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## The effect of the ryanodine receptor gene on the reproductive traits of Welsh sows

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The reproductive performance of sows largely determines the efficiency of the entire pig farming industry. The purpose of our work is the evaluation of polymorphism of the ryanodine receptor gene and its impact on the reproductive traits of sows of the Welsh breed of pigs. For this study, 148 pigs of the Welsh breed were used. The reproductive traits of sows were evaluated in two adjacent generations. We conducted a comprehensive assessment of the reproductive ability of sows using the SIRQS (selection index of reproductive qualities of sows), determined phenotypic consolidation coefficients and assessed the genetic potential of the animals' productivity. The polymorphism of the RYR1 gene was determined using polymerase chain reaction-restriction fragment length polymorphism analysis (PCR-RFLP). Data processing was performed using single-factor analysis of variance (ANOVA). Polymorphism of the ryanodine receptor gene in sows of the Welsh pig breed was evaluated. 8.0% of the animals were identified as carriers of the mutant allele of the RYR1 gene. However, no homozygous RYR1-nn animals were found. Pigs of the maternal generation carrying the homozygous NN genotype had better reproductive performance in all indicators. Sows that were carriers of the mutant allele were characterized by lower values of the genetic productivity potential compared with the entire estimated population for all productive traits. Sows which were free of the mutant allele of the RYR1 gene were characterized by large values of the SIRQS index. The values of the coefficients of phenotypic consolidation of the number of live born piglets in sows without the mutant allele were lower than in sows with the mutant allele n. Better performance of sows free of the mutant allele of the RYR1 gene was established over sows carrying it in all evaluated traits of reproductive capacity (for different traits P ranged from 0.021 to  $1.0 \cdot 10^{-4}$ ), except for number of piglets born alive per sow in the daughter generation. Sows with the NN genotype had better selection index values by 15.7% in the maternal generation and by 10.2% in the daughter generation. In order to increase the reproductive ability of sows in the studied population of Welsh pigs and achieve similar results in other herds of this breed, animals free from the mutant allele of the RYR1 gene should be selected for further reproduction in the process of breeding, while on the contrary, carriers of this gene should be gradually eliminated from the herd. To carry out breeding work, further research is needed on the entire population of Welsh pigs for the RYR1 gene.

**Keywords:** pigs; reproductive capacity; genetic potential; selection index; phenotypic consolidation; RYR1 gene; mutant allele; stress sensitivity.

### Introduction

In the structure of world production and consumption of all types of meat, pork occupies a leading place, and its production is steadily increasing. The number of pigs that are bred in the world is about a billion animals that deliver more than 100 million tons of pork to people for consumption. The effective development of pig enterprises and the increasing of pork production is due to the biological characteristics of pigs, such as the precociousness of the offspring and the ability to give fattening pigs high daily gains (McGlone, 2013). As well as throughout the world, in Ukraine, pork production occupies a leading position of animal husbandry, which is tasked with providing the population of the country with high-energy protein food. The meat product subcomplex is an important source of income for peasants, an inviolable component of rural life, a means of strengthening the rural community, and a source of indispensable and essential food (Mykytyuk, 2021). Pork production is the main component of the country's food security (Vashchenko, 2003). Population and income growth in developing countries is exacerbating the trend in

per capita consumption of animal protein (Kopytets, 2018; Samokhina & Myhalko, 2018; Boltovska, 2022).

In recent decades, precision livestock farming technologies have been introduced, feed rations have been improved, genetic potential of livestock has been renewed, and a number of other aspects of livestock production have been improved. Further increasing the competitiveness of production in the pig industry on the domestic market requires a transition to a more intensive level of its management (Vranken & Berckmans, 2017; Shin et al., 2018; Gómez et al., 2021). More attention is paid to the conditions of farming pigs (Kanis et al., 2004; López-Vergé et al., 2018; Mylostyva et al., 2022), their balanced feeding and growth intensity (Spring, 2020a, 2020b), the latest approaches to meat quality assessment are used (Bankovska et al., 2020; Tarczyński et al., 2021), modern DNA-technologies are increasingly involved (Wang, 2012; Rudoman et al., 2017). The group of traits characterizing the reproductive qualities of pigs is no exception. Indices of sows' reproductive ability largely determine the level of overall efficiency of pig breeding technology (Peltoniemi et al., 2019; Stoyanovskyy et al., 2020; Muro et al., 2022). In recent decades,

