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The effect of maturation and aging on the quality of mammalian oocytes

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Abstract: The aim of this review was to summarise current knowledge regarding the effects of maturation, activation and aging on oocyte quality. Two main forms of aging were distinguished: (*i*) postovulatory aging, which occurs after ovulation due to a prolonged period before fertilisation and (*ii*) age-related aging, which is associated with a gradual decline in ovarian reserve and oocyte quality. Proper embryo development strongly depends on oocyte quality, which is most often assessed according to morphology. Numerous observations have demonstrated the influence of oocyte maturation, during which controlled cytoplasmic and nuclear modifications occur, and the influence of the timing of oocyte activation by the fertilising sperm. Post-ovulatory aging of an oocyte, which was not fertilised during the optimal period, manifests as impaired embryo development and results in fragmentation and embryonic mortality. Age-related oocyte aging leads to mitochondrial damage due to the long-term effects of reactive oxygen and nitrogen species (RONS), which play a key role in regulating physiological processes in the ovaries, including ovulation and oocyte maturation. Overall, it can be concluded that oocyte quality is the result of a complex interaction of meiotic, metabolic and redox mechanisms, which are significantly influenced by age, hormonal stimulation and the follicular microenvironment. Oocyte aging is associated with predominantly irreversible structural and functional changes leading to aneuploidy, mitochondrial dysfunction and failure of embryonic development.

Keywords: cattle; embryonic development; fertilisation; ovulation

INTRODUCTION

Proper embryo development strongly depends on oocyte quality, which is most often assessed based on morphology (Fluks et al. 2024). It has been noted that various morphological characteristics of oocytes, such as *zona pellucida* thickness (Bertrand et al. 1995), cytoplasmic granulation

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(Kahraman et al. 2000), perivitelline space size (Xia 1997) and oocyte shape (Ebner et al. 2008) correspond to the ability of embryos to develop and implant. Fluks et al. (2024) focused their study on the size of the spindle in oocytes and demonstrated that the shape and volume of the spindle in the oocyte are related to the quality of the resulting embryos, including the probability of blastocyst formation. The most important part of oocyte morphology assessment is determining oocyte maturity, with metaphase II (MII) oocytes being suitable for IVF (Ebner et al. 2003; Rienzi et al. 2011). However, there are more factors influencing oocyte quality in cattle, e.g. season of the year, heat stress, age of cows, metabolic stress etc. Milk production, fat/protein ratio and *post-partum* period also can be related to both quality and quantity of retrieved oocytes and to the number of flushed (transferable) embryos (Stadnik et al. 2017, 2022, 2024; Bezdicek et al. 2021; Toralova et al. 2025). The overall management of dairy cattle farming is also a significant factor (Saro et al. 2024, 2026).

The general goal is to ensure fertilisation in the optimal period after ovulation, known as the fertilisation window. After this period, the oocyte undergoes degradation processes, known as postovulatory aging. In the case of age-related aging, the quality of oocytes deteriorates already at ovulation. However, impaired fertility during this period is a multifactorial process, influenced by several external and internal factors. The aim of this review was to summarise current knowledge on the influence of maturation, activation and aging on oocyte quality, distinguishing between two main forms of aging: post-ovulatory aging, which occurs after ovulation as a result of prolonged time before fertilisation and age-related aging, which is associated with a gradual deterioration of ovarian reserve and oocyte quality. The overall consequences of postovulatory and age-related oocyte aging on the oocyte quality are presented in Table 1.

OOCYTE MATURATION AND ACTIVATION

Oocyte maturation refers to the transition from the germinal vesicle (GV) stage to the metaphase II (MII) stage, which occurs shortly before ovulation (Schultz and Kopf 1995). This is a process involving precisely controlled cytoplasmic and nuclear modifications aimed at achieving full fertilisation and developmental competence of the oocyte (Fissore et al. 2002). Oocyte activation is ensured by the fertilising sperm, which initiates long-lasting repeated oscillations of the free intracellular calcium (Ca^{2+}) concentration, leading to the release of cortical granules and, thus, to the blockade of polyspermy, the completion of meiosis, the formation of male and female pronuclei and the subsequent initiation of the first mitotic division (Schultz and Kopf 1995).

Ca^{2+} oscillations are induced only in oocytes that have almost completed maturation (Jones et al. 1995). In their study on hamster oocytes, Fujiwara et al. (1993) observed a gradual increase in Ca^{2+} during the first 5 h of maturation. The second and more pronounced increase occurs 10–12 h after the start of maturation, between prometaphase II and metaphase II. At the same time, in both mouse and hamster oocytes, the endoplasmic reticulum (ER), which is a Ca^{2+} reservoir, undergoes rearrangement during maturation. The ER disperses throughout the oocyte cortex (Shiraishi et al. 1995), which may alter the properties of Ca^{2+} channels or the Ca^{2+} reservoir itself. Aging oocytes show abnormal Ca^{2+} oscillations with higher frequency and lower amplitude, which are associated with the onset of apoptosis after fertilisation (Lord and Aitken 2013).

