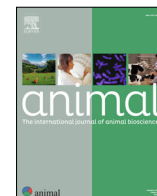




Animal

The international journal of animal biosciences



Dietary supplementation with carnosine reduces the prevalence of breast muscle myopathies without altering performance, meat yield or quality in broiler chickens



A. Askri^a, Y. Martel-Kennes^b, E. Pouliot^c, L. Saucier^{a,d,e}, N. Alnahhas^{a,e,*}

^a Department of Animal Science, Faculty of Agricultural and Food Sciences, Université Laval, 2425 Rue de l'Agriculture, Québec City G1V 0A6 Québec, Canada

^b Sollio Agriculture, 9001 Boulevard de l'Acadie, Bureau 200, Montréal H4H 3H7 Québec, Canada

^c Olymel S.E.C./L.P., Boucherville, 1580 Rue Eiffel, Boucherville J4B 5Y1, Québec, Canada

^d Institute of Nutrition and Functional Foods, Faculty of Agricultural and Food Sciences, Université Laval, 2440 Boulevard Hochelaga, Québec City G1V 0A6 Québec, Canada

^e Swine and Poultry Infectious Diseases Research Center, Faculty of Veterinary Medicine, Université de Montréal, 3200 Rue Sicotte, St-Hyacinthe J2S 2M2 Québec, Canada

ARTICLE INFO

Article history:

Received 24 May 2024

Revised 4 April 2025

Accepted 7 April 2025

Available online 15 April 2025

Keywords:

Broilers

Carnosine

Nutrition

White striping

Wooden breast

ABSTRACT

Breast muscle myopathies such as White striping and Wooden breast represent a major challenge for the poultry industry due to the deterioration of breast meat quality induced by these myopathies. Previous research has demonstrated that oxidative stress and subsequent oxidative damage in the *Pectoralis major* muscle were predisposing factors for the development of breast muscle myopathies. More specifically, research has shown that myopathic muscle content of histidine-containing dipeptides such as carnosine that is well-known for its antioxidant properties was almost entirely depleted, exposing the muscle to oxidative stress and predisposing it to the development of myopathies. The aim of the present study was thus to investigate the effect of dietary carnosine supplementation on growth, meat yield, meat quality and the prevalence of breast muscle myopathies. To achieve this, a total of 1 080 1-day-old male Ross 308 chicks were distributed into two treatment groups in a randomized complete block design with 12 replicates per treatment. The experimental groups included a basal diet and the same basal diet supplemented with 500 mg of carnosine/kg that were fed from d 1 to d 35. The data analysis revealed that apart from a slightly lower ($P = 0.03$) BW at d 21 in the carnosine group compared to the control, final weight, growth and feed conversion were not influenced by the experimental diet. Similarly, carcass weight, carcass yield, yield of carcass cuts and technological quality traits of breast meat did not differ between groups. However, carnosine supplementation was associated with a reduction of the prevalence of White striping ($P < 0.001$), Wooden breast ($P < 0.001$) and the co-occurrence of these two myopathies ($P < 0.001$). Moreover, carnosine supplementation increased ($P < 0.001$) the antioxidant potential of breast muscles while malonaldehyde and carbonyl concentrations remained similar in the experimental group relative to the control group. In conclusion, carnosine supplementation provided promising results with regard to breast muscle myopathies. Further research is needed to elucidate the mechanisms underlying the effect of carnosine on these myopathies.

© 2025 The Author(s). Published by Elsevier B.V. on behalf of The animal Consortium. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Implications

Breast muscle myopathies of non-infectious origin are associated with alteration of the visual aspect of breast meat and with increased hardness of breast fillets which significantly impact consumer satisfaction and their purchase decision. Additionally, these myopathies deteriorate breast meat water-holding capacity and processing ability leading to increased economic losses for the

industry. The importance of the present study is that it demonstrated that the prevalence of these myopathies could be reduced by supplementing broiler diets with 500 mg of carnosine/kg of feed without altering growth performance, feed efficiency, carcass yield or meat quality.

Introduction

In modern commercial broiler chickens, the improved growth rates, higher feed efficiency and greater breast meat yield are mainly achieved through genetic selection (Kuttappan et al.,

* Corresponding author.

E-mail address: nabee.lalnahhas@fsaa.ulaval.ca (N. Alnahhas).

2012a; Petracci and Cavani, 2012; Zuidhof et al., 2014). However, the genetic progress that has been achieved in these traits of economic importance over the years has also been associated with the development of meat quality issues (Alnahhas et al., 2016; Orłowski et al., 2021). Selection-induced myofiber hypertrophy in the pectoral muscles of boiler chickens not only alters muscle metabolism (Boerboom et al., 2018; Boerboom et al., 2023) but also muscle structure which leads to the occurrence of these meat quality issues (Velleman, 2019; Velleman, 2020). In the last decade, three novel breast muscle myopathies (BMM) have been identified in broiler breast muscles: white striping (WS), wooden breast (WB) and spaghetti meat (SM). The occurrence of these abnormalities is associated with an adverse impact on meat quality and on further processed products (Hammemi et al., 2024). Some studies reported that the presence of BMM negatively impacted consumer acceptance and purchasing behavior of chicken breast meat (de Carvalho et al., 2020; Kuttappan et al., 2012b). Additionally, these myopathies have been shown to have a negative effect on technological quality traits by increasing cooking loss and reducing marinade uptake compared with normal fillets (Hammemi et al., 2024; Mudalal et al., 2015). Moreover, meat nutritional quality is significantly modified by these growth-related abnormalities, where a significant decrease in muscle protein content, an increase in collagen content and an increase in intramuscular fat have been reported in affected breast fillets (Baldi et al., 2018; Mudalal et al., 2014; Sammari et al., 2023).

Selection-induced myofiber hypertrophy has been highlighted as a key factor triggering the onset of BMM as this hypertrophy is associated with hypoxia and oxidative damage that predispose the muscle to the development of BMM (Alnahhas et al., 2023; Soglia et al., 2019a). Hypoxia is the result of decreased muscle capillary density which is a known consequence of myofiber hypertrophy (Pampouille et al., 2019; Velleman, 2019). As for oxidative damage, muscles severely affected by WS and WB abnormalities are characterized by an increased oxidative stress resulting in an increased oxidation of lipids and proteins (Li et al., 2022). This increased oxidative stress in myopathic muscles is mainly related to the depletion of muscle reserves of antioxidant molecules (Abasht et al., 2016; Soglia et al., 2019b).

Given their negative economic consequences, solutions to reduce the occurrence of BMM and alleviate their severity are needed. Several studies have investigated the possibility of modifying broiler growth rate using many approaches including varying diet content in energy and protein (i.e., qualitative approach) and applying feed restriction (i.e., quantitative approach; Flees et al., 2024; Rault et al., 2017; Vieira et al., 2021). However, the benefits from these strategies are variable and sometimes confounded by their impact on BW gain and/or breast yield which makes it difficult to draw any meaningful conclusions.

