac{1 + 0.5(n-1)h^2}{n} \end{bmatrix}^{-1} \begin{bmatrix} h^2 \\ 0.5h^2 \end{bmatrix} \qquad [2]$$

where h^2 is the polygenic heritability of the trait. To account for heterogeneity in the number of offspring between hens, we used the reliability (R^2) of this index as a statistical weight in the QTL analyses:

$$R^2 = \frac{\begin{bmatrix} b_1 \\ b_2 \end{bmatrix}' \begin{bmatrix} \sigma_a^2 \\ 0.5\sigma_a^a \end{bmatrix}}{\sigma_a^2} \qquad [3]$$

where σ_a^2 is the additive genetic variance of the trait. When only information on offspring is used, Eq. [3] reduces to:

$$R^2 = \frac{0.25h^2 n}{1 + (n-1)0.5h^2} \qquad [4]$$

A second trait score was defined by using the EBV of the G2 hens, adjusted for information coming from other relatives besides their offspring by deducting the mean of the parental EBV of each hen. The weighting factor that was used in the QTL analysis was the same as that for the OYD. For traits that were inferred to have a significant direct and or maternal genetic effect, the estimated effects from ASREML for each hen were included as a separate trait in the QTL analyses.

Power Calculations

The power of the half-sib design was assessed with the deterministic formulae proposed by Van Der Beek et al. (1996). The formulae assume all grandsires to be heterozygous for the markers and also assume a balanced design with equal family sizes. Other relevant parameters, such as heterozygosity for the QTL, distance between markers, number of offspring, and size of effect, can be varied to test their effect on the power of the experiment. In the planning stages of the experiment, it became clear that family size, QTL effect, and heterozygosity of grandsires for the QTL were the major factors affecting the power of the experiment. For the results presented here, we used the realized half-sib family size and number of G3 offspring. Assuming a polygenic heritability of 0.35, a marker spacing of 10 cM, and a significance threshold of $P < 0.05$, we evaluated 1) the power for different QTL effects given a heterozygosity of 50% and 2) the power for different heterozygosities, given a QTL effect of 0.40 phenotypic SD.

Quantitative Trait Locus Analyses

Quantitative trait locus analyses were performed under a half-sib model using the QTL Express software at http://qtl.cap.ed.ac.uk/ (Seaton et al., 2002). The analysis uses the multimarker approach for interval mapping in half-sib families, as described by Knott et al. (1996) and applied to QTL mapping studies in cattle (De Koning et al., 1998) and pigs (De Koning et al., 1999). Within every half-sib family, a QTL was fitted at 1-cM intervals along the chromosome:

$$y_{ij} = m_i + b_i p_{ij} + e_{ij} \qquad [5]$$

where y_{ij} is the trait score of hen j (either adjusted

EBV or OYD), originating from male i; m_i is the average effect for half-sib family i; b_i is the substitution effect for a putative QTL; p_{ij} is the conditional probability for individual j of inheriting the first paternal haplotype; and e_{ij} is the residual effect. The test statistic is calculated as an F-ratio for every map position across families, whereas within families, a t-test is calculated for most likely position of a QTL. Because this study was aimed at confirmation of QTL and not at detecting new QTL, we imposed a nominal threshold of $P < 0.05$ on the across-family F ratio to claim confirmation of a QTL. Once a QTL was detected in the across-family analyses, tabulated values ($P < 0.05$) of the t-tests for the individual families were used to infer which families were likely to be segregating for the QTL.

Results

Power Assessment

Table 1 includes an overview of the average number of G3 offspring for every trait. This shows that the traits can be divided in three groups: 1) the body weight traits, with an average of 35 informative hens/family that have an average of 29 offspring/hen; 2) carcass traits with an average half-sib family size of 31 and 11 offspring/dam; and 3) feed-conversion traits with an average half-sib family size of 29 and 5 offspring/dam. The difference in power between the three groups is apparent across a wide range of QTL effects and grandsire heterozygosities (Figure 1). The design was considered suitable to confirm a QTL of moderate to large effect (>0.4 SD), provided it was segregating at a sufficient frequency (>30%). It must be noted that the curve for body weight and feed conversion-related traits do not take the G2 observations into account, which means the values in Figure 1 are an underestimation of the actual power.

