Reprod. Nutr. Dev. 43 (2003) 105–115

DOI: 10.1051/rnd:2003009

Original article

The effects of overfeeding on myofibre characteristics and metabolical traits of the breast muscle in Muscovy ducks (*Caïrina moschata*)

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(Received 17 March 2002; accepted 20 December 2002)

Abstract — The aim of this experiment was to study the consequences of precise feeding on the myofibre characteristics and metabolic traits of the breast muscle (*Pectoralis major*, *Pm*) of Muscovy ducks. Twenty-four samples of breast muscle, without skin or subcutaneous fat, from two groups of ducks, control and overfed respectively, were collected at 14 weeks of age. We assayed different chemical (water content, crude proteins, total lipid ashes, total and thermosoluble collagen), biochemical (activities of the CS, LDH and β-HAD enzymes), histological (muscle fibre typing and intramuscular adipocyte measurements) and technological (drip and cooking losses, texture) determinations. At the force-feeding period, the overfed ducks weighed 6366 g and the control ducks 4606 g of body weight. In the PM muscle, some modifications of the biochemichal parameters and enzyme activities were observed but neither the shear force nor the histological characteristics of the breast muscle were affected by the fattening treatment. The overfed birds had an increased total lipids content (correlated to an increase in the intramuscular area occupied by the adipocyte) and a different fatty acid profile as the result of a higher energy feed intake. The lipids of the *Pm* muscle of the overfed ducks contained more C16:0, C16:1n-7 and C18:1n-9, but less C18:0, C18:2n-6 and C20:4n-6 than the control birds. These results show that in response to high energy feeding, the muscle is able to respond quickly on a metabolic basis (by increasing the activities of the oxydative enzymes) without changing its typology or morphology. Additionally, fattening was correlated to a degradation in the technological qualities of the breast muscle, especially an increase in the cooking losses.

muscovy duck / force feeding / *Pectoralis major* / muscle typing / fatty acid

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1. INTRODUCTION

An important part of the French waterfowl production is related to fatty liver commercialisation. The most commonly used species in France is the Mule duck, but, in the south west of the country, the Muscovy duck has always been traditionally used. France ranks first in Europe for the production of duck meat (213 000 t in 2000), with a large part of this being Muscovy ducks (45%).

Precise-fed ducks ingest large amounts of corn over a period of 14 to 15 days (ranging from 250 to 900 g/day/animal). Abundant information is available about the effect of overfeeding on the metabolic changes in waterfowl [1–3] especially on steatosis development [4] and on growth performance [5].

Metabolic response to precise feeding varies considerably and depends on genetic factors. The hepatic lipogenesis induced by overfeeding can be summarised into two major facts; storage in situ, beginning the steatosis of the liver, and exportation of lipids, giving an increase in peripheral fat deposition [6]. At the end of the precise feeding time, muscle lipid content is therefore high because of both storage in the myofibres and adipocytes located between the fasciculi [7]. The effects of overfeeding on both intramuscular adipose tissue development and muscle fibre characteristics have not been clearly investigated in the Muscovy ducks yet. Therefore, the aim of this study was to use histochemical, enzymological and biochemical measurements to evaluate in detail the metabolical changes observed in the *Pectoralis major* (*Pm*) muscle of Muscovy ducks after precise feeding. Furthermore, it was of interest to ascertain whether an increase in intramuscular fat stores could have any consequences on meat quality traits such as shear force and cooking losses.

2. MATERIAL AND METHODS

The experiment was carried out on 40 Muscovy male ducks. Until the 10.5th week, the animals were fed with standard diets provided ad libitum as follow: diet I (1 day to 4 weeks old, 189 $g \cdot kg^{-1}$ crude protein (CP) and 2888 kcal metabolisable energy (ME)$\cdot kg^{-1}$) and diet II (4 to 10.5 weeks old, 182 $g \cdot kg^{-1}$ CP and 2750 kcal ME$\cdot kg^{-1}$). Two groups (control and overfed) were constituted at 10.5 weeks. Between 10.5 and 12 weeks, the two groups were fed with diet II but control birds were fed only 200 g/day/bird, while the overfed birds received increasing amounts daily, ranging from 210 to 380 g/day/bird. During the overfeeding period (12th to 14th week), the control ducks remained on diet II (200 g/day/bird) while the overfed ducks were fed with a diet mainly constituted of whole grain corn, corn flour and water (26, 35 and 39 $g \cdot kg^{-1}$ respectively). The main components of the corn are proteins (8.9%), carbohydrates (62.2%), lipids (4.1%) and water (12.3%). The main fatty acids of corn are palmitic (C16:0), oleic (C18:1n-9) and linoleic (C18:2n-6) acids which represent respectively 10, 25 and 50% of the total fatty acid content [8].

