Growth performance, carcass traits and meat quality of heavy lambs reared in a warm or cold environment during winter

É. Pouliot[1], C. Gariépy[2], M. Thériault[1,3], C. Avezard[2], J. Fortin[2], and F. W. Castonguay[1,3]

[1]*Département des sciences animales, 2425, rue de l'Agriculture, Université Laval, Québec, Québec, Canada G1V 0A6;* [2]*Food Research and Development Centre, Agriculture and Agri-Food Canada, 3600 Casavant Blvd. West, Saint-Hyacinthe, Quebec, Canada J2S 8E3; and* [3]*Dairy and Swine Research and Development Centre, Agriculture and Agri-Food Canada, PO Box 90, Lennoxville Stn., Sherbrooke, Quebec, Canada J1M 1Z3.*
Received 29 September 2008, accepted 21 January 2009.

Pouliot, É., Gariépy, C., Thériault, M., Avezard, C., Fortin, J. and Castonguay, F. W. 2009. **Growth performance, carcass traits and meat quality of heavy lambs reared in a warm or cold environment during winter.** Can. J. Anim. Sci. **89**: 229–239. The goal of this study was to evaluate the impact of winter rearing environment on the growth performance and meat quality of heavy lambs. Half of sixty-four Dorset lambs (32 males and 32 females) were raised in each of two different environments: warm and cold with average temperature of 10.9 ± 0.7°C and -2.0 ± 5.2°C, respectively. The lambs were slaughtered at live weights of 41–45 kg for females and 46–50 kg for males. Cold environment had no adverse effect on either growth performance or carcass quality. The rate of longissimus dorsi muscle deposition ($P = 0.049$) and its depth at slaughter ($P = 0.027$) were rather greater in lambs reared in the cold environment and a higher proportion of oxido-glycolytic fibres ($P = 0.047$) was also observed in this muscle. Rearing environment had only a minor effect on the organoleptic qualities, with the cold environment promoting juiciness of the meat ($P = 0.043$). Therefore, cold environment rearing such as used in this study represents an economic advantage for lamb producers by reducing the costs associated with the construction of insulated barns, while maintaining growth performance, as well as carcass and meat quality.

Key words: Lamb, rearing environment, temperature, growth, carcass, meat quality

Pouliot, É., Gariépy, C., Thériault, M., Avezard, C., Fortin, J. et Castonguay, F. W. 2009. **Performances de croissance, caractéristiques de la carcasse et qualité de la viande des agneaux lourds élevés dans un environnement tempéré ou froid durant l'hiver.** Can. J. Anim. Sci. **89**: 229–239. Cette étude avait pour objectif d'évaluer l'impact de l'environnement d'élevage durant la période hivernale sur les performances de croissance et la qualité de la viande des agneaux lourds. Soixante-quatre agneaux Dorset (32 mâles et 32 femelles) ont été répartis et élevés dans deux environnements d'élevage : tempéré ou froid sous des températures moyennes de $10{,}9 \pm 0{,}7$°C et $-2{,}0 \pm 5{,}2$°C respectivement. Les agneaux ont été abattus aux poids vifs de 41–45 kg pour les femelles et 46–50 kg pour les mâles. Aucun impact négatif de l'élevage en environnement froid n'a été observé sur la croissance ni sur la qualité des carcasses. Au contraire, la vitesse de dépôt musculaire du longissimus dorsi ($P = 0{,}049$) et l'épaisseur de ce muscle à l'abattage ($P = 0{,}027$) ont été supérieures chez les agneaux élevés au froid et une proportion supérieure de fibres oxydo-glycolytiques ($P = 0{,}047$) a aussi été observée dans ce muscle. Finalement, l'environnement d'élevage n'a eu qu'un faible impact sur la qualité organoleptique de la viande, l'environnement froid favorisant la jutosité ($P = 0{,}043$). L'élevage sous un environnement froid pourrait donc représenter un avantage économique pour les producteurs en permettant de réduire les coûts de production reliés à la construction de bergeries isolées tout en maintenant les performances de croissance et la qualité de la carcasse et de la viande.

Mots clés: Agneau, environnement d'élevage, température, croissance, carcasse, qualité de la viande

Weather conditions in Canada influence production methods in all agricultural sectors. In eastern Canada, harsh winter conditions, with average temperature of approximately -10°C, but often falling as low as -20 to -30°C (Environment Canada 2008), necessitate the construction of structures that can provide a suitable environment for livestock. In sheep production, this has led to the use of completely enclosed buildings and has steered the industry toward an indoor production model in winter. However, the cost of building and maintaining such infrastructures is substantial for sheep producers. The use of "cold" sheep barns, which are not insulated, represents an economical alternative. They provide slightly warmer temperatures than those recorded outdoors (Vachon et al. 2007). But it is known that rearing animals in a cold environment can affect both the growth performance and the meat quality.

In sheep and cattle, acclimatization to cold has been shown to result in both higher resting metabolism and heat production rates (Webster et al. 1969; Slee 1972; Young 1975) and increased maintenance requirements by as much as 41% in steers (Delfino and Mathison 1991). In addition, Ames and Brink (1977) reported increasing feed intake levels along with decreasing

average daily gains (ADG) in shorn lambs as temperatures decreased from 15 to −5°C. However, such an effect on ADG was not observed in other studies conducted with either shorn (0 vs. 23°C; Ekpe and Christopherson 2000; Moibi et al. 2000) or unshorn lambs (−7.5 vs. 6.3°C, trial 1; −4.7 vs. 10.5°C, trial 2; Vachon et al. 2007).

At the muscle level, exposure to cold during growth is known to promote the development of muscle fibres with a higher oxidative metabolism. Higher proportions of type I (oxidative) and type IIA (oxido-glycolytic) fibres have been observed in various muscles of pigs raised in colder temperatures (8–12 vs. 23–28°C; Lefaucheur et al. 1991; Herpin and Lefaucheur 1992). Similar observations were reported in rats (Behrens and Himms-Hagen 1977), in guinea pigs (Ratzin Jackson et al. 1987) and in ducks (Duchamp et al. 1992). Numerous findings of mitochondrial changes (Depocas 1966; Buser et al. 1982; Kinnula et al. 1983) or changes in the activity of certain enzymes (Dauncey and Ingram 1988, 1990; Lefaucheur et al. 1991) support the hypothesis that muscle oxidative activity increases in animals after a period of cold exposure. Increased lipid content in some muscles of cold-adapted animals has also been reported (Buser et al. 1982; Lefaucheur et al. 1991; Soni and Katoch 1997).

In addition to its effect on growth performance, previous studies suggest that exposure to cold may influence the quality parameters of the meat. However, no such research has been conducted on lambs. Therefore, the goal of this study was to evaluate the impact of winter rearing environments (warm vs. cold) on the growth performance, carcass characteristics, longissimus dorsi (LD) fibre composition and fibre metabolism of heavy lambs, as well as meat organoleptic qualities.

MATERIALS AND METHODS

Animal Management

Lambs used in this experiment were handled in accordance with the guidelines of the Canadian Council on Animal Care (1993).

Group Formation and Treatment

Sixty-four Dorset lambs (32 males BW = 25.5 kg ± 0.7 and 32 females BW = 23.5 kg ± 0.7) were selected 1 wk after weaning, at an average age of 62 ± 1.85 d. Within genders, lambs were divided into two groups of similar body weights and ages. Sixteen lambs of each sex were then randomly assigned to one of two housing units of the experimental farm of CEPOQ (Centre d'expertise en production ovine du Québec, La Pocatière, QC): a sheep barn with thermal insulation and backup heating (the "warm" environment – WE), the other with no thermal insulation or backup heating (the "cold" environment – CE). Lambs of the same sex were randomly placed by four in four pens measuring 1.80 × 2.40 m, providing approximately 1.1 m^2 per lamb.