Oocyte maturation is precisely coordinated in time, so that sperm entry and activation are maximised within a few hours after ovulation. In mammalian oocytes, the fertilisation window is limited to less than ten hours after ovulation. Oocytes that have spent a longer period in the oviduct without fertilisation, show gradual inactivation of calcium release mechanisms, leading to low developmental success of the zygote after delayed fertilisation (Fujiwara et al. 1993).

Calcium oscillations (and other ions, e.g. K^+) during oocyte maturation and fertilisation, have been found in several animal species. In cattle, Tosti et al. (2002) demonstrated that fertilisation is associated with hyperpolarisation of the membrane potential, mediated by Ca^{2+} and K^+ ions. These processes are dependent primarily on the internal release of Ca^{2+}. The authors also demonstrated that sensitivity on various activators (sperm, chemicals etc.) is increased in bovine oocyte during maturation. In addition, Meng et al. (2021) demonstrated that Ca^{2+} is one of the factors involved in nuclear reprogramming in bovine oocyte.

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Table 1. Consequences of postovulatory and age-related oocyte aging on the oocyte quality

The type of aging	Consequences of aging
Postovulatory aging	structural disorders of cell organelles
	abnormal Ca^{2+}oscillations
	inactivation of calcium release mechanisms
	increased lipid peroxidation causing reduced oolemma permeability
	changes in the protein mRNA composition
	changes in the methylation of imprinted genes
	errors in chromosome segregation
	lower DNA repair capacity
	impaired development of embryos
	damages to mitochondria caused by a long-term exposure to reactive oxygen (ROS) and nitrogen (NOS) species
	disturbed balance between ROS, NOS and antioxidants
Age-related aging	chromosome segregation disorders during meiosis
	smaller volume and width of the spindle
	damages to mitochondria caused by ROS and NOS
	decline in mRNA
	disturbed balance between ROS, NOS and antioxidants
	reduced oxygen supply to the ovaries due to insufficient vascularisation
	obesity
	higher level cholesterol
	abnormal glucose tolerance
	lower level of anti-Müllerian hormone (AMH)

POSTOVULATORY AGING OF THE OOCYTE

Any oocyte abnormalities can activate a developmental checkpoint leading to apoptosis and termination of development. The changes that occur during oocyte maturation are transient and, in the absence of fertilisation, undergo rapid degradation, leading to the activation of an alternative developmental program characterized by fragmentation and abnormal development (Fissore et al. 2002). A similar development occurs in oocytes fertilised after the optimal period, when they already show signs of post-ovulatory aging manifested by impaired development and ending in fragmentation and embryonic mortality (Fissore et al. 2002). This can be attributed to biochemical and functional changes occurring in the post-ovulatory oocyte, e.g. increased lipid peroxidation causing reduced oolemma permeability, thereby reducing the likelihood of fertilisation. In mouse oocytes, delayed fertilisation by 12 h was associated with slowed embryonic development (Fissore et al. 2002) with premature exocytosis of cortical granules and hardening of the *zona pellucida* (Lord and Aitken 2013). Changes in the *zona pellucida* have been demonstrated in the post-ovulatory period and during age-related aging. From this point of view, Ishikawa-Yamauchi et al. (2024) reported that the *zona pellucida* of older mice undergoes age-related structural changes, subsequently associated with impaired fertility. The authors demonstrate a different structure and composition of *zona pellucida* proteins in oocytes of older females, as well as reduced communication between oocytes and cumulus cells due to a decrease in transzonal projections, forming a communication link between the oocyte and granulosa cells (Ishikawa-Yamauchi 2024).

Changes in the methylation of imprinted genes have also been demonstrated in post-ovulatory oocytes and in the developing placenta (Liang et al. 2011).

Post-ovulatory aging of oocytes is further manifested by structural disorders of cell organisation, with visible abnormal areas of microfilaments above the meiotic spindle, its disruption, abnormal localisation and chromatin disorganisation (Fissore et al. 2002).

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The aim of *in vitro* fertilisation processes in cattle is to reverse postovulatory aging, because prolonged time (over 20–22 h) is associated with decreased oocyte quality and viability, mainly due to higher amount of reactive oxygen species (Yin et al. 2023). That is why the effort has been made to delay oocyte aging through the supplementation of some antioxidants. Yin et al. (2023) attempted to decline oocyte aging using ferulic acid. The addition of this antioxidant (5 μM) to aged bovine oocyte improved antioxidant capacity, mitochondrial activity and ATP levels. The authors concluded that ferulic acid has a positive effect in preventing *in vitro* aging of bovine oocytes.