At 14 weeks, 12 animals of each group were randomly selected and slaughtered by sectioning of the neck. Just after bleeding (< 10 min), the *Pm* muscles were rapidly harvested. The right muscle was divided into different samples used to determine the biochemical composition (water, proteins, lipids and mineral contents). These samples were immediately frozen in liquid nitrogen, while the samples used to determine the metabolic enzyme activities and histological characteristics were frozen in isopentane cooled by liquid nitrogen. The left *Pm* was used to determine the technological parameters, remained intact, vacuum bagged and frozen in cold ethanol (–20 °C). All samples were stored at –80 °C until analysis, except the whole left *Pm* muscle samples (–20 °C).

2.1. Meat quality traits

The whole left *Pm* muscles were thawed at 4 ºC during an overnight period. A sample of this muscle was weighed, individually bagged and cooked in an 80 ºC water bath to reach an end-point temperature of 75 ºC at the thermal centre of the sample. After cooking, the samples were allowed to equilibrate at room temperature in a water bath. The samples were rapidly wiped and weighed again to determine the cooking losses [Cooking loss (%) = (initial weight – cooked weight)/initial weight × 100].

The objective texture of the raw and cooked meat was determined using a Warner-Bratzler single blade shear placed on a universal testing machine (MTS Synergie 200 – MTS Systems, Ivry-sur-Seine, France). Adjacent 1.0 cm wide strips were cut from the medial portion of the muscle, parallel to the longitudinal axis of the myofibres and sheared according to the procedure described by Honikel [9].

2.2. Metabolic enzyme activity determinations

The enzyme activities were measured from frozen tissues. Rapidly, the samples were thawed and homogenised in ice-cold phosphate buffer with an ultra-homogeniser (Ultraturrax – Ika-Werke, Staufen, Germany). The homogenate was centrifuged (1500 *g*, 10 min, 4 ºC) and the supernatant was collected. The activities of lactate deshydrogenase (LDH, E.C 1.1.1.27), citrate synthase (CS, E.C 4.1.3.7) and β-hydroxyacyl CoA deshydrogenase (HAD, E.C 1.1.1.35) were measured according to Bass et al. [10]. Enzyme activities were determined at 30 ºC using spectrophotometric techniques.

2.3. Histochemical determinations

All samples were taken at a comparable relative position from each *Pm* muscle (right side) and serial cross-sections (14 μm thick) were cut from the frozen samples on a cryostat at –20 ºC.

Fibre types were determined on the basis of the ATPase activity, after preincubation at pH 4.2 and 10.4 [11], and succinate dehydrogenase (SDH) activities. Myofibres were classified on the basis of their contractile and metabolic properties as types βR, αR and αW according to the terminology of Ashmore and Doerr [12].

The αR and αW fibres were labile after acid pre-incubation (and stable after alkaline pre-incubation). The subtypes R and W of the α myofibres were distinguished as having strong (R) or weak (W) reactions to the SDH determination. The muscle samples of the animals from the control and from the overfed group were placed on the same slide to rule out the possibility of artefactual differences between fibres due to the histochemical procedure.

One other section of the muscle was stained with red azorubin, which permits clear identification of the interfibre network and stains myofibres. In this section, mean cross-sectional areas (CSA) of each fibre type were determined using a computerised image analysis system [13]. For image acquisition and treatment, the software, called RACINE, was implemented on a UNIX workstation equipped with a graphic card linked with a CCD video camera placed on a microscope (Leitz – Laborlux 2 – Leitz, Wetzlar, 6330, Germany).

Other sections were stained with oil red 0 as described by Dubowitz [14]. Adipocyte cells were stained in red/orange. The mean relative area of clusters of adipocytes was measured on three random fields after image digitalisation and analysed with VISILOG (Noesis, Quebec, H4T-27A, Canada) software [15]. It was expressed as a percentage of the total area of the microscopic field.