methodological approaches to the evaluation of DNA polymorphisms have made it possible to significantly accelerate the speed of selection in pig breeding (Rexroad et al., 2019; Wang et al., 2021; Dilger et al., 2022). It should be noted that the most well-known candidate genes responsible for the expression of main features of the reproductive qualities of sows are the estrogen receptor (ESR1) and prolactin (PRLR) genes (Balatsky et al., 2015; Vashchenko et al., 2019). There is also evidence of the influence of certain genotypes of the ryanodine receptor gene (RYR1) on the expression of reproductive qualities of sows (Szyndler-Nędza et al., 2019). First of all, in our opinion, this can be connected with the general resistance of animals to the influence of adverse factors.

Preliminary analysis of QTL genes' polymorphism is important for the expansion and development of methodological approaches to increasing the productivity of pigs (Buske et al., 2006; Bovo et al., 2020; Vashchenko et al., 2022). In the future, these approaches can be implemented on a large herd. Identifying certain regularities in the formation of the reproductive capacity of pigs, establishing existing relationships between different allelic variants of QTL genes and the expression of productivity in animals of different breeds are promising tasks of applied agricultural genetics (Uemoto et al., 2021; Ding et al., 2022; Xue et al., 2022). Development of these methodological approaches should be carried out, first of all, on small populations and local breeds. For conducting such research, the Welsh breed of pigs is of great interest. This breed has been bred in Ukraine for a long time and is used in various hybridization systems, both as a maternal and as a parental form. Therefore, animals of this breed should have a high level of reproductive capacity of sows and boars (Wilkinson et al., 2012; Tserenyuk et al., 2018).

The purpose of the research presented in this paper is to evaluate ryanodine receptor gene polymorphism in Welsh sows and the effect of RYR1 on their reproductive capacity.

## Materials and methods

The research was conducted at the Shubske farm (Bogodukhiv district, Kharkiv region, Ukraine). 148 sows of the Welsh breed of different maternal lines (74 sows each in the daughter and maternal generations) were evaluated. This number is 91.9% of the total number of sows of this breed in Ukraine (N = 161 sows). Formation of groups and assessment of animals were carried out in compliance with the general principles of research organization (Ibatullin & Zhukorskiy, 2017). All experiments were conducted in compliance with the requirements of the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (Strasbourg, 1985) and the Order of the First National Congress of the Bioethics (Kyiv, 2001), as well as the law of Ukraine "On the protection of animals against ill-treatment" No. 3447-IV as of 21/02/2006 last amended on 04/08/2017. The conditions for keeping pigs of both generations and both genotypes were the same throughout the entire period of research.

Reproductive qualities of sows were evaluated in two adjacent generations. The number of live born piglets, the number of weaned piglets and their weight at the time of weaning at 28 days were taken into account. A comprehensive evaluation of the reproductive capacity of sows was carried out using the SIRQS index (selection index of reproductive qualities of sows). The value of the index was calculated according to the formula (1) proposed by Tserenyuk O. M. (described in Patent for Utility Model No 100641 Ukraine, IPC A01K 67/02 Method of selection of sows. u201411117: 2015.15.3):

$$\text{SIRQS} = 6X_1 + 9.34 \left( \frac{X_2}{X_3} \right) \quad (1)$$

where SIRQS – selection index of reproductive qualities of sows,  $X_1$  – number of piglets born alive per farrowing (animals),  $X_2$  – litter's weight at weaning (kg),  $X_3$  – weaning age (days).

The value of the index of 100 points characterizes the reproductive capacity of sows of the elite class, according to the grading instructions in force in Ukraine. Sows with an index value of more than 100 points were selected for reproduction. The hair follicles of pig bristles were used as biological material (Fig. 1).

DNA isolation was performed using the DNA-sorb-B kit, according to the manufacturer's instructions (AmpliSens, Russia). The polymor-

phism of the RYR1 gene (exon 17, position 1843 C→T) was studied using the PCR-RFLP technology (amplification of the gene region in the polymerase chain reaction with subsequent determination of the restriction fragment length polymorphism) at the Laboratory of Molecular Genetic, Physiological and Biochemical Research in Animal Husbandry of the Institute of Animal Husbandry, National Academy of Agrarian Sciences (Kharkov, Ukraine) and the Institute of Pig Breeding and Agro-Industrial Production of National Academy of Agrarian Sciences (Poltava, Ukraine).