Analyses of Phenotypic Traits and Map Construction

The estimated heritabilities and maternal effects are summarized in Table 1. In general, these values are slightly lower than those published by Van Kaam et al. (1998; 1999), but they were estimated on a crossbred population. Body weight showed both a significant direct maternal and maternal genetic effect, whereas a significant direct maternal effect was present for residual feed intake, conformation score, dissection weight, and thigh meat weight (Table 1).

The initial map with four markers spanned 56 Kosambi cM, which is consistent with the consensus map (Schmid et al., 2000). The order of markers on the consensus map was confirmed using the flips option of Crimap (Green et al., 1990). From the additional four markers, two mapped within the region spanned by the initial four markers, whereas the linkage group was extended toward the distal end of GGA4 by the
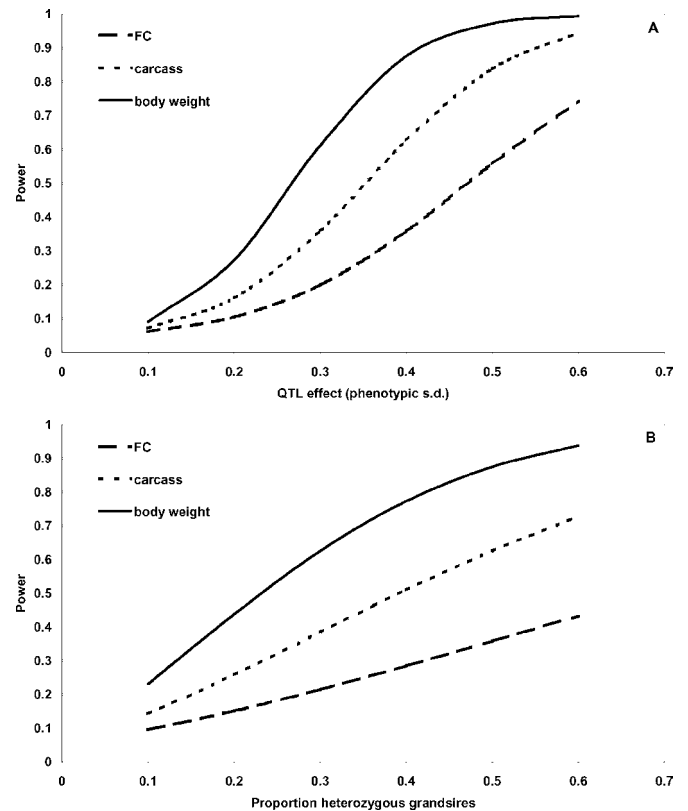

Figure 1. Power of the half-sib design for three different trait groups given different QTL effects (A) or proportion of informative grandsires (B).

other two markers. The final linkage map spanned 87 Kosambi cM. For the QTL analyses these distances were converted to Haldane cM, which extended the region analyzed to 102 cM.

Quantitative Trait Locus Analyses

The results were very similar whether we analyzed adjusted EBV or OYD. However, using adjusted EBV generally gave slightly higher F-ratios, and the results presented in this section are those obtained with the adjusted EBV. The results of the QTL analyses are summarized in Table 2. The initial analyses using four markers showed highly significant QTL for body weight and thigh muscle weight. Further evidence for QTL ($P < 0.05$) was found for residual feed intake, thighbone weight, and the direct maternal effect affecting body weight (Table 2). These QTL explained between 9 and 15% of trait variance at the population level (Table 2).

