ACTA VET. BRNO 2024, 93: 289–298; https://doi.org/10.2754/avb202493030289

Seasonal ovarian activity and oocyte size in ovarian follicles of sexually mature gilts

Petronela Kyzeková, Katarína Bárdová, Peter Reichel, Róbert Link, Jaroslav Novotný, Gabriela Čonková-Skybová

University of Veterinary Medicine and Pharmacy in Košice, Clinic of Swine, Košice, Slovakia

Received June 14, 2023
Accepted July 11, 2024

Abstract

The aim of this study was to evaluate ovarian activity and the size of oocytes in ovarian follicles of sexually mature Landrace-Yorkshire gilts in relation to the seasons of the year. The size and weight of the ovaries, the number of follicles and corpora lutea (CL) according to individual size categories were evaluated on 240 gilts slaughtered at an abattoir during the four seasons of the year. Our evaluation of the ovary size showed that they were the largest in autumn when their mean length reached 25.8 ± 3.4 mm, whereas in winter their mean length was 24.2 ± 2.9 mm ($P < 0.05$). During the autumn months, the largest number of follicles in the ovaries of the gilts was recorded, with a predominance of follicles up to 3 mm (mean number 17.9 ± 7.5). The smallest number of corpora lutea was observed in winter (mean number 6.1 ± 1.1) and the largest in spring (mean number 12.1 ± 2.6). The oocytes, from follicles of up to 3 mm size, were the smallest in spring (mean size $16.99 \times 10^3 \pm 3.42 \times 10^3$ μm^2). In total, the largest oocytes were aspirated from 4–6 mm follicles in autumn (mean size $19.60 \times 10^3 \pm 5.37 \times 10^3 \pm$ μm^2). The findings of the study indicate that the ovarian activity and growth of oocytes in gilts are affected by the seasons of the year.

Sows, reproduction, sesonal infertility

Successful reproductive performance of gilts and sows is based upon the active functioning of their ovaries, characterised by intensive folliculogenesis. Numerous growing and ripening ovarian follicles ensure conditions for favourable conception abilities of gilts and sows and are an optimum source of oocytes for the use in embryo transfers.

Folliculogenesis is a process of development of follicles which are the basic structures of mammalian ovaries. It is one of the most important phases of development of the female reproductive organs that commences already during foetal life (Rybska et al. 2018). Extensive studies have shown that after reaching sexual maturity, folliculogenesis involves ripening and ovulation of minimally 14–20 follicles during each subsequent oestrous cycle. However, every population of these follicles is morphologically and biochemically heterogenic. Differences in the number of granulosa cells, activation of lutropin receptors or concentration of steroids in the follicular fluid are recorded even in follicles of the same size.

It is evident that the quality of follicles affects the quality of oocytes. The pre-ovulation development of follicles and oocytes can thus positively or negatively affect the formation, development, and survival of embryos. The economic efficiency of pig breeding largely depends on the effective reproductive management of sows (Knox 2016). Achieving such efficiency primarily involves reducing non-productive days, which will allow more piglets to be weaned per sow and year (Peltoniemi and Virolainen 2006; Knox 2014).

Sows with one or more piglets represent approximately 80% of the total sow population on pig farms. They are inseminated immediately during the first oestrus after weaning, most often between the third and fifth day after weaning (Knox and Zas 2001). Unfortunately, a variable number of weaned sows do not show oestrus during this period, which

Address for correspondence:
Katarína Bárdová
Clinic of Swine
University of Veterinary Medicine and Pharmacy in Košice
Komenského 73, 041 81 Košice, Slovakia
E-mail: katarina.bardova@uvlf.sk
http://actavet.vfu.cz/

delays their insemination and increases the number of non-productive days (Lopes et al. 2014). Moreover, long intervals from weaning to oestrus are associated with increased losses during pregnancy, reduced number of farrowings and reduced number of litters (Lopes et al. 2014; Knox 2019). The number of litters is determined by the number of oocytes released during ovulation that are fertilized and successfully develop into a viable piglet (Ferguson et al. 2006). Between 5% and 15% of oocytes released at ovulation are not fertilized and up to 30% of embryos fail to develop after day 30 of pregnancy (Hälli et al. 2008) and these reproductive losses represent lost economic potential for the pig industry (Lopes et al. 2014). Recent studies suggest that oocyte quality may be a primary determinant of embryo viability and survival (Bagg et al. 2004). The quality of oocytes is influenced by the maternal environment, especially the nutritional status, the age of the animal, the external environment, as well as the season (Tast et al. 2002; Bertoldo et al. 2011; Swinbourne et al. 2014).

The aim of this study was to analyse ovarian activity in sexually mature gilts and to evaluate the size of oocytes according to individual size categories of follicles in the individual seasons of the year.

