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Segregation of QTL for production traits in commercial meat-type chickens

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Summary

This study investigated whether quantitative trait loci (QTL) identified in experimental crosses of chickens provide a short cut to the identification of QTL in commercial populations. A commercial population of broilers was targeted for chromosomal regions in which QTL for traits associated with meat production have previously been detected in extreme crosses. A three-generation design, consisting of 15 grandsires, 608 half-sib hens and over 15 000 third-generation offspring, was implemented within the existing breeding scheme of a broiler breeding company. The first two generations were typed for 52 microsatellite markers spanning regions of nine chicken chromosomes and covering a total of 730 cM, approximately one-fifth of the chicken genome. Using half-sib analyses with a multiple QTL model, linkage was studied between these regions and 17 growth and carcass traits. Out of 153 trait × region comparisons, 53 QTL exceeded the threshold for genome-wide significance while an additional 23 QTL were significant at the nominal 1% level. Many of the QTL affect the carcass proportions and feed intake, for which there are few published studies. Given intensive selection for efficient growth in broilers for more than 50 generations it is surprising that many QTL affecting these traits are still segregating. Future fine-mapping efforts could elucidate whether ancestral mutations are still segregating as a result of pleiotropic effects on fitness traits or whether this variation is due to new mutations.

1. Introduction

In chicken, as in other species, crosses between extreme lines have been used to detect quantitative trait loci (QTL) that explain phenotypic differences between the lines. These experimental populations include crosses between native jungle fowl and White Leghorn (Carlborg *et al*., 2003), broiler and White Leghorn (Sewalem *et al*., 2002) and 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 as to whether these QTL are segregating within current commercial lines that have been selected for at least 50 generations. Indeed, following more than 50 generations of selection for efficient growth, it is expected that loci with major effects on growth will be fixed for the high-growth alleles within the broiler lines, unless there are other mechanisms that maintain variation at these loci. Hence, most of the extreme crosses have been analysed under the assumption that the founder breeds are completely fixed for alternative QTL alleles (Haley *et al*., 1994). However, for successful implementation of marker-assisted selection within a population, segregation of QTL needs to be verified within the commercial 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 study designs and statistical analyses compared with line-cross experiments. Following the preliminary results

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Table 1. *Trait means and genetic parameters for 13 traits in a commercial broiler breeding population*

Trait	Mean[a]	SD	$h^2 \pm$ SE	Maternal effect[b]	Average reliability[c]
Body weight 40 days, g	2415	276	0·11 ± 0·01	0·02/0·01	0·30
Feed conversion during test	1·82	0·31	0·07 ± 0·01	–	0·10
Residual feed intake during test, g	1042	223	0·11 ± 0·02	0·02	0·16
Conformation score	3·35	0·88	0·23 ± 0·02	0·01	0·43
Dissection weight at 41 days, g	2291	268	0·10 ± 0·03	0·04	0·18
Abdominal fat weight, g	28	10	0·00 ± 0·01	–	–
Breast muscle weight, g	450	67	0·43 ± 0·04	–	0·33
Thighbone weight, g	20	4·5	0·06 ± 0·02	–	0·10
Thigh muscle weight, g	92	13	0·10 ± 0·03	0·02	0·16
Thigh meat to bone ratio	4·8	1·1	0·10 ± 0·02	–	0·10
Drumbone weight, g	33	7·3	0·07 ± 0·02	–	0·12
Drum muscle weight, g	76	13	0·16 ± 0·03	–	0·21
Drum meat to bone ratio	2·4	0·7	0·04 ± 0·02	–	0·08

[a] Raw phenotypic means.
[b] Proportion of total variance explained by the direct maternal effect. Second value is for the maternal genetic effect.
[c] Expected fraction of additive genetic variance explained by breeding values (EBV).
– Indicates that the direct maternal effect was not significant.

for a region on chicken chromosome 4 (De Koning *et al*., 2003), we have tested eight additional candidate regions for which QTL have been reported in extreme crosses on a commercial broiler line.

