African Journal of Biotechnology Vol. 11(68), pp. 13235-13243, 23 August, 2012
Available online at http://www.academicjournals.org/AJB
DOI: 10.5897/AJB12.556
ISSN 1684–5315 ©2012 Academic Journals

Full Length Research Paper

Tissue and ontogenic expression profiles of *FATP1* and *FATP4* genes in goose

Fanli Kong[1], Juan Luo[1], Jing Sun[1], Daqian He[2], Zhiqing Yang[1], Qing Zhu[1] and Yiping Liu[1]*

[1]College of Animal Science and Technology, Sichuan Agricultural University, Ya'an, Sichuan Province, 625014, China.
[2]Institute of Animal Husbandry and Veterinary Medicine, Shanghai Academy of Agricultural Sciences, Shanghai, 201106, China.

Accepted 8 August, 2012

Fatty acid transport proteins (FATPs) are a family of proteins involved in fatty acid uptake and activation. The tissues and ontogenic expression profiles of the critical genes participating in fatty acid metabolism have little been systematically investigated in goose. To gain insight into the gene-regulation processes in goose fatty acid metabolism, we detected the expression profiles of *FATP1* and *FATP4* transcripts in goose tissues using the quantitative real-time PCR method in two goose breeds: Zhejiang white goose and Landes goose. The results show that *FATP1* and *FATP4* genes were ubiquitously expressed in all seven studied geese tissues. Both genes exhibited tissue-specific expression pattern in mRNA level with the highest expression level in leg muscle and the lowest in abdominal fat. The liver and heart were also two important tissues for both of genes expression. The growth points at 35 and 56 days were important points for both of genes expression. In addition, for the two breeds, both genes showed Zhejiang white goose had higher expression than Landes goose. It can be speculated that the expression of *FATP1* and *FATP4* genes may have breed-specific. The results could serve as a primary reference for the expression profile of goose fatty acid metabolism.

Key words: Expression pattern, *FATP1*, *FATP4*, Landes goose, Zhejiang white goose.

INTRODUCTION

Globalization and a growing demand for meat products in developing regions in recent years have led to rapid expansion of the livestock sector. The goose is considered as an ideal and healthy food for its high protein, low fat and low cholesterol, and it contains all kinds of amino acids which are needed for human. Goose has the ability to store energy in its liver through overfeeding to form fatty liver (Hermier et al., 1994), which serves as food product. In poultry, triglycerides (TG) are synthesized mainly in the liver, then transported and stored in subcutaneous fat, visceral fat, and other organs, such as liver and muscle (Hirsch et al., 1998). This tissue-specific distribution of fat is a crucial factor to determine carcass quality and appropriate fat deposition in muscle can improve the tenderness, juiciness, and the flavor of meat. Within two to three weeks, the goose liver accumulates large TG in response to overfeeding, and its weight may increase up to 10-fold (Hermier et al., 1994). This change is different among different goose breeds, so their fatty liver performances are also different (Mourot et al., 2000). Accordingly, the molecular mechanism of tissue-specific fat deposition in poultry has been one of focused issues in the field of animal nutrition and physiology. Landes goose, a well-known goose breed, can produce large fatty liver. However, Chinese indigenous goose breeds Zhejiang white goose, with the features of fast growth and good meat quality, showed a

*Corresponding author. E-mail: liuyp578@yahoo.com. Tel: 0086-835-2882509. Fax: 0086-835-2886080.

relatively poor fatty liver performance. So far, because of the weak capability of fatty acid's *de novo* synthesis, TG accumulation in poultry adipose tissues depended greatly on transmembrane fatty acid transportation (Bartov et al., 1974; Griffin et al., 1992; Zhang, 1995), which gave rise to a hypothesis that the fat tissue-specific deposition of poultry is probably based on the differences of tissue expression and function of specific fatty acid transport proteins.

