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Interaction of *ESR*1 gene with the *FSHB* and *MYOG* genes: effect on the reproduction and growth in pigs*

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The study aimed at determining whether the combination of three selected genes can be used for selection in small populations of pigs. The estrogen receptor (*ESR*1), follicle stimulating hormone (*FSHB*) and porcine myogenin (*MYOG*) genes were selected to detect their combined effect. Although over the last decades considerable progress in pig production was achieved, reproduction in this species still remains unsatisfactory. The marker-assisted selection (MAS) is considered to bring progress in pig reproduction. If MAS is to be used efficiently, the complexity of reproduction process should be taken into consideration. The effects were studied of interaction between the mentioned three genes and selected production and reproduction traits of pigs. Interactions between the effects of particular gene markers are important because of possible negative effect(s) of a single-path selection as well as possible co-selection. No significant interaction between the effects of genes studied was found. It is concluded that in small populations co-selection is effective only when highly significant effects of selected auxiliary genes occur.

KEY WORDS: *ESR*1 / *FSHB* / growth rate / marker-assisted selection / *MYOG* / pigs / reproduction

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The estrogen receptor gene (*ESR*1) and follicle-stimulating hormone gene (*FSHB*) are considered to be candidate genes for reproduction. *ESR*1 reached special attention after Rothschild *et al*. [1996] observed its impact on litter size in the synthetic line of Meishan pigs. Since then, numerous studies on the effect of these genes have been performed [Depuydt *et al*. 1999, Van Rens *et al*. 2000, Goliášová and Wolf 2004]. Estrogens are steroid hormones which together with their receptors play an important role in reproductive processes. The function of estrogens is mediated *via* binding to estrogen receptors α (*ESR*1) and β (*ESR*2) – Nilsson *et al*. [2001]. In the *ESR*1 gene the *Pvu*II polymorphism was found by Rothschild *et al*. [1991].

The *FSHB* genes code the β subunit that is specific for all animals [Mellink *et al*. 1995]. The follicle-stimulating hormones enter the reproduction cycle during maturation of small and medium follicles into ovulating large follicles [Wang and Greenwald 1993, Mannaertz *et al*. 1994]. *FSHB* association with reproduction of pigs was reported by Li *et al*. [1998].

Production of pork depends mainly on the number of piglets weaned from a sow per year and their ability to growth. As the methods based on marker-assisted selection expanded, the comprehensiveness of selection models used was emphasized. In this paper interaction effects were studied between the genes influencing the reproduction and production traits of pigs. Generally, the lean meat growth capacity of pigs depends upon the number of muscle fibres at birth that in turn is regulated by *MYOD* gene family [Händel and Stickland 1988]. *MYOD* family consists of four related genes: *MYOD1*, *MYOG* (*MYF4*, myogenin), *MYF5* and *MYF6 (MRF4*, herculin). The authors decided to include into the study the *MYOG* gene which is the only one being expressed in all skeletal muscle cell lines [Wright *et al*. 1989, Edmondson and Olson 1989]. Within *MYOD* family polymorphisms have been described in *MYOD1* [Knoll *et al*. 1997], *MYOG* (Te Pas *et al*. 1996], *MYF5* [Stratil and Čepica 1999] and *MYF6* [Vykoukalova *et al*. 2003] and some of them have been studied for association with performance traits [Cieślak *et al*. 2000, Te Pas *et al*. 1999].

In the present report the investigation is described conducted on the Czech Large White sows and aiming at evaluating the effects of interactions between the three genes potentially important for reproduction in pigs.

Material and methods

Animals and data collection

The data concerning sows were collected from the records of three purebred herds of Czech Large White pigs (CLW – herd 1, 2 and 3) kept and reproduced independently. Numbers of animals with known genotypes of *ESR*1 were 289, 73 and 24, of *FSHB* – 161, 64 and 23, and of *MYOG* – 199, 64 and 23, in herd 1, 2 and 3, respectively. Studied traits included the number of live piglets born in first and subsequent litters (NBA 1 and NBA2), lean meat content of carcass (LMC), and mean daily live weight gain (MDG). The growth rate of all gilts was assessed under the same feeding and

maintenance conditions. The MDG test commenced when the gilts were 84 days (±4) old and terminated after eight weeks. At the end of MDG test the LMC was estimated with Sonomark device 100 by one-point method (at the site "P2" between the second and third from the last rib, 70 mm off the dorsal midline) and consequently the mean daily live weight gain from the birth to the end of the test was calculated.