THE EFFECT OF OOCYTE AGING ON DNA

Sharma et al. (2024) demonstrated a lower DNA repair capacity in aging oocytes, leading to the damage to chromosome integrity and division. At the same time, they observed premature loss of cohesion, which may be one of the causes of errors in chromosome segregation in older oocytes. Aging oocytes of some mouse strains produce more aneuploid oocytes characterized by depleted cohesin and shugoshi protein in centromeres (Eichenlaub-Ritter 2012). A particularly high loss of sister centromere cohesion was observed in older oocytes from stimulated cycles. There is evidence from mouse models of a negative effect of hormonal stimulation on cohesion between sister chromatids (Merriman et al. 2012). It is very important to determine whether the loss of cohesion in human oocytes is influenced by age, the microenvironment in spontaneous or stimulated cycles or the influence of reproductive life (Eichenlaub-Ritter 2012).

In general, mammalian oocytes are among the longest-surviving cells in the body. Meiosis begins in the foetal period, when primary oocytes enter prophase I of meiosis and remain in this stage for a long period of time until maturation is complete. Especially in cattle, primordial, primary and secondary follicles were first observed in *in vivo* experiments around 90, 140, and 210 days of gestation (Yang and Fortune 2008). From this view point it is questionable which factors determine the size of the follicular reserve. Fortune et al. (2013) reported that maternal nutrition status and health in cattle can play a significant role. The authors present that nutrition during early pregnancy of cows is very important, because gonadal differentiation occurs during this period. Authors summarize that deterioration of nutrition or health during early bovine gestation negatively can affect the future size of follicular reserve in heifers. Thus, higher somatic cell count in milk during gestation relates to udder infection and lower concentration of AMH (anti-Mullerian hormone) in the blood of female calves. At the same time, lower concentrations of AMH have been correlated with lower count of antral follicle. Similarly, endocrine-disrupting chemicals (e.g. phytoestrogens, environmental oestrogens etc.) can affect formation of foetal ovaries follicle and overall bovine size of follicular reserve (Fortune et al. 2013).

Most primordial follicles undergo atresia, while only a small proportion are recruited into the growth phase and reach the MII stage. The supply of follicles in the ovaries is limited, and its gradual depletion leads to the cessation of ovulation and menopause (Eichenlaub-Ritter 2012). Long-term meiotic arrest is a significant risk factor for meiotic errors. Aneuploidy is very common in human oocytes, most often resulting from chromosome segregation disorders during meiosis, particularly premature chromatid separation (Holubcova et al. 2015), and is the main cause of preimplantation and post-implantation arrest of embryo development, implantation failure and spontaneous miscarriages (Nagaoka et al. 2012). According to Holubcova et al. (2015), human oocytes assemble the meiotic spindle independently of centrosomes or other microtubule organising centres. In her experiment, spindle assembly took up to 16 hours and was marked by internal spindle instability with abnormal kinetochore attachments to microtubules. This can lead to incorrect chromosome segregation and embryonic aneuploidy (Holubcova et al. 2015; Vazquez-Diez et al. 2019). The importance of spindle compactness has also been suggested previously in studies of human oocytes using polarized light microscopy (Fluks et al. 2024). A difference in the volume and width of the spindle was observed between younger and older oocytes, which corresponds to the reduced developmental potential of oocytes in older mothers (Cimadomo et al. 2018). Several components were used for optimizing spindle morphology during oocyte aging. Zhang et al. (2025) studied regulatory effects of palmitoyl oleoyl phosphatidyl choline (POPC) in bovine oocytes. POPC is a natural component of many tissues, such as brain, kidney,

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liver etc., where it stabilizes membrane structure, which is also important during *in vitro* manipulations. Supplementation of POPC improved spindle integrity and function in bovine oocytes, furthermore, reduced the content of reactive oxygen species and upregulated some antioxidant genes (Zhang et al. 2025).

As reported by Fishman et al. (2018), the centrosome derived from the sperm recruits maternal proteins to acquire its function in the fertilised egg. Therefore, age-related decline in maternal mRNAs important for centrosome function may explain the reduced developmental capacity of eggs from women of advanced reproductive age. Recent evidence confirms that the egg transcriptome changes with reproductive aging (Porokh et al. 2024). While aneuploidy in human sperm reaches only 1–2%, approximately 20% of all oocytes are aneuploid with aneuploidy found in more than 50% of cases in oocytes from older women (Fragouli et al. 2011). Fragouli and Wells (2011) even report up to 75% aneuploid blastocysts obtained from women over 40 years of age. Another topic discussed is the mtDNA content in relation to oocyte aging and its fertilisation capacity. In this context, Ferreira et al. (2023) summarize that in older cows (also in other animal species) a lower mtDNA content has been found, indicating lower mitochondrial biogenesis and fertilisation capacity of older oocytes. In general, mature oocyte contains high levels of mtDNA, suggesting that mitochondrial biogenesis is tightly controlled during oocyte maturation (Ferreira et al. 2023). It has also been shown that ovarian aging is associated with a higher incidence of mtDNA deletions as well as lower mtDNA copy numbers (Chan et al. 2005). Mitochondrial DNA is also an important topic from the point of oxidative stress, because mtDNA is located near to electron transport chain, does not have a histone protection system and lacks effective repair system. Therefore, a disruption of the oxidative/antioxidant balance is very critical for the deterioration of the quality of mitochondria, as well as its DNA (Zhang et al. 2017).