The lambs were exposed to a daily photoperiod of 16 h of light. The indoor temperature and humidity of both barns were recorded every 2 h using an automatic temperature data logger (Dickson Pro Series Data Loggers TP120, Dickson, Addison, IL). In the warm barn, the ambient temperature was maintained at approximately 11°C while the indoor temperature of the cold barn fluctuated with the outside temperature, which was monitored by the La Pocatière weather station (Environment Canada 2005). The experiment was carried out from 2004 Dec. 30 to 2005 Mar. 24.

Feed

During the first 3 wk of treatment, lambs had ad libitum access to a second-cut hay (mainly timothy grass and brome grass; CP, 12.8%; ADF, 42.3%; NE, 0.42 Mcal kg^{-1}) and a pelleted feed (Puranio 18%, Agribrands Purina; CP, 19.91%; ADF, 15.55%; Ca, 1.33%; P, 0.60%; NEg, 2.53 Mcal kg^{-1}). When they reached an average live weight of 31.8 ± 3.4 kg and an average age of 83.4 ± 1.9 d, the percentage of protein in the pelleted feed was reduced (Puranio 16%, Agribrands Purina; CP, 18.13%; ADF, 14.45%; Ca, 1.37%; P, 0.58%; NEg, 2.53 Mcal kg^{-1}). This diet would be similar to that fed to commercial lambs in Quebec. The quantity of pelleted feed consumed per pen was calculated weekly. Hay consumption could not be measured precisely, since hay feeders allowed some hay wastage. Nevertheless, hay disappearance represented only around 5% of DMI (data not shown), which was very similar to previous study (Vachon et al. 2007). Fresh water was available at all times.

Live Measurements

At three times during the growth period (average age of 76, 97 and 118 d), blood samples were collected from the jugular vein of eight male lambs in each treatment group using Vacutainer® serum tubes (Model 366430, Becton Dickinson, Franklin Lakes, NJ). The tubes were left at room temperature for approximately 30–60 min and then centrifuged at 2000 × *g* for 20 min. The serum was recovered and stored at −20°C until metabolic profile analyses could be performed.

At the start of the protocol and every 2 wk thereafter, ultrasound subcutaneous fat and LD muscle depth measurements were taken between the 3rd and 4th lumbar vertebrae on the left side of the live animal. A last measure was also taken the day before slaughter for each animal. These measurements were performed by an experienced technician using a real-time ultrasound scanner (Ultrascan50, Alliance Medical, Montreal, QC).

Except for the ultrasound measurement site, which was closely clipped before each scanning session, lambs were not shorn before or during the experimental period. They were weighed once a week and were slaughtered when they reached the targeted fasting weight of 46–50 kg for males and 41–45 kg for females; fasting weight

was estimated by subtracting 7% from the live weight. The lambs were fasted for approximately 12–15 h prior to slaughter.

Slaughter and Post-slaughter Sampling

Lambs were slaughtered at a commercial slaughterhouse located 130 km from the experimental farm. Carcasses were weighed prior to being conveyed to the cooling chambers following the commercial practice of the slaughterhouse.

Within 30 to 60 min postmortem, a $\pm$15-g muscle sample was taken adjacent to the vertebral column at the last rib from the right LD muscle. Smaller cubes of about 8 mm were prepared and frozen in -80°C isopentane using a quick freezing device (Shandon Histobath II, Thermo Electron Corporation, Waltham, MA) before being stored at -80°C until histochemical and biochemical analyses. The remainder of the sample was coarsely cut up, frozen in liquid nitrogen and stored at -80°C for subsequent enzyme analyses.

After 24 h of cooling at 4°C, the cold carcass weight was recorded. Carcasses were then graded according to the Agriculture Canada method (1992), which assesses each of the shoulder, loin and leg conformation using a scale from 1 (deficient muscling) to 5 (excellent muscling). The average of these three scores was calculated to establish an average conformation score. Total tissue depth was measured using a ruler at the 12th rib, 11 cm from the vertebral column (GR measurement). On the same day, meat samples needed for the various analyses were also prepared. The right loins were cut up into short loins and racks. The short loins were transferred to the laboratory for pH, drip loss and meat colour measurements on fresh LD muscle. A 1-cm-thick slice collected from the rack near the last rib was vacuum-packed and frozen at -20°C for sarcomere length measurements. After an aging period of 7 d at 4°C, the short loins and racks were vacuum-packed and frozen at -20°C for subsequent analysis. For sensory analyses, 32 left loins and 32 left semimembranosus (SM) muscles were also collected (8 LD and 8 SM muscles/sex/treatment), packaged and frozen after the same aging period. The 32 subjects were randomly selected in proportion of the number of individuals slaughtered per week in each treatment group.

Laboratory Analyses

Drip Loss, Colour and pH

Approximately 27 ± 1 h after slaughter, a slice of meat from the anterior end of the right short loins was extracted and trimmed of visible fat and connective tissue. The slices were then weighed and suspended for 48 h in a hermetic plastic container maintained at 4°C following the recommendations of Honikel (1987). Drip loss was then determined as the difference between the initial and final weights, expressed in percentage.

The freshly cut surface of the short loin was exposed to air for a 30-min oxygenation period and colour measurements (L^*, a^* and b^*) were taken in triplicate using a colorimeter (Chroma Meter CR-300, Minolta Co., Ltd., Osaka, Japan). Approximately 48 h post-slaughter, triplicate pH measurements were taken along the longitudinal surface of the right short loins with a probe electrode (Mettler-Toledo LoT406-M6-DXK-S7/25, Mettler Toledo Ingold Inc., Bedford, MA).

Cooking Loss and Shear Force

For shear force measurements, the racks were thawed at 2°C for 48 h, after which the LD muscle was isolated and stripped of its fat cover and epimysium. The LD muscles were weighed before being individually vacuum-packed. Thermocouples were inserted in two pieces, representative of the batch in term of size, to accurately monitor internal temperatures during autoclave cooking (Autoclave Pilot Rotor 900, Herman Stock Maschinenfabrik Gmbh, Neumunster, Germany). Cooking was stopped with the cold shower of the autoclave when the internal temperature reached 68°C as used by Gariépy et al. (1999). It has to be noted that uniform cooking pattern and doneness were achieved among the samples despite some variation in their lengths and widths since LD muscle thickness, which represented the smallest dimension, was similar and allowed for comparable heat transfer among all samples. Once cooked, the meat was stored overnight at 4°C. The following day, the meat samples were kept at room temperature for 2 h prior to weighing for cooking loss determination. Each piece of meat was then subjected to a shear force test using a texturometer (TA-XT2i Texture Analyser, Stable Micro System, Godalming, Surrey, United Kingdom). At least nine 1-cm^2 meat "sticks" from each sample were cut parallel to the fibre axis before being sheared perpendicular to the muscle fibre orientation using a Warner-Bratzler cutting device.

Sarcomere Length

Sarcomere length was measured with a phase contrast microscope on 25 myofibrils having at least 10 sarcomeres following the procedure described in Gariépy et al. (1992).

Water, Fat, Protein and Myoglobin

Composition analyses were performed on ground samples from the short loins that were vacuum packed and frozen. Meat samples were first placed in a Lyo-Tech lyophilizer (Lyo-San Inc., Lachute, QC) at 20°C for approximately 68 h to determine the water content. The dried samples were ground to powder and were placed in sealed tubes kept at room temperature for subsequent fat and protein content assessment, which were carried out with the LECO TFE2000 extractor (LECO Corporation, St. Joseph, MI) and the LECO FP-428 protein extractor (LECO Corporation, St. Joseph, MI) based on

Association of Official Analytical Chemists (AOAC 2000) procedures 991.36 and 992.15, respectively.

Myoglobin concentration was determined on 3 g of ground meat according to Trout (1991).