2. Material and methods

(i) *Experimental population and phenotypic traits*

Following power calculations (De Koning *et al*., 2003), 15 males of a broiler dam line (The Cobb Breeding Company Ltd, Chelmsford, UK) were selected as grandsires in a three-generation half-sib design. Blood samples were collected on the grandsires (G1), their mates (104) and 608 second-generation (G2) hens. For 80 hens only their own observations for body weight, conformation and test data were available, leaving 524 G2 hens with phenotypic data on at least one offspring with an average family size of 35. On 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 days and conformation score. Prior to selection, a proportion of the birds were randomly selected for carcass dissection to allow sufficient numbers for QTL analysis. Following truncation selection on body weight, a proportion (~20%) of birds was tested for 2 weeks for feed consumption and growth, while the remaining birds were culled at 40 days of age. Thirteen traits were derived from the observations (Table 1). For body weight and conformation score observations were available on >50 000 birds (15 000 G3 offspring and their contemporaries) with an average of 28 offspring for every G2 hen. For nine carcass-related traits, an average of nine offspring phenotypes were available for each of 477 G2 hens. For the feed intake and growth data during a 2 week test, an average of five offspring was available for 440 G2 hens. Following exploratory analyses using GENSTAT (Lawes Agricultural Trust, Harpenden, UK), variance components were estimated using ASREML (Gilmour *et al*., 2000). The initial model included the fixed effects (sex, hatch within flock, and age of dam for all traits), covariates (body weight for all carcass proportions, mid-weight and growth during test for feed efficiency traits) as well as a random polygenic component. The initial model included all the fixed effects and covariates as well as a random polygenic component:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}, \quad (1)$$

where **y** is a vector of phenotypes, **b** is a vector of fixed effects and covariates, **u** is a vector of random direct polygenic effects (estimated breeding values: EBV) and **e** is a vector of residuals. **X** is an incidence matrix relating fixed effects and covariates to observations and **Z** is an incidence matrix relating observations to random direct polygenic effects. Subsequently a direct maternal effect was added to the model and tested against a polygenic model with a likelihood ratio test.

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Vc} + \mathbf{e}. \quad (2)$$

Variables are as in (1) with the addition of **c**, a vector of random direct maternal effects and **V**, an incidence matrix relating direct maternal effects to observations. When the direct maternal effect was significant the model was extended with a genetic maternal

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Table 2. *Candidate regions from four experimental crosses*

Chromosome	Marker interval (positions)[a]	QTL in experimental crosses[b]
1	MCW0011–MCW0112 (98–205)	Body weight[1,3,4], feed intake[1], thigh yield[3]
3	ADL0237–MCW0037 (275–317)	Body weight[4], fatness[3]
4	ADL0241–LEI0076 (80–182)	Body weight[2,3,4], feed intake[1,2]
5	MCW0090–MCW0032 (57–128)	Body weight[4], fatness[3], lean-to-bone ratio[3]
7	LEI0064–MCW0236 (0–109)	Body weight[3,4], leg yield[3], fatness[3], lean-to-bone ratio[3]
8	ROS0026–MCW0100 (14–46)	Body weight[3,4], breast yield[3]
9	ROS0078–MCW0135 (0–57)	Body weight[4], fatness[3], lean-to-bone ratio[3]
11	LEI0110–ROS0112 (18–88)	Body weight[4]
13	MCW0213–ADL0214 (22–74)	Body weight[3,4], fatness[3], leg yield[3], lean-to-bone ratio[3]

[a] Positions on consensus linkage map in Schmid *et al*. (2000).
[b] Restricted to traits that resemble those in the present study. Superscripts indicate in which cross the QTL was detected: [1] Wageningen University extreme broiler cross (Van Kaam *et al*., 1998, 1999*a*, *b*); [2] Agrifood Research Finland extreme layer cross (Tuiskula-Haavisto *et al*., 2002); [3] Roslin Institute broiler × layer cross (Ikeobi *et al*., 2002; Sewalem *et al*., 2002; Ikeobi *et al*., 2004); [4] Uppsala Red Jungle Fowl × White Leghorn cross (Carlborg *et al*., 2003).

component and its significance evaluated with a likelihood ratio test against model (2):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wd} + \mathbf{Vc} + \mathbf{e}, \quad (3)$$

where **d** is a vector of random maternal genetic effects and **W** is an incidence matrix relating maternal genetic effects to observations. For the QTL analyses, trait scores for the G2 dams were derived from 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. An alternative to using adjusted EBV is to calculate offspring yield deviations (OYD) as was done by Van Kaam *et al*. (1998) and in our previous work (De Koning *et al*., 2003). However, the adjustment of the EBV is more straightforward than obtaining the OYD, especially because the EBV of the G2 sires (mated to our G2 hens) may be biased when they were mated only to a single or few hens. Furthermore, Dolezal *et al*. (2003) showed that adjusted EBV and OYD are very closely correlated. To account for different numbers of offspring between G2 hens, the reliability of the EBV was used as a weighting factor in the QTL analyses (Table 1). The estimation of direct maternal (MD) and the maternal genetic (MG) effects used additional information compared with the EBVs for traits that were also measured on the G2 hens. Therefore, the estimated maternal effects from ASREML for body weight (direct and genetic), conformation score and residual feed intake were included as four additional traits in the QTL analyses. For a more detailed description of the phenotypes and the derivation of QTL trait scores see De Koning *et al*. (2003).