THE EFFECT OF OXIDATIVE STRESS ON OOCYTE QUALITY

Another theory of oocyte aging is based on the action of free radicals and assumes damage to mitochondria as a result of long-term exposure to reactive oxygen species (Eichenlaub-Ritter 2012), leading to the accumulation of mitochondrial DNA mutations (Tatone et al. 2011). The maturation of mouse oocytes in vitro is accompanied by specific changes in mitochondria and bursts in ATP production (Yu et al. 2010), while a reduced supply of high-energy substrates, particularly ATP, negatively affects the formation and regulation of the meiotic spindle, intracellular signalling and Ca^{2+} homeostasis (Eichenlaub-Ritter et al. 2011).

Reactive oxygen and nitrogen species (RONS) play a key role in the regulation of physiological processes in the ovaries, including ovulation, oocyte maturation, luteal function and angiogenesis. The process of follicle growth itself causes an increase in reactive oxygen species, with the accumulation of advanced glycation end products responsible for age-related mitochondrial damage and an increase in DNA breaks (Su et al. 2009). A number of studies have shown that hydrogen peroxide and superoxide anion accumulate in oocytes with increasing time after ovulation (Tatone et al. 2011; Lord and Aitken 2013). Detoxification enzymes appear to be less expressed in the cumulus of older mice compared to young mice (Tatone et al. 2011). The cumulus, in turn, supplies the oocytes with metabolites such as amino acids, lactate and pyruvate, which are essential for maintaining mitochondrial activity, ATP production and ionic and redox homeostasis in the oocyte (Su et al. 2009). In contrast, the course of meiosis II is supported by antioxidants, demonstrating that there is a complex relationship between ROS and antioxidants in the ovary that is influenced by hormonal action (Bezdicek et al. 2025). A slight increase in ROS levels is necessary for the activation of the physiological process of ovulation, where oxygen deficiency stimulates follicular blood supply but also promotes apoptosis. Antioxidants, such as glutathione, together with FSH, balance this process in the growing follicle. At the same time, increasing amounts of oestrogen trigger the production of catalase, which also prevents apoptosis. After an increase in LH, the level of inflammatory precursors increases, generating ROS. On the other hand, premature depletion of these precursors disrupts ovulation (Sies and Jones 2020). The oocyte protects itself against oxidative stress using the antioxidant glutathione, but this is reduced in the post-ovulatory oocyte (Lord and Aitken 2013). Excessive ROS production or impaired antioxidant protection leads to oxidative stress, damage

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to cellular components and pathological changes in the ovary. An imbalance between ROS production and the effectiveness of the antioxidant system contributes to faster aging, reduced oocyte quality and overall negative effects on female reproduction. These general conclusions have been demonstrated in a number of animal species. In particular, Takeo et al. (2013) found higher level of ROS in *in vitro* matured bovine oocytes from aged cows compared to the oocytes derived from younger counterparts. Oocytes isolated from aged cows also displayed higher mitochondrial dysfunction. Authors also found association between oocytes derived from aged cows and lower total number of blastocyst cells and higher count of abnormal fertilisation (Takeo et al. 2013).

Age is also associated with the depletion of primordial follicles, which alter the microenvironment of follicles and oocytes and hormonal homeostasis. The aging of blood vessels in the ovaries leads to insufficient vascularisation, resulting in a reduced supply of nutrients and oxygen, which disrupts proper follicle development (Liu et al. 2025). For example, older mice have increased body weight, and some strains of laboratory mice have higher serum cholesterol levels, abnormal glucose tolerance and lower AMH hormone levels compared to younger and leaner control groups (Hirshfeld-Cytron et al. 2011).

THE EFFECT OF VITRIFICATION ON OOCYTE QUALITY

Cryopreservation of oocytes can also be a significant cause of oxidative stress in the context of assisted reproduction. It induces oxidative stress through osmotic damage, increased oxidative metabolism in mitochondria, decreased ATP levels and activation of the intrinsic apoptotic pathway (Len et al. 2019). Vitrification can lead to lipid peroxidation, DNA damage, disorganisation of the meiotic spindle, loss of microtubules and epigenetic alterations in developing embryos (Chen et al. 2016). After thawing, damaged mitochondria are eliminated and synthesized de novo, which can partially restore mitochondrial function (Iwata 2021). Antioxidants such as melatonin, resveratrol, N-acetylcysteine, coenzyme Q10, glutathione and ascorbic acid have been shown to alleviate the oxidative stress associated with vitrification and improve oocyte quality in various mammalian species (Olexikova et al. 2023; Bezdicek et al. 2024). In particular, Olexikova et al. (2023) demonstrated, that 5 mmol l^{-1} glutathione added to the oocyte recovery culture, reversed the harmful effect of vitrification on cattle oocytes. In this study, protective role of glutathione was confirmed, which reflected in lower ratio of apoptotic cells in blastocyst and higher quality of actin cytoskeleton. The protective effect of glutathione during vitrification is actual topic and this antioxidant has been successfully used also in ram sperm during cooling storage (Makarevich et al. 2022).