The fatty acid transport protein (FATP) represents a family of six related proteins (FATP1-6) that are highly conserved during evolution with representatives in all vertebrate and invertebrate species as well as in yeast (Stahl, 2004). Several lines of evidence demonstrated that FATPs were a key transporter family for exogenous fatty acid transmembrane transport and directly took part in the fat deposition process as well (Schaffer and Lodish, 1994; Dirusso et al., 2000; Chiu et al., 2005). FATPs also have enzymatic activity. Recently, a good number of studies showed good correlation between FATP expression and fatty acid uptake (Marotta et al., 2004; Heather et al., 2006; Larqué et al., 2006). And mRNA and/or protein levels of different FATP family members are regulated by hormones such as insulin, by inflammatory mediators such as endotoxin, and by activators of peroxisome proliferator activated receptor (Pohl et al., 2004; Stahl, 2004; Doege and Stahl, 2006). *FATP1*, as the first discovered using an expression clone strategy in these 6 members, is a 71-kDa transmembrane protein (Schaffer and Lodish, 1994), which is mainly expressed in fatty acid utilization and storage tissues, such as muscle and adipose tissue (Marotta et al., 2004). It is an insulin-sensitive LCFA transporter. Insulin-induced *FATP1* translocation coincides with increased LCFA uptake (Stahl et al., 2002), which suggests that hormonal regulation of FATP activity may play a vital role in energy homeostasis. It is also considered as one of important candidate genes that can influence the obesity because of its active role in mediating fatty acid uptake (Doege and Stahl, 2006). The polymorphism of human *FATP1* intron was also closely related to intracellular triglyceride (TG) concentration (Meirhaeghe et al., 2000). Furthermore, *FATP1* could channel exogenous fatty acids into cells, preferentially for intracellular TG biochemical synthesis (Hatch et al., 2002). *FATP1* knockout significantly reduced the TG content in adipocytes (Lobo et al., 2007). And FATP1 deletion does not alter food intake, but increases liver fatty acid oxidation and liver expression of PPARα target genes, suggesting that increased energy expenditure due to increased liver fatty acid uptake may underlie the protection from obesity (Wu et al., 2006). The expression of *FATP1* gene presents a gender-related variance in skeletal muscle of lean individuals and might not actively contribute to the alterations of fatty acid uptake in patients with obesity and/or type 2 diabetes (Binnert et al., 2000). *FATP4* is most closely related to *FATP1* and like *FATP1* is expressed in adipose tissue, skeletal muscle, and the heart (Doege and Stahl, 2006). FATP4 expression and polymorphisms have been linked to markers of insulin resistance and obesity in humans (Doege and Stahl, 2006; Gertow et al., 2006). In addition, *FATP4* is the only member expressed in intestine (Stahl et al., 1999) and in muscle tissues *FATP1* and *FATP4* are co-expressed (Hirsch et al., 1998; Gimeno et al., 2003). Compared with previous studies of FATPs in human and mice, few studies are done in domestic animals. In recent study, Wang et al. (2010a, b) identified the SNPs and detected the expression pattern of *FATP1* gene in chicken. They found the polymorphisms of *FATP1* gene were associated with chicken carcass traits and the expression of *FATP1* mRNA in chicken tissues exhibited specific developmental changes and age-related patterns. So this gene may be used as a potential marker during chicken breeding. Several genes have been demonstrated to be involved in the regulation of hepatic steatosis in geese fatty liver, such as SCD, Elov1-6, and ACSL1 (Zhu et al., 2011). Whether *FATP1* and *FATP4* genes are involved in goose fatty acid metabolism are still unknown.

Here, the main objectives of this study are to reveal the relationship between fat deposition and the *FATP1* and *FATP4* genes expression in goose by using fluorescence qRT-PCR reaction. So, these results provide an experimental basis for fatty acid metabolism in goose and may improve the goose carcass composition and meat quality.

MATERIALS AND METHODS

Animals and tissues

One-day-old geese, 300 Zhejiang white geese and 80 Landes geese provided by Shanghai Academy of Agricultural Sciences, raised by special staff at the same levels of nutrition and management in poultry house, were housed on the deep-litter bedding, and then transferred to the growing pens at the age of 63 days. Zhejiang white goose is a famous native breed of Zhejiang Province in China, with fast-growing and a favorable meat quality. Landes goose is an introduced breed originally from France for fatty liver production. At 1, 14, 21, 28, 35, 42, 49, 56 and 63 days, 5 Zhejiang white geese and 5 Landes geese were sacrificed. The samples of heart, liver, leg muscle, breast muscle, intestines, abdominal fat and subcutaneous fat were collected. We isolated and weighted the liver, leg muscle, breast muscle and abdominal fat at 63 days. All experimental procedures in the present study were in accordance with the guidelines described by the guiding principles for the care and use of research animal in biology of reproduction. All tissue samples were snap frozen in liquid nitrogen and stored at -80°C.

Total RNA extraction and cDNA synthesis

Total RNA of all samples was extracted from about 50 mg tissue samples of geese using TRIzol reagent (TaKaRa Biotechnology Co.

Table 1. Gene and primers used in this study.

