Physiological Functions of -Alanine and Its Applications in Animal Production: A Postprint

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Abstract

-Alanine is an amino acid that does not participate in protein synthesis and serves as a precursor for the synthesis of muscle-derived bioactive peptides such as carnosine and anserine. As a sports nutrition supplement for enhancing muscle endurance, it has been widely applied in clinical nutrition. Studies have shown that -alanine can improve animal production performance, regulate muscle growth and the content of muscle-derived bioactive peptides, and enhance meat quality. This article aims to review the sources and metabolism, physiological functions, and applications of -alanine in the field of animal production, thereby providing a theoretical basis for its application in animal nutrition regulation and production practice.

Full Text

Physiological Functions of -Alanine and Its Application in Animal Production

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Abstract

-Alanine is a non-proteinogenic amino acid that serves as a precursor for the synthesis of muscle-derived bioactive peptides such as carnosine and anserine. Widely used as a sports nutrition supplement to enhance muscular endurance in clinical nutrition, -alanine has been shown to improve animal growth performance, regulate muscle growth and muscle-derived bioactive peptide content, and enhance meat quality. This review summarizes the sources and metabolism of -alanine, its physiological functions, and its applications in animal production, providing a theoretical basis for the use of -alanine in animal nutrition regulation and production practices.

Keywords: -alanine; muscle-derived active peptide; physiological function; animal production

With rapid economic development and improving living standards, consumer demands for meat quality have increased annually. Consumers now focus not only on the nutritional properties of meat products but also on their health-promoting functional characteristics. Currently, the development of meat products remains in its early stages with limited novel varieties, making the development of functional meat products significant for the advancement of the meat industry. Meat, eggs, and milk are the primary sources of animal protein for humans, with poultry meat particularly rich in functional peptides known as imidazole dipeptides (carnosine and its derivative anserine). -Alanine is the simplest -amino acid and serves as the limiting amino acid for endogenous imidazole dipeptide synthesis in humans and mammals, with demonstrated effects on increasing imidazole dipeptide content in muscle, enhancing antioxidant capacity, improving muscle buffering capacity, and reducing fatigue. As production costs have decreased in recent years, research has begun to explore the application of -alanine in animal production. Studies have shown that rational use of -alanine in livestock and poultry production can regulate muscle growth and improve animal product quality. This review examines the sources and metabolism, physiological functions, and practical applications of -alanine in animal production to provide theoretical support and reference for its application in this field.

1 Sources and Metabolism of -Alanine

-Alanine is the only naturally occurring -amino acid and does not participate in protein synthesis. It is not only a catabolic product of uracil and cytosine but also a component of pantothenic acid and coenzyme A, combining with histidine to form carnosine and its derivative anserine found in animal muscle. -Alanine exists in free form in the root nodules of legumes, tea leaves, and mammalian brain hydrolysates. In bacteria, aspartic acid can be decarboxylated by aspartate decarboxylase to produce -alanine.

In animals, -alanine is primarily synthesized in the liver through three main pathways: pyrimidine degradation, carnosine hydrolysis, and L-aspartate decarboxylation [Figure 1: see original paper], with pyrimidine degradation being the major source. -Alanine can also be synthesized through chemical methods and microbial transformation. The chemical synthesis method primarily involves ammoniation and hydrolysis of acrylonitrile, where acrylic acid is aminated to produce -aminopropionitrile, which is then hydrolyzed under acidic or alkaline conditions to generate -alanine. However, this process produces large amounts of inorganic salts, resulting in low product purity and yield. Microbial transformation utilizes recombinantly expressed L-aspartate -decarboxylase genes in *E. coli* and *Corynebacterium glutamicum* to convert L-aspartate into -alanine. When the enzyme dosage is 3,000 U/g, the conversion rate of 100 g/L L-aspartate substrate reaches 97.8%. This process offers simple equipment, mild conditions, few byproducts, easy purification, and high yield, meeting the requirements for industrial production and gaining increasing application.