Adding the additional four markers increased significance for all the QTL that were detected using the four initial markers (Table 2). Additional QTL were detected for the maternal genetic effect on body weight ($P < 0.01$), the direct maternal effect for residual feed intake ($P < 0.001$) and conformation score ($P < 0.05$), feed conversion ($P < 0.05$), and dissection weight ($P < 0.01$). The test statistics along the GGA4 region for

Table 2. Overview of quantitative trait loci results for chicken
chromosome 4 using four and eight markers

Trait[a]	Four markers			Eight markers		
	Position, cM	F ratio	Effect[b]	Position, cM	F ratio	Effect[b]
Body weight	41	2.44**	0.14	37	3.30***	0.21
MD	41	1.87*	0.10	38	2.47**	0.16
MG	37	1.59	0.06	103	2.15**	0.11
Feed conversion	41	1.10	0	22	1.7*	0.04
Residual feed intake	6	2.05*	0.10	9	2.33**	0.14
MD	0	1.89*	0.12	15	2.71***	0.22
Conformation score	27	1.33	0.03	97	1.43	0.04
MD	61	1.45	0.05	91	1.88*	0.10
Dissection weight	0	1.05	0.01	22	2.08**	0.13
Abdominal fat	1	0.88	0	85	0.94	0
Breast muscle	0	1.36	0.04	18	1.41	0.05
Thighbone	44	1.96*	0.13	41	2.06*	0.14
Thigh muscle	61	2.12**	0.15	96	2.12**	0.15
Thigh meat:bone ratio	45	1.58	0.08	40	1.67	0.09
Drumbone	41	1.32	0.04	41	1.21	0.03
Drum muscle	0	0.80	0	30	1.20	0.03
Drum meat:bone ratio	41	1.21	0.03	41	1.51	0.08

[a]MD and MG denote respectively, the direct maternal and the maternal genetic effect of the preceding trait.

[b]Proportion of variance explained by the QTL, assuming a polygenic heritability of 0.10.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

four traits with the additional markers are presented in Figure 2. The most likely position of a QTL affecting body weight and thighbone weight has shifted to the left of marker ADL0194 compared with the analysis with four markers. Note that the most likely position for the QTL affecting the maternal genetic effect on body weight is at the distal end of the region (Table 2). The most likely position for the QTL affecting thigh muscle weight has also shifted to the distal end, although the curve is very flat (Figure 2).
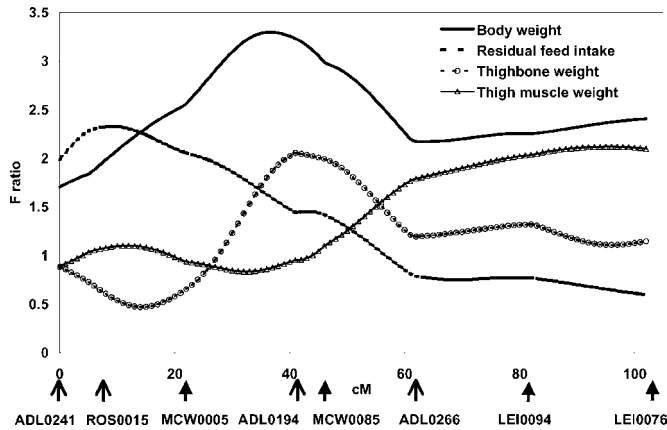

Figure 2. Test statistic along chicken chromosome 4. The horizontal line denotes the nominal threshold of $P < 0.05$. Marker names and positions are indicated under the x-axis. Open arrows indicate the locations of the initial four markers, whereas closed arrows depict the additional four markers.

The markedly different QTL positions suggest that there could be up to three different QTL segregating on this region of GGA4. One QTL affecting feed intake and two other QTL affecting different aspects of growth. Statistical proof for different QTL would be given by nonoverlapping confidence intervals for the QTL affecting different traits. Unfortunately, bootstrapping analyses following Visscher et al. (1996) showed that the 90% confidence interval for the body weight QTL comprised the entire length of the analyzed region on GGA4. This is common in half-sib designs and largely reflects the heterogeneity in best QTL positions between individual families (De Koning et al., 1998). Another approach is to look at the families that are inferred to be segregating for the QTL. If the same QTL is affecting several traits, the same families are expected to be informative for these QTL. Table 3 summarizes the effects for the informative families, for all QTL that had $P < 0.01$ in the analyses using eight markers. For body weight, the families that are segregating for the QTL affecting the adjusted EBV and the direct maternal effect are different from those segregating for the maternal genetic effect. Family 5 was segregating for the QTL affecting residual feed intake and dissection weight, but not for the body weight QTL ($P > 0.60$). The families that were inferred to be segregating for the thigh muscle QTL were not segregating for any of the other QTL. This points toward the existence of multiple QTL affecting different traits on this region of GGA4 rather than a single pleiotropic QTL.