The adjusted EBVs for all traits were analysed jointly by GENSTAT to obtain estimates of the correlations between trait scores. A principal component analysis was also performed to assess the number of independent traits among the 17 traits that were analysed.

(ii) *Genotyping and map construction*

Nine regions on chicken chromosomes 1, 3, 4, 5, 7, 8, 9, 11 and 13 were selected because they showed evidence for body-weight-related QTL in one or more genome scans. Marker coverage of these chromosomal regions and the QTL identified in these regions in four experimental populations are summarized in Table 2. Microsatellite markers in the candidate regions were selected from the consensus linkage map (Schmid *et al*., 2000) and tested for heterozygosity in the 15 grandsires. Genotypes were obtained on the G1 and G2 animals for 52 microsatellite markers with three to ten markers per candidate region. Details on PCR amplification and gel electrophoresis are given by Sewalem *et al*. (2002). Marker distances were estimated using the 'build' option of Crimap (Green *et al*., 1990), subsequently using the 'flips' option to evaluate alternative marker orders compared to the marker order of the consensus map.

(iii) *QTL analysis*

The methodology is based on the half-sib analyses proposed by Knott *et al*. (1996). Exploratory QTL analyses were performed using the QTL Express

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software at http://qtl.cap.ed.ac.uk/ (Seaton *et al.*, 2002), followed by analyses under a multiple QTL model using a modification of the methodology proposed by De Koning *et al.* (2001). In the first step of the multiple QTL analyses, the candidate regions are analysed individually fitting a single QTL within every family:

$$Y_{ij} = \mu_i + b_i X_{ij} + e_{ij}, \quad (4)$$

where Y_{ij} is the phenotype of j, offspring of sire i, μ_i is the mean of sire family i, b_i the allele substitution effect of the QTL within family i, X_{ij} the probability that animal j inherited the (arbitrarily assigned) first haplotype of sire i, and e_{ij} is the residual effect. In the second step, the best positions on every chromosome that exceeded a point-wise 5% threshold were identified and all the regions were re-analysed with the QTL that were on all other chromosomes as cofactors:

$$Y_{ij} = \mu_i + b_i X_{ij} + \sum_{k=1}^{n} b_{ik} X_{ijk} + e_{ij}, \quad (5)$$

where variables are identical to (1), except for the term $\sum_{k=1}^{n} b_{ik} X_{ijk}$, which describes the multiple regression of the n cofactors that are on chromosomes other than the one under study. If this analysis revealed additional putative QTL, or the best positions of the QTL change, the selection of cofactors was modified and the regions were re-analysed. This step was repeated until no new QTL were identified or dropped from the model, and the positions of the QTL were stable. The difference between this analysis and that of De Koning *et al.* (2001) is that in the present study the cofactors were maintained in the model continuously, while De Koning *et al.* (2001) adjusted the trait scores for cofactor effects prior to re-analysing the chromosomes. The proportion of within-family variance explained by each QTL (h^2_{QTL}) was approximated following Knott *et al.* (1996):

$$h^2_{QTL} = 4*[1-(MSE_{full}/MSE_{reduced})], \quad (6)$$

where MSE_{full} is the mean squared error of the model including the QTL (4) and $MSE_{reduced}$ is the mean squared error of the model fitting only a family mean. For comparison, we also estimated the proportion of variance explained (r^2) by the joint QTL and cofactors. Empirical thresholds were obtained using permutation tests (Churchill & Doerge, 1994). Marker genotypes for the region under study were permuted within half-sib families, while the phenotypes and the genotype scores for the cofactors were maintained. Note that this provides an empirical test for the region under study, not for the cofactors, but the significance of every cofactor was tested when its region was re-analysed. For significance testing we imposed two thresholds: (1) Following the recommendations of Lander & Kruglyak (1995) we used an empirical point-wise threshold (not accounting for multiple testing) of $P<0{\cdot}01$ to claim confirmed linkage when a QTL for a given trait had already been reported for a certain region. (2) Because each region represented on average 1/50 of the chicken genome, we imposed an empirical 'region-wise' threshold (accounting for multiple tests on part of a linkage group) of $P<0{\cdot}001$ to claim genome-wide significant linkage (Lander & Kruglyak, 1995).

It is not trivial to determine which QTL are confirming published QTL and which QTL are 'new'. Trait definitions vary between studies and some traits are measured in only a single study. Published studies use different molecular markers, further compromising any comparison of QTL positions. This is no problem for genome-wide significant QTL because they do not rely on published results for interpretation of their significance. Accounting for the imprecision of QTL detection, we used a maximum distance of 30 cM from a published QTL to infer whether that QTL had been confirmed in the present study.