The metabolism of -alanine occurs primarily in the brain and muscle, with malonate semialdehyde (MS) as the primary metabolic product, which under normal conditions is ultimately converted to acetic acid. -Alanine synthesized in the liver is transported to tissues and organs through the taurine transporter (TauT) and proton-coupled amino acid transporter (PAT1) via blood circulation, where it produces carnosine and MS to exert its effects. As shown in Figure 1, MS can directly generate acetyl-CoA or be decarboxylated to produce acetaldehyde. Research indicates that -alanine primarily functions in animals through imidazole dipeptides, which possess biological activities such as buffering muscle pH, anti-fatigue effects, antioxidant capacity, and memory improvement. shows the imidazole dipeptide content in various animal products, revealing that poultry breast muscle contains relatively high levels of imidazole dipeptides.

2 Physiological Functions of -Alanine

As the sole limiting amino acid for imidazole dipeptide synthesis, -alanine is a potential functional amino acid with multiple physiological functions. Current research has identified several roles: regulating metabolism as a neurotransmitter or hormonal modulator, serving as an intermediate metabolite for various active substances (such as coenzyme A and pantothenic acid), combating fatigue and improving exercise capacity, and enhancing memory with anti-aging effects. These diverse physiological functions have attracted widespread attention.

2.1 As a Neurotransmitter

In mammalian nervous systems, -alanine functions as a neurotransmitter to synthesize neural dipeptides (carnosine and anserine). Studies have shown that in the sacral dorsal commissural nucleus (SDCN), -alanine can activate chloride channel-regulating systems and act as an agonist for strychnine-sensitive glycine receptors. In vitro experiments demonstrate that -alanine, as a neuromodulator, can activate both GABA_A and glycine receptors, which are important regulators of progesterone and steroid hormones that control metabolism. -Alanine may also serve as a lead detoxifying agent, with its mechanism potentially related to its neurotransmitter function.

2.2 As an Intermediate Metabolite of Active Substances

-Alanine is a key intermediate for various active substances. While plants and microorganisms can synthesize pantothenic acid, animals cannot, and exogenous -alanine supplementation can promote pantothenic acid and coenzyme A formation. In insect pigmentation, -alanyldopamine synthase (BAS) transfers -alanine to dopamine to form N- -alanyldopamine (NBAD), reducing melanin deposition on the body surface and altering insect cuticle color. NBAD is the primary component of yellow pigments in swallowtail butterfly wings. Additionally, N- -alanylnorepinephrine (NBANE) and NBAD are precursors for arthropod cuticle sclerotization, with -alanine serving as the substrate for NBANE and NBAD synthesis, thereby promoting cuticle sclerotization.

2.3 Enhancing Exercise Capacity and Combating Fatigue

As a precursor for carnosine synthesis (a muscle buffer), -alanine is one of the few scientifically-supported exercise enhancers and has been widely applied in clinical research. Carnosine acts as a non-carbonate proton buffer in muscle, reducing skeletal muscle acidosis caused by high-intensity exercise, though its buffering duration may be limited. Clinical studies show that young volunteers taking 6.4 g of -alanine daily for 23 days exhibited significantly elevated carnosine levels. Research also indicates that -alanine supplementation has no effect on exercise lasting less than 60 seconds, demonstrates strong positive effects on exercise lasting 60-240 seconds, and shows even more pronounced benefits for exercise exceeding 240 seconds. As a dietary supplement with anti-fatigue effects, approximately 100 tons of -alanine are consumed annually. College football players taking 4.5 g/d of -alanine for 30 days showed significantly reduced subjective fatigue, demonstrating that -alanine can alleviate fatigue, particularly during high-intensity anaerobic exercise. -Alanine also increases endocrine hormone levels in athletes, enhancing training volume and tolerance. When -alanine (4.8 g/d) was supplemented immediately, 15 minutes, and 30 minutes after resistance training, immediate and 15-minute post-exercise supplementation significantly increased growth hormone levels, while all -alanine supplementation groups showed significantly increased corticosterone levels.