Sudan black B was used to stain lipids in adipocytes or in myofibres according to

Dubowitz [14]. Sudan black stain intensity was measured in individual myofibres as the mean pixel luminance determined from 100 pixels around the central area of the fibres, expressed on a 256 grey level scale (0 to 255) and named LumSB.

All histochemical characteristics were determined on 200–300 fibres counted in three different fields.

2.4. Biochemical analyses

The frozen samples from the right *Pm* were crushed in liquid nitrogen and freeze-dryed. The dry matter was determined after 24 h at 103 ºC according to JOCE [16]. The mineral content of the samples was determined after total calcination in an oven at 550 ºC [17]. The total lipid content was determined according to Folch et al. [18] and the composition of the major fatty acids was determined after transmethylation [19]. The fatty acids were analysed using a gas chromatograph (Hewlett-Packard 5890 series II, Avondale, PA, USA) fitted with a 0.25 µm film thickness reticulated polyethyleneglycol phase 30 m × 0.25 mm i.d. capillary column (Innowax, Hewlett-Packard, Avondale, PA, USA), with nitrogen as the carrier gas. The temperatures of the injector and the detector were 250 ºC for both, and the column temperature was set from 200 to 250 ºC with a 5 ºC·min^{-1} rise.

The nitrogen content of the samples was determined using the LECO (St-Joseph, MI, USA) analyser (FP 428 model) after total combustion of the samples and the results were expressed as total protein (N × 6.25).

The total hydroxyproline content was determined after HCl hydrolysis according to the procedure of Woessner [20], with subsequent hydroxyproline concentration analysed by spectrophotometry (λ_{DO} = 557 nm). The total quantity of collagen was estimated by multiplying the percentage of total hydroxyproline of the samples by 7.14 [21]. The thermo-soluble collagen was determined according to Hill [22] after 60 min heating at 77 ºC.

2.5. Statistics

Data were analysed by variance analysis using the general linear model procedure of Minitab (State College, Pa, USA) software [23]. Among the different groups, significant differences between means were shown according to the Student Newman-Keul test. The Pearson correlation criteria were computed using the same software.

3. RESULTS

As expected, between 4 and 12 weeks of age, the mean body weights in the two groups were identical (4500 g at 12 weeks of age). At the end of the fattening period (14 weeks of age), the overfed birds were far heavier than the control birds (6366 ± 270 g and 4606 ± 334 g, body weight respectively, $P < 0.001$). The chemical composition of the *Pm* muscle is presented in Table I. A lower concentration of water, proteins, total collagen content and collagen solubility was observed in the overfed animals. Conversely, a higher quantity of lipids was found in the muscle samples from the overfed animals (4.4 vs. 2.1%, in fat and lean animals, respectively).

The percentages of the main fatty acids (> 2% of the total fatty acids effectively detected) found in the total muscle lipids are presented in Table II. Overfeeding changed the fatty acid composition of the breast muscle, including an increase in the percentage of palmitic, palmitoleic and oleic acids, with a concomitant reduction in the proportion of stearic, linoleic and arachidonic acids ($P < 0.001$). Overfed animals exhibited significant differences in groups of fatty acids (saturated, SFA; mono, MUFA and poly-unsaturated, PUFA). Overfed animals had a higher (MUFA+PUFA)/SFA ratio

Table I. Chemical composition of *Pm* muscle of 14-week old Muscovy ducks[a]. The values are means ±SEM.

	Group		Overfeeding effect	
Characteristics	Control (n = 12)	Overfed (n = 12)	Sign[b]	F
Moisture[1]	75.70 ±0.96	73.70 ± 0.95	***	24.22
Crude protein[1]	21.90 ± 0.79	21.20 ± 0.44	*	7.25
Ash[1]	0.60 ± 0.03	0.70 ± 0.03	NS	1.57
Total lipids[1]	2.10 ± 0.33	4.40 ± 0.49	***	190.28
Total Collagen[2]	23.90 ± 1.05	18.90 ± 0.87	**	12.42
Thermo-soluble Collagen[2]	4.60 ± 0.41	2.20 ± 0.33	***	20.98
Solubility %	18.90 ± 1.10	11.20 ± 1.22	***	21.58

[a] All measures were done in duplicate. [b] NS, non significant; *P < 0.05; **P < 0.01; ***P < 0.001.
[1] % of fresh tissue, [2] % of total proteins.

