



International Journal of Veterinary Sciences and Animal Husbandry



ISSN: 2456-2912

NAAS Rating (2026): 4.61

VET 2026; 11(6): 36-41

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www.veterinarypaper.com

Received: 22-03-2026

Accepted: 26-04-2026

Publication: 02-06-2026

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Dietary flaxseed supplementation modulates ovarian histoarchitecture and CTSS gene expression in adult female rabbits

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DOI: <https://www.doi.org/10.22271/veterinary.2026.v11.i6a.3309>

Abstract

Ovarian function is regulated by coordinated structural and molecular events that control follicular growth, steroidogenesis, and tissue remodeling. Nutritional bioactive compounds have recently gained attention as natural modulators of reproductive physiology, yet their influence on ovarian histology and local regulatory gene expression remains poorly understood in rabbits. The present study investigated the effects of dietary flaxseed supplementation on ovarian histomorphology and ovarian Cathepsin S (CTSS) gene expression in adult female rabbits. Thirty clinically healthy adult female New Zealand White rabbits were randomly assigned into two equal groups ($n = 15/\text{group}$). The control group received a standard basal diet, whereas the treatment group received the same ration supplemented with 5% ground flaxseed for 30 days. At the end of the feeding period, ovarian tissues were collected for histological examination and quantitative real-time PCR analysis, using β -actin (ACTB) as the housekeeping gene. Histological evaluation revealed marked ovarian structural enhancement in flaxseed-fed rabbits, characterized by a significant increase in primary follicles (9.8 ± 0.7 vs. 6.1 ± 0.5 follicles/section; $p=0.0024$), secondary follicles (7.2 ± 0.5 vs. 4.6 ± 0.4 ; $p=0.0018$), and antral follicles (5.9 ± 0.4 vs. 3.7 ± 0.3 ; $p=0.0011$). Granulosa cell layer thickness increased significantly by 31.6% ($p=0.0036$), while the number of atretic follicles decreased markedly ($p=0.0052$). Molecular analysis demonstrated a significant 2.87-fold upregulation of ovarian CTSS mRNA expression in treated rabbits compared with controls ($p=0.0009$). CTSS expression showed strong positive correlations with antral follicle number ($r=0.79$, $p=0.0005$) and granulosa cell thickness ($r=0.83$, $p=0.0002$), while showing a negative correlation with follicular atresia ($r=-0.71$, $p=0.0017$). These findings indicated that dietary flaxseed supplementation improved ovarian tissue organization and activated local reproductive regulatory pathways involving CTSS, suggesting a novel nutritional strategy for supporting female reproductive health in rabbits.

Keywords: Flaxseed supplementation, ovarian histology, Cathepsin S (CTSS), rabbit reproduction

Introduction

In rabbits, the ovaries are at the center of the developing egg cell and ovulate egg cell, and hormone and metabolic activity. In the fields of animal reproduction, the activity of the ovaries of the female rabbit is of great importance. Events like follicular recruitment, the complete formation of the follicle, and the endocrine activity of the follicle are crucial. Recent work has shown that the nutritional and health status of rabbits can be modified by using certain feeding techniques. The added presence of omega-3 fatty acids in the diet of female rabbits was associated with omega-3 fatty acid sources from plants, flax, and algae, and was linked to enhanced rabbit reproduction and gut health. Interest has also been established with omega-3 diets in rabbits. Quattrone *et al.* (2025) ^[9] has shown this using flexible or adaptable diets, metabolic linseed diets, and supportive diets in rabbit production. Quattrone *et al.* (2024) ^[8] suggest that the use of flax, and its by-products like lignans and bioactive fibers, as a high source of the omega-3 fatty acid, could enhance the health of the reproductive tissue and the metabolism of the rabbits. These results help to validate the purpose of this study. Flaxseed has become popular in animal nutrition because it is a source of omega-3s, phytoestrogenic lignans, antioxidants and fermentable fiber. These nutrients can influence

