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Quantitative trait loci for meat yield and muscle distribution in a broiler layer cross

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Abstract

An F_2 cross of male and female chickens from broiler and layer lines was used to detect and map quantitative trait loci (QTL) affecting muscle yields and the relative weights of different muscles. Phenotypic data from 442 individuals in 30 families were analysed by within-family regression analyses using 102 microsatellite markers in 27 linkage groups with genome-wide significance thresholds. Interactions of the QTL with sex or family were unimportant and, for each trait, there was no evidence for imprinting or of multiple QTL on any chromosome. There were 30 significant QTL on 12 chromosomes (chromosomes 1 to 9, 13, 27 and Z) for 11 traits. Significant dominance effects were detected for 10 of the QTL and several were of relatively large effect. The magnitude of each QTL accounted for 3.2–5.7% of the residual phenotypic variation and the additive effects for 0.2–0.8 phenotypic standard deviations (S.D.). The results suggest that there are QTL affecting relative yield of carcass parts and of breast muscle in particular.

Keywords: Broiler; Layer; QTL; Muscle distribution; Muscle yields

1. Introduction

Commercial poultry breeders have achieved rapid increases in the body weight and relative proportion of the breast muscle in the carcass of broiler chickens in the last 40 years (Nicholson, 1998). The identification of quantitative trait loci (QTL) for these traits is the first step to characterising the genetic changes that have occurred at the level of the gene and DNA. This is of intrinsic interest and also opens the way for dissecting the adverse effects on disease and reproduction that may have accompanied this success (Sandøe et al., 1999; Sørensen, 1989) and providing effective solutions to overcome them.

We have previously described QTL for live weight at 3, 6 and 9 weeks of age and QTL or fatness traits at 9 weeks in a broiler × layer cross (Ikeobi et al., 2002; Sewalem et al., 2002). The objective of this report is to describe the location of a large number of QTL for

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Table 1
Number of microsatellite markers, chromosome (linkage) group, map length and the first marker on each chromosome that were used for a whole genome scan of a broiler layer cross

Chromosome	Number of markers used	Map length (cM)	First marker
1	24	542	*MCW0168*
2	12	474	*LEI0163*
3	11	282	*ADL0131*
4	4	232	*ADL0317*
5	6	167	*LEI0082*
6	4	89	*ROS0062*
7	3	109	*LEI0064*
8	2	94	*ADL0179*
9	4	132	*ROS0078*
10	1	–	*ADL0209*
11	5	70	*MCW0097*
12	2	33	*ADL0240*
13	3	70	*MCW0340*
14	1	–	*MCW0123*
15	2	45	*LEI0083*
17	1	–	*ADL0199*
18	2	23	*ROS0022*
23	2	1	*LEI0090*
24	1	–	*ROS0113*
E25C31	1	–	*ROS0102*
26	1	–	*ADL0285*
27	1	–	*ROS0071*
28	2	40	*ROS0095*
E32	1	–	*ALVE3*
E38	1	–	*ROS0073*
W25	1	–	*MCW0249*
Z	3	127	*ROS0072*

carcass yield, the relative yields of body parts (breast, thigh, drumstick and wing) and measures of muscling in the same population.

2. Materials and methods

2.1. Animals and husbandry

Details of the origin, mating structure and husbandry of the grandparent, F_1 and F_2 birds were presented in an earlier paper (Sewalem et al., 2002). The grandparents were a line of White Leghorn egg laying (L) chickens and a commercial broiler (B) sire-line that had been genetically selected for high growth rates and breast muscle yields. Two males from both lines were each mated to a female from the other line to create four F_1 families. At 30 weeks of age eight male and 32 female F_1 were selected for breeding the F_2 generation in a balanced mating scheme (Sewalem et al., 2002). A total of 546 F_2 chicks from five hatches were reared in floor pens and fed ad libitum.