Table II. Overfeeding effect on the fatty acid composition (in % of total fatty acids) of *Pm* muscle of 14-week old Muscovy ducks[a]. The values are means ±SEM. Only the main fatty acids (representing more than 2% of the total) are reported.

	Group		Overfeeding effect	
Characteristics	Control (n = 12)	Overfed (n = 12)	Sign[b]	F
Palmitic (C16:0)	23.03 ± 0.18	25.87 ± 0.20	***	113.89
Palmitoleic (C16:1 n-7)	2.77 ± 0.08	3.40 ±0.09	***	28.16
Stearic (C18:0)	11.23 ±0.25	9.89 ±0.014	***	20.93
Oleic (C18:1 n-9)	34.15 ±0.66	40.50 ±0.36	***	73.88
Linoleic (C18:2n-6)	16.23 ±0.17	12.36 ±0.18	***	246.76
Arachidonic (C20:4n-6)	6.10 ±0.08	3.54 ±0.05	***	45.51
Saturated (SFA)	34.26 ±0.19	35.77 ±0.23	***	25.096
Monounsaturated (MUFA)	36.92 ±0.72	44.00 ±0.38	***	75.26
Poly-unsaturated (PUFA)	22.33 ±0.4	15.9 ±0.34	***	149.77
(MUFA ±PUFA) / SFA	1.73 ±0.02	1.68 ±0.02	*	4.63
PUFA / SFA	0.65 ±0.01	0.45 ±0.01	***	163.96

[a]All measures were done in duplicate. [b] *P < 0.05; ***P < 0.001.

Table III. Muscle fibre characteristics of *PM* muscle of 14-week old Muscovy ducks[a].

	Group		Overfeeding effect	
Characteristics	Control (n = 12)	Overfed (n = 12)	Sign[b]	F
αW myofibres (%)	20.30 ±9.35	21.00 ±8.20	NS	0.04
αR myofibres (%)	79.70 ±9.35	79.00 ±8.20	NS	0.04
CSA[c] αW (μm^2)	2074.20 ±228.90	2262.90 ±411	NS	1.93
CSA[c] αR (μm^2)	983.10 ±127.90	1122.50 ±217.40	NS	3.66
LumSB[d] αW	211.40 ±13.50	209.00 ±24.90	NS	0.08
LumSB[d] αR	176.10 ±16.60	161.40 ±26.40	NS	2.67
Adipocytes (%)	0.95 ±0.40	2.54 ±0.90	***	31.92

[a] Values are means ±SEM. [b] NS, non significant; ***$P < 0.001$. [c] Cross sectionnal area. [d] Luminance due to the staining with Black Sudan B.

($P < 0.05$) and a lower PUFA/SFA ratio ($P < 0.001$).

Pm muscle fibre characteristics are presented in Table III. The myofibre composition of *Pm* muscle presented a higher proportion of αR than that of αW fibres (about 80 vs. 20%). The CSA was higher in the αW than in the αR fibres (about 2 fold). The LumSB was also higher in the αW than in the αR fibres, indicating that there is more intracellular lipids in the αR myofibres.

Overfeeding did not modify muscle myofibre architecture because neither muscle fibre type nor CSA nor LumSB were significantly different in the control and overfed ducks. On the contrary, the relative area of clusters of adipocytes was higher in the birds from the overfed group than in the control group ($P < 0.001$).

It was observed that the overfed birds exhibited a higher activity of CS and β-HAD enzymes, with a similar activity of the LDH enzyme (Tab. IV). Thus the LDH/HAD and CS/HAD ratios were not modified by overfeeding while the LDH/CS ratio was significantly decreased (approximately 30%).

Figure 1 shows the results of Warner-Bratzler shear values and cooking losses. No significant differences were observed between the two groups for the texture of the raw or cooked meat, but cooking losses were different in the control and overfed birds ($P < 0.05$) (14.7 vs. 17.0%, respectively).

4. DISCUSSION

In palmipeds, the marked increase in body and liver weights after overfeeding results from a dramatic increase in the synthesis and accumulation of lipids as peripheral and intramuscular fat deposition [24]. This is a direct result of the large quantity of carbohydrates (from the corn) ingested during the fattening period. As reported by Salichon et al. [25], the meat of lean Muscovy ducks contains fewer lipids than that of overfed birds. This is due to the fact that, in birds, even though lipids are mainly synthesised in the liver, their final storage takes place in the muscle and adipose tissue.