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ovarian function by altering steroidogenesis, oxidative balance, inflammatory tone and follicular-cell survival. In the rabbit, improvement in reproductive and maternal performance after the addition of omega-3s in the diet has been documented to be associated with the improvement of the quality of the diet lipids (Agradi *et al.*, 2023) ^[1]. In addition, the rabbit studies have recently documented that ovarian granulosa cells, because they have a role in controlling the development of the follicle, secretion of the hormones of the follicle, and the destiny of the follicle, are subject to nutritional-metabolic shifts. Song *et al.* (2022) ^[13] documented that blocking rabbit coprophagy was associated with a reduction in reproductive performance and a reduction in the incidence of granulosa-cell apoptosis. These flourishes suggest that rabbit ovarian function is associated with the physiological and nutritional balance, and therefore, it is likely that analyzing the effects of flaxseed on rabbit ovarian histology will clearly demonstrate the compensatory physiological and nutritional balance with respect to the follicle development, granulosa-cell arrangement, and follicular atresia.

At the molecular level, Cathepsin S (CTSS) is an interesting candidate gene that emerges from rabbit ovarian studies. CTSS, a member of the cysteine protease family, participates in tissue remodeling and the cellular and reproductive regulatory processes. Song and Colleagues (2021) ^[11] reported that CTSS facilitated the regulation of progesterone and estradiol secretion as well as granulosa-cell proliferation and apoptosis in rabbit ovarian granulosa cells. This makes CTSS a relevant candidate gene in studies involving the ovarian follicle and the structural integrity of the ovary. More recently, CTSS polymorphisms have also shown potential in trait determination of litter size in rabbits and have strengthened the hypothesis of its role in the reproductive efficiency of rabbits. To date, however, most of the studies have either been on the cellular level or on the genetic level, and studies on basic *in vivo* histology that link CTSS expression in the ovary of rabbits to the supplementation of flax seeds in their diet are, to our knowledge, nonexistent. Therefore, the present study was conducted to fill that gap and proposes to test female's health flaxseeds to see if they will positively impact the histoarchitecture of the ovary and the level of expression of the CTSS gene in these rabbits.

Materials and Methods

Experimental animals and housing conditions

A total of thirty (30) clinically healthy adult female New Zealand white rabbits aged 5-6 months and of 2.7-3.2 kg were included in this study. These rabbits were acquired from an approved rabbit breeding unit. The rabbits were acclimatized in animal housing units for 2 weeks before the start of the experiment. Each rabbit was in its own unit made with welded wire. The dimensions of the unit were 60 x 50 x 40 cm. The experiment room was well ventilated, and the experiment was conducted under conditions of normal circadian cycles with a temperature of 21 ± 2 °C and a relative humidity of 55-65%. Water was available for the rabbits in the units via water nipples. Health, feed intake and the activity of the rabbits in the units were observed and recorded. The implementers of the study prepared the basal diet according to the nutritional requirements of rabbits. The diet consisted of 17.5% crude protein, and 2.8% of crude fat and 14% crude fiber, and 2,550 kJ/kg of metabolizable energy. Procedures undertaken in the experiment were in agreement with the Laboratory animal (rabbits) welfare codes.

Experiment structure and diet additive

There were thirty rabbits involved in this experiment. They were split into two groups of fifteen. The control group received no supplemental diet while the experimental group

received a base diet with a 5% flaxseed diet additive for thirty days. Commercial flaxseed (*Linum usitatissimum*) was used; the seeds were supplied to us for agriculture, cleaned, dried, and then ground into fine fibers using a metal lab grinder. The flaxseed was combined into the base diet in the weeks to follow, with supplemental animal diet stored in opaque airtight vessels in a 4 °C environment to prevent the oxidation of fatty acids and to increase the bioactivity during the supplemental diet.

Collection of ovarian samples and recording of body weights

The starting and ending body weights for the experimental animals were collected using an Adam Equipment Co. UK. CKT 16UH electronic scale. In the last day of the feeding trial, the rabbits were fasted for 7 hours and then euthanized. Euthanasia was performed via the intramuscular administration of 35 mg/kg of body weight of ketamine hydrochloride, and the 5 mg/kg of body weight of xylazine hydrochloride. The ovaries were dissected, and the surrounding fat and connective tissue were removed before being weighed using an analytical balance from Sartorius AG, Germany, cat. No. Entris II BCE224I-1S. The ovarian index was calculated by dividing the weight of the ovary by the body weight and multiplying by 100. One ovary was fixed for further histological analysis. The other ovary was washed in cold phosphate buffer saline (pH 7.4), snap frozen in liquid nitrogen, and stored at -80 degrees Celsius until further molecular analysis was conducted.