Gene	Primer sequence (5'-3')	Annealing temperature (°C)	Product length (bp)	Standard curve	Correlation coefficient (r^2)
β-actin	F:TGATGGAGTTGAAGGTGGTCTC R: TCCCTGGAGAAGAGCTACGAG	60	113	Y=-3.358X+34.851	0.985
FATP1	F:CAGGAGATGTGTTGGTGATGG R:CGTCTGGTTGAGGATGTGACT	60	137	Y=-3.367X+35.741	0.982
FATP4	F: GCAGACAGCTCTTCGCCACC R: GCAGCCTTGGGCATTCCCGT	60	102	Y=-3.378X+31.429	0.977

A slope of -3.32 indicates the PCR reaction has 100% efficiency (Ginzinger, 2002). The slopes of all primer pairs were close to each other, from -3.37 to -3.35, suggesting a close efficiency of the amplification between reference and target genes in qPCR. The close efficiency of amplification between target and reference validates the quantification of genes by either the standard curve or the $2^{-\Delta\Delta Ct}$ methods in further experiments.

Ltd., Dalian, China) according to the manufacturer's protocol, and dissolved in RNase-free water. The quality of RNA was measured by the $A_{260/280}$ absorbance ratio of 1.6-1.8 and the integrity of the 18S and 28S rRNA bands was detected by using 1% agarose gel in Tris-EDTA buffer, and stored at -70℃ for further analysis. For cDNA synthesis, we used ImProm-II Reverse Transcription System (TaKaRa Biotechnology Co. Ltd., Dalian, China) using 1 ng/μL of digested RNA in every tissue in total volume of 10 μL, according to the manufacturer's instruction, and ended with incubation at 15 min at 37°C, and 85°C for 5 s, and the cDNA product was stored at -20°C.

All PCR products were sequenced in order to confirm their identity and to eliminate the possibility of DNA contamination.

Quantitative real-time PCR (qRT-PCR) assay for *FATP1* and *FATP4* genes

Without any available goose sequences, the primers designed for qRT-PCR were based on the chicken sequence: *FATP1* (accession number: NM001039602) and *FATP4* (accession number: FJ868804) mRNA sequences in GenBank and synthesized by TaKaRa Biotechnology Co. Ltd., (Dalian, China), and the housekeeping gene *β-actin* (Genbank accession number: AF047874) used as an internal control was also synthesized (Table 1). The qRT-PCR products was cloned into a pMD 18-T vector (TaKaRa) and then sequenced by Shanghai Yingjun Biology Technique Corporation (Shanghai, China). All the PCR products had high homology with chicken *FATP1* and *FATP4* genes.

qRT-PCRs were performed on iQ5 Real Time PCR thermal cycle instrument (Bio-Rad, German) using SYBR Green I detection chemistry in a final reaction volume of 25 μL containing 12.5 μL SYBR Premix Ex TaqTM 2× (TaKaRa Biotechnology Co. Ltd., Dalian, China), 0.5 μL of each primer (10 μM) (listed in Table 1), 2 μL cDNA and 9.5 μL ddH_2O. The reaction carried out without template was used as negative control. PCR amplification was performed in triplicate wells, using the following conditions: 35 cycles of denaturing at 94°C for 30 s, annealing at 60°C for 30 s and extension at 72°C for 50 s.

The specificity of amplifications was checked by melting curve analyses and 2% agarose gel. All primers gave specific melting curves and electrophoresis bands as expected (data not shown).

In addition, the efficiency of the amplification for each primer pair was assessed by a slope of the equation of a standard curve generated from the 8-fold dilutions (10^{-3}, 10^{-4}, 10^{-5}, 10^{-6}, 10^{-7}, 10^{-8}, 10^{-9}, and 10^{-10}) of a purified specific intestine PCR product (Table 1).

Statistical analysis

The values were expressed as the mean ± standard deviation (SD). Comparison of variables between breeds was analyzed by using one-way ANOVA and an independent-samples t-test with SAS 8.0 for Windows Software (SAS Institute Inc., Cary, NC). Statistical significance was interpreted as values of $P< 0.05$.

RESULTS

Ontogenic expression of goose *FATP1* mRNA level

The *FATP1* transcripts were ubiquitously expressed in all collected tissues at all growth points in this study. Relative to the *β-actin* gene, the *FATP1* transcripts had a relatively higher expression level in leg muscle, liver and heart. Especially, the leg muscle had the highest expression at every growth points, while the liver had a relatively higher expression before 35 days, and the heart had a high expression level after 35 days. However, the adipose tissues had relatively low expression level (Figure 1). The breast muscle also had a relatively low expression level. We also detected that the *FATP1* gene in intestines also had a little expression level.

The ontogenic expression of *FATP1* gene in geese with different growth points was also analyzed. As shown in Figure 3, the liver, heart and leg muscle had the highest expression at 56 days. Especially, the heart had a rise development change before 56 days. In total, the breast muscle had a significant higher expression level after 35 days than before ($P<0.05$). In addition, the intestines tissue made a "decline-rise-decline" development changes, the abdominal fat tissue had a "rise-decline" development changes, and the subcutaneous fat tissue had a decline development change after 21 days.