Muscle Fibre Typing

Fibre typing of the LD muscle was performed on 14-μm-thick serial sections as prepared with a cryostat (Model 840, Reichert-Jung, Buffalo, NY). Two successive sections were stained in duplicate to highlight both ATPase activity for the determination of the contraction speed according to Guth and Samaha (1970) after preincubation in an acidic medium (pH = 4.35) and succinate dehydrogenase (SDH) activity for the determination of the oxidative capacity according to Nachlas et al. (1957). The Image-Pro Express 4.0 software (MediaCybernetics, Silver Spring, MD) was used to determine percentage of slow-twitch oxidative (SO), fast-twitch glycolytic (FG) and fast-twitch oxido-glycolytic (FOG) fibres from the digitalized micrographs. More than 350 fibres were typed per sample.

Enzyme Activity

The activity of lactate dehydrogenase (LDH; Bass et al. 1969), citrate synthase (CS; Srere 1969) and β-hydroxyacyl-CoA dehydrogenase (HAD; Bass et al. 1969) were measured to provide a complementary assessment of the glycolytic and oxidative capacity of the muscle.

The activity of the meat tenderizing calpain-calpastatin system was also measured. The method developed by Iversen et al. (1993) was used to determine μ-calpain and m-calpain activity. Separation of these two enzymes was achieved using a chromatography system (FPLC Waters 650E, Water Division, Millipore, Milford, MA) with a multisolvent delivery system (Waters 600E, Water Division, Millipore, Milford, MA). Calpastatin was isolated using the approach developed by Shackelford et al. (1994), based on Koohmaraie (1990). Enzyme caseinolytic activity was measured by spectrophotometry.

Sensory Evaluation

Sensory evaluation was done according to Meilgaard et al. (1999). A sensory profile in which seven trained judges were asked to indicate the perceived intensity of flavour, juiciness and firmness characteristics was carried out on 32 left LD muscles and 32 left SM muscles. Flavour intensity was evaluated on a scale of 0 to 7, while texture characteristics (firmness and juiciness) were evaluated on a scale of 0 to 15.

At each of the seven sessions, each judge was given a sample from both the short loin and the leg for the evaluation of flavour, while juiciness and firmness were assessed from a sample from the rack only. For the flavour, the order of the muscles to be evaluated was reversed for each session. Once all three samples from one of the treatments had been evaluated, the second treatment was presented, and so on until the fourth treatment, based on a random order that was predetermined for each judge at each session. This testing was carried out in a sensory evaluation room with multiple partitioned work stations under positive pressure to eliminate odours, and under red light to mask potential differences in sample appearance.

Statistical Analyses

The data were analyzed using the MIXED procedure of SAS (SAS Institute Inc. 2001). The sources of variation included in the model were sex (male vs. female), rearing environment (warm vs. cold) and their interaction. It is important to note that the sex effect includes a weight at slaughter effect, since the female lambs were slaughtered at a lower weight than the males in order to represent the commercial conditions.

Main effects and interactions were considered to be significant at $P<0.05$. Pearson correlations between the various growth parameters, as well as carcass quality, muscle characteristics and meat quality, were also established.

RESULTS AND DISCUSSION

Unlike studies conducted in controlled environments (Brink and Ames 1975; Ames and Brink 1977; Ekpe and Christopherson 2000; Li et al. 2000; Moibi et al. 2000), the level of cold in the present experiment fluctuated with outside environmental conditions that are representative of the winter temperatures in which livestock are raised in eastern Canada. This aspect must be taken into consideration when interpreting the results, since it has been observed that metabolic responses in sheep differ depending on whether they are exposed to constant cold or to fluctuating temperatures (Webster et al. 1969; Slee 1970, 1972). The average daily temperature (Fig. 1a) was $10.9 \pm 0.7^{\circ}$C (min. $= 8.8^{\circ}$C and max. $= 12.3^{\circ}$C) in the warm environment (WE) and $-2.0 \pm 5.2^{\circ}$C (min. $= -10.9^{\circ}$C and max. $= 9.3^{\circ}$C) in the cold environment (CE). The average humidity measured inside the sheep barns was $57.8 \pm 9.7\%$ and $75.2 \pm 8.2\%$ for the WE and CE respectively (Fig. 1b).

Growth Performance

Significant differences in some growth parameters between males and females were observed (Table 1) consequent with male lambs generally growing faster than female (Dragomir 2005; Vachon et al. 2007). However, no negative effects on growth were observed between CE and WE for either males or females (Table 1). This observation is consistent with the findings of two trials conducted by Vachon et al. (2007) under comparable rearing conditions (average temperatures of -7.5 and 6.3°C for the CE and WE in the first trial, and -4.7 and 10.5°C for the CE and WE in the second trial).

The ADGs recorded in the present study did not change with rearing environment and are consistent with those reported for similar Dorset lambs (Dragomir 2005). Other studies, however, carried out with lambs

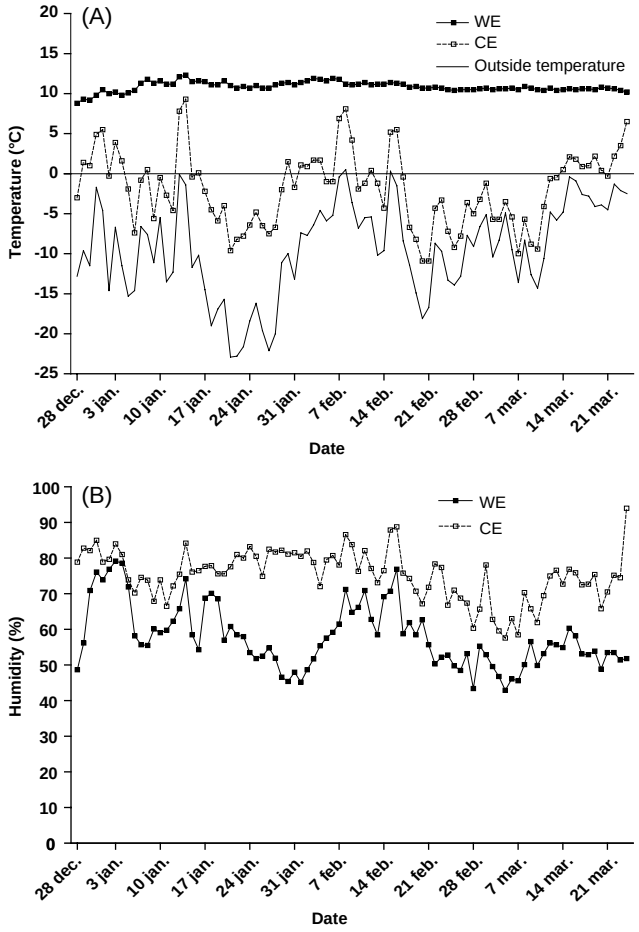

Fig. 1. Variations in average daily temperature (A) and humidity (B) in two experimental sheep barns during the winter period (WE: warm environment and CE: Cold environment).

shorn twice weekly, to maintain constant thermal neutral temperature, and kept for 12 d at −5, 0, 5, 10, 15, 20, 30 and 35°C have shown temperature to have a quadratic effect with ADG increased between −5 and 15°C and decreasing thereafter (Brink and Ames 1975; Ames and Brink 1977). According to these authors, the poor growth performance observed under the coldest temperatures was due to increased maintenance requirements caused by thermal stress combined with an increase in feed intake that was not sufficient to meet the higher energy demand.

With unshorn lambs however, Vachon et al. (2007) have observed that those raised in CE tend to show higher ADG rates ($P = 0.06$) and to reach market weight sooner ($P = 0.09$) compared with lambs raised in WE. Ekpe and Christopherson (2000) and Moibi et al. (2000) have confirmed higher ADG rates in lambs raised at colder temperatures. In these studies, feed intake was greater in the CE, which partially explains the difference in weight gain.