Materials and Methods

Ovarian activity was evaluated on ovaries from 240 Landrace-Yorkshire gilts, 9–10 months old and weighing 150–160 kg. The ovaries were obtained after the animals were slaughetered at the abattoir. The ovaries were evaluated for their size and weight and the number of follicles and corpora lutea (CL), according to individual size categories. In follicles the size categories were up to 3 mm, 4–6 mm, 7–9 mm, 10–11 mm and 12 mm and more, in corpora lutea up to 5 mm, 6–9 mm, 10–11 mm and 12 mm and more. Using an insulin syringe BD Micro-Fine Plus 0.5 ml (BD Medical, Franklin Lakes, USA), the follicular fluid with oocytes was aspirated and applied to Petri dishes (Gama group, a. s., České Budejovice, Czech Republic) and filled up to one third with sodium chloride 0.9% infusion solution (KO, Košice, Slovakia). The Petri dishes were marked with the size category of follicles from which the oocytes were aspirated. The identification of the oocytes in the dishes was carried out under a stereoscopic microscope STM 723 (Kapaoptic, Kvant, Bratislava, Slovakia) at a 20–40-fold magnification. Using an adjusted Monoject tuberculin syringe 1 cc (Covidien, Mansfield, England) with a piece of IUI pipette, we transferred the oocytes to the Petri dishes containing clear sodium chloride 0.9% infusion solution and after calibration of the microscope we photographed them using a camera 1,3 MP Moticam 1SP (Motic China Group Co., Ltd., Hong Kong, China). The size of oocytes was measured by the software Motic Images Plus 2.0 (Motic China Group Co., Ltd., Hong Kong, China).

This study was carried out in accordance with the Ethics Committee at the UVMP in Košice, Slovakia under the number EKVP/2022-03.

The statistical evaluations of the results were carried out by the software Microsoft Office Excel 2013 (Microsoft Corporation, Redmond, USA) and the significance of differences of two sets of data were determined using Student's *t*-test ($P < 0.05$; $P < 0.01$; $P < 0.001$).

Results

The results obtained in this study confirmed the influence of seasons on ovarian activity and oocyte growth in gilts and sows.

Our evaluation of the ovary size (Fig. 1) revealed that the smallest ovaries were observed in winter (mean size 24.2 ± 2.9 mm) and the largest in autumn (mean size 25.8 ± 3.4 mm). The ovaries of gilts reached the highest weight (Fig. 2) in spring (mean weight 6.2 ± 2.2 g) and the lowest one in autumn (mean weight 5.7 ± 1.4 g).

The above findings correspond with the largest number of ovarian follicles in gilts (mean number 24.8 ± 7.7) in autumn (Fig. 3) that resulted in enlarged volume of ovaries, and the highest number of corpora lutea (mean number 12.1 ± 2.6) in spring (Fig. 4) that affected the weight of the gilts' ovaries. In autumn, the predominant size of the follicles was up to 3 mm. The ovarian follicles of size 4–9 mm were found most frequently in autumn and winter (mean number 6.9 ± 2.0 and 6.9 ± 1.8, respectively).

When evaluating the size of oocytes collected from gilts' follicles of size up to 3 mm, we detected different sizes of oocytes during individual seasons (Fig. 5). The smallest were oocytes collected from follicles up to 3 mm size in spring (mean size $16.99 \times 10^3 \pm 3.42 \times 10^3$ μm^2) and the largest were those collected in winter (mean size $18.90 \times 10^3 \pm 2.99 \times 10^3$ μm^2). In total, the largest oocytes were collected from 4–6 mm follicles in autumn (mean size $19.60 \times 10^3 \pm 5.37 \times 10^3$ μm^2).

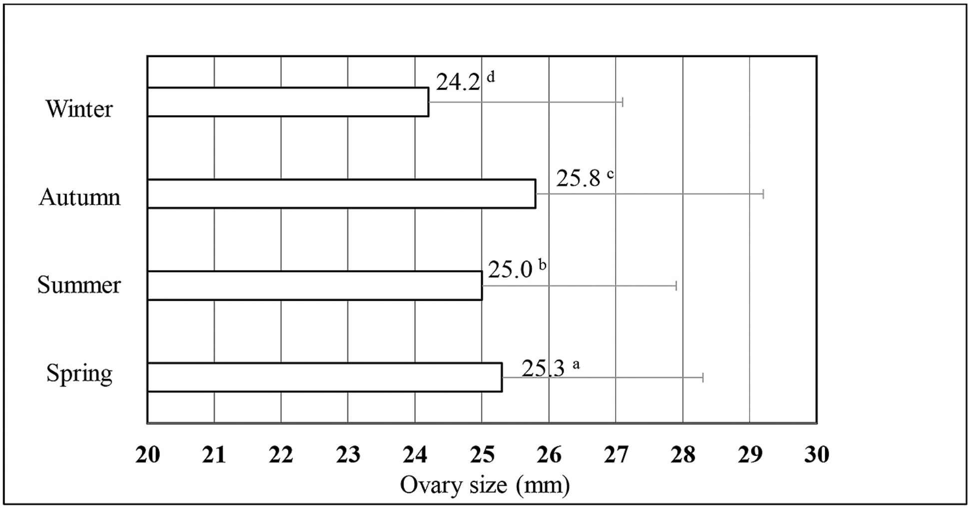

Fig. 1. The mean size of ovaries of gilts during the different seasons of the year.
Student's *t*-test: a:b,c = $P > 0.05$; c:b,d = $P < 0.05$; a:d = $P < 0.01$