3. Results

(i) *Trait heritabilities and correlations*

Heritabilities were low to moderate (Table 1) and significant direct maternal effects were detected for body weight, residual feed intake, conformation, dissection weight and thigh muscle weight. For body weight, the maternal genetic effect was also significant.

Many of the traits were closely correlated and a principal component analysis on all adjusted breeding values showed that five independent vectors explained 99% of all the variation in the 17 traits. The principal component vector loadings and the partial correlations between the EBVs show that conformation, bodyweight and dissection weight grouped together with correlations ranging from 0·30 to 0·96. Residual feed intake and feed conversion ratio were a separate group with a correlation of 0·64. Correlations of the feed intake traits with the other traits were all within −0·10 to 0·10, with the exception of feed conversion ratio and dissection weight (0·17). The thigh and drum proportion traits were at least moderately correlated with the absolute correlation varying between 0·20 and 0·81.

(ii) *QTL analyses*

The multiple QTL analyses found 53 genome-wide significant QTL, varying from a single genome-wide significant QTL for body weight and conformation score up to six genome-wide significant QTL for

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residual feed intake and thighbone weight. Twenty-three additional putative QTL exceeded the threshold for confirmed linkage. An overview of all these QTL and a comparison with published QTL is given in Fig. 1. Seventeen genome-wide significant QTL map to regions where similar QTL have been published (Fig. 1). From the 23 QTL exceeding the threshold for confirmed linkage, 10 map within 30 cM of published QTL for a similar or identical trait, while the remaining 13 putative QTL have to be classified as suggestive new QTL because they do not map to a published QTL. Fig. 1 also shows that the QTL appear clustered rather than uniformly distributed across the candidate regions. Many of these QTL clusters may reflect pleiotropic action of a single QTL, with the actual number of genome-wide significant QTL between 9 and 53. Although Schrooten & Bovenhuis (2002) propose a method to identify pleiotropic effects of QTL in a half-sib design there is at present no multi-trait software available to distinguish between linked and pleiotropic QTL in half-sib designs.

(iii) *QTL effects*

The approximate proportions of within-family variance explained by the QTL (h^2_{QTL}) are summarized in Table 3 and range between 0·04 and 0·26 for the genome-wide significant QTL. Summed together, the QTL and QTL used as cofactors have r^2 (Table 3) between 0·16 (body weight) and 0·52 (direct maternal effect for residual feed intake). Multiplying the r^2 by 4 to approximate the within-family variance explained by the joint QTL would give very unrealistic values, thus illustrating that the variances explained by the joint QTL are overestimated. Hayes & Goddard (2001) quantified the level of upward bias using empirical pig and dairy cattle data and the present results agree with their trend. The total overestimation of the QTL variances increases with the number of QTL that are detected.

To evaluate the proportion of the additive genetic variance that is explained by the joint QTL it is important to note that the trait scores are EBV that would explain all additive genetic variance (i.e. have a 'heritability' of 1·0) if there were an infinite number of offspring. The reliability of the EBV, also defined as the squared correlation between the estimated and true EBV, is an indicator of the proportion of additive genetic variance explained by the EBV. The average reliabilities vary between $\sim$0·1 for the thigh and drum traits and 0·4 for conformation score, clearly reflecting the effect of the estimated heritability (Table 1) on the reliability. Although the QTL explain up to half of the variance in adjusted EBV (Table 3), this only accounts for a small part of the additive genetic variance because of the low to modest reliabilities of the EBV (Table 1).

