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Polymorphisms at *loci* of leptin (*LEP*), *Pit1* and *STAT5A* and their association with growth, feed conversion and carcass quality in Black-and-White bulls*

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The association was studied between the polymorphism at leptin (*LEP*), *Pit1*, and *STAT5A loci* and meat production traits in 145 Black-and-White growing/fattening bulls. Genotypes of *LEP*, *Pit1* and *STAT5A* were determined with the PCR-RFLP technique. Over the 8th month of age the 28-day performance test was introduced to assess growth rate and feed conversion during which the full-concentrate diet was offered *ad libitum*. At the age of 15 months the bulls were slaughtered, and their carcasses cut and dissected into lean, fat and bone.

The allele frequencies were 0.85, 0.07, and 0.08 for A, B and C *LEP* variants, 0.25 and 0.75 for A and B *Pit1* variants, and 0.90 and 0.10 for C and T *STAT5A* variants, respectively. Polymorphism of leptin significantly affected some carcass traits, and among them the weight of carcass-side that was highest in the AA homozygotes. The effect of *Pit1* genotype was observed on carcass dimensions only. The AA homozygotes had higher chest circumference, chest depth, and circumference of round, but BB homozygotes had a higher round width. CT genotype of the STAT5A-encoding gene significantly affected four out of 36 carcass traits measured and was related to higher weight of bone of best + fore ribs (4.2 *vs* 3.8 kg) and of sirloin (1.6 *vs* 1.3 kg) as well as to oblique carcass length (140.5 *vs* 138.5 cm). The CC *STAT5A* genotype was associated with significantly higher live weight gain from 8 to 15 months (1.04 *vs* 0,97 kg daily).

KEY WORDS: cattle / carcass / fattening / gene /polymorphism

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Genes affecting polygenic traits characterizing milk or meat production are difficult to identify. However, a number of potential candidate genes have been recognized. They may be selected on the basis of a known relationship between physiological or biochemical processes and production traits, and can be tested as quantitative trait *loci* (QTLs).

Pituitary transcription factor Pit1, belonging to a large POU domain family, is a positive regulatory factor for synthesis of growth hormone, prolactin, and thyrotropin subunit β in the mammalian pituitary. Therefore, the gene encoding for Pit1 was chosen as a candidate gene to investigate its association with growth, carcass traits, and lactating performance in cattle [Stancekova *et al.* 1999]. The *POU1F1* gene encoding Pit1 transcription factor has been assigned to cattle chromosome 1 [Moody *et al.* 1995]. Its sequence is known [Showalter *et al.* 2002] and available in GenBank database at accession number AF453512.

Leptin, the product of the *ob* gene, is secreted from white adipose tissue and regulates food intake and whole-body energy metabolism [Friedman and Halaas 1998]. Leptin is an important regulator of energy metabolism, adiposity and reproduction, and is perhaps linked to meat quality determinants such as marbling [Hossner 1998]. Leptin is also involved in the regulation of body weight and can, probably, be considered as one of the best biological markers reflecting body fatness in both animals and humans. In the cattle leptin gene has been mapped to chromosome 4 and its full sequence is available in GenBank database at accession number U50365.

STAT5 is a key intracellular mediator of prolactin signalling and can activate transcription of milk protein genes in response to prolactin [Wakao *et al*. 1994]. It is also known as a main mediator of growth hormone (GH) action on target genes [Argetsinger and Carter-Su 1996]. In cattle the STAT5A gene (*STAT5A*) has been assigned to chromosome 19q17 within 40 Kpz *STAT locus* containing also STAT3 and STAT5B genes [Seyfert *et al*. 2000, Moleenar *et al*. 2000]. The full sequence of the bovine *STAT5A* is available in GenBank database, accession numbers AJ 237937, AJ 242522 and AY 280369.

In this study an association was investigated between the polymorphism at *LEP* and *Pit1 loci* and traits related to meat production in growing Black-and-White bulls. These genes are considered promising candidates for markers of economically important quantitative traits. Moreover, the effect of a newly found polymorphism in the bovine STAT5A gene in exon 7 was investigated accordingly.