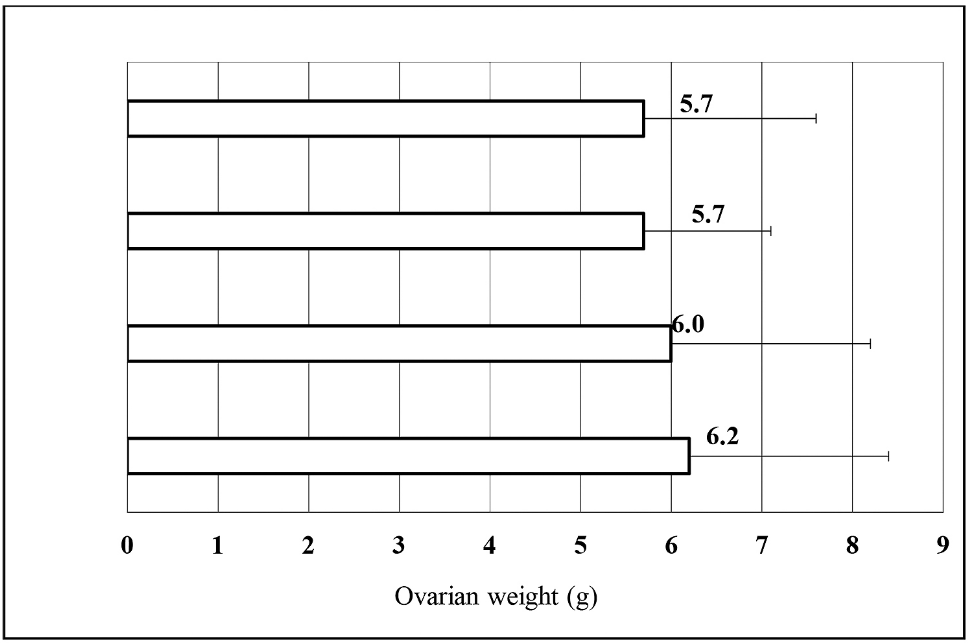

Fig. 2. The mean weight of ovaries of gilts during the different seasons of the year.
Student's *t*-test: $P > 0.05$

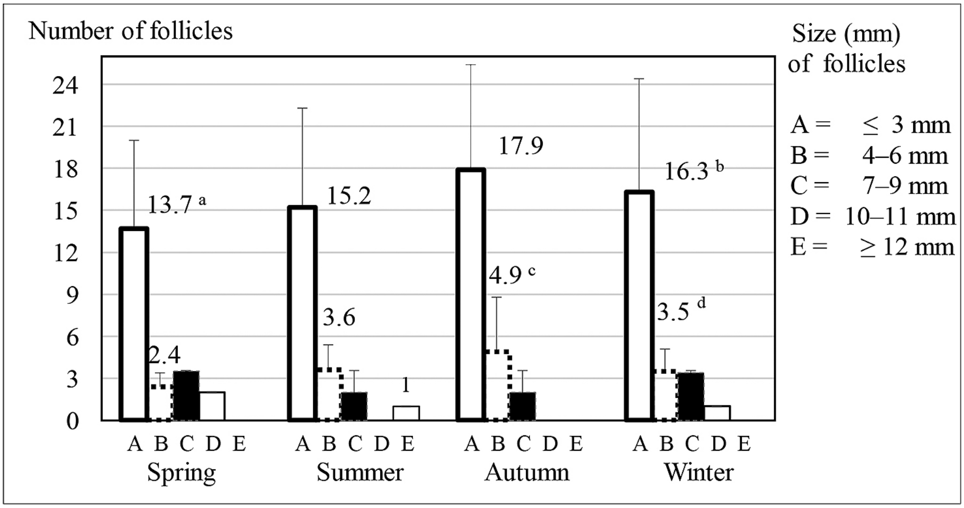

Fig. 3. Comparison of the mean number of follicles per ovary in individual groups (A–E) according to their size in gilts during the seasons

Student's *t*-test: c:d = $P < 0.05$; a:b = $P < 0.01$

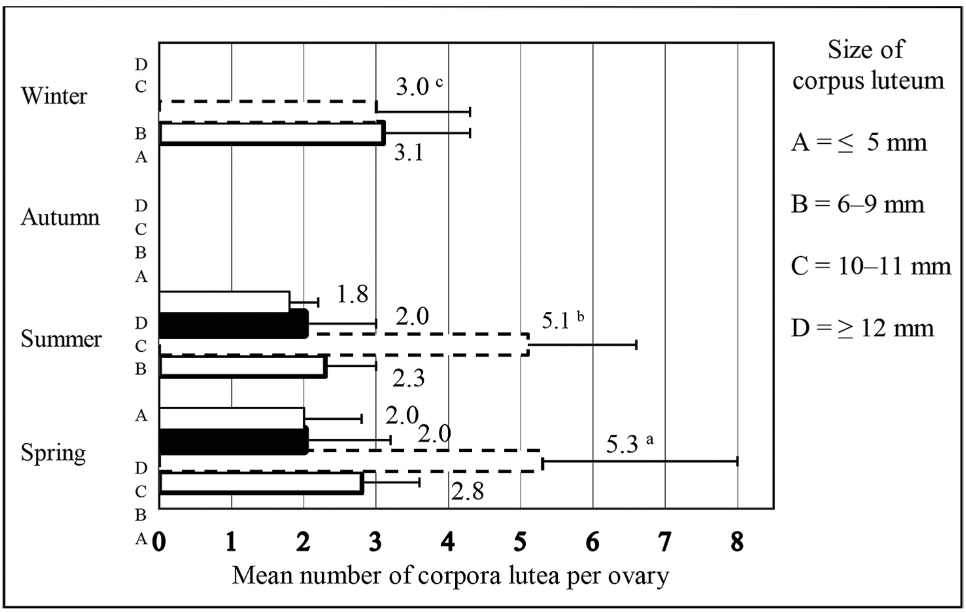

Fig. 4. Comparison of the mean number of corpora lutea per ovary in individual groups (A–D) according to their size in gilts during the seasons