2.2. Observations

The birds were weighed at slaughter at 2 kg live weight when they were 9 weeks of age ($n = 510$). The feeders were withdrawn 2 h before the birds were crated for removal to the processing area. The birds were killed by dislocating their necks, the blood vessels of the neck were cut and the body was suspended by the feet to bleed out. The carcasses were immersed in a tank of hot water (58 °C) for 15 s and immediately plucked in an automatic wet defeathering machine. The neck skin was loosened and the head and neck were removed at the anterior edge of the breast and the feet and shanks were cut off at the hock joint. The crop and respiratory tract

Table 2
Means (g) and S.D. of carcass traits and phenotypic correlations between them ($n = 442$, both sexes combined)

Trait	Mean	S.D.	Carcass weight	Breast muscle	Thighs	Thigh muscle	Drums	Drum muscle	Wings	Drum + thigh muscles
Carcass weight	1349	235								
Breast muscles	288	54	0.92							
Thighs	230	45	0.97	0.88						
Thigh muscles	168	34	0.97	0.89	0.99					
Drums	187	37	0.95	0.85	0.95	0.96				
Drum muscles	127	24	0.94	0.86	0.95	0.96	0.99			
Wings	161	28	0.96	0.86	0.94	0.94	0.95	0.93		
Drum + thigh muscles	295	57	0.97	0.89	0.98	0.99	0.98	0.99	0.95	
Drum + thigh bones	69	17	0.92	0.82	0.92	0.93	0.96	0.94	0.93	0.94

Table 3
QTLs for carcass weight and carcass parts in an F_2 population of chickens derived from a broiler × layer cross

Trait (g)	Covariate (g)	Chromosome	F [a]	Position, cM[b]	Flanking markers (FM)	Position from first FM[c]	95% confidence interval
Carcass	Live weight	4	8.6*	154	*ADL0266–LEI0073*	28	81–175
		7	7.1$^+$	42	*LEI0064–ROS0019*	42	0–108
		28	6.7$^+$	0	*ROS0095–ADL0299*	0	0–22
Breast muscle	Carcass	1	5.0$^+$	68	*MCW0010–ADL0188*	20	0–119
		2	6.9$^+$	240	*ADL0196–LEI0147*	15	160–282
		7	5.8$^+$	51	*LEI0064–ROS0019*	51	0–70
		8	9.9*	0	*ADL0179–ROS0075*	0	0–46
		13	7.5$^+$	37	*ADL0147–ADL0225*	37	15–38
		18	5.0$^+$	0	*ROS0022–ROS0027*	0	0–23
Thigh	Carcass	1	11.1**	82	*MCW0010–ADL0188*	34	64–144
		4	8.1*	0	*ADL0317–ROS0015*	0	0–81
		7	5.1$^+$	40	*LEI0064–ROS0019*	40	0–100
		13	5.6$^+$	20	*ADL0147–ADL0225*	20	6–36
		27	5.5$^+$	0	*ROS0071*	0	0
Thigh muscle	Carcass	1	9.1*	136	*LEI0146–LEI0068*	10	108–160
		7	6.6$^+$	36	*LEI0064–ROS0019*	36	0–70
Drum	Carcass	1	6.0$^+$	121	*ADL0188–LEI0068*	12	68–165
		4	8.0*	231	*ADL0266–LEI0073*	105	179–231
		5	8.6*	15	*LEI0082–MCW0090*	15	10–54
		7	10.1**	41	*LEI0064–ROS0019*	41	0–83
		13	11.1**	28	*ADL0147–ADL0225*	28	12–36
		Z	8.1*	106	*LEI0111–LEI0075*	19	40–127
Drum muscle	Carcass	1	5.9$^+$	72	*MCW0010–ADL0188*	24	18–162
		4	6.6$^+$	225	*ADL0266–LEI0073*	99	156–231
		6	10.2**	29	*ROS0062–ROS0003*	29	11–61
		7	8.1*	45	*LEI0064–ROS0019*	45	0–79
		13	11.0**	27	*ADL0147–ADL0225*	27	12–38
		Z	5.6$^+$	98	*LEI0111–LEI0075*	11	20–127
Wing	Carcass	1	7.5$^+$	523	*ROS0025–MCW0107*	20	499–541
		4	8.2*	231	*ADL0266–LEI0073*	105	167–231
		5	5.5$^+$	120	*ROS0084–ADL0298*	63	74–145
		7	11.3**	26	*LEI0064–ROS0019*	26	0–56
		8	6.4$^+$	42	*ADL0179–ROS0075*	42	12–80
		27	8.7*	0	*ROS0071*	0	0
		Z	5.7$^+$	110	*LEI0111–LEI0075*	23	69–126
Drum and thigh muscle	Carcass	1	8.3*	75	*MCW0010–ADL0188*	27	5–126
		4	5.4$^+$	208	*ADL0266–LEI0073*	82	160–228
		6	8.1*	33	*ROS0062–ROS0003*	33	6–65
		7	7.2$^+$	43	*LEI0064–ROS0019*	43	0–68
		13	9.1*	26	*ADL0147–ADL0225*	26	10–38
		Z	5.4$^+$	99	*LEI0111–LEI0075*	12	86–127
Drum and thigh muscle	Leg bones	1	6.0$^+$	156	*LEI0146–MCW0018*	11	144–180
		1	6.8$^+$	479	*ADL0183–ROS0025*	60	446–528
		2	5.3$^+$	116	*LEI0163–ADL0176*	116	96–168
		3	6.3$^+$	60	*MCW0083–ADL0370*	9	40–154
		4	7.5$^+$	99	*ROS0015–ADL0266*	29	62–162
		5	11.0**	57	*ADL0292–ROS0084*	6	21–92
		6	8.5*	18	*ROS0062–ROS0003*	18	4–58
		7	13.8**	55	*LEI0064–ROS0019*	55	39–105
		9	10.9**	39	*ROS0078–MCW0135*	39	18–90
		13	11.5**	17	*ADL0147–ADL0225*	17	2–33
		Z	8.6*	127	*LEI0111–LEI0075*	40	117–127