**Fig. 1.** Experimental pigs during the taking of biological material for DNA analysis

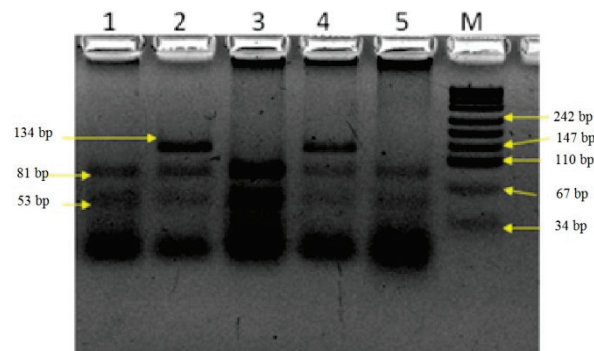
Amplification of the RYR1 gene fragment (134 bp) was carried out using the Amply-4 thermal cycler (Biomom, Russia, 2014) using primers of the following structure (Brem & Brening, 1993; Balatsky et al., 2015): F: 5'- GTGCTGGATGTCCTGTGTTCCCT- 3', R: 5'- CTGGTGAC ATAGTTGATGAGGTTTG- 3'.

PCR amplification program: 1 cycle of denaturation 94 °C – 4 minutes, 35 cycles – denaturation 94 °C – 1 minute, annealing 69 °C – 1 minute, elongation 72 °C – 1 minute, 1 cycle – final elongation 72 °C – 4 minutes. The volume of the reaction mixture was 20 µL, which contained MgCl<sub>2</sub> – 2 mM, dNTP – 200 µM each, Tag DNA polymerase – 2 units activities, primers – 0.2 µM each, 1 x Tag buffer, DNA – 50–100 ng.

The restriction products were separated in a 3.5% agarose gel with the addition of ethidium bromide (0.5 µg/mL) at a voltage of 5 V/cm with subsequent visualization on a transilluminator in UV light (312 nm).

The size of the amplification and restriction fragments was determined using a marker pUC19DNA/MspI ("Thermo scientific", USA).

Restriction analysis was performed using HhaI endonuclease, according to the manufacturer's protocol ("Thermo scientific", USA). HhaI-polymorphism of the studied fragment is caused by the presence of one restriction site for the specified enzyme, which occurs as a result of the C/T transition and leads to the formation of restriction fragments with a length of 81 and 53 bp. Restriction patterns correspond to genotypes: n/n – 134 bp; N/n – 134, 81, 53 bp; N/N – 81, 53 bp (Fig. 2).



**Fig. 2.** Electropherogram of the products of HhaI restriction DNA locus *RYR1* in a 3.5% agarose gel: 2, 4 – experimental animals with the Nn genotype; 1, 3, 5 – with the NN genotype; M is a marker of molecular weight pUC19 DNA/MspI

The genetic potential (GP) of various productivity traits was determined according to the method (Basovskiy, 1991), as described in (Kovalenko & Nezhlukchenko, 2008), based on all evaluated traits of reproductive capacity of sows (number of piglets born alive per farrowing, number of weaned piglets and litter weight at 28 days weaning) according to formula (Kovalenko & Nezhlukchenko, 2008).

Calculations of the genetic potential were carried out between two adjacent generations of “mother–daughter” separately for the entire estimated population, for the part of the population with the *RYR1<sup>NN</sup>* and *RYR1<sup>Nn</sup>* genotypes. Determination of GP was carried out only for those groups in which the generation of daughters exceeded the indicators of mothers.

Based on the obtained absolute indicators, the coefficients of phenotypic consolidation were determined both through the root mean square deviation (K1) and through the coefficient of variation (K2), using formulas (Polupan, 2001). Data processing was performed using SAS/STAT(R) 15.1 statistical software (SAS Institute Inc., USA, 2018). The tables show the arithmetic mean values and their standard errors ( $\bar{x} \pm SE$ ). The significant of differences between the genotypes was assessed using single-factor analysis of variance (ANOVA). Fisher’s F-test was used to assess

the ratio of intergroup and intragroup variability. Differences were considered significant at  $P < 0.05$ . Tukey’s HSD test was used to test for significant differences in multiple comparisons.