Material and methods

One-hundred-and-forty-five young Black-and-White (Friesian) bulls were used, born in herds yielding 4500-5000 kg milk and being the progeny of 24 AI sires. The number of half-sibs varied from 3 to 9. The bulls were housed in a tie-stalls, and fed *ad libitum* silage, hay and concentrate up to the age of 15 months. Within month 8 of age the growth rate and feed conversion were both investigated in a 28-day performance test during which the only feed used was concentrate offered *ad libitum*. Two weeks

of adaptation to concentrate feeding preceded the test. Body weight at start and at the end (month 7 to 8), as well as body dimensions at the end of the test, were recorded. Moreover, mean daily energy and protein, dry matter, INRA feed units for maintenance and meat production (UFV), PDI (INRA), as well as net energy and protein intake per kg live body weight gain were calculated. All bulls were slaughtered at the age of 15 months, after 24 hours fasting. The carcasses were chilled for 24 hours at 4°C. From the right carcass-sides the valuable cuts (round, shoulder, tenderloin, best ribs + fore ribs) were obtained and dissected into lean, fat and bone.

Investigations were carried out over four consecutive years. Data were analysed by the SAS General Linear Model Procedure as follows:

$$y_{ijkl} = \mu + G_i + Y_j + S_k + \beta(w_{ijk} - \bar{w}) + e_{ijkl}$$

where:

y_{ijkl} – mean value of the trait;

μ – general mean;

G_i – effect of genotype (*LEP*, *Pit1*, *STAT5*; i = 1,2,3);

Y_j – effect of year (1994, 1995, 1996, 1997; j = 1, 2, 3, 4);

S_k – effect of season (January-March, April-June, July-September, October-December; k = 1, 2, 3, 4);

$\beta(w_{ijk} - \bar{w})$ – regression on body weight at the age of 7 months

e_{ijkl} – random error.

The association of carcass traits with the genotypes was evaluated using regressions on body weight at slaughter. The differences between genotypes were tested by Duncan's test.

The reference genotypes were AA, AB and AC for *locus LEP*, AA, AB and BB for *Pit1*, and CC and CT for *STAT5A*.

Using this model the effect of particular *loci* may be biased due to failing to account for the sire. The structure of data was very close to paternal half-sib group design. With small progeny groups, not all possible genotypes were present within a sire.

DNA isolation from blood

Blood samples for DNA genotyping were collected from jugular vein by authorized veterinarian (procedure approved by the Local Ethics Commission, No 67/2001). Blood was collected on K_2EDTA and stored at -25°C for few weeks or at -75°C up to several months. The isolation of DNA from whole blood was performed according to Kanai *et al*. [1994].

***LEP* polymorphism**

LEP genotypes were identified according to Pomp *et al.* [1997]. The 1820-bp fragment of the bovine leptin gene was amplified using following primers: 5´GTCAC-CAGGATCAATGACAT3´ and 5´AGCCCAGGAATGAAGTCCAA 3´. The PCR amplification cycles were: 95°C – 1 min, then 32 cycles of 95°C – 1min, 60°C – 2 min, 72°C – 3 min, followed by 7 min at 72°C. The PCR product was digested with *Sau3*AI nuclease.

***Pit1* polymorphism**

Genetic variants of the Pit1 gene were identified according to Moody *et al*. [1995]. The sequences of primers were: 5'-CAATGAGAAAGTTGGTGC-3' and 5'-TCTGCAT-TCGAGATGCTC-3'. Initial cycle of 95°C – 2 min, 55°C – 1 min and 72°C – 2 min was followed by 29 amplification cycles: 94°C – 45 s; 55°C – 1 min; 72°C – 1 min, and concluded with a final extension at 72°C for 2 min. The amplified 1355-bp-long DNA fragment was digested with *Hinf*I restriction nuclease.

***STAT5A* polymorphism**

The following PCR primers were designed: 5'-CTGCAGGGCTGTTCTGAGAG-3'; 5'-TGGTACCAGGACTGTAGCACAT-3' [Flisikowski *et al*. 2003]. The polymerase chain reactions were performed using a PCR-mix with: primers, both at concentration 5.0 pmol/ml, 1 U Taq polymerase (SIGMA), 1 µl Taq polymerase buffer, four dNTPs, each at final concentration of 0.2 mM, ca 100 ng of genomic DNA, and H_2O up to 10 µl. The following PCR protocol was used: 1 min at 94°C, 1 min at 61°C and 1 min at 72°C – 34 cycles. Ten µl of PCR products were digested with 10 U of *Ava*I restriction nuclease (New England BioLabs, USA) for 3 hours at 37°C.

