



QTL for percentage of carcass and carcass parts in a broiler x layer cross

E. E. Baron^{*,2}, A. S. A. M. T. Moura^{†,2}, M. C. Ledur[‡], L. F. B. Pinto[§], C. Boschiero[†], D. C. Ruy^{*}, K. Nones^{*}, E. L. Zanella^{‡,1}, M. F. Rosário^{*}, D. W. Burt[¶] and L. L. Coutinho^{*}

*Animal Biotechnology Laboratory, Department of Animal Science, ESALQ-USP. Av. Pádua Dias 11, Piracicaba-SP, 13418-900, Brazil.

†Department of Animal Production, FMVZ, São Paulo State University (UNESP), Botucatu, SP, 18618-000, Brazil. ‡Embrapa Suínos e Aves. BR 153, Km 110, Concórdia, SC, 89700-000, Brazil. §Universidade Federal da Bahia, Av. Ademar de Barros, 500, Ondina Salvador, BA, 40170-110, Brazil. ¶Roslin Institute, Edinburgh University, Midlothian EH25 9PS, UK

Summary

An F₂ experimental population, developed from a broiler layer cross, was used in a genome scan of QTL for percentage of carcass, carcass parts, shank and head. Up to 649 F₂ chickens from four paternal half-sib families were genotyped with 128 genetic markers covering 22 linkage groups. Total map length was 2630 cM, covering approximately 63% of the genome. QTL interval mapping using regression methods was applied to line-cross and half-sib models. Under the line-cross model, 12 genome-wide significant QTL and 17 suggestive linkages for percentages of carcass parts, shank and head were mapped to 13 linkage groups (GGA1, 2, 3, 4, 5, 7, 8, 9, 11, 12, 14, 18 and 27). Under the paternal half-sib model, six genome-wide significant QTL and 18 suggestive linkages for percentages of carcass parts, shank and head were detected on nine chicken linkage groups (GGA1, 2, 3, 4, 5, 12, 14, 15 and 27), seven of which seemed to corroborate positions revealed by the previous model. Overall, three novel QTL of importance to the broiler industry were mapped (one significant for shank% on GGA3 and two suggestive for carcass and breast percentages on GGA14 and drums and thighs percentage on GGA15). One novel QTL for wings% was mapped to GGA3, six novel QTL (GGA1, 3, 7, 8, 9 and 27) and suggestive linkages (GGA2, 4, and 5) were mapped for head%, and suggestive linkages were identified for back% on GGA2, 11 and 12. In addition, many of the QTL mapped in this study confirmed QTL previously reported in other populations.

Keywords breast, carcass, chickens, drums and thighs, QTL, shank, wings.

Introduction

Carcass quality becomes a critical issue as chicken meat sales worldwide move from retailers to food service companies, implying portioning of whole carcasses and further processing (Arthur & Albers 2003). Although carcass traits have moderate to high heritabilities (Zerehdaran *et al.*

2004), phenotypes on the relative yield of carcass parts are difficult and expensive to obtain in breeding programs, because slaughtering and dissection in sib tests are required. Finding genomic regions associated with yield of specific carcass parts could facilitate genetic progress.

Some studies have already focused on mapping genomic regions responsible for carcass traits (reviewed by Abasht *et al.* 2006; Gao *et al.* 2009; Le Mignon *et al.* 2009; Terčič *et al.* 2009; Uemoto *et al.* 2009). The breast muscle, which is the most valuable part of the chicken carcass, has received more attention in those studies, followed by the drum and thigh muscles. A few reports have covered other carcass parts, such as wings, shank and head (Ikeobi *et al.* 2004; Park *et al.* 2006; Gao *et al.* 2009), but none have included the dorsal portion of the carcass (back).

The Brazilian F₂ Chicken Resource Population, developed from a broiler x layer cross, was designed to map quanti-

Address for correspondence

L. L. Coutinho, Laboratório de Biotecnologia Animal, ESALQ-USP. Av Pádua Dias 11, Piracicaba, SP, 13418-900, Brazil.
E-mail: llcoutin@esalq.usp.br

¹Present address: Universidade de Passo Fundo, Curso de Medicina Veterinária, Passo Fundo, RS, 99001-970, Brazil.

²Both authors contributed equally to this study.