2.4 Other Functions

-Alanine can influence cold resistance mechanisms in insects and regulate body temperature, improve memory function, and provide potential health benefits for the elderly, including anti-aging effects.

3 Application of -Alanine in Animal Production

-Alanine can improve feed conversion efficiency and production performance, increase muscle content of muscle-derived active peptides, enhance muscle antioxidant capacity, improve meat quality, and increase taurine consumption in vivo.

3.1 Improving Production Performance

Current reports on the effects of -alanine on animal production performance are inconsistent. Research in poultry is relatively extensive, but definitive conclusions remain elusive. One study found that 2-day-old broiler chicks orally administered -alanine (22 mmol/kg) twice daily for 5 days showed reduced feed intake and improved feed efficiency. However, a subsequent dose-response trial with 2-day-old broilers given 0.176, 0.880, 4.400, or 22.000 mmol/kg -alanine for 5 days found no effects on production performance. Earlier research demonstrated that dietary supplementation with 2.5% -alanine significantly reduced feed intake and improved feed efficiency in broiler chicks. Four-week-old broilers fed diets containing 1% and 2% -alanine for 4 weeks showed significantly reduced body weight gain, with the 2% -alanine group also exhibiting significantly reduced feed intake but no change in feed efficiency. Other studies indicate that dietary supplementation with 500 mg/kg -alanine showed a trend toward increased body weight gain and feed conversion ratio in carp, while dietary supplementation with 1.2% -alanine had no significant effect on mouse production performance, and 0.225% -alanine supplementation did not affect pig production performance. The potential for -alanine to improve animal production performance may be attributed to its role as a neurotransmitter regulating growth hormone secretion, though effects are also influenced by animal species, management practices, environment, and administration methods. Therefore, further research is needed to clarify the effects of -alanine on animal production performance.

3.2 Regulating Imidazole Dipeptide Content in Muscle

Carnosine is an endogenous functional dipeptide found primarily in skeletal and breast muscle, with biological activities including intracellular pH stabilization, lipid peroxidation inhibition, free radical scavenging, and Ca^{2} regulation. Studies show that dietary supplementation with 0.5% -alanine increased carnosine content in broiler thigh muscle by 45%, while 1% supplementation increased breast muscle carnosine content by 20%. In mice, -alanine supplementation via drinking water (1.2%) increased tibialis anterior muscle carnosine content by 160% (6.47 mmol/kg vs. 2.48 mmol/kg), whereas direct high-dose carnosine supplementation (1.8%) only increased tibialis anterior carnosine content by 30% (3.22 mmol/kg vs. 2.48 mmol/kg), demonstrating that -alanine supplementation in drinking water is far more effective than direct carnosine supplementation. Tomonaga et al. found that the administration method (drinking water vs. feed) may affect tissue carnosine content, with increased carnosine levels likely resulting from abundant histidine availability and synthesis rates being primarily limited by -alanine availability. Exogenous -alanine supplementation can increase the Km value of carnosine synthetase, thereby increasing carnosine content. Recent research indicates that -alanine-fed broilers show significantly increased muscle imidazole dipeptide content, with anserine concentration doubling after heat treatment of the muscle, suggesting that -alanine regulation of imidazole dipeptide content continues to exert effects post-mortem, though the specific mechanisms require further investigation.