In general, several ways to increase the cryotolerance of oocytes have been investigated. However, the addition of various antioxidants, hormones or growth factors, which ensure less damage to oocytes and a higher number of subsequent blastocysts, still remains in the forefront of interest. To mitigate toxicity, the combination of several cryoprotectants in vitrification medium also appears to be a more advantageous strategy than higher concentrations of a single cryoprotectant (Dujickova et al. 2021).

THE INFLUENCE OF OOCYTE QUALITY ON THE SUBSEQUENT EMBRYO QUALITY

Closely linked to age is a decline in embryo quality, which is influenced by a number of factors. These include the aging of the cytoplasm, which is no longer able to support embryo development and changes in the composition of oocyte mRNA proteins, especially during prolonged ovulation. Numerous studies have shown a slowdown in aging after the injection of mitochondria from younger mitochondria into older oocytes. After 24 h of cultivation, a decrease in apoptosis levels was observed compared to control oocytes (Perez et al. 2000).

Furthermore, there are chromosomal abnormalities occurring in embryos. In some species, such as cattle, a disorder of the *zona pellucida* associated with polyspermy has been demonstrated (Chian et al. 1992). The effect of post-ovulatory oocyte aging on offspring has also been demonstrated, as well as a significant decrease in live births and an increased incidence of abnormalities in offspring, such as growth retardation, delayed development and reduced longevity (Tarin et al. 2002).

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Fertilisation failure, where the sperm has entered the egg but no zygote has been formed, can be caused not only by abnormalities in egg maturation, but also by paternal factors, such as a defect in the PLCζ protein (phospholipase C zeta), which is found in the acrosome of sperm and whose role is to trigger Ca^{2+} oscillations, or a defect in the sperm centrosome. It has also been shown that microinjection of PLCζ RNA into the oocyte can cause intense Ca^{2+} oscillations in oocytes of cows, pigs, mice and humans (Swann 2018). PLCζ has been found in sperm in several animal species. Various isoforms of PLCζ are known (currently 13), which share a similar structure and function in different tissues, where they act as a key regulatory mechanism. It appears that absence or significantly reduced expression of PLCζ is associated with the inability to induce Ca^{2+} release and oocyte activation. On the other hand, the higher levels of PLCζ are associated with greater fertilisation success (Abdulsamad et al. 2023). However, the question of relation between the intensity of the PLCζ signal and the ability to activate development in aged oocytes is still open.

CONCLUSION

Overall, oocyte quality is the result of a complex interaction of meiotic, metabolic and redox mechanisms, which are fundamentally influenced by age, hormonal stimulation and the microenvironment of the follicle. Oxidative stress plays a major role in affecting the oocyte itself, reducing mitochondrial function and, thus, the onset of apoptosis in aging oocytes after ovulation. Damage to mitochondrial DNA could also be the reason for mitochondrial disorders in offspring derived from aging oocytes.

Oocyte aging is associated with largely irreversible structural and functional changes leading to aneuploidy, mitochondrial dysfunction and embryonic development failure.

Currently, the possibilities for therapeutic intervention in the quality of aging oocytes remain limited, with early cryopreservation of oocytes in social freezing programs being one of the few effective strategies for preserving female reproductive potential. One of the biggest problems with oocyte vitrification is the age of the mother at the time of vitrification, as age has a strong negative impact on the outcome of treatment after oocyte thawing.

Conflict of interest

The authors declare no conflict of interest.

REFERENCES

Abdulsamad HMR, Murtaza ZF, AlMuhairi HM, Bafleh WS, AlMansoori SA, AlQubaisi SA, Hamdan H, Kashir J. The therapeutic and diagnostic potential of phospholipase C zeta, oocyte activation, and calcium in treating human infertility. Pharmaceuticals (Basel). 2023 Mar 15;16(3):441.

Bertrand E, Van den Bergh M, Englert Y. Does zona pellucida thickness influence the fertilization rate? Hum Reprod. 1995 May;10(5):1189-93.

Bezdicek J, Nesvadbova A, Duchacek J, Sekaninova J, Stadnik L, Janku M. Changes in the oxidative biochemical status in dairy cows during the transition period affecting reproductive and health parameters. Czech J Anim Sci. 2024 Sep 27;69(9):345-55.

Bezdicek J, Nesvadbova A, Makarevich A, Kubovicova E. Negative impact of heat stress on reproduction in cows: Animal husbandry and biotechnological viewpoints: A review. Czech J Anim Sci. 2021 May 28;66(8):293-301.