Accepted for publication 31 May 2010

tative trait loci for traits relevant to the poultry industry and consumers. Previous reports described genome scans for growth- (Ambo *et al.* 2009) and fatness-related traits (Campos *et al.* 2009) in this population. Weights of carcass and carcass parts, but not the percentages relative to BW, were also included in a former study restricted to GGA1 (Nones *et al.* 2006). This study reports the results of a QTL search of 22 linkage groups for percentages of carcass, carcass parts, shank and head, including novel QTL mapped in the chicken genome.

Material and methods

Experimental population and phenotypes

The F₂ chicken resource population used in this study was developed from the crossbreeding of a broiler and a layer line as previously described by Nones *et al.* (2006). F₂ chickens were reared as broilers in floor pens up to 35 days and individually caged from 35 to 41 days. Chickens were weighed and slaughtered on day 42, after 6-h fasting and transportation to the slaughterhouse. Carcasses were eviscerated, stored at -4 °C for six hours, and then dissected. Weights of carcass parts (breast with bones and skin, drums and thighs with bones and skin, wings and back, which corresponds to the dorsal portion of the carcass, after removing carcass parts), carcass (the summation of carcass parts), shank (including the metatarsus and phalanges) and head (including the neck) were recorded. Weight of breast muscle separated from skin and bones was not acquired, because of the large number of animals and phenotypes recorded. Percentages of carcass, carcass parts, shank and head were calculated relative to body weight at 42 days of age and used in the QTL search. Blood samples were collected at slaughter for DNA analyses.

QTL mapping analyses

Up to 649 F₂ chickens belonging to seven full-sib and four paternal half-sib families were genotyped with 128 genetic markers covering 22 linkage groups. Total map length was 2630 cM, corresponding to approximately 63% of genome coverage. Genotyping and linkage map construction were conducted as described by Campos *et al.* (2009).

Two genetic models, line-cross (Haley *et al.* 1994) and half-sib (Knott *et al.* 1996), were applied for QTL interval mapping analyses using the regression method in the *QTL Express* software (Seaton *et al.* 2002). In the line-cross analysis, the fixed effects of hatch, sex and family were included in the model for QTL mapping. The line-cross analysis was initiated with an additive model. If the statistical test for a QTL exceeded the suggestive threshold level, models including additive + dominance and additive + dominance + parent-of-origin effects were also tes-

ted. When an indication of a second QTL was found, based on *F*-value profile, the two-QTL model was tested and the best model (1 vs. 2 QTL) was chosen based on the log of odds (LOD) scores. The percentage of phenotypic variance explained by the QTL was obtained as the percentage of reduction in the residual mean squares after fitting the fixed effects. In the half-sib analyses, three to four half-sib sire families were used depending on the chromosome being analysed. Additional relationships within half-sib groups were ignored. The fixed effects of hatch and sex were included in the model.

Significance thresholds were computed using 10 000 permutations (Churchill & Doerge 1994) for probability levels of 1 and 5% (genome-wide) and for suggestive linkage (Lander & Kruglyak 1995). Confidence intervals for QTL positions were estimated with bootstrapping according to Visscher *et al.* (1996).

Results and discussion

Descriptive statistics for body weight at 42 days and percentages of carcass and carcass parts are described in Table 1.

QTL mapped under the line-cross model

A total of 12 QTL and 17 suggestive linkages were mapped to 13 chicken linkage groups in the line-cross analysis (Table 2). Parent-of-origin effects were not detected for any of the QTL. The two-QTL model showed a better fit than the one QTL model for breast% on GGA2 (LOD = 5.1).

For carcass%, a QTL showing 1% genome-wide significance was positioned at 202 cM on GGA2, and two suggestive linkages were mapped to GGA3 and 14 (Table 2). The QTL on GGA2 is in agreement with Atzmon *et al.* (2007) and Terčič *et al.* (2009). The suggestive linkages on GGA3 and GGA14 may indicate a novel QTL for this trait. All three QTL acted in an additive manner, and the alleles increasing carcass% came from the broiler line.

Table 1 Descriptive analysis of traits used in QTL mapping.

Trait ¹	Number of records	Mean	SD	Minimum	Maximum
BW42 (g)	1056	997.5	176.9	402.0	1631.0
Carcass %	1051	65.0	2.1	55.5	79.3
Breast %	1054	16.2	1.1	9.3	23.8
Drums and thighs %	1055	21.5	1.2	14.0	28.2
Wings %	1053	8.32	0.45	6.75	13.19
Back %	1055	19.0	1.0	14.5	22.4
Shank %	1055	4.07	0.36	2.61	5.38
Head %	1055	3.50	0.34	2.62	5.56

¹BW42, body weight at 42 days of age; Percentages of parts are relative to BW42.