The allele substitution effects of the body weight QTL ranged from 14 to 23 g in EBV, 9 to 16 g for the

de Koning et al.

Table 3. Standardized quantitative trait loci effects for the families that were inferred to be segregating for the most significant ($P < 0.01$) QTL from the analyses with eight markers

Trait[a]	Family effects standardized to within-family trait standard deviations								
Family	3	5	6	7	8	11	12	14	15
Body weight	0.38**	—	—	0.41*	—	—	0.38*	0.51**	—
MG		—	0.42*	—	0.45*	—	—	—	—
MD	0.38**	—	—	0.40*	—	—	0.32*	0.40*	—
Residual feed intake	—	0.47*	—	—	—	—	0.51**	—	—
MD	—	0.80***	—	—	—	—	—	—	—
Dissection weight	0.41**	0.62**	—	—	—	—	—	—	—
Thigh muscle	—	—	—	—	—	0.51**	—	—	0.34**

[a]MD and MG denote the direct maternal and the maternal genetic effect of the preceding trait, respectively.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ for the t-test on the within-family substitution effect.

direct maternal effect, and 6 to 8 g for the maternal genetic effect. The size of these effects approximates 0.3 to 0.5 within family trait deviations (Table 3). For residual feed intake, the allele substitution effects were 8 to 9 g in EBV and 6 g in direct maternal effect. For dissection weight and thigh muscle weight, the effects for EBV were 13 to 17 g and 0.7 to 0.9 g, respectively. The largest standardized effect was for the direct maternal effect on residual feed intake (0.80 SD), which was also the QTL that explained most variance across the population (Table 2). The heterozygosity of grandsires for the QTL was 0.3 or lower. However, this was probably underestimated because for some QTL, up to five additional families show t-tests with $0.15 > P > 0.05$, and some of these grandsires will contribute significantly to the reduction in variance across families.

Discussion

The results of this study show the feasibility of a QTL confirmation experiment within a commercial broiler-breeding program. The results for GGA4 confirm the predictions made by the power calculations that the design has considerable power to detect QTL with an effect >0.4 SD. It must be noted that the initial four markers were sufficient to confirm the QTL for body weight and residual feed intake. The four additional markers were added to verify whether the QTL for body weight, residual feed intake, and thigh muscle weight mapped to different marker intervals on GGA4. The higher power when using eight markers (Table 2) is largely a result of the increased information content in the interval between ROS0015 and ADL0194 compared to the analyses with four markers (data not shown).

The use of a point-wise threshold of $P < 0.05$ might be considered too liberal because we had been testing >100 positions on GGA4 for 13 traits. However, when attempting to confirm a published QTL in an independent study, Lander and Kruglyak (1995) proposed to impose a point-wise threshold of $P < 0.01$ to claim confirmed linkage. Imposing these guidelines would

imply confirmed linkage for QTL affecting (residual) feed intake and body weight. To our knowledge, no QTL for conformation score, thighbone weight, and thigh muscle weight have been reported for GGA4, so these findings should formally be adjusted for multiple testing. By doing so, the QTL affecting thigh muscle weight could still be considered to be a new, suggestive QTL.

In poultry, maternal effects have been reported for body weight and a range of other traits (Koerhuis and Thompson, 1997; Van Kaam et al., 1998; Pakdel et al., 2002). There is the maternal genetic component, which is an additive effect of the hen that is expressed in the offspring, and the direct maternal effect, which reflects a permanent environmental maternal effect. Although maternal effects may have a genetic component, they are an environmental source of variation with regard to the offspring (Lynch and Walsh, 1998). Any maternal effects in poultry have to be egg-related because there is no permanent "litter" environment. Al-Murrani (1978) showed a significant effect of egg weight and protein content on body weight from hatching up to 56 d of age. Because the effect on body weight is apparent for several weeks, it is actually not that surprising that significant maternal effects were also observed for residual feed intake. Although egg weights were not available for this study, Tuiskula-Haavisto et al. (2002) detected an egg weight QTL in the same region on GGA4 that harbored the QTL for body weight. Therefore, the present QTL for a maternal effect on body weight and residual feed intake could be the correlated response of an egg weight QTL. Unlike Koerhuis and Thompson (1997) and Pakdel et al. (2002), we have only maternal full-sibs and no maternal half-sibs. As a result, we cannot distinguish a maternal genetic effect from a dominance effect because the two are completely confounded in our data. Results for the maternal effects on the slaughter traits were omitted because for these traits, there is only information on the G3 birds. The correlation between the EBV for any of these traits and the estimates for the maternal effect for a G2 hen are bound to be close to 1 because they are derived from exactly the same