Ontogenic expression of goose *FATP4* mRNA level

As shown in Figure 2, the expression of *FATP4* gene was also detected in all collected tissues and varied

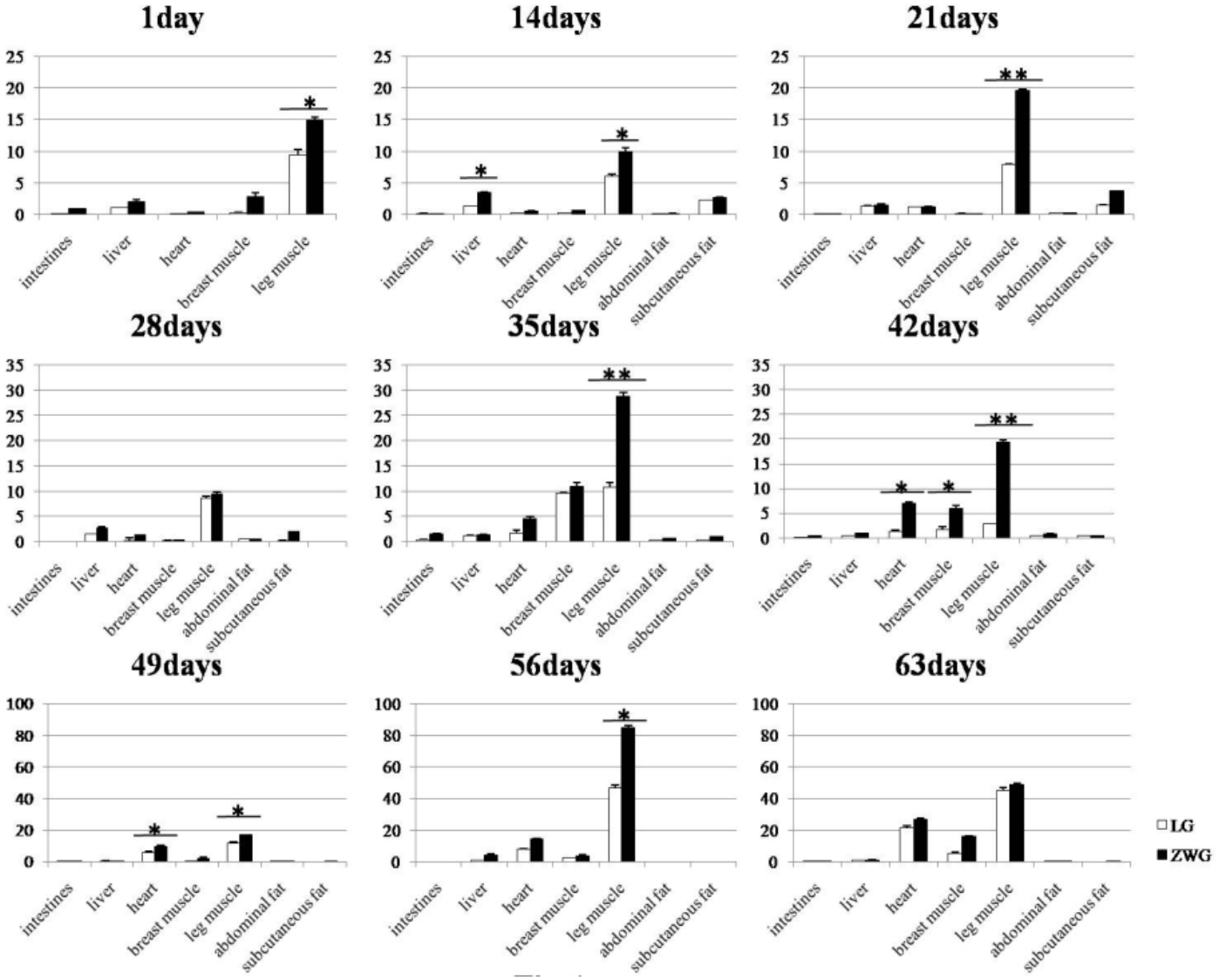

Figure 1. The relative expression level of *FATP1* gene in seven goose tissues at different growth points. The relative expression amount was calculated as $2^{-\Delta\Delta Ct}$ and the Ct value of intestine at 1day of Zhejiang white goose was used as a reference in each respective reaction to normalize the deviation. The means marked by asterisks was significantly different of *FATP1* mRNA in the same tissues between Zhejiang white goose and Landes goose (* for $P<0.05$ and ** for $P<0.01$) and the abscissa was on behalf of every tissue, the ordinate was on behalf of the relative expression level for mRNA. For each growth point, at least four geese were analyzed, and the results reflect the mean ± SD. LG, Landes goose; ZWG, Zhejiang white goose.

considerably in different tissues. The *FATP4* transcript had a relative higher expression in leg muscle, liver, heart and subcutaneous fat. However, the leg muscle, liver and subcutaneous fat had relative higher expression level at 35 days and younger and the heart tissue after the 35 days. In addition, *FATP4* in liver and subcutaneous fat may display concomitant. The intestines, breast muscle and abdominal fat tissues had relative lower expression level.

