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Impact of heat stress on redox homeostasis in the liver of laying hens and the protective role of antioxidant supplements

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PDB: Investigation; Data curation; Formal analysis; Validation; Visualization; Writing — original draft, review & editing.
SYT: Conceptualization; Methodology; Project administration; Supervision.

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None to declare.

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All procedures involving animals were conducted in compliance with the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (Strasbourg, 2005), EU Directive 2010/63, and the Law of Ukraine no. 3447-IV "On Protection of Animals from Cruelty" (no. 440-IX from 14.01.2020). The experimental protocol was approved by the Bioethics Committee of the Institute of Animal Biology NAAS (protocol no. 115a from 28.09.2022).

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None.

Under intensive poultry farming conditions, heat stress (HS) is a major factor negatively affecting the productivity of laying hens. Elevated ambient temperatures can lead to systemic imbalances, particularly by disrupting the redox homeostasis in liver cells. A primary consequence of HS is the onset of oxidative stress (OS), marked by increased production of reactive oxygen species (ROS) and impaired function of the antioxidant defense system. Recent studies suggest that dietary supplementation with antioxidants such as betaine, taurine, and myo-inositol can enhance the liver's resistance to oxidative injury. These compounds are thought to stabilize cellular membranes, stimulate antioxidant enzyme activity, and reduce the overall OS burden in the liver of laying hens. This study aimed to evaluate the combined effects of betaine, taurine, and myo-inositol on oxidative stress markers in the liver of laying hens under HS conditions. Thirty-two laying hens were used. The experiment was conducted at the vivarium of the Institute of Animal Biology NAAS, and consisted of two phases: during the first phase, birds were kept at 20 °C for one week (thermoneutral conditions); in the second phase, HS was induced by raising the ambient temperature to 30 °C for 6 hours daily over 7 days. The birds were divided into two groups: a control group fed a standard diet, and an experimental group whose diet was supplemented with 0,5 g/kg betaine, 5 g/kg taurine, and 2 g/kg myo-inositol. Under HS conditions, the control group exhibited a 1.5-fold increase in hepatic LOOH levels ($P<0.001$), indicating heightened OS. SOD and CAT activities decreased by 30 % ($P<0.01$) and 25 % ($P<0.001$), respectively, compared to thermoneutral conditions. GPx and GR activities declined by 25 % ($P<0.05$) and 38 % ($P<0.05$), respectively. In contrast, antioxidant supplementation reduced LOOH levels by 1,4-fold ($P<0.001$) and increased SOD and CAT activities by 21 % ($P<0.05$) and 18 % ($P<0.05$), respectively. GPx activity rose 1.5-fold ($P<0.01$) relative to the control group. These findings confirm the beneficial effects of betaine, taurine, and myo-inositol on the hepatic antioxidant system in laying hens under HS. Their inclusion in poultry diets may serve as a promising strategy to mitigate oxidative damage and support liver function during periods of elevated ambient temperature.

Key words: heat stress, antioxidant supplements, antioxidant protection, enzymes, catalase, superoxide dismutase, hydroperoxides, lipid peroxidation, glutathione peroxidase, reduced glutathione, TBA-active products

Introduction

Heat stress is one of the key factors that negatively affect the productivity and physiological condition of laying hens, especially under elevated ambient temperatures. Due to limited thermoregulatory capacity, birds rely on alternative mechanisms such as increased respiratory rate, which disrupts water-electrolyte balance and induces metabolic disturbances [6, 18]. In laying hens, the effects of HS are particularly detrimental as they directly affect egg formation processes. Reduced feed intake leads to an energy and mineral deficit, impairs eggshell quality, and decreases egg mass. In severe cases, laying regularity is also disrupted [5]. Moreover, prolonged HS contributes to oxidative stress development, damaging cellular structures and impairing the overall condition of the liver, the central metabolic organ involved in lipid and protein synthesis and detoxification [4].

Oxidative stress in the liver arises due to excessive ROS production and insufficient activity of the antioxidant defense system [1]. Elevated ROS levels trigger lipid peroxidation, damaging cell membranes and disrupting hepatocyte function. One of the indicators of OS is an increased level of thiobarbituric acid reactive substances (TBARS), which reflect the intensity of oxidative damage. Simultaneously, the activity of key antioxidant enzymes — SOD, CAT, and GPx — is reduced, weakening cellular detoxification [8].