Table 2 Quantitative trait loci mapped in the line-cross analysis.

Trait ¹	GGA (cM) ²	Confidence interval	F-Ratio ³	Flanking markers	Additive effect (SE)	PV (%) ⁴
Carcass %	2 (202)	146–236	18.58**	MCW0291–LEI0147	0.60 (0.14)	3.07
	3 (47)	0–271	7.99 [†]	MCW0169–MCW0222	0.55 (0.19)	1.33
	14 (2)	0–24	11.78 [†]	ADL0200–LEI0098	0.49 (0.14)	2.74
Breast %	2 (156)	NE ⁵	12.13 [†]	MCW0062–ADL0373	0.35 (0.10)	3.85
	2 (242)	NE ⁵	15.32*	MCW0185–MCW0264	0.34 (0.09)	5.14
	3 (45)	2–246	10.57 [†]	MCW0169–MCW0222	0.30 (0.09)	1.81
	8 (61)	4–89	11.61 [†]	ABR0345–ADL0172	0.31 (0.09)	2.50
	12 (6)	0–86	10.76 [†]	ADL0372–ADL0044	0.28 (0.09)	2.49
	18 (6)	0–21	12.38*	MYHE–MCW0217	0.29 (0.08)	2.89
Drums & thighs %	3 (154)	4–256	10.65 [†]	ADL0371–LEI0118	–0.24 (0.07)	1.81
	4 (121)	95–176	15.78*	MCW0240–LEI0063	0.31 (0.08)	2.66
Wings %	1 (176)	83–332	12.80 [†]	LEI0138–MCW0068	–0.09 (0.02)	1.90
	3 (153)	98–166	19.41**	ADL0371–LEI0118	–0.13 (0.03)	3.43
Back %	2 (196)	119–235	10.07 [†]	MCW0291–LEI0147	0.20 (0.06)	1.61
	11 (20)	3–109	10.37 [†]	LEI0143–ADL0123	–0.26 (0.08)	2.38
	12 (15)	0–86	10.02 [†]	ADL0372–ADL0044	0.29 (0.09)	2.30
Shank %	1 (195)	155–392	10.92 [†]	MCW0068–ADL0020	–0.07 (0.02)	3.22
	2 (195)	40–212	11.99 [†]	MCW0291–LEI0147	–0.07 (0.02)	2.00
	3 (112)	12–166	18.65**	LEI0029–ADL0371	–0.08 (0.02)	3.27
	4 (180)	124–189	49.67**	LEI0085–MCW0174	0.17 (0.02)	8.24
	27 (100)	54–110	14.07 [†]	MCW0300–MCW0328	0.08 (0.02)	3.34
Head %	1 (178)	121–217	30.02**	LEI0138–MCW0068	–0.11 (0.02)	4.54
	2 (224)	25–251	8.52 [†]	LEI0147–MCW0185	–0.06 (0.02)	1.43
	3 (112)	20–273	10.50*	LEI0029–ADL0371	–0.06 (0.02)	1.71
	4 (10)	0–152	8.17 [†]	LEI0100–LEI0122	–0.09 (0.03)	1.30
	5 (46)	2–138	7.25 [†]	MCW0090–LEI0145	–0.06 (0.02)	1.17
	7 (82)	21–125	10.87*	ADL0279–MCW0236	–0.08 (0.02)	2.32
	8 (34)	27–76	12.88**	MCW0095–ADL0154	–0.09 (0.02)	2.80
	9 (29)	0–123	9.54*	ROS0078–ADL0021	–0.10 (0.03)	4.28

¹Percentage of parts relative to body weight at 42 days of age.

²Position in cM from the first marker in the set for the chromosome.

³Suggestive genome-wide, *5% genome-wide, **1% genome-wide.

⁴PV, percent of phenotypic variance explained by the QTL.

⁵NE, non-estimated because there were two QTL for this trait in the same chromosome. In the one QTL model, the QTL position was at 227 cM and the confidence interval was from 11 to 248 cM.