The developmental changes of the *FATP4* mRNA expression in geese at different growth points shows that the liver, heart and leg muscle had the highest expression at 56 days. Especially, the leg muscle and heart at 56 days had significant difference from other growth points (P<0.05). Totally, the abdominal fat tissue had a “rise-decline” development changes, and the subcutaneous fat tissue had a decline development change after 21 days. However, the intestines made a “rise-decline” development changes after 1 day but the development changes of breast muscle were not evident

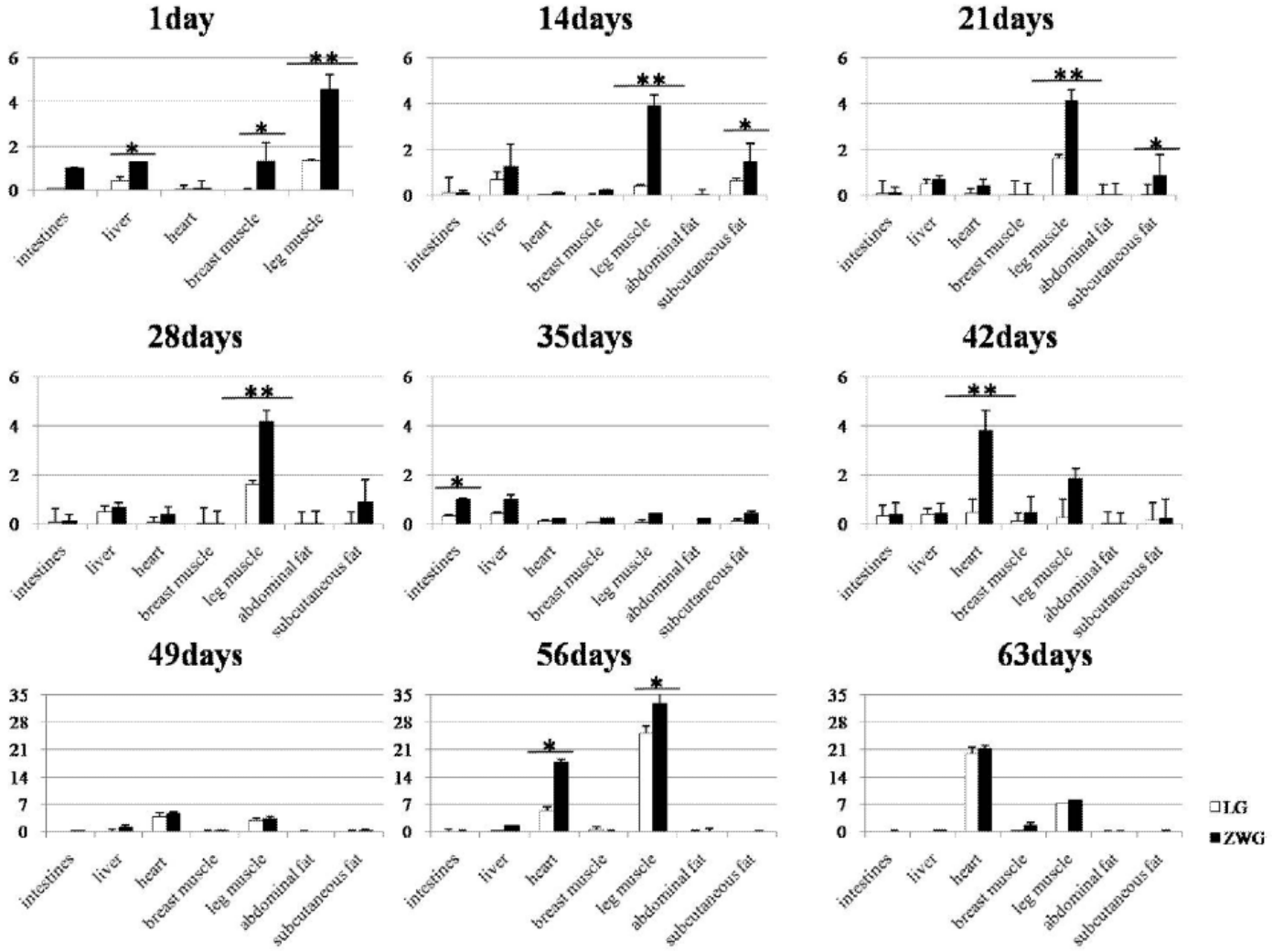

Figure 2. The relative expression level of *FATP4* gene in seven goose tissues at different growth points. The relative expression amount was calculated as $2^{-\Delta\Delta Ct}$ and the Ct value of intestine at 1day of Zhejiang white goose was used as a reference in each respective reaction to normalize the deviation. The means marked by asterisks was significant difference of *FATP1* mRNA in the same tissues between Zhejiang white goose and Landes goose (* for $P<0.05$ and ** for $P<0.01$). The abscissa was on behalf of every tissue, the ordinate was on behalf of the relative expression level for mRNA. For each growth point, at least four geese were analyzed, and the results reflect the mean ± SD. LG, for Landes goose; ZWG, for Zhejiang white goose.

in all selected growth points (shown Figure 4).

The difference of *FATP1* and *FATP4* genes expression pattern between Zhejiang white goose and Landes goose

To characterize differences of *FATP1* and *FATP4* genes expression pattern between breeds, we analyzed the expression level of both genes in all collected tissues between the two goose breeds. In total, the expression of both genes in the Zhejiang white goose tissue was higher than Landes goose (Figures 1 and 2). Especially in leg muscle and heart, the difference of both genes was great significant at some growth points ($P<0.01$) and both of breeds showed the same developmental change in every tissue at every growth points.

DISCUSSION

It is well known that *FATP1* and *FATP4* genes have close relationship in fatty acid uptake (Lobo et al., 2007). As a development step for clarifying the mechanism for expression differentiation, our results reveal that *FATP1* and *FATP4* transcripts were ubiquitously expressed in all

