

Role of genetic markers in the prediction of classification of Czech Large White gilts to a hyperprolific line

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Abstract

The objective of statistical evaluation (discriminant analysis) was to find out whether the genetic endowment the gilt was born with is a high-quality discriminator for prediction of its future classification to a hyperprolific line (HPL). Based on the results a conclusion is drawn that the gilt with genotype *CC* of *ESR* gene will be classified to HPL in high probability – if the effect of this gene is not reduced by an interaction with other genes. The statistical analysis did not reveal a significant effect of *FSHB* gene in Czech Large White sows on their future classification to HPL. On the contrary, *PRLR* gene is a high-quality discriminator. Obviously, it is highly probable that the gilt with genotype *BB* will be classified to HPL. It is to state from the analysis of pairs of the studied genes that the adult gilt with genotype *CC* of *ESR* gene and genotype *BB* of *FSHB* gene and/or *PRLR* gene will be classified to HPL in all probability. *PRLR* gene has a dominant effect in the pair *ESR* and *PRLR*. Genotype *BB* of *PRLR* gene (the most beneficial of the genotypes from the aspect of future classification of gilts to HPL) markedly increases posterior probability of alleles of *ESR* gene. If the classification of a gilt to HPL is predicted from the analysis of all three genes, the results of partial analyses are confirmed in most cases. The results of the experiment indicate a possible prediction of gilts on the basis of their genotype for classification to HPL but it cannot be confirmed that the identified »beneficial« genotype will always be expressed in different populations by an increase in reproductive traits.

Keywords: pig, Czech Large White, litter size, candidate genes, *ESR*, *FSHB*, *PRLR*

Zusammenfassung

Eignung genetischer Marker für eine Voraussage von Sauen des Tschechischen Weißen Edelschweins für eine superfruchtbare Linie

Das Ziel der Arbeit bestand in der mittels Diskriminanzanalyse vorgenommenen Prüfung ob die angeborene genetische Ausstattung als hochwertiger Marker für eine Voraussage einer Einordnung in eine superfruchtbare Sauenlinie (HPL) genutzt werden kann. Es wurde festgestellt, dass Sauen mit dem Genotyp *CC* des *ESR* Gens dieser Linie zugeordnet werden können wenn dieser Effekt nicht durch Interaktionen mit anderen Genen verringert wird.

Kein signifikanter Effekt ergab sich diesbezüglich bei dem *FSHB* Gen in der untersuchten Population. Das galt das nicht für das *PRLR* Gen bei dem die *BB* Genotypen für diese Linie prädestiniert waren. Die größte Wahrscheinlichkeit, dass Sauen in die HPL Linie eingeordnet werden bestand in der Kombination *CC* Genotyp des *ESR* Gens und *BB* Genotyp des *FSHB* und/oder des *PRLR* Gens. Der *BB* Genotyp des *PRLR* Gens, welches aus der Sicht einer Einordnung der Sauen in die HPL als der günstigste Genotyp angesehen wird, erhöht wahrscheinlich merklich den Anstieg der *ESR* Gen Allele. Erfolgt mit Hilfe der Analyse aller drei Gene eine Einordnung der Sauen in die HPL Linie so bestätigten sich in den meisten Fällen die Ergebnisse der Teilanalysen. Die Ergebnisse der Untersuchungen lassen eine mögliche Voraussage der Einordnung von Sauen in die HPL auf Grund ihres Genotyps erwarten. Es konnte nicht bestätigt werden, dass die hier als günstige Genotypen ermittelten auch in anderen Populationen eine Verbesserung der Fruchtbarkeitsleistungen erwarten lassen.

Schlüsselwörter: Schwein, Tschechisches Weißes Edelschwein, Wurfgröße, Kandidatengen, *ESR*, *FSHB*, *PRLR*

Introduction

In France the method of hyperprolific lines (HPL) contributed to an increase in the genetic potential of pigs to a high level. BIDANEL and DUCOS (1994) reported that HPL of daughters of HPL boars of Large White breed exhibited a genetic improvement of the litter size by 0.9 piglet per litter. A need to increase the level of prolificacy in dam breeds resulted in development of methodology for the production of HPL also in the Czech Republic.