Carnosine content varies by sex and tissue, with male animals showing greater increases in breast muscle carnosine content than females when consuming equivalent amounts of alanine. Dietary supplementation with 1% and 2% -alanine significantly increased carnosine and anserine content in broiler brain but had no significant effect on superficial pectoral, deep pectoral, or biceps femoris muscles. -Alanine promoted growth in carp but did not affect carnosine and anserine content, possibly due to low carnosine storage and insensitivity in fish. Expression of -alanine transporters such as TauT and PAT1, as well as differential sensitivity to carnosine among animals, can affect carnosine synthesis. Research indicates that plasma carnosine, rather than muscle carnosine, plays a role in counteracting inflammation or metabolic stress induced by high-fat diets in rats. In humans, plasma carnosine is undetectable after ingestion of pure carnosine, beef, chicken, or chicken broth, while plasma anserine increases significantly and urinary carnosine and anserine increase by more than 10-fold, suggesting that ingested imidazole dipeptides are rapidly metabolized by plasma carnosinase and excreted in urine. These findings demonstrate that imidazole dipeptide content and ratios differ among body compartments. The metabolic pathways and key products of imidazole dipeptides in blood, liver, muscle, and other tissues after -alanine consumption require further investigation to elucidate the tissue-specific mechanisms of -alanine function. Therefore, the effects of -alanine on imidazole dipeptide content in different animals need further study.

3.3 Improving Meat Quality

-Alanine can increase muscle fiber density and tenderness, reduce muscle fiber diameter, decrease muscle shear force, alleviate lipid oxidation and stress, and improve meat quality. Studies show that dietary supplementation with 0.12% -alanine significantly increased mRNA expression of slow-twitch and fast-oxidative myosin heavy chain genes while decreasing fast-glycolytic myosin heavy chain gene expression in broiler breast muscle, significantly increased leg muscle fiber density at 42 days, and reduced muscle fiber area and diameter. -Alanine (2%) also increased the ratio of slow-oxidative to fast-oxidative fibers in broiler thigh muscle, improved muscle tenderness, and regulated muscle growth. Supplementation with 1% -alanine reduced breast muscle shear force and lightness (L*) values, with increased carnosine concentrations accelerating calpain activation, thereby accelerating muscle maturation, improving tenderness, and enhancing meat quality.

Reports indicate that combined application of -alanine and -hydroxy- -methylbutyrate can reduce muscle protein degradation in aged, sedentary rats, though without significantly improving muscle function, leaving open the possibility of effectiveness under extreme conditions. The synergistic effects and mechanisms of -alanine combined with other muscle metabolism regulators (creatine, -hydroxy- -methylbutyrate, N-carbamylglutamate, etc.) on increasing muscle yield and improving meat quality in meat-producing animals represent a promising approach for systematic investigation.

3.4 Enhancing Muscle Antioxidant Capacity

-Alanine can increase carnosine content, reduce lipid peroxidation in muscle, and enhance antioxidant capacity. Mouse studies demonstrate that -alanine increases superoxide dismutase (SOD) and glutathione peroxidase (GSH-Px) activities while reducing malondialdehyde (MDA) content in gastrocnemius muscle, thereby improving skeletal muscle antioxidant capacity. Research also shows that dietary supplementation with 0.12% -alanine significantly reduced MDA content and increased GSH-Px activity in broiler breast muscle at 42 days. -Alanine supplementation at 0.5% and 1.0% showed a trend toward reduced MDA content in broiler breast muscle. By increasing muscle carnosine content, -alanine can reduce lipid oxidation and stress during the feeding process, enhancing overall antioxidant capacity. These findings demonstrate that -alanine can improve muscle antioxidant capacity.

3.5 Increasing Taurine Consumption in vivo

Taurine is a sulfur-containing amino acid that exists in free form and is not directly involved in protein synthesis but participates in amino acid metabolism. Due to competitive relationships in absorption and metabolism, -alanine can cause taurine depletion. Injection of -alanine in mice induces taurine depletion in brain and muscle, and -alanine acts as a taurine inhibitor that increases taurine consumption, though no changes in animal health status have been observed in these studies.

Research indicates that -alanine can inhibit taurine uptake and reduce Ca^{2} regulatory effects, possibly due to competition for taurine transporters that can transport both -alanine and taurine. Neurobiological studies show that -alanine and -aminobutyric acid (GABA) can share transporters, suggesting that -alanine may affect GABA function and feeding regulation, though no relevant animal studies have been conducted. Future research should employ systems biology approaches to investigate the effects of -alanine on taurine and GABA in animal tissues, particularly neural tissue.