Two different regions associated with breast% were identified on GGA2: a significant QTL at 242 cM plus a suggestive linkage at 156 cM. Another QTL influencing breast% was mapped to GGA18 and three additional suggestive linkages to GGA3, 8 and 12 (Table 2). The same region on GGA3 affected both carcass% and breast%, which could be owing to a pleiotropic QTL. All six QTL acted additively, had positive effects on breast%, and seemed to corroborate results from previous studies on GGA2 (Ikeobi *et al.* 2004; McElroy *et al.* 2006; Zhou *et al.* 2006; Terčič *et al.* 2009), GGA3 (McElroy *et al.* 2006; Park *et al.* 2006), GGA8 (Ikeobi *et al.* 2004; Zhou *et al.* 2006; Gao *et al.* 2009), GGA12 (Zhou *et al.* 2006) and GGA18 (Ikeobi *et al.* 2004).

One QTL and a suggestive linkage were mapped for drums and thighs% on GGA4 and 3, respectively. No other study except that of Ikeobi *et al.* (2004) has considered the combined percentage of drums and thighs. However, some authors have associated the region of GGA4 mapped in this study with traits such as drumstick% (Zhou *et al.* 2006), adjusted drum, drum muscle, drum and thigh muscle weights (Ikeobi *et al.* 2004) and adjusted thigh muscle weight (De Koning *et al.* 2003). Similarly, a suggestive QTL was reported for adjusted thigh meat weight on GGA3 (Gao *et al.* 2009).

One QTL and a suggestive linkage were mapped for wings% on GGA3 and 1, respectively. Suggestive linkages for adjusted wing weight were previously reported on

GGA1, but they were mapped either to the proximal (Nones *et al.* 2006) or to the distal portion of the chromosome (Ikeobi *et al.* 2004; Gao *et al.* 2009), as opposed to the intermediate portion in this study. No QTL was previously reported for wings% or adjusted wing weight on GGA3. Common features were identified between the suggestive linkage for drums and thighs% and the QTL for wings% on GGA3. First, they were both positioned in the same region (*ADL0371–LEI0118*), only one cM apart, suggesting that a group of linked loci in this region or a pleiotropic QTL could be influencing limb development; second, they both showed negative additive effects, meaning that the alleles that conferred higher proportions of limbs came from the layer line. This is not surprising considering that, in the broiler founder line, selection emphasis was placed mainly on body weight and breast yield (Figueiredo *et al.* 2003), which may have caused negative correlated responses for limb yield.

Three suggestive linkages were detected for back%, which corresponded to the dorsal portion of the carcass, after breast, drums, thighs and wings were removed (Table 2). Two of these showed positive additive effects; one was mapped to the same interval as the QTL for carcass% and shank% on GGA2 (*MCW0291–LEI0147*) and the other to GGA12 (*ADL0372–ADL0044*), where a suggestive linkage for breast% was mapped. The third suggestive linkage, which had negative additive effects, was mapped to GGA11, where no QTL for any carcass part was previously mapped. Although back% has no economic importance *per se*, it is directly related to the proportion of economically important parts. The relative proportions of all parts, on the other hand, would contribute to a balanced body structure.

Two QTL (on GGA3 and 4) and three suggestive linkages (GGA1, 2 and 27) were mapped for shank% (Table 2). Interestingly, QTL for body weight at 35 and 41 days of age were previously reported for this population in these same chromosomes and similar intervals (Nones *et al.* 2006; Ambo *et al.* 2009). In this study, the QTL with the largest effect on shank%, explaining 8.24% of the phenotypic variance, was located in the same region of GGA4 where Ambo *et al.* (2009) mapped the QTL with the largest effects on body weight at 41 days of age, which explained 5.26% of the phenotypic variance. Moreover, the allele that conferred the higher value for both traits originated from the broiler line. Accordingly, Nadaf *et al.* (2009) mapped QTL that explained 14% of the phenotypic variance for BW and around 20% for shank length and diameter to the same portion of GGA4, in an intercross of high- and low-growth chicken lines. Taken together, these results are an indication that linked genes or genes with pleiotropic effect might be acting to increase both body weight and shank% in this region of GGA4.

A similar situation may have occurred with the suggestive linkage for shank% found on GGA27 in this study and the QTL for body weight at 35 days detected by Ambo *et al.* (2009).

However, not all the alleles that increased shank% came from the broiler line. For the suggestive linkages on GGA1 and 2, and also for the highly significant QTL for shank% on GGA3, additive effects were negative, and therefore the alleles increasing shank% in these cases originated from the layer line. Selection for high egg production has probably brought about an increase in shank%, because leg bones act as stores for much of the calcium deposited in eggshells (Whitehead *et al.* 2003). Unraveling alleles that increase shank%, independently of body weight, could be useful to alleviate the incidence of leg disorders in broilers resulting from rapid gain in body weight (Whitehead *et al.* 2003). Additionally, the QTL for shank% on GGA1 showed dominance effects ($d = 0.06 \pm 0.02$). A corresponding suggestive linkage with similar traits had been found for adjusted feet weight on GGA1 by Nones *et al.* (2006).