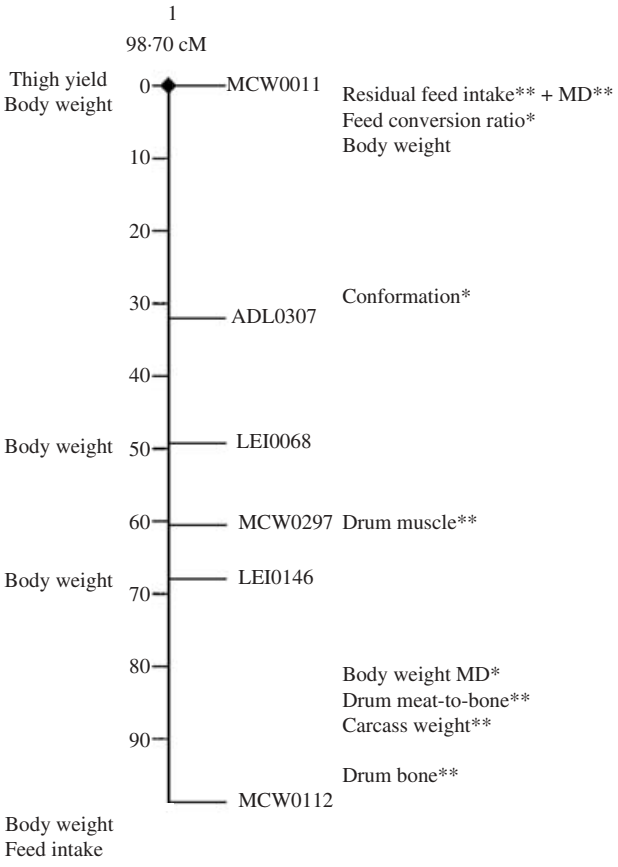
4. Discussion

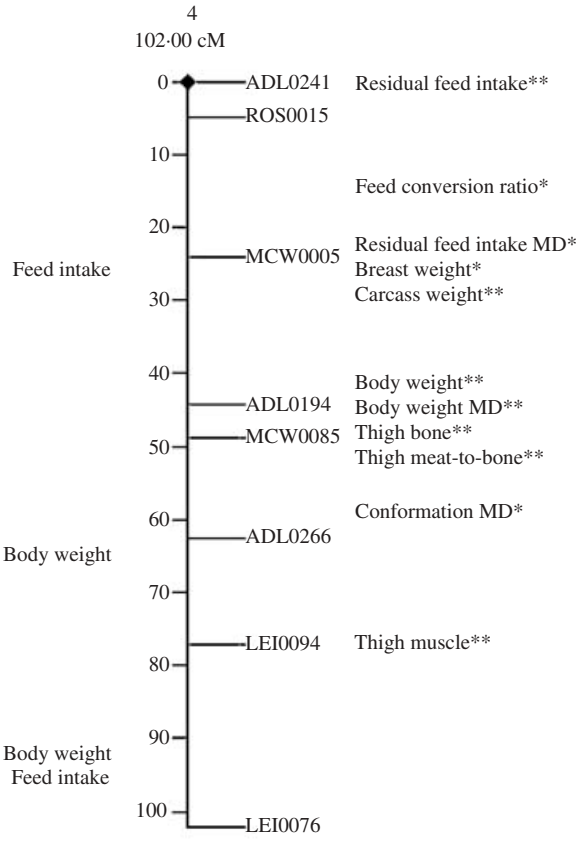
(i) *Multiple QTL analysis*

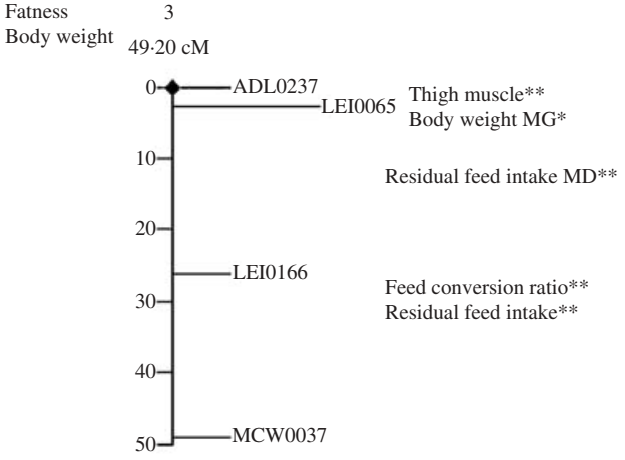
The number of genome-wide significant QTL (53) is very high compared with published studies of poultry QTL, even accounting for the fact that many of the QTL are counted more than once because they affect multiple traits (Fig. 1, Table 3). The only comparison with a family based experimental design is offered by the studies of Van Kaam *et al.* (1998, 1999*a*, *b*) who identified only four genome-wide QTL. They used a cross between two different broiler strains that is expected to be segregating for more QTL than the present study of a single closed population. One possible explanation for this discrepancy could be the use of cofactors to account for unlinked QTL in the present analyses. Using only single QTL analyses we detected 24 instead of 53 genome-wide significant QTL. De Koning *et al.* (2001) first introduced the use of cofactors for the analyses of half-sib designs in dairy cattle. Despite the apparent effectiveness of this approach and its relatively straightforward implementation, it has not been widely used in the analyses of experimental data except for the population where it was first implemented (Viitala *et al.*, 2003). The present results use a refined approach of the cofactor analysis where cofactors are continuously included in the analyses rather than adjusting the phenotypic data for the cofactor effects (De Koning *et al.*, 2001). Fig. 2 shows the effect of multiple QTL analyses on the test statistic along chromosome 1 for two traits. The main effect of using cofactors is the reduction in the residual variance leading to a higher test statistic.