Histological preparation and microscopic evaluation

Ovarian tissues were preserved in 10% neutral buffered formalin (Sigma-Aldrich, USA, Cat. No. HT501128). Formalin fixation was then done for 48 hours and then the samples were processed for paraffin embedment. The steps in paraffin processing were 70%, 80%, 90%, 95% and 100% ethanol dehydration, xylene for wax penetration, and paraffin wax for embedment. Using rotary microtome (Leica Biosystems, Germany; Model RM2235), 5-micron sections were taken and put in clean glass slides. The sections were deparaffinized and were stained by hematoxylin and eosin. Digital light microscopy (Olympus BX53, Olympus Corporation, Japan) was used for samples histopathological examination. The sections evaluated were then counted for the presence of primordial, primary, secondary, and antral follicles and atretic follicles, and also the thickness of the granulosa cell layer, and the presence of corpus luteum. Photographic documentation was done of every histological microscopy. Measurements were taken in 10 non-overlapping microscopic fields from each ovary and were photographed for documentation of histological changes.

RNA extraction & quality assessment

Total RNA from frozen ovarian tissue was obtained via TRIzol™ Reagent (Invitrogen, Thermo Fisher Scientific, USA, Cat. No. 15596026). About 50 mg of frozen ovarian tissue was homogenized in a 1000 µL of TRIzol reagent in a digital homogenizer (IKA T25 ULTRA-TURRAX, Germany). After homogenization, 200 µL of chloroform was added and mixed vigorously for 15 s. The mixture was allowed to sit for 3 min at room temperature before centrifuging at $12,000 \times g$ for 15 min at 4 °C. The RNA-containing upper layer was removed and added to a fresh RNase free tube. RNA was precipitated from this layer by adding 500 µL of isopropanol, centrifugation, and washing with 75% ethanol. After drying, the RNA was finally dissolved in nuclease-free water. The quality of the RNA was assessed with a spectrophotometer (NanoDrop One, Thermo Fisher Scientific, USA, Cat. No. ND-ONE-W) by ensuring the spectral purity of the RNAs was between 1.8 and 2.1 at the 260/280 nm wavelength. Prior to reverse transcription, RNAs

that fell within this spectral purity criterion (A260/A280) were used.

The cDNA Synthesis Kit was used to produce complementary DNA from 1 µg of total RNA (Thermo Fisher Scientific, Lithuania, Cat. No. K1622). As per the manufacturer's protocol, each 20 µL reaction was made of random hexamer primers, reaction buffer, dNTPs, RiboLock, reverse transcriptase enzyme, and water. Reverse transcription was first put at 25 °C for 5 min and then at 42 °C for 60 min, and then was enzyme was inactivated at 70 °C for 5 min. After this, the PowerUp™ SYBR™ Green Master Mix (Applied Biosystems, Thermo Fisher Scientific, USA; Cat. No. A25742) was used for the quantitative real-time PCR. This came to a total of 20 µL containing 10 µL of the master mix, 1 µL forward a primer, 1 µL reverse primer, 2 µL of the cDNA template, and the rest, water. This was then put in a machine for denaturing at 95 °C for 2 min, followed by 40 cycles of denaturing at 95 °C for 15 s, then at 60 °C for 30 s. This was followed by extending at 72 °C for 30 s. and a melting curve range from 65-95 °C the machine. This was used to determination of the specificity of the amplification. The $2^{-\Delta\Delta C_t}$ method was used to keep in mind the housekeeping gene β -actin (ACTB) to find the relative expression, which in this case was ovarian Cathepsin S (CTSS).