## Results

A high level of reproductive performance of sows of the Welsh breed has been established. Animals exceeded the requirements for the elite class by 35.0% in the number of piglets born alive and by 8.2% in weaning litter weight. The main indicators of reproductive capacity in sows of the maternal and daughter generations of the evaluated population did not differ significantly (Table 1).

There was a slight increase in the productivity of all evaluated traits in subsequent generations, although this was due to chance rather than organized causes. Consequently, we can state the absence of genetic progress in reproductive capacity.

In the evaluated population, 8.0% of animals carrying the mutant allele *n* of the *RYR1* gene were found. However, no homozygous *RYR1<sup>nn</sup>* animals were found (Table 2).

**Table 1**

Reproductive capacity of sows of the Welsh breed in two generations

Trait	Maternal generation, n = 74, $\bar{x} \pm SE$	Daughter generation, n = 74, $\bar{x} \pm SE$	F	P	Genetic potential
Number of piglets born alive per sow, animals	13.50 ± 0.17	13.53 ± 0.20	0.009	0.922	13.55
Number of weaned piglets per sow, animals	11.13 ± 0.14	11.15 ± 0.17	0.010	0.920	11.17
Weaning litter weight, kg	194.8 ± 2.4	195.1 ± 2.9	0.009	0.923	195.5

**Table 2**

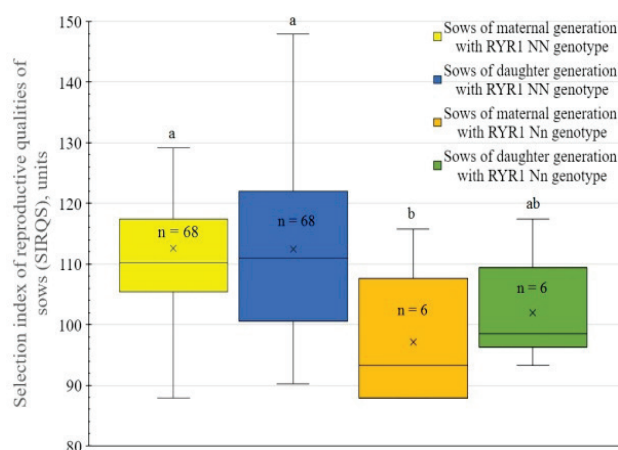
Reproductive capacity of maternal and daughter generation of sows of the Welsh breed with different genotypes of *RYR1* gene

Generation	Maternal				Daughter				All genotypes	
	Genotype	NN (n = 68)	Nn (n = 6)	F	P	NN (n = 68)	Nn (n = 6)	F		P
Statistical parameter		$\bar{x} \pm SE$	$\bar{x} \pm SE$			$\bar{x} \pm SE$	$\bar{x} \pm SE$			genetic potential
Number of sows (n)		68	6	–	–	68	6	–	–	74
Number of piglets born alive per sow, animals		13.64 ± 0.17	11.93 ± 0.50	8.66	0.004	13.62 ± 0.22	12.52 ± 0.58	2.18	0.144	13.1
Number of piglets weaned per sow, animals		11.28 ± 0.12	9.37 ± 0.83	17.61	1.0*10 <sup>-4</sup>	11.26 ± 0.17	9.87 ± 0.31	5.60	0.021	10.4
Weaning litter weight, kg		197.5 ± 2.1	163.9 ± 14.5	14.94	2.0*10 <sup>-4</sup>	197.1 ± 3.0	172.7 ± 5.5	5.93	0.017	181.4

Pigs of the maternal generation carrying the homozygous NN genotype had better reproductive performance in all indicators. For a more accurate characterization of the evaluated populations and individual groups of animals, the genetic potential of productivity was calculated. Realization level of genetic productivity potential in animals with the *RYR1-n* allele according to the following traits: number of piglets born alive per sow – 95.6%, number of piglets weaned per sow – 95.1% and weaning litter weight – 95.2%. Traits measured at weaning were characterized by a lower percentage of realization of genetic potential compared to the number of piglets born alive per sow, which can be explained by a greater influence of paratypic factors. Comparing the data shown in Tables 1 and 2, we can see that sows carrying the *RYR1-n* mutant allele had lower values compared to the entire evaluated population for all indicators. In sows that did not have a mutant allele, the genetic potential of productivity was not determined due to the lack of progress in the next generation.