A different approach based on reducing oxidative stress by using exogenous antioxidants in broiler diets has also been investigated (Bodle et al., 2018; Cemin et al., 2018; Sirri et al., 2016). In their study, Sirri et al. (2016) supplemented broiler diets with high and low doses of organic and inorganic trace minerals including Zn, Mn and Cu. Neither the source nor the dose of trace minerals had any impact on the occurrence of WS (60 to 61% of all evaluated fillets) or on WB (11 to 16% of all evaluated fillets). Cemin et al. (2018) also supplemented broiler diets with increasing doses (0.0 to 1.0 PPM) of an organic source of selenium (Zn-L-selenomethionine) and evaluated the impact of this supplementation on the occurrence of BMM. These authors reported that breast fillets from the control group that did not receive the dietary supplement had a significantly ($P < 0.05$) higher percentage of normal fillets than all treatment groups that received the Zn-L-SeMe. This result could be explained by the higher BW gain and breast meat

yield that were reported in this study in the treatment groups compared to the control group.

Another well-known class of potent antioxidants that are naturally present in high concentrations in muscle tissue is histidine-containing dipeptides (HCD). Previous studies have reported a significant depletion of muscle content of HCD including carnosine and anserine in breast fillets exhibiting BMM and have linked their depletion to oxidative stress and consequently to the development of BMM (Abasht et al., 2016; Soglia et al., 2019b). Carnosine is a dipeptide composed of β -alanine and L-histidine, which acts as a natural antioxidant, pH buffer, and metal ion chelator in skeletal muscle tissue (Lackner et al., 2021). It could thus be hypothesized that supplementing broiler diets with carnosine could improve their oxidative status leading to reduced occurrence and severity of BMM. The current study was designed to test this hypothesis. More specifically, it aimed to investigate the effect of dietary carnosine supplementation on (1) the occurrence and severity of BMM, (2) growth performance, meat yield and quality.

Material and methods

Birds, experimental design and housing

The trial was conducted at the Deschambault Research Centre in Animal Science (Deschambault, Quebec, Canada) from May to June 2023. A total of 1 080 1-day-old male Ross 308 chicks were obtained from a local commercial hatchery (Sollio, Quebec, Canada) and assigned to a randomized complete block design with two treatments in 12 blocks. Each treatment was replicated 12 times with 45 chicks placed in each floor pen. Each pen was equipped with a bell drinker and a manual feeder, and the floor was bedded with wood shavings. Stocking density was 30 kg/m² at 35 days of age. Ambient temperature was maintained at 33 °C during the first week, and then, it was gradually reduced to 22 °C by the end of the third week and maintained at 22 °C until the end of the experiment. A lighting program meeting the requirement of Ross 308 was applied during this experiment.

Experimental diets

The composition of the experimental diets used in the current study is presented in Table 1. A corn/soybean-based diet was formulated to meet birds' nutritional requirements according to Rostagno et al. (2024) and was used as a basal diet for each growth phase. The experimental diets were distributed *ad libitum* during the starter (d 0 – d 10), grower (d 11 – d 21) and finisher (d 22 – d 35) phases. These diets included a control (basal) and an experimental diet which was the same basal diet supplemented with 500 mg/kg of L-Carnosine (LCARNO250, Bulk Supplement, USA). This dose of carnosine was chosen based on findings from a previous study showing that a dietary carnosine supplementation of 400 mg/kg of feed had induced a significant increase in the activity of antioxidant enzymes in the serum and a significant decrease in oxidation products in broiler breast muscles at 21 and 42 d (Cong et al., 2017a). Given the severe oxidative damage that BMM induce (Abasht et al., 2016), we increased this dose to 500 mg/kg. Diets were presented in mash form, and the supplement was mixed in the diet according to the above-mentioned dose using a commercial scale feed mixer.

Growth performance, processing, yield of carcass and carcass cuts

Per pen BW was recorded on d 0, 10, 21 and 35. BW gain and feed intake were measured at the end of each growth phase to cal-

Table 1
Composition and calculated nutrient content of the basal broiler diet.

Ingredient ¹ (kg)	Diet		
	Starter	Grower	Finisher
Corn	475.63	512.49	552.54
Soybean meal	246.00	193.00	105.00
Soft wheat	100.00	100.00	100.00
Soya Trituro 44%	100.00	100.00	105.00
Meat meal	47.00	39.00	31.00
Corn gluten 60%	0.0	18.00	19.00
Animal fat	8.00	16.00	21.00
Methionine MHA® 88%	4.46	3.70	3.32
Limestone	4.40	4.80	5.40
Lysine sulfate 70%	3.40	3.20	3.00
NaCl	2.70	2.70	2.80
Threonine 98.5%	1.80	1.40	1.22
NaCO ₃	1.60	1.60	1.80
Vitamin E 50 000 IU	1.00	0.70	0.60
Vitamin premix	1.00	1.00	0.90
Myco-curb	1.00	1.00	1.00
Liquid choline 75%	0.61	0.61	0.54
L-Isoleucine, 98.5%	0.46	0.26	0.36
Phytase	0.34	0.34	0.34
Vitamin D HY®	0.30	0.20	0.18
L-Valine 97%	0.30	0.0	0.0
Calculated nutrients (as fed basis) ²			
CP, %	23.09	21.50	19.54
AMEn ³ , Kcal/kg	2 998.10	3 102.30	3 202.20
D-Lysine, %	1.29	1.15	1.03
D-Met+D-Cys/D-Lys	0.74	0.76	0.78
D-Met/D-Lys	0.54	0.54	0.55
D-Thr/D-Lys	0.67	0.67	0.67
D-Try/D-Lys	0.20	0.20	0.19
D-Arg/D-Lys	1.07	1.07	1.07
D-Hist/D-Lys	0.37	0.39	0.40

¹ The premix contained 12 000 000 IU of vitamin A/kg, 3 500 000 IU of vitamin D/kg, 30 000 IU of vitamin E/kg, 120 000 mg of Zn/kg, 20 000 mg of Cu/kg, 100 mg of Se (as sodium selenite) and 200 mg of organic Se/kg.

² DM content: 87.93, 87.73 and 87.57% for the starter, grower and finisher diets, respectively.

³ AMEn = Apparent metabolizable energy corrected for nitrogen balance.

culate the feed conversion ratio. Mortality was recorded daily, and mortality rate was calculated per growth phase.

On d 35, a total of 80 birds (n = 40 birds/treatment) were randomly selected, individually identified using a leg band, weighed, and transported to a commercial processing unit (Adstock, Quebec, Canada) where they were processed as described by Benahmed et al. (2023). After processing, carcasses were individually placed in plastic bags with their identifiers and brought back on ice to the Food Science laboratory (Faculty of Agricultural and Food Sciences, Université Laval, Quebec, Canada) where they were immediately transferred into a cold room (4 °C). Next, carcass weight and weight of individual carcass parts (whole breast, *Pectoralis major*, *Pectoralis minor*, whole thigh, upper thigh, drumstick and wing) were recorded. The yield of the whole carcass and that of the carcass cuts were then evaluated relative to BW at slaughter (Benahmed et al., 2023).