In summary, -alanine can regulate muscle metabolism, enhance muscle antioxidant capacity, and improve meat quality, demonstrating good potential for application in animal production. Current research on the mechanisms of -alanine in animal production is limited, and further systematic and in-depth studies are needed in several areas: (1) optimal dietary supplementation levels of -alanine for different animals, as current research on -alanine as a feed additive is insufficient, with no consensus on dosage ranges for increasing carnosine content in broilers; (2) pathways and mechanisms through which -alanine functions in different body compartments; (3) effects and mechanisms of -alanine on livestock and poultry under stress or adverse conditions; and (4) synergistic effects of -alanine combined with other muscle nutrition supplements on animal muscle metabolism. The rational application of -alanine in animal production, practical technologies, and mechanisms of action through carnosine in animal bodies require further research and exploration. As understanding of -alanine mechanisms deepens, it will play an increasingly important role in the feed industry and animal production.

References

[1] ABE H.Role of histidine-related compounds as intracellular proton buffering constituents in vertebrate muscle (review)[J].Biochemistry (Mosc),2000,65(7):757-765. [2] BAKARDJIEV A,BAUER K.Transport of -alanine and biosynthesis of carnosine by skeletal muscle cells primary culture[J].European Journal Biochemistry,1994,225(2):617-623. [3] DUNNET M,HARRIS R C.Influence of oral beta-alanine and L-histidine supplementation carnosine content gluteus medius[J].Equine Veterinary Journay,1999,31(S30):499-504. [4] HARRIS R C,TALLON M J,DUNNETT M,et al.The absorption of orally supplied -alanine its effect on muscle carnosine synthesis in human vastus lateralis[J].Amino Acids,2006,30(3):279-289. [5] HILL C A,HARRIS R C,KIM H J,et al.Influence of beta-alanine supplementation on skeletal muscle carnosine concentrations and high intensity cycling capacity[J].Amino Acids.2007,32(2):225-233. [6] 张国强. 日粮肌苷酸、-丙氨酸和组氨酸对肉鸡肉品质的营养调控 [D]. 博士学位论文. 北京: 中国农业大学,2008. [7] 罗积杏, 薛建萍, 沈寅初. -氨基丙酸的合成与应用 [J]. 氨基酸和生物资源,2005,27(1):52-55. [8] 赵连真. 酶转化法合成 -丙氨酸关键基因的重组表达及转化研究 [D]. 硕士学位论文. 无锡: 江南大学,2013. [9] GRIFFITH O W. -amino acids:mammalian metabolism and utility as -amino acid analogues[J].Annual Review of Biochemistry,1986,55(1):855-878. [10] JACOB J P,BLAIR R,HART L E,et al.The effect of taurine transport antagonists on cardiac taurine concentration and the incidence of sudden death syndrome in male broiler chickens[J].Poultry Science,1991,70(3):561-567. [11] HARRIS R C,MARLIN D J,DUNNETT M,et al.Muscle buffering capacity and dipeptide content in the thoroughbred horse,greyhound dog and man[J].Comparative Biochemistry and Physiology Part A:Physiology,1990,97(2):249-251. [12] GALLANT S,SEMYONOVA M,YUNEVA M.Carnosine as a potential anti-senescence drug[J].Biochemistry,2000,65(7):866-868. [13] DJENANE D,MARTÍNEZ L,SÁNCHEZ-ESCALANTE A,et al.Antioxidant effect of carnosine and carnitine in fresh beef steaks stored under modified atmosphere[J].Food Chemistry,2004,85(3):453-459. [14] WANG D S,ZHU H L,LI J S. -alanine acts on glycine receptors in the rat sacral dorsal commissural neurons[J].International Journal of Neuroscience,2003,113(3):293-305. [15] WU F S,GIBBS T T,FARB D H.Dual activation of GABAA and glycine receptors by -alanine:inverse modulation by progesterone and 5 -pregnan-3 -ol-20-one[J].European Journal of Pharmacology,1993,246(3):239-246. [16] EL-WASSEF A.Beta-alanine antidote[J].Oriental Journal Chemistry,1988,4(1):102-103. [17] WHITE W H,GUNYUZLU P L,TOYN J H.Saccharomyces cerevisiae is capable of de Novo pantothenic acid biosynthesis involving a novel pathway of -alanine production from spermine[J].Journal of Biological Chemistry,2001,276(14):10794-10800. [18] KOCH P B,BEHNECKE B,WEIGMANN-LENZ M,et al.Insect pigmenta-

