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Original article

Age-related changes in plasma porcine growth hormone (GH) profiles and insulin-like growth factor-I (IGF-I) concentrations in Large White and Meishan pigs

I Louveau [1,*], M Bonneau [1], DN Salter [2]

[1] *INRA, Station de Recherches Porcines, Saint-Gilles, 35590 L'Hermitage, France;*
[2] *AFRC, Institute of Grassland and Animal Production, Pig Department, Shinfield, Reading RG2 9AQ, UK*

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Summary — Plasma GH profiles and IGF-I concentrations were determined in Large White intact male (LW-M), female (LW-F) and castrated male (LW-C) and in Meishan intact male (MS-M) pigs between 10 and 140 d of age. Mean GH levels slightly increased between 10 and 45 d of age in LW pigs, in connection with an alteration in the temporal distribution of GH peaks, whereas neither interpulse GH level nor maximum GH level were affected. Mean GH levels decreased after 45 d of age, in connection with a decline in maximum and interpulse GH levels. IGF-I concentrations were low between 10 and 45 d of age and increased thereafter. GH secretory profiles did not differ significantly between LW-M and LW-F at either age. Castration had no effect at 45 d of age whereas LW-C exhibited lower mean, maximum and interpulse GH levels and smaller sum of GH pulse areas and widths than LW-M or LW-F at 140 d of age. IGF-I was lower in LW-C or LW-F than in LW-M at 140 d of age. The pattern of age-related changes in GH and IGF-I was similar in MS and LW pigs. However, interpulse GH level was higher and sum of GH pulse widths was smaller in MS-M than in LW-M, whatever the age. The results indicate that: i), GH and IGF-I secretions were similar in Meishan, and Large White pigs; ii), in both breeds, GH secretion declined after 45 d of age, due to decreased maximum and interpulse GH levels; iii), sex and/or castration effects on GH and IGF-I secretion were observed after 45 d of age only.

pig / age / breed / GH / IGF-I

Résumé — Évolution avec l'âge des profils d'hormone de croissance porcine (GH) et des concentrations d'*insulin-like growth factor-I* (IGF-I) dans le plasma de porcs Large White et Meishan. *Les profils de GH et les concentrations d'IGF-I ont été déterminés entre 10 et 140 j d'âge dans le plasma sanguin périphérique de porcs mâles entiers (LW-M), femelles (LW-F) et mâles castrés (LW-C) de race Large White et de porcs mâles entiers de race Meishan (MS-M). La concentra-*

* Correspondence and reprints

tion moyenne de GH augmente légèrement entre 10 et 45 j d'âge chez les porcs LW, en relation avec un changement dans la répartition temporelle des pics de GH, alors que ni le niveau de GH entre pics, ni le niveau maximum de GH ne sont affectés. La concentration moyenne de GH décroît après 45 j d'âge, en relation avec un déclin des niveaux entre pics et maximum de GH. La concentration d'IGF-I est basse entre 10 et 45 d'âge, puis augmente. Les profils de secrétion de GH ne diffèrent pas significativement entre LW-M et LW-F, quel que soit l'âge. La castration n'a aucun effet à 45 j d'âge, alors que les niveaux moyen, maximum et entre pics de GH et les sommes des aires et des durées des pics de GH sont plus faibles chez LW-C que chez LW-M ou LW-F à 140 j d'âge. La concentration d'IGF-I est plus faible chez LW-C ou LW-F que chez LW-M à 140 j d'âge. L'évolution avec l'âge des secrétions de GH et d'IGF-I est similaire chez les porcs MS et LW. Cependant, le niveau de GH entre pics est plus élevé et la somme des durées des pics de GH est plus faible chez MS-M que chez LW-M, quel que soit l'âge. Les résultats indiquent que :
– les secrétions de GH et d'IGF-I sont similaires chez les porcs Meishan et Large White;
– dans les 2 races, la secrétion de GH est plus faible après 45 j d'âge, en raison du déclin des niveaux maximum et entre pics de GH;
– les effets du sexe et/ou de la castration ne s'observent qu'après 45 j d'âge.