Animal management

All sows were bred under the same conditions. The artificial insemination or natural mating was applied. The inseminations were carried out twice a day by a conventional artificial insemination technique with 2.5 x 10^9 motile spermatozoa in 80 ml of extended semen. When the "standing reflex" became quit, each sow was moved to the naturally ventilated house (4-8 sows per pen, *i.e*, 1.2 m^2 per sow). In these groups, the sows were kept until 10 days before the expected farrowing. For parturition, the stab lings of 2.1 m length and 0.7 m width (30 cm area for piglets) were separated on both sides with heated mattress (33°C). The sows were fed twice a day. Throughout the growing period, the gilts had free access to a standard cereal-soybean feed mix containing 13.0 ME, 9.8 g lysine and 150g crude protein/kg. The diet based on barley, wheat and soybean was used during the pregnancy of sows (12.6 ME, 6.6 g lysine and 160 g crude protein/kg). The diet of similar composition but different parametres – 13.0 ME, 8 g lysine and 200 g crude protein/kg – was offered to sukling sows.

Genotyping

PCR conditions and determination of DNA polymorphisms according to Short *et al*. [1997] (restriction enzyme *Pvu*II), Rohrer *et al*. [(1994] (restriction enzyme *Hae*III) and Te Pas *et al*. [1996] (restriction enzyme *Msp*I) were applied for detection of genotypes within the *ESR*1, *FSHB* and *MYOG* genes, respectively**.** Two alleles: *B* (55 and 65 bp) and *A* (120 bp); *A* (332 bp) and *B* (173 and 159 bp); *A* (219 and 134 bp) and *B* (353 bp) were detected within *ESR*1, *FSHB* and *MYOG* genes, respectively.

Statistical

To estimate the interactions of *ESR*1 gene with either *FSHB* or *MYOG* gene the four- trait animal model in PEST software [Groeneveld *et al*. 1990] was used. In the models the following factors were included:

– linear regression on the live body weight at the end of test (Weight);
– fixed effect of the device used to estimate the lean meat content (LMC) of carcass (Device);
– fixed effect of test type (Test);
– random effect of herd-year-season (HYS);
– random effect of litter (Litter);
– fixed effect of genotype interactions (Interactions);
– random effect of animal (Animal);

– linear regression on age at first farrowing (Age 1);
– square regression on age at first farrowing (Age 2);
– fixed effect of mating type (Mating: artificial insemination or natural);
– linear regression on farrowing interval (Interval 1);
– square regression on farrowing interval (Interval 2);
– fixed effect of parity (Parity);
– random permanent environmental effect of the sow (Permanent).
Individual models are shown in Table 1.

Table 1. Animal models used to determine the effects of interactions of the *ESR*1 gene with the *FSHB* gene or *MYOG* gene

Factor	Type	Trait			
		LMC	MDG	NBA 1	NBA 2
Weight	*C*	*X*	-	-	-
Device	*F*	*X*	-	-	-
Test	*F*	*X*	*X*	-	-
HYS	*F*	*X*	*X*	*X*	*X*
Litter	*R*	*X*	*X*	-	-
Interaction	*F*	*X*	*X*	*X*	*X*
Animal	*R*	*X*	*X*	*X*	*X*
Age 1	*C*	-	-	*X*	-
Age 2	*C*	-	-	*X*	-
Mating	*F*	-	-	*X*	*X*
Interval 1	*C*	-	-	-	*X*
Interval 2	*C*	-	-	-	*X*
Parity	*F*	-	-	-	*X*
Environment	*R*	-	-	-	*X*

F – fixed effect, R – random effect, C – regression. LMC – lean meat content of carcass; MDG – mean daily live weight gain; NBA 1 and NBA 2 – numbers of piglets born alive in first and subsequent litters, respectively.

Results and discussion

During the past few decades, advances in molecular genetics led to development of marker-assisted selection (MAS) technique which could help to achieve the maximum genetic gain. As breeding and selection are often conducted in small elite populations, the authors of the present report decided to find out whether such breeding work can be conducted based upon the combination of three interacting genes. The profitability of using MAS was assessed by Hayes and Goddard [2003] who used a computer simulation in population of 20 sows from a pedigree herd. To achieve this objective the animal model in PEST software [Groeneveld *et al*. 1990] was used along with the

information about the *ESR*1, *FSHB* and *MYOG* genotypes whose effect on the studied population has already been confirmed [Humpolicek *et al*. 2007].