Primers and molecular targets

Primers were customized for the amplification of rabbit oocyte CTSS and the internal control gene ACTB. The CTSS primer set stemmed from the published work of Guangli Song *et al.* (2021) [12]. They demonstrated a regulatory role for CTSS in rabbit granulosa-cell proliferation, apoptosis, and the secretion of steroid hormones. The sequence for the forward primer for CTSS was 5'-CTACGGCAAGCAATACAA-3', and the reverse was 5'-TCTCAGGGAAGTCATCAA-3', generating an amplicon of 127 bp. For ACTB, the forward primer was 5'-ATGCAGAAGGAGATCACCGC-3' and the reverse was 5'-ACTCCTGCTTGCTGATCCAC-3', generating an amplicon of 148 bp. All twelve primers were purchased from the company Macrogen (Seoul, South Korea), and were reserved of a row concentration of 100 pmol/µL and dispenses were made of a working concentration of 10 pmol/µL. The lengths of the amplicons were below 150 bp, and therefore real-time PCR amplification would be efficient.

Statistical analysis

IBM SPSS and GraphPad Prism Statistical were the programs used for analysis of the data. The data are reported as the mean $\pm$ standard error. The Shapiro Wilk test was used test for normality of distribution of data. An independent sample t-test was used for the comparisons of the control and flaxseed treated groups. Pearson (r) correlation was used for the analysis

of the relationship of CTSS gene expression vs. ovarian histological dimensions. The p-value for significance was set to be under 0.05.

Results

Impact of flaxseed supplementation on body weight and ovarian index

The addition of flaxseed to the diet of adult female rabbits over a 30-day period led to changes in the physiologic and reproductive structure in the rabbits. Body weight at the end of the study period was greater in the flaxseed group (3.38 ± 0.07 kg) in comparison to the control group (3.21 ± 0.08 kg). The weight difference was statistically significant ($p=0.0412$). Enhancement of the rabbits' ovarian weight was also noted in the treated group (0.42 ± 0.02 g) in comparison to the control group (0.31 ± 0.01 g), ($p=0.0027$). This resulted in a significant increase in the ovarian index ($0.124 \pm 0.006\%$ vs. $0.097 \pm 0.005\%$; $p=0.0019$). Positive changes in the ovarian morphology and development were noted in the flaxseed group. The development of the ovarian follicles in the flaxseed group showed a greater number of visible follicular protrusions. This demonstrates a greater activity in the reproductive tissues (Table 1).

Table 1: Effect of dietary flaxseed supplementation on body weight and ovarian index in adult female rabbits

Parameter	Control group	Flaxseed-treated group	P-value	Significance
Initial body weight (kg)	2.86 ± 0.06	2.88 ± 0.05	0.781	NS
Final body weight (kg)	3.21 ± 0.08	3.38 ± 0.07	0.0412	S
Body weight gain (kg)	0.35 ± 0.03	0.50 ± 0.04	0.0194	S
Ovarian weight (g)	0.31 ± 0.01	0.42 ± 0.02	0.0027	S
Ovarian index (%)	0.097 ± 0.005	0.124 ± 0.006	0.0019	S

Values are expressed as mean $\pm$ SE. S = Significant at $p < 0.05$; NS = non-significant

Impact of flaxseed on ovarian histomorphology

Flaxseed supplementation caused several histomorphological changes in ovaries of rabbits. When compared with the control group, the ovaries of treated rabbits demonstrated greater numbers of developing follicles spanning various stages including primary follicles (9.8 ± 0.7 vs. 6.1 ± 0.5 follicles/section, $p=0.0024$), secondary follicles (7.2 ± 0.5 vs. 4.6 ± 0.4 , $p=0.0018$), and antral follicles (5.9 ± 0.4 vs. 3.7 ± 0.3 , $p=0.0011$). The average thickness of the granulosa cell layer was significantly increased ($p=0.0036$) by 31.6%, from 62.6 ± 2.9 µm to 82.4 ± 3.6 µm. The count of atretic follicles significantly decreased ($p=0.0052$) from 3.4 ± 0.3 to 1.7 ± 0.2 follicles/section. The ovaries of treated rabbits demonstrated a more even and organized stroma, with follicles exhibiting less degenerative change and a more oocyte clear architectural appearance, suggestive of improved follicle maturity (Table 2).