Student's *t*-test: c:a,b = $P < 0.05$

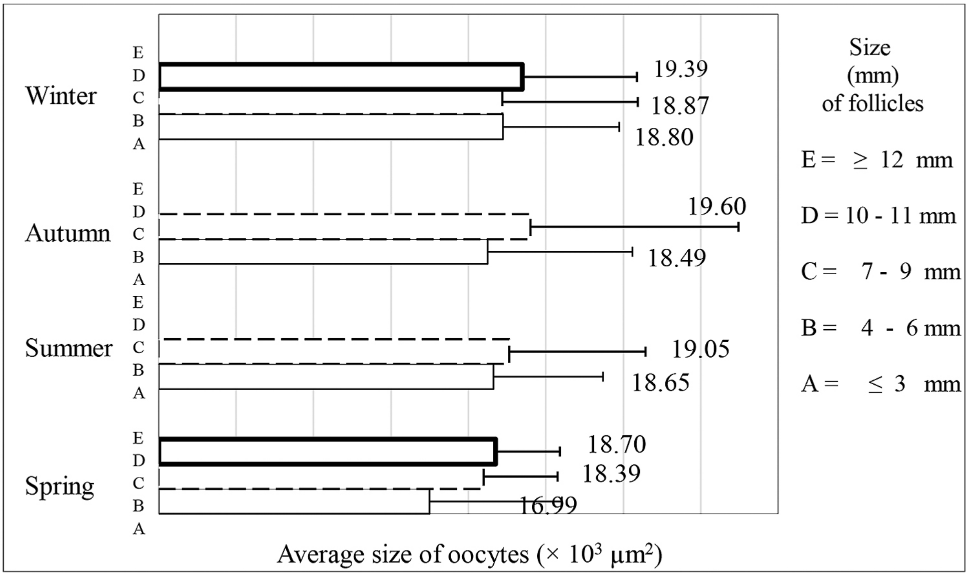

Fig. 5. The average size of oocytes of gilts during the different seasons of the year
Student's *t*-test: $P > 0.05$

Discussion

The functionality of the reproductive apparatus in sows is affected by a number of factors. One of them is the season of the year. It has been demonstrated that the seasonal variability of conception abilities of gilts and sows may cause disturbances of the oestrous cycle and occurrence of embryonic deaths. The reasons for these disorders are alterations of synthesis and release of gonadotropins from the hypophysis, particularly insufficient production of lutropin, which affects the activity of the luteal cells of the corpora lutea and causes a decreased production of progesterone. The low production of progesterone by the ovaries of gilts results in the reduced developmental competence of the oocytes (Bertoldo et al. 2010). Yoshizawa et al. (2009) stated that an optimum concentration of progesterone during folliculogenesis in gilts is necessary for the oocyte to reach its full developmental potential. Gupta et al. (2007) and Bertoldo et al. (2011) reported that oocytes obtained from the corpora lutea containing ovarian follicles of gilts and sows exhibited higher developmental potential than oocytes obtained from follicles that did not possess corpora lutea. It was recorded that the progesterone concentration varies with the seasons and its marked decrease is associated with a reduced conception rate or increased embryonic and foetal mortality rates in gilts and sows.

Pigs, as well as several other mammals (cattle, sheep and others, including the human population), are born with a highly varied number of ovarian follicles and oocytes in the ovaries, which decrease during aging and never replenish. This change in ovarian reserve is reflected in the number of antral follicles in the ovaries at all ages after birth (Evans et al. 2012). As the factors causing this variability in ovarian follicle size at weaning are not yet fully explanated (Knox 2019) their elucidation would help design effective management strategies to achieve and maintain optimal weaning-to-oestrus intervals. Seasons, parity, body condition and duration of lactation are considered to be the main factors influencing the growth of ovarian follicles in sows (Knox 2019). Elucidation of the role played by the season would be of particular interest, as seasonal changes in daylight and air temperature are well-known factors affecting the reproductive performance of sows, which significantly affects the economics of pig farming (Quesnel et al. 2005; Peltoniemi and Virolainen 2006; Auvigne et al. 2010; Bertoldo et al. 2011).