porc / âge / race / hormone de croissance / IGF-I

INTRODUCTION

Blood porcine growth hormone (GH) concentration declines with age in the growing pig (Siers and Swiger, 1971; Chappel and Dunkin, 1975; Althen and Gerrits, 1976; Wangness *et al,* 1977; Scanes *et al,* 1987). To date, none of the studies that have examined the pulsatile nature of GH secretion have investigated the whole range of postnatal ages (Klindt and Stone, 1984; Klindt, 1986; Dubreuil *et al,* 1987, 1988, 1989; Arbona *et al,* 1988,1989). Similary, descriptions of the age-related elevation of insulin-like growth factor-I (IGF-I) concentration in pigs were restricted either to the first 2 months of postnatal life (Scanes *et al,* 1987; Simmen *et al,* 1988; Osborne *et al,* 1989) or to older ages (112–168 d; Arbona *et al,* 1989).

In animals younger than 2 months, blood GH concentrations are not affected by sex or castration (Dubreuil *et al,* 1987; Trudeau *et al,* 1988). In older pigs, blood GH and IGF-I are higher in intact males than in females and depressed by castration in males (Arbona *et al,* 1988, 1989; Dubreuil *et al,* 1987, 1989). However, the effects of sex and castration on IGF-I concentrations in young post-natal pigs have not been investigated.

GH and IGF status differs among the various models of slow growing fat breeds of pigs. In comparison with conventional pigs, GH and IGF-I secretions are not impaired in Yucatan mini pigs (Lauteric *et al,* 1988), IGF-I but not GH is depressed in Yucatan micro and Hanford mini pigs (Buonomo *et al,* 1987; Lauteric *et al,* 1988) and both GH and IGF-I concentrations are lower in Ossabaw pigs (Kasser *et al,* 1981; Martin *et al,* 1985; McCusker *et al,* 1985). Meishan breed is a particularly interesting model of slow growing fat animal. Growth rate is 30% and 50–60% lower in Meishan than in Large White pigs during the suckling and growing periods respectively and 90 kg Meishan pigs contain 41% more body fat than their Large White counterparts (Bonneau *et al,* 1990). No information is available concerning GH and IGF secretion in Meishan pigs.

The aim of the present study was to investigate the influence of age, from 10 to 140 d, on blood GH profiles and IGF-I con-

centrations in growing Large White and Meishan pigs. Moreover, the effects of sex and castration were investigated in the Large White breed.

MATERIALS AND METHODS

Large White animals

Twelve intact male (LW-M), 12 female (LW-F) and 6 castrated male (LW-C) Large White pigs, chosen from 6 litters, were used in the experiment. Blood samples were collected from 6 LW-M and 6 LW-F at 10 d of age. Six LW-M, 6 LW-F and 6 LW-C, from the same 6 litters, were then sampled at 45 and at 140 d of age. At 10 d of age, the animals were housed in the farrowing crate and were allowed to suckle during blood collection time. Weaning and castration were performed at 30 d of age. The animals were then fed *ad libitum* a cereal–soya diet containing 17.3% crude protein and 0.88% lysine.

Meishan animals

A total of 40 intact male pigs (MS-M) were used in the experiment. The animals were the descendents of the 1 boar and 2 gilts imported to France in 1979 and of 3 animals (1 sow and 2 boars) subsequently imported from China in 1982. Inbreeding level was 10%.

Eight animals were sampled at each of the following ages: 10, 30, 45, 70 and 140 d. At 10 and 30 d of age, the animals were housed in the farrowing crate and allowed to suckle during blood collection time. Weaning was performed at 30 d of age. The animals were then fed *ad libitum* a cereal–soya diet containing 17.3% crude protein and 0.88% lysine.

Ages at sampling for Meishan animals were chosen so that comparisons could be made with Large White pigs either at the same ages (10, 45, 140 d) or at similar stages of sexual development (Meishan at 10, 30 and 70 d *vs* Large White at 10, 45 and 140 d age, respectively). Meishan pigs were 25–30% lighter than Large White animals of similar ages.

Blood sampling procedure

Three days prior to blood collection, a catheter was inserted into the jugular vein of the animal under general anaesthesia. Blood samples (1.2 ml at 10 d, 1.5 ml at older ages) were collected through the catheter at 20-min intervals, starting at 09 00, for a 6-(10 d of age) or 8-h period (30–140 d of age). Blood was kept on ice and centrifuged. Porcine GH was measured on individual plasma samples. From each plasma sample, a 0.2-ml aliquot was pipetted to make a pool for each animal over the 6 or 8-h period of blood sampling. Insulin-like growth factor-I (IGF-I) concentrations were measured on plasma pools.

