Asian-Aust. J. Anim. Sci.
Vol. 21, No. 10 : 1389 - 1394
October 2008

www.ajas.info

Microsatellite Markers Linked to Quantitative Trait Loci Affecting Fatness in Divergently Selected Chicken Lines for Abdominal Fat

Hui Zhang[a], Shouzhi Wang[a], Hui Li*, Xijiang Yu[1], Ning Li[2], Qin Zhang[3], Xiaofeng Liu Qigui Wang, Xiaoxiang Hu[2], Yuxiang Wang and Zhiquan Tang

College of Animal Science and Technology, Northeast Agricultural University, Harbin 150030, China

ABSTRACT : Abdominal fat characters are complex and economically important in the poultry industry. Their selection may benefit from the implementation of marker-assisted selection (MAS). The objective of this study was to identify the markers linked to QTL responsible for fatness traits. The Northeast Agricultural University broiler lines divergently selected for abdominal fat content (NEAUHLF) were used in the study. A total of 596 individuals from the divergent tails from the 6th to the 10th generations were genotyped at 23 microsatellite markers on chromosome 1. The differences of allele frequencies of all marker alleles between the divergent tails across the five generations were recorded. The allele frequencies of five markers, including LEI0209, LEI0146, MCW0036, ADL328 and MCW0115, had significant differences between the two tails in all five generations. The resulting p-values using Fisher's exact test on eleven markers, containing MCW248, MCW0010, MCW0106, LEI0252, LEI0068, MCW0018, MCW0061, LEI0088, MCW200, MCW283 and ROS0025, had a decreasing tendency from the 6th to the 10th generation. Statistical analysis showed that polymorphisms of the eight markers, including LEI0209, LEI0146, ROS0025, MCW0115, MCW0010, MCW0036, MCW283, ADL328, were significantly ($p<0.0011$) or suggestively ($p<0.05$) associated with abdominal fat content (AFW and AFP) across generations. It is concluded that the eight markers could be associated with the QTL affecting the deposition of abdominal fat in broiler chickens. (**Key Words :** Chicken, Abdominal Fat Traits, QTL, Microsatellites, Allele Frequencies)

INTRODUCTION

In addition to being a widely raised farm animal in agriculture, chicken also serve as an excellent animal model in genetic selection/evolution research. Selecting for an increased growth rate or, reducing of the age at which the commercial slaughter weight is reached often resulted in a higher body fat content. Therefore, excessive body fatness has long been of interest to both researchers on human obesity and producers of farm animals. It is well known that excessive fat in poultry depresses feed efficiency resulting in a lower commercial value, and less appreciation by consumers. Considerable research efforts have been therefore applied around the world to search factors associated with fat deposition and methods to reduce adiposity (Jennen, 2004).

Substantial advances had been made in the improvement of some important traits in livestock by artificial selection. However, most of such selections were initiated decades ago on the basis of observable phenotypes without knowledge of genetic architecture of the selected characteristics (Dekkers and Hospital, 2002) and thereby the improvement on the traits of interest is very limited. The development of molecular biology techniques for uncovering variation at the DNA level has opened new avenues to identify genes affecting quantitative traits (Beckman and Soller, 1983; Haley and Knott, 1992; Lander and Kruglyak, 1995), in which molecular maker-assisted selection (MAS) acts as a promising tool to improve the trait progression through conventional means. Such phenotypic traits are doomed of low heritability, difficulty in observation, or highly-priced in cost (Dekkers and Hospital, 2002).

To date, a number of QTLs affecting abdominal fat content in chickens were identified mainly using

* Corresponding Author: Hui Li. Tel: +86-451-55191516, Fax: +86-451-55103336, E-mail: lihui@neau.edu.cn
[1] College of Animal Science and Technology, Shandong Agricultural University, Tai'an, 271018, China.
[2] National Laboratories for Agribiotechnology, China Agricultural University, Beijing 100094, China.
[3] College of Animal Science and Technology, China Agricultural University, Beijing 100094, China.
[a] These authors contributed the same to this work.
Received December 17, 2007; Accepted April 23, 2008

microsatellite markers (van Kaam et al., 1998, 1999; Tatsuda and Fujinaka, 2001; de Koning et al., 2003; Zhu et al., 2003; Carlborg et al., 2004; Jennen et al., 2004; Sasaki et al., 2004; Siwek et al., 2004; Schreiweis et al., 2005). More recently, we identified QTLs affecting body weight (BW) and abdominal fat traits on chromosome 1 in the Northeast Agricultural University F_2 Resource Population (NEAURP) (Liu et al., 2007). Combining the previous results, the objective of the current study was to identify the markers linked to QTLs responsible for fatness traits by investigating the allelic distribution of microsatellite markers and evaluating association between markers and fatness traits in the two unique lines divergently selected for abdominal fat content.