Meat quality measurements

Meat quality measurements were conducted as previously described (Benahmed et al., 2023; Hammemi et al., 2024). Briefly, after 24 h at 4 °C, the ultimate pH (pHu) and the color parameters including lightness (L*), redness (a*) and yellowness (b*) were measured on the dorsal (bone side) surface of the cranial (the thickest) part of the *Pectoralis major* muscle. The color intensity (chroma, C*) was calculated using Eq. (1) and the hue angle (h) was determined by Eq. (2) as described previously (Andy King et al., 2023).

$$C^* = \sqrt{(a^*^2 + b^*^2)}$$
 (1)

$$h = \text{Tan}^{-1} (b^* / a^*)$$
 (2)

Additionally, drip loss, cooking loss and Warner-Bratzler shear force of cooked fillets were evaluated as described by Hammemi et al. (2024). After 4 months at −20 °C, the other breast fillet of each bird was thawed at 4 °C overnight. On the next day, thawed fillets were weighed to evaluate the freezing-thawing loss that was calculated as the difference in fillet weight before freezing and after thawing and then expressed as a percentage. Next, a sample (60 ± 2 g) was taken from the middle part of each fillet and marinated as described previously (Mudalal et al., 2015). Marinade uptake was evaluated as the difference in weight of meat sample before and after marination. To determine cooking loss after freezing, thawing and marination, meat samples were cooked in an oven using the hot air mode (Rational, SelfCookingCenter® 5 Senses 102E) with the cooking temperature set at 85 °C until an internal sample temperature of 76 °C. After cooking, samples were left to cool down at room temperature, weighed again and the cooking loss was expressed as a percentage of sample weight before cooking.

Breast muscle myopathies

On d 36, a total of 500 birds (n = 250 birds/treatment) were randomly selected from the 12 pens/treatment (10 pens × 21 birds + 2 pens × 20 birds), transported to a commercial federally inspected processing unit (Berthierville, Quebec, Canada) and processed according to commercial practices. Next, the occurrence and severity of BMM including WB, WS and SM were evaluated using the scales described by Tijare et al. (2016), Kuttappan et al. (2016) and Baldi et al. (2021b), respectively, for the three myopathies.

Muscle oxidation parameters

On d 35, 15 birds per treatment were randomly selected without considering their status regarding BMM, weighed, euthanized by cervical dislocation, and samples were taken from the cranial part of the *Pectoralis major* muscle to evaluate oxidation parameters. Samples taken from the *Pectoralis major* muscle were transported on dry ice to the laboratory and then were stored at −80 °C until analysis.

The secondary products of lipid peroxidation were measured using the thiobarbituric acid reactive substances (TBARS) assay, as described by Sammari et al. (2023) with slight modifications. Samples (1 g) were homogenized with 1 mL of 0.88% butylated hydroxytoluene and 9 mL of 30% trichloroacetic acid at a speed of 12 000 rpm. After centrifugation at 3 000 × g for 10 min at 4 °C, 1 mL of the supernatant was transferred to a new tube and mixed with 1 mL of 30% trichloroacetic acid and 1 mL of either the sample or standard solution. Then, 1 mL of 0.09 M thiobarbituric acid was added, and the mixture was thoroughly vortexed. Next, the tubes were incubated in a water bath at 95 °C for 45 min. Samples were then cooled at room temperature for 10 min. Absorbance was measured at 532 nm using a spectrophotometer (Varioskan, Thermo Fisher Scientific, Waltham, MA, USA). The results were expressed in mg of malondialdehyde/kg of meat. This analysis was conducted in triplicates. For the control group, the intra-sample CV ranged from 0.55 to 12.20% and was 6.59% on average, while in the carnosine group, it varied from 1.0 to 10.61% and was 5.41% on average.

Protein carbonylation was quantified in muscle samples from the *Pectoralis major* using the DNPH (2,4-dinitrophenylhydrazine)-based method described by Sammari et al. (2023), with the modifications described by Soglia et al. (2016) aiming to increase protein unfolding and improving carbonyl group labeling with

DNPH. A sample of 1.5 g of meat was homogenized with 10 mL of phosphate buffer (50 mM phosphate buffer pH 6.7 containing 1 mM EDTA) using an Ultraturrax (IKA, Wilmington, NC, USA). Samples were then centrifuged at 4 °C, $4\,700 \times g$ for 10 min. To remove nucleic acids, 100 μ L of 10% streptomycin sulfate (S6501-50G, Sigma-Aldrich, Ontario, Canada) was added to 900 μ L of supernatant and incubated at room temperature for 15 min prior to centrifugation at 4 °C, $6\,000 \times g$ for 10 min. After collecting 200 μ L of supernatant in a new tube and adding 800 μ L of DNPH, the samples were incubated in the dark while vortexing for 15 min. Once the incubation was completed, 1 mL of 20% trichloroacetic acid was added and the samples were centrifuged at 4 °C, $10\,000 \times g$ for 15 min. Next, 400 μ L of 5% SDS were added to the pellet obtained after precipitation in trichloroacetic acid, heating the preparation at 100 °C for 10 min followed by ultrasonication at 40 °C for 30 min. Excess DNPH was removed by three washes with 1 mL of ethanol/ethyl acetate (1:1) followed by vortex mixing and centrifugation at 4 °C, $10\,000 \times g$ for 15 min. After each wash, the supernatant was discarded. Following the last wash, 500 μ L of guanidine hydrochloride (6 M) was added, vortexed to resuspend the precipitated protein pellet, and then centrifuged at 4 °C, $10\,000 \times g$ for 15 min. Absorbance was measured on the supernatant using a spectrophotometer (Varioskan, Thermo Fisher Scientific, Waltham, MA, USA) at 370 nm to determine carbonyl concentration. The concentration of DNPH was expressed in nmol of carbonyls/mg of protein. Calculations were performed as described in [Soglia et al. \(2016\)](#). This analysis was conducted on one replicate per sample.

Antioxidant potential of breast muscles

Antioxidant capacity of muscle samples was measured according to [Wu et al. \(2004\)](#), with some modifications to sample preparation. Muscle samples were powdered in liquid nitrogen using a mortar and pestle. Powdered muscle samples were then extracted in 20% ethanol as described in [Wu et al. \(2008\)](#) with modifications. Briefly, 250 mg of sample powder was extracted in 5 mL ethanol 20% using an ultrasound bath heated at 37 °C for 10 min then agitated on a horizontal shaker for 10 min. Extracts were then centrifuged for 10 min at $3\,400 \times g$, and the resulting pellets were extracted a second time using the same conditions. Both supernatants were combined and diluted in phosphate buffer 0.075 M to measure the antioxidant capacity as described by [Wu et al. \(2004\)](#). Hydrophilic ORACFL assays were carried out on a FLUOstar Galaxy plate reader equipped with an incubator and one injection pump. The incubator was set to a temperature of 37 °C. The AAPH solution was used as peroxy generator and Trolox as a standard. Twenty μ L of sample, blank, and Trolox calibration solutions were transferred to 96-well microplates in triplicate. A total of 200 μ L of fluorescein solution was added per well (7.5 nmoles), and 75 μ L of AAPH (8.6 mg/mL) was added by the injector in the microplate reader at cycle 4. The plate reader was programmed to record the fluorescence of fluorescein each cycle, and the parameters and calculations are exactly as described by [Wu et al. \(2004\)](#). This assay was performed in triplicates. In the control group, the intra-sample CV ranged from 0.62 to 8.21% with an average of 3.56% across all samples. In the carnosine group, the intra-sample CV varied from 0.36 to 8.21% with an average of 4.26% across all samples.