Oestrogen receptor gene is one of the best-known genes studied in relation with sow prolificacy. According to ROTHSCCHILD (1996) the preferred allele *D* of *ESR* gene was associated with an increase in the number of piglets in the Large White breed by 0.4-0.5 piglet per litter. A significant effect of *ESR* locus on the number of weaned piglets ($P \leq 0.01$) in Large White breed was reported by OMELKA *et al.* (2006). However, they observed a negative effect of *DD* genotype on this trait. The influence of the *ESR* gene as a quantitative trait locus (QTL) for litter size in a German Landrace population was analysed by DRÖGEMÜLLER *et al.* (1999). They did not find any *Pvu II* polymorphism. The associations of *ESR* genotypes with reproduction traits of hybrid sows were studied by DEPUYDT *et al.* (1999). The assumed effect of *ESR* genotypes on fertility was not confirmed. BUSKE *et al.* (2006) investigated if the genotype of the gene *ESR2* was associated with litter size in a commercial pig cross population. Sows were divided into two extreme performance groups, with large (≥ 14.3) and with small litter size (≤ 11.3). No association was found between different *ESR2*.

The results of ZHANG *et al.* (2004) showed that the polymorphism of *FSHB* locus was significantly associated with litter size. Total number born and number born alive of sows with genotype *BB* were higher, with the additive effect 1.02-1.42 and 1.04-1.27 piglets per litter, respectively. LINVILLE *et al.* (2001) did not prove any significant associations between polymorphic markers and studied genotypes of *FSHB* gene. Nevertheless, they admitted that other genetic changes within candidate genes influenced the studied traits (linear model). HUMPOLICEK *et al.* (2006) examined the effects of *FSHB* on the performance

of Large White sows in three different herds. The influence of *FSHB* was not very conclusive in the studied populations; it was different depending on the herd in which the sows were kept or on the set of analyzed litters. The polymorphisms of *ESR1*, *FSHB* and *RBP4* genes (PCR-SSCP, PCR and PCR-RFLP) in a Large White herd and in a Landrace herd were detected by WANG *et al.* (2006). They found polymorphisms for the three genes in Large White besides the *ESR1* and *RBP4* genes in Landrace. The results showed that the highest genotype effects were exerted by *ESR1* among these three genes.

According to VINCENT *et al.* (1998) *PRLR* gene seems to have a similar effect like *ESR* gene, but rather in the lines of Landrace origin, while the effect of *ESR* receptor is expressed mainly in Large White and Meishan breeds. DRÖGEMÜLLER *et al.* (2000) reported that in the Duroc breed a difference between genotypes *AA* and *BB* was 1 piglet born alive per litter; VAN RENS and VAN DER LENDE (2002) stated that (Large White × Meishan) gilts of genotype *AA* of *PRLR* genotype delivered more piglets born and born alive than gilts of genotype *BB*.

The objective of statistical evaluation was to find out whether the genetic endowment of the gilt was born with is a high-quality discriminator for prediction of its future classification to the HPL.

Material and methods

Data from performance testing of reproductive traits of Czech Large White sows coming from three elite breeding herds were used in this study. We evaluated 98 sows with known genotypes of three candidate genes for reproduction:

- oestrogen receptor (*ESR*) with alleles *C* (120 bp) and *D* (65, 55 bp)
- follicle-stimulating hormone (*FSHB*) with alleles *A* (208, 173, 159, 84 bp) and *B* (332, 208, 84 bp)
- prolactin receptor (*PRLR*) with alleles *A* (85, 59, 19 bp) and *B* (104, 59 bp).

It is so called »training set« (in accordance with statistical terminology). Out of the studied sows, 51 sows were classified to the HPL while 47 sows were classified to the basic herd (*x*). Genotypes were determined by molecular genetics methods PCR-RFLP in Laboratory of Applied Genetics of Mendel University of Agriculture and Forestry in Brno (LamGen). DNA was isolated from blood samples with the addition of anticoagulant EDTA.

The statistical analysis of data was based on methods of discriminant analysis when we used the discriminant analysis for two groups (HPL, basic herd). The genotypes (*ESR*, *FSHB* and *PRLR*) are specific because they are discrete random variables. Therefore the methods of discrimination for categorical data were used (AITCHISON & AITKEN 1976, HALL 1981, ČERMÁKOVÁ & FORBELSKÁ 2004). The personal study was employed for these purposes because commercial statistical software packages do not comprise any discrete models.