(continued on next page)

Table 3 (*continued*)

Trait (g)	Covariate (g)	Chromosome	F [a]	Position, cM[b]	Flanking markers (FM)	Position from first FM[c]	95% confidence interval
Breast muscle	Drum and thigh muscle	1	7.8^{+}	81	*MCW0010–ADL0188*	33	36–108
		1	7.5^{+}	306	*ROS0044–ADL0148*	0	306–386
		2	8.7*	238	*ADL0196–LEI0127*	13	179–314
		3	9.3*	246	*ADL0306–LEI0265*	23	179–282
		6	6.9^{+}	15	*ROS0062–ROS0003*	15	0–69
		8	11.3**	38	*ADL0179–ROS0075*	38	13–57
		13	12.4**	37	*ADL0147–ADL0225*	37	21–38
Drum muscle	Thigh muscle	5	9.2*	48	*ROS0013–ADL0292*	1	18–57
		8	6.0^{+}	52	*ADL0179–ROS0075*	52	28–78
		13	5.6^{+}	28	*ADL0147–ADL0225*	28	3–38

Different covariates were used in each analysis as indicated in the second column.

[a] +, suggestive linkage; *, significant linkage at 5%; **, significant linkage at 1%.

[b] Position of QTL relative to the first marker in the set for this chromosome (Table 1).

[c] Position of QTL relative to the first flanking marker i.e. independent of the marker set.

were removed and the carcasses were eviscerated by hand. The eviscerated carcass weight was noted and the bodies were stored at −20 °C. They were subsequently thawed overnight and dissected according to established guidelines (Jensen, 1983). The weights of the breast meat, breast skin, legs, thighs, wings and residual carcass were recorded. The legs and thighs from both sides were dissected into bone, muscle and skin (including adhering fat) and their respective weights were recorded.