Statistical analysis

The effect of treatment on measured quantitative traits was analyzed using a linear mixed-effects model that was fitted to the data using the R package *lmerTest* ([Kuznetsova et al., 2017](#)). The model included the treatment as a fixed effect while the effect of the block was fitted as a random effect when the sampling unit

was the pen. When the sampling unit was the bird, a pen intra-block was also fitted as a random effect to account for random variations between pens. The results of these analyses were reported as the least squares means and their SEs. Differences between treatment means were tested for significance using the Tukey method as implemented in the *emmeans* package of R ([R Core Team, 2020](#)). For breast muscle myopathies that were evaluated on a discrete scale, Fisher's Exact test as implemented in R was used to analyze the effect of treatment on these myopathies. Treatment effects and differences between treatment groups were considered statistically significant at $P < 0.05$.

Results

Effect of dietary treatments on performance, carcass yield, yield of carcass cuts and meat quality

The effect of dietary treatments on BW, feed intake, feed conversion ratio and mortality rate for the starter, grower and finisher phases is presented in [Table 2](#). The statistical analysis revealed that carnosine supplementation did not alter any of the above-mentioned performance traits except for BW on d 21 that was significantly lower in the carnosine-fed group compared to the control.

In this study, the statistical analysis did not reveal any significant effect of carnosine supplementation on carcass or meat yield in comparison to the control group ([Table 3](#)). The effect of treatment on the technological quality traits of breast meat and on its aptitude for further transformation is presented in [Table 4](#). As can be seen in this table, supplementing boiler diets with carnosine was not associated with significant changes in the quality attributes of breast meat.

Effect of dietary treatments on breast muscle myopathies

The effect of the treatment on the prevalence of WS and WB is presented in [Table 5](#). In the total population of samples ($n = 500$), the percentage of normal breast fillets and breast fillets exhibiting mild and moderate WS was 49.80, 42.66, and 7.14%, respectively. Very few fillets (0.40%) exhibited severe WS. The effect of treatment on the prevalence and severity of WS was highly significant. Carnosine-fed broilers had a significantly higher percentage of normal breast fillets and a significantly lower percentage of mildly WS-affected fillets in comparison to the control group.

As for WB, 60.52% of evaluated breast fillets ($n = 500$) exhibited some degree of this myopathy. In this population of WB-affected breast fillets, 32.14, 24.21 and 4.17% were mildly, moderately, and severely affected, respectively. Similar to WS, Fisher's Exact test revealed a significant treatment effect on WB. Birds from the carnosine-fed group exhibited a significantly lower percentage of moderately WB-affected fillets and a significantly higher percentage of normal breast fillets than the control group.

In the current study, 40.08% of evaluated breast fillets ($n = 500$) exhibited either WS or WB, while 35.32% of these fillets exhibited some degree of both myopathies simultaneously. In comparison to the control group, the carnosine-fed group exhibited a significantly lower percentage of breast fillets affected by both myopathies simultaneously ([Table 6](#)).

Effect of dietary treatments on the antioxidant potential, lipid, and protein oxidation in the breast muscles

Dietary carnosine supplementation was associated with a significant increase in the antioxidant potential of the *Pectoralis major* muscle compared to the control group ([Table 7](#)). However, this

Table 2
Effect of the control and carnosine-supplemented diets on broiler performance¹.

Age (d)	Trait ²	Diet ³		SEM	P-value
		Control	Carnosine		
0–10	BW, g	257.0	260.0	4.78	0.56
	FI, g/bird	268.0	264.0	4.03	0.10
	FCR	1.28	1.22	0.02	0.10
	Mortality, %	1.66	0.93	0.41	0.21
11–21	BW, g	1 046.0	1 020.0	8.96	0.03
	FI, g/bird	993.0	990.0	13.20	0.92
	FCR	1.37	1.36	0.01	0.86
	Mortality, %	0.56	0.75	0.36	0.68
22–35	BW, g	2 724.0	2 704.0	40.10	0.68
	FI, g/bird	2 140.0	2 130.0	29.50	0.52
	FCR	1.56	1.58	0.02	0.53
	Mortality, %	0.78	0.18	0.39	0.18

¹ Values are least squares means of 12 pens per treatment, with their respective standard errors (SEM).² FI = feed intake, FCR = feed conversion ratio.³ Control: a basal control diet without supplementation, Carnosine: the same basal diet supplemented with 500 mg of carnosine/kg of feed from day 1 to day 35.**Table 3**
Effect of the control and carnosine-supplemented diets on broiler carcass and meat yields¹.

Trait ²	Diet ³		SEM	P-value
	Control	Carnosine		
BW35, g	2 380.0	2 340.0	48.10	0.57
Carcass, %	74.1	73.2	0.44	0.10
BMV, %	19.20	19.40	0.35	0.58
TY, %	28.70	28.40	0.21	0.37
UTY, %	18.60	18.30	0.19	0.34
Drumstick, %	10.10	10.07	0.11	0.71
Wings, %	7.78	7.64	0.09	0.23

¹ Values are least squares means of 40 samples per treatment, with their respective standard errors (SEM).² BW35 = BW at slaughter, BMV = breast meat yield, TY = thigh yield, UTY = yield of the upper part of the thigh.³ Control: a basal control diet without supplementation, Carnosine: the same basal diet supplemented with 500 mg of carnosine/kg of feed from day 1 to day 35.**Table 4**
Effect of the control and carnosine-supplemented diets on broiler breast meat quality traits¹.

Trait ²	Diet ³		SEM	P-value
	Control	Carnosine		
pHu	5.77	5.76	0.02	0.59
L*	59.5	59.8	0.42	0.55
a*	5.95	6.89	0.43	0.12
b*	17.10	17.60	0.29	0.19
C*	18.20	19.10	0.38	0.07
h*	1.24	1.21	0.02	0.41
DL, %	7.36	7.26	0.86	0.90
CL, %	19.30	18.70	0.45	0.17
WBSF, N/cm2	21.10	19.90	1.95	0.21
Freeze-Thaw, %	9.77	10.80	1.55	0.63
Marinade uptake, %	7.98	7.91	0.27	0.85
CLTM, %	12.40	11.80	0.28	0.22

¹ Values are least squares means of 40 samples per treatment, with their respective standard errors (SEM).² pHu = ultimate pH of the *Pectoralis major* muscle, L* = lightness, a* = redness, b* = yellowness, C* = chroma, h* = hue angle, DL = drip loss, CL = cooking loss, WBSF = Warner-Bratzler shear force, CLTM = cooking loss after thawing and marination.³ Control: a basal control diet without supplementation, Carnosine: the same basal diet supplemented with 500 mg of carnosine/kg of feed from day 1 to day 35.

increase in the antioxidant potential was not associated with changes in lipid peroxidation, as measured by the TBARS index, or in protein oxidation, as measured by the concentration of carbonyls (Table 7).