Table 2: Effect of dietary flaxseed supplementation on ovarian histomorphology in adult female rabbits

Parameter	Control group	Flaxseed-treated group	P-value	Significance
Primary follicles (No./section)	6.1 ± 0.5	9.8 ± 0.7	0.0024	S
Secondary follicles (No./section)	4.6 ± 0.4	7.2 ± 0.5	0.0018	S
Antral follicles (No./section)	3.7 ± 0.3	5.9 ± 0.4	0.0011	S
Atretic follicles (No./section)	3.4 ± 0.3	1.7 ± 0.2	0.0052	S
Granulosa cell layer thickness (µm)	62.6 ± 2.9	82.4 ± 3.6	0.0036	S
Corpus luteum frequency (No./section)	1.3 ± 0.2	2.4 ± 0.3	0.0147	S

Values are expressed as mean $\pm$ SE. Significant differences were considered at $p < 0.05$

Ovarian CTSS gene expression in response to flaxseed supplementation

Results showed that flaxseed supplementation increased the expression of Cathepsin S in the ovaries. When measurements of mRNA expression were adjusted against levels of ACTB,

large increases among the flaxseed supplemented group were measured, at an average of 2.87-fold ($p=0.0009$), in comparison to the control. The result of the amplification showed highly consistent and rapid exponential amplification for all biological replicates; melting-curve analysis supported

rapid and consistent separation for the labeled samples. The increased CTSS expression in the ovaries indicated the activation of the local signaling mechanisms for granulosa cell proliferation and extracellular matrix remodeling, steroidogenic support indicative of the healthy functional dynamics of ovarian and follicle development (Figure 1).

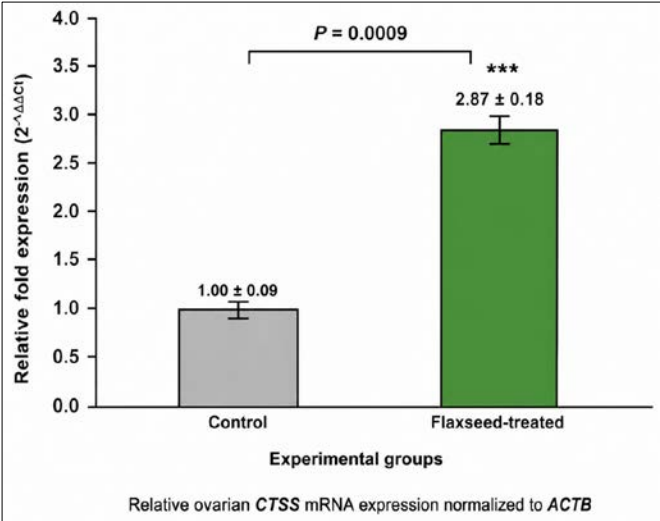


Fig 1: Relative ovarian Cathepsin S (CTSS) mRNA expression in control and flaxseed-treated adult female rabbits

Relationship of CTSS to histological measures

Correlation analysis showed that CTSS expression is strongly related to the parameters of follicular development. That is to say, the expression of CTSS showed positive correlations to the count of primary follicles ($r=0.68$; $p=0.0028$), secondary follicles ($r=0.73$; $p=0.0011$), and antrals ($r=0.79$; $p=0.0005$). There was also a highly positive correlation to the count of granulosa cell layers ($r=0.83$; $p=0.0002$), confirming transactivation of CTSS and structural follicular maturation. Significantly high CTSS expression being associated with low rates of follicular atresia was also indicative of local regulatory functions and follicular maturation (Table 3 and Figure 2).