The effects of season and mild nutritional restriction on ovarian function and oocyte nuclear maturation in cyclic gilts were pointed out by Swinbourne et al. (2014) who reported that the number of large follicles (≥ 6 mm) was lower in summer (S) compared to winter (W) (S: 10.7 ± 1.74 vs W: 15.5 ± 1.15, $P < 0.05$), as was the proportion of oocytes in the germinal vesicular stage of meiosis (S: 0.06 ± 0.02 vs W: 0.08 ± 0.02, $P < 0.05$). However, the proportion of oocytes that reached MII was similar in summer and winter (S: 0.72 ± 0.04 and W: 0.69 ± 0.06, $P > 0.05$). Intrafollicular concentrations of luteinizing hormone were higher in summer (S: 43.05 ± 6.44 vs W: 12.05 ± 5.12 ng/ml, $P < 0.001$), while oestradiol was lower (S: 1.27 ± 0.36 vs W: 27.52 ± 5.59 ng/ml, $P < 0.001$). The results demonstrated that in summer the growth of follicles above 6 mm is impaired during the periovulatory period without affecting the meiotic competence of the oocytes. Importantly, these data also demonstrated that ovarian follicle growth and the ability of oocytes to achieve MII *in vitro* appear to be unaffected by mild nutritional restriction during the preceding oestrous cycle. In agreement with our findings, Lopes et al. (2020) in a field study after transrectal ovarian scanning, recorded a comparable mean follicle size in weaned (n = 191) and lactating (n = 40) sows as in our experiment and concluded that the growth of ovarian follicles during lactation determines the reproductive performance of weaned sows, as already lactating sows showed large variability in ovarian follicle diameter, suggesting that variability at weaning already existed during early lactation and carried over to weaning.

Likewise, the results of several other experimental works confirmed that sows show significant variability in the size of ovarian follicles at weaning (Bracken et al. 2003), whereas sows with small follicles at weaning had a longer interval from weaning to oestrus (Lucy et al. 2001; Lopes et al. 2014). Kumar et al. (2016) aimed to assess the effect of different seasons on pig ovarian biometry, oocyte collection and oocyte quality in the northeastern hilly region of India. Pig ovaries (1886) were collected over a 12-month period from local slaughterhouses. Morphological studies revealed mulberry-shaped ovaries with an average weight of 4.435 ± 0.622 g. The mean number of follicles and corpora lutea was significantly higher in winter than monsoon but not significantly different from pre-monsoon/summer. The number of retrieved oocytes from visible follicles in the oocyte collection medium was significantly higher in winter than in the other two seasons. The percentage of class I (10–12 mm), class II, (7–9 mm), class III (4–6 mm) and class IV (≤ 3 mm) oocytes was found to be 24, 36, 23 and 17%, respectively. Cultivable oocytes were significantly higher in winter than in summer and monsoon seasons. The season had a significant effect on the quality and quantity of pig ovaries, which could be well utilized for *in vitro* maturation and fertilization by reproductive and biotechnology research. Currently, little is known about the aetiology of seasonal infertility in sows. Recent findings represent a significant advance in the understanding of sow reproductive physiology and implicate poor oocyte developmental competence as a contributing factor to infertility during the seasonal period. It has also been shown that ovarian activity is reduced during the seasonal period of infertility. Decreased oocyte quality is associated with reduced progesterone levels in the follicular fluid during final oocyte maturation *in vivo* (Bertoldo et al. 2012). In sows, summer and early autumn are the periods when reproductive indicators show the lowest values. This period is often referred to as summer infertility or, more appropriately, as seasonal infertility, as the effects may occur outside of the summer months (Tast et al. 2002; Martinat-Botté et al. 2010). Manifestations of seasonal infertility include delayed puberty (Martinat-Botté et al. 2010), prolonged or irregular weaning to oestrous intervals (Belstra et al. 2004; Seyfang et al. 2016), reduced birth rate (Tantasuparuk et al. 2000; Hansen et al. 2001), anoestrus and reduced number of litters (Tast et al. 2002). Seasonal infertility can be attributed to a variety of factors, but is primarily associated with seasonally high environmental temperatures that negatively affect nutrient intake for lactation (Tast et al. 2002). Reduced feed intake may also interact with the photoperiod, as feeding restriction has been shown to lead to higher melatonin circulation in sows (Langendijk 2022).

In general, seasonal infertility occurs more often in gilts and young sows than in older sows (Tummaruk 2012; Iida and Koketsu 2013). Heat stress and long photoperiods during the warm season can cause a decrease in feed intake and an imbalance of the hypothalamic-pituitary-ovarian axis. Increased variability of the interval between the onset of oestrus and ovulation leads to an increased number of poorly timed inseminations. Altered endocrine activity threatens the development of follicles and luteal bodies, reduces oocyte quality and increases embryo mortality (De Rensis and Kirkwood 2016; Hale et al. 2017; De Rensis et al. 2017). It has been assumed that the quality of oocytes and their fertilization ability as well as maturation competence are affected by the size of the follicles from which they originated (Alwarez et al. 2009). Oocytes are present in ovarian follicles in all stages of folliculogenesis and can be obtained already from follicles 2–5 mm in size (Marcha et al. 2002). However, there is an assumption that with the increasing size of the follicle, the environment that affects the quality of the oocyte and its fertilization ability improves as its maturation competence improves. With the growth of follicles, the number of layers and counts of columnar cells surrounding the oocytes increase (Liu et al. 2002). Oocytes obtained from larger follicles (3–8 mm) exhibit increased intensity of meiotic maturation and higher cytoplasmic activity than oocytes obtained from small follicles (up to 3 mm). It was reported that higher proportion of oocytes collected from larger follicles developed to metaphase II compared to oocytes from small follicles (Liu et al. 2002). During *in vitro* cultivation, such oocytes exhibit a higher ability to develop to the blastocyst stage than oocytes collected from smaller follicles. The concentrations of steroid hormones, particularly progesterone (P4) and 17-beta oestradiol (E2) increases in the follicular fluid of growing follicles which is positively reflected in terms of an increased developmental competence of oocytes (Liu et al. 2002). Differences in the concentrations of these steroid hormones were recorded also between ovarian follicles of pre-pubertal and sexually mature gilts (Grupen et al. 2003). The concentration of these hormones was substantially lower in follicles of pre-pubertal gilts compared to follicles of the same size collected from sexually mature gilts. Similarly, oocytes obtained from follicles of pre-pubertal gilts at *in vitro* fertilization showed markedly a higher degree of polyspermy than oocytes from follicles of sexually mature gilts. This indicates insufficient cytoplasmic maturation in pre-pubertal gilts and the fact that the age of gilts also affects the developmental competence of oocytes. Griffin et al. (2006) observed that the developmental competence of oocytes during *in vitro* fertilization correlated with the size of oocytes; the larger the oocyte, the higher the probability of its good developmental competence. The size of oocytes is again in correlation with the size of the follicles. Only sufficiently large follicles contain the optimum number of cells necessary for the adequate developmental competence of oocytes, numerous receptors for gonadotropic hormones and optimum concentrations of steroids in the follicular fluid.