Table 2. Relative frequencies (R) of genotypes and alleles at the *loci ESR1*, *FSHB* and *MYOG* (chi-square test)

Herd		Genotype	R	Chi-square test	Allele	R
ESR1	1 (n=289)	ESR^{AA}	0.2585	0.05 ns	ESR^{A}	0.51
		ESR^{AB}	0.5068		ESR^{B}	0.49
		ESR^{BB}	0.2347			
	2 (n=73)	ESR^{AA}	0.4384	0.05 ns	ESR^{A}	0.66
		ESR^{AB}	0.4384		ESR^{B}	0.34
		ESR^{BB}	0.1233			
	3 (n=24)	ESR^{AA}	0.0870	0.02 ns	ESR^{A}	0.28
		ESR^{AB}	0.3913		ESR^{B}	0.72
		ESR^{BB}	0.5217			
FSHB	1 (n=161)	$FSHB^{AA}$	0.1478	18.10**	*A*	0.29
		$FSHB^{AB}$	0.2906		*B*	0.71
		$FSHB^{BB}$	0.5616			
	2 (n=64)	$FSHB^{AA}$	0.0615	14.50**	*A*	0.11
		$FSHB^{AB}$	0.1077		*B*	0.89
		$FSHB^{BB}$	0.8308			
	3 (n=23)	$FSHB^{AA}$	0.0455	0.46 ns	*A*	0.27
		$FSHB^{AB}$	0.4545		*B*	0.73
		$FSHB^{BB}$	0.5000			
MYOG	1 (n=199)	$MYOG^{AA}$	0.4424	0.32 ns	*A*	0.66
		$MYOG^{AB}$	0.4303		*B*	0.34
		$MYOG^{BB}$	0.1273			
	2 (n=64)	$MYOG^{AA}$	0.3182	1.08 ns	*A*	0.59
		$MYOG^{AB}$	0.5455		*B*	0.41
		$MYOG^{BB}$	0.1364			
	3 (n=23)	$MYOG^{AA}$	0.5000	5.96*	*A*	0.61
		$MYOG^{AB}$	0.2273		*B*	0.39
		$MYOG^{BB}$	0.2727			

The population was not in the Hardy-Weinberg Equilibrium. *P ≤ 0.05, **P ≤ 0.01; ns = not significant.

The differences between genotype combinations are shown in Table 3. Significant differences were identified in two cases only, both in MDG. They were related to ESR^{BB} genotype which was rarely represented in herd 1 and 2 (Tab. 3). In the first case it was in combination with $FSHB^{AA}$ genotype whereas in the second – in combination with genotype $MYOG^{BB}$. Particularly remarkable is the effect of *ESR1* and *FSHB* genotype combination on MDG (Tab. 3). Earlier the effect of this gene on the reproduction but not on the MDG has been found. Whereas the genotypes combination $ESR^{BB}/FSHB^{AA}$ affected the MDG, its effect on litter size was not found. It is remarkable that not only the present results, but also those of Linville *et al*. [2001] or Cassady *et al*. [2001] outlined that the *FSHB* gene had no reliable effect on the litter size. Although that, the