MATERIALS AND METHODS

Experimental populations

The Northeast Agricultural University broiler lines divergently selected for abdominal fat content (NEAUHLF) were used in the current study. The lean and fat lines have been selected divergently using abdominal fat percentage (AFP) and plasma very low-density lipoprotein (VLDL) concentration as selection criteria since 1996. The 0 generation of the two lines came from the same grandsire line originating from the Arbor Acres breed, which was then divided into two lines according to plasma VLDL concentration at 7wk of age. Birds with plasma VLDL concentration lower than the average population mean value were grouped and defined lean line, and higher than the average population mean value were grouped and defined fat line. Selection was continued for 10 generations, with 15 sires and 4 hens per sire in each line for the 0 to 5 generations and 25 sires and 4 dams per sire in each line for generations 6th to 10th. From 1st to 10th, birds of each line were raised in two hatches and housed in pens with five birds per cage. Plasma VLDL concentration were measured for all birds at 7 wk of age. Abdominal fat weight (AFW) of the male birds was measured and adjusted (AFP) for body weight (BW) after slaughtered at 7 wk of age. For lean line, birds of plasma VLDL concentration and AFP lower than the population average mean value were selected as candidates of breeders, considering the body weight of male birds and egg production of female birds. 25 families were established to produce offspring of next generation. The mating ratio was 1 sire to 4 dams; for fat line birds of plasma VLDL concentration and AFP higher than the population average mean value were selected as candidates of breeders. The breeder selection and mating program was the same as described above for lean line and also 25 families were established to produce offspring of next generation. Only male birds of each generation were kept in this study. All chickens from the two lines of each generation were ranked according to their abdominal fat percentage (AFP) from the highest to the lowest. In each generation, the chickens with highest 15% and lowest 15% of AFP were selected, belonging to the fat line and the lean line respectively. In other words, birds from two tails of each generation were used in the current study. The numbers of individuals selected from the five generations (the 6th to the 10th) were 70, 86, 120, 120 and 200, respectively, and the total number reached 596.

The birds had free access to feed and water. Commercial corn-soybean-based diets that met all NRC requirements (National Research Council, 1994) were provided in the study. From hatch to 3 wk of age, birds received feed (3,000 kcal ME/kg and 210 g/kg CP) and from 3 to 7 wk of age, birds were fed a grower diet (3,100 kcal ME/kg and 190 g/kg CP).

Phenotyping

The body weight (BW) was measured at hatch and in 2-wk intervals from 1 up to 7 wk of age. All male birds were slaughtered at 7 wk of age and the carcass weight (CW) and abdominal fat weight (AFW) was measured, and abdominal fat percentage (AFP) was calculated (AFW expressed as percentage of BW7).

Genotyping

According to Liu et al. (2007), the linkage map on chromosome 1 was constructed using 23 microsatellite markers. The distances between adjacent markers vary from 9.0 to 50.5 cM and the average distance was about 30.0 cM. In the current study, these 23 microsatellite markers were genotyped in all individuals selected. The genomic DNA was isolated from venous blood samples using a phenolchloroform method. The primers of the 23 markers were synthesized in Shanghai Sangon Biological Engineering Technology & Services Co. Ltd. The polymerase chain reactions for each marker were carried out separately in a reaction volume of 25 μl included 100 ng of template DNA, 1×PCR reaction buffer (10 mM of Tris-HCl, 50 mM of KCl, and 1.5 mM of $MgCl_2$, pH 8.3), 0.25 μM of each primer, 200 μM of each deoxynucleotide triphosphate, and 1 U of *Taq* polymerase (Takara Biotechnology Co., Ltd., Dalian, China). The following amplification conditions were applied: 5 min of denaturation at 94°C, followed by 35 cycles of denaturation at 94°C for 45 s, annealing at 50-65°C for 45 s, and extension at 72°C for 30 s. The PCR products were electrophoresed in 6% denaturing polyacrylamide gels using an ABI377 sequencer (Applied Biosystems, Foster City, CA). A total of 596 individuals from the five generations were genotyped and the genotype data was collected using GeneScan 3.1 and Genotyper 2.1 (Applied Biosystems).