For discrimination were applied both parametric discrimination (see models with the multinomial estimator) and nonparametric discrimination based on kernel estimators of probability functions figuring in decision rules (see models with binary or nominal kernel estimator). The quality of discrimination was evaluated by estimations of probabilities of misclassification, applying two methods: plug-in method and resubstitution method (ČERMÁKOVÁ & FORBELSKÁ 2004). These methods of statistical analyses were used

because of the relatively small size of the training set. If we obtained significantly different results by different methods, generalisation for the population would not be correct. It is to note that we took advantage of nonparametric methods enabling to estimate posterior probability even when the particular combinations of alleles (e.g. *DD*, *AB*, *BB*) did not occur in the training set. Parametric methods do not provide such a possibility. The statistical analysis considered all theoretical variants, i.e. it was carried out for each separate gene, for combinations of two genes and for the vector of three genes. Taking into account the small size of the training set it can considerably be deduced from the results whether in relation to prolificacy the genes act either autonomously or it is possible to expect their interaction.

Results and discussion

The summary of classification results of parametric (multinomial) model and two nonparametric (binary and nominal kernel) models and error rates are presented in Figures 1 through 7. The left horizontal stacked bar graph shows estimated posterior probabilities of individual genotypes. The right horizontal bar graph shows the achieved contribution of individual genotypes (*scores* q_i) to the total error rate (ER) based on posterior probabilities (plug-in estimates). For estimating error rates, the resubstitution method (apparent error rate APER) is also available.

Figures 1-7 show that the results obtained by parametric and nonparametric methods do not differ significantly from each other.

Therefore we can draw a conclusion that gene *ESR* (Figure 1) if its effect is not decreased through interaction with other genes influences reproductive traits in this sense: the gilt that will be born with genotype *CC* of *ESR* gene will be classified in high probability to HPL ($p_{HPL,CC}=0.75$). The probability of misclassification of *CC* genotype to HPL is not very high. The two remaining genotypes are indifferent for the prediction of future classification of gilts to HPL (posterior probability is slightly below the level 0.5, so it is not possible to draw a conclusion concerning the future with sufficient reliability). LEGAULT *et al.* (1996) did not report any significant differences in the genotype frequency of *ESR* gene between HPL and control group of Large White breed, the genotypes did not show a significant effect on litter size in any line. MATOUŠEK *et al.* (2003) analysed the relationship of *ESR* genotypes with the traits of litter size in sows in two elite breeding herds. In one herd, sows of genotype *DD* had a significantly higher number of piglets while in the other herd the examined reproductive traits were higher in sows of genotype *CC*.

The statistical analysis did not indicate a significant effect of *FSHB* gene on their future classification to HPL (Figure 2). The value of posterior probabilities is about 0.5; so *FSHB* gene does not appear to be a high-quality discriminator between the two classes in the Czech Large White breed. But it does not imply that it does not contribute to discrimination in interaction with other genes. HUANG *et al.* (2000) found out by 0.55-2.21 piglets born alive more per litter in gilts of genotype *BB* compared to gilts of genotype *AA*.

PRLR gene belongs to high-quality discriminators. Figure 3 illustrates that the gilt with genotype *BB* will be classified in high probability to HPL ($p_{HPL,BB}=0.8$). This conclusion is supported by the fact that the probability of misclassification of the gilt with genotype

BB of *PRLR* gene is low (it lies deep below the mean value of scores). The gilt with genotype *AA* would seem not to have a very high chance to be classified to HPL. But we cannot draw such a conclusion due to high probability of misclassification. According to DVOŘÁK (1999) the average effect of allele *B* of *PRLR* gene in parity 1 is 0.25 piglet more. DRÖGEMÜLLER *et al.* (2001) observed a small additive effect of allele *B* of *PRLR* gene on litter size in the Duroc line (linear model). VAN RENS *et al.* (2003) believed that *PRLR* gene was a candidate gene for ovulation rate rather than for litter size (linear model).