Park *et al.* (2006) detected two highly significant QTL for adjusted shank weight in a cross between a high- and low-weight selection lines: one on GGA1 (between *LEI0162* and *LEI0134*) and another on GGA27 (in the *MCW0076–MCW0292* interval). We found suggestive linkages for a similar trait (shank%) on both chromosomes, but the positions were different (Table 2). For those authors, the alleles that increased shank weight came from the high growth line. Gao *et al.* (2009) detected two QTL (on GGA1 and 5) and two suggestive linkages (on GGA2 and 4) for adjusted shank and claw weights. The suggestive linkage on GGA4 was found in the same region as the highly significant QTL for shank% mapped in this study. The 1% genome-wide significant QTL for shank% identified on GGA3 (Table 2) is a new QTL and explains 3.27% of the phenotypic variation.

Five QTL (on GGA1, 3, 7, 8 and 9) and three suggestive linkages (on GGA2, 4 and 5) were mapped for head%. Based on the additive effects, the alleles conferring higher head% came, in all cases, from the layer line. A possible explanation was that the broiler founder line was selected for body weight and breast yield, which may have resulted in desired negative correlated responses on head%. The QTL for head% on GGA9 showed dominance effects ($d = -0.26 \pm 0.08$).

QTL mapped under the half-sib model

Six QTL and 18 suggestive linkages were detected on nine chicken autosomes under the paternal half-sib genetic model (Table 3). Seven of these 24 regions identified by the half-sib model seemed to reinforce regions mapped with the line-cross model, because they were mapped either to the same or to an adjacent interval: for breast%, drums and thighs%, wings%, and shank% on GGA3, for back% on GGA12 and for shank% on GGA4 and 27. All QTL (or suggestive linkage) positions for shank% were identified on the same chromosomes (GGA1, 2, 3, 4 and 27) in both analyses, which may indicate important candidate regions for this trait.

QTL for carcass and breast% on GGA1 as well as the suggestive linkages for these two traits on GGA5 were

Table 3 Quantitative trait loci mapped in the paternal half-sib analysis.

Trait ¹	GGA (cM) ²	Confidence interval	F-Ratio ³	Flanking markers	Sire	Allele substitution effect (SE) ⁴
Carcass %	1 (172)	121–325	6.70*	<i>LEI0138–MCW0068</i>	7716	0.56 (0.33)
					7769	0.98 (0.24)
					7822	0.37 (0.35)
	2 (168)	67–231	5.25 [†]	<i>ADL0373–LEI0096</i>	7716	1.29 (0.39)
					7797	0.65 (0.35)
					7822	1.19 (0.57)
					7977	0.92 (0.68)
	5 (0)	0–150	4.43 [†]	<i>LEI0082–MCW0193</i>	7716	0.48 (0.31)
					7797	0.04 (0.28)
7822					1.02 (0.31)	
Breast %	1 (172)	0–325	6.66*	<i>LEI0138–MCW0068</i>	7716	0.001 (0.18)
					7769	0.55 (0.13)
					7822	0.31 (0.19)
	3 (20)	4–272	4.06 [†]	<i>MCW0169–MCW0222</i>	7716	0.34 (0.16)
					7797	0.26 (0.14)
					7822	0.35 (0.17)
	5 (0)	0–143	4.99 [†]	<i>LEI0082–MCW0193</i>	7716	0.04 (0.15)
					7797	0.003 (0.13)
					7822	0.58 (0.15)
	14 (16)	0–50	5.37 [†]	<i>LEI0098–MCW0123</i>	7716	0.23 (0.19)
					7769	0.26 (0.28)
					7822	0.65 (0.18)
Drums & thighs %	2 (136)	8–196	5.48 [†]	<i>MCW0062–ADL0373</i>	7716	0.60 (0.25)
					7797	0.13 (0.22)
					7822	1.24 (0.44)
					7977	1.37 (0.49)
	3 (160)	0–264	4.60 [†]	<i>ADL0371–LEI0118</i>	7716	0.19 (0.17)
					7797	0.03 (0.17)
					7822	0.64 (0.18)
	5 (148)	0–150	4.24 [†]	<i>ADL0233–ADL0298</i>	7716	0.02 (0.47)
					7797	0.28 (0.17)
					7822	0.66 (0.21)
	15 (24)	0–61	5.32 [†]	<i>LEI0120–MCW0231</i>	7716	0.09 (0.17)
					7769	0.63 (0.24)
7822					0.66 (0.23)	
Wings %	1 (132)	86–280	6.06 [†]	<i>ADL0319–MCW0058</i>	7716	0.26 (0.06)
					7769	0.03 (0.06)
					7822	0.07 (0.06)
	3 (152)	20–272	5.83 [†]	<i>ADL0371–LEI0118</i>	7716	0.10 (0.08)
					7797	0.17 (0.08)
					7822	0.26 (0.08)
	5 (20)	11–150	4.90 [†]	<i>MCW0193–MCW0090</i>	7716	0.12 (0.07)
					7797	0.06 (0.06)
					7822	0.21 (0.06)
Back %	12 (0)	0–86	5.46 [†]	<i>ADL0372–ADL0044</i>	7716	0.13 (0.18)
					7769	3.16 (0.90)
					7822	0.35 (0.18)