Bezdicek J, Sekaninova J, Janku M, Makarevic A, Luhova L, Dujickova L, Petrivalsky M. Reactive oxygen and nitrogen species: Multifaceted regulators of ovarian activity. Biol Reprod. 2025 May 13;112(5):789-806.

Chan CC, Liu VW, Lau EY, Yeung WS, Ng EH, Ho PC. Mitochondrial DNA content and 4977 bp deletion in unfertilized oocytes. Mol Hum Reprod. 2005 Dec;11(12):843-6.

Chen H, Zhang L, Deng T, Zou P, Wang Y, Quan F, Zhang Y. Effects of oocyte vitrification on epigenetic status in early bovine embryos. Theriogenology. 2016 Aug;86(3):868-78.

Chian RC, Nakahara H, Niwa K, Funahashi H. Fertilization and early cleavage in vitro of ageing bovine oocytes after maturation in culture. Theriogenology. 1992 Mar;37(3): 665-72.

Cimadomo D, Fabozzi G, Vaiarelli A, Ubaldi N, Ubaldi FM, Rienzi L. Impact of maternal age on oocyte and embryo competence. Front Endocrinol (Lausanne). 2018 Jun;9:327.

Dujickova L, Makarevich AV, Olexikova L, Kubovicova E, Strejcek F. Methodological approaches for vitrification of bovine oocytes. Zygote. 2021 Feb;29(1):1-11.

Ebner T, Moser M, Sommergruber M, Tews G. Selection based on morphological assessment of oocytes and embryos at different stages of preimplantation development: A review. Hum Reprod Update. 2003 May-Jun;9(3):251-62.

Ebner T, Shebl O, Moser M, Sommergruber M, Tews G. Developmental fate of ovoid oocytes. Hum Reprod. 2008 Jan;23(1):62-6.

https://doi.org/10.17221/77/2026-CJAS

Eichenlaub-Ritter U, Wieczorek M, Luke S, Seidel T. Age related changes in mitochondrial function and new approaches to study redox regulation in mammalian oocytes in response to age or maturation conditions. Mitochondrion. 2011 Sep;11(5):783-96.

Eichenlaub-Ritter U. Oocyte ageing and its cellular basis. Int J Dev Biol. 2012;56(10-12):841-52.

Ferreira AF, Soares M, Almeida-Santos T, Ramalho-Santos J, Sousa AP. Aging and oocyte competence: A molecular cell perspective. WIREs Mech Dis. 2023 Sep-Oct;15(5):e1613.

Fishman EL, Jo K, Nguyen QPH, Kong D, Royfman R, Cekic AR, Khanal S, Miller AL, Simerly C, Schatten G, Loncarek J, Mennella V, Avidor-Reiss T. A novel atypical sperm centriole is functional during human fertilization. Nat Commun. 2018 Jun 7;9(1):2210. Erratum in: Nat Commun. 2018 Jul 13;9(1):2800.

Fissore RA, Kurokawa M, Knott J, Zhang M, Smyth J. Mechanisms underlying oocyte activation and postovulatory ageing. Reproduction. 2002 Dec;124(6):745-54.

Fluks M, Milewski R, Tamborski S, Szkulmowski M, Ajduk A. Spindle shape and volume differ in high- and low-quality metaphase II oocytes. Reproduction. 2024 Mar 19;167(4):e230281.

Fortune JE, Yang MY, Allen JJ, Herrick SL. Triennial Reproduction Symposium: The ovarian follicular reserve in cattle: What regulates its formation and size? J Anim Sci. 2013 Jul;91(7):3041-50.

Fragouli E, Alfarawati S, Goodall NN, Sanchez-Garcia JF, Colls P, Wells D. The cytogenetics of polar bodies: Insights into female meiosis and the diagnosis of aneuploidy. Mol Hum Reprod. 2011 May;17(5):286-95.

Fragouli E, Wells D. Aneuploidy in the human blastocyst. Cytogenet Genome Res. 2011;133(2-4):149-59.

Fujiwara T, Nakada K, Shirakawa H, Miyazaki S. Development of inositol trisphosphate-induced calcium release mechanism during maturation of hamster oocytes. Dev Biol. 1993 Mar;156(1):69-79.

Hirshfeld-Cytron JE, Duncan FE, Xu M, Jozefik JK, Shea LD, Woodruff TK. Animal age, weight and estrus cycle stage impact the quality of in vitro grown follicles. Hum Reprod. 2011 Sep;26(9):2473-85.

Holubcova Z, Blayney M, Elder K, Schuh M. Human oocytes. Error-prone chromosome-mediated spindle assembly favors chromosome segregation defects in human oocytes. Science. 2015 Jun 5;348(6239):1143-7.