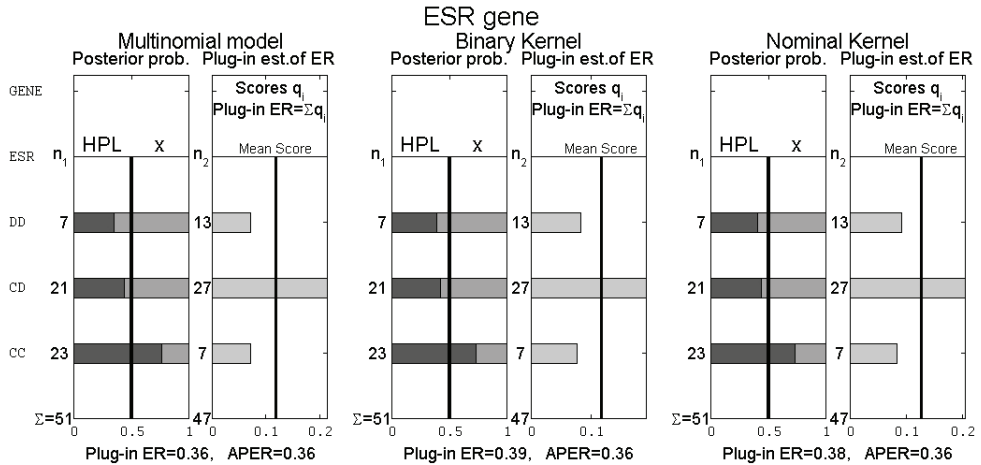
If we predict future classification of sows from the aspect of genetic endowment on the basis of parallel analysis of two or even three genes (Figures 4-7), we have to be considerate because only very few animals can have the particular genotype combination.

It seems that *FSHB* gene that was not a good discriminator (Figure 2) will express itself in combination with *ESR* (Figure 4) or *PRLR* (Figure 6) gene. Genotype *BB* of *FSHB* gene in synergy with the genotype of *ESR* gene or *PRLR* gene increases more or less the probability that the adult gilt will be classified to HPL. E.g. in the combination of genotype *BB* of *FSHB* gene and genotype *CC* of *ESR* gene posterior probability will increase from the value $p_{HPL,CC}=0.75$ (Figure 1) to the value $p_{HPL,CC\&BB}=0.85$ (Figure 4). In the combination of genotype *BB* of *FSHB* gene and genotype *BB* of *PRLR* gene (Figure 6) posterior probability increased from $p_{HPL,BB}=0.8$ (Figure 3) to $p_{HPL,BB\&BB}=0.9$ (Figure 6). Genotype *AB* of *FSHB* gene and genotype *DD* of *ESR* gene significantly increase the probability of classification to HPL from $p_{HPL,DD}<0.5$ (Figure 1) to $p_{HPL,DD\&AB}>0.5$ (Figure 4) while genotype *AB* of *FSHB* gene and genotype *BB* of *PRLR* gene decrease such probability (Figure 6). It is possible to conclude from the analysis of pairs of these genes that the adult gilt born with genotype *CC* of *ESR* gene and genotype *BB* of *FSHB* gene will have the highest probability of being classified to HPL whereas the prediction score is low (Figure 4); the same will apply to genotype *BB* of *PRLR* gene and *FSHB* gene, also with the low score of prediction error (Figure 6). On the contrary, very low probability of classification to HPL was determined in gilts with scarce combinations of genotypes, i.e. genotype *CD* (and/or *CC*) of *ESR* gene and genotype *AA* (and/or *AB*) of *FSHB* gene (Figure 4) and genotype *AA* of *PRLR* gene and *FSHB* gene (Figure 6). CHEN *et al.* (2001) drew a conclusion that the effect of *ESR* and *FSHB* genes on litter size made it possible to improve reproductive traits through marker-assisted selection.

The analysis of the pair of *ESR* and *PRLR* genes provided interesting results (Figure 5). The effect of *PRLR* gene was dominant in this pair. Genotype *BB* of *PRLR* gene (it is the most beneficial of all genotypes from the aspect of future classification of a gilt to HPL) markedly enhances posterior probability of *ESR* gene alleles. E.g. in genotype *CD* of *ESR* gene ($p=0.4$), i.e. on the basis of the analysis through *ESR* gene only, it is not possible to predict the classification of a gilt to HPL, but in the combination of genotype *CD* of *ESR* gene and genotype *BB* of *PRLR* gene it can be stated in high probability that this gilt will be classified to HPL. Genotype *AB* of *PRLR* gene behaves indifferently in relation to *ESR* gene while genotype *AA* of *PRLR* gene decreases the effect of *ESR* gene with respect to the future classification of gilts to HPL. E.g. if we analysed *ESR* gene only, the probability of the gilt with genotype *CC* to be classified to HPL would be high. However, if we also consider *PRLR* gene and if the gilt is of genotype *AA*, its probability of being classified reliably to HPL at an adult age will decrease to $p=0.5$. VAN RENS (2001) analysed the