All PCR reactions were performed in MJ Research TETRAD thermal cycler. The restriction fragments were subjected to electrophoresis in 2% agarose/ethidium bromide gels (GIBCO, BRL, England) in 1 × TBE buffer (0.09 M Tris-boric acid, 0.002 M EDTA). Gels were visualised under UV light and documented in FX Molecular Imager apparatus (Bio-Rad).

Results and discussion

The overall means of traits studied are shown in Table 1. At the beginning of the test period (the end of month 7) the bulls' mean live weight was 200 kg, and at the end (the end of month 8) – 243 kg. Over 28 days of the test period the overall mean live weight gain was 43 kg/bull (1530 g/bull/day). Over that time the mean daily intake was 6.3 kg dry matter, 0.94 kg crude protein, 6.5 feed units for maintenance and meat production (UFV) and 695 g PDI. Mean weight at slaughter was 460 kg and mean dressing percentage 52.8%.

The allele frequencies at the studied *loci* were: 0.85/0.07/0.08 for *LEP* A/B/C variants, 0.25/0.75 for *Pit1* A/B variants, and 0.90/0.10 for *STAT5A* C/T variants,

Table 1 Overall means (n = 145) and their standard deviations of analysed traits in the Black-and-White bulls

No.	Trait	Mean	SD
	Live weight (kg)		
1	age 7 months	300.0	29.7
2	age 8 months	341.0	32.0
3	age 15 months	560.0	50.0
	Daily live weight gain (kg)		
4	0–7 months	0.82	0.14
5	7–8 months	1.51	0.25
6	8–15 months	1.01	0.11
7	0–15 months	0.91	0.09
	Daily feed intake, records 7 to 8		
8	consumed (kg)	6.5	1.00
9	dry matter (kg)	6.1	0.90
10	crude protein (kg)	0.9	0.1
11	fodder units for maintenance and weight production (LJPW)	6.5	0.9
12	FCE[1] (%)	61.1	8.6
	Feed conversion, records 7 to 8		
13	consumed (kg/kg LWG)	7.1	0.7
14	dry matter (kg/kg LWG)	7.1	0.7
15	crude protein (kg/kg LWG)	0.61	0.1
16	fodder units for maintenance and weight production (kg/kg LWG)	7.1	0.7
17	FCE[1] (%)	14.6	1.9
	Carcass traits, age 15 months		
18	dressing percentage (cold)	51.6	1.6
19	cold carcass (kg)	317.1	31.1
20	right carcass-side (kg)	158.1	15.9
21	valuable cuts of carcass-side (kg)	79.7	8.5
22	valuable cuts share in carcass (%)	61.1	1.1
23	lean weight of valuable cuts (kg)	58.7	7.7
24	lean share in valuable cuts (%)	69.1	1.6
25	lean of carcass-side (kg)	71.7	6.6
26	fat of carcass-side (kg)	18.6	7.6
27	bone of carcass-side (kg)	31.7	3.1
28	conformation (kg)	1.6	0.1
29	round (kg)	73.5	7.1
30	lean (kg)	57.5	5.1
31	fat (kg)	7.5	0.9
32	bone (kg)	7.7	0.5
33	shoulder (kg)	35.9	3.7
34	lean (kg)	30.9	3.0
35	fat (kg)	3.1	0.7
36	bone (kg)	1.6	0.1

Table 1. Continued

(No.)	Trait	Mean	SD
(37)	sirloin (cut)	6.4	0.6
(38)	lean (kg)	4.4	0.4
(39)	fat (kg)	0.7	0.2
(40)	bone (kg)	1.4	0.5
(41)	best ribs + fore ribs (kg)	16.1	2.0
(42)	lean (kg)	10.7	1.5
(43)	fat (kg)	2.1	0.6
(44)	bone (kg)	3.9	0.8
(45)	carcass length (cm)	164.3	5.3
(46)	carcass oblique length (cm)	139.0	5.6
(47)	carcass length from pubic symphysis to I lumbar vertebra (cm)	60.6	1.9
(48)	carcass width over the III thoracic vertebra (cm)	67.8	2.4
(49)	carcass width over the VIII thoracic vertebra (cm)	61.3	4.5
(50)	carcass length of the thoraco-lumbar section (cm)	110.7	4.6
(51)	width of round (cm)	44.8	4.7
(52)	depth of round (cm)	25.9	4.6
(53)	circumference of round (cm)	111.9	4.3
(54)	length of round (cm)	77.0	2.6
	Body dimensions, age 8 months (cm)		
(55)	withers height	101.4	4.0
(56)	chest girth	141.5	7.2
(57)	chest width	34.8	2.3
(58)	chest depth	55.4	3.6
(59)	width at thurls	37.5	5.2