(ii) *Segregation of QTL within a selected line*

The selection line for this experiment is a broiler-dam line with about 50 000 contemporaries at any given time in overlapping generations. Although all birds are potential selection candidates the effective population size is much smaller, which is exemplified by the present experiment where 15 grandsires give rise to approximately one-third of the animals in the G3. The initial selection of candidate parents is based on body weight at 6 weeks of age and conformation score. The selected birds are then entered into a 2 week feed efficiency trial, while a proportion of unselected relatives is dissected to provide carcass measurements. From the 53 genome-wide QTL, 21 are for traits for which selection is applied directly on the selection candidates (body weight, feed intake, conformation) and 32 for carcass-related traits that have been measured on relatives of the selection candidates. For many decades selection has been mainly been on juvenile growth and conformation. This may be reflected in the present results because we find the least number







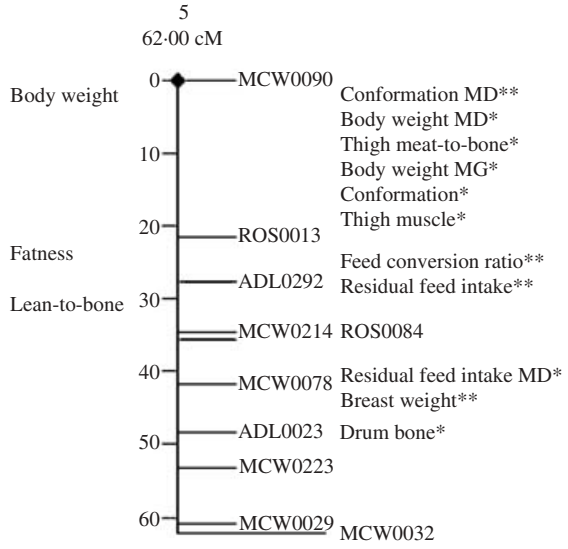


Fig. 1. (*Cont.*)

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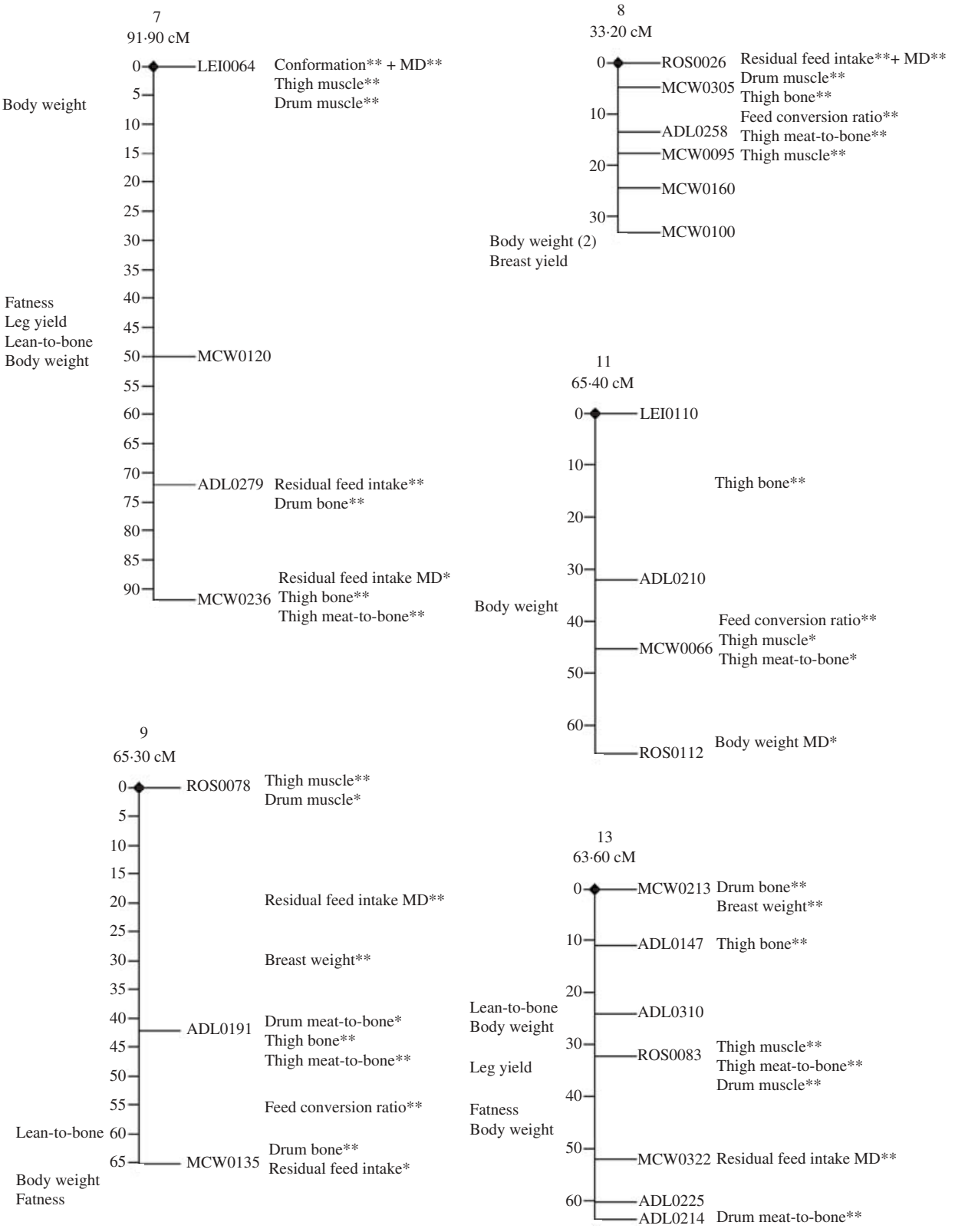