The lack of difference in feed intake in our study differs with the results published by various authors on the relationship between feed intake and thermal environment in sheep (Brink and Ames 1975; Ekpe and Christopherson 2000; Moibi et al. 2000) and, more generally, in a variety of species [Webster 1970; National Research Council (NRC) 1981; Herpin and Lefaucheur 1992]. In fact, the NRC (1981) reports a negative correlation between ambient temperature and ingestion of dry matter in shorn lambs, based on the results of Brink and Ames (1975).

However, intake appears not to be affected when daily temperatures fluctuate near the thermal neutral zone (NRC 1987). Accordingly, the results of the present study, where feed intake did not increase and rate of weight gain did not decrease in CE, suggest that, at the ambient temperatures evaluated, unshorn growing lambs were in their comfort zone. The findings of Vachon et al. (2007) also support this interpretation. These authors observed an interaction between the year and the environment in terms of concentrate intake; the intake of lambs raised in the CE being higher only in the trial carried out under the coldest conditions. It should be noted that, in Vachon et al. (2007), the average temperatures in the CE during the 2-yr experiment were lower than those recorded in the present study, which may explain the presence of statistical trends in their study and the absence of effect in the present study. Unfortunately, the thermal neutral zone of unshorn growing lambs fed ad libitum with a high energy diet is not well established.

Among livestock species, sheep is the most tolerant to cold owing to their fleece (NRC 1981). The temperature associated with maximum growth in shorn lambs is 13°C, but this value decreases in unshorn lambs (NRC 1981). Works by Slee (1970, 1971, 1972) have shown that exposing sheep to intermittent cold, as opposed to constant cold, causes only a weak metabolic responses and even promotes a facultative temporary reduction in body temperature. This type of adaptation to stress, referred to as "habituation" (Glaser 1966; Slee 1971, 1972), would enable lambs to tolerate temperatures that temporarily fall below their comfort zone without experiencing an increase in metabolism or energy requirements.

Unexpectedly, LD muscle depth was greater in lambs raised in the CE than in those raised in the WE ($P = 0.027$), which translates into a faster rate of muscle deposition (expressed in mm d^{-1}) in lambs raised in the CE ($P = 0.014$; Table 1). No such results have been reported before. Some authors have reported enhanced urea recycling, increased non-ammonia nitrogen (NAN) intake, and improved duodenal NAN flow in sheep fed forage and raised at 0–5°C compared with those raised at 20–25°C, a situation that would appear to promote nitrogen balance (Christopherson and Kennedy 1983; Kennedy et al. 1986). However, no such difference was observed when the diet was oat-based or canola-based

Table 1. Growth parameters of lambs reared in warm (WE) or cold (CE) environments

	Males		Females			P value[z]		
Growth traits	WE	CE	WE	CE	SEM	S	E	S × E
Initial weight (kg)	25.6	25.4	23.6	23.4	0.7	0.011	0.771	0.980
Initial age (d)	62.5	61.8	62.9	62.3	0.6	0.521	0.252	0.917
Initial fat depth[y] (mm)	5.7	5.7	5.6	5.8	0.2	0.964	0.716	0.814
Initial loin muscle depth[y] (mm)	25.0	24.9	24.6	24.6	0.6	0.493	0.967	0.992
Live weight at slaughter (kg)	50.4	51.0	45.3	45.4	0.3	<0.001	0.223	0.443
Slaughter age (d)	119.5	118.8	127.3	124.5	2.5	0.019	0.491	0.682
Fat depth at slaughter[y] (mm)	9.0	8.3	9.3	9.0	0.3	0.112	0.125	0.685
Loin muscle depth at slaughter[y] (mm)	32.8	34.4	31.8	33.4	0.6	0.144	0.027	0.955
ADG (g d^{-1})	0.455	0.474	0.355	0.374	0.013	<0.001	0.161	0.996
Fat deposition[x] (mm d^{-1})	0.061	0.048	0.061	0.055	0.005	0.482	0.068	0.535
Muscle deposition[x] (mm d^{-1})	0.142	0.170	0.119	0.149	0.010	0.049	0.014	0.886
Concentrate consumption[w] (kg pen^{-1})	379.0	388.8	391.7	368.6	11.4	0.726	0.532	0.139
Feed conversion[v] (kg concentrate kg^{-1} gain)	3.82	3.80	4.53	4.19	0.14	0.001	0.186	0.245

[z]S = sex; E = environment; S × E = sex × environment interaction.
[y]Loin muscle and fat depths measured by ultrasound between the 3rd and 4th lumbar vertebrae.
[x]Muscle and fat deposition measured by ultrasound between the 3rd and 4th lumbar vertebrae and expressed in mm d^{-1}.
[w]Total average pelleted feed consumption per four-lamb pen.
[v]Total quantity of pelleted feed consumed per four-lamb pen, divided by the total weight gain per pen.

(Kennedy et al. 1982), which is more comparable with the one used in the present study. Conversely, a reduction in nitrogen retention was reported by McBride and Christopherson (1984) in lambs raised at 0 vs. 21°C. According to Sano et al. (1995), increased oxidation of non-protein substrates in sheep exposed to cold (0 vs. 20°C) could help maintaining protein balance despite increased heat production, which suggests that endocrine changes are involved in this metabolic response. Several hormones are known to influence tissue synthesis and growth in animals exposed to cold [for a review consult Sasaki and Weekes (1986)]. In particular, thyroid hormone levels increased in sheep raised under cold conditions (Sasaki and Weekes 1986; Ekpe and Christopherson 2000). These hormones can promote protein synthesis in skeletal muscles, but if the level is too high, protein catabolism is activated (Cassar-Malek et al. 1998). Exposure to cold has also been reported to increase both plasma insulin concentrations (Sasaki and Weekes 1986; Ekpe and Christopherson 2000) and its tissue response (Weekes et al. 1983), with consequent reduction in protein catabolism and hence, synthesis at the muscle level (Brockman 1986; Cassar-Malek et al. 1998). Therefore, it appears quite plausible that a cold rearing environment could promote protein deposition. However, the parameters measured in this experiment do not allow for an explanation. It is nevertheless worthy of mention that, throughout the experiment, plasma urea concentration was lower in CE lambs, which support the hypothesis of a more efficient nitrogen utilization (Fig. 2).

Subcutaneous fat deposition rate (mm d^{-1}) tended to be lower ($P = 0.068$) in the animals raised in CE (Table 1). However, no significant differences were observed between CE and WE for live ultrasound fat depth at slaughter or GR measurements performed on the carcass (Table 2). Li et al. (2000) have measured thicker backfat layers in shorn castrated male lambs raised at 0°C compared with those raised at 20°C, which could reportedly promote insulation and reduce heat loss. This suggests that fleece provided an excellent insulation in our environmental conditions.

Overall, we can conclude from these observations that the cold environment had no negative effects on growth performance. On the contrary, only positive effects were observed, even though feed intake levels were similar. These results were comparable with those of Vachon et al. (2007) who also observed positive effects of CE on growth performance.

Although health problems were not more prevalent in any of the two environments during the experiment, this does not rule out possible subclinical differences. It is possible that the microbial load is reduced in a CE and that energy requirements for combating infection therefore decrease as well. In fact, Daniel et al. (2006) report a higher prevalence of pulmonary lesions in lambs born in the spring compared with those born in the fall as well as lower ADG and loin eye area and attributed these results to seasonal differences, considering housing conditions were the same. The average spring and fall temperatures they measured were 10.2 and −1.1°C, respectively, which is very close to the temperatures recorded in the present study. We must therefore consider the possibility that the CE could have a positive impact on the health of lambs and may indirectly favour muscle deposition.