SOD acts as the first line of defense by catalyzing the dismutation of superoxide anion (O_2^-) into hydrogen peroxide (H_2O_2) and oxygen [16]. However, H_2O_2 is also toxic and must be further neutralized. This is accomplished by CAT and GPx. Catalase decomposes H_2O_2 into water and oxygen, preventing its accumulation, while GPx reduces lipid peroxides and H_2O_2 using GSH. Glutathione is a major non-enzymatic antioxidant that supports cellular redox balance and detoxification [13].

Since HS disrupts the balance between ROS production and antioxidant protection, it is essential to explore compounds that preserve cellular homeostasis and maintain liver function. Betaine, taurine, and myo-inositol are among such agents that help protect hepatocytes against oxidative damage. Betaine functions as an osmoprotectant and methyl group donor, reducing homocysteine levels, stabilizing membranes, and supporting liver metabolism [7]. Taurine is a potent antioxidant and ion homeostasis modulator that prevents calcium dysregulation and lipid peroxidation [15]. Myo-inositol is involved in lipid metabolism and improves endoplasmic reticulum function, helping reduce hepatocyte oxidative accumulation [2]. Supplementing these compounds into the diet of laying hens mitigates the effects of HS, supports antioxidant status, and preserves productivity under high temperatures [10].

This study aimed to investigate the combined effects of betaine, taurine, and myo-inositol on several markers of the antioxidant defense system — specifically LOOH, and the activity of GPx, GR, SOD, and CAT — as well as on the concentration of GSH in the liver of laying hens exposed to heat stress induced under experimental conditions in a vivarium.

Materials and Methods

The study involved 32 laying hens randomly assigned to two groups. The control group (n=16) was fed a standard diet without additives. The experimental group (n=16) received feed supplemented with betaine (0.5 g/kg), taurine (5 g/kg), and myo-inositol (2 g/kg) based on dry matter. The experiment was conducted at the vivarium of the Institute of Animal Biology NAAS. Birds were housed in metal cages equipped with automated feeders and drinkers. All birds had access to a balanced diet containing essential nutrients, vitamins, and minerals, as well as unlimited access to clean water. Temperature, humidity, and lighting were controlled throughout the trial.

The study was carried out in two phases. During the first week, birds were maintained under thermoneutral conditions (20 °C, relative humidity 60 %; temperature-humidity index = 66) [3]. On day 7, birds were euthanized by decapitation, and liver samples were collected for biochemical analysis. From day 8, the temperature was raised to 30 °C for 6 hours daily, with relative humidity maintained at 70 % (temperature-humidity index = 81) [3]. On day 14, after one week of heat stress exposure, the birds were euthanized, and liver tissues were again collected.

All procedures involving animals were conducted in compliance with the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (Strasbourg, 2005), EU Directive 2010/63, and the Law of Ukraine no. 3447-IV “On Protection of Animals from Cruelty” (amended by no. 440-IX from 14.01.2020). The experimental protocol was approved by the Bioethics Committee of the Institute of Animal Biology NAAS (Protocol no. 115a, dated 28.09.2022).

The content of LOOH was determined spectrophotometrically at 480 nm following the interaction of blood plasma with ammonium thiocyanate. Optical density was measured over 10 minutes, and the LOOH concentration was calculated as the difference between control and experimental samples, expressed in arbitrary units per 1 mL of blood [14].

TBARS determination is based on the formation of a colored complex between malondialdehyde (MDA) and thiobarbituric acid (TBA) under acidic conditions and elevated temperature. After protein precipitation and heating of the sample with TBA in a water bath for one hour, the resulting complex was centrifuged. Optical density was measured spectrophotometrically at 535 and 580 nm, and the results were expressed as nmol MDA per gram of tissue.

The content of GSH was measured colorimetrically based on its reaction with 5,5'-dithiobis-2-nitrobenzoic acid (Ellman’s reagent), which forms a colored product. After incubation and centrifugation, the sample was mixed

with Na_2HPO_4 (0.3 M) and Ellman's reagent, followed by optical density measurement at 412 nm [14].

GPx activity was assessed by the rate of GSH oxidation in the presence of tert-butyl hydroperoxide. After incubation with TRIS buffer (pH 8.5) containing EDTA and sodium azide, the substrate was added, the reaction was stopped, and the residual GSH concentration was determined spectrophotometrically at 412 nm [14].