Discussion

Due to their impact on the visual aspect of breast fillets and on the technological quality traits of breast meat, BMM represent an

important challenge for the poultry industry. Despite all the progress that has been made in terms of understanding the mechanisms underlying the development of BMM (Alnahhas et al., 2023; Petracci et al., 2019), solutions to reduce their prevalence and severity without deteriorating performance traits are still lacking. The current study was designed to investigate the effect of carnosine, a histidine-containing dipeptide, on broiler performances, meat quality and the occurrence of BMM. The dietary supplementation of carnosine used in this study is based on previous studies

Table 5Effect of the control and carnosine-supplemented diets on the prevalence (%) of broiler breast muscle myopathies¹.

Myopathy ²	Degree	Diet ³		P-Value ⁴
		Control	Carnosine	
WS	Normal	38.58 ^b	61.20 ^a	<0.001
	Mild	57.09 ^a	28.00 ^b	
	Moderate	4.30	10.00	
	Severe	0.00	0.80	
WB	Normal	27.95 ^b	51.2 ^a	<0.001
	Mild	33.10	31.2	
	Moderate	36.22 ^a	12.00 ^b	
	Severe	2.80	5.60	

Different superscripts (^{a–b}) within the same severity degree (Normal, Mild, Moderate, Severe) and within the same myopathy (WS, WB) indicate a significant difference between treatments at $P < 0.05$. Posthoc pairwise comparisons were conducted using the Chi-squared test, and the corresponding P -values were Bonferroni-adjusted. The absence of superscripts indicates a Bonferroni-adjusted P -value > 0.05 .

¹ Values presented in this table are expressed as percentages, based on 250 samples per group.

² WS = White striping, WB = Wooden breast.

³ Control: a basal control diet without supplementation, Carnosine: the same basal diet supplemented with 500 mg of carnosine/kg of feed from day 1 to day 35.

⁴ P -values of Fisher's Exact test.

Table 6Effect of the control and carnosine-supplemented diets on the co-occurrence (%) of white striping and wooden breast in broiler breast muscles¹.

Myopathy ²	Diet ³		P-Value ⁴
	Control	Carnosine	
Normal	15.35 ^b	34.00 ^a	<0.001
WS/WB	35.80	44.00	
WS+WB	48.82 ^a	21.60 ^b	

Different superscripts (^{a–b}) within the same category of myopathy indicate a significant difference at $P < 0.05$. Posthoc pairwise comparisons were performed using the Chi-squared test, and the corresponding P -values were Bonferroni-adjusted. The absence of superscripts indicates a Bonferroni-adjusted P -value > 0.05 .

¹ Values presented in this table are expressed as percentages, based on 250 samples per group.

² Normal = normal breast fillets, WS/WB = breast fillets exhibiting either white striping or wooden breast, WS+WB = breast fillets exhibiting white striping and wooden breast.

³ Control: a basal control diet without supplementation, Carnosine: the same basal diet supplemented with 500 mg of carnosine/kg of feed from day 1 to day 35.

⁴ P -values of Fisher's Exact test.

showing a severe depletion of HCD content in BMM-affected breast fillets (Abasht et al., 2016; Soglia et al., 2019b).

In terms of performance, supplementation with carnosine did not influence growth, feed efficiency or mortality rate. These findings are in line with previous reports from the literature. For instance, Cong et al. (2017b) supplemented broiler diets with increasing concentration of carnosine from 0.0 to 400 mg/kg of feed and noted that this supplementation had no impact on growth performance or feed conversion except for the feed-to-gain ratio that was slightly lower compared to the control group at the end of the starter phase. On the other hand, Kopec et al. (2020) supplemented broiler diets with a considerably higher dose (2 700 mg/kg) of carnosine and observed a significant increase in BW and in feed intake at d 28. However, an earlier study reported that carnosine supplementation at an even higher dose (5 000 mg/kg) in broi-

ler diets from d 1 to d 42 had no effect on BW, weight gain, feed intake or conversion ratio (Hu et al., 2009). These findings seem to suggest the presence of an optimal threshold where carnosine could enhance BW and beyond which carnosine no longer impacts performance. This dose-response relationship between carnosine and performances requires further investigation to be elucidated.

In the current study, carnosine supplementation had no impact on carcass yield or on the yield of carcass cuts compared to the control group. This finding is not in agreement with the findings reported in previous studies. In fact, both Kopec et al. (2020) and Hu et al. (2009) reported an increase in breast meat yield in the carnosine-supplemented groups compared to the control group in their respective studies. Both studies speculated that this increase in breast meat yield could have been induced by an increased secretion of insulin based on previous studies on rats

Table 7Effect of the control and carnosine-supplemented diets on the antioxidant potential, lipid peroxidation and protein oxidation of broiler breast muscles¹.

Parameter ²	Diet ³		SEM	P-value
	Control	Carnosine		
TBARS, mg of MDA ⁴ /kg of meat	0.21	0.20	0.009	0.30
Carbonyls, mg/g of protein	6.97	6.88	0.37	0.80
Trolox, μ mol equivalent /g of muscle	16.5	20.7	1.21	<0.001

¹ Values are the least squares means of 15 samples per group, with their respective standard errors (SEM).

² TBARS = the thiobarbituric acid reactive substances index, Trolox = the antioxidant potential of muscle tissue expressed as Trolox equivalent.

³ Control: a basal control diet without supplementation, Carnosine: the same basal diet supplemented with 500 mg of carnosine/kg of feed from day 1 to day 35.

⁴ MDA = Malondialdehyde.

and dogs (LeBlanc and Soucy, 1994; Yamano et al., 2001). One possible explanation for the lack of effect of carnosine on breast meat yield and on other carcass cuts in the present study is the dose of carnosine that was lower compared to previous studies. Additionally, differences in strain and age at processing between our study and previous studies could also have contributed to the differences in findings. It is worth mentioning that BW at slaughter, carcass yield and yield of carcass cuts were all within the range of values reported in the literature under Canadian (Quebec) conditions (Benahmed et al., 2023; Hammemi et al., 2024).

In this study, carnosine supplementation was not associated with significant changes in breast meat quality traits. These findings are in line with the ones reported in the literature. In the study of Cong et al. (2017a), the effect of carnosine on the pHu of the *Pectoralis major* muscle was not significant over a range of carnosine doses varying between 0.0 and 400 mg/kg. In fact, the only significant changes these authors reported in meat quality traits were a slight decrease ($P < 0.001$) in drip loss (2.32 vs 1.99% in the control and 400 mg/kg group, respectively) and a slight increase ($P = 0.043$) in redness (a^*) of breast fillets (1.88 vs 2.51 units in the control and 400 mg/kg group, respectively). However, meat shear force and texture properties were not influenced by carnosine supplementation. Similarly, Hu et al. (2009) did not evidence significant differences in pHu or in meat color except for a^* that was higher ($P < 0.05$) in the carnosine-supplemented group compared to the control group (4.11 vs 3.60 for the carnosine and control group, respectively) contrary to findings for a^* in the above-cited study. Additionally, water-holding capacity was not impacted by the carnosine supplementation in the study of Hu et al. (2009). A recent study suggested that a high concentration of HCD in breast muscles could reduce *postmortem* acidification and subsequent *postmortem* decline of pH due to an increase in the buffering capacity of breast muscles under the effect of HCD (Baldi et al., 2021a). Reduced *postmortem* acidification could help to understand the lack of effect of carnosine supplementation on meat quality. It is important to note that myopathic muscles have a lower glycogen content than normal muscles (Abasht et al., 2016) which also translates into lower *postmortem* acidification. However, it is unclear if carnosine supplementation could further decrease *postmortem* acidification in the presence of BMM. Overall, our findings and findings from the literature suggest that carnosine supplementation has a limited effect on breast meat quality traits when supplemented at doses in the range of 400 to 500 mg/kg of feed.