[1]PDI – protein digested in the small intestine. Source: Jarrige [1989].
[2]Live weight gain.

respectively (data not tabulated).

The effects of *LEP* genotype on feed intake and carcass quality indicators are presented in Table 2. During the testing period AA bulls consumed daily more dry matter, crude protein and PDI than heterozygotes AB or AC. The weight of carcass-side was highest in AA homozygotes which also showed a significantly higher carcass-side fat deposition (19.2 kg) than AC heterozygotes (17.9 kg). The per cent of valuable cuts was highest in AC genotype bulls – 62.7 as compared to 61.9 in AB and 62.2 in AA animals. In general, bulls of AA *LEP* genotype consumed more feed than those of remaining two heterozygotes.

As shown in Table 3, over 28 days of testing period the AB bulls at the *Pit1 locus* consumed more dry matter, crude protein, UFV and PDIA than those of AA or BB genotypes. The effect of *Pit1* genotype on carcass quality traits was observed only for carcass dimensions (Tab. 3). Moreover, the AA homozygotes had a higher chest girth and depth as well as circumference of round, while BB homozygotes showed higher length and width of round.

Table 2. Least squares means (LSM) and their standard errors (SE) for bulls' traits affected significantly by *LEP* genotypes AA, AB and AC

(No.)	Trait	AA (n=98)		AB (n=21)		AC (n=22)	
		LSM	SE	LSM	SE	LSM	SE
(9)	Dry matter intake (kg daily)	6.5[a]	0.10	6.3	0.18	6.2[a]	0.18
(10)	Crude protein intake (kg daily)	0.98[A]	0.02	0.95	0.03	0.91[A]	0.30
(11)	Feed units for maintenance and meat production intake (daily)	6.8[a]	0.10	6.6	0.20	6.3[a]	0.20
(12)	PDI[1] intake (daily)	0.64[A]	0.01	0.62	0.02	0.60[A]	0.02
(20)	Right carcass-side weight (kg)	114.6[a]	0.40	113.5	0.80	112.8[a]	0.80
(22)	Valuable cuts share in carcass-side (%)	62.2[a]	0.13	61.9[b]	0.30	62.7[ab]	0.30
(26)	Fat of carcass-side (kg)	19.2[a]	0.30	18.2	0.60	17.9[a]	0.60
(33)	Shoulder weight (kg)	16.0[a]	0.11	15.9	0.25	15.4[a]	0.24
(38)	Lean of sirloin (kg)	4.4[a]	0.03	4.3	0.07	4.2[a]	0.07
(41)	Best ribs + fore ribs weight (kg)	16.2[b]	0.30	15.5[ab]	0.26	16.4[a]	0.24
(48)	Carcass width over III thoratic vertebra (cm)	67.9[a]	0.20	67.6	0.40	67.1[a]	0.40
(53)	Circumference of round (cm)	112.3[A]	0.30	112.2[B]	0.70	110.2[AB]	0.60
(58)	Chest depth – age 8 months (cm)	55.6[a]	0.40	54.1[a]	0.70	54.6	0.70

[a,A] Within rows, means bearing the same superscript differ significantly at: small letters – P≤0.05; capitals – P≤0.01.
[1]PDI – protein digested in the small intestine. Source: Jarrige [1989].