2.3. Genotyping

Samples of fresh blood were collected at 6 weeks of age by superficial venepuncture of a wing vein and DNA was prepared by standard procedures. A total of 103 microsatellite markers covering 26 autosomal linkage groups and the sex chromosomes were used to genotype the eight F_0 grandparents, 40 F_1 parents and 510 F_2 offspring as described previously (Sewalem et al., 2002). Fragment sizes were determined by using GeneScan 3.1 DNA fragment analysis and Genotyper 2.1 software (PE Biosystems, USA). All pedigree, marker genotypes and trait data were recorded in resSpecies, a generic resource database (Law and Archibald, 2000; http://www.resSpecies.org). Information on the genetic markers can be viewed at http://www.thearkdb.org/browser?species=chicken; (Hu et al., 2001). After parentage checking and genotyping edits, complete data from 442 F_2 individuals from 30 families with genotypes on 101 microsatellite markers in 27 linkage groups were available for analysis (Table 1). The total map length, including an arbitrary 20 cM for the end markers and for each linkage group with a single marker was 2923 cM or about 75% of the consensus linkage map (Schmid et al., 2000).

2.4. QTL analyses

The QTL mapping method proposed by Haley et al. (1994) was implemented using QTL Express software (Seaton et al., 2001). A linear model for the additive (a) and dominance effects (d) of a QTL at a given position was analysed by least squares for each trait where the additive effect was defined as half the difference between the two homozygotes and the dominance effect as the difference between the means of the heterozygotes and homozygotes. Positive additive and dominance effects indicate that the broiler allele was greater than the allele from the layer line and negative genetic effects that the layer allele was larger than that from the broiler. The statistical model included family, sex, pen and a covariate as fixed effects (hatch was confounded with pen). The covariates were live weight for carcass weight, and carcass weight for the weights of carcass parts (breast muscles, thighs, drumsticks (drums) and wings). Additional analyses were conducted to investigate the relative growth of muscles and bone: total thigh and drum muscle weights with bone weight as a covariate; breast muscle

with drum plus thigh muscle as a covariate; and drum muscle with thigh muscle as a covariate.

If the test statistics in the initial analysis exceeded the threshold value we conducted a series of analyses based on conventional *F*-tests with appropriate degrees of freedom. A QTL by sex interaction was assessed to investigate whether the genetic effects differed between the two sexes. Evidence that a QTL was segregating in one or the other line was determined by an analysis of a model that included the interaction between the QTL effect and family. A model fitting an imprinting effect (parent of origin effect) was evaluated as described by Knott et al. (1998). A trait showing evidence for a single QTL was tested for the presence of two or more QTL in that linkage group by fixing one of the QTL and searching at 2 cM intervals along the chromosomes before moving the fixed QTL to the next location (also spaced at 2 cM). This model was tested by an *F*-ratio against a model with no QTL and against a model with only one QTL. Finally, for each QTL significant at the suggestive level in the initial interval

Table 4
Means and S.E. of additive and dominance effects for genome-wide statistically significant QTL, genetic effects as a proportion of the phenotypic S.D. and the proportion of the residual sum of squares that were removed by fitting the QTL model for carcass weight, carcass parts (breast muscle, thigh, drum, thigh muscle and drum muscle weights), the relative weights of breast, drum and thigh muscles, and drum and thigh muscle relative to drum and thigh bone weight