Carnosine is well known for its antioxidant properties and its concentration has been shown to improve oxidative stability of muscle and meat (Manhiani et al., 2011; O'Neill et al., 1998). Previous studies have shown that BMM-affected muscles were severely depleted of carnosine and suggested that this could predispose muscles to the occurrence of BMM under oxidative stress conditions such as those induced by greater muscle growth and development (Abasht et al., 2016; Soglia et al., 2019b). In the present study, incorporating carnosine in broilers' diets led to a significant increase in the total antioxidant potential of breast muscles. This result agrees with findings from previous reports showing that carnosine supplementation was associated with increased total antioxidant capacity and increased activity of antioxidant enzymes including glutathione peroxidase (Cong et al., 2017a; Kopec et al., 2020). The increase in the antioxidant potential of breast muscles from carnosine-fed broilers could thus partly explain the reduced prevalence of BMM in this study. However, contrary to findings from the above-cited studies, the increased antioxidant potential in breast muscles of the carnosine-fed group in the current work was not associated with a significant decrease in the concentrations of lipid and protein oxidation products in comparison to the control group. One possible explanation for this is that very few breast fillets exhibiting severe degrees of WS and

WB were found in the present study and that high levels of lipid and protein oxidation are usually associated with these severe forms of BMM (Alnahhas et al., 2023). Lipid and protein oxidation levels remained thus low in the breast muscles of both groups of the current study. Consequently, carnosine supplementation and the associated improvement in muscle antioxidant potential would only have a limited impact in terms of reducing an already low oxidation level. This statement is partly supported by the similar breast meat yield in both groups indicating similar muscle development and growth levels in birds from both groups. It is also important to note that in the current study, muscle samples were immediately frozen after sampling and stored at -80°C until they were analyzed. Samples thus remained somewhat fresh after a single freeze-thaw cycle. This could have limited the development of oxidative process and led to the low levels of oxidation products in muscle samples. Further research is needed to investigate and understand the underlying mechanism of action of carnosine in terms of reducing the prevalence of BMM.

Conclusion

Carnosine supplementation (500 mg/kg) in broilers' diets was not associated with noticeable changes in performance, meat yield or technological quality traits. However, it significantly reduced the prevalence of breast muscle myopathies including white striping and wooden breast. This reduction in the prevalence of breast muscle myopathies might be mediated by an increase in the antioxidant potential of breast muscles due to carnosine supplementation. Further research is required to understand the mechanisms underlying the effect of carnosine supplementation on breast muscle myopathies.

Ethics approval

The experimental procedures and animal care were reviewed and approved by the Institutional Animal Care and Use Committee of Université Laval (CPAUL) that is accredited by the Canadian Council of Animal Care (Project #2023-1272).

Data and model availability statement

The data/models were not deposited in an official repository. The data generated and analyzed in this study can be made available upon request from the corresponding author.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

Author ORCIDs

Askri, A.: <https://orcid.org/0000-0002-0162-6748>.

Saucier, L.: <https://orcid.org/0000-0003-2401-5891>.

Alnahhas, N.: <https://orcid.org/0000-0002-3760-9253>.

CRediT authorship contribution statement

A. Askri: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Y. Martel-Kennes:** Writing – review & editing, Methodology, Conceptualization. **E. Pouliot:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **L. Saucier:** Writing – review & editing, Supervi-

sion, Funding acquisition, Conceptualization. **N. Alnahhas:** Writing – review & editing, Supervision, Funding acquisition, Data curation, Conceptualization.

Declaration of interest

None.

Acknowledgements

The authors acknowledge the technical support they received from the staff of the Deschambault Research Centre in Animal Science (CRSAD), from the staff of the Centre de Développement du Porc du Québec (CDPQ) and from DSM-Firmenich (Ontario, Canada). The authors thank the Swine and Poultry Infectious Diseases Research Center (<https://www.cripa.center/>) for the financial support that was granted to Amani Askri.

Financial support statement

This research was supported by the MAPAQ Research Chair on meat quality and safety–Musculo (<https://musculo.fsa.ulaval.ca/>) funded under grant number PPIA13 by the Agri-Food Innovation Partnership Program, under the Canadian Agricultural Partnership, an agreement between the governments of Canada and of Quebec (Ministère de l'Agriculture des Pêcheries et de l'Alimentation du Québec MAPAQ), and by Olymel S.E.C./L.P., Choisy Laboratories Ltd., a subsidiary of the Kersia Group, and the Centre de développement du porc du Québec.