Table 1. Information on microsatellite markers used in the present study

No.	Name	Heterozygosity	PIC	Alleles[1]
1	MCW248	0.222	0.242	3
2	LEI0209	0.569	0.620	9
3	MCW0010	0.400	0.455	5
4	MCW0106	0.639	0.681	5
5	LEI0252	0.675	0.833	8
6	LEI0114	0.776	0.819	9
7	LEI0068	0.489	0.430	4
8	MCW0297	0.661	0.544	3
9	LEI0146	0.683	0.641	5
10	MCW0018	0.711	0.751	7
11	MCW0058	0.257	0.562	3
12	ADL251	0.466	0.665	4
13	MCW0061	0.579	0.740	5
14	LEI0088	0.518	0.658	6
15	MCW200	0.612	0.745	7
16	MCW0036	0.490	0.611	4
17	MCW283	0.536	0.612	7
18	LEI0107	0.536	0.680	4
19	LEI0079	0.457	0.486	4
20	ADL328	0.469	0.498	4
21	ROS0025	0.467	0.636	5
22	MCW0115	0.558	0.770	6
23	MCW0107	0.237	0.249	3
Mean		0.649	0.606	5.48

[1] The number of alleles detected in all the five generations.

Statistical analyses

The differences of allele frequencies between the two tails were examined by Fisher exact test, using SAS 8.1 software (SAS Institute Inc., Cary, NC, USA, 2001). The association between the markers and the phenotypic traits was analyzed using the GLM procedure of JMP 4.0 (SAS Institute Inc., 2002). The model was fitted with the genotype (G), the generations (g) and lines (L) as fixed effects; Due to relatively small sample size for individual generation and many alleles at each locus, G×L as interaction of G by L effect and the G×g as interaction of G by g effect were unavailable by JMP 4.0 (SAS Institute Inc., 2002). Thus, G×L and G×g are not included in the final model. F (L) represents family effect nested within the lines, and D (F,L) represents dam effect nested within the lines and families. They are considered as random effects. Body weight at 7 wk of age (BW7) as a linear covariate, as follows:

$$Y = \mu+G+L+F(L)+D(F, L)+BW7+e \quad (1)$$

$$Y = \mu+G+L+g+F(L)+D(F, L)+BW7+e \quad (2)$$

Model (1) and model (2) were used for the association of single marker on fat trait in individual generation and across generations, respectively. Where Y is the dependent variable, μ is population mean, and e is the random error. Significant differences between least squares means of the different genotypes were calculated using a contrast test. Suggestively significant threshold was determined as $p<0.05$, significant associations were defined by $p<0.0011$ (2 traits×23 markers = 46 independent tests) using a Bonferroni adjustment. The percentage contribution of marker to the total phenotypic variance of traits was estimated by using MTDFREML package (Boldman et al., 2002).

RESULTS

Allele frequency analyses

There are totally 120 alleles of all the 23 microsatellite markers examined. The number of alleles at each locus ranged from 3 to 9, and the average number was 5.48 (Table 1). Fisher exact test was used to test the differences of allele frequencies at every locus between the two tails in the five generations. The allele frequencies of five markers, including LEI0209, LEI0146, MCW0036, ADL328 and MCW0115, had significant differences between the two tails through all the five generations. The resulting p-values using Fisher's exact test on eleven markers, containing MCW248, MCW0010, MCW0106, LEI0252, LEI0068, MCW0018, MCW0061, LEI0088, MCW200, MCW283 and ROS0025, had a decreasing tendency from the 6th to the 10th generation (Figure 1).

Association analyses

Based upon allele frequency analyses of above markers, single marker association analysis was performed to detect the effects of the sixteen markers on AFW and AFP both in every generation and across generations. We found that significant or suggestive associations of all sixteen markers with AFW and AFP were only detected in certain generation(s). Four markers of them, including LEI0209, LEI0146, ROS0025 and MCW0115 had significant ($p<0.0011$) and another four markers including MCW0010, MCW0036, MCW283 and ADL328, had suggestive ($p<0.05$) association with AFW and AFP in the mixed population (across generations) (Table 2). Additionally, percentage of phenotypic variance explained by QTL linked to 16 markers was estimated, suggesting that phenotypic variance explained by QTL linked to above-mentioned eight markers was larger than that explained by others markers (Table 2).