tion:activities of beta-alanyldopamine synthase in wing color patterns of wild-type and melanic mutant swallowtail butterfly Papilio glaucus[J].Pigment Cell Research,2000,13(Suppl.8):54-58. [19] 王晓燕. -丙氨酸对甜菜夜蛾生长发育及体内酶活性的影响 [D]. 硕士学位论文. 武汉: 华中农业大学,2010. [20] HOFFMAN J R,RATAMESS N A,FAIGENBAUM A D,et al.Short-duration -alanine supplementation increases training volume and reduces subjective feelings of fatigue in college football players[J].Nutrition Research,2008,28(1):31-35. [21] 孙景权, 叶碧璇, 周海涛, 等. 天然 -丙氨酸提高运动能力及其机制的研究进展 [J]. 中国食物与营养,2015,21(6):64-68. [22] SHAFFER J E,KOCSIS J J.Taurine mobilizing effects of beta alanine and other inhibitors of taurine transport[J].Life Science,1981,28(24):2727-2736. [23] BEX T,CHUNG W,BAGUET A,et al.Muscle carnosine loading by beta-alanine supplementation is more pronounced in trained vs. untrained muscles[J].Journal of Applied Physiology,2014,116(2):204-209. [24] HOBSON R M,SAUNDERS B,BALL G,et al.Effects of -alanine supplementation on exercise performance:a meta-analysis[J].Amino Acids,2012,43(1):25-37. [25] SALE C,ARTIOLI G G,GUALANO B,et al.Carnosine:from exercise performance to health[J].Amino Acids,2013,44(6):1477-1491. [26] HOFFMAN J,RATAMESS N A,ROSS R,et al. -alanine and the hormonal response to exercise[J].International Journal of Sports Medicine,2008,29(12):952-958. [27] TOMONAGA S,KAJI Y,TACHIBANA T,et al.Oral administration of -alanine modifies carnosine concentrations in the muscles and brains of chickens[J].Animal Science Journal,2005,76(3):249-254. [28] HOFFMAN J R,EMERSON N S,STOUT J R. -Alanine supplementation[J].Current Sports Medicine Reports,2012,11(4):189-195. [29] TOMONAGA S,MATSUMOTO M,FURUSE M. -alanine enhances brain and muscle carnosine levels in broiler chicks[J].Journal of Poultry Science,2012,49(4):308-312. [30] TOMONAGA S,KANEKO K,KAJI Y,et al.Dietary -alanine enhances brain,but not muscle,carnosine anserine concentrations broilers[J].Animal Science Journal,2006,77(1):79-86. [31] GEDA F,DECLERCQ A,DECOSTERE A,et al. -Alanine does not act through branched-chain amino acid catabolism in carp,a species with low muscular carnosine storage[J].Fish Physiology and Biochemistry,2014,41(1):281-287. [32] EVERAERT I,STEGEN S,VANHEEL B,et al.Effect of beta-alanine and carnosine supplementation on muscle contractility in mice[J].Medicine & Science in Sports & Exercise,2013,45(1):43-51. [33] MEI L ,CROMWELL G L,CRUM A D,et al.Influence of dietary -alanine and histidine on the oxidative stability of pork[J].Meat Science,1998,49(1):55-64. [34] ARISTOY M C,TOLDRÁ F.Histidine dipeptides HPLC-based test for the detection of mammalian origin proteins in feeds for ruminants[J].Meat Science,2004,67(2):211-217. [35] KRALIK