Ishikawa-Yamauchi Y, Emori C, Mori H, Endo T, Kobayashi K, Watanabe Y, Sagara H, Nagata T, Motooka D, Ninomiya A, Ozawa M, Ikawa M. Age-associated aberrations of the cumulus-oocyte interaction and in the zona pellucida structure reduce fertility in female mice. Commun Biol. 2024 Dec 24;7(1):1692.

Iwata H. Resveratrol enhanced mitochondrial recovery from cryopreservation-induced damages in oocytes and embryos. Reprod Med Biol. 2021 Jun 27;20(4):419-26.

Jones KT, Carroll J, Whittingham DG. Ionomycin, thapsigargin, ryanodine, and sperm induced Ca2+ release increase during meiotic maturation of mouse oocytes. J Biol Chem. 1995 Mar 24;270(12):6671-7.

Kahraman S, Yakin K, Donmez E, Samli H, Bahce M, Cengiz G, Sertyel S, Samli M, Imirzalioglu N. Relationship between granular cytoplasm of oocytes and pregnancy outcome following intracytoplasmic sperm injection. Hum Reprod. 2000 Nov;15(11):2390-3.

Len JS, Koh WSD, Tan SX. The roles of reactive oxygen species and antioxidants in cryopreservation. Biosci Rep. 2019 Aug 29;39(8):BSR20191601.

Liang XW, Ge ZJ, Wei L, Guo L, Han ZM, Schatten H, Sun QY. The effects of postovulatory aging of mouse oocytes on methylation and expression of imprinted genes at midterm gestation. Mol Hum Reprod. 2011 Sep;17(9):562-7.

Liu X, Zhao Y, Feng Y, Wang S, Zhang J. Ovarian aging: Mechanisms, age-related disorders, and therapeutic interventions. MedComm (2020). 2025 Nov 16;6(12):e70481.

Lord T, Aitken RJ. Oxidative stress and ageing of the postovulatory oocyte. Reproduction. 2013 Oct;146(6):R217-27.

Makarevich A, Spalekova E, Kubovicova E, Bezdicek J, Chrenek P. Cooling storage of ram sperm in presence of antioxidant glutathione. Czech J Anim Sci. 2022 Sep 30; 67(9):356-64.

Meng L, Hu H, Liu Z, Zhang L, Zhuan Q, Li X, Fu X, Zhu S, Hou Y. The role of Ca2+ in maturation and reprogramming of bovine oocytes: A system study of low-calcium model. Front Cell Dev Biol. 2021 Oct 26;9:746237.

Merriman JA, Jennings PC, McLaughlin EA, Jones KT. Effect of aging on superovulation efficiency, aneuploidy rates, and sister chromatid cohesion in mice aged up to 15 months. Biol Reprod. 2012 Feb 29;86(2):49.

Nagaoka SI, Hassold TJ, Hunt PA. Human aneuploidy: Mechanisms and new insights into an age-old problem. Nat Rev Genet. 2012 Jun 18;13(7):493-504.

Olexikova L, Dujickova L, Makarevich AV, Bezdicek J, Sekaninova J, Nesvadbova A, Chrenek P. Glutathione during post-thaw recovery culture can mitigate deleterious impact of vitrification on bovine oocytes. Antioxidants (Basel). 2023;12(1):35.

Perez GI, Trbovich AM, Gosden RG, Tilly JL. Mitochondria and the death of oocytes. Nature. 2000 Feb 3;403(6769): 500-1.

Porokh V, Kyjovska D, Martonova M, Klenkova T, Otevrel P, Kloudova S, Holubcova Z. Zygotic spindle orientation defines cleavage pattern and nuclear status of human embryos. Nat Commun. 2024 Jul 29;15(1):6369.

https://doi.org/10.17221/77/2026-CJAS

Rienzi L, Vajta G, Ubaldi F. Predictive value of oocyte morphology in human IVF: A systematic review of the literature. Hum Reprod Update. 2011 Jan-Feb;17(1):34-45.

Saro J, Duchacek J, Stadnik L, Brozova H. Decision support systems in dairy cows farming: A 20-year scoping review of characteristics, applications, and future challenges. Czech J Anim Sci. 2026 May 5;71(5):191-207.

Saro J, Stadnik L, Blahova P, Huguet S, Brozova H, Duchacek J. A decision support system based on disease scoring enables dairy farmers to proactively improve herd health. Czech J Anim Sci. 2024 May 22;69(5):165-77.

Schultz RM, Kopf GS. Molecular basis of mammalian egg activation. Curr Top Dev Biol. 1995;30:21-62.

Sharma N, Coticchio G, Borini A, Tachibana K, Nasmyth KA, Schuh M. Changes in DNA repair compartments and cohesin loss promote DNA damage accumulation in aged oocytes. Curr Biol. 2024 Nov 18;34(22):5131-48.e6.