Radioimmunoassay of plasma GH

Plasma GH concentration was determined by a specific homologous double antibody radioimmunoassay. Antiserum (UCB Bioproducts, Brussels, Belgium) was used at a final dilution of 1/30 000. Cross-reactions with porcine prolactin, luteinizing hormone and follicle-stimulating hormone were < 0.4%. USDA-GH-I-1 (AFP-6400) was used for iodination and standard curve. Sensitivity was 1 ng/ml. Coefficients of variation for plasma samples containing 3.8, 12.0 and 25.0 ng/ml were as follows: intra-assay 9.2, 5.9 and 8.6% respectively, inter-assay 9.4, 12.7 and 14.7 respectively. Samples from the same breed were measured within a single assay.

Radioimmuoassay of plasma IGF-I

Porcine plasma IGF-I concentration was determined in acid–ethanol extracts with a single antibody radioimmunoassay as described by Morell *et al* (1989), using polyethylene glycol and bovine γ-globulin to separate bound from free IGF-I. UK polyclonal antiserum R557-A (a gift from D Morrell, Institute of Child Health, University of London, UK) was used at a final dilution of 1/5 000. Cross-reactivity against IGF-II was ≈ 4%. Recombinant Thr-59 human somatomedin C analogue (Amersham International plc, Amersham, UK) was used as standard. One unit of porcine IGF-I was defined as equivalent to 1 ng of standard. Human (^{125}I)IGF-I, specific activity 100

μCi/μg (a gift from J Pell, AFRC Institute for Grassland and Animal Production, Hurley, UK) was used as tracer. Sensitivity was 0.5 units/ml. Intra-assay coefficient of variations for samples containing 271 and 412 units/ml were 4.3% and 8.5% respectively. Plasma samples were extracted in duplicate. All extracts were set up in triplicate and measured within a single assay.

Determination of GH secretory profile criteria

GH secretory profiles were analyzed according to the procedure described by Merriam and Wachter (1982). For each profile, mean GH levels, mean interpulse GH levels, sum of GH pulse areas and widths, maximum within-pulse GH levels and number of detected GH pulses were calculated.

Statistical methods

Analysis of variance was performed on GH secretory profile criteria and IGF-I concentrations, using the General Linear Model procedure (SAS, 1989). Five different analyses were conducted to investigate the effects of: i), age (10, 45, 140 d) and sex (LW-M *vs* LW-F) in Large White pigs; ii), age (45 *vs* 140 d) and gender (LW-M, LW-F, LW-C) in Large White pigs; iii), age in Meishan pigs; iv), age and breed (LW-M *vs* MS-M at 10, 45 and 140 d); and v), age and stage (LW-M at 10, 45 and 140 d *vs* MS-M at 10, 30 and 70 d, respectively). Where relevant, multiple comparisons of the means were performed, using Duncan's test.

RESULTS

GH and IGF-I in Meishan pigs

Mean interpulse GH level increased from 10 to 30 d of age then decreased between 45 and 70 d of age (table I). Mean and maximum GH levels significantly declined between 45 and 70 d of age. Similary, sum of GH pulse areas decreased between 45 and 70 d of age ($P < 0.10$). Age-related decline was also observed for a number of GH pulses. IGF-I concentration was not significantly different at 10, 30 and 45 d of age, increased between 45 and 70 d and declined thereafter.

GH and IGF-I in Large White pigs

Plasma growth hormone (GH) profile criteria and insulin-like growth factor-I concentrations (IGF-I) in Large White pigs are reported in table II. Sex (LW-M *vs* LW-F) had no significant effect on any plasma GH profile criterion whereas age significantly affected all of them (table III). Mean GH level was significantly higher in 45- than in 10-d-old pigs and was higher at 10 than at 140 d of age. Mean interpulse GH level was lower in 140-d-old than in younger animals. Sum of GH pulse areas or widths was higher at 45 than at 10 or 140 d of age. Number of detected GH pulses was significantly higher in 10-d than in older pigs. Maximum GH levels decreased with age in LW-M, but this trend was less clear in LW-F.