Sows characterized by high values of one productive trait are not always marked by high values of other traits. This complicates a comprehensive assessment of their reproductive capacity. In order to obtain a generalized assessment of the productivity of sows based on several characteristics at the same time, the SIRQS index was determined. The animals were ranked according to the SIRQS index for further selection work. The mean values of SIRQS in groups of animals with the *RYR1 Nn* genotype were lower in both maternal and daughter generations (Fig. 3). Sows with the *RYR1Nn* genotype had worse SIRQS index values in both evaluated generations. Compared to sows carrying the *RYR1 NN* genotype, animals with the *Nn* genotype had SIRQS values lower by 15.68% ( $P = 0.015$ ) when comparing sows of the maternal generation and by 10.20% when comparing sows of the daughter generation.

In addition, the value of the phenotypic consolidation coefficients for both studied groups of sows was evaluated in comparison with the evaluated population as a whole (Table 3).



**Fig. 3.** The values of the selection index of reproductive qualities of sows (SIRQS) in pigs of the Welsh breed maternal and daughter generations with different genotypes of *RYR1* gene: cross – median, central horizontal line – mean, upper and lower borders of the rectangle – 25% and 75% quartiles, vertical line – minimum and maximum values; different letters within each figure indicate significant differences between groups according to the Tukey’s HSD test results

The values of the coefficients of phenotypic consolidation of the trait number of piglets born alive in sows without the mutant allele were lower than the similar values of sows with the *RYR1 n* allele. Sows of the maternal generation with the NN genotype had a consolidation ratio from 2.75 to 7.00 times higher compared to sows of the same generation, but with the *Nn* genotype. An even greater difference was established between the values of the coefficients of phenotypic consolidation of the



weight of the litter of piglets at weaning. Sows of the maternal generation with the NN genotype were more consolidated, whereas in the daughter generation heterozygous sows carrying the mutant allele n of the RYR1 gene were more consolidated.

**Table 3**  
Coefficients of phenotypic consolidation for reproductive capacity of the Welsh breed of sows in two generations

Genotypes of sows	Productivity trait	Maternal generation		Daughter generation	
		K1, units	K2, units	K1, units	K2, units
RYR1 NN (n = 68)	Number of piglets born alive per sow	0.03	0.04	-0.02	-0.01
RYR1 NN (n = 68)	Weaning litter weight	0.16	0.17	0.00	0.01
RYR1 Nn (n = 6)	Number of piglets born alive per sow	0.21	0.11	0.25	0.19
RYR1 Nn (n = 6)	Weaning litter weight	-0.57	-0.86	0.51	0.44

## Discussion

RYR1 gene polymorphism was mainly studied in order to determine its effect on stress sensitivity, meat quality and fattening productivity of pigs (Webb et al., 2010; Han et al., 2012; Rybarczyk et al., 2022). It is known that the RYR1 gene has significant effects on growth and meat quality except for ultimate pH value, initial conductivity and redness of the meat (Kadamdeen, 2007; Otto et al., 2007). Regarding the comparability of the data we obtained with the results of research conducted by other scientists on other breeds of pigs, it should be noted that there is no consensus regarding the level of reproductive capacity in animals with different genotypes of the RYR1 gene. In the studies of some scientists, a significant influence of the RYR1 gene polymorphism on reproductive ability of sows was not established (Nienartowicz-Zdrojewska et al., 2017). In other studies, between dominant NN homozygotes and hybrids with the Nn genotype, a significant difference was established at  $P \leq 0.01$  for all major traits (Lebret & Čandek-Potokar, 2021). Furthermore, significant differences were observed in the composition of the milk of sows in groups depending on the genotype at the RYR1 locus. The milk of sows with the RYR1 C/C genotype contained more dry matter. The impact of the RYR1 gene polymorphism on reproductive traits has been established. There was negative influence of the T nucleotide in the RYR1 gene on litter parameters (Babicz et al., 2012). The strength of the influence of the stressful genotype on the productive qualities of pigs may be due to the duration of the stress factor (Lebret & Čandek-Potokar, 2021). Other scientists emphasize the difficulty of conducting a comparative assessment of the productivity of animals with different genotypes, which is associated with a small percentage of animals carrying the mutant allele (Kmicic et al., 2000; Nienartowicz-Zdrojewska et al., 2017). In general, our research confirmed the existence of a dependence of the presence of a mutant allele of the RYR1 gene in the genotype on the reproductive capacity of sows of the Welsh breed. The results obtained by us indicate that sows carrying a mutant allele of the RYR1 gene had worse values of reproductive capacity compared to sows without this allele.