Table 3 (Continued)

Trait ¹	GGA (cM) ²	Confidence interval	F-Ratio ³	Flanking markers	Sire	Allele substitution effect (SE) ⁴
Shank %	1 (380)	44–392	4.52 [†]	MCW0020–ROS0025	7716	0.03 (0.06)
					7769	0.13 (0.08)
					7822	0.22 (0.06)
	2 (144)	127–241	8.68 ^{**}	MCW0062–ADL0373	7716	0.02 (0.06)
					7797	0.33 (0.06)
					7822	0.16 (0.12)
					7977	0.21 (0.14)
	3 (116)	20–272	5.50 [†]	LEI0029–ADL0371	7716	0.08 (0.05)
					7797	0.08 (0.05)
					7822	0.19 (0.05)
	4 (180)	106–198	7.08 ^{**}	LEI0085–MCW0174	7716	0.71 (0.24)
					7769	0.23 (0.12)
7797					0.24 (0.10)	
7975					0.14 (0.08)	
7977					0.31 (0.08)	
27 (108)	66–110	6.86 [†]	MCW0328–ADL0376	7716	0.11 (0.06)	
				7769	0.29 (0.08)	
				7822	0.12 (0.08)	
Head %	1 (144)	130–186	12.12 ^{**}	ADL0319–MCW0058	7716	0.27 (0.06)
					7769	0.18 (0.05)
					7822	0.05 (0.06)
	2 (124)	11–251	4.37 [†]	MCW0062–ADL0373	7716	0.03 (0.08)
					7797	0.20 (0.06)
					7822	0.29 (0.11)
					7977	0.10 (0.13)
	3 (108)	0–272	4.96 [†]	MCW0222–LEI0161	7716	0.03 (0.05)
					7797	0.14 (0.05)
					7822	0.13 (0.05)
	27 (20)	0–47	7.79 [*]	MCW0300–MCW0328	7716	0.37 (0.08)
					7769	0.05 (0.12)
7822					0.05 (0.09)	

¹Percentage of parts relative to body weight at 42 days of age.

²Position in cM from the first marker in the set for the chromosome.

³[†]Suggestive genome-wide, *5% genome-wide, **1% genome-wide.

⁴Absolute value.

detected in the half-sib analysis (Table 3). In each case, the flanking markers, positions and relative magnitudes of the allele substitution effects in the half-sib families were very similar for both traits, suggesting linked loci (or alternatively a pleiotropic QTL). Equivalent results involving GGA5 were reported by McElroy *et al.* (2006). In their detailed analysis of GGA5, Le Mignon *et al.* (2009) revealed three male-specific linked QTL for adjusted breast muscle weight in the F₂ progeny of a fat x lean broiler line cross. However, in contrast with this study, in which the QTL was mapped to the proximal portion of GGA5, those of Le Mignon were located in the central and distal portions of the chromosome. An additional suggestive linkage for breast% was mapped to GGA14 in this study, where no QTL for any

carcass trait was previously mapped, although three QTL for body weight have been already mapped to this chromosome (Jennen *et al.* 2004; Zhou *et al.* 2006).