information, only scaled by the proportion of variance attributed to the polygenic and direct maternal component. For the traits where the G2 hens also have their own observations, this correlation is <1, which is reflected by the QTL results for these traits. Even though we do not know the true nature of the maternal effects, they provide additional clues about the mode of action of a QTL.

Assuming that broiler breeding in its present form started in the 1950s, and that a generation interval of 8 to 12 mo is appropriate, the present broiler population has been through 50 to 75 generations of selection for increased growth and feed efficiency. The finding that a QTL that explains differences between broilers and layers also explains up to 20% of the genetic variance within a commercial broiler line is very surprising. It raises questions as to how selection affects the individual genes, and under which scenarios genes with such large effects could still be segregating in a commercial population. A possible explanation could be an effect on fitness-related traits that are not part of the present study, either as a pleiotropic effect of the gene(s) affecting growth and feed intake or the effect of a closely linked gene. Our results corroborate earlier suggestive evidence that genes with sizeable effects on body weight and feed intake are still segregating on GGA4 in broilers, as reported by Van Kaam et al. (1998; 1999), who analyzed a cross between two divergent broiler lines.

Although the QTL for residual feed intake, body weight, and thigh muscle weight map to different marker intervals and different families appear to be segregating for these QTL, we have no definite answer as to the number of QTL on this region of GGA4. The multiple-trait analyses of Knott and Haley (2000) provides a test for pleiotropic vs. linkage of multiple QTL, but their approach has not yet been implemented for half-sib designs. Fitting of multiple QTL is technically an option, but only for a single trait at the present time. Both a multivariate and a multiple-QTL approach would be hampered by heterogeneity of informativeness across the linkage group between different families (De Koning et al., 1998).

Farnir et al. (2002) and Meuwissen et al. (2002) demonstrated two approaches in which an outbred half-sib design was utilized to fine-map a QTL using historical recombinations. Single nucleotide polymorphisms provide a new tool to characterize the genome at the fine-mapping level. Using the present broiler population for fine mapping could identify haplotypes that are in linkage disequilibrium with the traits of interest. If there is more than one QTL, this should result in different haplotypes being identified for these traits. Furthermore, if the same region were targeted in an advanced intercross line (Darvasi and Soller, 1995) of the cross where the QTL were initially detected, comparison of haplotypes across studies would elucidate whether different studies detected the same gene or different genes that mapped to the same QTL area.

Confirmation of QTL within commercial lines provides the prospect of marker-assisted selection for these QTL within the commercial lines. However, until a conserved haplotype is identified, selection has to be done within families, and the phase between the QTL and the parental markers has to be re-estimated for every generation. A conserved haplotype would allow for association testing across the population, which gives a better estimation of the true effect. Before implementation in a breeding program, all pleiotropic effects of the QTL should be evaluated in order to avoid any unwanted correlated response.

Implications

A region of chicken chromosome 4, affecting body weight and feed intake in experimental chicken populations, has been shown to explain a significant proportion of genetic variance within a commercial broiler line. Other effects were found for the weight of the thigh muscle and a subjective score of fleshiness. The discovery that the same chromosome regions that explain differences between divergent lines also explain variation within lines that have been under selection for these traits for over 50 generations raises questions about effects of selection on gene frequencies and possible correlated effects of these genes. This detection of significant quantitative trait loci could be used to make broiler-breeding programs more efficient, but before this is attempted, further scrutiny of the effects on all relevant traits, and a refinement of the location of the quantitative trait loci are required.

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