DISCUSSION

Comparing the differences of gene frequencies between the two groups, which had divergent phenotypes, would help us to identify the genes affecting the trait of interest (Falconer and Mackay, 1996). Two tails analysis can be

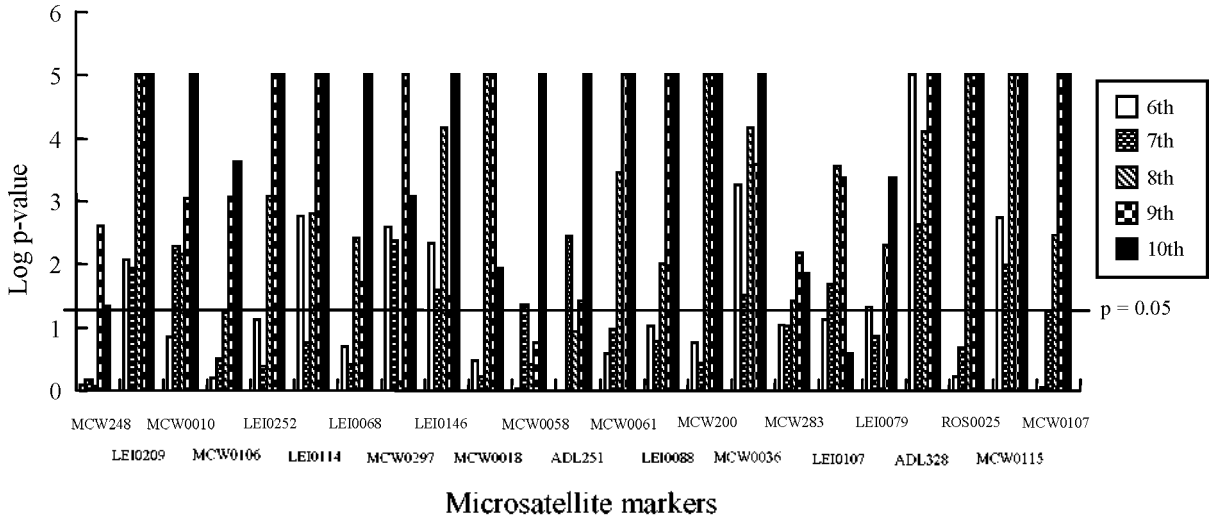

Figure 1. Comparisons of allele frequencies in two tail population (15%) of two lines of the 6th to 10th generation. There were 70, 86, 120, 120 and 200 individuals from 6th to 10th respectively.

used to study the difference of gene frequencies between two groups that had exact reverse phenotypes in the same trait, and to identify the genes that have a great effect on the traits of interest (Falconer and Mackay, 1996). Experimental and theoretical results showed that comparison between gene frequencies of two tails of a resource population, contributes tremendously to saving the requirements of genotyping efforts. Gene frequencies of the two tails are expected to be similar, except for genes controlling the trait under analysis (Hillel, 2004). Dunnington et al. (1992) used chickens that selected for high and low 8-wk body weight to detect QTL for desirable economic traits, and observed one fingerprint band associated with shank length at 12 wk of age and body weight at 8 wk. Plotsky et al. (1993) used tail analysis to compare fingerprints of DNA mixes from individuals at the two tails of a phenotypic distribution, detecting one sire-specific band associated with abdominal fat deposition.

The population used in the present study has been selected for abdominal fat trait for ten years. To date, the fat line is nearly three times of the lean line in the AFP at age of 49 d (Figure 2), and the BW at 7 wk of age was not significantly different between the two lines, suggesting that the selection for AFP was very effective in the continuing generations. The frequency of QTL allele affecting AFP may change due to this artificial selection. Therefore, if an

Table 2. Effects of sixteen markers on AFW and AFP both in every generation and across generations