Table 3. Detected interactions of the *ESR*1 gene with gene *FSHB* or *MYOG*

	LMC	MDG	NBA 1	NBA 2
$ESR^{BB}/FSHB^{BB}$	0.09±0.99	30.95±31.32	1.49±1.01	-0.06±0.58
$ESR^{BB}/FSHB^{AB}$	0.19±0.86	22.56±27.13	0.67±0.70	-0.39±0.47
$ESR^{BB}/FSHB^{AA}$	0.09±0.86	20.65±6.81*	0.81±0.67	0.02±0.46
$ESR^{AB}/FSHB^{BB}$	0.25±0.88	7.98±28.35	0.45±0.77	-0.16±0.53
$ESR^{AB}/FSHB^{AB}$	-0.13±0.82	23.71±26.05	0.59±0.63	-0.45±0.44
$ESR^{AB}/FSHB^{AA}$	0.25±0.82	11.32±26.04	0.66±0.59	-0.05±0.40
$ESR^{AA}/FSHB^{BB}$	0.00±0.41	0.00±13.79	0.56±0.96	-0.25±0.64
$ESR^{AA}/FSHB^{AB}$	0.21±0.94	31.18±29.82	-0.50±0.89	0.01±0.57
$ESR^{AA}/FSHB^{AA}$	-0.09±0.87	17.28±27.40	0.00±0.33	0.00±0.21
$ESR^{BB}/MYOG^{BB}$	-0.76±0.76	26.06±23.56	0.19±0.95	0.19±0.60
$ESR^{BB}/MYOG^{AB}$	0.42±0.67	11.35±21.06	0.99±0.85	-0.24±0.55
$ESR^{BB}/MYOG^{AA}$	-0.18±0.57	16.00±7.79*	0.30±0.76	0.00±0.45
$ESR^{AB}/MYOG^{BB}$	-0.58±0.65	8.21±20.32	0.54±0.86	0.01±0.53
$ESR^{AB}/MYOG^{AB}$	-0.45±0.62	4.46±19.54	0.31±0.80	-0.27±0.50
$ESR^{AB}/MYOG^{AA}$	0.00±0.22	0.00±7.55	0.00±0.35	0.00±0.20
$ESR^{AA}/MYOG^{BB}$	-0.57±0.68	11.77±21.25	-0.40±0.87	-0.16±0.56
$ESR^{AA}/MYOG^{AB}$	-0.38±0.77	-3.33±23.63	0.20±0.95	0.35±0.66
$ESR^{AA}/MYOG^{AA}$	-0.51±0.69	15.52±21.60	0.11±0.90	0.18±0.55

LMC – lean meat content of carcass; MDG – mean daily live weight gain; NBA 1 and NBA 2 – number of piglets born alive in first and subsequent litters, respectively.
*P≤0.05.

ESR1 and *FSHB* are both considered to be candidate genes for this trait. Particularly in *FSHB*, the results of published studies did not confirm the effect reported by Li *et al*. [1998]. Thus, the application of *FSHB* gene in pig selection and breeding may be recommended only if significant effect is confirmed in a given specific population.

Although the significant effect of genes considered in this report had already been found on litter size and growth in pigs, certain authors do not confirm that effect in some populations. Significant effect of *ESR*1 has first been detected in crossbred population by Rothschild *al*. [1996] and later confirmed by Depuydt *et al*. [1999], Isler *et al*. [2002] and Horogh *et al*. [2004], whereas Droegemueller *et al*. [1999] or Gibson *et al*. [2002] have not found such effect. The non-homogeneous effects of *MYOG* and *FSHB* genes were identified as well. Te Pas *et al*. [1999] observed that in the population of Large White pigs the $MYOG^{BB}$ genotype was associated with increased birth weight, higher growth rate and lean meat elevated content. Cieślak *et al*. [2000] noted that in one population of Large White the $MYOG^{AA}$ genotype was associated with higher carcass-side weight and higher lean meat content of carcass, higher ham meat weight, higher loin meat weight and elevated loin eye area, whereas in another population no such effects were found.

The objective of this study was to test the possibility of co-selection using gene markers in small population frequently used in practice. Earlier the considerable effects of tested genes have been confirmed. Nevertheless, when the effect of genotypes

interactions was tested, only two significant, but not convincing, effects were found. It is probably due to limited number of sows included in the study what is in accordance with above mentioned goal. The results shown here demonstrate that co-selection in small populations might be feasible only when the highly significant effects of selected auxiliary genes occur.

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Interakcja genu *ESR*1 z genami *FSHB i MYOG:* wpływ na wybrane cechy rozrodu i wzrost świń

Streszczenie

Aczkolwiek na przestrzeni ostatnich lat zarysował się znaczny postęp w produkcji trzody chlewnej, to jednak tempo reprodukcji tego gatunku należy uznać za niewystarczające. Badania zmierzały do twierdzenia, czy kombinacja wybranych genów może znaleźć zastosowanie w selekcji małych populacji trzody chlewnej. Opierając się na wynikach prac wcześniejszych, których wyniki świadczyły o istnieniu zależności między konkretnymi genami a cechami produkcji i reprodukcji świń, do badań wybrano geny *ESR*1, *FSHB* i *MYOG*. W przypadku selekcji wspomaganej markerami (marker-assisted selection) interakcje między efektami konkretnych genów mogą być ważne i przydatne wobec zagrożenia uzyskaniem ujemnego wyniku w przypadku pojedynczej ścieżki selekcyjnej lub koselekcji. Poza dwoma mało przekonującymi przypadkami nie stwierdzono istotności poszukiwanych interakcji. Autorzy wnioskują, że w małych populacjach koselekcja może być skuteczna wyłącznie wtedy, gdy efekt wybranych genów „wspomagających" jest wysoce istotny.