Suggestive linkages for drums and thighs% on GGA2, 5 and 15, for wings% on GGA5 and a QTL for head% on GGA27 were mapped only under the half-sib model (Table 3). These results agree with those from Ikeobi *et al.* (2004), who mapped a QTL for drumstick% and a suggestive linkage for adjusted wing weight on GGA5, and from Gao *et al.* (2009), who mapped a suggestive linkage for adjusted thigh meat weight on GGA5. There was no QTL previously detected for drum- and thigh-related traits on GGA15, but one for body weight (Jennen *et al.* 2005) and one for tibia bone mineral density (Schreiweis *et al.*

2005) were mapped to an interval including *LEI0120*. In our study, drums and thighs% included bone weight.

Sire allele substitution effects (Table 3) indicated that most QTL and suggestive linkages that were not detected under the line-cross model were, in fact, segregating exclusively in one sire family. Two exceptions were the suggestive linkages for drums and thighs% on GGA2 and 15.

A total of 46 putative QTL for carcass%, carcass parts%, shank% and head% were detected. From these, at least three were novel regions associated with traits of economic importance to the broiler industry, such as carcass% and breast% on GGA14, drums and thighs% on GGA15 and shank% on GGA3. Their importance relates to yield of valuable carcass cuts and prevention of leg disorders in lines with rapid gain in body weight. These QTL need to be further validated using higher marker density in those regions.

Acknowledgements

The authors thank Dr Jerry Dodgson and Dr Hans H. Cheng (United States Poultry Genome Project) for primer donation. E.E. Baron, L.F.B. Pinto, C. Boschiero, M.F. Rosário and K. Nones received scholarships from FAPESP. D.C. Ruy received a PICDT (CAPES) scholarship. A.S.A.M.T. Moura and L.L. Coutinho received scholarships from CNPq. Financial support was provided by EMBRAPA/PRODETAB and FAPESP. David Burt was sponsored by grants from BBSRC (UK).