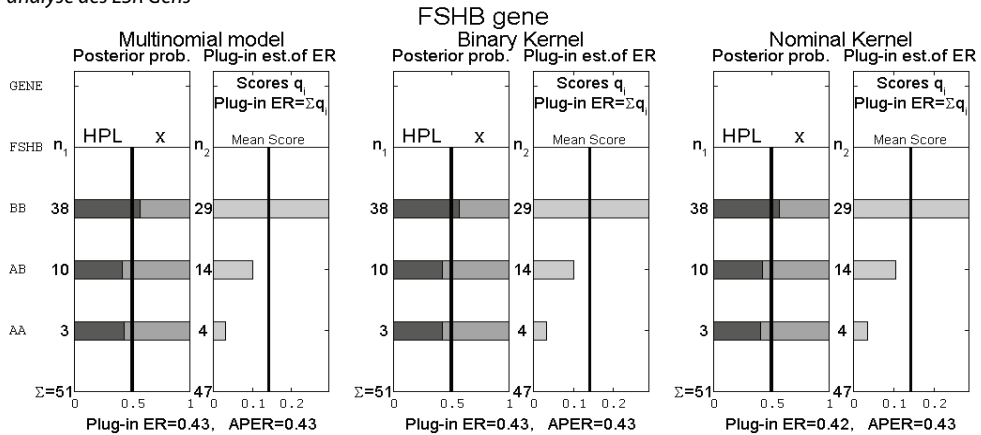
combinations of *ESR* and *PRLR* genotypes. She reported that each gene influenced different components of litter size. SOUTHWOOD *et al.* (1999) did not detect any interactions between genes for prolactin and oestrogen receptor.

If the gilt classification to HPL is predicted by the analysis of all three genes, the results of partial analyses are mostly confirmed: e.g. a marked contribution of genotype *CC* of *ESR* gene with the positive association of genotype *BB* of *FSHB* gene and augmentation effect of genotype *BB* of gene *PRLR*.



All estimated values of the total error rate are in the range: 0.36-0.39. Each of the methods classifies sow with genotype *DD* of *ESR* gene into not HPL (posterior probabilities $p_{HPL,DD} < p_{X,DD}$) and sow with genotype *CC* into HPL ($p_{HPL,CC} > p_{X,CC}$).

Figure 1
Probability of the future classification of sows to HPL determined by the analysis of genotypes of *ESR* gene
Wahrscheinlichkeit künftiger Sauenzuordnung in die superfruchtbare Linie (HPL) auf Grund der Genotypenanalyse des ESR Gens



All estimated values of the total error rate are about 0.43. Parametric and nonparametric methods classify sow with genotype *BB* of *FSHB* gene into HPL (posterior probabilities $p_{HPL,BB} > p_{X,BB}$) and sow with genotype *AA* into not HPL ($p_{HPL,AA} < p_{X,AA}$).

Figure 2
Probability of the future classification of sows to HPL determined by the analysis of genotypes of *FSHB* gene
Wahrscheinlichkeit künftiger Sauenzuordnung in die HPL auf Grund der Genotypenanalyse des FSHB Gens