Fig. 1. Overview of poultry QTL in nine candidate regions in four experimental crosses and the present study. The marker maps are in Kosambi cM. Trait names on the left of the maps indicate approximate locations of QTL in the four experimental crosses while trait names on the right indicate approximate locations of QTL in the present study. Significance exceeding the threshold for confirmed linkage (*); genome-wide significant linkage (**). MD and MG denote, respectively, the direct maternal and the maternal genetic effects of the trait.

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Table 3. *Approximate proportion of within-family variance* (h^2_{QTL}) *explained by QTL in nine candidate regions and the proportion of EBV variance* (r^2) *explained by joint QTL and cofactors*

Trait[a]	GGA1	GGA3	GGA4	GGA5	GGA7	GGA8	GGA9	GGA11	GGA13	r^2 joint cofactors and QTL
Body weight	0·07*		0·24**					C		0·16
MD	0·06*		0·16**	0·08*				0·08*		0·21
MG	C[b]	0·09*		0·12*			C			0·24
Feed conversion	0·09*	0·18**	0·09*	0·14**		0·14**	0·18**	0·18**		0·40
Residual feed intake	0·14**	0·10**	0·16**	0·15**	0·10*	0·11**	0·06*	C		0·41
MD	0·05**	0·04**	0·03*	0·05*	0·02*	0·08**	0·18**	C	0·06**	0·52
Conformation score	C[b]			0·11*	0·20**					0·15
MD	0·10*		0·10*	0·19**	0·20**					0·23
Dissection weight	0·24**		0·23**							0·13
Breast yield			0·04*	0·11**			0·20**		0·13**	0·26
Thighbone			0·12**		0·17**	0·10**	0·10**	0·10**	0·10**	0·38
Thigh muscle		0·15**	0·16**	0·03*	0·10**	0·10**	0·05**	0·05*	0·08**	0·47
Thigh meat to bone ratio			0·05**	0·04*	0·07**	0·09**	0·16**	0·04*	0·09**	0·39
Drumbone	0·30**			0·05*	0·14**		0·10**		0·26**	0·32
Drum muscle	0·18**				0·13**	0·15**	0·07*		0·21**	0·29
Drum meat to bone ratio	0·20**						0·08*		0·20**	0·20

* Denotes significance at the empirical $P<0·01$ (confirmed linkage) and ** denotes significance at the empirical region-wide $P<0·001$ ($\sim$genome-wide significant).
[a] MD and MG denote respectively, the direct maternal and the maternal genetic effect of the preceding trait.
[b] C indicates that the best position was included as a cofactor although this region was not significant.

of QTL for body weight and conformation. Breeding objectives have changed over time to include feed efficiency and breast yield, for which we find large numbers of QTL. Selection on carcass proportions is expected to be less effective because it is based on information coming from relatives. As more traits are combined in the selection index, the total efficiency of selection for any given trait will decrease. Although the development of broiler breeding over time may offer some explanations, it is nevertheless surprising that so many QTL with moderate to large effect are still segregating within this line. It is even more surprising that many of these QTL map to regions that explain phenotypic differences between broilers, layers and their wild progenitor. Furthermore the number of detected QTL suggests that the present design is at least as powerful as a moderately sized F2 design for the detection of QTL. This raises questions as to whether there is just as much variation within chicken lines as there is between lines, and whether the same loci or even the same alleles might be involved.

The large population size would certainly contribute to maintain considerable genetic variation by preventing fixation of alleles by drift and/or inbreeding. However, for QTL with moderate to large effects to be present it could be hypothesized that considerable mutation variance should have contributed (Keightley & Hill, 1987). If there were new mutations giving rise to many of the detected QTL it is not obvious why they would map to the same regions as QTL explaining differences between broilers and layers. However, no firm conclusions can be drawn because we do not know how many QTL are segregating outside the candidate regions nor whether the QTL that map to similar regions as published studies represent the same functional mutation. Furthermore, we do not know whether the QTL represent single Mendelian loci or complexes of multiple linked effects. Fine mapping efforts in both the commercial line and the experimental crosses would reveal conserved haplotypes around the mutation(s) that give rise to the QTL in each population. If these haplotypes are identical in the crosses and the commercial lines this points to the same mutation while different haplotypes and/or QTL locations point to independent mutations in different populations.