GR activity was evaluated based on the rate of oxidized glutathione (GSSG) reduction in the presence of NADPH. The incubation mixture contained K_2HPO_4, EDTA, and GSSG, and the reaction was initiated by the addition of NADPH. Optical density was measured at 340 nm, and enzyme activity was expressed in μmol NADPH/min × mg of protein [14].

SOD activity was determined by its ability to inhibit the reduction of nitro blue tetrazolium (NBT) to nitroformazan. Samples were incubated in phosphate buffer with phenazine methosulfate (PMS) and NADH, and the intensity of the resulting coloration was measured at 540 nm. Enzyme activity was expressed in arbitrary units per 1 mg of protein [14].

CAT activity was assessed by measuring the residual H_2O_2 level after incubation with the hemolysate. The reaction with ammonium molybdate was used, and the resulting complex was detected spectrophotometrically at 410 nm. The enzyme activity was calculated per 1 mg of protein [14].

Statistical analysis was performed as described by Petrovska [9]. Data are presented as mean ± standard deviation. All data were analyzed using the *Statistica 10* software. Statistical significance was determined using one-way analysis of variance (ANOVA). Student's *t*-test was used to assess differences between two groups. Differences were considered statistically significant at $P<0.05$.

Results and Discussion

Hyperactivation of lipid peroxidation (LPO) processes is an important biomarker of oxidative stress induced by heat stress, which triggers cell apoptosis by disrupting the stability, barrier, and transport functions of biological membranes [11]. Our results revealed a statistically significant difference in LOOH levels in liver homogenates of hens from the control group under thermoneutral (TN) conditions compared to those exposed to HS. Exposure to elevated temperatures resulted in a 1.5-fold increase in LOOH content ($P<0.001$, fig. 1). This indicates an increase in oxidative stress levels in liver cells under heat load conditions.

Including feed additives such as betaine, taurine, and myo-inositol in the diet of laying hens contributed to a 1.4-fold decrease ($P<0.001$) in LOOH levels in liver cells under HS compared to the control. This may suggest a reduction in oxidative stress levels in the birds, potentially due to the antioxidant properties of the aforementioned compounds and their ability to alleviate oxidative load induced by heat exposure. Their antioxidative activity may enhance the pro-antioxidant balance within cells [11, 17].

According to the data on TBARS (fig. 2), a 23 % increase ($P<0.05$) in their content was recorded in liver homogenates of laying hens from the control group under heat stress conditions compared to thermoneutral conditions. This indicates an intensification of lipid peroxidation processes in the liver under the influence of heat stress, reflecting the activation of oxidative stress and disruption of the prooxidant–antioxidant balance in the organism. The elevated level of TBARS serves as a marker of cellular membrane damage caused by excessive generation of reactive oxygen species [12].

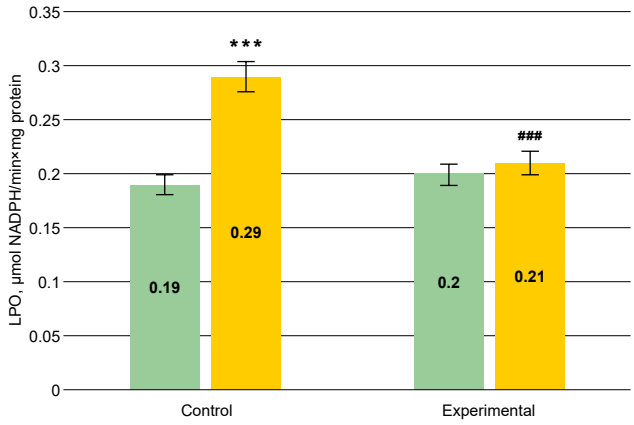

Fig. 1. Lipid hydroperoxide content in the liver of laying hens under TN and HS conditions after inclusion of betaine, taurine, and myo-inositol (M±m)