Significant age x gender interactions were observed for mean and maximum GH levels and sum of GH pulse areas ($P < 0.05$; table IV) as well as for sum of GH pulse widths ($P < 0.10$). Gender had no significant effect on GH profile criteria at 45 d. At 140 d of age, mean and maximum GH levels and sum of GH pulse areas were lower in LW-C than in LW-M or LW-F ($P < 0.05$). Mean interpulse GH level also tended to be lower in LW-C than in LW-M or LW-F ($P < 0.10$). Sum of GH pulse widths were significantly higher in LW-M than in LW-C, with LW-F being intermediate ($P < 0.05$).

Table I. Plasma GH profile criteria and IGF-I concentrations in intact male Meishan pigs (mean ± SEM).

Age (d) *No of animals*	*10* *7*	*30* *7*	*45* *6*	*70* *7*	*140* *8*	*Significance of age effect*
Mean GH level (ng/ml)	6.6 ± 0.8^{ab}	7.9 ± 1.2^{a}	7.4 ± 0.8^{a}	3.3 ± 0.3^{c}	4.5 ± 0.4^{bc}	***
Mean interpulse GH level (ng/ml)	4.4 ± 0.3^{bc}	6.4 ± 1.0^{a}	5.9 ± 0.8^{ab}	2.4 ± 0.2^{d}	3.8 ± 0.5^{cd}	***
Sum of GH pulse areas (μg.min/ml)	2.0 ± 0.5	1.8 ± 0.5	1.8 ± 0.3	0.9 ± 0.1	0.9 ± 0.1	NS
Sum of GH pulse widths (min)	188 ± 42	166 ± 36	190 ± 15	177 ± 25	154 ± 26	NS
Maximum within pulse GH level (ng/ml)	12.0 ± 1.3^{a}	12.8 ± 1.2^{a}	11.0 ± 0.7^{a}	7.0 ± 0.7^{b}	7.3 ± 0.8^{b}	**
No of detected GH pulses / 8 h	4.2 ± 0.8^{a}	2.9 ± 0.4^{ab}	3.3 ± 0.4^{ab}	3.0 ± 0.3^{ab}	2.0 ± 0.4^{b}	*
IGF-I level (units/ml)	18 ± 1^{c}	17 ± 1^{c}	31 ± 6^{c}	121 ± 17^{a}	79 ± 13^{b}	***

Means in the same line that do not have a common superscript letter differ ($P < 0.05$).

Table II. Plasma GH profile criteria and IGF-I concentration in Large White pigs (means ± SEM).

Age (d) *Gender* [1]	*10* *LW-M*	*10* *LW-F*	*45* *LW-M*	*45* *LW-F*	*45* *LW-C*	*140* *LW-M*	*140* *LW-F*	*140* *LW-C*
No of animals	*6*	*6*	*6*	*6*	*5*	*6*	*5*	*6*
Means GH level (ng/ml)	5.5 ± 1.3	4.4 ± 0.8	5.8 ± 0.8	7.6 ± 0.3	7.5 ± 1.0	3.3 ± 0.3	3.2 ± 0.5	2.0 ± 0.1
Means interpulse GH level (ng/ml)	2.9 ± 0.6	3.1 ± 0.5	2.9 ± 0.5	3.4 ± 0.2	3.8 ± 0.8	2.0 ± 0.3	2.2 ± 0.3	1.6 ± 0.1
Sum of GH pulse areas (μg.min/ml)	2.1 ± 0.6	1.2 ± 0.4	2.3 ± 0.5	3.2 ± 0.2	2.9 ± 0.4	1.1 ± 0.1	0.9 ± 0.2	0.5 ± 0.1
Sum of GH pulse widths (min)	232 ± 50	158 ± 32	283 ± 37	330 ± 33	288 ± 22	243 ± 33	188 ± 22	160 ± 24
Maximum within pulse GH level (ng/ml)	10.6 ± 1.5	8.6 ± 0.9	9.4 ± 1.1	12.8 ± 1.2	13.0 ± 1.6	7.1 ± 0.6	8.7 ± 1.3	4.3 ± 0.5
No of detected GH pulses / 8 h	5.3 ± 0.9	4.5 ± 0.7	3.5 ± 0.8	3.5 ± 0.4	3.3 ± 0.4	3.2 ± 0.3	2.8 ± 0.3	2.4 ± 0.4
IGF-I level (units/ml)	26 ± 3	30 ± 3	20 ± 3	18 ± 1	14 ± 1	117 ± 17	75 ± 9	69 ± 12

[1] LW-M = entire males; LW-F = females; LW-C = castrated males.