Markers	6th (n = 70)		7th (n = 86)		8th (n = 120)		9th (n = 120)		10th (n = 200)		Mixed population (n = 596)		% Phenotypic variance[1]	
	AFW	AFP	AFW	AFP	AFW	AFP	AFW	AFP	AFW	AFP	AFW	AFP	AFW	AFP
ADL328	0.0067	0.0166	0.0185	0.0046	NS	NS	NS	NS	NS	NS	0.0241	0.0205	6.31	5.81
MCW0036	0.0216	0.0448	NS	NS	NS	NS	NS	NS	NS	NS	0.0063	0.0022	3.28	3.77
LEI0146	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.0001	0.0001	9.12	8.67
LEI0209	NS	NS	NS	NS	NS	NS	NS	NS	0.0001	0.0001	0.0001	0.0001	13.76	12.29
MCW0115	NS	NS	0.0518	0.0346	NS	NS	NS	NS	NS	NS	0.0007	0.0001	4.58	5.71
MCW248	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NA	NA
MCW0010	NS	NS	0.0035	0.0056	NS	NS	NS	NS	NS	NS	0.0039	0.0014	4.02	4.23
MCW0106	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NA	NA
LEI0252	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	2.01	2.22
LEI0068	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	2.54	2.74
MCW0018	NS	NS	NS	NS	NS	NS	0.0081	0.0382	NS	NS	NS	NS	1.79	1.01
MCW0061	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.23	0.57
LEI0088	NS	NS	NS	NS	0.0322	0.0184	NS	NS	NS	NS	NS	NS	0.48	0.70
MCW200	NS	NS	NS	NS	0.0174	0.0541	0.0010	0.0106	NS	NS	NS	NS	0.02	0.02
MCW283	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.0049	0.0026	3.24	3.21
ROS0025	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.0001	0.0001	4.91	4.37

[1] % of phenotypic variance in the mixed population. NS = Not significant at p>0.05. NA = No convergence.

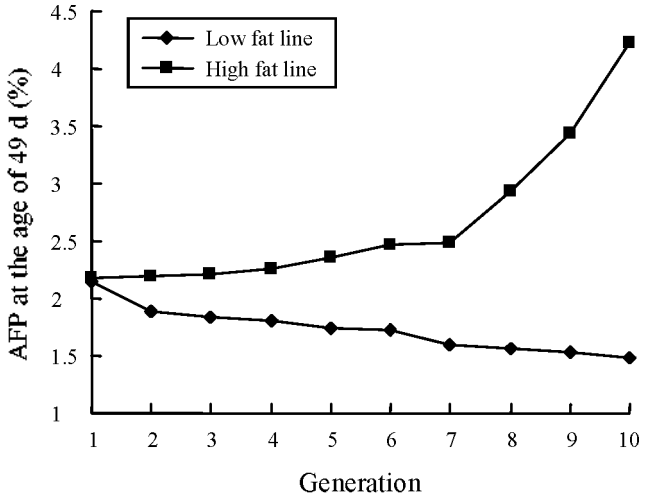

Figure 2. Selection effects of high and low fat lines. The number of fat line chickens from 1st to 10th was 82, 88, 75, 81, 80, 78, 179, 165, 186 and 336, respectively; and the number of lean line chickens from 1st to 10th was 124, 133, 127, 141, 139, 145, 258, 219, 197 and 291, respectively.

allele frequency of the marker used in the present study had significant difference between the two lines, it may indicate that the marker was closely linked with the QTL interested. In the current study, 23 microsatellite loci on chromosome 1 were used, and the differences of allele frequencies of these 23 markers between the two tails were conducted using Fisher exact test. The resulting p-values using Fisher's exact test on eleven markers of them, including MCW248, MCW0010, MCW0106, LEI0252, LEI0068, MCW0018, MCW0061, LEI0088, MCW200, MCW283 and ROS0025, had a decreasing tendency from the 6th to the 10th generation (Figure 1). Five of the 23 markers, including LEI0209, LEI0146, MCW0036, ADL328 and MCW0115, had significant differences in allele frequencies between the two tails in all the five generations. The results could indicate that QTL linked to those markers, responsible for abdominal fatness traits, segregate with selection for AFP in the consecutive generations.