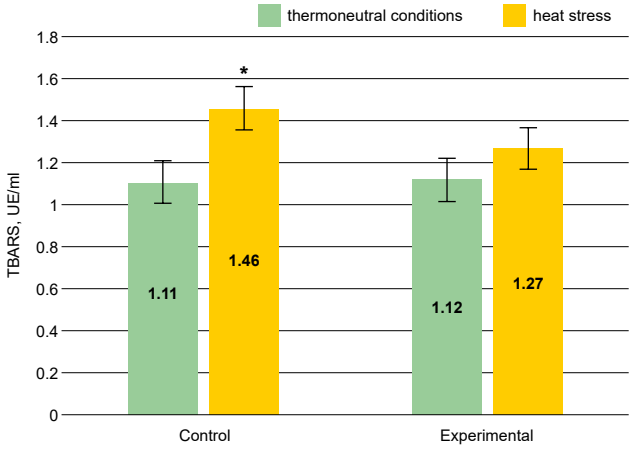

Fig. 2. TBARS content in the liver of laying hens under TN and HS conditions after inclusion of betaine, taurine, and myo-inositol (M±m)

Note: throughout this and the following figures, * — $P<0.05$; ** — $P<0.01$; *** — $P<0.001$ indicate statistically significant differences between HS and TN conditions. # — $P<0.05$; ## — $P<0.01$; ### — $P<0.001$ indicate statistically significant differences between experimental and control groups.

Analysis of SOD and CAT activity (table 1) shows that HS caused a marked decrease in their enzymatic activity in hepatocytes of laying hens in both control and experimental groups compared to TN conditions. Specifically, in the control group, SOD activity decreased by 30 % (P<0.01), and CAT activity by 25 % (P<0.001). In the experimental group (E), SOD activity dropped by 23 % (P<0.01), while CAT activity decreased by 11 % (P<0.001) relative to TN values.

These findings suggest that HS exerts a detrimental effect on both superoxide dismutase and catalase activity, leading to their inactivation, possibly due to an overload of the birds' antioxidant system. This overload likely diminishes the organism's ability to neutralize free radicals, thereby increasing the level of oxidative stress in laying hens [13, 16].

The supplementation of animal feed led to an increase in superoxide dismutase and catalase activity in liver tissue under stress conditions by 21 % (P<0.05) and 18 % (P<0.05), respectively, compared to the control. This may indicate a modest yet positive effect of betaine, taurine, and myo-inositol on the activation of SOD and CAT under stress conditions. These findings may suggest a slight enhancement of the primary antioxidant defense system in the liver against oxidative stress, contributing to the stabilization of cellular membranes and mitigation of the negative effects of heat stress on the birds' organism [17].

The analysis of GSH levels in hepatocytes of laying hens revealed no statistically significant changes under either normal or stress conditions (table 2). Similarly, dietary supplementation did not significantly affect its concentration in the liver. These results suggest an improvement in overall antioxidant capacity, which likely contributes to the stabilization of redox processes in hepatic cells and supports the balance of the prooxidant-antioxidant system [13].

The activity of GPx markedly decreased under HS conditions in both the control and experimental groups by 1.5- and 1.2-fold, respectively (P<0.05), compared to TN. However, dietary supplementation (experimental group) led to a 1.5-fold (P<0.01) increase in hepatic GPx activity under HS compared to the control group. These findings indicate the potential of the supplements to enhance cellular defense against OS, especially under heat stress conditions.

As for GR, exposure to HS in the control group led to a 38 % reduction in its activity (P<0.05), while in the experimental group, an increase of 40 % was observed (P<0.05) compared to TN. These findings may indicate a reduced load on the enzymatic component of the antioxidant defense system due to sufficient exogenous antioxidant support, as well as a decreased need for activation of endogenous antioxidant mechanisms [11].

Heat stress significantly increased LOOH levels in the liver homogenates of laying hens, indicating intensified lipid peroxidation processes and elevated OS. Adding betaine, taurine, and myo-inositol to the diet significantly reduced LOOH content, indicating decreased oxidative load and activation of antioxidant defense mechanisms. These bioactive compounds exhibit antioxidant properties that help alleviate the negative impact of HS on hepatocytes and maintain the prooxidant–antioxidant balance.

Table 1. Superoxide dismutase and catalase activity in the liver of laying hens under TN and HS conditions following dietary supplementation with betaine, taurine, and myo-inositol (M±m)

Indicators	Conditions	Control	Experimental
SOD, AU/mg protein	TN	40.74±2.45	46.86±5.7
	HS	28.68±4.83**	36.14±2.23**##
CAT, mmol H_2O_2/ min×mg of protein	TN	21.10±0.61	26.15±0.67##
	HS	19.53±0.28*	23.78±0.98*#

Table 2. Indicators of the glutathione-dependent antioxidant defense system in the liver of laying hens under TN and HS conditions following dietary supplementation with betaine, taurine, and myo-inositol (M±m)