The identification of reliable characteristics of follicular quality and developmental competence has been pursued in many studies, but with inconsistent results. They focused on identifying these characteristics by analyzing the profile of steroids (Jochems et al. 2021; Jochems et al. 2022) or other hormones and various metabolites (Bartkova et al. 2020) in the follicular fluid in relation to the cumulus-oocyte complex morphology and follicle size, followed by molecular rationale (Costermans et al. 2020).

Traditional methods of oocyte quality assessment are based on the morphological classification of follicle, cumulus-oocyte complex, polar body and meiotic spindle. Biochemical and morphological changes in oocytes and surrounding granulosa cells are very complex and depend on many factors, including intercellular communication. Granulosa cells have many functions, often crucial for proper oocyte viability and subsequent positive fertilization (Munakata et al. 2018; Kulus et al. 2020).

The results of several works (Bertoldo et al. 2013; Hu et al. 2020; Inoue et al. 2020; Gad et al. 2022) confirm that the microenvironment of the developing follicle is crucial for the acquisition of oocyte developmental competence, which is influenced by several factors, including follicle size and season. Ovarian follicular fluids contain several types of regulatory factors that maintain a suitable microenvironment for oocyte development. Extracellular vesicles are among the factors that play an essential role in the regulation of follicle and oocyte development through their microRNA (miRNA) molecules. It seems that in order to overcome the seasonal effect and achieve acceptable early embryonic development in pigs, experimental work will be pointed in this direction (Kwak et al. 2014; Tsakmakidis et al. 2017; Shibahara et al. 2020; Zhao et al. 2020).

In conclusion, the fertilization abilities and developmental competences of oocytes are affected by a number of factors including the gilts' age, their nutritional status during mating, the season, and follicle growth. Without accepting and optimising the influence of these factors on folliculogenesis and thus also on the development and maturation of oocytes, breeders will be unable to ensure the required reproductive indices in pig farming and experimental workers will not reach the expected results of *in vitro* fertilization in embryo transfer programmes developed for pigs.

Acknowledgements

The authors wish to thank the colleagues Drs Ján Varecha, Jozef Illár, and Jozef Kmec for their collaboration, and the company Dalton s.r.o. for assistance in obtaining the biological materials.

References

Alwarez GM, Dalvit GC, Ach M, Miguez MS, Cetica PD 2009: Immature oocyte quality and maturational competence of porcine cumulus-oocyte complexes subpopulations. Biocell **33**: 167-177

Auvigne V, Leneveu P, Jehannin C, Peltoniemi O, Sallé E 2010: Seasonal infertility in sows: a five year field study to analyze the relative roles of heat stress and photoperiod. Theriogenology **74**: 60-66

Bagg MA, Vassena R, Papasso-Brambilla E, Grupen CG, Armstrong DT, Gandolfi F 2004: Changes in ovarian, follicular, and oocyte morphology immediately after the onset of puberty are not accompanied by an increase in oocyte developmental competence in the pig. Theriogenology **62**: 1003-1011

Bartkova A, Morovic M, Strejcek F, Murin M, Benc M, Percinic FP, Laurincik J 2020: Characterization of porcine oocytes stained with Lissamine Green B and their developmental potential *in vitro*. Anim Reprod (Belo Horizonte) **17**: 1-11

Belstra BA, Flowers WL, See MT 2004: Factors affecting temporal relationships between estrus and ovulation in commercial sow farms. Anim Reprod Sci **84**: 377-394

Bertoldo MJ, Holyoake PK, Evans G, Grupen CG 2011: Seasonal effects on oocyte developmental competence in sows experiencing pregnancy loss. Anim Reprod Sci **124**: 104-111

Bertoldo MJ, Holyoake PK, Evans G, Grupen CG 2012: Seasonal variation in the ovarian function of sows. Reprod Fertil Dev **24**: 822-834

Bertoldo MJ, Nadal-Desbarats L, Gérard N, Dubois A, Holyoake PK, Grupen CG 2013: Differences in the metabolomic signatures of porcine follicular fluid collected from environments associated with good and poor oocyte quality. Reprod **146**: 221-231

Bertoldo M, Holyoake PK, Evans G, Grupen CG 2010: Oocyte developmental competence is reduced in sows during the seasonal infertility period. Reprod Fertil Dev **22**: 222-229