References

- Abasht B., Dekkers J.C.M. & Lamont S.J. (2006) Review of Quantitative Trait Loci Identified in the Chicken. *Poultry Science* **85**, 2079–96.
- Ambo M., Moura A.S.A.M.T., Ledur M.C. *et al.* (2009) Quantitative trait loci for performance traits in a broiler x layer cross. *Animal Genetics* **40**, 200–8.
- Arthur J.A. & Albers G.A.A. (2003) Industrial perspective on problems and issues with poultry breeding. In: *Poultry Genetics, Breeding and Biotechnology* (Ed. by W.M. Muir & S.E. Aggrey), pp. 1–12. CABI Publishing, Wallingford.
- Atzmon G., Blum S., Feldman M., Lavi U. & Hillel J. (2007) Detection of agriculturally important QTLs in chickens and analysis of the factors affecting genotyping strategy. *Cytogenetic and Genome Research* **117**, 327–37.
- Campos R.L.R., Nones K., Ledur M.C. *et al.* (2009) Quantitative trait loci associated with fatness in a broiler-layer cross. *Animal Genetics* **40**, 729–36.
- Churchill G.A. & Doerge R.W. (1994) Empirical threshold values for quantitative trait mapping. *Genetics* **138**, 963–71.
- De Koning D.J., Windsor D., Hocking P.M., Burt D.W., Law A., Haley C.S., Morris A., Vincent J. & Griffin H. (2003) QTL detection in commercial broiler lines using candidate regions. *Journal Animal Science* **81**, 1158–65.
- Figueiredo E.A.P., Rosa P.S., Scheurmann G.N., Jaenisch F.R.F., Schmidt G.S., Ledur M.C., Brentano L. & Costa C.A.F. (2003) Genetic gain in body weight, feed conversion, and carcass traits in White Plymouth Rock broiler strain Embrapa 021. In: *Proceedings of the IX World Conference on Animal Production*, 26–31 October 2003, Porto Alegre, Brazil.
- Gao Y., Du Z.Q., Wei W.H., Yu X.J., Deng X.M., Feng C.G., Fei J., Feng J.D., Li N. & Hu X.X. (2009) Mapping quantitative trait loci regulating chicken body composition traits. *Animal Genetics* **40**, 952–4.
- Haley C.S., Knott S.A. & Elsen J.M. (1994) Mapping quantitative trait loci in crosses between outbred lines using least squares. *Genetics* **136**, 1195–207.
- Ikeobi C.O.N., Woolliams J.A., Morrice D.R., Law A., Windsor D., Burt D.W. & Hocking P.M. (2004) Quantitative trait loci for meat yield and muscle distribution in a broiler layer cross. *Livestock Production Science* **87**, 143–51.
- Jennen D.G.J., Vereijken A.L.J., Bovenhuis H., Crooijmans R.P.M.A., Veenendaal A., Van Der Poel J.J. & Groenen M.A.M. (2004) Detection and localization of quantitative trait loci affecting fatness in broilers. *Poultry Science* **83**, 295–301.
- Jennen D.G., Vereijken A.L., Bovenhuis H., Crooijmans R.M., van der Poel J.J. & Groenen M.A. (2005) Confirmation of quantitative trait loci affecting fatness in chickens. *Genetics, Selection, Evolution* **37**, 215–28.
- Knott S.A., Elsen J.M. & Haley C.S. (1996) Methods for multiple-marker mapping of quantitative trait loci in half-sib populations. *Theoretical and Applied Genetics* **93**, 71–80.
- Lander E. & Kruglyak L. (1995) Genetic dissection of complex traits: guidelines for interpreting and reporting linkage results. *Nature Genetics* **11**, 241–7.
- Le Mignon G., Pitel F., Gilbert H. *et al.* (2009) A comprehensive analysis of QTL for abdominal fat and breast muscle weights on chicken chromosome 5 using a multivariate approach. *Animal Genetics* **40**, 156–64.
- McElroy J.P., Kim J.J., Harry D.E., Brown S.R., Dekkers J.C.M. & Lamont S.J. (2006) Identification of trait loci affecting white meat percentage and other growth and carcass traits in commercial broiler chickens. *Poultry Science* **85**, 593–605.
- Nadaf J., Pitel F., Gilbert H. *et al.* (2009) QTL for several metabolic traits map to loci controlling growth and body composition in an F₂ intercross between high- and low-growth chicken lines. *Physiological Genomics* **38**, 241–9.
- Nones K., Ledur M.C., Ruy D.C., Baron E.E., Melo C.M.R., Moura A.S.A.M.T., Zanella E.L., Burt D.W. & Coutinho L.L. (2006) Mapping QTLs on chicken chromosome 1 for performance and carcass traits in a broiler x layer cross. *Animal Genetics* **37**, 95–100.
- Park H., Jacobsson L., Wahlberg P., Siegel P.B. & Andersson L. (2006) QTL analysis of body composition and metabolic traits in an intercross between chicken lines divergently selected for growth. *Physiological Genomics* **25**, 216–23.
- Schreiweis M., Hester P.Y. & Moody D.E. (2005) Identification of quantitative trait loci associated with bone traits and body weight in an F₂ resource population of chickens. *Genetics Selection Evolution* **37**, 677–98.
- Seaton G., Haley C.S., Knott S.A., Kearsley M. & Visscher P.M. (2002) QTL Express: mapping quantitative trait loci in simple and complex pedigrees. *Bioinformatics* **18**, 339–40.
- Terčič D., Holcman A., Dovč P., Morrice D.R., Burt D.W., Hocking P.M. & Horvat S. (2009) Identification of chromosomal regions

- associated with growth and carcass traits in an F3 full sib intercross line originating from a cross of chicken lines divergently selected on body weight. *Animal Genetics* **40**, 743–8.
- Uemoto Y., Sato S., Odawara S. *et al.* (2009) Genetic mapping of quantitative trait loci affecting growth and carcass traits in F₂ intercross chickens. *Poultry Science* **88**, 477–82.
- Visscher P.M., Thompson R. & Haley C.S. (1996) Confidence intervals in QTL mapping by bootstrapping. *Genetics* **143**, 1013–20.
- Whitehead C.C., Fleming R.H., Julian R.J. & Soresen P. (2003) Skeletal problems associated with selection for increased production. In: *Poultry Genetics, Breeding and Biotechnology* (Ed. by W.M. Muir & S.E. Aggrey), pp. 29–52. CABI Publishing, Wallingford.
- Zerehdaran S., Vereijken A.L.J., van Arendonk J.A.M. & van der Waaij E.H. (2004) Estimation of genetic parameters for fat deposition and carcass traits in broilers. *Poultry Science* **83**, 521–5.
- Zhou H., Deeb N., Evock-Clover C.M., Ashwell C.M. & Lamont S.J. (2006) Genome-wide linkage analysis to identify chromosomal regions affecting phenotypic traits in the chicken. II. Body composition. *Poultry Science* **85**, 1712–21.