Table 3. Least squares means (LSM) and their standard errors (SE) for bulls' traits affected significantly by *Pit1* genotypes AA, AB and BB

(No.)	Trait	AA (n=9)		AB (n=53)		BB (n=82)	
		LSM	SE	LSM	SE	LSM	SE
(9)	Dry matter intake (kg daily)	6.3	0.20	6.6[a]	0.08	6.3[a]	0.07
(10)	Crude protein intake (kg daily)	0.95	0.03	0.99[A]	0.01	0.95[A]	0.01
(11)	Feed units for maintenance and meat production intake (daily)	6.5	0.20	6.8[a]	0.08	6.6[a]	0.07
(12)	PDI[1] intake (daily)	0.62	0.20	0.64[A]	0.08	0.62[A]	0.06
(51)	Width of round (cm)	40.9[AA]	1.30	45.0[A]	0.60	45.2[A]	0.30
(52)	Depth of round (cm)	29.2[ab]	1.30	25.5[a]	0.60	25.7[b]	0.30
(53)	Circumference of round (cm)	112.8	1.00	111.3[a]	0.40	112.3[a]	0.40
(54)	Length of round (cm)	75.7[AA]	0.60	77.4[A]	0.30	77.0[A]	0.20
(56)	Chest girth (cm)	144[ab]	0.90	141[a]	0.40	141[b]	0.30
(58)	Chest depth (cm)	57.0[a]	1.00	54.2[a]	0.40	55.1	0.40

[a,A] Within rows, means bearing the same superscript differ significantly at: small letters – P≤0.05; capitals – P≤0.01.
[1]PDI – protein digested in the small intestine. Source: Jarrige [1989].

Significant effects of *STAT5A* C/T genotypes are shown in Table 4. Affected were only four out of 36 carcass traits considered. The CC genotype was significantly associated with higher live weight gain from 8 to 15 months (1.04 *vs* 0,97 kg daily), while genotype CT with higher weight of bone of sirloin (1.6 *vs* 1.3 kg) and of best ribs (4.2 *vs* 3.8 kg) and with longer thoraco-lumbar section (112 *vs* 110 cm).

The body weight gain appearing during the 28 days of test period (1530 g/day) was extremely high, but a complete mix *ad libitum* feeding of young stock is not routinely used. Diets containing a high proportion of silage have sustained lower growth rates

Table 4. Least squares means (LSM) and their standard errors (SE) for bulls' traits affected significantly by *STAT5A* (RFLP/*Ava*I) genotypes: CC and CT

(No.)	Trait	CC (n=115)		CT (n=30)	
		LSM	SE	LSM	SE
(6)	Daily live weight gain 8-15 months (kg)	1.04^{a}	0.01	0.97^{A}	0.02
(40)	Bone of sirloin (kg)	1.30^{A}	0.05	1.60^{A}	0.09
(44)	Bone of best ribs (kg)	3.80^{A}	0.07	4.2^{A}	0.12
(50)	Length of the thoraco-lumbar section (cm)	110.3^{A}	0.40	112.0^{A}	0.70

^{a,A} Within rows means bearing the same superscript differ significantly at: small letters – $P \leq 0.05$; capitals – $P \leq 0.01$.

and resulted in a greater proportion of fat in the carcass than high-concentrate diets. The effect of change in energy intake on the performance and carcass composition of beef cattle is therefore likely to depend on whether the change is achieved by restricting the quality of dry matter offered, or increasing the forage to concentrate ratio in a diet offered ad libitum [Steen and Kilpatrick 2000]. The distribution of muscle, fat and bone is largely a function of maturity. Cattle at the same maturity stage demonstrate a higher variation in distribution of fat than of any other tissue.

Only few studies have been performed of the effect of leptin gene polymorphism on performance traits in cattle. Leifers *et al.* [2002] have reported on the association between the leptin genotype and milk production traits in Holstein-Friesian cows where AB genotype was associated with higher milk yield. They concluded that *LEP* allele B can determine a higher milk yield without negatively affecting energy balance and fertility. In this study the estimated frequency of *LEP* A allele in the Black-and White bulls studied was 0.85, being slightly higher than previously reported for Holstein cattle (0.71) by Pomp *et al.* [1997], but about the same as in another population of Polish Black-and-White cattle (0.80) as reported by Klauzińska *et al.* [2000]. The frequency of variant C was 0.10. This variant of the leptin gene appeared favourable for some milk production traits in Polish Black-and-White cattle: cows carrying this allele (genotype AC) showed higher daily yield of milk components – fat, protein, and lactose – than those with AA and AB genotypes [Zwierzchowski *et al.* 2002].