Table 3: Pearson correlation coefficients between ovarian CTSS gene expression and histological parameters

Parameter	Correlation coefficient (r)	P-value	Correlation type
Primary follicles	+0.68	0.0028	Strong positive
Secondary follicles	+0.73	0.0011	Strong positive
Antral follicles	+0.79	0.0005	Very strong positive
Granulosa cell thickness	+0.83	0.0002	Very strong positive
Corpus luteum frequency	+0.64	0.0041	Moderate positive
Atretic follicles	-0.71	0.0017	Strong negative

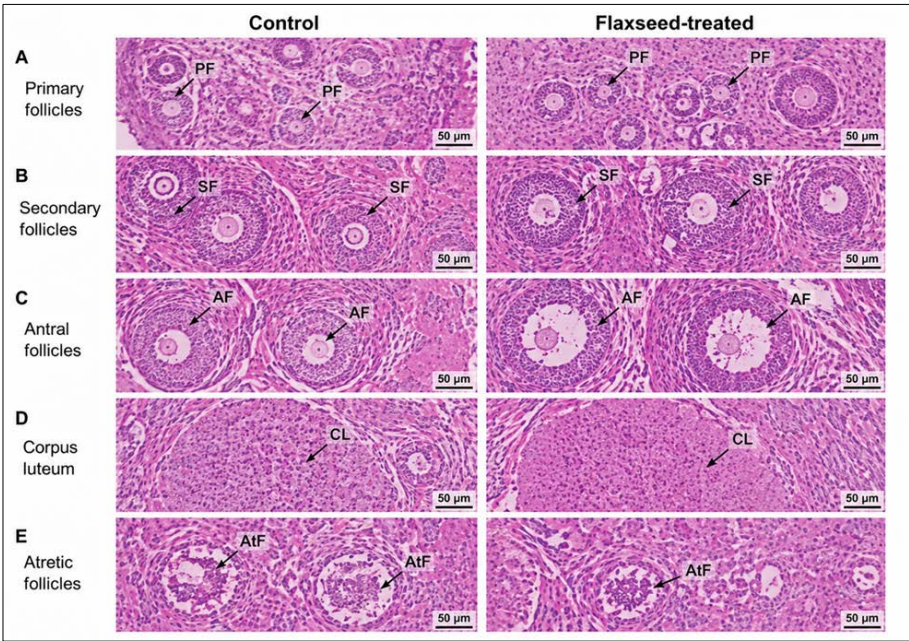


Fig 2: Histological sections of ovary stained with H&E showing follicular development in control and flaxseed-treated adult female rabbits. A: Primary follicles (PF). B: Secondary follicles (SF). C: Antral follicles (AF). D: Corpus luteum (CL). E: Atretic follicles (AtF). Flaxseed-treated rabbits showed increased numbers of developing follicles, thicker granulosa-cell layers, more prominent corpus luteum formation, and reduced follicular atresia compared with the control group. 50 μm

Discussion

This study showed that dietary flaxseed supplement led to improvement in adult female rabbit characteristics denoting ovarian development which includes increased ovarian weight and ovarian index, enhancement of follicular development and granulosa-cell, and increased expression of ovarian CTSS gene. The result of this study corroborates recent research in rabbit reproduction which indicates that ovarian response to dietary and metabolic modification is apparent. The increased ovarian index in rabbits treated with flaxseed is indicative of heightened ovarian activity and advanced development of reproductive tissues. This result is consistent with Hadjadj *et al.* (2025) [7], who stated that feeding modification caused changes in rabbit ovarian folliculogenesis, cell proliferation and apoptosis, and the production of regulatory peptides. The improvement in this case was flaxseed providing omega-3 fatty acids, lignans, and antioxidant. In the study of Hadjadj *et al.* (2025) [7], food restriction led to the development of stress-related changes in the ovary while the study under consideration reported positively as the omega-3 fatty acids, lignans, and antioxidants provided by the flaxseed eased the stress. This comparison corroborates that rabbit ovarian fabric is versatile in nutrition and that the dietary quality has a pronounced impact on follicular activity.