Carcass Quality

As expected, the difference in slaughter weights for males and females were reflected in hot and cold carcass

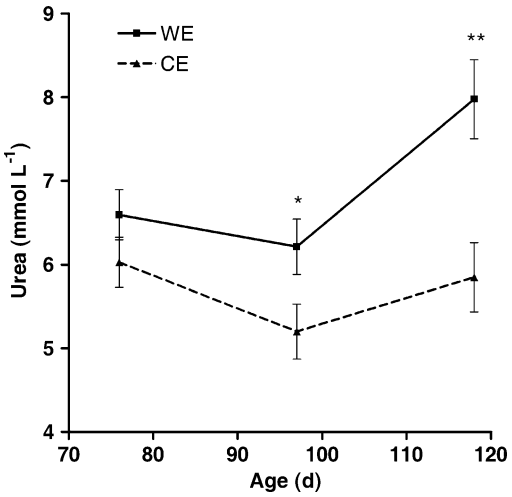

Fig. 2. Plasma urea concentration (least-squares means ± SEM) in male lambs reared in warm (WE) or cold (CE) environments (*$P < 0.05$; **$P < 0.01$).

weights ($P < 0.001$; Table 2). Females were fatter than males as shown by GR values ($P < 0.001$), had higher carcass yield ($P = 0.002$) and lower lean and saleable meat yields ($P = 0.001$ and $P < 0.001$, respectively) consequent with intact males being leaner than females and having also lower carcass yields (Lawrence and Fowler 2002).

Carcass weights were higher for lambs raised in the CE ($P = 0.025$ and $P = 0.027$ for hot and cold carcasses weights, respectively) despite similar live weights. The difference in carcass weights was also reflected in carcass yields ($P = 0.044$). This result was contrary to those reported by Li et al. (2000) showing no difference in the carcass yields of male lambs that had been castrated, shorn and fed ad libitum, regardless of whether they were raised at 0 or 20°C. Cold acclimatization is known to increase various organ weights (Héroux 1961). In shorn sheep, cold has been shown to increase the weight of the digestive tract, an effect due in part to increased feed intake (Graham et al. 1982). In fact, McBride and Christopherson (1984) showed no significant difference in organ weights from lambs raised at 0 or 21°C when feed intake were similar. In the present study, there was no difference in the quantity of feed ingested, and lambs in CE had higher carcass weight and yield, which does not appear to support the hypothesis of heavier digestive tracts and organs. Because there was no difference in slaughter weight, differences in carcass weights and yields could be due to reduced fasting loss or to a smaller amount of perirenal and mesenteric fat tissues removed at evisceration in CE lambs. Unfortunately, these data were not collected.

Biochemical and Chemical Characteristics of the LD Muscle

Fibre type composition of the LD muscle along with its energetic enzyme activities are presented in Table 3 and suggest altogether a fairly important glycolytic metabolism. These results are consistent with those of Dragomir (2005) using lambs of similar genetics, ages and weights.

A larger number of FOG fibres were observed in lambs raised in the CE ($P = 0.047$; Table 3), but no significant differences between treatments were measured for CS, LDH or HAD activities. Cold acclimatization in many species can induce an increase in the proportion of SO and/or FOG fibres in various muscles (Behrens and Himms-Hagen 1977; Ratzin Jackson et al. 1987; Lefaucheur et al. 1991; Duchamp et al. 1992; Herpin and Lefaucheur 1992; Lebret et al. 2002). Other researchers have also shown that cold exposure increases the oxidative capacity of the muscle to promote heat production (Buser et al. 1982; Barre et al. 1987; Ratzin Jackson et al. 1987; Duchamp et al. 1992). Although no such information has been reported for lambs, the increased proportion of FOG fibres supports the hypothesis that an adaptation of some kind took place in the muscles of lambs raised in CE. However, it seems that the physiological response was not sufficient to influence metabolic activity, which supports the hypothesis that the lambs in this experiment experienced conditions close to the lower limit of their comfort zone.

Table 2. Carcass quality parameters of lambs reared in warm (WE) or cold (CE) environments

	Males		Females			*P* value[z]		
Carcass traits	WE	CE	WE	CE	SEM	S	E	S × E
Hot carcass weight (kg)	24.1	25.1	22.6	22.8	0.2	<0.001	0.025	0.093
Carcass yield (%)	47.7	49.2	49.9	50.1	0.4	0.002	0.044	0.124
Cold carcass weight (kg)	22.9	23.9	21.5	21.7	0.2	<0.001	0.027	0.128
GR[y] (mm)	16.3	14.9	20.3	19.8	1.0	<0.001	0.336	0.634
Average conformation score	4.5	4.6	4.6	4.6	0.1	0.955	0.442	0.593
Lean meat yield[x] (%)	55.1	55.5	53.7	53.9	0.4	0.001	0.400	0.698
Saleable meat yield[w] (%)	76.2	77.1	74.3	74.6	0.5	<0.001	0.275	0.566

[z]S = sex; E = environment; S × E = sex × environment interaction.
[y]Total tissue depth measured on the carcass at the 12th rib, 11 cm from the vertebral column.
[x]LMYeq = 65.8 – (0.074 hot carcass weight) – [0.432 × (6.38 + 0.88 GR)] (Jones et al. 1992).
[w]SMYeq = 78.92 − 0.51 GR + 1.25 average conformation score (Jones et al. 1996).

Table 3. Chemical and biochemical characteristics of longissimus dorsi of lambs reared in warm (WE) or cold (CE) environments

	Males		Females			*P* value[z]		
Biochemical traits	WE	CE	WE	CE	SEM	S	E	S × E
SO fibres[y] (%)	8.8	7.7	8.1	7.0	0.7	0.284	0.139	0.991
FOG fibres[y] (%)	52.1	53.6	52.0	55.0	1.0	0.522	0.047	0.475
FG fibres[y] (%)	39.1	38.7	39.9	38.1	1.0	0.904	0.276	0.467
Water (%)	73.7	73.6	72.6	72.9	0.2	0.003	0.554	0.312
Fat (%)	3.2	3.3	3.8	3.7	0.3	0.098	0.999	0.620
Protein (%)	21.7	21.5	21.6	21.5	0.2	0.866	0.403	0.780
CS[x] (IU g^{-1} meat)	16.4	17.2	15.5	18.1	1.0	0.957	0.107	0.377
LDH[x] (IU g^{-1} meat)	1466.4	1491.5	1596.5	1721.5	124.3	0.169	0.553	0.692
HAD[x] (IU g^{-1} meat)	1.01	1.16	0.96	1.18	0.16	0.908	0.221	0.812
u-calpain (IU g^{-1} meat)	2.43	1.60	2.31	2.14	0.54	0.702	0.381	0.562
m-calpain (IU g^{-1} meat)	6.59	5.83	4.41	4.28	0.39	<0.001	0.261	0.426
Calpastatin (IU g^{-1} meat)	20.7	19.0	12.9	14.1	1.1	<0.001	0.824	0.241
Sarcomere length (mm)	1.676	1.750	1.682	1.690	0.024	0.263	0.099	0.181
Myoglobin (mg g^{-1} meat)	3.19	3.13	3.22	3.22	0.10	0.550	0.744	0.774

[z]S = sex; E = environment; S × E = sex × environment interaction.
[y]SO fibres: slow oxidative fibres; FOG fibres: fast oxidative-glycolytic fibres; FG fibres: fast-twitch glycolytic fibres.
[x]CS: citrate synthase; LDH: lactate dehydrogenase and HAD: β-hydroxyacyl-CoA dehydrogenase.

A lower percentage of water ($P = 0.003$) and a tendency for a higher proportion of fat ($P = 0.098$) were observed in females compared with males (Table 3), as the results obtained by Dragomir (2005) with lambs of similar genetics. However, no significant difference was found between the two rearing environments in terms of water, fat, protein and myoglobin content of the LD muscle.