Table III. Significance of the effects of age (10, 45, 140 d) and sex (males *vs* females) on plasma GH profile criteria and IGF-I concentrations in Large White pigs.

	Effects			*Within age means* [1]		
	Age	*Sex*	*Age x sex*	*10 d*	*45 d*	*140 d*
Mean GH level	***	NS	NS	4.9^{b}	6.7^{a}	3.3^{c}
Mean interpulse GH level	*	NS	NS	3.0^{a}	3.1^{a}	2.1^{b}
Sum of GH pulse areas	***	NS	NS	1.6^{a}	2.8^{a}	1.0^{b}
Sum of GH pulse widths	**	NS	NS	196^{b}	306^{a}	218^{b}
Maximum within pulse GH level	***	NS	NS	9.7^{ab}	11.0^{a}	7.7^{b}
No of detected GH pulses	**	NS	NS	4.9^{a}	3.5^{b}	3.0^{b}
IGF-I level	***	NS	*	28^{b}	19^{b}	98^{a}

[1] Means in the same line that do not have a common superscript letter differ ($P < 0.05$). NS: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

IGF-I was similar in 10 and 45-d old pigs while it significantly increased between 45 and 140 d of age. Age-related IGF-I increase differed between sexes and genders (age x sex and age x gender interactions: $P < 0.05$). IGF-I level was higher in LW-M than in LW-F or LW-C at 140 d of age ($P < 0.05$).

Comparison between GH and IGF-I in Meishan vs *Large White pigs*

Similar results were obtained from the comparisons of Large White and Meishan pigs at either the same age or similar stages of sexual maturation (table V). Mean inter-

Table IV. Significance of the effects of age (45 *vs* 140 d) and gender (males, females, castrates) on plasma GH profile criteria and IGF-I concentrations in Large White pigs.

	Effects			*Gender effect*	
	Age	*Gender*	*Age x gender*	*at 45 d*	*at 140 d*
Mean GH level	***	NS	*	NS	**
Mean interpulse GH level	***	NS	NS	NS	NS
Sum of GH pulse areas	***	NS	*	NS	**
Sum of GH pulse widths	***	NS	NS	NS	*
Maximum within pulse GH level	***	NS	*	NS	**
No of detected GH pulses	NS	NS	NS	NS	NS
IGF-I level	***	*	*	NS	*

NS: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Table V. Significance of the effects of age or stage and breed on plasma GH profile criteria and IGF-I concentrations in intact male pigs.

	Analysis of age [1] *and breed* [3] *effects*			*Analysis of stage* [2] *and breed* [3] *effects*		
	Age	*Breed*	*Age x breed*	*Stage*	*Breed*	*Stage x breed*
Mean GH level	**	NS	NS	***	NS	NS
Mean interpulse GH level	*	***	NS	***	***	*
Sum of GH pulse areas	*	NS	NS	*	NS	NS
Sum of GH pulse widths	NS	**	NS	NS	*	NS
Maximum within pulse GH level	**	NS	NS	***	NS	NS
No of detected GH pulses	**	NS	NS	*	NS	NS
IGF-I level	***	NS	NS	***	NS	NS

[1] 10, 45 and 140 d of age (30 and 70-d-old MS pigs were ignored). [2] Stage 1: LW and MS 10 d; stage 2: LW 45 d and MS 30 d; stage 3: LW 140 d and MS 70 d (45 and 140-d-old MS pigs were ignored). [3] Large White (LW) *vs* Meishan (MS). NS: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

pulse GH level was higher and sum of GH pulse widths was lower in MS-M than in LW-M whatever the age or stage considered. In most cases, age x breed or stage x breed interactions were not significant, indicating that age-related changes in GH profile criteria or IGF-I levels were similar in LW-M and in MS-M.

DISCUSSION

The frequency of GH measurements (every 20 min) may have been insufficient for an accurate determination of GH peak frequency and amplitude. Indeed, frequent bursts of GH secretion may have been unresolved in our study, so that the number of detected GH pulses may be an underestimation of the real number of GH peaks.