References

- Abasht, B., Mutryn, M.F., Michalek, R.D., Lee, W.R., 2016. Oxidative stress and metabolic perturbations in wooden breast disorder in chickens. *PLoS One* 11, e0153750. <https://doi.org/10.1371/journal.pone.0153750>.
- Alnahhas, N., Berri, C., Chabault, M., Chartrin, P., Boulay, M., Bourin, M.C., Le Bihan-Duval, E., 2016. Genetic parameters of white striping in relation to body weight, carcass composition, and meat quality traits in two broiler lines divergently selected for the ultimate pH of the pectoralis major muscle. *BMC Genetics* 17, 61. <https://doi.org/10.1186/s12863-016-0369-2>.
- Alnahhas, N., Pouliot, E., Saucier, L., 2023. The hypoxia-inducible factor 1 pathway plays a critical role in the development of breast muscle myopathies in broiler chickens: a comprehensive review. *Frontiers in Physiology* 14, 1260987. <https://doi.org/10.3389/fphys.2023.1260987>.
- Andy King, D., Hunt, M.C., Barbut, S., Claus, J.R., Cornforth, D.P., Joseph, P., Kim, Y.H. B., Lindahl, G., Mancini, R.A., Nair, M.N., Merok, K.J., Milkowski, A., Mohan, A., Pohlman, F., Ramanathan, R., Raines, C.R., Seyfert, M., Sorheim, O., Suman, S.P., Weber, M., 2023. American meat science association guidelines for meat color measurement. *Meat and Muscle Biology* 6, 1–81. <https://doi.org/10.22175/mmb.12473>.
- Baldi, G., Soglia, F., Mazzoni, M., Sirri, F., Canonico, L., Babini, E., Laghi, L., Cavani, C., Petracci, M., 2018. Implications of white striping and spaghetti meat abnormalities on meat quality and histological features in broilers. *Animal* 12, 164–173. <https://doi.org/10.1017/s1751731117001069>.
- Baldi, G., Soglia, F., Laghi, L., Meluzzi, A., Petracci, M., 2021a. The role of histidine dipeptides on postmortem acidification of broiler muscles with different energy metabolism. *Poultry Science* 100, 1299–1307. <https://doi.org/10.1016/j.psj.2020.11.032>.
- Baldi, G., Soglia, F., Petracci, M., 2021b. Spaghetti Meat Abnormality in Broilers: Current Understanding and Future Research Directions. *Frontiers in Physiology* 12, 684497. <https://doi.org/10.3389/fphys.2021.684497>.
- Benahmed, S., Askri, A., de Rauglaudre, T., Létourneau-Montminy, M.-P., Alnahhas, N., 2023. Effect of reduced crude protein diets supplemented with free limiting amino acids on body weight, carcass yield, and breast meat quality in broiler chickens. *Poultry Science* 102, 103041. <https://doi.org/10.1016/j.psj.2023.103041>.
- Bodde, B.C., Alvarado, C., Shirley, R.B., Mercier, Y., Lee, J.T., 2018. Evaluation of different dietary alterations in their ability to mitigate the incidence and severity of woody breast and white striping in commercial male broilers. *Poultry Science* 97, 3298–3310. <https://doi.org/10.3382/ps/pey166>.
- Boerboom, G.M., Navarro-Villa, A., van Kempen, T.A.T.G., 2023. Metabolomic analysis of wooden breast myopathy shows a disturbed lipid metabolism. *Metabolites* 13, 20. <https://doi.org/10.3390/metabo13010020>.
- Boerboom, G., van Kempen, T., Navarro-Villa, A., Perez-Bonilla, A., 2018. Unraveling the cause of white striping in broilers using metabolomics. *Poultry Science* 97, 3977–3986. <https://doi.org/10.3382/ps/pey266>.
- Cemin, H.S., Vieira, S.L., Stefanello, C., Kindlein, L., Ferreira, T.Z., Fireman, A.K., 2018. Broiler responses to increasing selenium supplementation using Zn-L-selenomethionine with special attention to breast myopathies. *Poultry Science* 97, 1832–1840. <https://doi.org/10.3382/ps/pey001>.
- Cong, J., Zhang, L., Li, J., Wang, S., Gao, F., Zhou, G., 2017a. Effects of dietary supplementation with carnosine on meat quality and antioxidant capacity in broiler chickens. *British Poultry Science* 58, 69–75. <https://doi.org/10.1080/00071668.2016.1237767>.
- Cong, J.H., Zhang, L., Li, J.L., Wang, S.H., Gao, F., Zhou, G.H., 2017b. Effects of dietary supplementation with carnosine on growth performance, meat quality, antioxidant capacity and muscle fiber characteristics in broiler chickens. *Journal of the Science of Food and Agriculture* 97, 3733–3741. <https://doi.org/10.1002/jsfa.8236>.
- de Carvalho, L.M., Ventanas, S., Olegario, L.S., Madruga, M.S., Estévez, M., 2020. Consumers awareness of white-striping as a chicken breast myopathy affects their purchasing decision and emotional responses. *LWT – Food Science and Technology* 131, 109809. <https://doi.org/10.1016/j.lwt.2020.109809>.
- Flees, J.J., Keel, A.J., Gregg, C.R., Starkey, C.W., Starkey, J.D., 2024. Effects of light intensity and reduction of starter diet digestible lysine and metabolizable energy on broiler chicken growth performance, breast meat yield, and meat quality defects. *Poultry Science* 103, 103222. <https://doi.org/10.1016/j.psj.2023.103222>.
- Hammami, C., Askri, A., Létourneau-Montminy, M.P., Alnahhas, N., 2024. Current state of breast meat quality in standard-yielding broiler strains. *Journal of Applied Poultry Research* 33, 100383. <https://doi.org/10.1016/j.japr.2023.100383>.
- Hu, X.X., Hongtrakul, K., Ji, C., Ma, Q.G., Guan, S., Song, C.L., Zhang, Y., Zhao, L.H., 2009. Effect of carnosine on growth performance, carcass characteristics, meat quality and oxidative stability in broiler chickens. *Poultry Science* 46, 296–302. <https://doi.org/10.2141/jpsa.46.296>.
- Kopec, W., Jamroz, D., Wilczkiewicz, A., Biazik, E., Pudlo, A., Korzeniowska, M., Hikawczuk, T., Skiba, T., 2020. Antioxidative characteristics of chicken breast meat and blood after diet supplementation with carnosine, L-histidine, and β -alanine. *Antioxidants* 9, 1093. <https://doi.org/10.3390/antiox9111093>.
- Kuttappan, V.A., Brewer, V.B., Apple, J.K., Waldrup, P.W., Owens, C.M., 2012a. Influence of growth rate on the occurrence of white striping in broiler breast fillets. *Poultry Science* 91, 2677–2685. <https://doi.org/10.3382/ps.2012-02259>.
- Kuttappan, V.A., Lee, Y.S., Erf, G.F., Meullenet, J.F., McKee, S.R., Owens, C.M., 2012b. Consumer acceptance of visual appearance of broiler breast meat with varying degrees of white striping. *Poultry Science* 91, 1240–1247. <https://doi.org/10.3382/ps.2011-01947>.
- Kuttappan, V.A., Hargis, B.M., Owens, C.M., 2016. White striping and woody breast myopathies in the modern poultry industry: a review. *Poultry Science* 95, 2724–2733. <https://doi.org/10.3382/ps/pew216>.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lackner, J., Albrecht, A., Mittler, M., Marx, A., Kreyenschmidt, J., Hess, V., Sauerwein, H., 2021. Effect of feeding histidine and β -alanine on carnosine concentration, growth performance, and meat quality of broiler chickens. *Poultry Science* 100, 101393. <https://doi.org/10.1016/j.psj.2021.101393>.
- LeBlanc, J., Soucy, J., 1994. Effects of carnosine on insulin and glucagon secretion in the dog. *Nutrition Research* 14, 1655–1660. [https://doi.org/10.1016/S0271-5317\(05\)80320-3](https://doi.org/10.1016/S0271-5317(05)80320-3).
- Li, B., Dong, X., Puolanne, E., Ertbjerg, P., 2022. Effect of wooden breast degree on lipid and protein oxidation and citrate synthase activity of chicken pectoralis major muscle. *LWT – Food Science and Technology* 154, 112884. <https://doi.org/10.1016/j.lwt.2021.112884>.
- Manhiani, P.S., Northcutt, J.K., Han, I., Bridges, W.C., Scott, T.R., Dawson, P.L., 2011. Effect of stress on carnosine levels in brain, breast, and thigh of broilers. *Poultry Science* 90, 2348–2354. <https://doi.org/10.3382/ps.2011-01426>.
- Mudalal, S., Babini, E., Cavani, C., Petracci, M., 2014. Quantity and functionality of protein fractions in chicken breast fillets affected by white striping. *Poultry Science* 93, 2108–2116. <https://doi.org/10.3382/ps.2014-03911>.
- Mudalal, S., Lorenzi, M., Soglia, F., Cavani, C., Petracci, M., 2015. Implications of white striping and wooden breast abnormalities on quality traits of raw and marinated chicken meat. *Animal* 9, 728–734. <https://doi.org/10.1017/s175173111400295x>.
- O'Neill, L.M., Galvin, K., Morrissey, P.A., Buckley, D.J., 1998. Inhibition of lipid oxidation in chicken by carnosine and dietary α -tocopherol supplementation and its determination by derivative spectrophotometry. *Meat Science* 50, 479–488. [https://doi.org/10.1016/s0309-1740\(98\)00061-8](https://doi.org/10.1016/s0309-1740(98)00061-8).
- Orlowski, S.K., Dridi, S., Greene, E.S., Coy, C.S., Velleman, S.G., Anthony, N.B., 2021. Histological analysis and gene expression of satellite cell markers in the pectoralis major muscle in broiler lines divergently selected for percent 4-day breast yield. *Frontiers in Physiology* 12, 71209. <https://doi.org/10.3389/fphys.2021.71209>.
- Pampouille, E., Hennequet-Antier, C., Praud, C., Juanchich, A., Brionne, A., Godet, E., Bordeau, T., Fagnoul, F., Le Bihan-Duval, E., Berri, C., 2019. Differential expression and co-expression gene network analyses reveal molecular mechanisms and candidate biomarkers involved in breast muscle myopathies in chicken. *Scientific Reports* 9, 14905. <https://doi.org/10.1038/s41598-019-51521-1>.