Meat Quality

The loins from males had a slightly higher ultimate pH than those from females ($P = 0.035$; Table 4), which is consistent with the findings of Johnson et al. (2005) and Bickerstaffe et al. (2000). These latter authors attributed the difference in pH to a higher activity level for the males during the pre-slaughter period because both sexes were grouped, as in our study. This small pH effect had no influence on L^* values. The a^* and b^* colour parameters of the LD muscle, however, were slightly higher ($P = 0.001$) in females, which is in accordance with the results of Johnson et al. (2005). Other studies have not found that sex influences the colour of lamb meat (Dransfield et al. 1990; Vergara and Gallego 1999; Diaz et al. 2003). This lack of agreement among studies may be due to differences in breed or slaughter weights (Dragomir 2005).

Drip loss differed according to sex ($P = 0.032$), with females showing less water holding capacity. Other studies have reported a similar difference (Vergara and Gallego 1999; Diaz et al. 2003), but Dragomir (2005) found that sex had no impact on this parameter. In terms of cooking loss, no sex effect was observed, which is consistent with the findings of several other studies (Dransfield et al. 1990; Dragomir 2005; Johnson et al. 2005).

Sex was found to have an impact on meat tenderness, with males producing less tender meat than females, as reflected in both shear force ($P < 0.001$) and firmness ($P = 0.088$). A similar sex effect on meat tenderness has also been reported (Dawson et al. 2002; Gonçalves et al. 2004; Dragomir 2005; Johnson et al. 2005), while other authors observed no difference (Corbett et al. 1973; Dransfield et al. 1990; Vergara and Gallego 1999). The higher calpastatin activity in loin meat from males ($P < 0.001$; Table 3) could contribute to explain the reduced tenderness although the μ-calpain activity did not differ between genders. According to Koohmaraie (1994) and Lonergan et al. (2001), shear force is positively correlated with calpastatin activity. The m-calpain activity was also higher in males ($P < 0.001$), but m-calpain is known to play a lesser role in meat tenderization compared to μ-calpain (Koohmaraie 1996; Ilian et al. 2001; Veiseth et al. 2001). It has been reported that the meat of male lambs contains more intramuscular collagen (Pommier et al. 1989; Dransfield et al. 1990), which may also play a role in reducing their meat tenderness.

Flavour was more intense in both LD ($P = 0.084$) and SM ($P = 0.026$) muscles from males than females (Table 4). Several other differences in the profile of perceived flavours were reported between intact males, castrated males and females in a Canadian study in commercial lambs (Jeremiah 1998). Differences in flavour appear to be linked to the concentration of certain branched short-chain fatty acids, a concentration which differs according to the sex and age of the lambs (Young and Braggins 1998).

Rearing environment had no effect on the physico-chemical measurements of meat quality. From the trained panel evaluation, however, meat from lambs raised in the CE was juicier than that from lambs raised in WE ($P = 0.043$). This effect is difficult to explain, considering that temperature had no effect on various parameters closely associated with the juiciness of the

Table 4. Meat quality parameters of longissimus dorsi of lambs reared in warm (WE) or cold (CE) environments

	Males		Females			*P* value[z]		
Quality traits	WE	CE	WE	CE	SEM	S	E	S × E
pH	5.69	5.65	5.62	5.59	0.03	0.035	0.275	0.797
Colour								
*L**	37.4	38.0	36.7	37.7	0.5	0.397	0.176	0.756
*a**	15.2	15.0	16.3	17.1	0.4	0.001	0.498	0.190
*b**	8.1	8.4	9.2	9.6	0.3	0.001	0.267	0.850
Drip loss (%)	1.8	1.5	2.0	2.0	0.1	0.032	0.337	0.264
Cooking loss (%)	20.8	21.0	20.1	20.7	0.6	0.454	0.525	0.687
Shear force (g)	2486.6	2790.9	1701.9	1812.0	147.0	<0.001	0.167	0.504
Sensory qualities								
Loin flavour	3.93	3.80	3.64	3.43	0.18	0.084	0.373	0.820
Loin firmness	4.27	4.30	3.86	3.65	0.30	0.088	0.750	0.697
Loin juiciness	3.29	3.77	3.61	3.83	0.17	0.257	0.043	0.420
Leg flavour[y]	3.82	3.86	3.27	3.48	0.20	0.026	0.510	0.675

[z]S = sex; E = environment; S × E = sex × environment interaction.
[y]Semimembranosus.

meat such as water and fat content, pH, drip loss and cooking loss. Very few studies have looked at the impact of the rearing environment on meat quality. One study in lambs reported that the temperature the night before slaughter has an impact on meat quality (Furnival et al. 1977). A drop in temperature from 13 to −1°C was associated with increases in pH (0.25 units) and shear force values (26%). However, these authors pointed out punctual effects of temperature on meat quality rather than rearing conditions to explain their observations. In pigs, which are more sensitive to temperature than lambs, some effects of temperature have been reported for meat and ham quality (Lefaucheur et al. 1991; Lebret et al. 1998, 2002). In beef, a higher incidence of dark-cutting beef (higher pH and darker meat) was found from September to January; the authors suggest a number of possible causes, including temperature-related stress (Tarrant and Sherington 1980). So there is a possibility that rearing conditions influence meat quality, but this particular aspect needs further investigation.

CONCLUSIONS AND IMPLICATIONS

The use of cold barns that are not insulated allowed the efficient and economical production of unshorn heavy lambs in a cold environment typical of winter in eastern Canada. No negative impact on feed intake, growth parameters and carcass and meat quality were observed. Rather, the few significant effects obtained were positive such as deeper LD muscle and improved juiciness of the meat. Therefore, using CE represents an economic advantage for producers by reducing the costs associated with the construction of heated sheep barns, while maintaining growth performance, as well as carcass and meat quality.

ACKNOWLEDGEMENTS

This study was made possible by the financial support of the Conseil pour le développement de l'agriculture du Québec (CDAQ), Agriculture and Agri-Food Canada and the Centre d'expertise en production ovine du Québec (CEPOQ). The authors also wish to thank Sélection BERARC, Abattoir Pouliot and the staff of the CEPOQ and of Agriculture and Agri-Food Canada's Food Research and Development Centre.

Agriculture Canada. 1992. Livestock and poultry carcass grading regulation (SOR/92-541). Canada Gazette, Part II. **126**: 3848.

Ames, D. R. and Brink, D. R. 1977. Effect of temperature on lamb performance and protein efficiency ratio. J. Anim. Sci. **44**: 136–140.

Association of Official Analytical Chemists. 2000. Official methods of analysis of AOAC International. 17th ed. AOAC International, Gaithersburg, MD.

Barre, H., Bailly, L. and Rouanet, J. L. 1987. Increased oxidative capacity in skeletal muscles from cold-acclimated ducklings: a comparison with rats. Comp. Biochem. Physiol. B. **88**: 519–522.

Bass, A., Brdiczka, D., Eyer, P., Hofer, S. and Pette, D. 1969. Metabolic differentiation of distinct muscle types at the level of enzymatic organization. Eur. J. Biochem. **10**: 198–206.

Behrens, W. A. and Himms-Hagen, J. 1977. Alteration in skeletal muscle mitochondria of cold-acclimated rats: association with enhanced metabolic response to noradrenaline. J. Bioenerg. Biomembr. **9**: 41–63.

Bickerstaffe, R., Palmer, B. R., Geesink, G. H., Bekhit, A. E. D. and Billington, C. 2000. The effect of gender on meat quality of lamb longissimus dorsi. Proc. 45th Int. Congr. Meat Sci. Technol., Yokohama, Japan. pp. 104–105.

Brink, D. R. and Ames, D. R. 1975. Effect of ambient temperature on lamb performance. J. Anim. Sci. **41**: 264 (Abstr.).