Trait (g)	Covariate (g)	Chromosome	Additive effect (g)			Dominance effect (g)			Phenotypic [a] variance (%)
			Mean	S.E.	S.D.[b]	Mean	S.E.	S.D.[b]	
Carcass	Live weight	4	105.1	25.7	0.6	− 34.4	74.6	− 0.2	3.6
Breast muscle	Carcass	8	13.5	3.1	0.5	− 9.3	7.3	− 0.4	4.0
Thigh	Carcass	1	7.2	1.8	0.5	− 11.7	4.3	− 0.8	4.6
		4	4.3	1.1	0.3	1.7	1.6	0.1	3.2
Thigh muscle	Carcass	1	3.0	0.9	0.3	− 3.5	1.5	− 0.3	3.7
Drum	Carcass	4	3.4	0.9	0.3	2.0	1.3	0.2	3.2
		5	− 2.6	1.2	− 0.2	6.3	1.8	0.5	3.8
		7	− 4.3	2.3	− 0.3	28.6	7.1	2.1	4.3
		13	− 0.9	1.3	− 0.1	− 10.7	2.4	− 0.8	4.6
		Z	− 4.7	1.2	− 0.3	1.6	2.0	0.1	3.4
Drum muscle	Carcass	6	− 3.1	0.7	− 0.3	1.6	1.2	0.2	4.2
		7	− 2.0	1.6	− 0.2	19.3	5.1	2.3	3.4
		13	0.2	0.9	0.0	− 7.8	1.7	− 0.9	5.0
Wing	Carcass	4	2.8	0.7	0.3	0.3	1.0	0.0	3.6
		7	− 2.5	1.3	− 0.3	15.1	3.5	1.6	5.1
		27	3.7	0.9	0.3	0.2	1.2	0.0	3.5
Drum and thigh muscle	Carcass	1	7.2	2.7	0.4	− 23.4	7.2	− 1.2	3.6
		6	− 5.3	1.4	− 0.3	3.4	2.1	0.2	3.3
		13	2.0	2.0	0.1	− 15.6	3.7	− 0.8	4.1
Drum and thigh muscle	Drum and thigh bones	5	6.5	1.4	0.3	1.2	2.0	0.1	4.6
		6	− 6.6	1.7	− 0.4	− 2.4	3.1	− 0.1	3.5
		7	16.0	3.1	0.8	2.7	9.7	0.1	5.7
		9	10.3	2.2	0.6	0.6	5.2	0.0	4.9
		13	9.7	2.0	0.5	− 0.4	4.1	− 0.0	5.1
		Z	5.3	1.3	0.3	− 1.4	1.8	− 0.1	3.6
Breast muscle	Drum and thigh muscle	2	7.8	2.0	0.4	6.4	3.6	0.3	3.8
		3	6.7	1.8	0.3	− 7.1	3.6	− 0.3	4.0
		8	18.3	4.6	0.8	32.8	18.2	1.5	5.1
		13	7.3	1.9	0.3	8.3	3.0	0.3	5.1
Drum muscle	Thigh muscle	5	− 2.3	0.5	− 0.4	− 1.2	0.8	− 0.2	4.1

[a] Proportional decrease in the residual sums of squares by fitting the model with the QTL compared to the reduced model.
[b] Standardized effect (the mean additive effect divided by the residual S.D.).

mapping analysis we reanalysed the data accounting for the background genetic effects of the significant QTL following Jansen (1993) and Zeng (1993).

2.5. Significance thresholds and confidence intervals

Genome-wide significant linkage thresholds were calculated on the basis of 1000 iterations (not 100 as erroneously presented in Sewalem et al., 2002). Genome-wide thresholds for significance as defined by Lander and Kruglyak (1995) were $F = 8.2$ for the 5% level of probability, $F = 10.0$ for the 1% level and $F = 5.0$ for suggestive linkage. An approximate confidence interval for the localisation of each of the significant and suggestive QTL was obtained using the bootstrap technique (Knott et al., 1998; Visscher et al., 1996) with a total of 500 samples. The 95% intervals presented were chosen to be of minimum length after removal of background bias associated with marker locations (Walling et al., 2002).

3. Results

The overall means and standard deviations (S.D.) of the seven primary traits and the sums of the drum and thigh muscles and bones are listed in Table 2. The phenotypic correlations between weights of the various carcass parts were in excess of 0.9 except those involving the weight of breast muscles that were in the range 0.8–0.9 (Table 2).

Suggestive and significant QTL locations, flanking markers, confidence intervals and the estimated location relative to the first marker on the chromosome (Table 1) are presented in Table 3. The genetic distance from the first flanking marker is also given to facilitate comparison with the current (Schmid et al., 2000) and future consensus linkage maps. There were 30 significant QTL for 11 traits on 12 chromosomes (chromosomes 1 to 9, 13, 27 and Z). Means and standard errors (S.E.) of estimated additive and dominance effects and genetic effects in standardised measure (effect divided by residual S.D.) are presented in Table 4. The proportion of the phenotypic variation explained by each significant QTL (additive and dominance effects) is given in the last column of Table 4. Significant dominance effects were detected for 10 QTL and the magnitude of the dominance effect was generally larger than the corresponding additive effect. Significant additive effects ranged from 0.2 to 0.8 phenotypic S.D. and individual QTL accounted for 3.2–5.1% of the phenotypic variation.