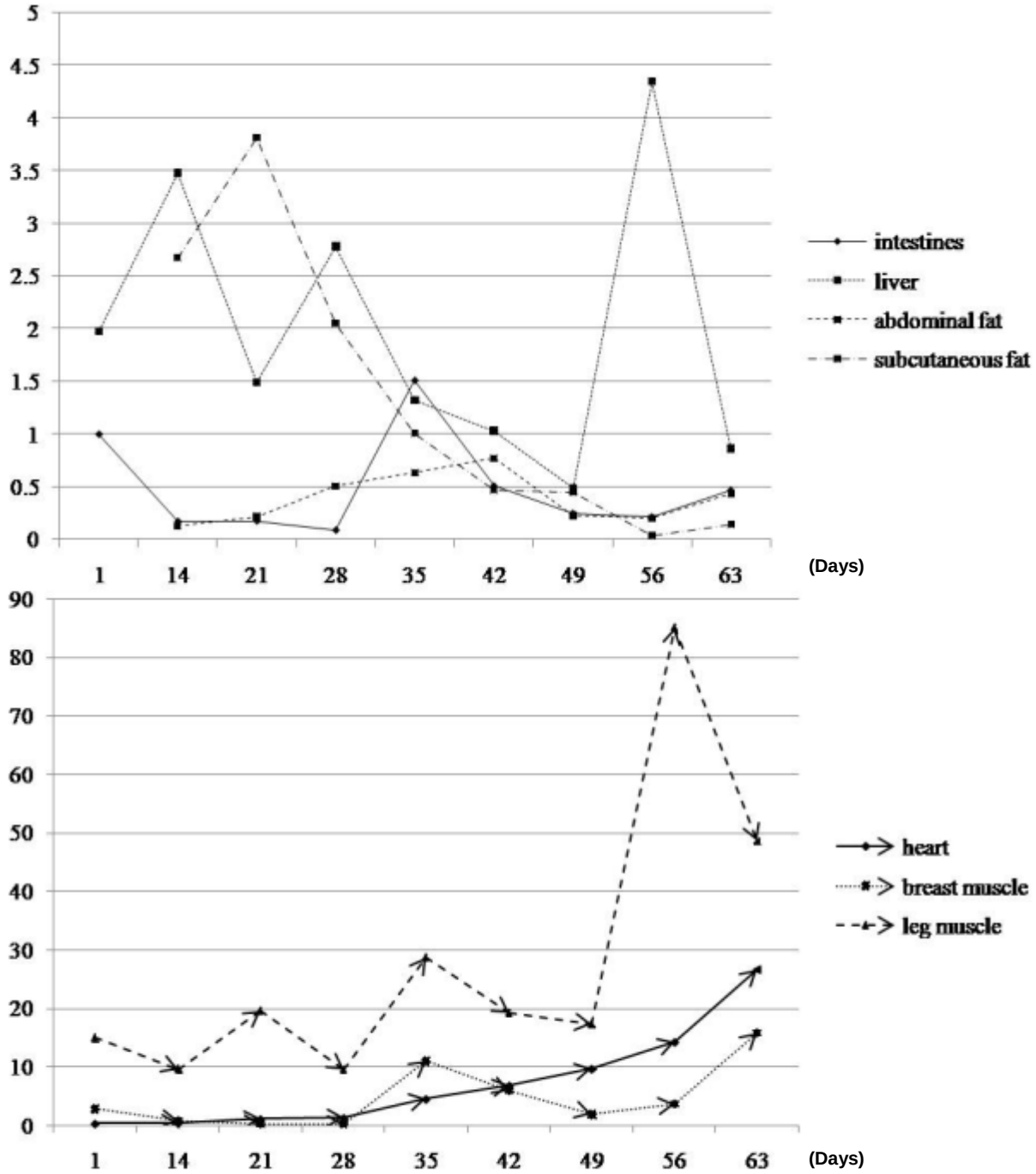

Figure 3. The expression quality of *FATP1* in different growth point for Zhejiang white goose. The relative expression amount was calculated as $2^{-\Delta\Delta Ct}$ and the Ct value of intestine at 1day of Zhejiang white goose was used as a reference in each respective reaction to normalize the deviation. The abscissa was on behalf of the growth points of every tissue, the ordinate was on behalf of the relative expression level for every tissue mRNA. For each growth point, at least four geese were analyzed, and the results reflect the mean ± SD.

collected tissues at every growth points in geese. Compared to its expression in other tissues, the geese *FATP1* and *FATP4* mRNA expression levels were abundant in leg muscle (Figures 1 and 2), which was in accordance with chicken (Marotta et al., 2004; Wang et al., 2010b). The results display that both genes may be