(iii) *Conclusions*

The use of nine candidate regions from experimental crosses to target a commercial line has proved very powerful. By typing only approximately 20% of the chicken genome we detected QTL explaining between 14% and 50% of the variation in the analysed traits, although this is most likely an inflated estimate. The detection of many QTL within a selection line is the first step to the implementation of marker-assisted selection within this line. With the present knowledge this would require large amounts of genotyping and analyses because the QTL effects have to be estimated within every family. However, if these QTL can be fine-mapped to the level of a functional haplotype by

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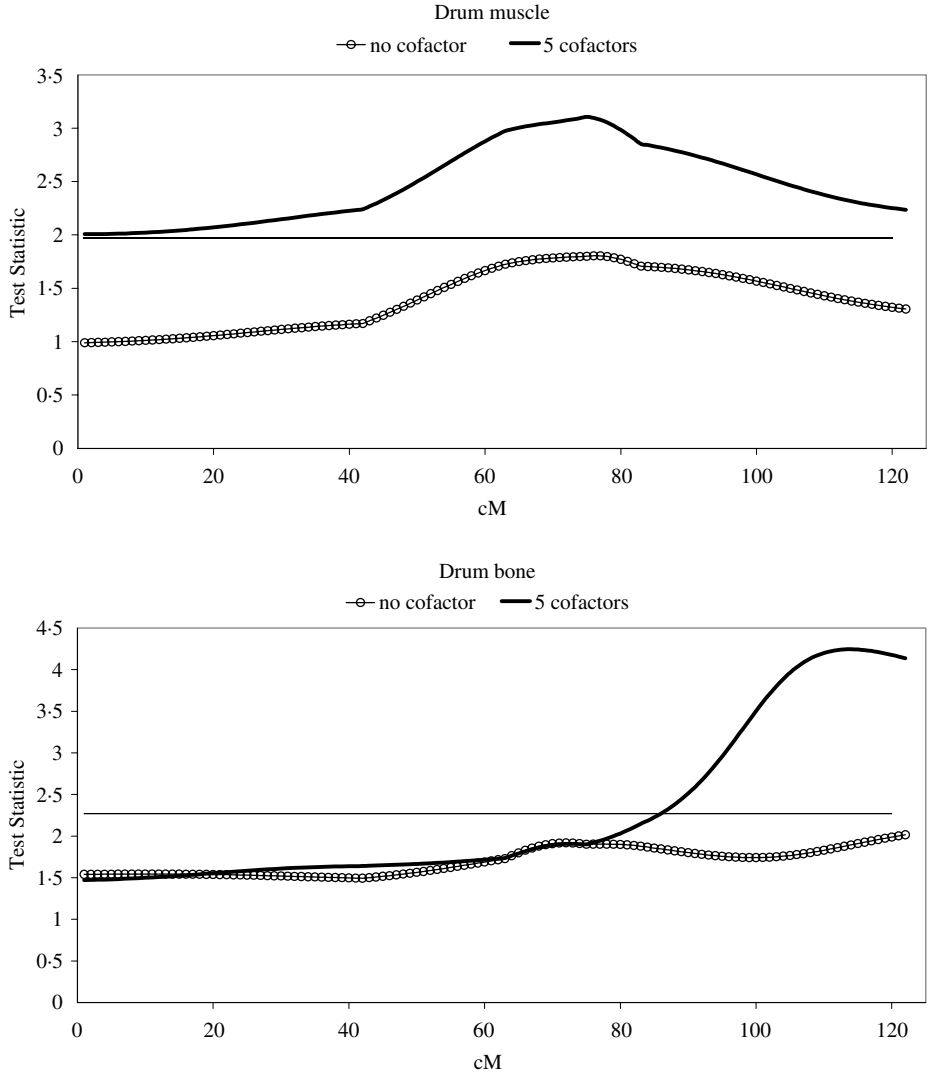

Fig. 2. Effect of cofactors on the test statistic along chromosome 1 for two traits. The horizontal line denotes the approximate threshold for genome-wide significance under the multiple QTL model.

using across-family haplotype comparison (Riquet *et al*., 1999), they could be used for direct association and selection at the population level.

Our results inspire some interesting hypotheses about variation within versus between lines and whether the same loci could be involved. The present results lack precision of QTL positions and information about QTL on the remaining chromosomes that would be required to draw any firm conclusions, but clearly point to commercial populations as a valuable addition to experimental crosses for the location of QTL that affect performance traits.

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