Interactions of the QTL with sex or family were not statistically significant. There was also no evidence of imprinting or of more than one QTL affecting a given trait in any linkage group. Fitting background effects did not result in any of the suggestive QTL becoming statistically significant.

4. Discussion

Analyses of the primary muscling traits without a covariate detected the same major QTL for live weight at 9 weeks of age (results not presented) that were previously reported by Sewalem et al. (2002). Three of these QTL, respectively, on chromosomes 4 (177 cM), 13 (15 cM) and 27 (at marker ROS0071), affected several of the traits in the current experiment and all of the remaining QTL for the unadjusted traits were also detected in the analyses with a covariate. We, therefore, present only the results for the covariance analyses as these adjust for the effect of size per se and provide evidence of QTL affecting relative growth of body parts and muscles.

The magnitude of the additive effects for these traits as a proportion of the phenotypic variation was comparable with those for body weight (Sewalem et al., 2002) and measures of fatness (Ikeobi et al., 2002) accounting for 0.2–0.8 phenotypic S.D. or 3–5% of the phenotypic variation. The carcass weight of the broiler line in this experiment was about 6-fold, and the weight of breast muscle 9-fold heavier than a strain of White Leghorns at 63 days of age (unpublished observations); corresponding values for thighs, drums and wings were 6-, 5- and 4-fold heavier.

The effect of the QTL on chromosome 4 represents an increase of carcass weight as a proportion of live weight of the F_2 of nearly 8% attributable to the broiler allele. In general the absolute values for the additive effects of the carcass parts relative to body weight were relatively small compared with those for body weight (Sewalem et al., 2002). Prescott et al. (1985), using data from a number of experiments from the 1920s to

the present day, showed that a linear relationship existed between the weight of breast muscle and live weight over a wide range of chicken lines and body weights from less than 0.2–10 kg. Their results are consistent with the proposal that the relative size of individual muscles is related in a functional manner and is invariant (Berg and Butterfield, 1976). However, the QTL on chromosome 8 increases relative breast muscle yield by almost 5%, and the sum of the QTL effects for the breast muscles adjusted to the average weight of leg and thigh muscles combined is 40 g or 3% of the mean carcass weight. It should also be noted that these values must be doubled to estimate the effect of replacing both layer alleles with their broiler equivalents, and therefore, represent QTL of significant economic importance. Our results suggest that there may be genes that increase the relative weight of breast muscle at the same carcass weight. Relatively small but economically significant differences in muscle distribution were demonstrated in a multi-strain study of adult body composition in chickens (Hocking et al., 1985) and in comparisons of different breeds of larger farm animals (e.g. Kempster et al., 1982a,b).

Significant dominance effects were detected for 10 of the 30 QTL in Table 4. This is a comparable proportion to that reported for fat traits (Ikeobi et al., 2002) and contrasts with the relative absence of dominance for body weight (Sewalem et al., 2002) in this population. Indeed several of the estimated dominance effects are relatively large compared with the size of the additive effects. It is possible that the lack of functional differences in relative muscle mass referred to above is associated with an exhaustion of additive genetic variation and the retention of non-additive genetic effects for these traits. Considerable caution is justified in interpreting these results because dominance effects are poorly estimated, and they should also not be confused with gene effects.

A consequence of analysing the data with a covariate for a trait of which it is part is that a positive QTL effect for one trait may result in a negative effect for another. Specifically, a positive effect of a QTL on the proportion of breast muscle may result in a numerical decrease in leg and thigh muscle. Indeed, the largest QTL for carcass parts were for breast muscle and breast muscle adjusted for drum and thigh muscle with a positive sign, indicating a broiler origin, whereas those for the drum and drum muscle, but not thigh or thigh muscle were generally negative.

Differences in the proportions of different carcass parts, especially the breast muscle, are economically important, as are the relative weights of different muscles in the body that were analysed by covariance analysis. Additional QTL were detected for breast muscle at the same weight of drum plus thigh muscle and for different traits of the drum and several of them were not associated with measures of the thigh (Table 4). In particular, there was a QTL on chromosome 5 that affected drum muscle and drum relative to thigh that do not have an effect on thigh muscle.