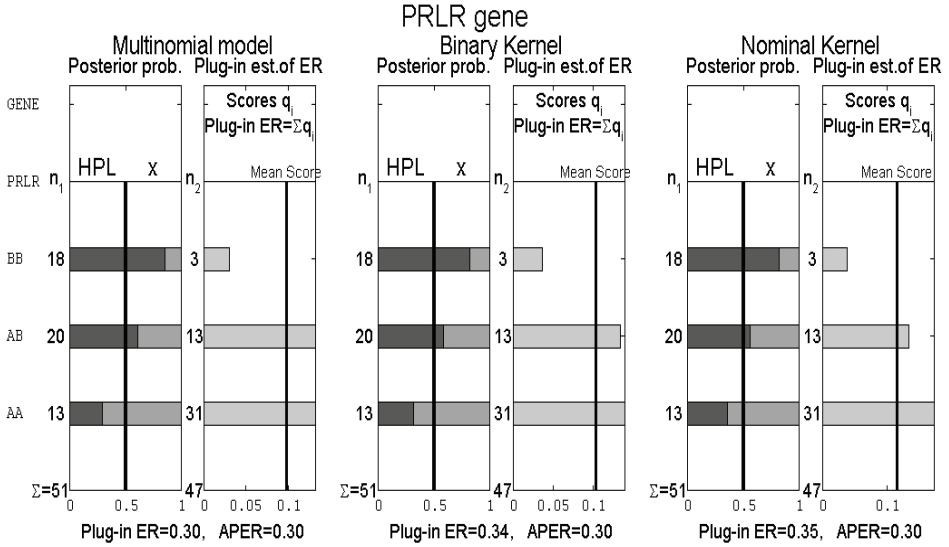


Figure 3
 Probability of the future classification of sows to HPL determined by the analysis of genotypes of *PRLR* gene
Wahrscheinlichkeit künftiger Sauenzuordnung in die HPL auf Grund der Genotypenanalyse des PRLR Gens

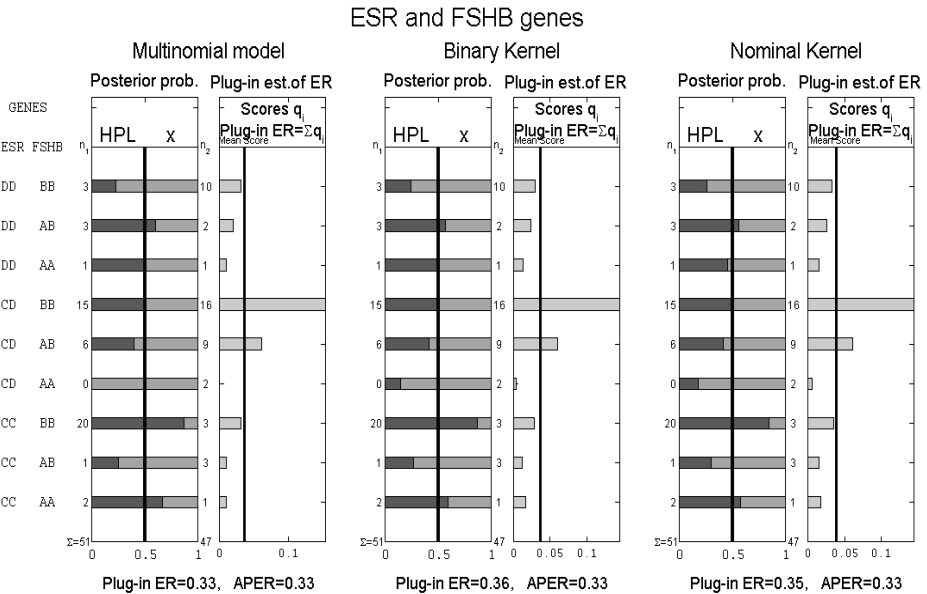
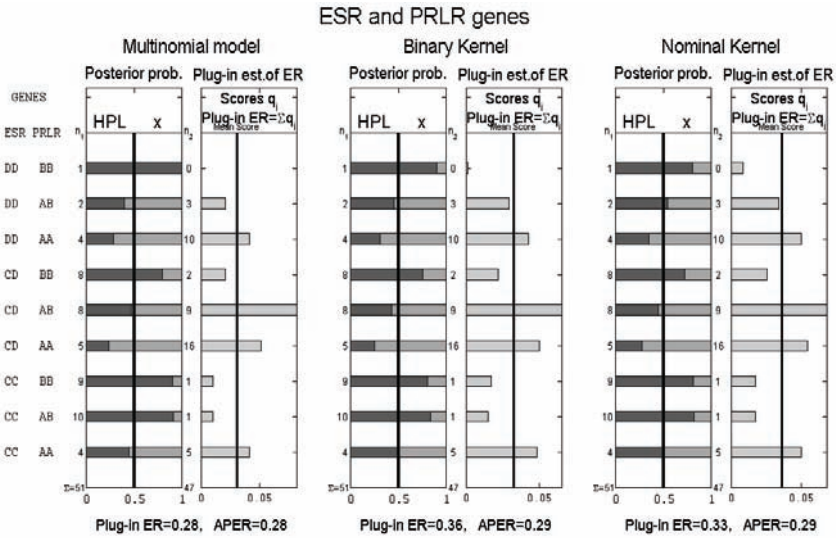