Bracken CJ, Lamberson WR, Safranski TJ, Lucy MC 2003: Factors affecting follicular populations on Day 3 postweaning and interval to ovulation in a commercial sow herd. Theriogenology **60**: 11-20

Costermans NGJ, Soede NM, Tricht F, van Blokland M, Kemp B, Keijer J, Teerds KJ 2020: Follicular fluid steroid profile in sows: relationship to follicle size and oocyte quality. Biol Reprod **102**: 3740-3749

De Rensis F, Kirkwood RN 2016: Control of estrus and ovulation: Fertility to timed insemination of gilts and sows. Theriogenology **86**: 1460-1466

De Rensis F, Ziecik AJ, Kirkwood RN 2017: Seas onal infertility in gilts and sows: Aetiology, clinical implications and treatments. Theriogenology **96**: 111-117
Evans ACO, Mossa F, Walsh SW, Scheetz D, Jimenez-Krassel, F, Ireland JLH, Smith GW, Ireland JJ 2012: Effects of maternal environment during gestation on ovarian folliculogenesis and consequences for fertility in bovine offspring. Reprod Domest Anim **47**: 31-37
Ferguson EM, Slevin J, Edwards SA, Hunter MG, Ashworth CJ 2006: Effect of alterations in the quantity and composition of the pre-mating diet on embryo survival and foetal growth in the pig. Anim Reprod Sci **96**: 89-103
Gad A, Murin M, Bartkova A, Kinterova V, Marcollova K, Laurincik J, Prochazka R 2022: Small-extracellular vesicles and their microRNA cargo from porcine follicular fluids: the potential association with oocyte quality. J Anim Sci Biotechnol **13**: 1-16
Griffin J, Emery BR, Huang I, Peterson CM, Carrell DT 2006: Comparative analysis of follicle morphology and oocyte diameter in four mammalian species (mouse, hamster, pig and human). J Exp Clin Assist Reprod **3**: 5-9
Grupen CG, McIlfatrick SM, Ashman RJ, Boquest AC, Armstrong DT, Nottle MB 2003: Relationship between donor animal age, follicular fluid steroid content and oocyte developmental competence in the pig. Reprod Fertil Dev **15**: 81-87
Gupta MK, Uhm SJ, Lee HT 2007: Sexual maturity and reproductive phase of oocyte donor influence the developmental ability and apoptosis of cloned and parthenogenetic porcine embryos. Anim Reprod Sci **108**: 107-121
Hale B, Hager CL, Seibert JT, Selsby JT, Baumgard LH, Keating AF, Ross JW 2017: Heat stress induces autophagy in pig ovaries during follicular development. Biol Reprod **97**: 426-437
Hansen PJ, Drost M, Rivera RM, Paula-Lopes FF, Mal-Katanani Y, Krininger CE, Chase CC Jr. 2001: Adverse impact of heat stress on embryo production: causes and strategies for mitigation. Theriogenology **55**: 91-103
Hälli O, Peltoniemi OAT, Tast A, Virolainen JV, Munsterhjelm C, Valros M, Heinonen A 2008: Photoperiod and luteinizing hormone secretion in domestic and wild pigs. Anim Reprod Sci **15**: 99-106
Hu JH, Dong JY, Zeng Z, Wu J, Tan XS, Tang T, Yan J, Jin ChZ 2020: Using exosomal miRNAs extracted from porcine follicular fluid to investigate their role in oocyte development. BMC Vet Res **16**: 1-13
Iida R, Koketsu Y 2013: Interactions between climatic and production factors on returns of female pigs to service during summer in Japanese commercial breeding herds. Theriogenology **80**: 487-493
Inoue Y, Munakata Y, Shinozawa A, Kawahara-Miki R, Shirasuna K, Iwata H 2020: Prediction of major microRNAs in follicular fluid regulating porcine oocyte development. J Assist Reprod Genet **37**: 2569-2579
Jochems R, Gaustad AH, Styrishave B, Zak LJ, Oskam IC, Grindflek E, Myromslien FD, Kommisrud E, Krogenæs AK 2022: Follicular fluid steroid hormones and *in vitro* embryo development in Duroc and Landrace pigs. Theriogenology **190**: 15-21
Jochems R, Gaustad AH, Zak LJ, Grindflek E, Zeremichael TT, Oskam IC, Myromslien FD, Kommisrud E, Krogenæs AK 2021: Ovarian characteristics and *in vitro* nuclear and cytoplasmic oocyte maturation in Duroc and Landrace pigs. Vet Med Sci **7**: 1845-1853
Knox RV, Zas SL 2001: Factors influencing estrus and ovulation in weaned sows as determined by transrectal ultrasound. J Anim Sci **79**: 2957-2963
Knox RV 2014: Impact of swine reproductive technologies on pig and global food production. Adv Exp Med Biol **752**: 131-160
Knox RV 2016: Artificial insemination in pigs today. Theriogenology **85**: 83-93
Knox RV 2019: Factors influencing follicle development in gilts and sows and management strategies used to regulate growth for control of estrus and ovulation. J Anim Sci **97**: 1433-1445
Kulus M, Kranc W, Sujka-Kordowska P, Mozdziak P, Jankowski M, Konwerska A, Kulus J, Bukowska D, Skowrońsk M, Piotrowska-Kempisty H, Nowicki M, Kempisty B, Antosik P 2020: The processes of cellular growth, aging, and programmed cell death are involved in lifespan of ovarian granulosa cells during short-term IVC – study based on animal model. Theriogenology **148**: 76-88
Kumar S, Devi B, Purkayastha A, Bharti PK, Doley S, Kadirve, G 2016: Porcine ovarian biometry, oocyte retrieval and quality of oocytes under different seasons in north east hill region. Ind J Anim Sci **86**: 300-330
Kwak SS, Yoon JCD, Cheong SA, Jeon YY, Lee ES, Hyun SH 2014: The new system of shorter porcine oocyte in vitro maturation (18 hours) using ≥8 mm follicles derived from cumulus-oocyte complexes. Theriogenology **81**: 291-301
Langendijk P 2022: Four feeding practices for supporting gestating and lactating sows. International Pig Topics **37**: 22-23
Liu RH, Li YH, Jiao LH, Wang XN, Wang H, Wang WH 2002: Extracellular and intracellular factors affecting nuclear and cytoplasmic maturation of porcine oocytes collected from different sizes of follicles. Zygote **10**: 253-260
Lopes TP, Padilla L, Bolarin A, Rodriguez-Martinez H, Jordi R 2020: ovarian follicle growth during lactation determines the reproductive performance of weaned sows. Animals (Basel) **10**: 1012
Lopes TP, Sanchez-Osorio J, Bolarin A, Martinez EA, Roca J 2014: Relevance of ovarian follicular development to the seasonal impairment of fertility in weaned sows. Vet J **199**: 382-386
Lucy MC, Liu J, Boyd CK, Bracken CJ 2001: Ovarian follicular growth in sows. Reprod Suppl **58**: 31-45