G,SAK-BOSNAR M,KRALIK Z,et al.Effects of -alanine dietary supplementation on concentration of carnosine and quality of broiler muscle tissue[J].Journal of Poultry Science,2014,51(2):151-156. [36] ŁUKASIEWICZ M,PUPPLEL K,KUCZYŃSKA B,et al. -Alanine as a factor influencing the content of bioactive dipeptides in muscles of Hubbard Flex chickens[J].Journal of the Science of Food and Agriculture,2015,95(12):2562-2565. [37] INTARAPICHET K O,MAIKHUNTHOD B.Genotype and gender differences in carnosine extracts and antioxidant activities of chicken breast and thigh meats[J].Meat Science,2005,71(4):634-642. [38] 胡新旭. 日粮肌肽、 -丙氨酸和黄芪多糖对肉鸡肉品质的营养调控 [D]. 博士学位论文. 北京: 中国农业大学,2009. [39] STEGEN S,STEGEN B,ALDINI G,et al.Plasma carnosine,but not muscle carnosine,attenuates high-fat diet-induced metabolic stress[J].Applied Physiology,Nutrition,and Metabolism,2015,40(9):868-876. [40] YEUM K J,ORIOLI M,REGAZZONI L,et al.Profiling histidine dipeptides in plasma and urine after ingesting beef,chicken chicken broth humans[J].Amino Acids,2010,38(3):847-858. [41] MANNION A F,JAKEMAN P M,DUNNETT M,et al.Carnosine and anserine concentrations in the quadriceps femoris muscle of healthy humans[J].European Journal of Applied Physiology and Occupational Physiology,1992,64(1):47-50. [42] 韩婷婷, 曹建民, 谭海, 等. 补充 -丙氨酸对间歇运动大鼠肌肉能量代谢生物学指标的影响 [C]//2014 年中国运动生理生化学术会议论文集. 贵阳: 贵州省体育科学学会,2014. [43] RUSS D W,ACKSEL C,BOYD I M,et al.Dietary HMB and -alanine co-supplementation does not improve in situ muscle function in sedentary,aged male rats[J].Applied Physiology,Nutrition,and Metabolism,2015,40(12):1294-1301. [44] WU H C, SHIAU C Y,CHEN H M.Antioxidant activities of carnosine,anserine,some free amino acids their combination[J].Journal Analysis,2003,11(2):148-153. [45] SMITH A E,STOUT J R,KENDALL K L,et al.Exercise-induced oxidative stress:the effects of -alanine supplementation in women[J].Amino Acids,2012,43(1):77-90. [46] HU X X,HONGTRAKUL K,JI C,et al.Effect of carnosine on growth performance,carcass characteristics,meat quality and oxidative stability in broiler chickens[J].Journal of Poultry Science,2009,46(4):296-302. [47] JONG C J,ITO T,MOZAFFARI M,et al. Effect of -alanine treatment on mitochondrial taurine level 5-taurinomethyluridine content[J].Journal of Biomedical Science,2010,17(1):325-332. [48] 刘虹, 刘贺, 王新, 等. 牛磺酸跨膜转运的研究进展 [J]. 中国饲料,2007(14):8-11. [49] MATHERS D A,MCCARTHY S M,COOKE J E,et al.Effects of the -amino acid antagonist TAG on thalamocortical inhibition[J].Neuropharmacology,2009,56(8):1097-1105. [50] JUGE N,OMOTE H,MORIYAMA Y.Vesicular GABA transporter (VGAT) transports -alanine[J].Journal of Neurochemistry,2013,127(4):482-486.

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