Shiraishi K, Okada A, Shirakawa H, Nakanishi S, Mikoshiba K, Miyazaki S. Developmental changes in the distribution of the endoplasmic reticulum and inositol 1,4,5-trisphosphate receptors and the spatial pattern of $Ca2^{+}$ release during maturation of hamster oocytes. Dev Biol. 1995 Aug;170(2):594-606.

Sies H, Jones DP. Reactive oxygen species (ROS) as pleiotropic physiological signalling agents. Nat Rev Mol Cell Biol. 2020 Jul;21(7):363-83.

Stadnik L, Bezdicek J, Makarevich A, Kubovicova E, Louda F, Fellnerova I, Hegedusova Z, Holasek R. Ovarian activity and embryo yield in relation to the postpartum period in superovulated dairy cows. Acta Vet Brno. 2017 Feb 17; 86(1):51-7.

Stadnik L, Duchacek J, Pytlik J, Gasparik M, Codl R, Vrhel M. Cow metabolic status assessed from fat/protein ratio in milk affected ovarian response and number of transferable embryos after superovulation. Czech J Anim Sci. 2022 Jan 13;67(2):39-46.

Stadnik L, Kinterova V, Sichtar J, Duchacek J, Gasparik M, Nemcova L, Prochazka R, Codl R. Comparison of selected data acquisition models using on-farm production records on qualitative parameters of oocytes in dairy cows. Czech J Anim Sci. 2024 Jan 16;69(1):1-10.

Su YQ, Sugiura K, Eppig JJ. Mouse oocyte control of granulosa cell development and function: Paracrine regulation of cumulus cell metabolism. Semin Reprod Med. 2009 Jan;27(1):32-42.

Swann K. The role of Ca2+ in oocyte activation during in vitro fertilization: Insights into potential therapies for rescuing failed fertilization. Biochim Biophys Acta Mol Cell Res. 2018 Nov;1865(11 Pt B):1830-7.

Takeo S, Kawahara-Miki R, Goto H, Cao F, Kimura K, Monji Y, Kuwayama T, Iwata H. Age-associated changes in gene expression and developmental competence of bovine oocytes, and a possible countermeasure against age-associated events. Mol Reprod Dev. 2013 Jul;80(7):508-21.

Tarin JJ, Perez-Albala S, Perez-Hoyos S, Cano A. Postovulatory aging of oocytes decreases reproductive fitness and longevity of offspring. Biol Reprod. 2002 Feb;66(2):495-9.

Tatone C, Heizenrieder T, Di Emidio G, Treffon P, Amicarelli F, Seidel T, Eichenlaub-Ritter U. Evidence that carbonyl stress by methylglyoxal exposure induces DNA damage and spindle aberrations, affects mitochondrial integrity in mammalian oocytes and contributes to oocyte ageing. Hum Reprod. 2011 Jul;26(7):1843-59.

Toralova T, Duchacek J, Gasparik M, Kinterova V, Maresova N, Codl R, Stadnik L. The serum levels of triacylglycerols, nonesterified fatty acids, and beta-hydroxybutyrate as markers of reproductive capability of primiparous dairy cows. J Anim Sci. 2025 Jan 4;103:skaf276.

Tosti E, Boni R, Cuomo A. Fertilization and activation currents in bovine oocytes. Reproduction. 2002 Dec;124(6): 835-46.

Vazquez-Diez C, Paim LMG, FitzHarris G. Cell-size-independent spindle checkpoint failure underlies chromosome segregation error in mouse embryos. Curr Biol. 2019 Mar 4;29(5):865-73.e3.

Xia P. Intracytoplasmic sperm injection: Correlation of oocyte grade based on polar body, perivitelline space and cytoplasmic inclusions with fertilization rate and embryo quality. Hum Reprod. 1997 Aug;12(8):1750-5.

Yang MY, Fortune JE. The capacity of primordial follicles in fetal bovine ovaries to initiate growth in vitro develops during mid-gestation and is associated with meiotic arrest of oocytes. Biol Reprod. 2008 Jun;78(6):1153-61.

Yin YJ, Zhang YH, Wang Y, Jiang H, Zhang JB, Liang S, Yuan B. Ferulic acid ameliorates the quality of in vitro-aged bovine oocytes by suppressing oxidative stress and apoptosis. Aging (Albany NY). 2023 Nov 8;15(21):12497-512.

Yu Y, Dumollard R, Rossbach A, Lai FA, Swann K. Redistribution of mitochondria leads to bursts of ATP production during spontaneous mouse oocyte maturation. J Cell Physiol. 2010 Sep;224(3):672-80.

Zhang D, Keilty D, Zhang ZF, Chian RC. Mitochondria in oocyte aging: Current understanding. Facts Views Vis Obgyn. 2017 Mar 30;9(1):29-38.

Zhang X, Wang D, Cheng X, Zhang Y, Jian R, Zhang J, Cao G. POPC enhances both the maturation of bovine oocytes and the subsequent development and quality of embryos. Animals (Basel). 2025 Oct 31;15(21):3172.

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