Marcha R, Vigneron C, Perreau C, Bali-Papp A, Mermillod P 2002: Effect of follicular size on meiotic and developmental competence of porcine oocytes. Theriogenology **57**: 1523-1532
Martinat-Botté F, Venturi E, Guillouet G, Driancourt MA, Terqui M 2010: Induction and synchronization of ovulations of nulliparous and multiparous sows with an injection of gonadotropin-releasing hormone agonist (Receptal). Theriogenology **73**: 332-342
Munakata Y, Ueda M, Kawahara-Miki R, Kansaku K, Itami N, Shirasuna K, Kuwayama T, Iwata H 2018: Follicular factors determining granulosa cell number and developmental competence of porcine oocytes. J Assist Reprod Genet **35**: 1809-1819
Peltoniemi OAT, Virolainen JV 2006: Seasonality of reproduction in gilts and sows. Soc Reprod Fertil Suppl **62**: 205-218
Quesnel H, Boulot S, Le Cozler Y 2005: Seasonal variation of reproductive performance of the sow. INRA Prod Anim **18**: 101-110
Rybska M, Knap S, Jankowski M, Jeseta M, Bukowska D, Antosik P, Nowicki M, Zabel M, Kempisty B, Jaśkowsk JM 2018: Characteristic of factors influencing the proper course of folliculogenesis in mammal. Med J Cell Biol **6**: 33-38
Seyfang J, Langendijk P, Chen TY, Bouwman E, Kirkwood RN 2016: Human chorionic gonadotrophin in early gestation induces growth of estrogenic ovarian follicles and improves primiparous sow fertility during summer. Anim Reprod Sci **172**: 21-25
Shibahara H, Ishiguro A, Inoue Y, Koumei S, Kuwayama T, Iwata H 2020: Mechanism of palmitic acid-induced deterioration of *in vitro* development of porcine oocytes and granulosa cells. Theriogenology **141**: 54-61
Swinbourne AM, Kelly JM, Kind KL, Kennaway DJ, van Wettere WHEJ 2014: The effects of season and moderate nutritional restriction on ovarian function and oocyte nuclear maturation in cycling gilts. Theriogenology **82**: 1303-1309
Tantasuparuk W, Lundeheim N, Dalin AM, Kunavongkrit A, Einarsson S 2000: Reproductive performance of purebred Landrace and Yorkshire sows in Thailand with special reference to seasonal influence and parity number. Theriogenology **54**: 481-496
Tast A, Peltoniemi OAT, Virolaine JV, Love RJ 2002: Early disruption of pregnancy as a manifestation of seasonal infertility in pigs. Anim Reprod Sci **4**: 75-86
Tsakmakidis IA, Tsantarliotou M, Michos IA, Basioura AG, Tsousis G, Boscos CM 2017: Selected steps of swine ICSI method to overcome seasonal effect and achieve acceptable early embryonic development, a preliminary study. Pol J Vet **20**: 607-609
Tummaruk P 2012: Effects of season, outdoor climate and photo period on age at first observed estrus in Landrace×Yorkshire crossbred gilts in Thailand. Livest Sci March **144**: 163-172
Yoshizawa M, Watanabe H, Fukui Y 2009: Effects of the presence and the numbers of corpora lutea in non-delivered and delivered pigs on *in vitro* oocyte maturation and embryonic development. J Reprod Dev **55**: 655-660
Zhao H, Xie S, Zhang N, Ao Z, Wu X, Yang L, Shi J, Mai R, Zheng E, Cai G, Wu Z, Li Z 2020: Source and follicular fluid treatment during the *in vitro* maturation of recipient oocytes affects the development of cloned pig embryo. Cell Reprogram **22**: 71-81