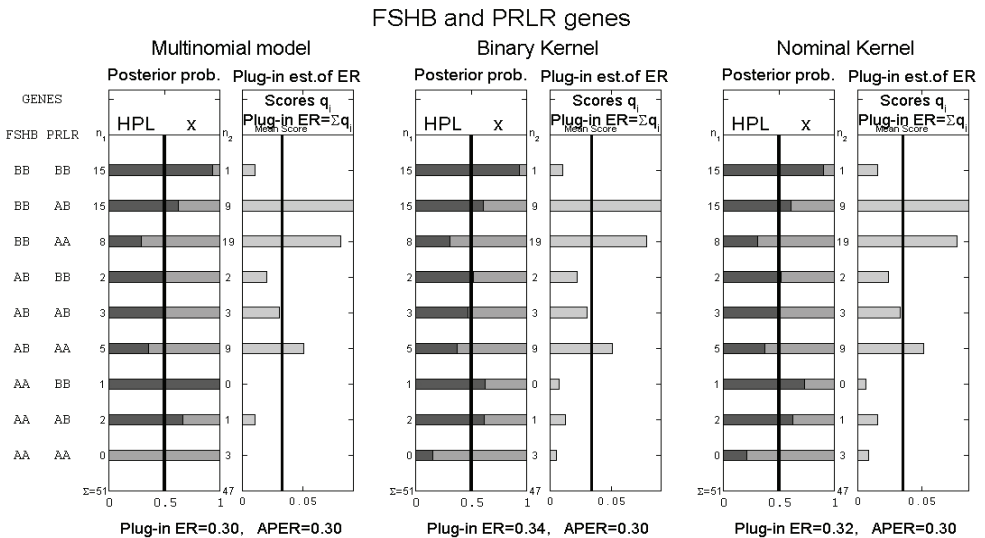
Figure 4
 Probability of the future classification of sows to HPL determined by the analysis of genotypes of *ESR* and *FSHB* genes
Wahrscheinlichkeit künftiger Sauenzuordnung in die HPL auf Grund der Genotypenanalyse der ESR-FSHB Gene



All estimated error rates are in the range: 0.28-0.36. Each of the methods evidently classifies sow with genotype *CC* of *ESR* gene and with genotype *BB* of *PRLR* gene into HPL (see posterior probabilities). The similar result is also for genotypic combination *CC* and *AB*.

Figure 5
Probability of the future classification of sows to HPL determined by the analysis of genotypes of *ESR* and *PRLR* genes

Wahrscheinlichkeit künftiger Sauenzuordnung in die HPL auf Grund der Genotypenanalyse der *ESR*-*PRLR* Gene