Brockman, R. P. 1986. Pancreatic and adrenal hormonal regulation of metabolism. Pages 406–419 *in* L. P. Milligan, W. L. Grovum, and A. Dobson, eds. Control of digestion and metabolism in ruminants. Prentice-Hall, Englewood Cliffs, NJ.

Buser, K. S., Kopp, B., Gehr, P., Weibel, E. R. and Hoppeler, H. 1982. Effect of cold environment on skeletal muscle mitochondria in growing rats. Cell Tissue Res. **225**: 427–436.

Canadian Council on Animal Care. 1993. Guide to care and use experimental animals. CCAC, Ottawa, ON. 211 pp.

Cassar-Malek, I., Listrat, A. and Picard, B. 1998. Contrôle hormonal des caractéristiques des fibres musculaires après la naissance. INRA Prod. Anim. **11**: 365–377.

Christopherson, R. J. and Kennedy, P. M. 1983. Effect of the thermal environment on digestion in ruminants. Can. J. Anim. Sci. **63**: 477–496.

Corbett, J. L., Furnival, E. P., Southcott, W. H., Park, R. J. and Shorthose, W. R. 1973. Induced cryptorchidism in lambs. Effect on growth rate, carcass and meat characteristics. Anim. Prod. **16**: 157–163.

Daniel, J. A., Held, J. E., Brake, D. G., Wulf, D. M. and Epperson, W. B. 2006. Evaluation of the prevalence and onset of lung lesions and their impact on growth of lambs. Am. J. Vet. Res. **67**: 890–894.

Dauncey, M. J. and Ingram, D. L. 1988. Influence of environmental temperature and energy intake on skeletal muscle respiratory enzymes and morphology. Eur. J. Appl. Physiol. Occup. Physiol. **58**: 239–244.

Dauncey, M. J. and Ingram, D. L. 1990. Respiratory enzymes in muscle: interaction between environmental temperature, nutrition and growth. J. Therm. Biol. **15**: 325–328.

Dawson, L. E. R., Carson, A. F. and Moss, B. W. 2002. Effects of crossbred ewe genotype and ram genotype on lamb meat quality from the lowland sheep flock. J. Agric. Sci. **139**: 195–204.

Delfino, J. G. and Mathison, G. W. 1991. Effects of cold environment and intake level on the energetic efficiency of feedlot steers. J. Anim. Sci. **69**: 4577–4587.

Depocas, F. 1966. Concentration and turnover of cytochrome c in skeletal muscles of warm- and cold-acclimated rats. Can. J. Physiol. Pharmacol. **44**: 875–880.

Diaz, M. T., Velasco, S., Perez, C., Lauzurica, S., Huidobro, F. and Caneque, V. 2003. Physico-chemical characteristics of carcass and meat Manchego-breed suckling lambs slaughtered at different weights. Meat Sci. **65**: 1085–1093.

Dragomir, L. 2005. Influence de la race, du sexe et du poids d'abattage sur la qualité de la viande d'agneau lourd. M.Sc. thesis, Université Laval, Québec, QC. 99 pp.

Dransfield, E., Nute, G. R., Hogg, B. W. and Walters, B. R. 1990. Carcass and eating quality of ram, castrated ram and ewe lambs. Anim. Prod. **50**: 291–299.

Duchamp, C., Cohen-Adad, F., Rouanet, J. L. and Barre, H. 1992. Histochemical arguments for muscular non-shivering thermogenesis in muscovy ducklings. J. Physiol. **457**: 27–45.

Ekpe, E. D. and Christopherson, R. J. 2000. Metabolic and endocrine responses to cold and feed restriction in ruminants. Can. J. Anim. Sci. **80**: 87–95.

Environment Canada. 2005. Températures moyennes. (Online). Available: http://www.climate.weatheroffice.ec.gc.ca/advanceSearch/searchHistoricData_f.html [2006 Nov. 15].

Environment Canada. 2008. Normales et moyennes climatiques au Canada 1971–2000. (Online). Available: http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_f.html [2008 Nov. 28].

Furnival, E. P., Corbett, J. L. and Shorthose, W. R. 1977. Meat properties of lambs grown to 32 kg at various rates on phalaris or lucerne pastures and an apparent effect of pre-slaughter ambient temperature. J. Agric. Sci. **88**: 207–216.

Gariépy, C., Amiot, J., Pommier, S. A., Flipot, P. M. and Girard, V. 1992. Electrical stimulation and 48 hours aging of bull and steer carcasses. J. Food Sci. **57**: 541–544.

Gariépy, C., Seoane, J. R., Cloteau, C., Martin, J. F. and Roy, G. L. 1999. The use of double-muscled cattle breeds in terminal crosses: Meat quality. Can. J. Anim. Sci. **79**: 301–308.

Glaser, E. M. 1966. The physiological basis of habituation. Oxford University Press, London, UK. 102 pp.

Gonçalves, L. A. G., Zapata, J. F. F., Rodrigues, M. P. and Borges, A. S. 2004. The effects of sex and aging on lamb meat quality. Ciênc. Tecnol. Aliment., Campinas **24**: 459–476 [in Portuguese, English abstract].

Graham, A. D., Nicol, A. M. and Christopherson, R. J. 1982. Rumen motility responses to adrenaline and noradrenaline and organ weight of warm- and cold-acclimated sheep. Can. J. Anim. Sci. **62**: 777–786.

Héroux, O. 1961. Climate and temperature-induced changes in mammals. Rev. Can. Biol. **20**: 55–68.

Herpin, P. and Lefaucheur, L. 1992. Adaptative changes in oxydative metabolism in skeletal muscle of cold-acclimated piglets. J. Therm. Biol. **17**: 277–285.

Honikel, K. O. 1987. Critical evaluation of methods detecting waterholding capacity in meat. Pages 225–239 *in* A. Romita, C. Valin, and A. A. Taylor, eds. Accelerated processing of meat. Elsevier Applied Science, London, UK.

Ilian, M. A., Morton, J. D., Kent, M. P., Le Couteur, C. E., Hickford, J., Cowley, R. and Bickerstaffe, R. 2001. Intermuscular variation in tenderness: association with the ubiquitous and muscle-specific calpains. J. Anim. Sci. **79**: 122–132.

Iversen, P., Ertbjerg, P., Larsen, L. M., Monllao, S. and Moller, A. J. 1993. An FPLC method for determination of calpains and calpastatin in porcine longissimus dorsi. Biochimie **75**: 869–872.

Jeremiah, L. E. 1998. The influence of lamb chronological age, slaughter weight and gender. Flavor and texture profiles. Food Res. Int. **31**: 227–242.

Johnson, P. L., Purchas, R. W., McEwan, J. C. and Blair, H. T. 2005. Carcass composition and meat quality differences between pasture-reared ewe and ram lambs. Meat Sci. **71**: 383–391.

Jones, S. D. M., Jeremiah, L. E., Tong, A. K. W., Robertson, W. M. and Gibson, L. L. 1992. Estimation of lamb carcass composition using an electronic probe, a visual scoring system and carcass measurements. Can. J. Anim. Sci. **72**: 237–244.

Jones, S. D. M., Robertson, W. M., Price, M. A. and Coupland, T. 1996. The prediction of saleable meat yield in lamb carcasses. Can. J. Anim. Sci. **76**: 49–53.

Kennedy, P. M., Christopherson, R. J. and Milligan, L. P. 1982. Effects of cold exposure on feed protein degradation, microbial protein synthesis and transfer of plasma urea to the rumen of sheep. Br. J. Nutr. **47**: 521–535.

Kennedy, P. M., Christopherson, R. J. and Milligan, L. P. 1986. Digestive response to cold. Pages 285–306 *in* L. P. Milligan, W. L. Grovum, and A. Dobson, eds. Control of digestion and metabolism in ruminants. Prentice-Hall, Englewood Cliffs, NJ.