Table IV. Muscle enzyme activities (in µmol of substrate degraded/min/g of total protein) in *Pm* muscles of 14-week old Muscovy ducks[a]. The values are means ± SEM.

	Group		Overfeeding effect	
Characteristics	Control (n = 12)	Overfed (n = 12)	Sign[b]	F
LDH	4643 ± 709	4755 ± 528	NS	1.33
CS	23.18 ± 5.98	35.29 ± 9.4	**	12.34
HAD	42.57 ± 11.14	56.10 ± 17.83	*	4.55
LDH/CS	208.00 ± 39.80	146.80 ± 30.89	**	16.39
LDH/HAD	131.30 ± 96.20	103.13 ± 43.60	NS	0.77
CS/HAD	0.65 ± 0.52	0.78 ± 0.43	NS	0.16

[a]All measures were done in duplicate. [b]NS, non significant; *P < 0.05; **P < 0.015.

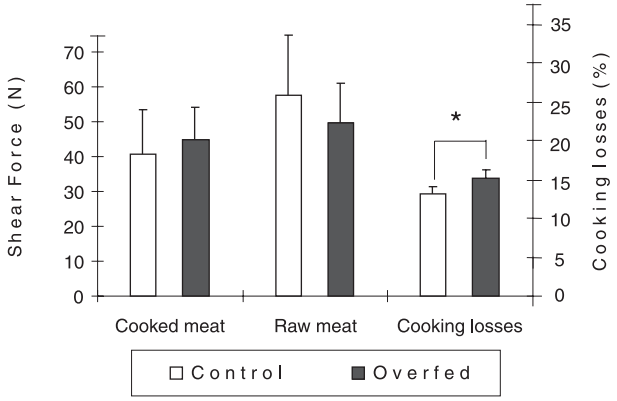

Figure 1. Warner-Bratzler shear force value and cooking losses of *Pm* muscle samples of 14-week old Muscovy ducks. The values are means ± SEM, n = 12 per group, *P < 0.05.

During overfeeding, the liver synthesises lipids continuously leading to an increase in fat deposition in storage tissues, such as subcutaneous or intramuscular adipose tissues. As a consequence of this fattening increase, a decrease in the protein and water content of the *Pm* muscle of the overfed group was observed. This balance between polar and non-polar constituents of the muscle can also be observed between fat and lean animals (in the pig, [26]) and in the rabbit, [27]). The decrease in whole muscle proteins in overfed birds is also illustrated by the small decrease observed in the proportion of the total collagen content. Since the proportion of collagen content is normally constant during growth [28], it could be hypothesised that overfeeding has slightly modified the muscle protein turn-over, leading to this little decrease in the proportion of muscle collagen content.

These modifications of collagen metabolism may also have affected the structure of the molecule because its solubility has slightly decreased in overfed ducks. The negative correlation (r = –0.66) between

total lipid content and collagen solubility also supports the idea that intramuscular fat content could act as a protector of thermal denaturation of collagen during cooking.

As previously observed in other works, the nutritional fatty acid profile plays a determining role in the muscle fatty acid composition (in rabbit, [29] and in bulls [30]). On the contrary, in overfed geese, Cazeils et al. [31], found that the modulation of the fatty acid composition by dietary lipid intake can be masked if not strongly limited.

Muscle fatty acid composition determined previously by Fristrom and Weihrauch (in geese [32]) is similar to the present results in the lean breast muscle. The significant changes observed in (PUFA+MUFA)/SFA and PUFA/SFA ratios were obviously the consequence of alterations in the proportion of fatty acids. These results are consistent with those reported by Salichon et al. [25] in lean Muscovy ducks.

A decrease in the incorporation of linoleic acid was observed despite the high proportion of this essential fatty acid in the diet (more than 50% of the total fatty acid content in corn). It can be hypothesised that in overfed palmipeds, de novo hepatic lipogenesis prevails over dietary lipid intake to modulate the profile of muscle fatty acids as observed in the liver plasma membrane of overfed geese [31]. As a consequence of this prevalence of the de novo hepatic lipogenesis over dietary lipid intake, the high proportion of oleic acid indicates a higher activity of hepatic lipogenesis in overfed ducks.