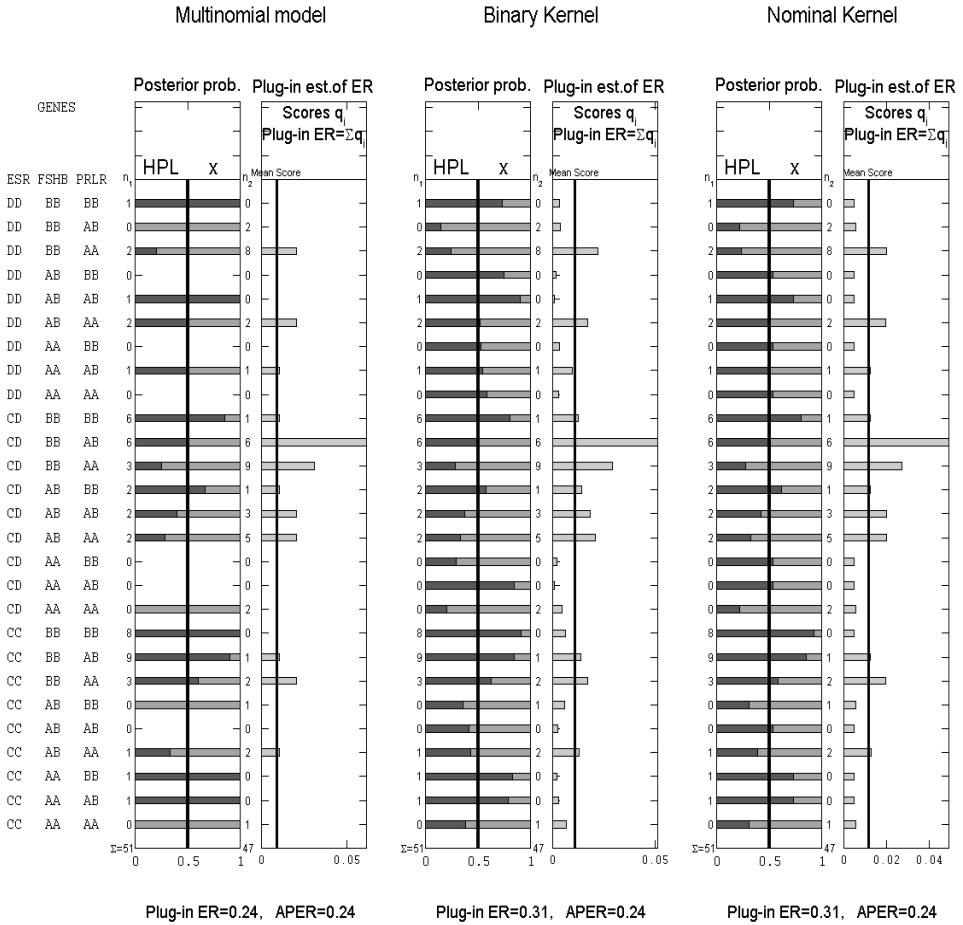


All estimated error rates are in the range: 0.30-0.34. Parametric and nonparametric methods classify sow with genotype *BB* of *FSHB* gene and of *PRLR* gene into HPL (posterior probabilities $p_{HPL, BB&BB} > p_{x, BB&BB}$) and sow with genotype *BB* (or *BA*) of *FSHB* gene and *AA* of *PRLR* into not HPL ($p_{HPL, BB&AA} < p_{x, BB&AA}$ and $p_{HPL, AB&AA} < p_{x, AB&AA}$).

Figure 6
Probability of the future classification of sows to HPL determined by the analysis of genotypes of *FSHB* and *PRLR* genes

Wahrscheinlichkeit künftiger Sauenzuordnung in die HPL auf Grund der Genotypenanalyse der *FSHB*-*PRLR* Gene

ESR, FSHB and PRLR genes



All estimated values of the total error rate are in the range: 0.24-0.31. The sows with genotype CC of ESR gene, genotype BB of FSHB gene and genotype BB of PRLR gene are evidently classified into HPL (posterior probabilities $p_{HPL,CC&BB&BB} > p_{X,CC&BB&BB}$). In this case we can see advantage of the nonparametric methods which allow probabilities to be attached to empty cells in the training set.

Figure 7
Probability of the future classification of sows to HPL determined by the analysis of genotypes of ESR, FSHB and PRLR genes

Wahrscheinlichkeit künftiger Sauenzuordnung in die HPL auf Grund der Genotypenanalyse der ESR-FSHB-PRLR Gene

The results of the experiment indicate a possible prediction of sows on the basis of their genetic »endowment«, i.e. of a particular genotype for the classification of sows to HPL, but it is not possible to prove that the identified »beneficial« genotype will always be expressed by an increase in reproductive traits in different populations. The results of DRÖGEMÜLLER'S *et al.* (2001) study demonstrated that the expressions of alleles between lines or populations differed. It may be caused by diverse linkages between alleles of markers and by random mutations of different lines. The results may also be explained by a high number of minor genes influencing the litter size. The authors are convinced that a

selection strategy should be defined for each line separately and possible pleiotropic effects should always be considered.

The originality of the paper consists in the application of discriminant analysis to predict the classification of gilts to a HPL when three selected genetic markers are determined. The studies that have been published until now demonstrate in different pig populations that the association of the genotype and alleles of genetic markers in relation to reproductive traits is not quite unambiguous. But these authors carried out »ex post« analyses, i.e. analyses of a reality only when such reality existed. The isolated evaluation of a single gene will always have a limited informative capacity and will provide applicable results only if the effect of this gene is very high and relatively independent of the genome residue and environmental conditions.

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