- Petracci, M., Cavani, C., 2012. Muscle growth and poultry meat quality issues. *Nutrients* 4, 1–12. <https://doi.org/10.3390/nu4010001>.
- Petracci, M., Soglia, F., Madruga, M., Carvalho, L., Ida, E., Estevez, M., 2019. Wooden-breast, white striping, and spaghetti meat: causes, consequences and consumer perception of emerging broiler meat abnormalities. *Comprehensive Reviews in Food Science and Food Safety* 18, 565–583. <https://doi.org/10.1111/1541-4337.12431>.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria doi: <https://www.r-project.org/>.
- Rault, J.-L., Clark, K., Groves, P.J., Cronin, G.M., 2017. Light intensity of 5 or 20 lux on broiler behavior, welfare and productivity. *Poultry Science* 96, 779–787. <https://doi.org/10.3382/ps/pew423>.
- Rostagno, H.S., Teixeira, G., Donzele, J.L., Gomes, P.C., Oliveira, R., Lopes, D.C., Ferreira, A., Barreto, S.T., Albino, L.F.T., Oliveira, R., Ferreira, A.d.S., Barreto, S.T., Teixeira-Carvalho, A., Euclides, R., 2024. Brazilian Tables for Poultry and Swine: composition of feedstuffs and nutritional requirements, fifth ed. Department of Animal Science, Federal University of Viçosa, Viçosa, Brazil.
- Sammari, H., Askri, A., Benahmed, S., Saucier, L., Alnahhas, N., 2023. A survey of broiler breast meat quality in the retail market of Quebec. *Canadian Journal of Animal Science* 103, 298–311. <https://doi.org/10.1139/cjas-2023-0001>.
- Sirri, F., Maiorano, G., Tavaniello, S., Chen, J., Petracci, M., Meluzzi, A., 2016. Effect of different levels of dietary zinc, manganese, and copper from organic or inorganic sources on performance, bacterial chondronecrosis, intramuscular collagen characteristics, and occurrence of meat quality defects of broiler chickens. *Poultry Science* 95, 1813–1824. <https://doi.org/10.3382/ps/pew064>.
- Soglia, F., Petracci, M., Erbjerg, P., 2016. Novel DNPH-based method for determination of protein carbonylation in muscle and meat. *Food Chemistry* 197, 670–675. <https://doi.org/10.1016/j.foodchem.2015.11.038>.
- Soglia, F., Mazzoni, M., Petracci, M., 2019a. Spotlight on avian pathology: current growth-related breast meat abnormalities in broilers. *Avian Pathology* 48, 1–3. <https://doi.org/10.1080/03079457.2018.1508821>.
- Soglia, F., Silva, A.K., Liao, L.M., Laghi, L., Petracci, M., 2019b. Effect of broiler breast abnormality and freezing on meat quality and metabolites assessed by H-1-NMR spectroscopy. *Poultry Science* 98, 7139–7150. <https://doi.org/10.3382/ps/pez514>.
- Tijare, V.V., Yang, F.L., Kuttappan, V.A., Alvarado, C.Z., Coon, C.N., Owens, C.M., 2016. Meat quality of broiler breast fillets with white striping and woody breast muscle myopathies. *Poultry Science* 95, 2167–2173. <https://doi.org/10.3382/ps/pew129>.
- Velleman, S.G., 2019. Recent developments in breast muscle myopathies associated with growth in poultry. *Annual Review of Animal Biosciences* 7, 289–308. <https://doi.org/10.1146/annurev-animal-020518-115311>.
- Velleman, S.G., 2020. Pectoralis major (breast) muscle extracellular matrix fibrillar collagen modifications associated with the wooden breast fibrotic myopathy in broilers. *Frontiers in Physiology* 11, 461. <https://doi.org/10.3389/fphys.2020.00461>.
- Vieira, S.L., Simões, C.T., Kindlein, L., Ferreira, T.Z., Soster, P., Stefanello, C., 2021. Progressive in vivo detection of wooden breast in broilers as affected by dietary energy and protein. *Poultry Science* 100, 101120. <https://doi.org/10.1016/j.psj.2021.101120>.
- Wu, X., Beecher, G.R., Holden, J.M., Haytowitz, D.B., Gebhardt, S.E., Prior, R.L., 2004. Lipophilic and hydrophilic antioxidant capacities of common foods in the United States. *Journal of Agricultural Food Chemistry* 52, 4026–4037. <https://doi.org/10.1021/jf049696w>.
- Wu, C., Duckett, S.K., Neel, J.P., Fontenot, J.P., Clapham, W.M., 2008. Influence of finishing systems on hydrophilic and lipophilic oxygen radical absorbance capacity (ORAC) in beef. *Meat Science* 80, 662–667. <https://doi.org/10.1016/j.meatsci.2008.03.003>.
- Yamano, T., Nijima, A., Iimori, S., Tsuruoka, N., Kiso, Y., Nagai, K., 2001. Effect of L-carnosine on the hyperglycemia caused by intracranial injection of 2-deoxy-D-glucose in rats. *Neuroscience Letters* 313, 78–82. [https://doi.org/10.1016/S0304-3940\(01\)02231-5](https://doi.org/10.1016/S0304-3940(01)02231-5).
- Zuidhof, M.J., Schneider, B.L., Carney, V.L., Korver, D.R., Robinson, F.E., 2014. Growth, efficiency, and yield of commercial broilers from 1957, 1978, and 2005. *Poultry Science* 93, 2970–2982. <https://doi.org/10.3382/ps.2014-04291>.