Flaxseed-treated rabbits presented with more numerous primary, secondary, and antral follicles and fewer atretic follicles in comparison to the control group. Flaxseed supplementation appeared to encourage follicular recruitment and survival. These findings corroborated with the results of Bao *et al.* (2024) [2], who identified those molecular regulators and proteins, such as CRABP1, were involved in rabbit follicle development and that follicular development relies on dynamics of cellular and molecular constituents. Flaxseed supplementation also demonstrated improved rabbit ovarian granulosa cells, corroborating the findings of (Bao *et al.*, 2024) [3] rabbit ovarian granulosa cells as an appropriate cell line in reproductive biology. Granulosa cells are at the center of folliculogenesis and oocyte support and steroidogenesis. In this study, enhanced cellular layering of granulosa cells in the animals of the flaxseed group was suggestive of improved follicular health and cellular support and lipid stress support. Flaxseed treatment demonstrated a notable decrease in follicular atresia. Follicular atresia is related to granulosa cell apoptosis, oxidative damage, and an unfavorable follicular microenvironment. The results align with the findings of Xue *et al.* (2024) [14], who studied the effects of oxidative ovarian damage and the protective effects of N-Acetylcysteine in their rabbit model of premature ovarian failure. The present findings were also in agreement with the results of Cai *et al.* (2024) [5], who investigated the effects of oxidative stress and apoptosis on rabbit ovarian granulosa cells, and found oxidative damage was mitigated with the provision of antioxidants. Although N-Acetylcysteine and flaxseed are different compounds, they both may impact the same protective mechanism, reducing oxidative stress. It is, therefore, plausible to suggest that a possible mechanism for the lower number of atretic follicles reported in the current study was due to the flaxseed antioxidant contents, such as omega-3 fatty acids and lignans. The study's primary observation was the increased expression of CTSS in flaxseed-treated rabbits, with the expression of CTSS closely linked to tissue remodeling and granulosa-cell regulation. The increase in CTSS expression in the flaxseed-treated group was correlated with an increase in the number of follicles, and a thicker granulosa cell layer was also observed. This was in agreement with previously reported molecular

studies supporting the observation that the regulation of rabbit ovarian function was related to the specific molecular gene networks related to the regulation of the growth of follicles and the efficiency of reproduction. Yang *et al.* (2024) [15] reported on the role of MTHFR as a candidate gene associated with litter size in rabbits, thus supporting the idea that the control of reproductive performance was also related to the genetic and ovarian regulatory networks. Furthermore, Bao *et al.* (2024) [4] reported on the role of exosomal miR-10a-5p in ovarian failure, acting through the BDNF/TrkB/Akt/mTOR pathway, thus elucidating the control of the ovarian function through the modulation of active molecular signaling. Here, the study shows that ovarian CTSS is another marker for nutrition-based functional follicular improvement.

The correlation findings enhanced both the histological and molecular findings. CTSS expression was positively correlated to 1°, 2°, and antral follicles, and to the number of granulosa cells. It was negatively correlated to follicular atresia. These correlations also indicated that CTSS was increased after flaxseed supplementation and was associated with improved ovarian tissue. A similar trend was observed within the last studies of rabbit ovarian tissue, where molecular alterations were observed that were linked to follicle formation, granulosa cell preservation and the overall reproductive performance. Improvement of flaxseed supplementation presented with histological findings and RT-qPCR analysis was observed, thereby supporting the flaxseed supplementation hypothesis and the flaxseed aid enhancement of ovarian function and both histological and molecular aspects of research.

Conclusion

The present research indicated that the supplementation of flaxseed in the diets of the adult female rabbits advanced the histoarchitecture of the ovary, enhanced CTSS, and molecular remodeling. In comparison to the majority of recent studies that examined the effect of flaxseed on oxidative injury, food restriction, granulosa cell cultures, and reproductive markers, the present study was able to utilize an uncomplicated nutritional model to connect with CTSS and ovarian histology. The promotion of granulosa cell thickness and the reduction of atresia showed that flaxseed supplementation supported the ovary function.

Acknowledgement

The author would like to express they're thanks to the College of Veterinary Medicine, University of Al-Qadisiyah for their support with the laboratories.

Funding

No external funding sources were available for the current study. It only was self-funded by the author.

Conflict of interest

No conflict of interest is found.

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How to Cite This Article

Jawad MS. Dietary flaxseed supplementation modulates ovarian histoarchitecture and CTSS gene expression in adult female rabbits. *International Journal of Veterinary Sciences and Animal Husbandry.* 2026; 11(6): 36-41.

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