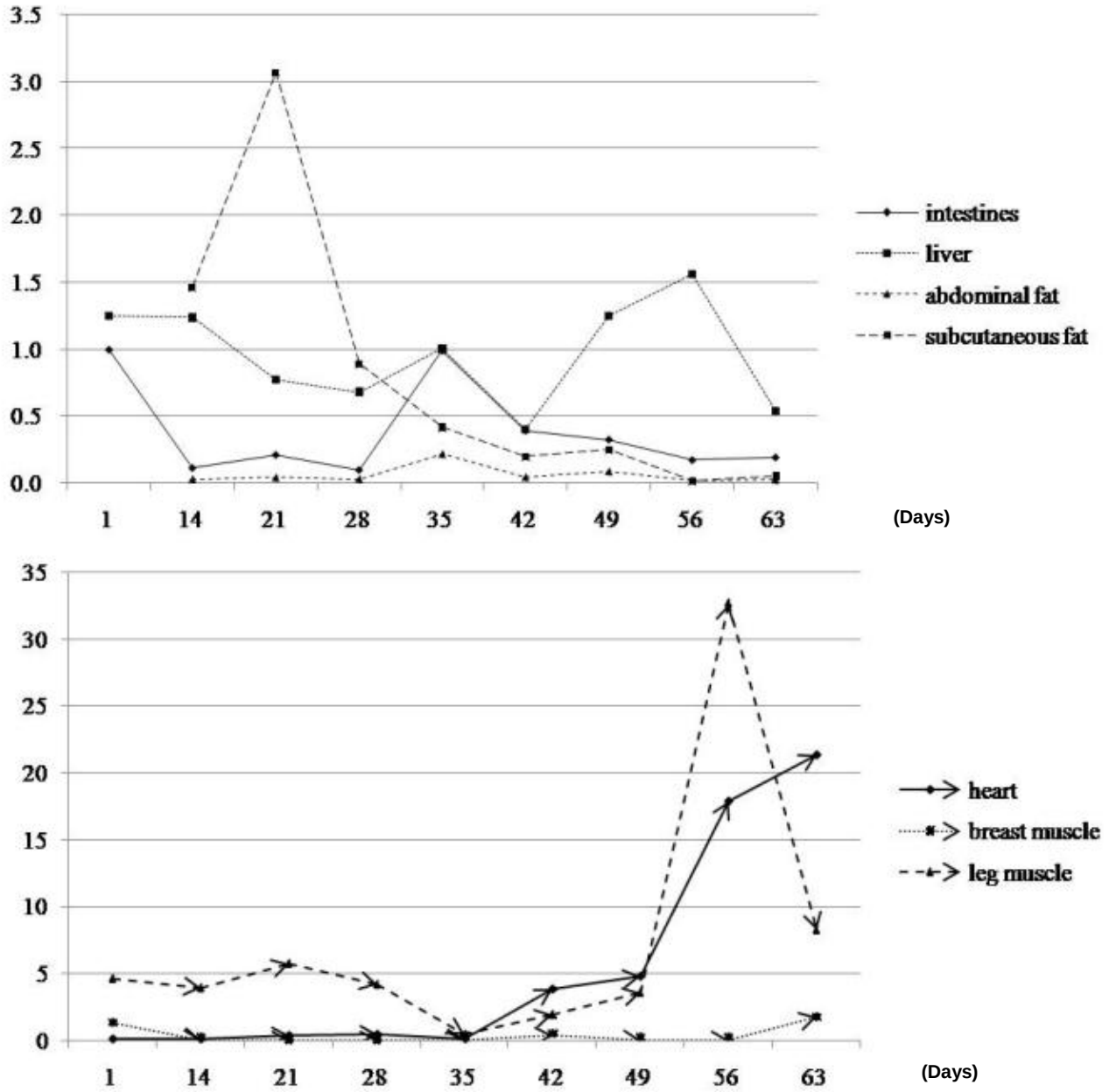

Figure 4. The expression quality of *FATP4* in different growth point for Zhejiang White Goose. The relative expression amount was calculated as $2^{-\Delta\Delta Ct}$ and the Ct value of intestine at 1day of Zhejiang White Goose was used as a reference in each respective reaction to normalize the deviation. The abscissa was on behalf of the growth points of every tissue, the ordinate was on behalf of the relative expression level for every tissue mRNA. For each growth point, at least four geese were analyzed, and the results reflect the mean ± SD.

active in fatty acid uptake for leg muscle. It was paralleled with the intramuscular fat deposition in muscle (Hatch et al., 2002) and this may be connected with the fiber type in goose's leg muscle. The leg muscle is made up of type 1 fiber which utilized the energy form aerobic oxidation of fatty acid (Hatch et al., 2002). This also may suggest that these proteins, as a vital transporter of long chain fatty acids, possibly play an important role in the metabolism type of regulation and intramuscular fat deposition in muscles. Meanwhile, the liver and heart also had a relatively higher expression level. This could be due to differences in lipid mobilization within tissues and levels of hormone-induced *FATP1* and *FATP4* genes activity that caused a remarkable increase plasma lipids and very

low density lipoprotein in production in avian species (Dashti et al., 1983). And the low expression level of both genes in goose abdominal fat most likely reflects the fact that lipogenesis, in birds, occurs primarily in liver (O'hea and Leveille, 1968). Previous study has shown that *FATP4* was the principal FATP expression member in the intestine (Stahl et al., 1999), and that reduction of *FATP4* protein levels result in reduced LCFA. Consistent with this observation, we also detected expression of *FATP4* gene in goose intestines. The expression of *FATP1* mRNA in intestines was first observed in this experiment, which could be speculated as being related to the utilization of unsaturated fatty acid and synthesis of bioactive substances in this organ. In addition, the growth points at 35 and 56 days may be important for goose lipid transporting. It may be related with the goose fattening.