In the present study, single marker association analysis was performed to detect the effects of the sixteen markers on AFW and AFP both in every generation and across generations. The results revealed that the four markers of them, including LEI0209, LEI0146, ROS0025 and MCW0115 had significant ($p<0.0011$) and another four markers including MCW0010, MCW0036, MCW283 and ADL328, had suggestive ($p<0.05$) associations with AFW and AFP in the mixed population (across generations). Significant or suggestive associations of all sixteen markers with AFW and AFP were only detected in certain generation(s), which is very likely attributed to the relatively small sample size of individual generation. A mixed population (a total of 596), from five generations, however, was used to enhance statistical power to a great extent. It is therefore relatively reliable to investigate associations with traits of interest in the mixed population. Meanwhile, an interesting finding was that phenotypic variance explained by QTL linked to eight markers with significant association was larger than that explained by others markers without significant association (Table 2), which was consistent with single marker analysis. Based upon frequency and association analyses, it is plausible to conclude that these eight markers are associated with QTL affecting the abdominal fat content.

Liu et al. (2007) reported a QTL affecting AFW and AFP near the marker ADL328 which was also detected in the current study. Zhou et al. (2006) reported a QTL affecting AFW and AFP in both the broiler-Fayoumi and broiler-Leghorn crosses and this QTL was also located near ADL328. Lagarrigue et al. (2006) identified a QTL affecting fatness in meat-type chicken lines divergently selected on abdominal fatness. The QTL was located between ADL328 and LEI0061. Jennen et al. (2005) detected a QTL flanked by MCW0297 and MCW0018 that affects AFW and AFP in an advanced intercross line (AIL) population. The marker LEI0146 used in the current study was located between these two markers. Nones et al. (2005) detected a QTL that affects abdominal fat weight between LEI0146 and LEI0174. Despite lacking in reports that the six markers, including LEI0209, ROS0025, MCW0115, MCW0010, MCW0036, MCW283, were linked to QTL for abdominal fat traits, the results in the study demonstrated that the six markers are linked to QTL affecting above traits.

To sum up, based upon makers frequencies differences in the two tail populations, marker-trait association analyses, and the previous QTL mapping results, here, we concluded that the eight markers identified in the present study may be associated with the QTL affecting AFW and AFP in chickens.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the members of the Poultry Breeding group of the College of Animal Science Technology in the Northeast Agricultural University for help in managing the birds and collecting the data. This research was supported by National Natural Science Foundation Key Project (N0. 30430510), National 863 project of China (2006AA10A120), and National 973 project of China (N0. 2006CB102105).

REFERENCES

Beckman, J. S. and M. Soller. 1983. Restriction fragment length polymorphisms in genetic improvement-methodologies, mapping and costs. Theor. Appl. Genet. 67:35-43.

Boldman, K. and D. V. Vleck. 2002. MTDFREML manual, United States Department of Agriculture, USA.

Carlborg, O., P. M. Hocking, D. W. Burt and C. S. Haley. 2004. Simultaneous mapping of epistatic QTL in chickens reveals clusters of QTL pairs with similar genetic effects on growth. Genet. Res. 83:197-209.

Dekkers, J. C. M. and F. Hospital. 2002. The use of molecular genetics in the improvement of agricultural populations. Nature 3:22-32.

de Koning, D. J., D. Windsor, P. M. Hocking, D. W. Burt, A. Law, C. S. Haley, A. Morris, J. Vincent and H. Griffin. 2003. Quantitative trait locus detection in commercial broiler lines using candidate regions. J. Anim. Sci. 81:1158-1165.

Dunnington, E. A., A. Haberfeld, L. C. Stallard, P. B. Siegel and J. Hillel. 1992. Deoxyribonucleic-acid fingerprint bands linked to loci coding for quantitative traits in chickens. Poult. Sci. 71:1251-1258.

Falconer, D. S. and T. F. C. Mackay. 1996. Introduction to Quantitative Genetics. Longman: New York.

Haley, C. S. and S. A. Knott. 1992. A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. Heredity 69:315-324.

Hillel, J. 2004. Detection of production trait loci in the chicken genome. Animal Science Papers and Reports 1:89-93.

Jennen, D. G. J. 2004. Chicken fatness: From QTL to candidate gene. PhD Diss. Wageningen University, The Netherlands.

Jennen, D. G., A. L. Vereijken, H. Bovenhuis, R. P. Crooijmans, A. Veenendaal, J. J. van der Poel and M. A. Groenen. 2004. Detection and localization of quantitative trait loci affecting fatness in broilers. Poult. Sci. 83:295-301.