Previous studies have reported that the breast muscle of ducks is composed of 2 fibre types, αW and αR (in Pekin ducks [33]; in Mallard ducks [34] and in Muscovy ducks [35]). It can be concluded from the present results that overfeeding for 14 days is not sufficient to modify this fibre type composition or the histological characteristics of the *Pm* muscle of Muscovy ducks. The observed values of the CSA of the αW or αR myofibres were similar to those obtained by Baéza et al. [35] in lean Muscovy ducks, indicating that overfeeding does not induce any large structural modification of the muscle. Because numerous other studies have also reported that feed restriction has no effect on the percentage of oxydative myofibres (in cattle [36]; in lambs [37]; in pigs [38] and in rabbits [39]), it can further be concluded now that nutrition seems to have limited effects on muscle typology.

Enzyme activities are used to describe the muscle metabolism pattern. The LDH enzyme characterises the glycolytic pathway while the CS and β-HAD enzymes characterise the oxydative pathway. In this study, overfeeding ducks induced significant variations in muscle enzyme activities. The high activities of HAD and CS suggest that the muscle is able to rapidly adapt its metabolism to use lipids. In 1969 and 1970, Bass et al. [10, 40] proposed to characterise the activities of the metabolic energetic in measuring different ratios of enzyme activities such as LDH/CS. In this study, the decrease of the ratio of LDH/CS observed in the *Pm* muscle of the overfed ducks also confirmed that increasing muscle fattening leads to an increase of the oxydative metabolism activity. In contrast, there is no significant difference of the CS/HAD ratio between overfed and control ducks indicating that there is no dysfunction all along the oxidative metabolic pathways after overfeeding.

The relative area of adipocyte clusters per field was higher in the overfed group indicating that muscle fattening largely contributes to a body weight increase after overfeeding. The same observations have already been made by Baéza et al. [41] in overfed geese. Because no difference in LumSB values was seen (indicating no modifications in the total lipid content of myofibres), it can be concluded that muscle fattening in ducks mainly lies in lipid storage tissues rather than in contractile tissues. In this study, in response to a fat storage

increase, it was verified that the muscle increases its own oxydative activity to predominantly produce energy from lipid oxidation. This adaptability of muscle metabolism has already been observed in rabbits by Gondret et al. [39] who reported that the activity of glucose-6-phosphodehydrogenase (G6PDH) and malic enzyme was related to a capacity of the muscle to accumulate lipids in interfascicular adipocytes.

During cooking of the meat, water and lipids are lost by evaporation but are also the results of tissue denaturation which reduces the water-holding ability of the protein muscle. In the present work, it was observed that overfed birds lost more juices during cooking than control birds (+15.64%). The increase in intramuscular fat is generally considered as a mean to enhance the texture and the taste of the meats [41, 42], but Éssen-Gustavsson et al. (in pigs [43]) observed a negative correlation between fat deposition and shear force. In the present work, the higher level of intramuscular fat observed in overfed birds did not improve the texture of *Pm* muscle. Additionally, the differences observed in total and thermosoluble collagen contents seems to play a secondary role in the determination of the texture of raw or cooked meat.

5. CONCLUSION

Differences between overfed and control ducks were observed in the chemical composition of their *Pm* muscle, but markedly, overfeeding increased the total lipid content of the muscles. This was closely related to greater hepatic lipogenesis, resulting in increased peripheral and intramuscular fat deposition, as observed by the increase in the relative area of adipocyte clusters.

Corn overfeeding for 14 days was sufficient to induce modifications of some enzymatic activities of breast muscle without inducing modifications of the morphology or the characteristics of *Pm* myofibres.

Changes in the fatty acid profile were related to the lipogenesis induced by a high carbohydrate intake. Consequently, this profile can be altered by nutritional means, which agrees with other studies.

The present results did not support the hypothesis that higher fat levels enhance per se the mechanical properties of the meat. It seems that the structural characteristics of myofibres and muscle fibre type composition play a major role. Furthermore, the only technological characteristic deteriorated significantly by the increases of the fat content of the meat were the cooking losses.

Finally, further studies must be conducted to better understand the rate of development of the adipocytes in the muscles of birds. It will be of particular interest to determine if there is any variation between the different lines or species, and if these differences exist how they could be better used to improve meat quality (specially the aroma and flavour) in fat or lean ducks. Concerning the relationships between intramuscular fat level and tenderness of the duck meat, it would be interesting to know which level of fattening is needed.

ACKNOWLEDGMENTS

J. Zanusso is a Ph.D. student supported by a grant scholarship (CAPES, Brasilia, Brazil).

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