Covariance analysis of muscling (drum plus thigh muscle weight adjusted for bone weight) was conducted in preference to muscle: bone ratios for mathematical reasons. Four QTL for thigh or drum muscle weight on chromosomes 1, 4, 6 and 9 were not associated with muscle weight at the same bone weight. The results demonstrate that different genes affect muscle and bone growth and that genetic selection has made use of this variation.

Comparisons of the magnitude of the 95% confidence intervals of QTL for different traits on the same chromosome provide an estimate of the likely presence of two or more QTL on that linkage group. Of the 12 chromosomes with QTL, only chromosome 4 showed evidence for more than one QTL for different carcass traits based on non-overlapping confidence intervals. The estimated locations of QTL from the present results were also compared with those of live weight at 3, 6 and 9 weeks from Sewalem et al. (2002). There was no evidence for more than one QTL affecting live weight or muscling on chromosomes 2, 5, 6, 7, 8, 9, 13, 27 and Z. Only three chromosomes (5, 6 and 9) had a QTL for at least one muscling or yield trait that did not also posses a live weight QTL. Of the chromosomes with two or more possible QTL, there was evidence for three non-overlapping QTL on chromosome 1 and two locations on chromosomes 3 and 4. Multi-trait analyses (Knott and Haley, 2000) could be used to confirm these multiple QTL and might also locate additional multiple QTL on other chromosomes.

Van Kaam et al. (1999) published data for two suggestive QTL in a broiler × broiler cross affecting carcass percentage on chromosome 1 at 466 cM, and for leg score adjusted for body weight at 565 cM. The

latter is on a similar position to the QTL for drum plus thigh muscle weight adjusted for carcass weight at 479 cM in this analysis (Table 3). The present results confirm the importance of an area on chromosome 4 that has a relatively large effect, in addition to carcass yield, on body weight (Sewalem et al., 2002) and also on egg weight, body weight and feed intake in a layer × layer cross (Tuiskula-Haavisto et al., 2002).

There was no evidence for sex × QTL interactions, implying that QTL effects were similar in both sexes, a result that is consistent with the effects of QTL for live weight and fatness (Ikeobi et al., 2002; Sewalem et al., 2002). The lack of significant QTL × family interactions suggest that the QTL were not segregating in the birds chosen from the parental lines and is consistent with one of the basic assumptions of the analysis that the QTL were fixed in the four birds sampled from each of the two populations.

Imprinting was not detected in these data for any trait nor in the analyses of live weight and fatness (Ikeobi et al., 2002; Sewalem et al., 2002). The lack of evidence for imprinting in this analysis contrasts with several reports of the effects of imprinting for muscle mass in the domestic pig (De Koning et al., 2000; Jeon et al., 1999; Nezer et al., 1999). The insulin like growth factor 2 (IGF2) gene is located on chromosome 5 (Yokomine et al., 2001) in the confidence interval for the QTL for drum weight (Table 3) and is frequently imprinted in mammalian species (Morison et al., 2001; http://www.otago.ac.nz/IGC). However, there are conflicting reports of the presence of imprinting in molecular studies of the expression of the IGF2 gene in chicken embryos (Koski et al., 2000; O'Neill et al., 2000) and we have failed to find evidence for imprinting of the IGF2 gene in embryos from parents of the same lines as in this cross (C. Bruley, unpublished observations).

5. Conclusion

In conclusion, we have detected QTL for carcass yield and carcass parts (breast, drum, thigh and wing) at equal carcass weight. QTL were also identified that affected muscle weight in the drum and thigh at constant bone weight and QTL for the weights of different muscles adjusted by covariance analysis for the weight of other muscles. There was also evidence that different QTLs affected different carcass parts and muscle weights. The magnitude of effects was relatively small but cumulative effects of all QTL affecting a given trait are of economic significance. Important dominance effects were detected for one-third of the QTL and in some cases additive effects were not significant.

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