Davail et al. (2000) showed that there is evident breed or species-related differences in the process of lipogenesis among different geese breeds, and probably under genetic control. In order to characterize the breed effect on the goose expression of *FATP1* and *FATP4*, we analyzed the expression level of these two genes in two goose breeds. The Zhejiang White Goose is a famous native breed of Zhejiang Province in China, with fast-growing and a favorable meat quality. In contrast, Landes Goose is an introduced breed for fatty liver production. We found that both genes in Zhejiang White Goose exhibited a higher expression level than Landes Goose (Figures 1 and 2), which indicate that the different expression levels of both genes may be correlated with the characters of these two breeds. It has been reported that the susceptibility to fatty liver varies in different species and the fatty liver serves as an energy storage organ (Hermier et al., 2003). But there is little report about the relationship between the mechanisms of molecular regulation and the expression of lipogenic gene. In our work, we also found that the expression level of both genes in the liver tissue showed different developmental changes between the two breeds (data not shown). It may be that in the process of liver fattening, the metabolism of the liver changed dramatically in goose (Davail et al., 2000), so the expression level in fatty liver is also different.

In conclusion, we report first the experimental evidence for *FATP1* and *FATP4* genes expression level in goose tissues using qRT-PCR method. Especially, leg muscle had higher expression level than other tissues even great significance in some growth points of both genes. We also found both genes may have breed-difference expression. Thus, our study may provide a new conclusion to understand the expression pattern of *FATP1* and *FATP4* genes in goose.

ACKNOWLEDGEMENTS

We thank Bing Zhou and Huali Wu for the sample collection and technical support. This study was supported by the National Natural Science Foundation of China (31172181), the Program from Sichuan Province (11TD007; 2011JTD0032) and the Program from Shanghai (2009-2-1).

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