Indicators	Conditions	Control	Experimental
GSH, mmol/L	TN	0.31±0.09	0.34±0.06
	HS	0.26±0.11	0.34±0.09
GPx, nmol GSH/ min×mg protein	TN	40.67±3.715	44.81±3.16
	HS	26.29±5.48*	38.15±4.97*##
GR, μmol NADPH/ min×mg protein	TN	2.5±0.39	0.47±0.15###
	HS	1.56±0.42*	1.48±0.36*

In the control group, HS notably decreased the activities of SOD and CAT in hepatocytes, indicating a reduced capacity to neutralize free radicals. In the experimental group, bioactive compounds led to a partial increase in SOD and CAT activity, suggesting a positive impact on strengthening antioxidant defense. Enhanced activity of these enzymes helps stabilize membrane structures and mitigate the harmful effects of HS on liver function.

HS also caused a decline in the activity of GPx and GR in the liver, reflecting depletion of the glutathione-dependent antioxidant defense system. Dietary inclusion of betaine, taurine, and myo-inositol increased GPx activity, thereby ensuring effective cellular protection against OS and improving the organism's resistance to thermal stress.

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Вплив теплового стресу на окисно-відновний баланс печінки курей-несучок та роль антиоксидантних добавок

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В умовах інтенсивного птахівництва одним із ключових факторів, який негативно впливає на продуктивність курей-несучок, є тепловий стрес (ТС). Підвищена температура навколишнього середовища може спричиняти дисбаланс в організмі птиці, зокрема впливати на окисно-відновний стан клітин печінки. Одним із основних наслідків ТС є розвиток оксидативного стресу (ОС), що супроводжується підвищеним утворенням активних форм кисню (АФК) та порушенням функціональної активності антиоксидантної системи захисту організму. Сучасні дослідження вказують на ефективність введення у корм курей певних антиоксидантних добавок — таких, як бетаїн, таурин та міо-інозитол, які здатні підвищувати резистентність печінкових клітин до оксидативного пошкодження. Завдяки своїм властивостям, ці речовини можуть сприяти стабілізації мембран, активізації антиоксидантних ферментів та загальному зниженню рівня ОС у печінці курей-несучок. Метою дослідження є оцінка комплексного впливу бетаїну, таурину та міо-інозитолу на рівень оксидативного стресу в печінці курей-несучок за умов теплового навантаження. У дослідженні було використано 32 курки-несучки. Експеримент проведено у віварії Інституту біології тварин НААН у два етапи: на першому курей утримували при температурі 20 °С протягом тижня, на другому створювали умови ТС підвищенням температури до 30 °С на 6 годин на добу протягом 7 днів. Птахів поділили на дві групи: контрольну (споживала стандартний корм) та дослідну (отримувала корм із додаванням 0,5 г/кг бетаїну, 5 г/кг таурину та 2 г/кг міо-інозитолу). Результати дослідження показали, що за умов ТС у контрольній групі спостерігали зростання рівня ГПЛ у печінці курей у 1,5 раза ($P<0,001$), що свідчить про посилення ОС. При цьому активність СОД знижувалася на 30 % ($P<0,01$), а КАТ — на 25 % ($P<0,001$) порівняно з ТН. Водночас спостерігалося зниження активності ГП на 25 % ($P<0,05$) та ГР на 38 % ($P<0,05$). Введення у раціон антиоксидантних добавок сприяло зниженню рівня ГПЛ у печінці в 1,4 раза ($P<0,001$), а також зростанню активності СОД на 21 % ($P<0,05$) та КАТ на 18 % ($P<0,05$) в умовах ТС. Крім того, активність ГП у печінці дослідної групи підвищувалася у 1,5 раза ($P<0,01$), порівняно з контрольною групою. Отримані дані підтверджують позитивний комплексний вплив бетаїну, таурину та міо-інозитолу на антиоксидантну систему курей-несучок при тепловому стресі. Використання цих добавок у раціоні може бути ефективною стратегією для зменшення оксидативного навантаження та підтримки стабільності клітинних мембран в умовах високих температур.

Ключові слова: тепловий стрес, антиоксидантні добавки, антиоксидантний захист, ферменти, каталаза, супероксиддисмутаза, гідропероксиди, перекисне окислення ліпідів, глутатіонпероксидаза, відновлений глутатіон, ТБК-активні продукти

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