Kinnula, V. L., Huttunen, P. and Hirvonen, J. 1983. Adaptive changes in skeletal muscle mitochondria of guinea-pig during acclimation to cold. Eur. J. Appl. Physiol. **51**: 237–245.

Koohmaraie, M. 1990. Quantification of Ca_2^+-dependent protease activities by hydrophobic and ion-exchange chromatography. J. Anim. Sci. **68**: 659–665.
Koohmaraie, M. 1994. Muscle proteinases and meat aging. Meat Sci. **36**: 93–104.
Koohmaraie, M. 1996. Biochemical factors regulating the toughening and tenderization processes of meat. Meat Sci. **43**: S193-S201.
Lawrence, T. L. J. and Fowler, V. R. 2002. Growth of farm animals. 2nd ed. CABI Publishing, Wallingford, UK. 347 pp.
Lebret, B., Massabie, P., Juin, H., Mourot, J., Clochefert, N., Mounier, A., Chevillon, P., Bouyssière, M. and Le Denmat, M. 1998. Influence des conditions d'élevage sur les performances de croissance du porc et la qualité des viandes. 2. Caractéristiques du muscle et du tissu adipeux et qualité technologique et organoleptique du jambon sel-sec. J. Rech. Porc. Fr. **30**: 43–50.
Lebret, B., Massabie, P., Granier, R., Juin, H., Mourot, J. and Chevillon, P. 2002. Influence of outdoor rearing and indoor temperature on growth performance, carcass, adipose tissue and muscle traits in pigs, and on the technological and eating quality of dry-cured hams. Meat Sci. **62**: 447–455.
Lefaucheur, L., Dividich, J. L., Mourot, J., Monin, G., Ecolan, P. and Krauss, D. 1991. Influence of environmental temperature on growth, muscle and adipose tissue metabolism, and meat quality in swine. J. Anim. Sci. **69**: 2844–2854.
Li, Y. Z., Christopherson, R. J., Li, B. T. and Moibi, J. A. 2000. Effects of beta-adrenergic agonist (L-644, 969) on performance and carcass traits of growing lambs in a cold environment. Can. J. Anim. Sci. **80**: 459–465.
Lonergan, S. M., Huff-Lonergan, E., Wiegand, B. R. and Kriese-Anderson, L. A. 2001. Postmortem proteolysis and tenderization of top loin steaks from Brangus cattle. J. Muscle Foods **12**: 121–136.
McBride, G. E. and Christopherson, R. J. 1984. Effects of cold exposure on young growing lambs. Can. J. Anim. Sci. **64**: 403–410.
Meilgaard, M., Civille, G. V. and Carr, B. T. 1999. Sensory evaluation techniques. 3rd ed. CRC Press, Boca Raton, FL. 387 pp.
Moibi, J. A., Christopherson, R. J. and Okine, E. K. 2000. In vivo and in vitro lipogenesis and aspects of metabolism in ovines: Effect of environmental temperature and dietary lipid supplementation. Can. J. Anim. Sci. **80**: 59–67.
Nachlas, M. M., Tsou, K. C., De Souza, E., Cheng, C. S. and Seligman, A. M. 1957. Cytochemical demonstration of succinic dehydrogenase by the use of a new p-nitrophenyl substituted ditetrazole. J. Histochem. Cytochem. **5**: 420–436.
National Research Council. 1981. Effect of environment on nutrient requirements of domestic animals. National Academy Press, Washington DC. 168 pp.
National Research Council. 1987. Predicting feed intake of food-producing animals. National Academy Press, Washington, DC. 96 pp.
Pommier, S. A., Fahmy, M. H., Poste, L. M. and Butler, G. 1989. Effect of sex, electrical stimulation and conditioning time on carcass and meat characteristics of Romanov lambs. Food Qual. Prefer. **1**: 127–132.
Ratzin Jackson, C. G., Sillau, A. H. and Banchero, N. 1987. Fiber composition and capillarity in growing guinea pigs acclimated to cold and cold plus hypoxia. Proc. Soc. Esp. Biol. Med. **185**: 101–106.
Sano, H., Nakamura, S., Kobayashi, S., Takahashi, H. and Terashima, Y. 1995. Effect of cold exposure on profiles of metabolic and endocrine responses and on responses to feeding and arginine injection in sheep. J. Anim. Sci. **73**: 2054–2062.
SAS Institute, Inc. 2001. Version 8.2. SAS Institute, Inc, Cary, NC.
Sasaki, Y. and Weekes, T. E. C. 1986. Metabolic responses to cold. Pages 326–343 *in* L. P. Milligan, W. L. Grovum, and A. Dobson, eds. Control of digestion and metabolism in ruminants. Englewood Cliffs, NJ.
Shackelford, S. D., Koohmaraie, M., Cundiff, L. V., Gregory, K. E., Rohrer, G. A. and Savell, J. W. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield, and growth rate. J. Anim. Sci. **72**: 857–863.
Slee, J. 1970. Resistance to body cooling in male and female sheep and the effects of previous exposure to chronic cold, acute cold and repeated short cold shocks. Anim. Prod. **12**: 13–21.
Slee, J. 1971. Physiological factors affecting the energy cost of cold exposures. Proc. Nutr. Soc. **30**: 215–221.
Slee, J. 1972. Habituation and acclimatization of sheep to cold following exposures of varying length and severity. J. Physiol. **227**: 51–70.
Soni, A. and Katoch, S. S. 1997. Structural and metabolic changes in skeletal muscle of cold acclimated rats. J. Therm. Biol. **22**: 95–107.
Srere, P. A. 1969. Citrate Synthase. Pages 3–5 *in* S. P. Colowick and N. O. P. Kaplan, eds. Methods in enzymology. Academic Press, New York, NY.
Tarrant, P. V. and Sherington, J. 1980. An investigation of ultimate pH in the muscles of commercial beef carcasses. Meat Sci. **4**: 287–297.
Trout, G. R. 1991. A rapid method for measuring pigment in porcine and other low pigmented muscles. Proc. 37th Int. Congr. Meat Sci. Technol., Kulmbach, Germany. pp. 1198–1201.
Vachon, M., Morel, R. and Cinq-Mars, D. 2007. Effects of raising lambs in a cold or warm environment on animal performance and carcass traits. Can. J. Anim. Sci. **87**: 29–34.
Veiseth, E., Shackelford, S. D., Wheeler, T. L. and Koohmaraie, M. 2001. Effect of postmortem storage on u-calpain and m-calpain in ovine skeletal muscle. J. Anim. Sci. **79**: 1502–1508.
Vergara, H. and Gallego, L. 1999. Effect of type of suckling and length of lactation period on carcass and meat quality in intensive lamb production systems. Meat Sci. **53**: 211–215.
Webster, A. J. F., Hicks, A. M. and Hays, F. L. 1969. Cold climate and cold temperature induced changes in the heat production and thermal insulation of sheep. Can. J. Physiol. Pharmacol. **47**: 553–562.
Webster, A. J. F. 1970. Direct effects of cold weather on the energetic efficiency of beef production in different regions of Canada. Can. J. Anim. Sci. **50**: 563–573.
Weekes, T. E. C., Sasaki, Y. and Tsuda, T. 1983. Enhanced responsiveness to insulin in sheep exposed to cold. Am. J. Physiol. **244**: E335-E345.
Young, B. A. 1975. Effects of winter acclimatation on resting metabolism of beef cows. Can. J. Anim. Sci. **55**: 619–625.
Young, O. A. and Braggins, T. J. 1998. Sheepmeat odour and flavour. Pages 101–130 *in* F. Shahidi, ed. Flavor of meat, meat products and seafoods. Blackie Academic & Professional, London, UK.