Age-related changes in GH secretion

The slight increase in mean GH level between 10 and 45 d of age in Large White animals is somewhat contradictory to the results of Klindt (1986) who observed a decline in mean GH concentrations between 9 and 18 d of age. However, the high GH concentrations reported by this author at 9 d of age were measured in 3 animals only. The increase in mean GH level between 10 and 45 d of age in LW pigs was mostly the result of an alteration in the temporal distribution of GH peaks, as neither interpulse GH levels nor maximum GH levels were altered. Increase in the sum of GH pulse widths and concomitant decrease in the number of detected GH pulses indicate that GH peaks were either less frequent and longer or less evenly distributed with time (unresolved peaks might result in seemingly "long" pulses).

In both Meishan and Large White pigs, mean and maximum GH levels and interpulse GH level decline after 45 d of age was in good accordance with previous results (Klindt and Stone, 1984; Dubreuil *et al,* 1987; Arbona *et al,* 1989).

GH and IGF-I secretion in Meishan vs Large White pigs

The pattern of age related changes in GH profile criteria was similar in Meishan and Large White animals. However, interpulse GH levels were higher in Meishan than in Large White pigs. Since GH measurements were performed in 2 different assays, it could be argued that the observed differences were the result of interassay variability. However, this can be ruled out as differences in interpulse GH levels between the 2 breeds ranged from 20 to 120%, while inter-assay coefficient of variation in this range of concentrations was only 9%. Lower sum of GH pulse widths in Meishan than in Large White pigs suggest a possible difference in the temporal distribution of GH peaks.IGF-I concentrations were similar in the 2 breeds.

Such results demonstrate that GH and IGF-I secretions were not dramatically impaired in the slow growing fat Meishan pig compared to conventional breeds. Therefore, as far as GH and IGF controls of growth are concerned, the Meishan pig seems to be similar to the Yucatan mini pig (Lauteric *et al,* 1988) and differs markedly from other slow growing fat pig models, such as the Hanford mini or Yucatan micro swine that have depressed IGF-I but not GH secretion (Buonomo *et al,* 1987; Lauteric *et al,* 1988) and the Ossabaw breed or the various lines selected for slow lean tissue growth, that all exhibit lower GH secretion than conventional animals (Lund-Larsen and Bakke, 1975; Althen and Gerrits, 1976; Kasser *et al,* 1981; Wangness *et al,* 1981; Hoffman *et al,* 1983; Martin *et*

al, 1985; McCusker *et al,* 1985; Stone *et al,* 1985; Norton *et al,* 1987; Arbona *et al,* 1988; Bark *et al,* 1988).

Sex and castration effects on GH and IGF-I secretion

The present study is, to our knowledge, the first report relating to the sex effect on GH secretion in pigs as young as 10 d of age. The absence of sex or castration effects on GH secretion in the 45-d old Large White animals is consistent with previous finding in 6 or 7-wk-old pigs (Dubreuil *et al,* 1987; Trudeau *et al,* 1988). The absence of sex effect on GH profile criteria in the 140-d old Large White pigs of the present study is in contrast with the results of Arbona *et al,* (1988, 1989) who reported higher mean GH levels and GH pulse amplitude in intact males than in females of the Landrace breed. The depressing effect of castration on GH secretion in male pigs over 2 months of age has already been reported (Dubreuil *et al,* 1989) and is consistent with the finding that GH secretion is higher in female than in castrated male swine (Dubreuil *et al,* 1987, 1988).

The absence of sex or castration effect on IGF-I concentrations in 10 and 45-d-old pigs is, to our knowledge, a new finding. The higher IGF-I concentrations in intact males than in females or castrates at 140 d of age are consistent with the results of Arbona *et al* (1989). The lower IGF-I concentrations in castrated than in intact male pigs may be related to the depressing effect of castration on GH secretion. However, IGF-I concentrations were lower in females than in males, although GH profiles were similar in the 2 sexes. The possible specific involvement of male sex steroids in the regulation of IGF-I production in pigs deserves further investigation.

From the present study it can be concluded that: i), GH and IGF-I secretion were similar in the slow growing fat Meishan pigs and in the conventional Large White animals; ii), GH secretory profiles were dramatically altered with age, resulting in an overall decrease in GH secretion after 45 d of age; iii), sex and/or castration effect on GH and IGF-I secretion were only observed in pigs older than 45 d.

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