Pit1 has been described as the critical cell-specific transcription factor responsible for

activating expression of prolactin (PRL) and GH genes in the anterior pituitary gland. To date, nine different mutations in the Pit1 gene have been described in mammals. Four of them affect DNA-binding, causing GH- and-PRL gene disorders [Renaville *et al.* 1997]. Because the PRL and the GH are essential for mammary gland development and milk yield, the *Pit1 locus* has potential as a marker for genetic variation in milk production traits. Polymorphism within bovine Pit1 gene – RFLP detected with *Hinf*I nuclease was first described by Woolard *et al*. [1994]. Within Italian Holstein-Friesian cattle the allele A of *Pit1* (frequency 0.18) showed a significant superiority over the allele B for milk and milk protein yields and body conformation traits [Renaville *et al.* 1997]. In this report the frequency of allele A in the *Pit1 locus* was 0.25, being similar to that previously found in Polish Black-and White cattle (0.26) by Klauzińska *et al*. [2000] and in Canadian Holstein bulls (0.21) by Sabour *et al.* [1996]. In the study by Renaville *et al*. [1997] and in our earlier study [Zwierzchowski *et al.* 2002] it was shown that allele A in the *Pit1 locus* positively affected milk production traits in Friesian cattle.

Only in few cases nucleotide sequence polymorphism has been detected in the bovine *STAT5A* gene. McCracken *et al*. [1997] found TG repeats of different length within the gene in the intron 12. Antoniou *et al*. [1999] described two SSCP variants of the gene fragment that encodes SH_2 domain in bovine STAT5A protein. In neither case an association with production traits was studied.

Recently, we identified 14 new polymorphic sites within the 5' region of the bovine *STAT5A* [Flisikowski and Zwierzchowski 2003a,b], most of them representing single nucleotide polymorphisms (SNPs). Moreover, the new nucleotide sequence polymorphism was found in the coding region of the bovine STAT5A gene, *i.e*. substitution C→T at position 6853 within the exon 7, recognizable by PCR-RFLP with the *Ava*I and *Dde*I restriction nucleases [Flisikowski *et al*. 2003]. Beef cattle with CC variant of the STAT5A-encoding gene were superior over CT animals for live weight gain, feed conversion and several carcass traits.

In conclusion, the results presented here confirm the value of *LEP* and *Pit1 loci* as markers for carcass traits and feed intake. The value of the *STAT5A locus* as a marker for carcass traits in cattle was also shown. These *loci* are candidate genes that may themselves produce differences in growth phenotypes.

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Związek między polimorfizmem *loci* leptyny, *Pit1* i *STAT5A* a tempem wzrostu, pobraniem i wykorzystaniem paszy oraz użytkowością rzeźną buhajów rasy cb

S t r e s z c z e n i e

Celem pracy było określenie genetycznej zmienności w obrębie *loci* genów *LEP*, *Pit1* i *STAT5A*, a także zbadanie wpływu ich alleli na tempo wzrostu, spożycie i wykorzystanie paszy oraz użytkowość rzeźną bydła czarno-białego. Materiał stanowiło 145 buhajków rasy cb opasanych do 15 miesiąca życia, a następnie ubijanych. Między 7 a 8 miesiącem życia buhajków przeprowadzono 28-dniowy test dla określenia pobierania i wykorzystania paszy, podczas którego zwierzęta żywiono wyłącznie paszą treściwą. Genotypy wymienionych czynników określono techniką PCR-RFLP. Analizie poddano 36 cech tuszy określonych w wyniku ich pomiarów liniowych, rozbioru i dysekcji na mięso, tłuszcz i kości. W obrębie genotypów leptyny zwierzęta o genotypie AA miały większą masę dysekowanej półtuszy. Osobniki AA pobierały więcej suchej masy, białka ogólnego oraz energii netto wyrażonej w jednostkach produkcji żywca (UFV) niż osobniki AB i AC. Wystąpiły różnice między zwierzętami o różnym genotypie *Pit1* – homozygoty BB pobierały mniej paszy i jej składników niż heterozygoty AB. Nie stwierdzono zależności między *Pit1* a masą mięsa, tłuszczu i kości w tuszy. W obrębie genotypów *STAT5A* buhajki CC miały mniejszą masę kości w antrykocie, rozbratelu i rozbefie, a ich tusze były krótsze niż buhajków CT. Jednocześnie osobniki CC wykazały istotnie wyższe przyrosty masy ciała.