Regarding the differences in the mechanism of implementation of the reproductive capacity of sows with different allelic variants of the RYR1 gene, it should be taken into account that the carriers of the mutant allele of this gene are more susceptible to stress. The mutant allele of this gene in the homozygous genotype causes a significant effect on the muscle tissue of pigs. The effect of the RYR1 gene was due to nn stress-susceptible pigs, in which the risk of PSE (pale soft exudative muscle) meat increased fourfold (Guàrdia et al., 2009; Liu et al., 2019; Zequan et al., 2022).

At the same time, sows at agro-industrial enterprises for the production of pork are in a state of temperature stress both during gestation and during lactation. A sharp increase in the ambient temperature above optimal values disrupts the thermal balance of the animal. This causes hyperthermia and, as a result, rapid breathing, excessive urination and hypersalivation. Stress-prone sows that were kept in stressful conditions are usually characterized by reduced reproductive traits (Mayorga et al., 2019; Rauw et al., 2020). The influence of the RYR1 genotype may also appear

during the restriction of the movement of sows with fixed maintenance in boxes for farrowing. A positive correlation was seen between cytokines (with the exception of IL-6) and plasma catecholamine (adrenaline and noradrenaline) concentrations in Nn heterozygous and nn homozygous pigs (Ciepielewski et al., 2013b). Stress-susceptible RYR1-mutated homozygotes develop a greater level of immune defense, including cytotoxic activity of NK cells, and this is accompanied by more pronounced stress-induced changes in neuroendocrine response than stress-resistant heterozygous (Nn) and homozygous (NN) pigs (Ciepielewski et al., 2013a). Sows carrying the mutant allele are more prone to stress, which can cause a decrease in their reproductive capacity.

Regarding the sensitivity to stress of different breeds of pigs, Pietren, Polish-Chinese pigs, Landrace, Hampshire and Yorkshire are considered quite susceptible to stress, while Chester White, Duroc, Large White and Berkshire are considered to be resistant to stress (Nevrkla et al., 2017; Shin et al., 2018; Mote & Rothschild, 2020). In our research, only 8.01% of animals carrying a mutant allele of the RYR1 gene were found, while no animals homozygous for the mutant allele of this gene were found at all. Accordingly, judging by the RYR1 gene, Welsh pigs of Ukrainian breeding can be classified as stress-resistant animals.

The process of phenotypic consolidation is usually a consequence of the reduction of genetic variability (Ladyka et al., 2019; Khalak et al., 2020). Therefore, the results obtained by us when determining the degree of phenotypic consolidation of experimental animals require explanation. More genetically homogeneous homozygotes with the NN genotype compared to heterozygotes had a lower consolidation coefficient for the trait number of piglets born alive in both generations and for the trait weaning litter weight in the daughter generation. A possible explanation may be the low influence of genetic factors on traits of reproductive ability.

## Conclusions

Polymorphism of the ryanodine receptor gene in sows of the Welsh pig breed was evaluated. 8.0% of the animals were identified as carriers of the mutant allele of the ryanodine receptor gene.

Better performance of sows free of the mutant allele of the RYR1 gene was established over sows carrying it in all evaluated traits of reproductive capacity (for different traits P ranged from 0.021 to  $1.0 \cdot 10^{-4}$ ), except for number of piglets born alive per sow in the daughter generation (no significant difference was established for this trait in this generation). The better performance of sows free from the mutant allele of the ryanodine receptor gene was also evident from the results of the index value (SIRQS). At the same time, significant differences in the level of consolidation of traits of the reproductive capacity of sows between animals with different allelic variants of the RYR1 gene were not detected.

In order to increase the reproductive capacity of sows in the studied population of Welsh pigs and to achieve similar results in other pig breeds, a methodological approach should be used, which consists in removing carriers of the mutant allele of the ryanodine receptor gene from the selection process.

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The authors declare no conflicts of interest.

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