Jennen, D. G. J., A. L. J. Vereijken, H. Bovenhuis, R. P. M. A. Crooijmans, J. J. der Poel, J. J. van der and M. A. M. Groenen. 2005. Confirmation of quantitative trait loci affecting fatness in chickens. Genet. Sel. Evol. 37:215-228.

Lagarrigue, S., F. Petel, W. Carré, B. Abstht, P. Le Roy, A. Neau, Y. Amigues, M. Sourdioux, J. Simon, L. Cogburn, S. Aggrey, B. Leclercq, A. Vignal and M. Douaire. 2006. Mapping quantitative trait loci affecting fatness and breast muscle weight in meat-type chicken lines divergently selected on abdominal fatness. Genet. Sel. Evol. 38:85-97.

Lander, E. and L. Kruglyak. 1995. Genetic dissection of complex traits: Guidelines for interpreting and reporting linkage results. Nat. Genet. 11:241-247.

Liu, X., H. Li, S. Wang, X. Hu, Y. Gao, Q. Wang, N. Li, Y. Wang and H. Zhang. 2007. Mapping quantitative trait loci affecting body weight and abdominal fat weight on chicken chromosome one. Poult. Sci. 86:1084-1089.

National Research Council 1994. Nutrient requirements of poultry. Natl. Acad. Press, Washington, DC.

Nones, K., M. C. Ledur, D. C. Ruy, E. E. Baron, C. M. R. Melo, A. S. Moura, E. L. Zanella, D. W. Burt and L. L. Coutinho. 2005. Mapping QTLs on chicken chromosome 1 for performance and carcass traits in a broiler x layer cross. Anim. Genet. 37: 95-100.

Plotsky, Y., A. Cahaner, A. Haberfeld, U. Lavi, S. J. Lamont and J. Hillel. 1993. DNA fingerprint bands applied to linkage analysis with quantitative trait loci in chickens. Anim. Genet. 24:105-110.

SAS Institute Inc. 2002. JMP User's Guide. Cary, NC: SAS Institute Inc.

Sasaki, O., S. Odawara, H. Takahashi, K. Nirasawa, Y. Oyamada, R. Yamamoto, K. Ishii, Y. Nagamine, H. Takeda, E. Kobayashi and T. Furukawa. 2004. Genetic mapping of quantitative trait loci affecting body weight, egg character and egg production in F2 intercross chickens. Anim. Genet. 35:188-194.

Schreiweis, M. A., P. Y. Hester and D. E. Moody. 2005. Identification of quantitative trait loci associated with bone traits and body weight in an F2 resource population of chickens. Genet. Sel. Evol. 37:677-698.

Siwek, M., S. J. Cornelissen, A. J. Buitenhuis, M. G. Nieuwland, H. Bovenhuis, R. P. Crooijmans, M. A. Groenen, H. K. Parmentier and J. J. van der Poel. 2004. Quantitative trait loci for body weight in layers differ from quantitative trait loci specific for antibody responses to sheep red blood cells. Poult. Sci. 83:853-859.

Tatsuda, K. and K. Fujinaka. 2001. Genetic mapping of the QTL affecting body weight in chickens using a F2 family. Br. Poult. Sci. 42:333-337.

van Kaam, J. B., J. A. van Arendonk, M. A. Groenen, H. Bovenhuis, A. L. Vereijken, R. Crooijmans, J. J. van der Poel and A. Veenendaal. 1998. Whole genome scan for quantitative trait loci affecting body weight in chickens using a three generation design. Livest. Prod. Sci. 54:133-150.

van Kaam, J. B., M. A. Groenen, H. Bovenhuis, A. Veenendaal, A. L. Vereijken and J. A. van Arendonk. 1999. Whole genome scan in chickens for quantitative trait loci affecting growth and feed efficiency. Poult. Sci. 78:15-23.

Zhou, H., N. Deeb, C. M. Evock-Clover, C. M. Ashwell and S. J. Lamont. 2006. Genome-wide linkage analysis to identify chromosomal regions affecting phenotypic traits in the chicken. II. Body Composition. Poult. Sci. 85:1712-1721.

Zhu, J. J., H. S. Lillehoj, P. C. Allen, C. P. Van Tassell, T. S. Sonstegard, H. H. Cheng, D. Pollock, M. Sadjadi, W. Min and M. G. Emara. 2003. Mapping quantitative trait loci associated with resistance to coccidiosis and growth. Poult. Sci. 82:9-16.